

Chapter 22

Ethology and Behavioral Ecology of the Walrus (*Odobenus rosmarus*), with Emphasis on Communication and Social Behavior



Edward H. Miller and Anatoly A. Kochnev

Abstract Large tusks characterize the extant walrus (*Odobenus rosmarus*) and its extinct relatives. Those socially selected organs vary between the walrus and fossil relatives, intraspecifically, and between the sexes. Tusks are used in innumerable interactions on land and in water, including fights during rut. “Play fighting” appears even in young calves that lack tusks. Complex sounds resembling those of rutting males underwater and at the water surface occur throughout the year; some are produced by young males. Short-range graded communication (acoustic; tactile; chemical) is important but has scarcely been investigated. Underwater communication within traveling or feeding groups is likely to occur, but also has not been investigated. Specialized integumentary “bosses” on the chests and necks of adult males probably function in optical signaling. Knowledge of movements, diving, feeding, rhythms, time-activity budgets, and effects of weather on behavior has increased greatly; little information is available on associated finer-scale behavioral structure. Field observations on benthic feeding and seabird predation have revealed previously unknown and ecologically interesting behaviors. Walruses are the most gregarious species of pinniped and are almost always in groups in the water and on land or ice, and in extensive body contact with one another. Gregariousness enables huddling for warmth and cultural transmission of information. Many anecdotes from over more than a century suggest more complex social structure than usually

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assumed, and the species expresses extensive social play that continues into adulthood. In light of those traits, plus the species' high intelligence and longevity, low reproductive rate, and site fidelity, it seems timely to investigate cultural aspects of the walrus social system.

Keywords Acoustic communication · Feeding behavior · Gregariousness · Maternal behavior · *Odobenus rosmarus* · Optical communication · Play behavior · Social structure · Tactile communication · Walrus · Weapon

22.1 Introduction

Explorers and scientists have reported on characteristics, natural history, and behavior of the walrus (*Odobenus rosmarus*) over centuries. They did so in the scientific contexts of their times, so early descriptions and illustrations have been succeeded by different and increasingly modern and more complete treatments. Before he traveled to the Pribilof Islands, Alaska, Elliott (1881) felt that he would learn little new about the walrus because of the extensive published material that he had consulted. He wrote (1881: 93; Fig. 22.1a)¹:

When, therefore, looking for the first time upon the walrus of Bering sea (*sic*), judge of my astonishment as I beheld the animal before me. It was a new species; it was a new creature, or all that had been written by five hundred authors in regard to the appearance and behavior of its Atlantic cousin had been in error.

Knowledge of the walrus has grown enormously since early scientific studies (Chapsky 1936; Belopolsky 1939; Freiman 1941; Nikulin 1941; Vibe 1950; Fay 1955; Mansfield 1958; Loughrey 1959), and through new forms of instrumentation, methods of analysis, and quantitative and modeling techniques. In addition, previously unknown behaviors are being observed in field and laboratory settings and contribute to increasingly comprehensive knowledge of the species' behavioral ecology.

We first discuss the iconic tusks of the walrus, which function mainly as a social organ. Tusk characteristics conform to widespread patterns of socially-selected structures (Sect. 22.2). We comment on behavioral description (Sect. 22.3) and elaborate on this topic in Supplementary Material III. Display behavior of rutting males has been described reasonably well and serves as an introduction to the subject of communication (Sect. 22.4). Most communication is subtle and involves much less conspicuous or stereotyped behavior than that of rutting males; examples are a specialization of the integument for passive optical signaling, and tactile communication (Sect. 22.5; the latter topic is also treated in Sect. 22.6). The extraordinary gregariousness and sociability of walruses are treated in two sections, on

¹Elliott himself made many errors of observation and interpretation, *e.g.* in regard to food habits (Fay 1982).

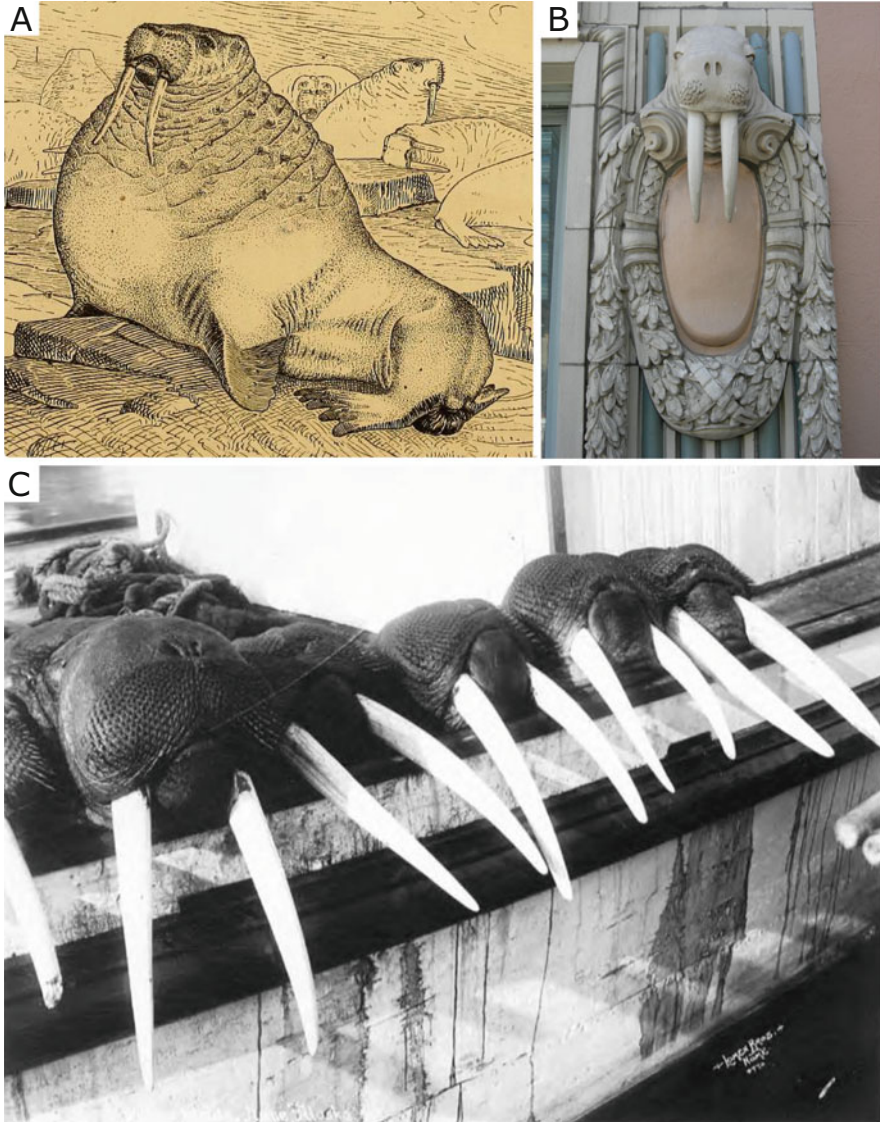


Fig. 22.1 (a) Henry Wood Elliott studied the walrus (*Odobenus rosmarus*) at the Pribilof Islands, Alaska. His drawing (a) clearly shows the largely naked skin, and large bumps on the neck and shoulder, that characterize adult males. (b) The walrus and its tusks are an icon for exploration and other activities in the Arctic. This image shows one of 27 walrus heads that decorate the outside of the Arctic Building (now the Arctic Club Hotel) in Seattle, Washington (the original ivory tusks were replaced with plastic copies in the 1940s). (c) Walrus heads were often killed just for their tusks. These heads were from Pacific walrus killed near Nome, Alaska, sometime between 1894 and 1904. a, After figure preceding p. 95 in Elliott (1881); b, Wikimedia Commons; c, University of Washington Libraries, Special Collections (PH Coll 328.228a; negative number UW12474)

gregariousness and thigmotaxis (Sect. 22.6) and herds and terrestrial haulouts (Sect. 22.7); the social system is discussed in Sect. 22.8. Technical and analytical advances have greatly improved knowledge of walrus behavior over large spatiotemporal scales; we discuss some aspects of movements and diving in Sect. 22.9. The walrus is probably the most specialized pinniped species in terms of feeding ecology and behavior, and in morphological traits related to its specialized trophic habits (Sect. 22.10). The concluding part is Sect. 22.11, in which we make some suggestions about research priorities, with an emphasis on social behavior. We encourage investigators to include descriptive anecdotes, illustrations, and personal impressions in their observations of walrus behavior. Knowledge of behavior contributes in many ways to fields other than science, such as welfare of captive animals; we comment on some such contributions.

In this chapter we emphasize communication and social behavior, and stress the need for information over multiple scales, from motor patterns to social structure. Behavioral studies over small spatiotemporal scales and that pertain to swimming, diving, and feeding are also desirable (*e.g.* locomotory patterns used in travel or diving). We include citations, descriptions, and data from older accounts, particularly from Soviet/Russian research, to emphasize the importance of natural history observations and subjective impressions of experienced observers, in building a broad understanding of the behavioral ecology of walrus.

22.2 Walrus Tusks as Social Organs

Tusks (greatly enlarged upper canines) are the most striking visible trait of the living walrus. The importance of tusks as a trade item led to targeted voyages to the Old World Arctic as early as the ninth century, and may have precipitated European settlement of both Iceland (c. 850–75 CE) and Greenland (c. 980–90 CE; Frei et al. 2015; Dectot 2018). Tusks were mainly shipped as raw tusks to a few centers where they were worked (*e.g.* Norway, Great Britain, and France; Dectot 2018). Carvings found their way throughout Europe, and even to the Middle East and China (Dectot 2018). Some walrus populations were over-exploited in and even extirpated from some places (*e.g.* Iceland; Dectot 2018; Keighley et al. 2019b; Barrett et al. 2020), or exploited over a long time (*e.g.* from eighth to the 20th centuries around the North Water polynya; Gotfredsen et al. 2018). The generation time of the walrus is 15–20 years (Lowry 2016; COSEWIC 2017), so it is possible that evolutionary changes in behavior have occurred in some populations due to exploitation. Here we describe some uses of tusks, the primary one being as a structure for display and striking in agonistic encounters. Like many other socially-selected² structures, tusks differ interspecifically, vary much within the species, and differ between the sexes.

²Social selection: “an alternative conceptual framework . . . in which sexual selection is one component of a more general form of selection resulting from all social interactions” (Tobias et al. 2012: 2274; Lyon and Montgomerie 2012; West-Eberhard 1983, 2014).

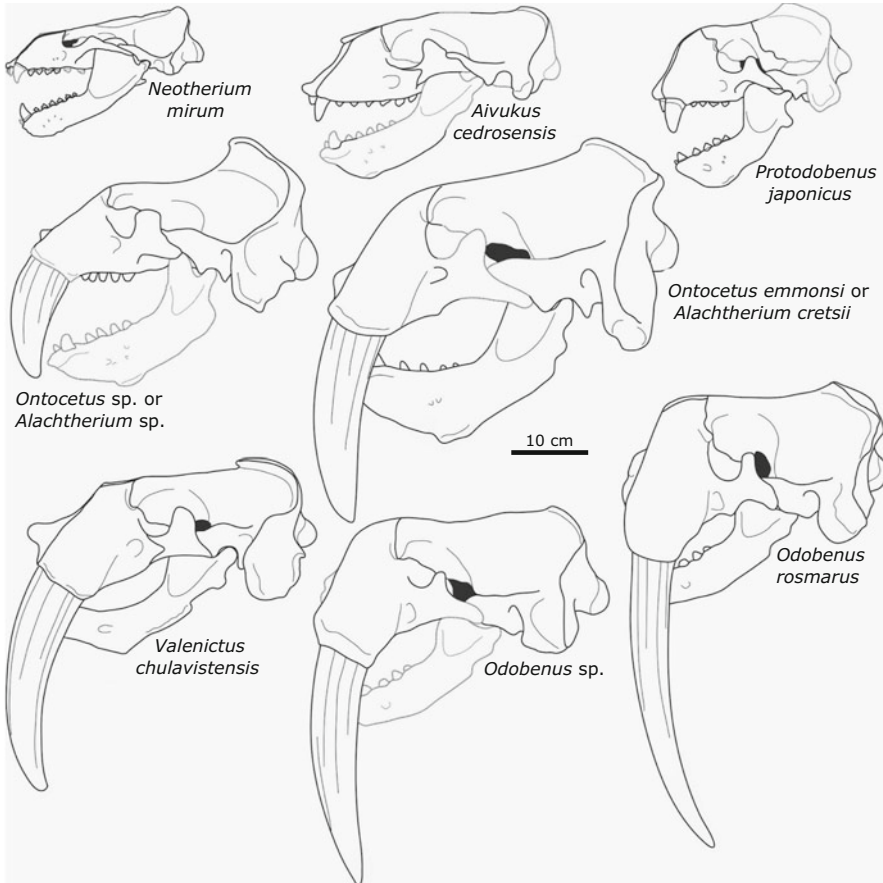


Fig. 22.2 The upper canine teeth varied in size and shape over the evolution of the Odobenidae. Skulls and tusks of some Miocene and Pliocene taxa, plus Pleistocene *Odobenus rosmarus*, are illustrated here. For divergence dates and recorded presence in the fossil record, see Berta et al. (2018). After illustration by R.W. Boessenecker (*in litt.*, 27 March 2020)

Throughout most of the clade's evolutionary history, and in most species, the dentition of Odobenidae was similar to that of their sister clade, the Otariidae. Extreme enlargement of the upper canines evolved independently several times and is a synapomorphy for the clade to which *Odobenus rosmarus* belongs (Odobenini; Boessenecker 2017; Berta et al. 2018; Magallanes et al. 2018; Biewer et al. 2020; Fig. 22.2).

The origins and current adaptive functions of social organs vary across and even within species, and functions almost certainly have changed and diversified even just within the Odobeninae (Stankowich 2011; Cabrera and Stankowich 2020; O'Brien 2019). A dominant old view was that tusks are used for rooting molluscs out of the sea floor, an interpretation that was unsound for multiple reasons (Fay 1981, 1982: 134–135, 1985). Some uses of tusks are as an aid to hauling out or in-air locomotion



Fig. 22.3 The large tusks (upper canines) of the walrus (*Odobenus rosmarus*) serve various non-social functions. (a) Tusks assist in locomotion on ice or land; here a thin ailing adult female is using her tusks as a fifth limb, pulling her body up the beach. (b) A male resting on land uses his tusks as props. (c) An adult male asleep in a breathing hole, holding himself in place by the tusks. (d) Most of the males (foreground) in this mixed herd hold themselves in place with their tusks against the ice. (e, f) Adult walrus threaten polar bears (*Ursus maritimus*) approaching them on sea ice and land. Credits: a, b, d, f, Anatoly A. Kochnev; c, Eliezer Gurarie; e, Svetlana Artemyeva

(probably a major cause of fractures, especially for hauling out on land), when animals on land or ice are resting on their ventral surface, to chop through ice, or to abrade the edges of ice at breathing holes by swinging the head rapidly from side to side (Fig. 22.3a, b; Tomilin and Kibal'chich 1975; Fay 1982: 136–137). Walrus commonly hook the tusks on ice while resting or sleeping in the water, when they serve both as prop and anchor (Fay 1982; Fig. 22.3c, d).

Tusks also serve as weapons in defense against predators, especially the polar bear (*Ursus maritimus*; Fig. 22.3e–h), which they sometimes kill (Freuchen 1921; Krylov 1971; Kiliaan and Stirling 1978; Calvert and Stirling 1990; Kochnev 2001; Thiemann et al. 2008), and the killer whale (*Orcinus orca*; Freuchen 1921; Nikulin 1941; Fay 1982; Born et al. 1995; Kochnev et al. 2008b; Kryukova et al. 2012; Kryukova 2016a; see further). Finally, walrus use the tusks to kill seals for food, and seabirds for food or in play (Freuchen 1935; Lowry and Fay 1984; Seymour et al. 2014; Giljov et al. 2017; see further).

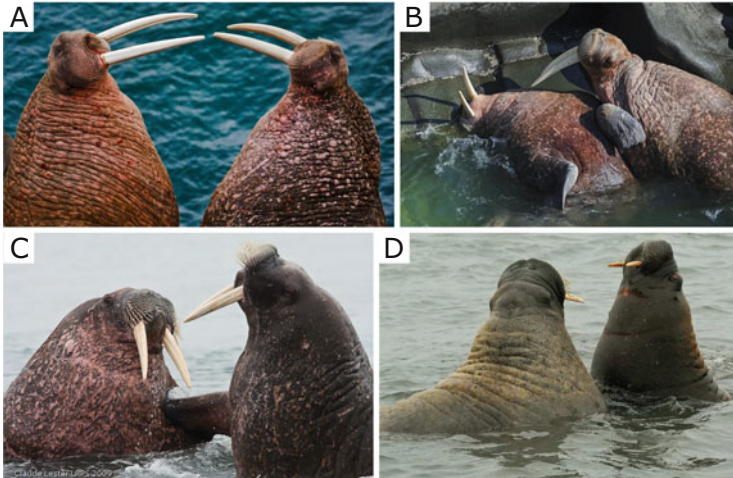


Fig. 22.4 Tusks are used extensively in almost all agonistic and most play interactions between walruses (*Odobenus rosmarus*). **(a)** Typical mutual tusk display between two adult males who are in upright postures on land. The tusks are approximately horizontal in an absolute frame of reference (see text); the oblique orientations of the animals enable them to see one another (Kastelein et al. 1993: Fig. 29B). **(b)** Dominant animal (on the right) orienting his tusks directly toward the head region of the other walrus, who is on his back and stretching away. Here a partner-wise frame of reference needs to be included in the description. **(c)** Dominant walrus (on the left) raises his tusks only slightly while oriented more-or-less directly at the other walrus, who has his tusks raised defensively while placing his right foreflipper against the dominant animal, rearing away, and barking with mystacial vibrissae erected. **(d)** Play-fighting between two young males; note the similarity of the postures to those in **a**. Sources: **a, b**, Pacific walrus, Lee Rentz; **c**, Atlantic walrus, Claude Lester; **d**, Laptev walrus, Anatoly A. Kochnev

Bud Fay had studied walruses for about 15 years when he read a landmark publication on the adaptive (behavioral) significance of horn-like structures in mammals (Geist 1966a), which shifted his thoughts about the functional significance of tusks. When he and EHM first met in 1971 he suggested that walrus tusks, like horn-like structures, may function as social organs. They investigated this possibility in a study of males at Round Island, Alaska, over two summers and found strong support for the hypothesis, even though their study took place well outside the period of rut: walruses brandish and strike one another with their tusks in a myriad of agonistic encounters whose outcomes are determined largely by tusk size and intactness, plus body size (Miller 1975a; Tomilin and Kibal'chich 1975; Salter 1979a; Krushinskaya and Lisitsyna 1983; Taggart 1987; Fig. 22.4). In addition, walruses exhibit formalized offensive, defensive, and submissive behavior in relation to the tusks during such encounters (Miller 1975a, b, 1985; Tomilin and Kibal'chich 1975; Krushinskaya and Lisitsyna 1983). The tusks are used similarly and invariably in innumerable agonistic encounters involving both sexes and all ages that take place on land or ice and in the water throughout year, ranging from play-fighting by very young animals to escalated fights between breeding adult males in

the water during rut (Miller 1975a, 1985; Ray and Watkins 1975; Fay et al. 1984b; Fig. 22.4). Play-fighting and agonistic encounters appear very early in development, even before tusks are erupted: in agonistic interactions between captive calves only a few months old, one individual struck the others “quite forcibly with the mandibular region” (Brown 1963: 15), and “the games of pups on ice consist in hitting and pushing one another with their heads, necks, and chests” (Krushinskaya and Lisitsyna 1983: 277; Supplementary Material I). Rutting males often strike the tusks forcefully against those of the opponent, which likely contributes to tusk breakage (Fay 1982). Sjare and Stirling (1996: 903) described a fight between adult male Atlantic walrus:

“Most mature males had scars and superficial bleeding wounds on their neck and shoulders, but surprisingly few fights . . . were observed and only one of these involved an attending male. In late April 1988, a silent mature satellite male . . . closely approached a female herd member. This action incited an intense fight with the attending male . . . One male reared out of the water to about midchest height and attempted to drive his tusks into the neck region of the other male. After striking one another two or three times the pair rolled around at or near the surface of the water . . . it appeared as though one male was trying to remain on top. The fight lasted about 2.5 min and when it was over the former attending male . . . became silent and left the area alone, while the satellite male . . . took over his position and sang³ for at least the rest of the afternoon. Both males had fresh wounds prior to the fight, indicating they had recently been involved in other aggressive interactions (not necessarily with each other).”

The primary functions of walrus tusks thus are social: in intraspecific offense and defense, and in optical signaling during agonistic interactions. In addition, they are visually obvious and hence informative to other individuals even when the bearer is not engaged in overt interactions. Fay (1982: 138) suggested that the shift from piscivory to molluscivory in walrus evolution emancipated the upper canines and they thereafter evolved principally as social organs; convergent evolution of tusks (enlarged upper incisors) in the bottom-feeding tusked odontocete *Odobenocetops* (de Muizon 2018) strengthens this inference (see also Born 2005; Magallanes et al. 2018).

Tusk size and shape vary over multiple levels: across species and populations, and between the sexes (Emlen 2008, 2014). For example, compared with *Ontocetus*, the tusks of *Odobenus rosmarus* are relatively thicker laterally than anteroposteriorly, and are more weakly curved (Fig. 22.5). Traits of tusks also vary across different walrus populations, being “much longer and thicker . . . less incurved and more convergent” in Pacific than in Atlantic walrus (Allen 1880: 158; Boeskorov et al. 2018; McLeod et al. 2014; Fig. 22.5b).⁴ Finally, tusks vary substantially within populations (Fay 1982; Miller 1991; MacCracken and Benter

³“Song” refers to the acoustic displays of rutting males at and below the water surface (Sect. 22.4).

⁴Atlantic and Pacific walrus diverged from one another nearly 1 mya (Andersen et al. 2017).

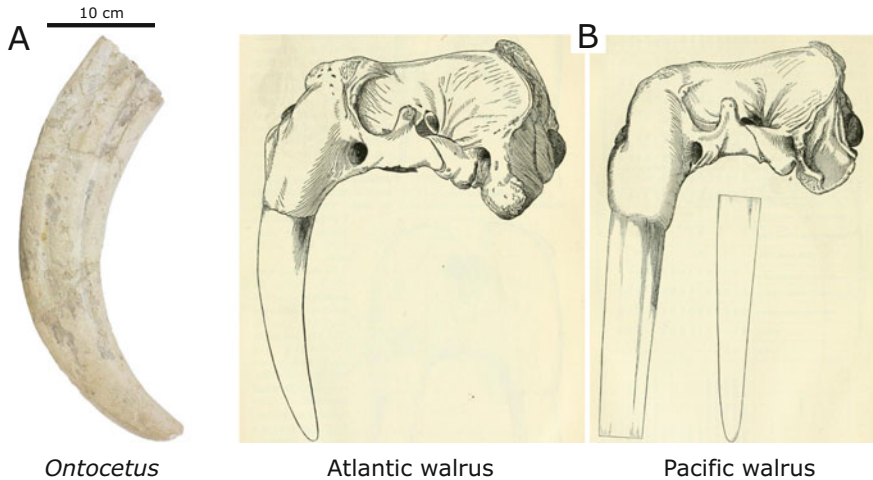


Fig. 22.5 Socially-selected structures like walrus tusks typically vary substantially among related species and across conspecific populations. (a) Tusk of Pleistocene specimen of the odobenid *Ontocetus emmonsi* (sister to *Valenictus* + *Odobenus*; see Fig. 22.2), which differs in basal thickness and curvature from the modern walrus *Odobenus rosmarus* (see panel b and Fig. 22.6). (b) Tusks of Atlantic and Pacific walruses differ in curvature and thickness. All images are shown in left lateral view; the 10-cm scale applies to *Ontocetus* only. (a) After Fig. 2 of Boessenecker et al. (2018); (b) After Figs. 15 and 14 (respectively) of Allen (1880)

2016). Fractures occur disproportionately in males with curved, highly divergent tusks (Fay 1982). Female walruses also possess tusks.

Sexual differences in social organs are common (Stankowich and Caro 2009), and walrus tusks conform to that trend (Nikulin 1941; Fay 1982; Fay et al. 1984a; Sjare and Stirling 1996; Kryukova 2019; Fig. 22.6). Adult males are 13–19% longer in body length and slightly larger (18–22%) in tusk length; however their tusks are much thicker: >40% on average (Supplementary Material II). Eberhard et al. (2018) and O’Brien et al. (2018) predicted that the size of social organs should generally scale positively on body size; this has not been investigated in the walrus.

Many explanations have been put forward to explain the presence of weapons or ornaments in female mammals, but none applies well to the walrus (Estes 1974, 1991, 2011; Stankowich and Caro 2009). Finally, female walruses protect their offspring from other walruses in densely packed herds through interactions that include tusk displays and strikes (Salter 1979a; Krushinskaya and Lisitsyna 1983; Miller and Boness 1983; Taggart 1987; Trillmich 1996). Females with longer tusks are dominant over females with shorter tusks and they display tusks to each other just like males, e.g. as females try to haul out and join a group (L.T. Quakenbush, *in litt.*, 23 April 2020).

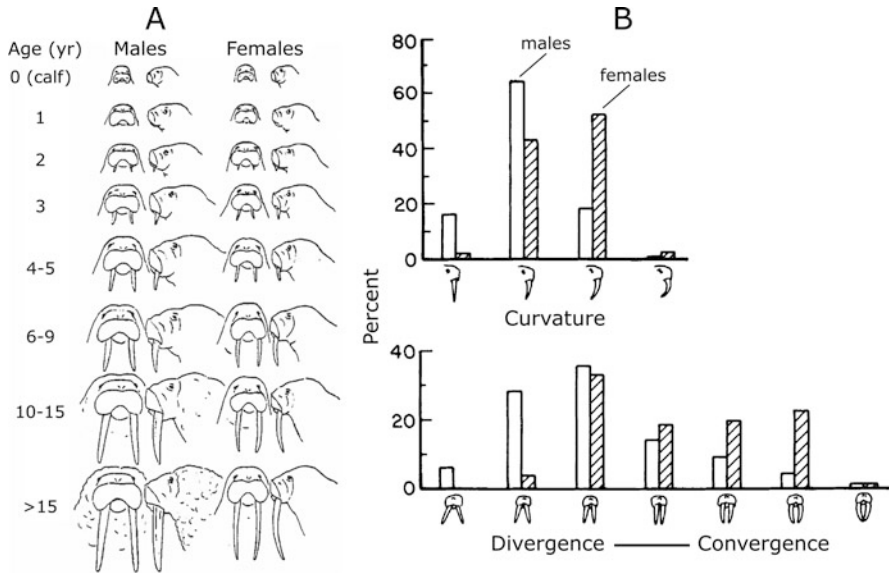


Fig. 22.6 Tusks of the walrus (*Odobenus rosmarus*) differ between the sexes in many ways apart from just size, e.g.: male tusks are less curved in lateral aspect (**a**; **b** top) and more divergent in frontal aspect (**a**; **b** bottom). **a**, After Fig. 2 of Fay et al. (1984a); **b**, After Figure 76 of Fay (1982)

22.3 Notes on Behavioral Description

Behavior can be described in many ways, according to the purposes of a study and the kind of behavior being described. We make three points here (see also Supplementary Material III). First, frames of reference (e.g. absolute; body-wise; partner-wise) need to be explicit even for descriptions of fairly simple motor patterns (Figs. 22.4, 22.7, 22.8). Second, animals rarely do only one thing at any time (e.g. sleeping animals at a haulout also are breathing and in physical contact with others). Third, even seemingly simple kinds of behavior like “sleep” may not be unitary, as they can have different underlying states (Fig. 22.9).

22.4 Walrus Breeding Behavior and Male Displays

The mating systems of pinnipeds have long fascinated biologists. The mating system of the walrus has been of particular interest, due to the species’ sister-group relationship with but completely different ecology from otariids (Fay 1982; Krushinskaya and Lisitsyna 1983; Fay et al. 1984b). However, direct observations of breeding animals were impossible because of the species’ remote breeding sites and the mid to late winter breeding period (Fay et al. 1984b; Born 2003; Sjare et al. 2003). The first observations of breeding behavior by scientists were made in the

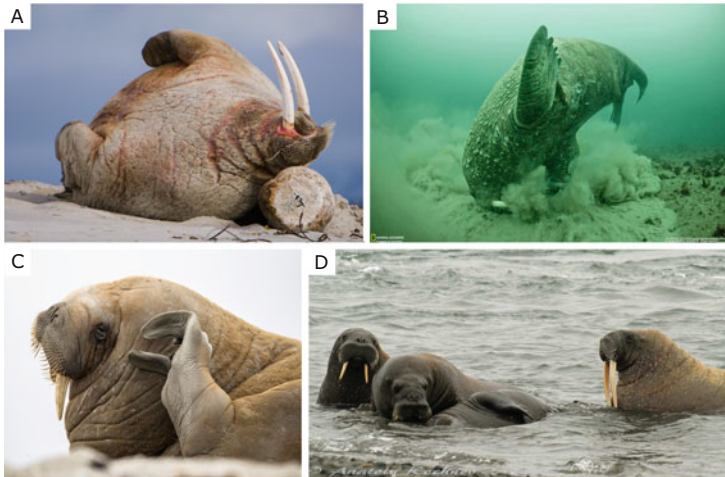


Fig. 22.7 The description of different kinds of motor behavior of walrus (*Odobenus rosmarus*) should be explicit with respect to the frame of reference used: the animals are orienting to external structures/stimuli in panels **a** and **b**, and these externalities should be used as points of reference for descriptions: **a**, Male Atlantic walrus resting against a log; **b**, Feeding male Atlantic walrus turning in the water while maintaining contact with the sea floor. Body-wise and partner-wise frames of reference are appropriate for describing motor patterns in **c** and **d**, respectively: **c**, Atlantic walrus scratching with a hind flipper; **d**, Juvenile (likely a 3–4-year-old male) Laptev walrus orients face to the bottom; the calf's mother (on the right) watches attentively. In all scenarios, descriptions should include details such as medium and posture. Photographers: **a**, Nick Garbutt; **b**, Phil Nicklin/National Geographic Society; **c**, Russell Millner/Alamy Stock Photo; **d**, Anatoly A. Kochnev

Bering Sea in March 1972 (Ray and Watkins 1975; Fay et al. 1984b). Those observations were opportunistic and short-term. Subsequently, Ian Stirling began a research program on breeding Atlantic walruses in the Canadian High Arctic (Stirling et al. 1987; Sjare 1993; Sjare and Stirling 1991, 1996; Sjare et al. 2003); this remains as the most important study of walrus breeding behavior to date (Supplementary Material IV).

Observations suggest a lek-like mating system in which large adult males display in water and compete with one another, through threats and fights, to be close to females in mixed herds on ice. Males appear to show site fidelity across breeding seasons (Sjare and Stirling 1996, Freitas et al. 2009). Males may stay by a particular group for several days at a time; a dominance-based system among males may prevail. Dominant males close to mixed herds may display for lengthy periods at and below the water surface (see further). Females occasionally enter the water and engage in facial and extensive body contact with males at and below the water surface, including mounting of males, before possible underwater copulation (McCord 2016). Below we focus on male behavior (Schevill et al. 1966; Ray and Watkins 1975; Fay 1982; Stirling et al. 1983, 1987; Sjare 1993; Verboom & Kastelein 1995; Sjare and Stirling 1996; Nowicki et al. 1997; Sjare et al. 2003; Denes 2014).

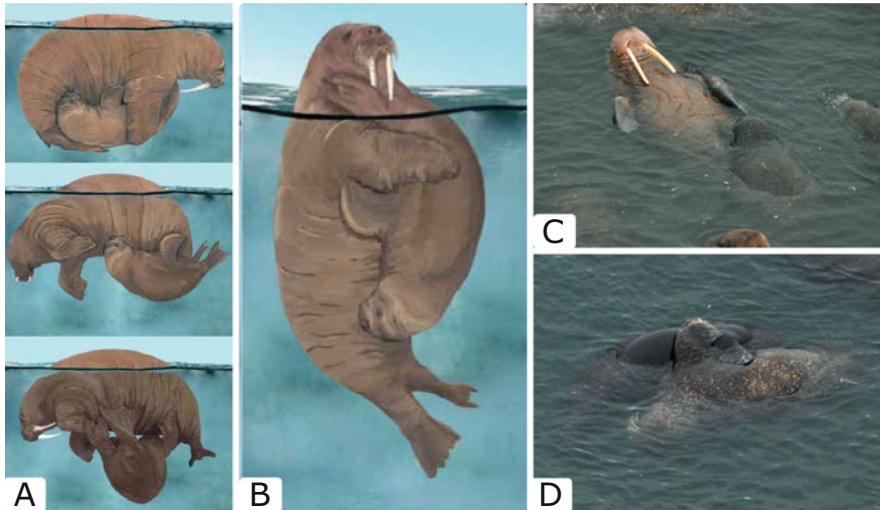


Fig. 22.8 The appropriateness of using a body-wise frame of reference for describing social interactions is exemplified by calf walrus (*Odobenus rosmarus*) nursing underwater. They do so in varied ways, determined by the mother's position, e.g. roughly horizontally below the mother (**a**), or approximately vertically upside-down (**b**). They also nurse at the water surface with the female on her back (**c**) or side (**d**). **a, b**, after Figs. 22.2 and 22.1 of Kryukova (2017); **c, d**, Anatoly A. Kochnev

Rutting adult male Atlantic walrus attending mixed herds dive repeatedly and give diverse sounds between dives at the water surface and under the water (at-surface time $\sim 1\text{--}2$ min long; dives $\sim 4\text{--}6$ min long; Fig. 22.10); see also Charrier (2021a). At the surface, males produce in-air *whistles* and underwater *knocks* and *taps* with the face submerged; during dives they give *knocks* and *taps* plus a *diving vocalization*, a *bell* sound (occasionally given by itself; Sjare 1993, X. Mouy *in litt.* 6 January 2020), and a *strum* sound.⁵ Thus they produce six kinds of sound,⁶ and these can be structured as compound sounds in various ways: through repetition of a single sound type, combinations of different sound types, or both (e.g. two *knocks* plus a *bell* sound); more complex sequences also occur. The *bell* sound is audible in air. The first example in Fig. 22.10b shows two non-harmonically related frequencies differing by ~ 300 Hz, and both frequencies differ from the single frequency of the second *bell* sound. Schevill et al. (1966: 104) made similar observations, and implied that two sound sources were responsible for examples like the first pulse in Fig. 22.10b (sometimes “there are two ‘bells’ involved”; see also Fig. 5d of Stirling et al. 1983). This is in keeping with the presence of paired pharyngeal pouches in

⁵In a captive study, *knocks* and *bells* also were given in air during the rut (Hughes et al. 2011).

⁶Correspondence between some sounds mentioned by Schevill et al. (1966; e.g. “rasp”), Gehrich (1984; e.g. “splutter”), and Schusterman and Reichmuth (2008; e.g. “moan”) with those named by Sjare and colleagues is not clear.

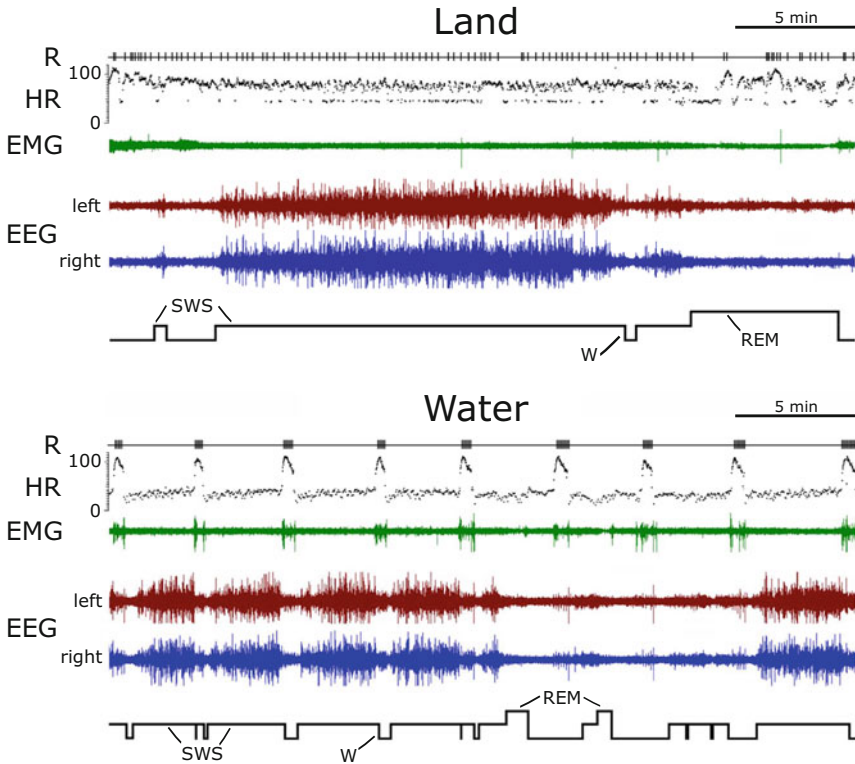


Fig. 22.9 Even seemingly simple categories of behavior in walrus (*Odobenus rosmarus*) like “sleep” can be physiologically complex and can differ physiologically between land and water. In this figure, polygrams at the bottom of each panel show wakefulness (W), slow-wave sleep (SWS), and rapid-eye-movement sleep (REM). Other abbreviations: EEG, electroencephalogram of left and right hemispheres; EMG, electromyogram of neck muscles; HR, instantaneous heart rate (beats·min⁻¹); and R, respiratory acts (breaths). After Fig. 25.8 of Lyamin and Siegel (2019; see also Lyamin et al. 2012)

male walruses, which are presumed to be responsible for the *bell* sound (Fay 1960, 1982; Schevill et al. 1966; Tyack and Miller 2002).⁷ Nuptial sounds of rutting male walruses have no counterpart in other species of the Otarioidea, although contrasting airborne and underwater sound repertoires typify ice-breeding pinnipeds (Van Opzeeland and Miksis-Olds 2011).

The size of pharyngeal pouches increases with age in male walruses, and pouches are sometimes present in females (one of four females examined by Fay 1960); this accounts for the production of *bell* sounds by some captive females (Schusterman and Reichmuth 2008). Pharyngeal pouch distension and production of *bell* sounds

⁷McCord (2016: 18) noted that the “neck area” of a captive male expanded “concurrent with a vocal (*sic*) resembling the scraping of a washboard followed by hitting a gong”.

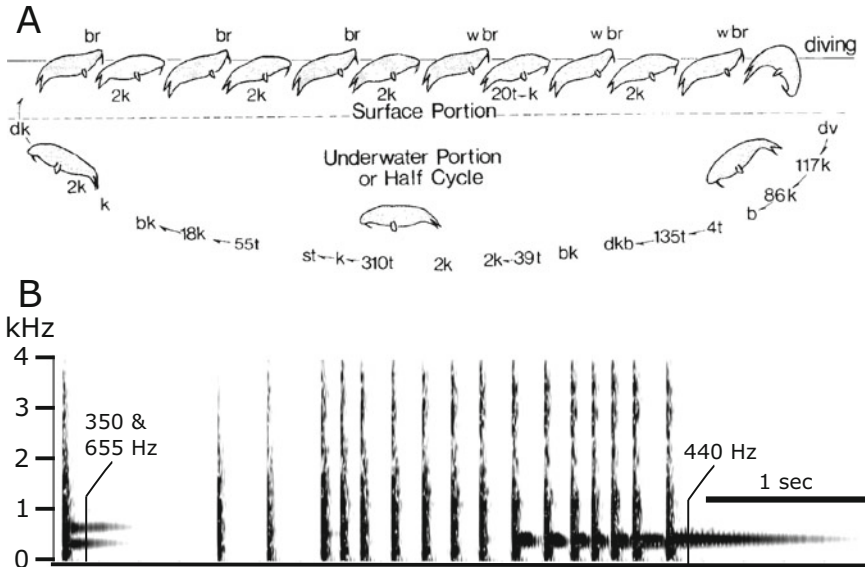


Fig. 22.10 Dominant adult male walrus (*Odobenus rosmarus*) position themselves in the water near mixed herds on ice, where they perform repeated displays at and below the water surface. (a) This diagram shows a male at the water surface, alternating breaths (br) and some airborne *whistle* sounds (w), with other kinds of phonation with the head below water: *knock* (k) and *tap* (t). They produce a *diving vocalization* (dv) when they begin a dive, and *bell* sounds (b), and *strum* sounds (st), plus *knocks* and *taps* alone, repeated, or in combination with other sound types (other abbreviations: *double-knock*, dk; *double-knock bell*, dkb) (The *double-knock bell* was later renamed, because it contains three pulses plus a tonal component (associated with the terminal pulse; Sjare 1993: 59)). (b) A typical part of the surface and underwater acoustic displays (“*bell knock coda*”; I. Stirling *in litt.* 2 January 2020), showing two *bell* sounds, each beginning with a pulse; the second longer *bell* sound also appears to be refreshed (hence lengthened) at each successive pulse. Finally, (a) the pulses differ in frequency and number of frequency bands, and (b) the two frequency bands in the first *bell* sound are not harmonically related. A, From Fig. 1 of Stirling et al. (1987); (b) Spectrogram prepared from Macaulay Library (Cornell University) recording #53276 (Becky Sjare, recordist)

occur commonly in males outside the breeding season, for example close to summer haulouts (Fay 1960; Miller 1975a; Kibal’chich 1978; Krushinskaya and Lisitsyna 1983; Mouy et al. 2012; Rideout et al. 2013), and in captivity (Gehrich 1984). Pharyngeal pouches also have another function, as males often rest/sleep suspended in the water with pouch(es) inflated (Vibe 1950; Bel’kovich and Yablokov 1961; Born 2005; Kryukova 2016b; see further).

Sjare and Stirling (1996) and Sjare et al. (2003) analyzed structure and variation of male “song”, and Denes (2014) detailed fine structure and temporal organization. Some principal findings of Sjare and colleagues were: song sequences range from stereotyped to variable (as noted); songs are individually distinctive, even across years; and song structure varies with social context (*e.g.* males displaying alone *vs.* adjacent to a mixed herd on ice). In addition, many continuous display/singing

performances lasted for long periods; for 24 observations of performances that were at least 8 h long, median duration = 13.5 h and the maximum was 81 h (data from Fig. 4 of Sjare et al. 2003). Therefore, adult males compete physically and through optical displays to establish positions close to adult females; they produce complicated and striking acoustic displays at such positions; and they expend considerable time and energy in the displays (though dive durations do not exceed the aerobic limit; Nowicki et al. 1997).

Kibal'chich (1978) stated that the intense *knocks* of male walrus (as young as 3–4 years old) are produced by the lower jaw striking the upper; preliminary results of research by Larsen and Reichmuth (2012) support this idea; publication of their study should further illuminate mechanisms of sound production. The *knock* sound is of high amplitude (177–186 dB; Hughes et al. 2011; Mouy et al. 2012; Denes et al. 2015). Therefore these and other display sounds can carry over considerable distances, which led Stirling et al. (1983) to propose their use in surveys and monitoring. Many techniques have been developed since then (e.g. passive acoustic monitoring) and have been used to detect or track walrus even outside the breeding period (Mouy et al. 2012; Denes 2014; Miksis-Olds et al. 2016; Marcoux et al. 2017; Chou et al. 2020; Fig. 22.11); at some sites, songs/song elements are not restricted to the period of rut (e.g. the A2W Bering Strait monitoring station of Chou et al. 2020; “a” in Part 2 of Fig. 22.11).

The rutting display of male walrus is a fairly discrete type of display. Display⁸ behavior, and behavior more generally, is rarely so simple to describe or enumerate (Supplementary Material V). For example, the airborne vocal repertoire of the walrus is unremarkable in structure, with much acoustic variation and intergradation, as is typical of short-range displays (Kibal'chich and Lisitsyna 1979; Krushinskaya and Lisitsyna 1983; Miller 1985, 1991; Kastelein et al. 1995; Charrier et al. 2010, 2011, 2021a). The high gregariousness of walrus enables other forms of important short-range communication as well.

22.5 Optical and Tactile Communication⁹

Here we discuss integumentary specializations of the walrus for protection against tusk strikes and optical signaling. We then address some general aspects of communication, much of which relies on general and unspecialized sources of information.

⁸In the field of animal communication, the term “display” conventionally refers to acts (often complex and stereotyped) that have evolved through the evolutionary process of ritualization. Overly restrictive use of the term seems undesirable however, and perhaps it is preferable to simply apply the term to acts that “appear to serve a signal or communication function, and to have been evolutionarily ‘designed’ to that end” (Beer 1977: 156). See Appendix V.

⁹See also Charrier (2021b).

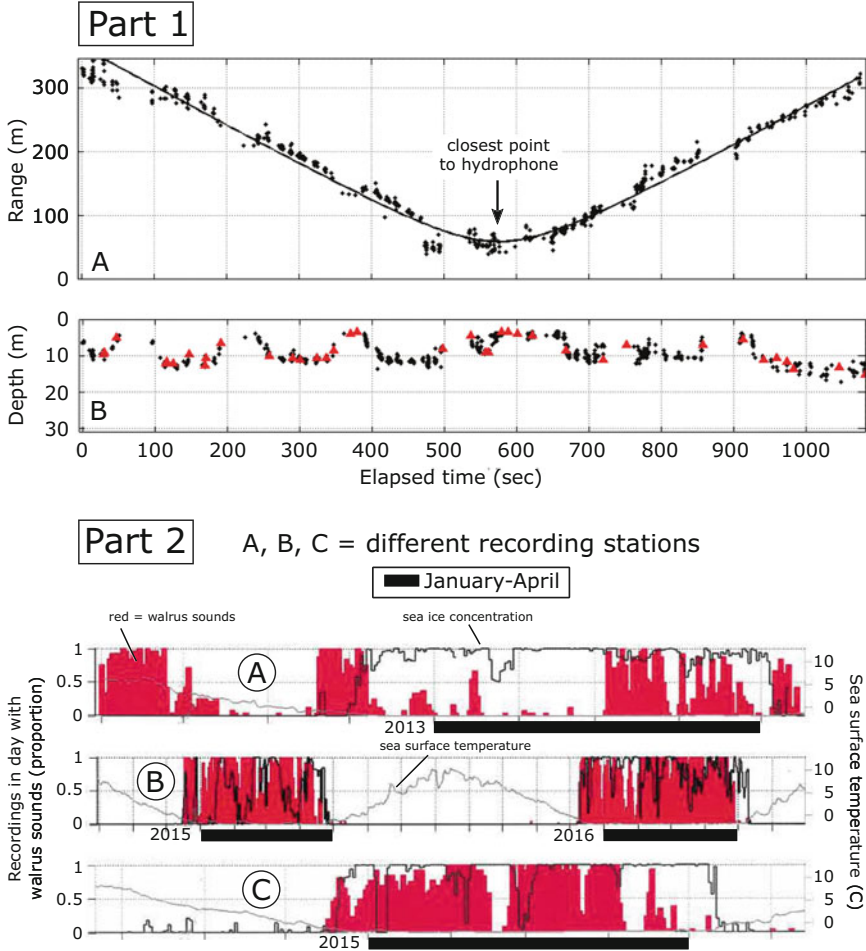


Fig. 22.11 Walrus (*Odobenus rosmarus*) produce underwater sounds throughout the year, not just during the rut. Part 1, movement track and depth of a walrus in the eastern Chukchi Sea, tracked by its display sounds (8 August 2007, hence well outside the rut). The symmetrical track in panel **a** shows that a single animal swam in a straight-line trajectory past the hydrophone. The animal was closest (~60 m) to the hydrophone at about 500–600 s from the beginning of the record and its horizontal velocity was $\sim 0.6 \text{ ms}^{-1}$. During its movement, it uttered both *bell* sounds and *knocks* (red and black symbols, respectively, in panel **b**); *knocks* were uttered at a rate of $\sim 75 \text{ min}^{-1}$. Part 2, long-term records of walrus sounds detected at three recording stations near Gambell and Savoonga (St. Lawrence Island, Alaska), and in the Bering Strait (**a**, **b**, and **c**, respectively). The black bars cover the period of January through April, which includes the period of rut. Note the regional differences in the circannual patterns of sounds. Part 1, After Fig. 9 of Mouy et al. (2012); Part 2, After Figs. 3, 4, and 5 of Chou et al. (2020)

Adaptive thickening of parts of the integument occurs in males of many species of mammal that use behavior like ramming or structures like horns in male-male combat. Thickened areas occur in body areas where contact is normally made in

combat. These thickened areas, or *dermal shields*, show recurrent seasonal thickening in some species (Geist 1966b; Sokolov 1982; Jarman 1989; Shadwick et al. 1992); this has not been investigated in the walrus. Dermal shields in adult male elephant seals (*Mirounga*) have been attributed to scarring (Bartholomew 1952; Laws 1953), but seem likely to also have a genetic contribution. In the Pacific walrus, the integument is thickest on the neck and shoulders, thickens with age, and is thicker in males than females (Fay 1982). Integument on the neck and shoulders of mature males is additionally thickened by rounded bosses that are about 1 cm thicker (sometimes more) than the surrounding skin; these bosses increase in number, thickness, and diameter with age and are present in all males (Fay 1982; Figs. 22.12, 22.13c). The bosses have long been regarded as a secondary sexual character unique to males (Chapsky 1936; Nikulin 1941; Freiman 1941; Mansfield 1958; Pedersen 1962; Burns 1965, citations in Fay 1982). Their possible communicative significance is summarized well by Fay (1982: 49):

“The thick, nearly hairless neck of the adult male, with its pale, “lumpy” skin contrasts markedly with the more slender, browner, and smoother neck of the adult female and of immature animals of either sex. Hence, it probably serves also as an important visual cue to other walruses of the sex and maturity of the individual.”

Finally, the view that bosses are a secondary sexual character is supported by geographic variation in the structure: they are more strongly developed in the Pacific walrus than in the Atlantic form (Pedersen 1962; Figs. 22.12a, c, e–g, 22.13c). Bosses, like tusks, are informative about sex, sexual maturity, and age of the bearer – general classes of information that are all important in social interactions. Other kinds of information are also available from unspecialized integumentary traits.

Some integumentary traits that are not selected for as signals *per se* provide socially useful information about age or sex available to other animals. At birth, calves are very dark, but this changes even in the first several weeks after birth (Burns 1965; Fay 1982: 44); do walruses behave differently toward calves of different ages, based in part on such characteristics? Old males can be nearly hairless and differ in appearance from younger males of the same size that retain pelage. The appearance of old hairless males can change strikingly due to peripheral blood flow, as individuals change from a pale appearance due to peripheral ischemia when in or just emerging from cold water, to a ruddy “sunburnt” appearance after resting in warm temperatures for some time; is such information available from hairlessness informative and hence useful to other males—do males appraise relative age partly by such appearance, *e.g.* when approached by or interacting with hairless mature males? (Burns 1965; Fay 1982: 44–45; Miller 1991; Fig. 22.13a–c)? Information about vision of the species is needed to assess this possibility, but walruses could detect such a difference simply by brightness, even if the species cannot distinguish color (F.D. Hanke, *in litt.* 12 March 2020).

Tactile behavior has been very poorly described in pinnipeds generally (Miller 1991), and in walruses has been described only incidentally and in general terms (Kastelein et al. 2015). This is ironic because body contact is so pronounced in the species, and ranges from brief to lengthy structured touching between interacting individuals, to protracted contact of much of the body surface between adjacent

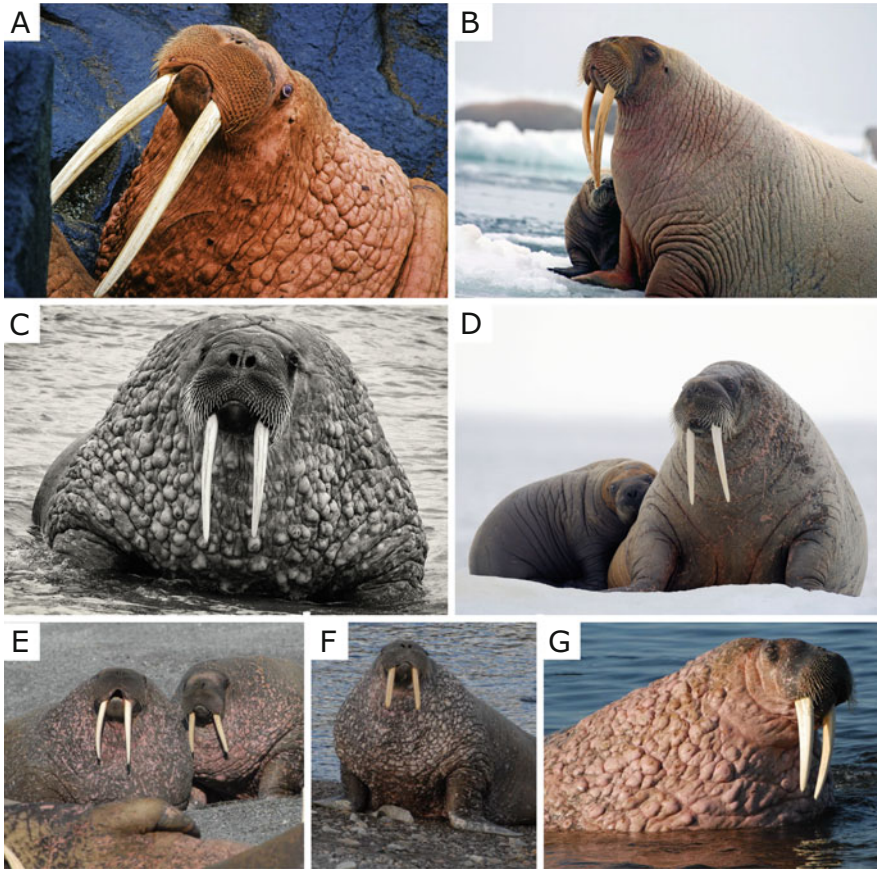


Fig. 22.12 Sexual differences in the walrus (*Odobenus rosmarus*) are expressed in many attributes, including tusk size and shape (Fig. 22.6), and external appearance. Sexual differences in appearance include the greater size and more massive neck and shoulders of old adult males (a, c), and in the “more slender, browner, and smoother neck of the adult female and of immature animals” (Fay 1982: 49; b, d). Raised “bosses” on the chest, neck, and shoulders of old males are generally more strongly developed in the Pacific walrus (a) than in the Atlantic form (c), but extremes are similar (a, G; see also Fig. 22.13c). The bosses grow over years; examples from a few small to many large bosses, and increasing loss of epidermal pigment, are shown in panels e–f–g (Barents Sea). (a) Pacific walrus, Klaus Steinkamp/Alamy Stock Photo; (b) Pacific walrus, Sarah A. Sonsthagen, U.S. Geological Survey; (c) Atlantic walrus, Andy Williams/Muench Workshops; (d) Atlantic walrus, agefotostock/Alamy Stock Photo; (e, f, g) Atlantic walrus, Anatoly A. Kochnev

animals in herds on land or ice. Examples of patterned touching are: in agonistic interactions, when one or both (but especially the subordinate) animals place a foreflipper against one another, to maintain control and distance (Miller 1975a; Fig. 22.4c); when calves are on the back of the mother or the mother and other adults, in rest or having climbed there to avoid disturbance (Fig. 22.14a); in nursing between offspring and mother on ice or land, at the water surface, or under the water

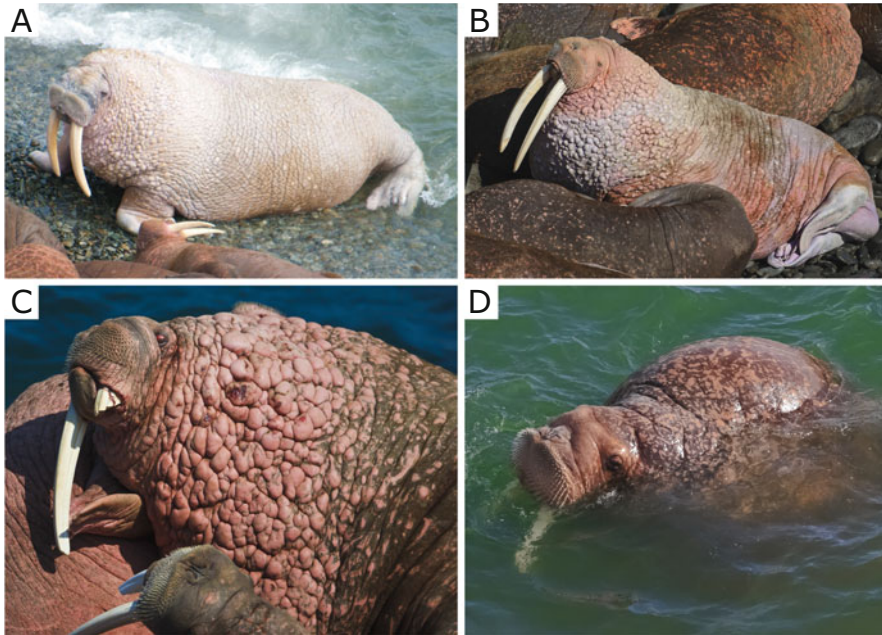


Fig. 22.13 Adult male walrus (*Odobenus rosmarus*) are nearly hairless. (a) In the summer, when they initially haul out, the skin is strikingly pale due to ischemia. This gradually (b) changes to a completely ruddy appearance coloration after they have been hauled out for some time (c). Therefore information about both physiological state and age is available to other individuals from the appearance of the skin of old males. (d) Near summer haulouts, male walrus spend much time in the water producing *knock*, *bell* and other sounds with a pharyngeal pouch inflated. (a) Hal Brindley/halbrindley.com; (b–d) Lee Rentz

(Fig. 22.8); and in nuzzling, when an animal may place its mystacial pad against another animal (often this is mutual), with or without open nostrils (it occurs frequently under the water, for example; Figs. 22.7d, 22.12b, d, 22.14b–d).¹⁰ Body contact or touching occur in innumerable other circumstances as well (e.g. Fig. 22.14e). Touching behavior has been investigated extensively in humans and other primates, and many of the questions asked in research on human tactile (“haptic”) communication could be adapted for studying this behavior in walrus; for example (Thayer 1986: 13):

“Consider ... the stimulus qualities of touch which can vary and alter the meaning of a touch: duration, frequency, intensity, breadth, continuity, rhythm, and sequence. Finally, consider the body parts involved, the settings in which touch occurs, the relation of touch to

¹⁰Fay (1982: 53) noted large sweat glands “in the anterior surface of the snout ... [and] ... associated with groups of small hairs in the spaces between the mystacial vibrissae”, and suggested that these might be important in chemical signaling. The mystacial vibrissae of walrus are numerous, mobile, and highly sensitive (Yablokov and Klevezal’ 1964; Ling 1977; Kastelein et al. 1989, 1990, 1991a; Kastelein & van Gaalen 1988; Milne et al. 2020).

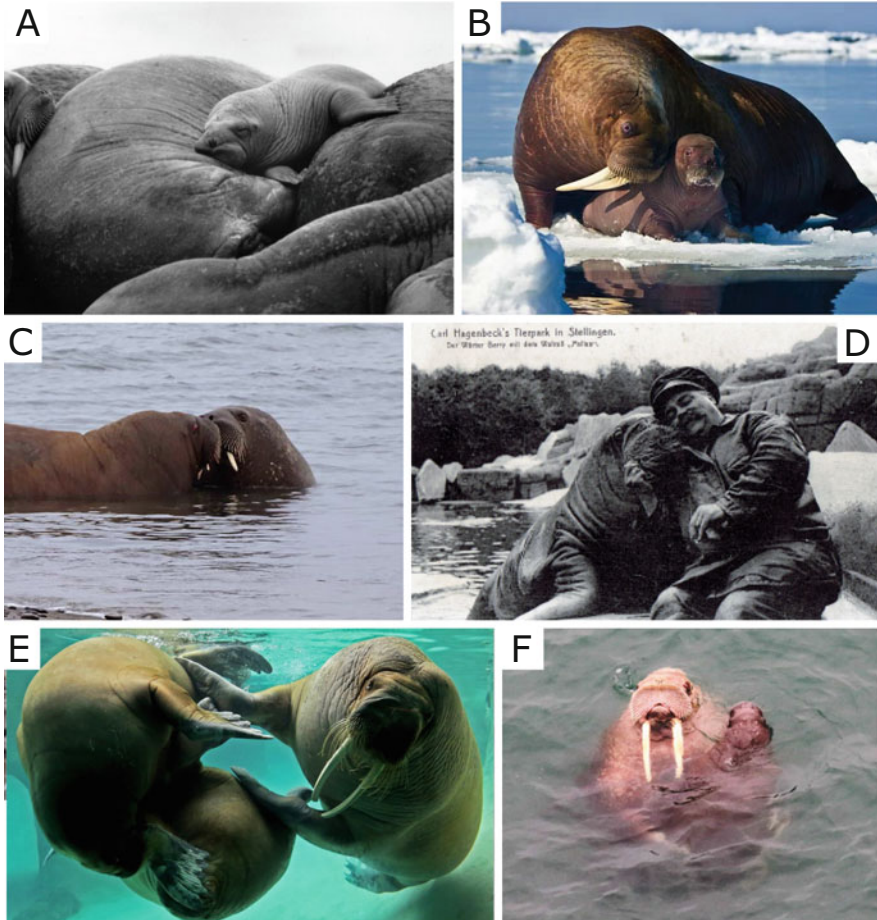


Fig. 22.14 Patterned touching takes many forms in the walrus (*Odobenus rosmarus*), as when a calf rest on top of its mother or other herd members (**a**); or when walrus nuzzle others (**b**, female nuzzles her calf; **c**, face-to-face nuzzling between two young males (note open nostrils of animal on the right)). Captive walrus also nuzzle and otherwise touch humans with whom they have social bonds (**d**). Walrus touch one another extensively under the water (**e**), and mothers and calves commonly are in extensive body contact with one another (**f**). **a**, After Figure 4.38 of Miller (1991); **b**, Rodney Ungwiluk Jr.; **c**, Anatoly A. Kochnev; **d**, Archiv Hagenbeck, Hamburg (see Svanberg 2010); **e**, The Seattle Times; **f**, After Karenina et al. (2017)

other communication signals, who initiates touch, whether touch is reciprocated, whether an expected touch is omitted, how a touch is responded to, and the relationship and roles of the individuals involved.”

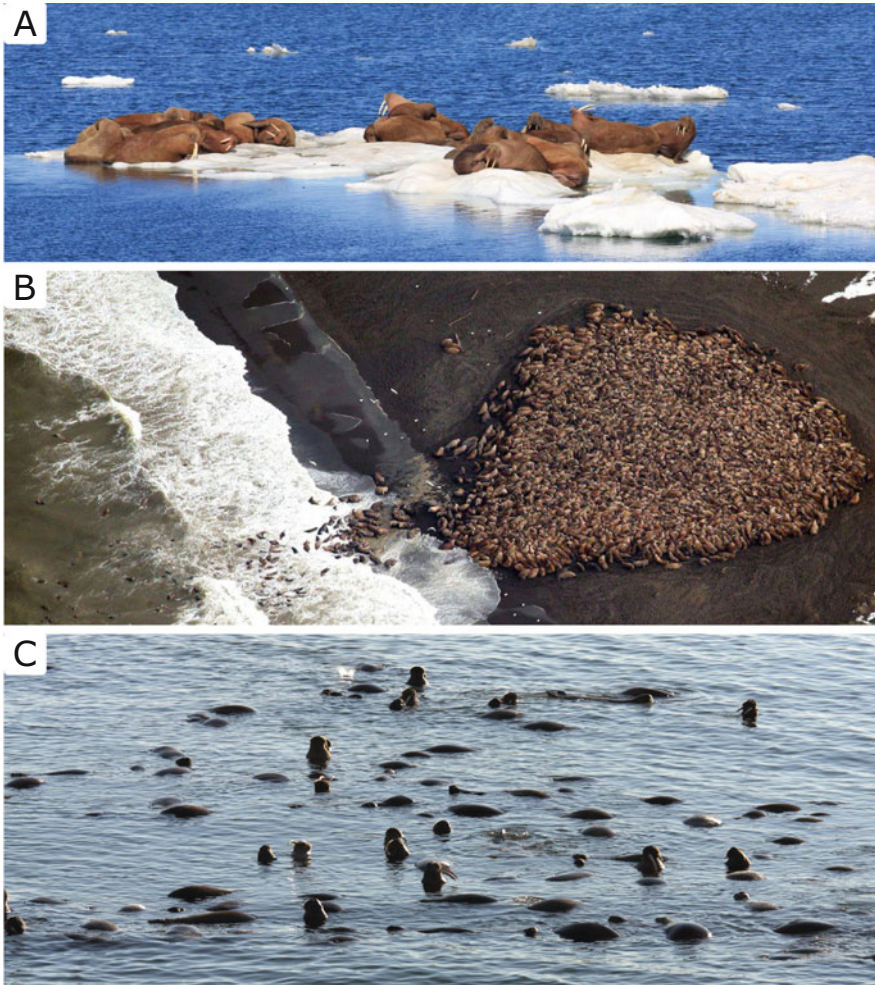


Fig. 22.15 Walrus (*Odobenus rosmarus*) are gregarious throughout the annual cycle and are invariably in body contact with other group members when hauled out. (a) Small group on sea ice, Chukchi Sea. (b) Large herd in the process of hauling out near Point Lay, Alaska, September 2014. Note the discreteness of the herd, due to animals seeking close proximity and contact with one another. (c) Group of males floating in the water with pharyngeal pouches inflated (Vankarem Cape, Chukchi Sea, Russia; August 2011). a, After Fig. 10 of Beatty et al. (2019); b, Photographer, Corey Accardo; c, Photographer, Natalia V. Kryukova

22.6 Gregariousness and Thigmotaxis

Characteristics, behavior, and adaptive significance of gregariousness in pinnipeds vary greatly. The walrus can be considered as the most gregarious pinniped for several reasons: group sizes can be enormous; walrus are gregarious throughout

the year; and walrus are invariably in groups, whether hauled out on land or ice, resting in the water, traveling, or feeding (Pedersen 1962; Fay and Ray 1968; Fay 1981, 1982, 1985; Fig. 22.15). It is important to have baseline information about herd behavior and characteristics because, in addition to inter- and intra-annual variations due to ecological factors, many aspects of walrus herds and their ecology are being affected increasingly both directly and indirectly by loss of sea ice due to climate change (predicted effects are not necessarily negative; Born 2005).

An obvious possible benefit of group living in the walrus pertains to locating patchily distributed food resources. Learning must be an important factor in facilitating the return to areas where walrus have fed in previous years (Born 2005); cultural knowledge and transmission may thus contribute substantially to this behavior.

Another possible advantage of gregariousness and group living is detection of predators.¹¹ In the case of polar bears, walrus at a terrestrial haulout in herds of a hundred or more may respond by fleeing when they detect a bear about 60 m away, or closer (Laptev walrus, and perhaps Atlantic walrus, are much calmer in the presence of polar bears than are Pacific walrus). Most walrus do not detect the bear directly, but instead respond to the behavior of other walrus and flee in response.¹² Reactions to killer whales differ. Walrus detect carnivorous *Orca* up to several km away, presumably by the whales' sounds. In response, all walrus swim quickly toward one another, resulting in a dense group. Killer whales do not approach such large groups and prefer to pursue small groups or single individuals. Hence the gregariousness of walrus facilitates predator detection in the case of polar bears, and protection (through predator discouragement) in the case of killer whales. Photographs of the reaction of walrus to killer whales are in Sect. 22.11.

Gregariousness also enables body contact that seems likely to afford thermal benefits.¹³ These are likely to be very important in the walrus, as they are substantial even in the low-latitude California sea lion (*Zalophus californianus*; Liwanag et al. 2014; Gilbert et al. 2010). Thermal benefits to body contact must be greatest in the winter and especially important for very young walrus, which have a thin insulative blubber layer (Liwanag et al. 2012). Walrus can regulate behaviorally how much surface and which body surfaces are exposed to the air *via* adjustments of body posture and positions of the flippers (Fay and Ray 1968). Additionally, most walrus in groups on ice or land are in extensive body contact with one another and, in cold weather, most calves are "brooded . . . against the mother's breast, between her forelimbs, and so completely concealed and sheltered that [a calf's] presence was

¹¹The following notes are based on observations of AAK, who saw >100 walrus-polar bear interactions over nearly four decades.

¹²The behavior of fleeing because other herd members are doing so is a generalized response that occurs in many circumstances, *e.g.* "disturbances can be caused by as little as a raven [*Corvus corax*] cawing" (M. Winfree in Robards and Garlich-Miller 2013: 26). Of course, a raven's call in turn could be a reaction to the presence of a polar bear.

¹³Advantages to being in a central position in a herd are suggested by Fig. 2c of Lydersen et al. (2012).

not detected until the mother became alarmed and began to flee” (Fay and Ray 1968: 4); in this position about half of the calf’s body surface is against its mother. In addition, as noted, calves often rest atop the mother or other walruses, which provides a warmer surface than the ice (Fig. 22.14a). Walruses huddle extensively throughout the year, indicating a strong social component to the behavior. Huddling behavior (and touching behavior generally) of the walrus is important energetically and socially, so merits detailed study (Miller 1991; Gilbert et al. 2010).

Regardless of the adaptive advantages to gregariousness and (separately) thigmotaxis, the affinity of walruses for one another’s close company is apparent from the facts that they (a) are rarely alone, and (b) form closely packed groups (regardless of whether the groups are small or large; Krushinskaya and Lisitsyna 1983). These behavioral tendencies have been well described by the walrus biologist Tony Fischbach¹⁴: “walruses love to be next to each other”; and “as soon as they’re concerned about something their first response is to turn to their companions and ... sniff them and nudge them”. Over larger distances, walruses are strongly attracted to and move toward distant airborne sounds from herds,¹⁵ which can carry considerable distances (Nyholm 1975); *e.g.* (Tomilin and Kibal’chich 1975: 5):

“... walruses resting on ice floes roar from time to time; this roar resounds through the air and attracts the attention of other walruses. The roar may be far enough away as to be still inaudible to the human ear, but the animals have perceived the call and head for the meeting points, orientating themselves by the direction from which the roar came. It may be that roars emitted from an ice floe are propagated through the water and thus perceived by those animals that are in the water. Upon hearing the call, feeding walruses interrupt their activities and head toward the assembly point (hunters note this direction when they are searching for walrus assemblages). Upon arrival at the floe from which the roar came, the new arrivals climb out of the water and join the others. If there is insufficient room on that ice floe, they climb onto the next one. Gregariousness is accompanied by synchronized behavior in groups (small or large) in the water as they travel or feed. In addition to just mothers and their dependent young, synchronous feeding occurs in larger groups of females and calves (Fay 1982). Tomilin and Kibal’chich (1975) observed small feeding groups of 2–3 animals at Wrangel Island diving and surfacing synchronously; for traveling groups in Greenland, Freuchen (1935: 6; 1921) noted that “whether there are many or only a few they always dive and surface together”.

Gregariousness in general, and the habit of forming large gatherings on land at traditional sites in some parts of the range, made walruses vulnerable to hunting by some indigenous populations; the impact of exploitation varied greatly

¹⁴<https://www.youtube.com/watch?v=pF-aNYhCr8k>

¹⁵Many observers have commented on the great distances over which airborne sounds of walruses can be transmitted, especially in calm conditions and fog (*e.g.* Pedersen 1962). Krushinskaya and Lisitsyna (1983: 264) remarked that even an injured or seriously ill individual may remain separate from herds “but ... always stays within earshot of the herd’s sound signals”; Kryukova and Ivanov (2012) made similar observations.

geographically, and also was affected by which other marine mammals were being hunted and which hunting technology was used (Drew et al. 2016; Hill 2011). The same traits predisposed the species to overexploitation and even extinction in certain areas after “discovery” by Europeans, who extirpated the distinctive populations of Iceland and that of Québec (Gulf of St. Lawrence) plus the Maritime Provinces of Canada (Fay et al. 1984a; Chugunkov 1991; Dyke et al. 1999; McLeod et al. 2014; Lydersen 2018; Keighley et al. 2019b; Barrett et al. 2020).

22.7 Herds and Terrestrial Haulouts

Size and composition of walrus groups vary generally according to substrate (smallest in the water, larger on ice, and largest on land; Fay 1982, 1985), size of area available,¹⁶ and stage of the annual cycle. The species mainly associates with moving pack ice over continental shelves where they feed. When ice is not available they will haul out on land (though this tendency may be overstated in the literature; Born 2005). Most populations are migratory, in accord with seasonal changes in the distribution of ice. For much of the year, adult males and mixed herds containing females and dependent young are segregated from one another (Fay 1982, 1985; Gjertz and Wiig 1994; Born et al. 1997; Lydersen et al. 2008; Monson et al. 2013). Group size and composition are important structural elements of a species’ social system (see further), and more information about herds on ice and in the water is desirable.

Sites of terrestrial haulout are well documented throughout most of their range (Fischbach et al. 2016; Lindqvist et al. 2016; Heide-Jørgensen et al. 2017; Semenova et al. 2019). A comprehensive review of historical and recent records of the Pacific walrus in Russia and the United States for the period 1852–2016 provides a valuable resource for long-term monitoring (Fischbach et al. 2016). Some haulout sites have been in use since they were first encountered by Europeans,¹⁷ whereas others have formed sporadically in recent decades at times when sea ice was unavailable. When the herds contain many females with calves, substantial mortality from crushing can occur. This has been observed since the 1960s in the Russian part of the Chukchi Sea (Kochnev 2002) and, with the reduction of ice cover since the 1990s, happens almost annually (AAK, unpubl.).

Large mixed herds of Pacific walruses are also forming on land more frequently in the absence of sea ice in the eastern part of the range. Monson et al. (2013) studied size, composition, and age-class assortment in mixed herds (mainly females and young animals) at haulouts in late summer. Walruses were not distributed randomly within the herds: dependent young in year classes 0, 1, and 2 tended to be closest to

¹⁶See photographs of confined beaches of different sizes in Kryukova et al. (2019).

¹⁷Use of traditional sites and the size of aggregations were strongly affected by European exploitation (Fay et al. 1984a).

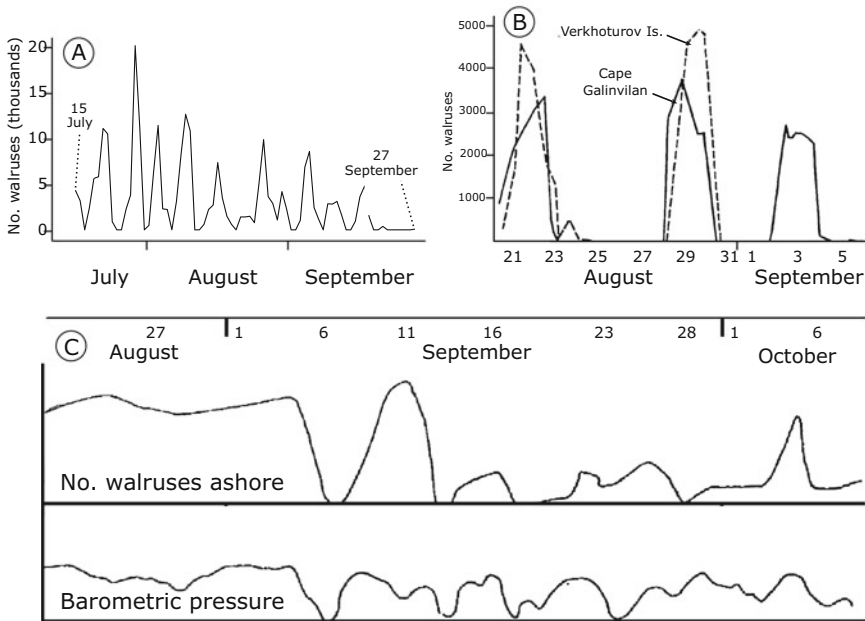


Fig. 22.16 Herds of walrus (*Odobenus rosmarus*) at terrestrial haulouts often display pronounced and rapid changes in numbers (a) and apparent synchrony across haulout sites in patterns of their presence and absence (b). Many early observations tied the presence or absence of walrus on land to weather, subjectively and through simple correlational analyses (c). **a**, Erratic changes in numbers at the Meyechkyn haulout site in the Gulf of Anadyr, Russia, in 1999. **b**, Nearly simultaneous changes in numbers hauled out at two Russian haulout sites that are separated by about 80 km; daily counts were made at each site over the period 21 August to 4 September 1987. **c**, Concurrent temporal trends in the number of walrus ashore and several meteorological measures at a haulout on Arakamchechen Island, Chukotska, for the period 20 August–10 September 1977. **a**, After Fig. 3 of Smirnov et al. (2000); **b**, After Fig. 2 of Semenov et al. (1988); **c**, After Fig. 2 of Kibal'chich (1988)

the water, a trend that strengthened over time as herds remained ashore. Socially subordinate walrus are over-represented peripherally in herds of summering male walrus (Miller 1976); non-random sex and age assortment in mixed summering herds that include males also has been noted in the Atlantic walrus, with females and dependent young closest to the water (Loughrey 1959; Krushinskaya and Lisitsyna 1983; Miller and Boness 1983); Vishnevskaya and Bychkov (1985, 1990) observed the same pattern, and tied it to the behavior of the females: mothers with first- or second-year calves did not attempt to enter the herd, but stayed at its periphery. In his 1977 study at Cape Kagynin, Kibal'chich (1978) noted that sick animals mainly occupied positions at the side of the haulout, and Freuchen (1935: 238) noted complete segregation of “bulls” and “cows” at a terrestrial haulout. Finally, at Russian haulouts, females and calves are more common on rocky sites, and males are more common on sandy beaches (Kochnev 2013).

Walrus aggregations on land often form and dissolve suddenly and erratically, a pattern that sometimes seems synchronous even across fairly distant haulout sites (Yablokov and Bel'kovich 1963; Vishnevskaya and Bychkov 1985, 1990; Taggart 1987; Chugunkov 1991; Kochnev 2001; Lydersen et al. 2008; Kryukova et al. 2019; Fig. 22.16a).¹⁸ The most parsimonious explanation of synchrony at different nearby sites is that walruses react similarly to common meteorological or sea conditions. Many early observers noted that weather affects presence on land (Belopolsky 1939; Nikulin 1941). Yablokov and Bel'kovich (1963), Kryukova (2012), and Kryukova et al. (2019) stressed the influence of wind; Kibal'chich (1978, 1988), Vishnevskaya and Bychkov (1985, 1990), and Hills (1992) noted the importance of air pressure, with departure associated with falling pressure and return to land occurring with increasing pressure (Fig. 22.16b). More recently, rigorous quantitative assessments of the relationships of haulout behavior to weather have identified wind speed and air temperature as important influences on haulout behavior, in addition to a diel pattern (Born and Knutsen 1997; Smirnov et al. 2000; Lydersen et al. 2008; Udevitz et al. 2009; Hamilton et al. 2015; Jay et al. 2017).¹⁹ The patterns are not uniform around the year, as temperature is an important factor mainly in winter, when mature males also spend much time in the water during the period of breeding (Hamilton et al. 2015). Haulout patterns and activity budgets also vary regionally and inter-annually due in part to ice availability and location (Garde et al. 2018). Behavioral observations at haulout sites are indispensable for understanding higher-level attributes of herds.

Aggregations on land appear to be established by adults who are initially cautious and halting in hauling out; the presence of some walruses on land appears to embolden others (Nikulin 1947; Chugunkov 1991; Supplementary Material VI). In mixed herds with only a small proportion of males, the males haul out first and females with young haul out several hours later (Kochnev 1999). Nikulin (1941: 43, see also Salter 1979b; Fay et al. 1984a) remarked on how animals become calmer over time after hauling out:

“After they get out on the firm ground, walrus behave very restlessly for the first few hours and it is very easy to frighten them at this time. But after lying for certain time they react very little or not at all to the approach of men or any foreign object”

Comparable information for the formation of herds on ice appears to be unavailable.

Individual walruses show site fidelity to particular haulout sites within and between years (Born and Knutsen 1997; Born et al. 2005; Jay and Hills 2005; Lydersen and Kovacs 2014). There is some evidence that individuals tagged at the

¹⁸In her detailed study, conducted for five months in each of five successive years, Hills (1992) observed no synchrony between two haulout sites separated by about 100 km.

¹⁹The animals' behavior is not directly observable in such studies, so “haulout” must be defined operationally. For example, Hamilton et al. (2015) defined the onset and termination of haulout as how long a sensor was continuously dry (≥ 15 min) or wet (≥ 40 s), respectively. Operational definitions vary across studies, and direct observations also would probably result in slightly different findings.

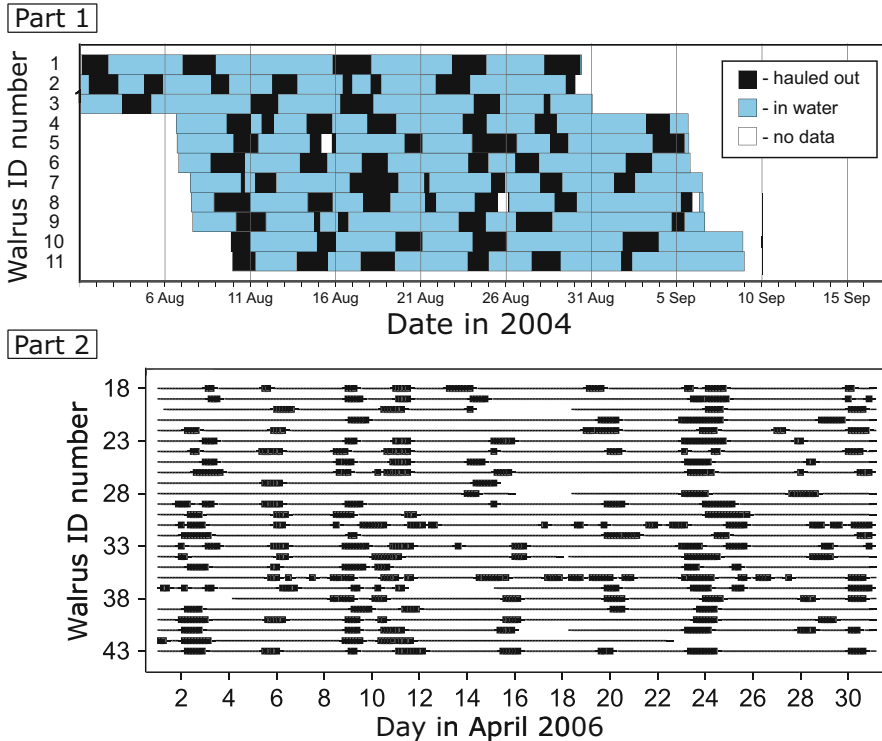


Fig. 22.17 Walruses (*Odobenus rosmarus*) in herds exhibit synchrony in patterns of haulout on land (male Atlantic walruses; Part 1) and ice (female Pacific walruses; Part 2). The patterns may be explained largely as responses to weather, but social factors likely also contribute. Assessment of synchrony depends on temporal scale, which differs between the two parts of this figure. Part 1, after Fig. 3 of Lydersen et al. (2008); Part 2, after Fig. 2 of Udevitz et al. (2009)

same time at a haulout site are synchronous in their at-sea/on-land activities thereafter (Fig. 22.17). This pattern could be explained most parsimoniously by similar behavioral reactions of individual animals to the same weather and sea conditions, but a social component may be involved and should be investigated, especially in small populations.

22.8 Social System

Walrus society can be considered within the framework of Kappeler (2019), who suggested that the term “social system” be standardized to include four core elements: mating system, social organization, social structure, and care system. We have adapted his treatment of the latter three elements for this part of the discussion:

Fig. 22.18 Females and their offspring are the core social unit in the walrus (*Odobenus rosmarus*), and remain together for years during and after weaning (a). For much of the year they associate in mixed herds containing other females and calves, plus young males (b). Multiple females and their calves sometimes associate closely, enabling calves to play among themselves (c). Photographs are of Pacific walrus. a, b, Sarah A. Sonsthagen, U.S. Geological Survey. c, Anatoly A. Kochnev



Social organization refers to three basic features of a social unit. Two of these are (i) *group size* and (ii) *group composition* (age; sex; reproductive status); many data on these features exist and more can be obtained for the walrus. The core social unit of walrus is the mother-calf pair, as they are inseparable throughout lactation and remain together for years thereafter (females longer than males: Fay 1981, 1982; Fig. 22.18). Fay (1982: 138) stated that “After [weaning] young males stay for 2 or 3 years longer with the adult females before joining all-male herds; the young females tend to stay with the adult females continuously”. Genetic analysis has refined this picture: analysis of samples from animals >2 years old in mixed herds disclosed slightly higher mean relatedness among herd members than expected by chance, and suggested that 3-year-old juveniles may associate and travel with the mother whereas offspring ≥ 4 years of age are wholly independent (Beatty et al. 2020). The long period of association between females and calves (especially female calves), coupled with strong individual recognition, could enable future “preferential interactions” between them (Trillmich 1996: 566).

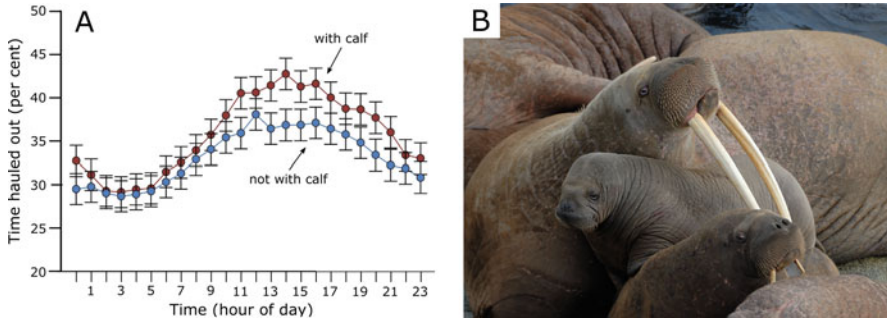


Fig. 22.19 Costs of motherhood: (a) female walrus (*Odobenus rosmarus*) with calves spend more time hauled out on ice (and hence not feeding) than do females without calves. Data for the graph are from tagged females in the Alaskan portion of the Chukchi Sea, June–September 2013–2015. Error bars represent 95% confidence intervals. (b) Females and calves often assume positions that could be interpreted as protective of the calf. a, After Figure 24 of Quakenbush et al. (2016); b, Anatoly A. Kochnev

Female walrus and their offspring travel and presumably feed together over their long period of association. Indications of high costs of walrus maternal care over this time include: observations of mothers defending or carrying their young; females with calves hauling out longer than females without calves; long female-calf bond; and high energetic costs of lactation (Kochnev et al. 2008a; Citta et al. 2014; Noren et al. 2016; Quakenbush et al. 2016; Fig. 22.19); see also Sepúlveda and Harcourt (2021).

Costs to female Pacific walrus with calves presumably are increasing due to global warming, because more feeding is taking place at greater depths (Kochnev 2004). Vishnevskaya and Bychkov (1985, 1990) noted that walrus with young-of-the-year hauled out on land and returned to the sea more often than did other adults, and interpreted this as reflecting their higher energetic requirements; they also observed that females with young-of-the-year occurred disproportionately in small mixed groups. Trillmich (1996) cautioned that energetic measures reflect maternal expenditure, not maternal investment; those measures are not static but vary greatly throughout the long reproductive lifetimes of female walrus. Female Pacific walrus are predicted to rest and forage less due to future changes in the distribution and amount of sea ice, which could have negative effects on multiple aspects of reproduction if females cannot replenish their endogenous reserves through winter feeding (Udevitz et al. 2017).

For these reasons, mixed herds outside the breeding period may be structured partly on (iii) *genetic relationships* (Beatty et al. 2019, 2020).²⁰ These three features

²⁰Fay (1981: 16) felt that this probably was not the case: “Apparently, the individual does not necessarily associate with the same retinue of companions and must re-affirm his or her social status continually in each new situation.” In contrast, Krushinskaya and Lisitsyna (1983: 267, 271) assumed that groups of adult females and young animals (up to the age of 7 years) consisted of related individuals, but commented for mature males that “ties of kinship are scarcely possible”.

provide a purely structural description that does not refer to or imply anything about how individuals in groups interact with each other. In addition, different age and sex classes of walrus are not distributed evenly across the range at any season. Such influences affect the composition of and hence the social dynamics within herds.

2. *Social structure* concerns the nature of social relationships within a group, as reflected in interactions among individuals (e.g. frequency or nature of social interactions). Characteristics of this element are usually positively related to high longevity and slow reproductive rate, as in the walrus. In walrus, the kind and frequency of interactions are influenced by age, sex, body size, and the female-offspring bond. Krushinskaya and Lisitsyna (1983) stressed the strength and nature of the female-calf bond, with young calves in essentially continuous body contact with their mothers from birth, whether hauled out or in the water, and with extensive vocal communication between them. Is walrus society also shaped by individual familiarity or kinship apart from females and their offspring? Does it reflect dominance relationships that emerge from repeated interactions involving animals familiar with one another in a group? Apart from females and their offspring, do individuals preferentially associate with other individuals?

3. *Care structure* refers to all forms of care. It includes maternal care but also care provided by kin or unrelated individuals, including seemingly altruistic behavior. For example, group defense against a polar bear has been observed (Stirling 1984, plus citations in Taggart 1987). This element too is often positively related to life-history traits of the species. Information on care is anecdotal but consistent: some reports suggest that young calves may be attended by other adult females when the mother is feeding; and many published descriptive accounts suggest that aid-giving is common. For example, many observers have noted that older walrus will attack hunters, especially when other group members are threatened or injured; Burns (1965) interpreted many (not all) of such observations as animals returning to young animals in response to their vocalizations (Supplementary Material I, VII; Bel'kovich and Yablokov 1961; Krushinskaya and Lisitsyna 1983). Care-giving and "mutual assistance" have been noted mainly in mixed herds of females and juveniles (Krushinskaya and Lisitsyna 1983); females were not seen to exhibit aggression toward first-year pups in herds dominated by that age class (Vishnevskaya and Bychkov 1990).

Behavioral development is intimately bound with social life in mammals, especially in group-living long-lived species like the walrus. It has not been studied specifically in the walrus, though diverse play behavior occurs throughout the year over all ages and in both sexes (see also Llamazares-Martín and Palagi 2021). It includes individual and social play with seabirds (wounded or and dead); play-fighting on land, ice, or in the water; mounting and apparent copulation; and diverse contact and rolling behavior (Miller 1975a; Vishnevskaya and Bychkov 1990; Giljov et al. 2017; Figs. 22.20, 22.21). Sometimes several females and their calves associate for some time, with the females moving together while monitoring the calves who play with one another (Fig. 22.18c). The most extensive descriptions of play are in Krushinskaya and Lisitsyna (1983; Supplementary Material I); here is an excerpt (p. 278):

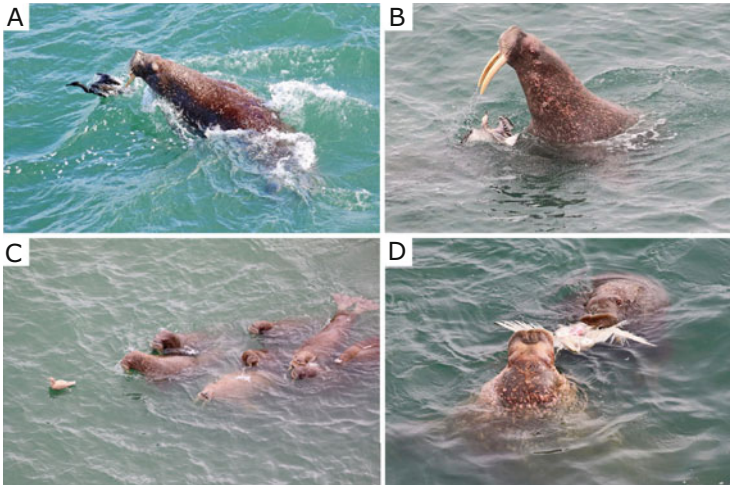


Fig. 22.20 Pacific walrus (*Odobenus rosmarus*) actively pursue, eat, and play with seabirds. (a) Young walrus (probably a 3–4-year-old male) pursuing a juvenile pelagic cormorant (*Phalacrocorax pelagicus*). (b) Male walrus (6–9 years old) about to strike a juvenile black-legged kittiwake (*Rissa tridactyla*) after upending it by rising quickly beneath it from below the water surface. (c) Mixed-age group of walrus approaching a juvenile glaucous gull (*Larus hyperboreus*), with a juvenile male in the lead. (d) Juvenile walrus “offers” the carcass of a juvenile black-legged kittiwake to an adult male (foreground), perhaps as an invitation to play. After Figs. 22.1, 22.2, and 22.3 of Giljov et al. (2017)

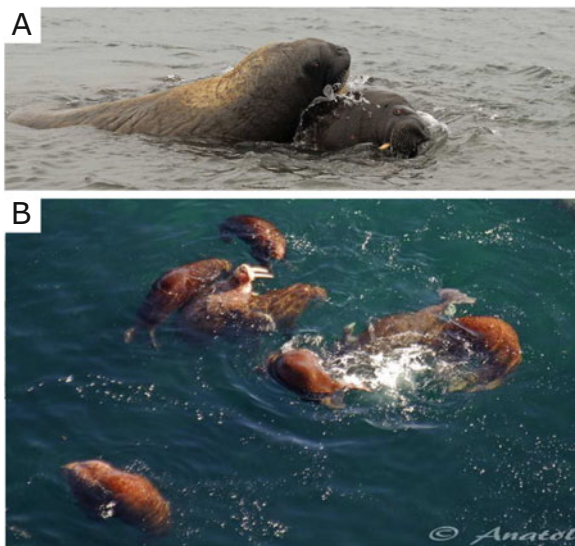


Fig. 22.21 Play in the walrus (*Odobenus rosmarus*). (a) Playing between two young males, when they were generally in extensive body contact while twisting and turning at and below the water surface. (b) Multiple males form a “water carousel” (see text); note also one male mounting another—slightly above and to the left of the carousel. Photographs, Anatoly A. Kochnev

“Males of different ages very often play in the water next to a costal rookery. The game is usually played by two, or less frequently, three animals, which can be of the same size, or one larger than the other. The playing pair surface simultaneously, and the animals touch with their vibrissae, then they dive, also simultaneously, and underwater one can see the walruses turning, so that a ring is formed in which the snout of one animal almost touches the rear flippers of the other. . .”

It is apparent that the social system of the walrus is poorly known and patchily known. Some information on social structure can come from focused investigations on particular topics like tactile communication or inter-individual associations (*e.g.* between individual animals at summer haulouts). Key information that will illuminate social processes can come from jointly investigating genetic structure, age/sex composition, and stability of mixed herds over the species’ range and through the annual cycle. Observations on social behavior mentioned above and in previous sections, and in Supplementary Material VII, are strikingly similar to some features of odontocete social systems, *e.g.*: fission-fusion dynamics; cooperative behavior; and aid-giving (Gowans 2019; McHugh 2019). Structure and dynamics of odontocete societies therefore may provide some direction to future research on walruses.

22.9 Movements and Diving: Descriptions Across Scales

Walruses travel great distances, feed on the sea floor in frigid water, and spend much time in areas that are remote or impossible to visit. For these reasons, researchers have tried to deploy instrumentation attached to walruses for many years. The first successful attachment of tags to walruses appears to have been in 1954; none of the 115 tags was recovered (Mansfield 1958; see Born et al. 1995: Fig. 14). Soviet biologists attached tags to 500 Pacific walruses in 1961 (Krylov 1965); none of those tags had been recovered as of 1976 (Krylov 1965: translator’s note). Later workers deployed diverse sophisticated instruments and used other techniques such as passive acoustic monitoring to document movements and diving. The investigations have yielded rich information on movements (sometimes over very long distances); travel time; diving; influences of weather on behavior; time-activity budgets; and within and between-year fidelity to terrestrial haulout sites, feeding grounds, and winter breeding areas; and other topics (Born and Knutsen 1992; Hills 1992; Wiig et al. 1993; Mouy et al. 2012; Rideout et al. 2013; Dietz et al. 2014; Marcoux et al. 2017; Semenova et al. 2019; Chou et al. 2020; *e.g.* Fig. 22.17). Most investigations of this kind have operated over large scales, so it is useful to consider smaller-scale studies that ask different questions, and provide complementary information that increases understanding across scales (Krupnik and Ray 2007; Schneider 2009; Robards and Garlich-Miller 2013; Kiszka et al. 2015). Swimming speed can serve as an example.

Many estimates of swimming speed from tracking studies are derived from long records (*e.g.*: 3.1 km h⁻¹; Born and Knutsen 1992: 281²¹). Heide-Jørgensen et al. (2017) gave estimates of 2.3 and 1.9 km h⁻¹ for records of ≤5 h and over a longer period (up to 24 h), respectively; for a 20-min sample of a walrus moving in a straight line, Mouy et al. (2012) estimated speed at <1 km h⁻¹ for 12- and 18-min records of walruses swimming in a straight line. Averages from long records will usually be lower than from short records, because animals rarely travel in straight lines for long periods, and they engage in other kinds of behavior than just traveling. Estimates of swimming velocity through direct observation are much greater: Loughrey (1959) estimated maximal swimming speed as 11–12 km h⁻¹; and Fay (1981: 14; 1982) estimated “normal cruising speed” at about 7 (up to 10) and “maximal ‘sprint’ speed” as ≥35 km h⁻¹. More important than the quantitative differences, the differing estimates for the different scales inform about different behavioral processes and differ in biological significance. Large-scale estimates may be useful in energetics analysis, bioenergetics modeling, or in relating travel velocity to sea-ice conditions; estimates at small scales can inform about whether swimming walruses can escape from a polar bear or killer whale, for example. Diving behavior is another example of scale differences.

Walruses dive when they travel to and feed on the sea floor. Most investigations of diving have concerned feeding and have interpreted dive characteristics in that light. Lowther et al. (2015) analyzed dive data for adult males in summer and winter, and noted an increase in shallow dives in the latter period. They interpreted the trend as an effect of rutting behavior, when males engage in many shallow dives during their displays. So-called “surface dives” are not observed directly so must be inferred from attached instruments and defined operationally. Wiig et al. (1993) considered “surface” to be ≤2 m from the water surface and “bottom” as ≥85% of a dive’s maximal depth; Garde et al. (2018) considered a dive to occur at >2 m; Lowther et al. (2015) recognized dives as submergences >4 m deep; and Jay et al. (2001) modified a criterion for maximal depth used by others. Analysis of coarse behavioral categories is also necessarily applied to data on rates of ascent and descent, and on various properties of feeding dives (*e.g.* do quantitatively defined classes of dives used in different studies mirror natural classes of behavior?). Observations on motor patterns of walruses while swimming at the surface, in non-feeding dives, and during ascent and descent, would illuminate all these matters. Basic knowledge of anatomy and motor patterns is available as a starting point for such investigations.

Anatomical traits associated with and motor patterns used by walruses swimming at and just below the water surface have been well described (Ray 1963; Fay 1981; English 1975; Gordon 1981, 1982; Pierce et al. 2011). Hind limbs are the major source of propulsion; the forelimbs are used mainly for maneuvering, and also as hydroplanes, to initiate dives, *etc.* (Gordon 1981, 1982). Motor patterns and basic quantitative aspects of locomotion during sustained traveling, or during ascent or descent from dives, have not been described in detail, although Levermann et al.

²¹The estimate of 3.08 is the grand mean of the seven individual means in their Table 6.

(2003: third page) made direct observations of feeding walrus and pointedly stated that “walrus dived directly to the bottom to feed, and when finished they went straight to the surface for air” (the motor behavior used, such as position or movements of flippers, *etc.*, remain undescribed; more descriptive details of behavior from that publication are in Supplementary Material VIII). Other aspects of motor patterns are important for understanding energetic costs: do the form of locomotion and energetic costs differ between large bulky adult males and more slender adult females, or between females with and without calves, or over development from calf to adulthood? Parenthetically, information on contextual details is invaluable in reporting on directly observed behavior, such as whether animals are alone or in groups (and if so, what is the group size?), whether a female is alone or diving with her offspring, and the age of her offspring.²²

22.10 Feeding

Abrasion patterns on tusks and mystacial vibrissae, and the strongly keratinized dorsal margin of the mystacial pad, suggested to Fay (1982 and earlier) that walrus root in the sea floor for their invertebrate prey. Sam Stoker, a Ph.D. student at the University of Alaska, made the first direct observations of feeding furrows in 1972 from an icebreaker-supported mini-submarine²³; furrow characteristics supported Fay’s inference (Ray et al. 2006). Further studies have provided more details about the structure and meaning of feeding signs.²⁴ As feeding walrus move forward on the sea floor (see further) they encounter prey, which they excavate in particular ways according to the type of prey that they encounter, and often leave identifying shells beside the excavation pits (Oliver et al. 1983; Nelson and Johnson 1987; Fig. 22.22a).

Detailed knowledge of the structure of feeding pits and how they are formed, coupled with knowledge of which prey species that were excavated, have enabled the use of excavations to be used as proxies for the prey that were eaten. The information has been used at different scales of analysis: Nelson et al. (1984, 1987) could resolve furrows but not pits; Bornhold et al. (2005: 296) could resolve furrows and pits, but not different kinds of pits. Nelson et al. (1987) described variation in the tracks of furrows and noted that the persistence (hence detectability) of furrows over time likely is affected by bottom-current water velocity and grain size of the substrate. Details of feeding behavior have been refined over time.

²²Some authors have suggested that very young calves cannot dive with their mothers (*e.g.* Loughrey 1959), but even very young calves dive with (and are carried by) their mothers (Krushinskaya and Lisitsyna 1983). Calves have accelerated development of physiological traits that are important to diving at a young age (Noren et al. 2015; Noren and Edwards 2020).

²³This was the same cruise on which the first observations on rutting behavior were made (Ray and Watkins 1975).

²⁴Such behavioral traces are termed *ichnofossils* in paleontology.

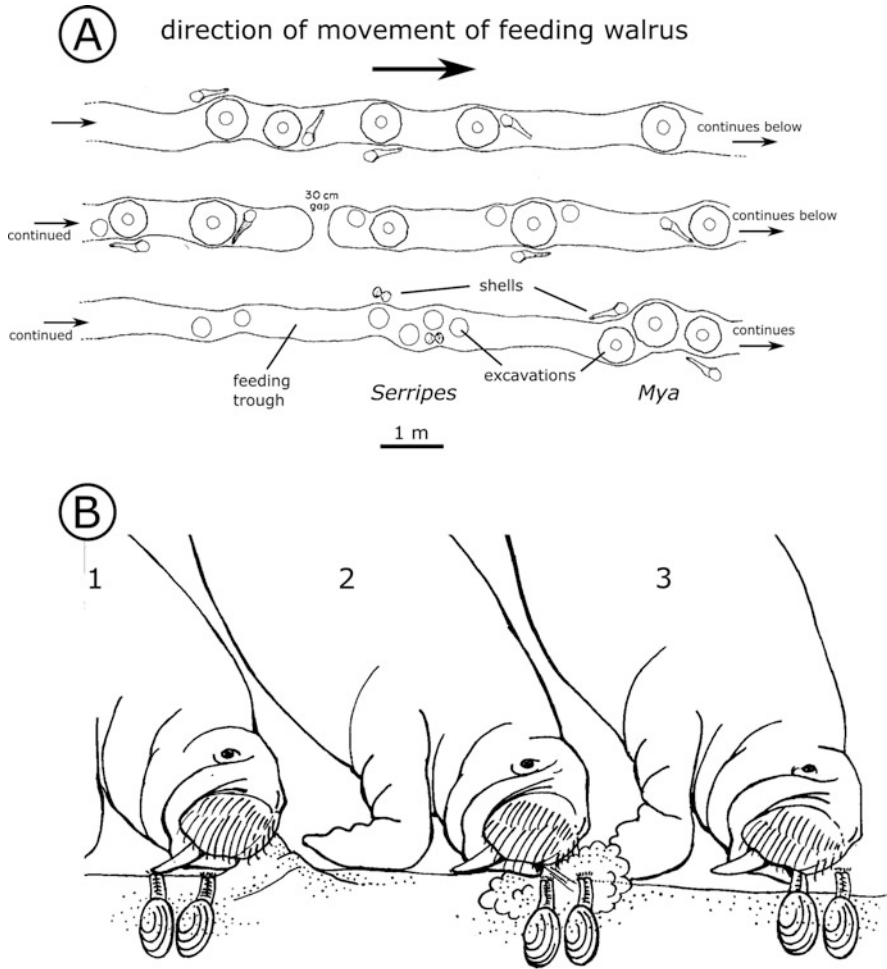


Fig. 22.22 (a) Walruses (*Odobenus rosmarus*) leave distinctive signs of feeding on the sea floor. They root in the substrate and, when they encounter prey, excavate them, and then suck out the soft parts and discard the shells. The excavations differ across prey types (here two are depicted: *Serripes* and *Mya*). (b) Sequence of feeding behavior by a captive walrus: 1, rooting in the substrate; 2, jetting with water to expose the food items (*Mya arenaria*); and 3, sucking the siphons from the *Mya* and ingesting them. Placement of the foreflippers on the substrate while feeding may have been related to the shallow placement of the prey items in the experiment; in the wild, prey are deeper in the substrate and flippers are needed to disperse overlying sediment (Levermann et al. 2003). a, After Fig. 3 of Oliver et al. (1983); b, After Fig. 2 of Kastelein and Mosterd (1989)

Vibe (1950: 34) offered the suggestion that walruses suck out the soft parts of molluscs and eject the shells: "[maybe] the Walrus takes the mussel into its mouth or between the lips, sucking out the firm portions, whereupon the rest of the mussel is spit out again . . . It is the general opinion among the Polar Eskimos that the Walrus in this way sucks out the mussel, spitting out the shells." The first direct observations

of feeding behavior were made on a captive animal (Kastelein and Mosterd 1989: 3–4; Fig. 22.22b):

“The animals showed the following behaviour. They positioned themselves on their front flippers on the sand, with their body at an angle of 30–90 degrees with the bottom surface . . . They slowly moved snout-first along the bottom, exploring it with their eyes open. The animals rooted in the sand with the upper edge of the snout and then made a pumping motion with the mouth cavity. This created a strong current in the water and stirred up the sand . . . The [food items] were found and excavated. After inspection with the vibrissae (which was difficult to see because it was done quickly between the snout and the substrate) the flesh was sucked from the shells. Afterwards the shells were dropped.”

The mechanics of suction include both fine and gross control of the tongue, which is used like a piston (Fay 1982; Kastelein and Gerrits 1990; Kastelein et al. 1991b, 1994). Walruses have a highly vaulted palate and greatly enlarged facial and labial muscles that are used to minimize the size of the mouth opening by (a) pursing the rostral lips and (b) occluding the lateral gape; this helps to maintain subambient (*i.e.* suction) pressure in the mouth (Marshall and Pyenson 2019; Horning et al. 2017). Hydraulic jetting is also used by the bearded seal (*Erignathus barbatus*), and suction is used widely in Phocidae and Otariidae (Marshall et al. 2008; Marshall 2016; Marshall et al. 2014, 2015; Kienle and Berta 2016, 2018; Kienle et al. 2018, 2019, references in Hocking et al. 2021).

Knowledge of how walruses feed has advanced a lot through direct observations and video analysis of 32 bottom sequences of 12 wild walruses by Levermann et al. (2003): walruses kept their eyes open and usually faced into the bottom current, perhaps so they could see most clearly, as they moved forward (walruses may detect some food items visually, such as *Mya* siphons protruding above the surface; Oliver et al. 1983; see Kastelein et al. 1993: Fig. 29D). The animals moved a foreflipper (usually the right one) to displace water that then removed sediment from an area in front of the head. Finally, the animals jetted water into the sediment to expose prey items, and rooted through the sediment with the muzzle, confirming the observations of Kastelein and Mosterd (1989) and the long-held view of Fay. Lateralization has also been noted in social interactions and during interactions with seabirds (Giljov et al. 2017, 2018; Karenina et al. 2017; Karenina and Giljov 2018; Fig. 22.14f).

22.11 Concluding Comments

Quantitative analyses of allometry and sexual differences in tusk size and shape would be informative. Many such analyses exist for socially-selected structures in other animals. Further, what are the quantitative relationships among tusk characteristics like length, thickness, curvature, *etc.*, and how are those related in turn to tusk strength and resistance to breakage, and to “condition” or “quality” of the bearer?

Socially-selected breeding displays in animals typically vary substantially across populations. Considering the substantial phenotypic differences between Pacific and



Fig. 22.23 Poorly understood aspects of walrus (*Odobenus rosmarus*) behavior range from individual behavior like nuzzling, to group behavior. **a**, Young male nuzzling a rock as it hauls out. **b**, Two sexually mature males, one 6–9 and the other 10–15 year old; (note the bosses) investigate a walrus carcass with the mystacial vibrissae (and smell?). **c**, Pacific walrus can detect the presence of carnivorous killer whales (*Orcinus orca*) up to several km away, presumably by the whales' underwater sounds. In response, all walrus swim quickly toward one another, resulting in a dense group (see also Kryukova 2016a; Kryukova et al. 2010). Killer whales do not approach such large groups and prefer to pursue small groups or single individuals (**d**). All photographs: Anatoly A. Kochnev

Atlantic walrus, and their long period of divergence, differences in breeding displays likely also occur. More information on displays of the Pacific walrus, more populations of the Atlantic walrus, and of the Laptev walrus, is desirable.

Walrus communicate extensively, mainly over short distances. Communication and the social system are intertwined, and knowledge about them will deepen our understanding of gregariousness and many other distinctive features of walrus biology. To date, only coarse patterns of the structure of conspicuous signals (“displays”) in a narrow range of situations have been studied. The broader structure of and variation in communicative signals in all modalities need to be described, and patterns of interaction documented. The program should include ontogeny of communicative signals. A striking gap in knowledge concerns communication within groups that are traveling or feeding, a situation in which some odontocete species engage in extensive tactile and acoustic communication (Norris 1991). The need for studies on behavior in relation to body contact and touching is noted above. Those studies should include special attention to the structure and contextual use of the extremely common behavior of social nuzzling, and to its sensory and behavioral significance. As noted, nuzzling occurs in air and under the water, so is not always associated with olfaction. However airborne nuzzling appears to be usually

associated with olfaction, judging by the open nostrils of nuzzling animals. Olfaction begs to be studied, considering the species' sensitivity to and alarm in reaction to smelling foreign odors (*e.g.* humans; smoke; Fay et al. 1984a), the common behavior of smelling conspecific animals, smelling the substrate when hauling out on land (Fig. 22.23), and in interactions between females and their calves and between individuals of other classes.

Understanding walrus society more fully will require knowledge about the presence and nature of inter-individual associations over time, both kin and non-kin, and about possible genetic structure and relationships within herds (Beatty et al. 2019, 2020; O'Corry-Crowe et al. 2020). Certainly the social bonds between females and their calves can be broken (and of course calves killed) in stampedes in large terrestrial aggregations, which are increasing in occurrence and size especially in Alaska and Russia. Much mortality can be experienced in such circumstances, and young animals are affected disproportionately directly through physical injuries, and indirectly through predation by polar bears on young animals (Tomilin and Kibal'chich 1975; Born et al. 1995; Kochnev 2002, 2004; Garlich-Miller et al. 2011; Jay et al. 2011; Udevitz et al. 2013; citations in Fischbach et al. 2016; Øren 2017). Separation of females and their calves also can result from stronger storms caused by reduction in the amount of and later seasonal formation of sea ice (Kochnev 2004). The importance of obtaining information from multiple haulout sites and over time is obvious from inter-annual and geographic fluctuations in and increasing loss of sea ice (Fischbach et al. 2016; Descamps et al. 2017; Kochnev 2019), and in the varied causes of mortality across different sites (Kibal'chich 1978; Gol'tsev 1968; Kochnev 2002, 2004).

Basic knowledge of individual and social behavior is relevant and important directly and indirectly to many aspects of walrus captive welfare, biology, and conservation. For example, through studies on anatomy and behavioral elements of feeding, we can understand better how walruses find, obtain, and consume their invertebrate prey, and what signs they leave behind when they do so (Kastelein and Mosterd 1989; Kastelein et al. 1991a, b, 1994). Improved conditions for captive animals have been developed using results from those studies plus increased knowledge of wild walruses (Kastelein and Wiepkema 1989; Kastelein et al. 1989, 2007, 1991b). Similarly, Fernandez and Timberlake (2019), recognizing the great amount of time that wild walruses spend foraging, and the highly specialized behavior that they use in feeding, developed methods to ameliorate behavioral stereotypes of captives such as repetitive swimming and sucking.

Understanding the social system and social culture of walruses is vital to conservation of the species. Genetic investigations like that of Beatty et al. (2019, 2020) will help to reveal the bases for herd structure, group, and care-giving behavior. As part of advancing knowledge in this area and in many other facets of walrus biology, it is important to incorporate natural history information and hence to train students in how to gather and report on such information (Estes and Gilbert 1978; Graham et al. 2011; Able 2016; Barrows et al. 2016); observer observations and impressions over the past century, despite seemingly casual interpretive references to "family groups" *etc.*, have been invaluable in building an overall picture of walrus society

that must be real in part (*e.g.* in respect to care-giving behavior) but needs to be built further through more critical observations. Only anecdotal evidence about behavioral development of any sort—individual or social—is available, yet behavioral development is a topic of great importance for deeper understanding of feeding and social structure, for example.

Knowledge of behavior is useful in diverse other kinds of studies. For example, information about time-activity budgets, haulout patterns, and influences of weather is vital for assessing survey data; for survey data as recent as 2006, the authors of one study could claim that it was “the first Pacific walrus survey to account for the proportion of the population in the water during the survey” (Speckman et al. 2011: 545). Subsequent studies on instrumented walruses have provided finer detail about activity budgets, time at and below the surface effects of weather, *etc.*

Assessment of effects due to human disturbance needs adequate understanding of many aspects of behavior, ranging from sensory biology to social structure: individuality (“personality”; de Vere et al. 2017; DeRango and Schwarz 2021); mechanics of feeding behavior; site fidelity; social structure; and walrus cultural traditions (Brakes and Dall 2016). Of course, the relevance of selected behaviors to a problem needs to be articulated, especially with respect to management problems (Greggor et al. 2016). Some forms of human disturbance occur directly at the hands of researchers, as in handling and marking or, over a longer period, effects of attached instruments (Rosen et al. 2017). For example, it is long been accepted that walrus tusks function as “runners” when feeding on the sea floor; this can account for patterns of wear on the anterior surface (Fay 1982). In addition, walruses appear to be lateralized and to favor the right flipper while feeding (Levermann et al. 2003), which may explain the generally greater wear on right tusks (MacCracken and Benter 2016; B. L. Benter *in litt.* 15 January 2020). What are the effects on feeding behavior and energy budgets of walruses resulting from instruments attached to tusks? Various kinds of instrument have been attached to walruses (Dietz et al. 2014). Horning et al. (2017; 2019) review some general concerns about instrumentation in their consideration of devices that are implanted or attached externally.

Species that have evolved in a setting of recurrent and predictable selective forces may lack sufficient behavioral flexibility to adjust to novel challenges over short, non-evolutionary time scales, or to rare, severe environmental events in general (Trillmich 1993; Kappeler et al. 2013). Knowledge of the walrus’s evolutionary history and adaptive traits therefore can inform about its resilience to anthropogenic climate change and other future challenges (Estes 1979; Born 2005); different populations of the species may differ in their responses (Born 2005). Ecological research and conservation concerns for the walrus presently address mainly small to moderate spatiotemporal scales, which is appropriate for investigating certain topics (*e.g.* effects of human disturbance; use of terrestrial haulouts in response to receding ice). Studies of behavior can contribute to planning and decision-making over multiple scales and can usually benefit by being integrated across different disciplines (Greggor et al. 2016; Keighley et al. 2019a).

Early observations on and interpretations of movements, diving, and feeding were based on direct observations or inference. Technical advances have led to a spectacular radiation of instrumentation and analyses that have illuminated our

knowledge and understanding of the behavioral ecology of walruses. However, knowledge of those subjects is mainly disconnected from knowledge of the behavior that underlies the patterns. For example, different motor patterns have different energetic costs, and those costs likely differ over ontogeny and whether a walrus is alone or moving in a group (Trillmich 1996).

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