Tyack, P. and E.H. Miller (2002) Vocal anatomy, acoustic communication and echolocation. Pp. 142-184 in Marine Mammal Biology: An Evolutionary Approach (A.R. Hoelzel, ed.). Blackwell Science, Oxford, England.

Vocal Anatomy, Acoustic Communication and Echolocation

Peter L. Tyack and Edward H. Miller

6.1 INTRODUCTION

In this chapter, we take the functional perspective of behavioural ecology to explore how marine mammals communicate, orientate, and echolocate in the sea. Most of the problems faced by marine animals are identical to those facing terrestrial animals: finding and capturing prey, avoiding predators, orienting in geographical space, finding and selecting a mate, and taking care of offspring. Yet the marine environment differs from the terrestrial environment in ways that have modified the costs and benefits of different sensory modalities that might be used to solve these problems. In particular, the marine environment favours the acoustic channel for rapid transmission of information over ranges of greater than a few tens of metres, and this has led to the evolution of auditory and vocal specializations in many marine mammals. These specializations are reflected in the morphology, functional anatomy and physiology of marine mammals (see Chapter 5).

Different communication problems have different requirements for how far signals should be transmitted, how long signals should last, how rapidly signals should travel, etc. For example, an alarm call intended for conspecific recipients would ideally travel rapidly only to them and would not be detectable by the predator, which is often more distant. To reduce the risk of interception by predators, alarm calls should be quiet, brief and difficult to locate (Klump & Shalter 1984). By contrast, reproductive advertisement displays of males are likelier to be detected by females if the displays are lengthy or repeated and have a large broadcast range; selection would also favour displays that can easily be located by females.

Animals live in different environments and move over different scales; these differences alter the costs and benefits of different sensory modalities for solving a specific communication or sensory problem. Many marine mammal species are social and highly mobile, so potentially large ranges for communication may be socially and ecologically important to them. Table 6.1 summarizes important differences between air and water for several sensory modalities. Small marine organisms use electrical and chemical signals to communicate over ranges of a few metres, but their limited ranges make them unsuitable for rapid communication over long ranges. The maximal ranges of propagation for long-distance optical or acoustic signals differ greatly in air versus water. Sunlight illuminates optical displays in open terrestrial environments during the daytime, often allowing them to be detected at ranges of a kilometre or more. Light scarcely attenuates as it passes through kilometres of clear air, but marine animals can seldom see an object more than a few tens of metres away. In contrast, sound attenuates less and travels faster in water than in air. Maximal ranges for detecting vocalizations of terrestrial animals are typically 1–10 km, but underwater microphones, called hydrophones, can detect low-frequency vocalizations of marine mammals at ranges of up to hundreds of kilometres (Tyack & Clark 2000). The limited range of vision and excellent propagation of sound under water not only favour acoustics for long-range communication, but also have selected for the evolution of echolocation in some marine mammals (Section 6.4).

When terrestrial mammals invaded the sea, they encountered new constraints and opportunities for sensing signals. Some marine mammals (sirenians, cetaceans, phocid seals and the walrus, *Odobenus*

Table 6.1 Comparison of the range, speed and locatability of different sensory modalities in air and under water. This table summarizes different physical attributes of acoustic, light, chemical and electrical cues in these two environments, along with features that are relevant for antidetection or location strategies.

Sensory modality	Mode of sensing	Mode of production	Range		Speed (m/s)		Locatability	Antidetection and location strategies
			Air	Water	Air	Water		
Acoustic	Hearing	Vocalization	1 km?	10–100 km	340	1500	Moderate	Faint hard-to-localize signal
Light	Vision	Luminescence	1–10 km	1–100 m	3×10^8	2.25×10^8	Good	Disruptive coloration; counter-illumination
Chemical	Olfaction	Pheromone	1 km?	10–100 m	Slow (wind)	Slow (current)	Moderate	Highly specific chemical signal and sense
Electrical	Electrical sense	Electric organ discharge	NA	Few metres	NA	Fast	Moderate	Jamming?

NA, not applicable.

rosmarus) evolved specializations for using sound to communicate under water and to explore the marine environment; others, including the otariid pinnipeds, sea otter (*Enhydra lutris*) and polar bear (*Ursus maritimus*), still communicate mainly in air. All sirenians and cetaceans live their entire lives in the sea, and cetaceans show the most elaborate and extreme specializations for acoustic communication under water (and rarely produce in-air vocalizations; Watkins 1967a). For example, the number of fibres in the auditory versus optic nerve is 2–3 times as high in cetaceans as in land mammals, suggesting an increased investment in audition compared to vision (Ketten 1997, 2000) (Chapter 4). Other than sirenians, the sea otter and cetaceans, all marine mammals spend critical parts of their lives on land or ice and some (mainly phocid seals) need to communicate both in air and under water. Kastak and Schusterman (1998) compared in-air and underwater hearing of three pinniped species. They argued that the California sea lion (*Zalophus californianus*) is adapted to hear best in air; the common seal (*Phoca vitulina*) can hear equally well in air and under water; and the auditory system of the northern elephant seal (*Mirounga angustirostris*) is adapted for underwater sensitivity at the expense of aerial hearing. These differences appear to reflect the relative importance of hearing in the two different environments for the different species.

6.2 SCOPE OF ACOUSTIC COMMUNICATION

6.2.1 Communicatively significant sounds: a continuum from incidental to highly specialized

> *When we speak of communicating, we commonly imply the use of specialized signals. These are not strictly necessary; we could define communication as any sharing of information from any source (Smith 1977, p. 13).*

Communication is usually defined in terms of a signal that provides information from a signaller to a receiver. Communication signals originally evolved in animals from useful but inadvertent sources of information, sources such as the sounds of respiration, locomotion or ingestion (Kenyon 1969; Watkins & Schevill 1976). If the sender benefits from transmitting information with a signal, evolution may select for more specialized signals or ritualized displays. A display that is 'ritualized' is defined as evolutionarily 'specialized in form . . . or frequency as an adaptation expressly to permit or facilitate communication' (Moynihan 1970, p. 86); ritualization can also take the form of a signal—even a simple signal—being used only in highly specific circumstances (Smith 1986, 1991a; Bain

1992). For example, when pinnipeds dive quickly upon detecting a potential predator the sounds they produce at the water surface commonly elicit reactions in conspecific animals, such as sudden diving or swimming away. When alarmed, some species (e.g. the harp seal, *Pagophilus groenlandicus*) loudly slap the water surface as they dive. Rapid submergence presumably was the original source of ritualized slapping of the surface by fore- or hind-flippers in pinnipeds, as in some aquatic displays of adult male common seals (Hewer 1974; Hanggi & Schusterman 1992, 1994). Male sea otters patrol the territory while swimming on the back with 'unusually vigorous kicking and splashing actions' (Calkins & Lent 1975, p. 529).

Information provided to receivers from sources other than displays is extremely important in communication over short distances. Bradbury and Vehrencamp (1998) recognized inadvertent **cues** as an important kind of non-display information. Examples of acoustic cues include:

1 Sounds produced by sea otters striking a food item on the belly with a stone while floating on the back.
2 Movement-related hydrodynamic or surface sounds (Watkins 1981; Watkins & Wartzok 1985).
3 Sounds produced by otariids rapidly walking on gravel (displacing it) or on a rock surface (especially if the animal is wet).

Sounds of locomotion may not be evolutionarily specialized as displays, but nevertheless can provide valuable information to receivers, for example in helping them to appraise body mass or to assess the success of feeding animals. Physical contact between fighting male marine mammals can generate loud percussive sounds by bodies or body parts (such as flippers, Miller 1991) making sudden forceful contact (e.g. humpback whales, *Megaptera novaeangliae*; Tyack & Whitehead 1983). Other males observing such interactions may be able to obtain information from them that is useful in their own future interactions with the fighting males.

There is a continuum in animal communication from unritualized cues to displays that are highly specialized for their signalling function. Distinctions between displays, unritualized actions and cues are conceptually useful but they may blur during the evolution of ritualized displays or countermeasures against interception (Andrew 1972; Beer 1982). For example, seismic vibrations are generated incidentally by locomotion of northern elephant seals on land and are perceptible to recipients up to 20 m distant (Shipley *et al.* 1992). In some instances vibrations appear to be produced deliberately. Males and females occasionally 'raise their forequarters and slap the sand with their head or chest without vocalizing' (Shipley *et al.* 1992, p. 559). These movements also generate sounds and may represent a ritualized display.

Some of the most obvious displays of cetaceans to human observers on a boat are the so-called 'aerial' displays of breaching, lobtailing and flipper slapping. We use vision to see these displays in the air, but the primary signal a cetacean sends to a conspecific whale with these 'aerial' displays is more likely to be the sound of the body hitting the water surface. Some of these sounds can be quite loud; for example, fluke and flipper slaps of humpback whales range in source level from 183 to 192 dB re 1 μPa at 1 m (Thompson *et al.* 1986), compared with a range of 144–174 dB for the species' song (Levenson 1972). These 'aerial' displays may be heard kilometres away, but animals at close range may sense both the optical and acoustic components.

Respiration and breathing have provided the raw material for the evolution of displays involving bubbles. 'Bubble blowing' in various forms occurs in displaying common seals, harp seals, bearded seals (*Erignathus barbatus*) and probably other pinniped species (Fig. 6.1a) (Ray *et al.* 1969; Hewer 1974; Møhl *et al.* 1975; Hanggi & Schusterman 1992, 1994). Cetaceans also produce bubble displays. Bottlenose dolphins (*Tursiops truncatus*) occasionally blow streams of bubbles that are highly synchronized with the production of whistle vocalizations (Caldwell & Caldwell 1972a; McCowan 1995; Herzing 1996). The bubble streams are a highly visible marker identifying who is vocalizing, but it is not known whether other dolphins use the information for this purpose or as an additional signal used to modulate interpretation of the whistle. During the breeding season, humpback whales form groups in which males compete for access to a female (Tyack & Whitehead 1983). Males in these competitive groups produce streams of bubbles up to 30 m long (Fig. 6.1b). When marine mammals exhale forcefully, they also create

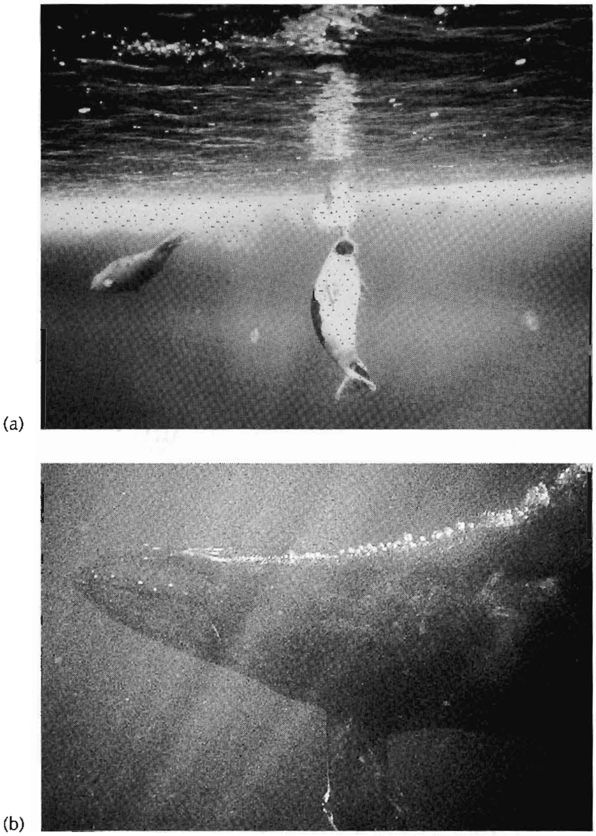


Fig. 6.1 Underwater exhalation of air is a common acoustic and optical display in marine mammals. (a) Adult male harp seal (*Pagophilus groenlandicus*) releasing air bubbles while vocalizing in threat. (From Merdsoy *et al.* 1976). (b) Adult male humpback whale (*Megaptera novaeangliae*) producing a stream of bubbles while challenging another male for access to a female in a competitive group (Tyack & Whitehead 1983). (© D. Glockner-Ferrari, Center for Whale Studies)

a non-vocal sound as the bubbles rise to the surface. Presumably air bubbles thus constitute a combined optical and acoustical display. Most terrestrial mammals exhale when they vocalize, but many marine mammals can vocalize without releasing bubbles and so must have anatomical specializations allowing the air passing the sound source to be held in some internal reservoir.

6.2.2 Vocal and non-vocal sounds

The terrestrial ancestors of marine mammals had vocal sound-production mechanisms typical of terrestrial mammals—air was passed under pressure from the lungs past laryngeal vocal folds that vibrated to produce sound energy (Kelemen 1963; Schneider 1964; Dorst 1973). It is possible to distinguish between 'vocal' sounds produced by specializations of the respiratory tract, and 'non-vocal' sounds produced by moving or striking body parts against one another or against some external structure. The term 'vocalization' is sometimes restricted to glottally produced sounds in the larynx, but we retain a broad interpretation of 'vocal sounds' in marine mammals to refer to sounds produced by air passing through specialized sound-producing structures in the body, whether these are vocal folds or some other organ. Some sounds we treat as vocal have simple mechanisms of production outside the larynx (e.g. snorts). For example, a male Forster's fur seal (*Arctocephalus forsteri*) arriving at a colony site in the spring may snort once or several times to announce its presence and willingness to compete for a territory (Winn & Schneider 1977). The pulse sequences produced under water by rutting male walruses using a non-laryngeal respiratory mechanism, and laryngeally produced sound sequences in other pinniped species can express complex ritualized temporal patterning even though the sounds themselves may be very simple (Fig. 6.2) (Bartholomew & Collias 1962; Le Boeuf & Petrinovich 1974; Ray & Watkins 1975; Sandegren 1976; Schusterman 1977; Shipley *et al.* 1981; Stirling *et al.* 1983; Miller 1991; Sanvito & Galimberti 2000a). Cetologists debate about whether the vocalizations of cetaceans are produced as air passes vocal folds in the larynx or as air flows past hard tissue in the nasal passages. The distinction of sounds as vocal or non-vocal based upon laryngeal origin is not useful for cetaceans given our current state of ignorance about the details of sound-production mechanisms.

6.3 SOUND PRODUCTION

6.3.1 Laryngeal anatomy and mechanisms of sound production

The larynx of terrestrial mammals functions both for respiration and sound production; in marine mammals the larynx also exhibits adaptations for

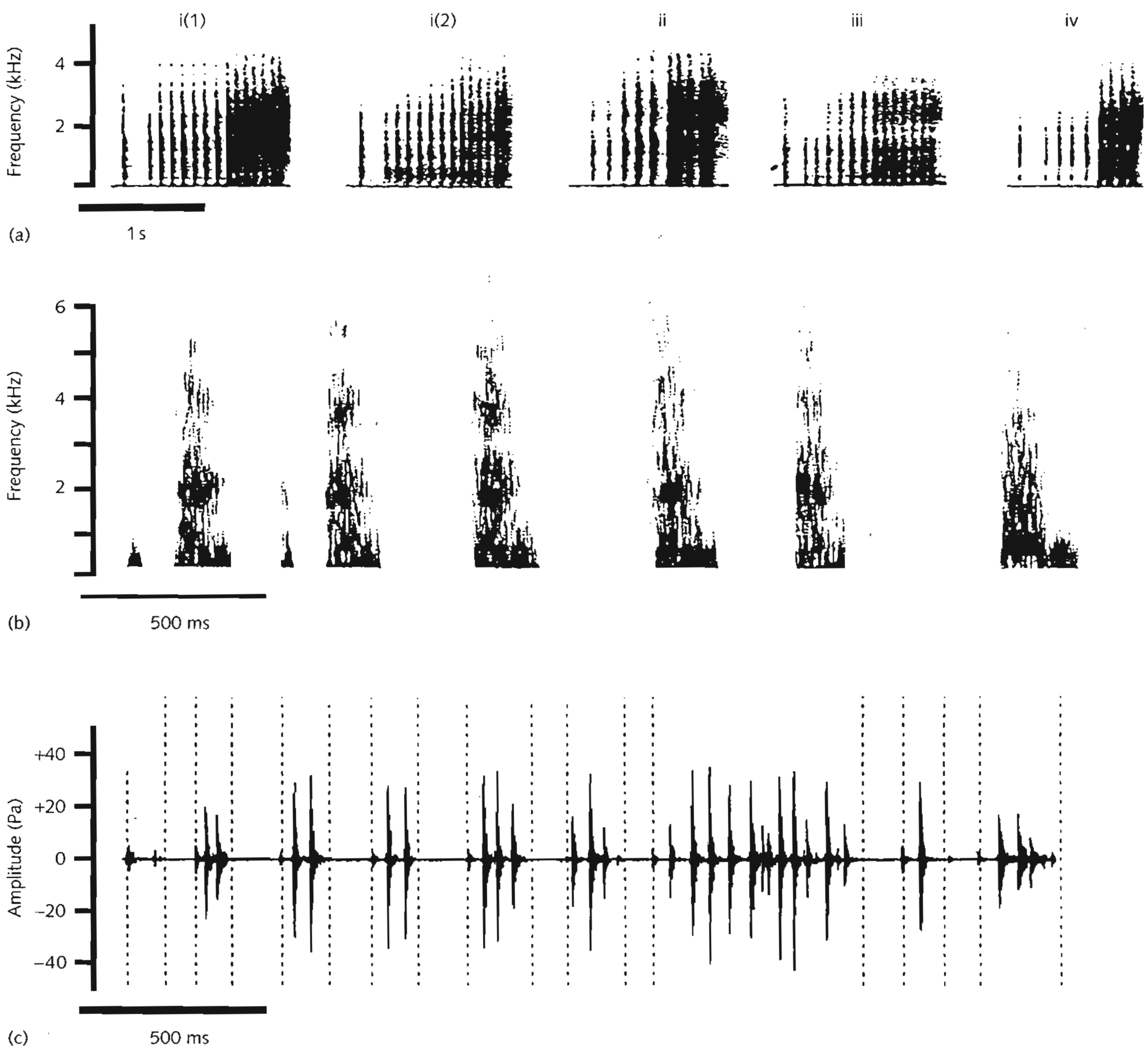


Fig. 6.2 Ritualization of acoustic displays can be expressed as stereotyped temporal patterning of simple sounds. (a) Spectrograms of pulse trains in underwater displays of rutting male Atlantic walruses (*Odobenus rosmarus rosmarus*). Four different individuals (i–iv) are represented; spectrograms i(1) and i(2) are from one male in successive years. (From Stirling *et al.* 1987.) (b) Spectrogram of chuffing vocalization of adult male polar bear (*Ursus maritimus*; the low-frequency sounds before the first two chuffs represent 'plop' component). (Adapted from Peters 1978.) (c) Waveform of drumming vocalization of a rutting male southern elephant seal (*Mirounga leonina*); the vertical dashed lines demarcate groupings of pulses in this airborne utterance. (From Sanvito & Galimberti 2000b.)

diving. The following review pertains mainly to pinnipeds and cetaceans because they have been studied the most and have diverse anatomical characteristics related to the production of vocalizations. For observations on the larynx and hyoid bone of sirenians and the polar bear see Kaiser (1974), Negus (1949) and Schneider (1963, 1964).

Cartilages and muscles of the mammalian pharynx, larynx and hyoid are well described, particularly for domestic species. The laryngeal skeleton comprises four main cartilages: thyroid, cricoid and paired arytenoids; smaller sesamoid cartilages and interarytenoid cartilages may also be present (Fig. 6.3). The musculus vocalis is present in pinnipeds and

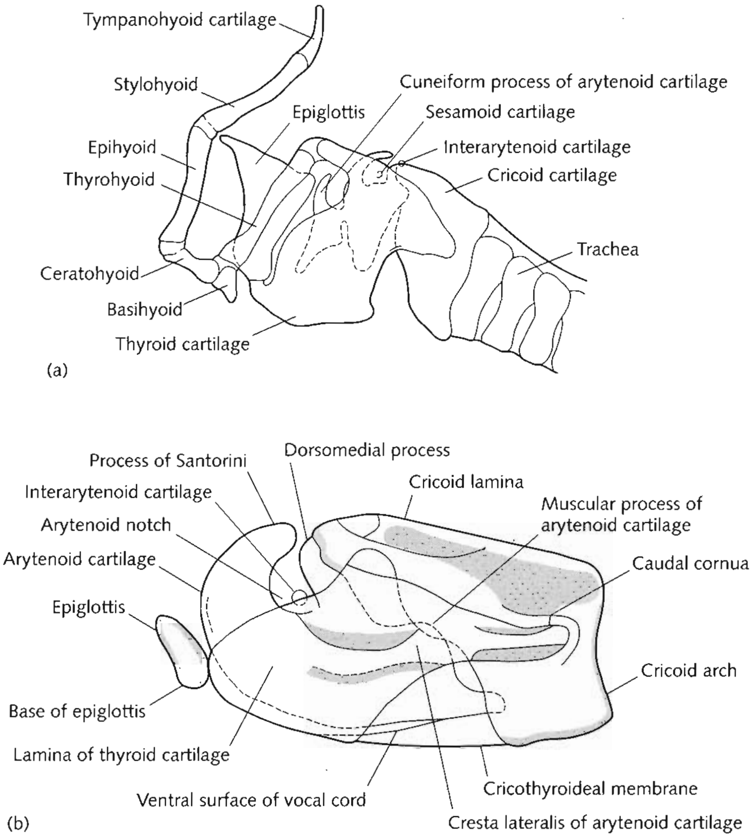


Fig. 6.3 (a) Hyoid, laryngeal cartilages and anterior end of the trachea in a left lateral view of the dog (*Canis familiaris*). (From Evans 1993.) (b) The laryngeal skeleton of a California sea lion (*Zalophus californianus*) in left lateral view. (Adapted from Odend'hal 1966.)

other Carnivora and plays an important role in the production and control of vocalizations (Schneider 1962, 1963, 1964; Odend'hal 1966; Piérard 1969; King 1983). The vocal folds are attached between the thyroid cartilage and the vocal process of the arytenoid cartilage on the left and right sides. The configuration of the laryngeal cavity, the space between the vocal folds, and the tension on the vocal folds are affected by the positions and shapes of the main cartilages and state of contraction of the laryngeal muscles. In pinnipeds, the size and shape of the laryngeal cartilages and muscles vary between species (Murie 1874; Chiasson 1955; Piérard 1965; Schneider 1963, 1964; Piérard 1969; King 1972, 1983), suggesting important species differences in the mechanisms of vocalization. There may also be differences within a species; in the northern fur seal (*Callorhinus ursinus*), for example, sesamoid cartilages are present only in males older than 5 years of age (Piérard 1969).

The larynx of baleen whales is similar to that of terrestrial mammals, as can be seen in Fig. 6.4, which compares the larynx of a terrestrial ungulate (the horse) with mysticete and odontocete cetaceans. Over two centuries ago, Hunter (1787) noticed an unusual laryngeal sac, called the diverticulum, on the lower side of the mysticete trachea, connected to the respiratory tract by an opening on the lower side of the thyroid cartilage (marked 'D' in Fig. 6.4b). Aroyan *et al.* (2000) modelled sound production in the blue whale (*Balaenoptera musculus*), and suggested that this laryngeal sac and the nasal passages may act as a resonator. Odontocetes have a larynx that differs from terrestrial mammals in that the arytenoid and epiglottal cartilages are elongated to form a beak-like structure that is held in the nasal duct by a sphincterlike palatopharyngeal muscle (Fig. 6.4c, d). This separates the respiratory tract from the mouth and oesophagus, reducing the risk of choking and

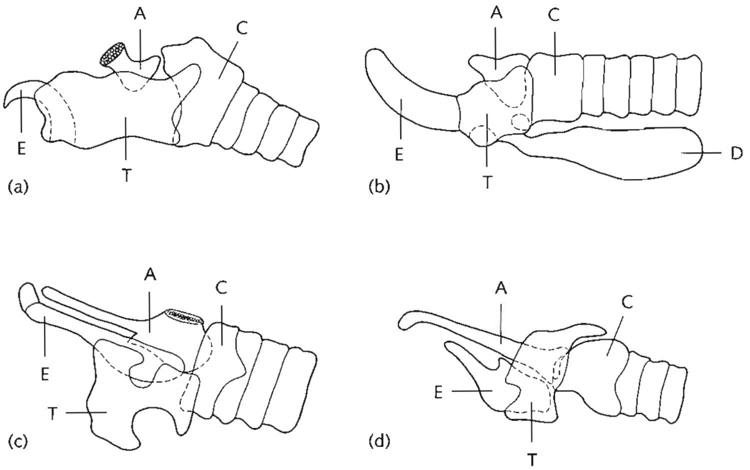


Fig. 6.4 Laryngeal anatomy in: (a) a terrestrial ungulate (horse), (b) a mysticete, and in two odontocete cetaceans, (c) a narwhal and (d) a pilot whale. A, arytenoid cartilage; C, cricoid cartilage; D, diverticulum; E, epiglottis; T, thyroid cartilage. (From Slijper 1979.)

allowing these animals to breathe and swallow at the same time.

There has been considerable debate about whether the larynx or nasal passages are the source of sounds such as clicks or whistles in odontocetes. The odontocete larynx is complex with a powerful musculature, and since the larynx is the source of vocalizations in most terrestrial mammals, many researchers have suggested that odontocete vocalizations are produced by the larynx (Lawrence & Schevill 1956; Purves 1966; Purves & Pilleri 1973, 1983). Reidenberg and Laitman (1988) reported vocal folds in the odontocete larynx, and argued that this supported the laryngeal-source hypothesis for odontocetes. Odontocetes also have a complex and specialized upper respiratory tract (Fig. 6.5). Since Norris *et al.* (1961) first proposed it, a growing group of biologists have suggested that the nasal passages may be the source of most odontocete vocalizations (Cranford 2000). In contrast to

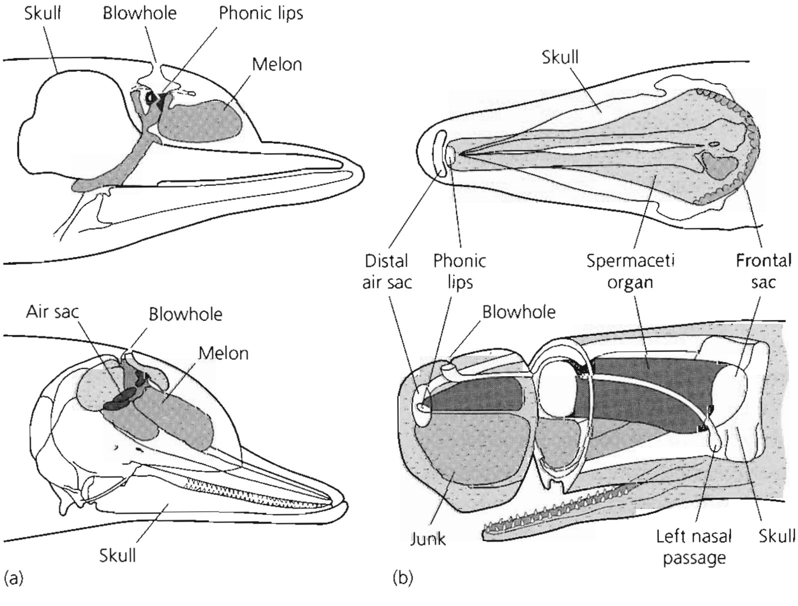


Fig. 6.5 Functional anatomy of sound production in two odontocete cetaceans: (a) the bottlenose dolphin, *Tursiops truncatus*, and (b) the sperm whale, *Physeter macrocephalus*. (Adapted from Au 1993; Cranford 2000.)

the primarily anatomical evidence for sound production in the cetacean larynx, there is strong physiological evidence for sound production in the nasal passages of odontocetes. This is reviewed in Section 6.3.2.3.

6.3.2 Anatomical mechanisms and specializations for sound production

6.3.2.1 Pinnipeds

The mechanism of vocalization in pinnipeds is essentially unstudied. Poulter (1965) localized the bark of California sea lions and suggested that the bark originates in the larynx. Brauer *et al.* (1966) reported on click vocalizations of California sea lions breathing heliox (a helium–oxygen mixture). Because of the low density of heliox, resonance effects due to gas-filled cavities are detectable by an upward shift in the frequency spectrum of vocalizations (Nowicki 1987). Sea lion clicks made in heliox displayed a significant upward shift in the frequency spectrum, suggesting resonance in air. California sea lions can bark successively under water without emitting bubbles and can emit two kinds of calls under water simultaneously, suggesting the possibility of alternative or multiple sound-generation mechanisms that do not require air to be expelled (Brauer *et al.* 1966).

Motor patterns that accompany the production of otariid roars and barks illustrate the complexity and interspecific diversity in mechanisms of sound production (Miller & Phillips 2001). For example, when breeding male South American sea lions (*Otaria flavescens*) bark they depress the lower jaw and simultaneously extend the tongue and flatten it enough to permit oral exhalation (and a bark); the nostrils remain completely or nearly closed. By contrast, the Australian sea lion (*Neophoca cinerea*) is reported to produce barks 'by vibrating the posterior part of the tongue against the soft palate at a rate of about 3 per second' (Marlow 1975, p. 186).

Walruses produce a great diversity of airborne vocalizations at all times of year (Miller 1985; Kastelein *et al.* 1995), and have diverse and elaborate displays below and at the water surface, especially during the rut (Fig. 6.2a) (Miller 1975, 1985, 1991; Ray & Watkins 1975; Fay 1982; Miller & Boness 1983; Stirling *et al.* 1983; Fay *et al.* 1984; Kastelein *et al.* 1995; Verboom & Kastelein 1995). The walrus may have more ways of producing sounds than any other pinniped species, including whistles produced by blowing air through the lips and gong-like sounds produced by pharyngeal sacs (Fig. 6.6a). Walruses have highly mobile tongues for feeding; supralaryngeal filtering by varied tongue shapes and positions may explain why even simple brief calls of the species are so diverse (Miller 1985; Kastelein *et al.* 1997).

Some phocid species have tracheal mechanisms for sound generation that were probably enabled by two respiratory adaptations for diving. One was the adaptive development of compressible airways in the form of flexible cartilage and membranes (Kooyman 1981). The other was increased tracheal width for rapid inspiration and expiration at the surface (Kooyman & Andersen 1969; Bryden & Felts 1974; Kooyman 1981; Ray 1981). Vocal folds are present in the Weddell seal (*Leptonychotes weddellii*) but may not generate vocalizations under water; rather, air movements between the larynx and trachea may generate sounds by vibration of the anterior tracheal membranes (Piérard 1969). Sufficient residual air is present for this kind of sound production even during dives to > 300 m or > 3030 kPa pressure (Kooyman *et al.* 1970). A similar mechanism of sound production may occur in the Ross seal (*Ommatophoca rossii*) (Bryden & Felts 1974; Ray 1981). The spectacular long (sometimes > 1 min) continuous underwater song of male bearded seals is followed, after an interval, by a terminal 'moan' when air is released (see Fig. 6.14a) (Ray *et al.* 1969). The song is probably produced by vibration of the expansive dorsal tracheal membrane that extends posteriorly to the lungs (Fig. 6.6b) (Burns 1981a). Adult male ribbon seals (*Histriophoca fasciata*) have a large air sac on the right side, which is connected via a valvular slit to the trachea near the tracheobronchial junction (Fig. 6.6c) (Sleptsov 1940; Abe *et al.* 1977; Burns 1981b). This sac is absent or more weakly developed in females, but it is unknown how this sac may contribute to sound production.

Intriguing observations on pulsation of the throat or chest in some vocalizing phocids suggest that involvement in sound production by the trachea and other parts of the respiratory tract may be widespread (Boness & James 1979; Gailey-Phipps 1984; Miller & Job 1992; Terhune *et al.* 1994a).

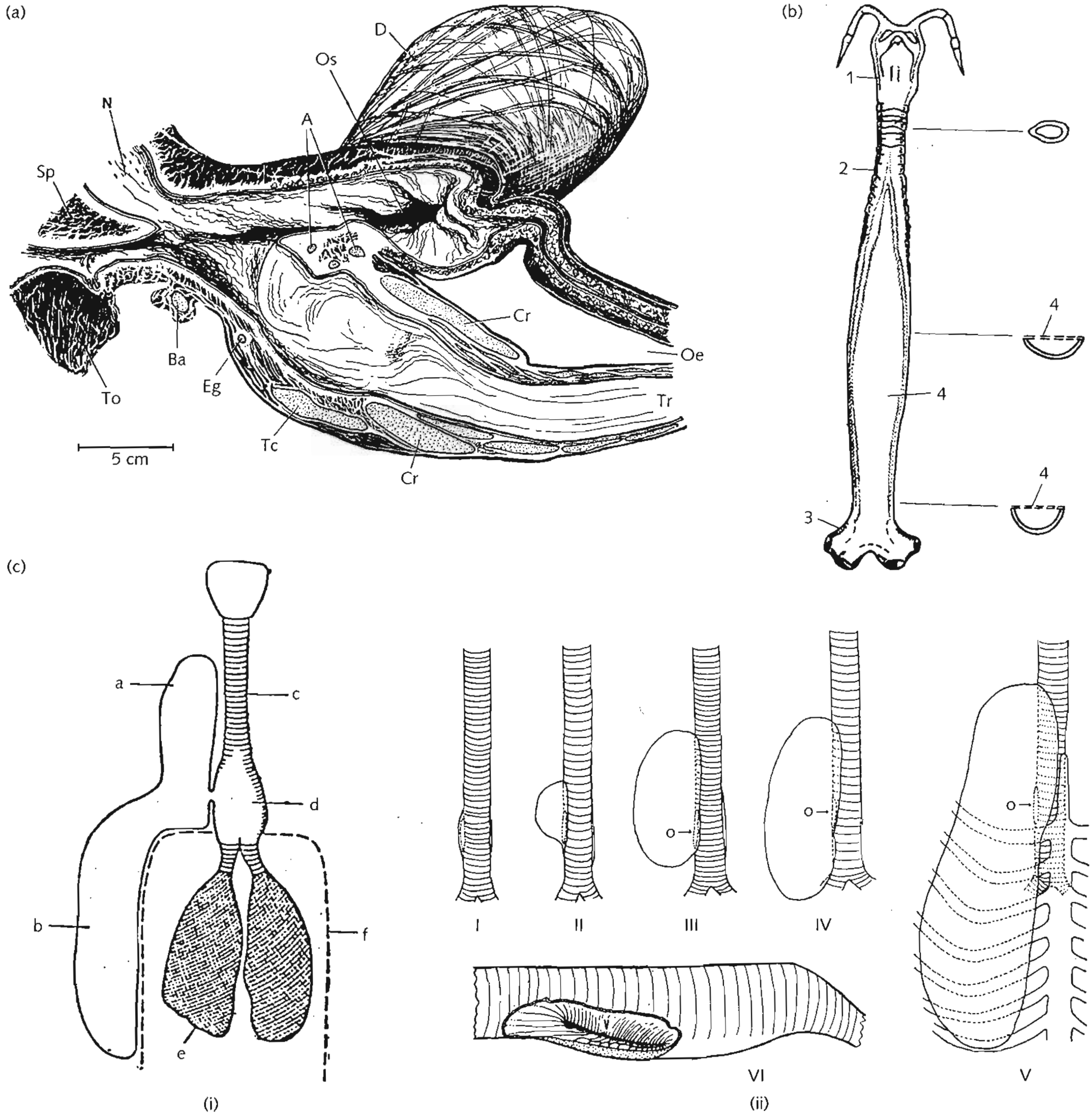


Fig. 6.6 Anatomical specializations for sound production in pinnipeds (the role of the air sac in sound production of the ribbon seal is likely but not established). (a) A sagittal section of the pharynx in the Pacific walrus (*Odobenus rosmarus divergens*; adult male), in left lateral view; note the partly distended pharyngeal pouch on the right side. A, arytenoid cartilage (cut); Ba, basihyoid (cut); Cr, cricoid cartilage (cut); D, diverticulum; Eg, epiglottis (cut); N, nasopharynx; Oe, oesophagus; Os, ostium diverticuli; Sp, soft palate; Tc, thyroid cartilage (cut); To, tongue; Tr, trachea. (From Fay 1960.) (b) The trachea (plus larynx, etc.) of the bearded seal (*Erignathus barbatus*) in dorsal aspect, showing the membranous section of the trachea between the larynx and lungs. 1, larynx; 2, trachea; 3, left bronchus; 4, membranous connective tissue. (From Sokolov *et al.* 1970.) (c) The tracheal air sac in the male ribbon seal (*Histriophoca fasciata*; ventral views): (i) in schematic outline, and (ii) of different sizes (specimens increase in size from I to V, except specimen III which was slightly larger than IV). The opening between the air sac and the trachea in a large male is shown in VI (right lateral aspect; membranous sac removed to reveal valve, 'v'). a, cervical portion of air sac; b, thoracic portion of air sac; c, trachea; d, expanded section of posterior trachea; e, lungs; f, rib cage; o, opening to air sac. (From Sleptsov 1940; Abe *et al.* 1977.)

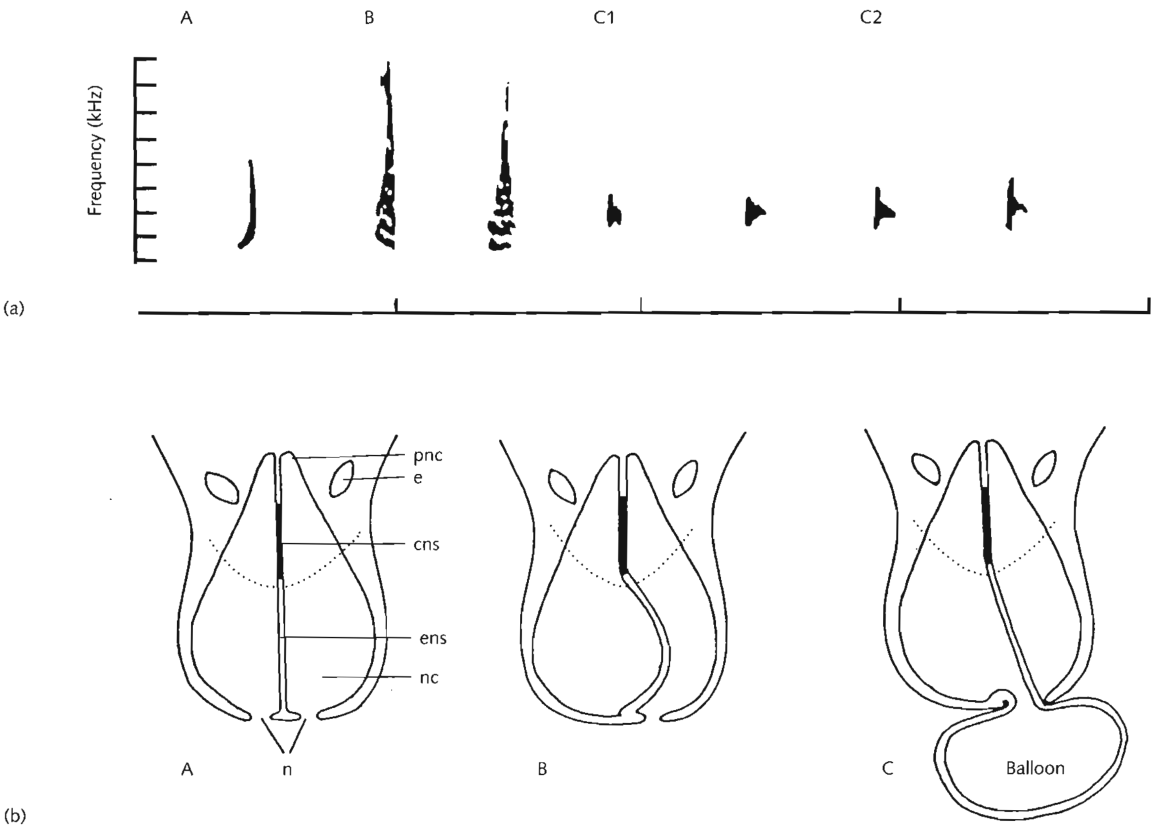


Fig. 6.7 Several kinds of mechanical non-vocal sounds are produced by the nasal hood and air-filled balloon (membranous nasal septum) of adult male hooded seals (*Cystophora cristata*). (a) Spectrograms of vocalizations produced: A, when fully inflated the hood is slightly deflated ('bloop'); B, when fully inflated the hood and septum are rapidly whipped downward ('whoosh'; two examples given); C, at the top of the upsweep of the hood and septum ('ping'; C1 and C2 represent separate recordings with the left spectrogram of each pair recorded in air and the other recorded simultaneously under water). (From Ballard & Kovacs 1995.) (b) Possible mechanism of balloon extrusion (schematic diagram, dorsal aspect): beginning from a relaxed position (A), one nostril is closed and the internal air pressure forces the anterior elastic nasal septum to bulge outwards (B), until it is extruded through one nostril as a large balloon (C). cns, cartilaginous part of nasal septum; e, eye; ens, elastic portion of nasal septum; n, nostril; nc, anterior part of nasal cavity; pnc, posterior part of nasal cavity. (Adapted from Berland 1966.)

Male hooded seals (*Cystophora cristata*) have a specialized inflatable nasal hood and septum that are used for a combined visual and acoustic display. Part of the nasal septum is highly elastic and can be extruded through one nostril as a large air-filled bladder, fiery red in colour (Fig. 6.7b) (Berland 1958, 1966; Popov 1961; Mohr 1963; Reeves & Ling 1981; Kovacs & Lavigne 1986; Lavigne & Kovacs 1988; Reeves *et al.* 1992). Distinctive 'bloop', 'ping' and 'whoosh' noises are produced during inflation or deflation of the hood and septum (Fig. 6.7a) (Terhune & Ronald 1973; Ballard & Kovacs 1995).

6.3.2.2 Polar bears and sirenians

The airborne sounds of the polar bear appear to be produced by laryngeal mechanisms typical of terrestrial mammals. The rapidly repeated chuff vocalization of the polar bear 'is produced with the mouth slightly open, and is characterized by visible chest and abdominal contractions and vertical and lateral motions of the upper lips overlying the cheek teeth . . . it appears that air is shuttled back and forth past the larynx with the emission of each burst of sound'; lip vibration may contribute to the sound

(Wemmer *et al.* 1976, p. 426). Sirenians vocalize under water and do not release air when vocalizing (Hartman 1971), but nothing is known about the functional anatomy of sirenian vocalization. Caribbean manatees (*Trichechus manatus*), Amazon manatees (*T. inunguis*) and dugongs (*Dugong dugon*) all contract the area behind the nostrils while vocalizing (R. S. de Sousa Lima, personal communication).

6.3.2.3 Cetaceans

Mechanisms of sound production in cetaceans are poorly understood. There has been considerable debate about which anatomical structures are the source of particular vocal sounds such as the clicks and whistles of odontocetes. Most cetaceans possess a well-developed larynx with vocal folds that might be capable of vibrating to produce sound when air passes over them (Reidenberg & Laitmann 1988). Aroyan *et al.* (2000) move beyond the debate about which structures excite vibrations, and they present a preliminary model of sound production in the blue whale. They suggest that when a blue whale vocalizes, much of the air stored in the lungs must flow through a valve that excites large pressure fluctuations in the nasal passages. They suggest that the relatively rigid nasal passages and the laryngeal sac act as a resonator for this sound. They note that the anatomical sites most commonly suggested as the oscillating valve for sound production are the vocal folds and the arytenoid cartilage, but either could function for this model. This work provides a good start for modelling sound production in mysticetes.

Over the past several decades, cetacean biologists have argued that odontocete cetaceans produce sound when air flows past the nasal passages in the skull. Evans and Maderson (1973) proposed that dolphin clicks were produced by a friction-based mechanism as air moved nasal plugs against the bony nares, with sound produced by the contact of hard tissues, as with stridulation in invertebrates. Cranford (1992, 1999, 2000) and Cranford *et al.* (1996) pointed out that the odontocete nasal passage can be blocked by a pair of internal nasal lips that he calls the 'phonic lips'. Cranford (2000) argued against the friction mechanism and suggested that odontocete cetaceans produce sound when air flows past these 'phonic' lips in a process similar to that by which terrestrial mammals produce glottal pulses with the larynx. Cranford (2000) used a high-speed endoscope to show that each pulse produced by a bottlenose dolphin is coincident with a movement that 'begins with the lips parting, followed by an explosion of air and fluid erupting from the gap between the lips, and concludes with closure of the lips' (p. 133).

Physiological experiments with dolphins support the hypothesis that the nasal passages are a source of sound production in odontocetes. Dormer (1979) made X-ray motion pictures of dolphins as they vocalized, and showed that air moved from the bony nares into the upper nasal passages. The X-ray images showed movement of the nasal plugs in the bony nares during vocalization, but did not show any movement of the larynx. Dormer (1979) associated movement of the right nasal plug with click production and movement of the left nasal plug with whistle production. MacKay and Liaw (1981) confirmed Dormer's results that the right nasal plug moves when clicks are produced. Ridgway *et al.* (1980) and Amundin and Andersen (1983) measured air pressure above and below the bony nares and measured electrical activity of the surrounding muscles. Before vocalization, air pressure built up below the nares. During vocalization, muscle activity occurred near the nares, but not near the larynx, and air pressure changed across the nares, suggesting that air flows across the nares and into the upper nasal sacs during vocalization. Aroyan *et al.* (1992, 2000) and Aroyan (1996) used structural acoustic models to calculate that the measured beam pattern from clicks of the common dolphin (*Delphinus delphis*) are consistent with a sound source about 1 cm below the right phonic lips. No such physiological studies have been made on mysticetes, which may use the larynx and the associated sac in sound production as proposed by Aroyan *et al.* (2000).

Identifying the source of sound is only part of the sound production story. Mechanisms for sound production must also match the acoustic impedance to the medium of air or sea water, and they may function to direct some sounds in a beam. The echolocation clicks of dolphins are known to be highly directional, pointing ahead of the dolphin in a beam about 6–10° in width (Au 1993). The dolphin has a fatty body called the melon in its forehead (Fig. 6.5a). This melon contains unusual fats with a sound velocity similar to that of sea water. The melon couples acoustic energy from the nasal area to sea water by matching the acoustic impedance of these different media. There is a gradient in sound velocity within the melon that causes some refraction of high-frequency sound, but Au (1993) states that this refraction is not enough on its own to account for the directionality of the dolphin click. The beam pattern of dolphin clicks stems from a complex interaction of reflection from the skull and air sacs, coupled with refraction in the soft tissues. Aroyan (1996) argues that the skull plays a predominant role in forming the beam of dolphin echolocation clicks.

We have a more detailed model of sound production for sperm whales (*Physeter macrocephalus*) than for other cetacean species. Sperm whales have a large organ called the spermaceti organ, which lies dorsal and anterior to the skull. Below the spermaceti organ is the 'junk', which is composed of a series of fatty structures separated by columns of dense connective tissue. Norris and Harvey (1972) argue that the spermaceti organ generates the clicks that are the dominant vocalization of sperm whales. Sperm whale clicks comprise a burst of pulses with equally spaced interpulse intervals (IPIs) (Backus & Schevill 1966; Goold & Jones 1995). Norris and Harvey (1972) suggest that the invariance of IPIs may result from reverberation within the spermaceti organ. They suggest that the spermaceti organ has a reflector of sound at the posterior end (frontal sac) and a partial reflector of sound at the anterior end (distal sac) (Fig. 6.5b). They further propose that the source of the sound energy in the click comes from a strong valve (i.e. the phonic lips of Cranford 1999) in the right nasal passage at the anterior end of the spermaceti organ (Fig. 6.5b). Norris and Harvey (1972) propose that the phonic lips act as a check valve, and that as pressure builds up behind these cornified lips in the right nasal passage, they open and close rapidly, producing an initial pulse of sound energy. Some of the energy from the first pulse within the click is hypothesized to be transmitted directly into the water. The remaining pulses are hypothesized to result as the initial sound reflects between the posterior and anterior reflectors within the spermaceti organ. Cranford (1999) proposes that some of the sound energy reflecting off the frontal sac becomes directed into the junk, and may be projected into the ocean medium, following a path that bypasses the reflective distal sac. Some of the sound energy reflecting back off the anterior reflector will reflect forward from the posterior reflector, leading to multiple pulses within a click. If this hypothesis is correct, then the IPI could represent an accurate indicator of the length of the spermaceti organ. Gordon (1991) measured the length of sperm whales in the wild and found the expected correlation between IPI and estimated size of the spermaceti organ.

The recent work of Cranford (1999), Cranford *et al.* (1996) and Aroyan *et al.* (1992) uses new techniques involving non-invasive three-dimensional imaging of animals, inferring the acoustic parameters from these images, and modelling the acoustic properties of the anatomy using structural mechanical models. These new techniques offer promise that this field will move from the decades of controversy regarding the source of sound production to a full analysis of how marine mammals produce sounds with particular time-frequency and directional qualities. This research is also shedding light on the evolution of sound production in odontocetes. In spite of the differences in form of sound-producing structures in dolphins and sperm whales (Fig. 6.5), Cranford *et al.* (1996) and Cranford (1999) suggest that the phonic lips of dolphins and sperm whales are homologous and that the junk in sperm whales may be homologous with the melon of dolphins.

6.3.2.4 Source–filter models of sound production

The controversy over the source of sound production in cetaceans appears to have inhibited the development of more sophisticated models that include not only the source but also the effects of filtering. Supralaryngeal filters are extremely important in shaping the acoustic properties of vocalizations of terrestrial mammals. Section 6.3.2.1 described how pinnipeds may change the shape of their oral and nasal cavities as they vocalize. As discussed above, the sperm whale has organs in

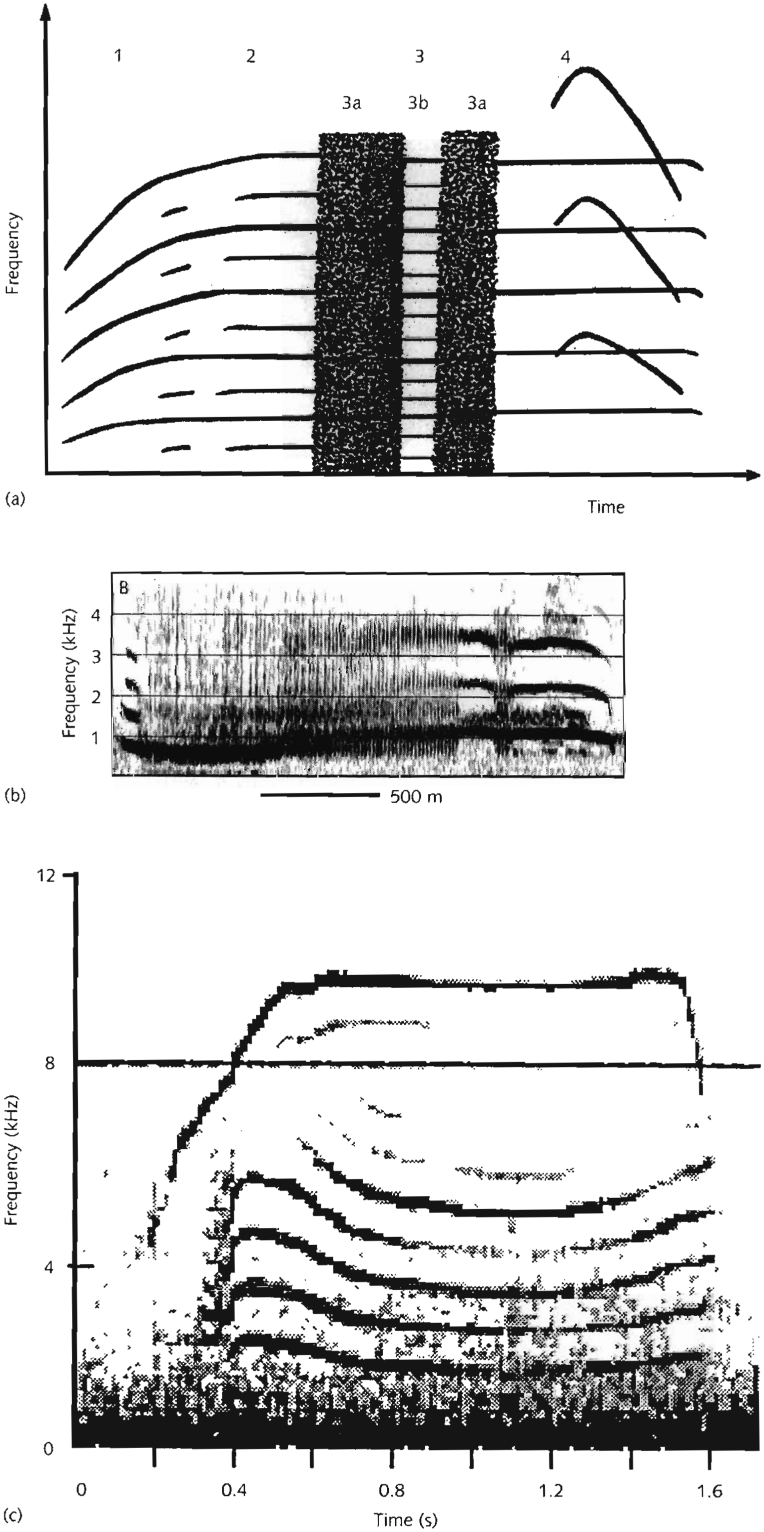


Fig. 6.8 Many communicatively important features of vocalizations result from non-linear processes in the vocal tract. (a) Schematic narrow-band spectrogram illustrating periodic phonation (1, 3b) and three phenomena resulting from non-linear processes: subharmonics (2), chaos (3a) and biphonation (4). (From Wilden *et al.* 1998.) (b) Spectrogram of the vocalization of an adult female South American fur seal (*Arctocephalus australis*) to her pup. A sharp transition from periodic to chaotic phonation occurs early in the call. (From E.H. Miller, unpublished data; see also Miller & Murray 1995.) (c) Spectrogram of a stereotyped, pulsed call N1 from a killer whale (*Orcinus orca*) showing a tonal high-frequency component harmonically unrelated to the pulsed call. (From data courtesy of P. Miller.)

the head that appear to be specialized to modify sounds emanating from the sound source. Odontocete cetaceans have a complex upper respiratory tract, with many air sacs, but their role in sound production has rarely been discussed for marine mammals (Miller & Job 1992). In humans, many of the effects of acoustic filtering are predictable from the shapes, dimensions and elasticity of the resonating cavities (Rubin & Vatikiotis-Bateson 1998). One important result of filtering is the production of **formants**—parts of the frequency spectrum that are reinforced by resonant properties of the vocal tract (Cherry 1978; Pierce 1983; Lieberman 1984). Supralaryngeal filters change continuously in size and shape during many vocalizations, imparting distinctive temporal patterns to formants. Because supralaryngeal filtering is effected mainly by a few key cavities, resulting vocalizations are informative about facial expression, tongue position and shape, body size, and other behaviourally and anatomically telling features of the pharynx of vocalizing animals (Andrew 1963, 1976; Rossing 1990; Shipley *et al.* 1991; Fitch 1997; Terhune *et al.* 1994a). Many cetacean vocalizations also appear to have formant-like features, but a more detailed model of vocal production in cetaceans is required in order to interpret such features in terms of vocal tract filtering.

Many features of vocalizations are not explainable just in terms of linear analysis of the sound source and resonant filters. Additional explanations in terms of non-linear phenomena are necessary. Three important phenomena that result from nonlinear dynamics during mammalian vocalization are subharmonics, biphonation and deterministic chaos (Fee *et al.* 1998; Wilden *et al.* 1998). Figure 6.8 gives a schematic illustration of how these phenomena appear on spectrograms, along with examples of such phenomena in vocalizations of pinnipeds and cetaceans (for sirenians, see Anderson & Barclay 1995). In the South American fur seal (*Arctocephalus australis*) there is 'residual' harmonic structure following the abrupt transition from periodic phonation (Fig. 6.8b), which provides evidence of chaotic phonation rather than turbulent noise (Wilden *et al.* 1998). Many stereotyped pulsed calls of killer whales (*Orcinus orca*) also have a tonal high-frequency component (Fig. 6.8c) (Hoelzel & Osborne 1986) similar to the biphonation phenomenon indicated in Fig. 6.7a (see also Tyack 1991).

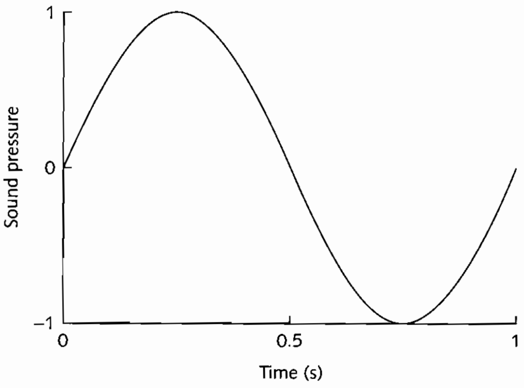
6.4 ECHOLOCATION

The term 'echolocation' was coined by Donald Griffin (1958) to describe the ability of flying bats to locate obstacles and prey by listening for echoes returning from high-frequency clicks that they emitted. A similar form of echolocation has been well documented for dolphins in captivity. Most dolphins produce high-frequency clicks produced in a narrow beam in front of the head. After producing a click, a dolphin usually waits and listens for echoes that may backscatter from targets within the click's beam. The large and successful body of experimental research on dolphin echolocation has been well summarized by Au (1993). When biologists think of echolocation, they think of an animal listening for echoes from its own high-frequency directional clicks, backscattered from targets ahead of it. Yet this is only one narrow example of the broad set of sonars that human engineers have developed to explore the environment (Tyack 1997). For example, sonars need not be high in frequency. Low-frequency sound can be propagated over greater distances than high frequencies in the sea, and man-made sonars designed to detect large targets at ranges of more than a few kilometres typically use much lower frequencies than the frequencies of dolphin or bat sonars. Some low-frequency animal sounds may be used in a similar manner, not just for communication, but also to explore or orientate in the ocean environment. In the rest of this section, we move from examples of marine mammal sonars with solid experimental data to more theoretical analyses of how marine mammals may use sound to explore their environment.

6.4.1 Dolphin echolocation

The best studied echolocation system in marine mammals is that of the bottlenose dolphin (Au 1993). Bottlenose dolphins produce clicks that can have very high peak-to-peak sound pressure levels (up to > 220 dB re 1 μPa at 1 m) but over very short periods (several microseconds), with a total click duration of only 50–80 μs (Au 1993). The clicks often have a relatively broad bandwidth (30–40 kHz) centred on high frequencies (often > 100 kHz).

BOX 6.1 UNDERWATER ACOUSTICS



Frequency (Hz, kHz), wavelength and bandwidth: A sound that we perceive as a pure tone has a sinusoidal pattern of pressure fluctuations. One full cycle of a sinusoidal sound is shown above. The *frequency* of these pressure fluctuations is measured in cycles per second. If the time it takes the sound to make a full cycle is t seconds, then the frequency of the sound is $f = 1/t$. The modern name for the unit of frequency is the *Hertz*, and just as 1000 metres are called a kilometre, 1000 Hertz are called a *kiloHertz*, abbreviated kHz. The sound illustrated above took 1 s for a full cycle, so it has a frequency of 1 Hz. The *wavelength* of this tonal sound is the distance from one measurement of the maximal pressure to the next maximum. Sound passes through a homogeneous medium with a constant speed, c. The speed of sound in water is approximately 1500 m/s, roughly five times the value in air, 340 m/s. The speed of sound c relates the frequency f to the wavelength λ by the following formula: $c = \lambda f$. Not all sounds are tonal. Sounds that have energy in a range of frequencies, say in the frequency range between 200 Hz and 300 Hz, would be described as having a *bandwidth* of 100 Hz.

Sound intensity, sound pressure: Sound *intensity* is the amount of energy per unit time (power) flowing through a unit of area. The intensity of a sound (I) equals the acoustic pressure (P) squared divided by a proportionality factor which is specific for each medium. This factor is called the specific acoustic resistance of the medium, and equals the density of the medium, ρ, times the speed of sound, c.

$$I = \frac{P^2}{\rho c} \qquad \text{(eqn 1)}$$

Decibel (dB); reference pressure = 1 microPascal (μPa): The primary definition of the decibel is as a ratio of intensities. The decibel always compares a pressure or intensity to a reference unit. Both intensities and pressures are referred to a unit of pressure. For underwater sound, the standard reference pressure is 1 μPa; for sound in air, the standard reference is 20 μPa, which is about the faintest sound a human can hear. The microPascal is a unit of pressure: 1 μPa = 10^{-6} Pa = 10^{-6} Newtons/m^2. The standard underwater reference I_{ref} is the intensity of a sound having a pressure level of 1 μPa (Urick 1983). If I and I_{ref} are two intensities, their difference in dB is calculated as follows:

$$\text{Intensity difference in dB} = 10\left[\log \frac{I}{I_{\text{ref}}}\right] \qquad \text{(eqn 2)}$$

For the intensity levels and pressure levels to be comparable in dB, the difference in sound pressure between a measured and reference pressure is defined in decibels as follows:

$$\text{Pressure difference in dB} = 20\left[\log \frac{P}{P_{\text{ref}}}\right] \qquad \text{(eqn 3)}$$

Most acoustic measurements actually measure the pressure fluctuations induced by a sound wave. Calibrated hydrophones relate the output voltage from a sound to the reference pressure of 1 μPa. Use of this with eqn 3 allows one to report the equivalent sound level for intensity or pressure. The difference in multiplier for intensity (10 log) and pressure (20 log) maintains the appropriate proportionality of intensity and pressure for sounds in the same medium. If $I \propto P^2$ by eqn 1, then log $I \propto 2 \log P$, or $10 \log I \propto 20 \log P$. As an example, take a sound measured to be 10 times the pressure reference. This would be 20 dB re 1 μPa by eqn 3. Since intensity is proportional to pressure squared, the intensity of this sound would be 10^2 or 100 times the intensity of the reference. This would still be 20 dB re the reference intensity, by the definition of intensity in eqn 2.

Use of these high frequencies allows dolphins to produce a directional click and to detect small objects. Sound energy will reflect efficiently from a rigid object with a circumference greater than or equal to the wavelength of the sound. Box 6.1 explains that the wavelength λ of a signal equals the speed of sound divided by the frequency. Since the speed of sound is about 1500 m/s in sea water, the wavelength of a 100 kHz sound = 1500/100 000 = 0.015 m or 1.5 cm. Thus dolphins producing clicks with energy above 100 kHz should be able to efficiently detect targets with a circumference of the order of 1 cm or larger. These kinds of calculations have been tested in careful experimental work with captive dolphins. Suggestive data on dolphin echolocation were collected in the 1950s, but the critical breakthrough came when Norris *et al.* (1961) blindfolded dolphins to rule out the possibility that they were using vision in detection tasks. Dolphins tested in an experimental apparatus for echolocation have demonstrated sophisticated echolocation abilities; e.g. an echolocating dolphin can detect a 2.5 cm metal target about 72 m away (Murchison 1980).

The brain of bottlenose dolphins is capable of very rapid auditory processing—their ears integrate high-frequency energy over an interval of about 0.25 ms (Nachtigall *et al.* 2000). This specialized hearing is an adaptation for receiving echolocation clicks. A bottlenose dolphin echolocates by producing a click and then waiting to detect the returning echo. If the dolphin detects a target, it will usually click again after a short delay for processing the echo information. Thus, if a dolphin does not detect an obstacle or a target nearby, it will usually produce clicks with a slow repetition rate. As it closes in on a target, the dolphin will often produce a train of clicks with an accelerating tempo and a decreasing interclick interval (ICI). Work with captive dolphins has shown that the ICI equals the round trip travel time of the click and echo (RT) plus a lag time (LT), which may represent the time the animal requires to process the sonar data. Bottlenose dolphins echolocating on targets 20–120 m away may have lag times of 19–45 ms (Au 1993).

$$\mathrm{ICI} = \mathrm{RT} + \mathrm{LT} \qquad \text{(eqn 6.4)}$$

Knowledge of the echolocation pattern just described has allowed investigators in the field to deduce when animals may be finding prey. Miller *et al.* (1995) studied patterns of clicks in wild narwhals (*Monodon monoceros*). They noted slow series of clicks with equal ICIs interspersed with accelerating rapid series, and suggested that these patterns reflect (respectively) orientation/detection and pursuit phases of foraging mediated by echolocation. However, the assumptions behind eqn 6.4 are not always justified. Beluga whales (*Delphinapterus leucas*) emit series of clicks with ICIs less than the round trip travel time to the sonar target (Turl & Penner 1989). Beluga whales do not have to process each pulse independently, waiting for the echo to return before emitting the next pulse, but rather appear to use a different kind of sonar processing in which they can process whole series of pulses together. Some other odontocetes also appear to have echolocation signals that differ from bottlenose dolphins, and they also may differ in their sonar signal processing. Pulsed signals of phocoenid porpoises and *Cephalorhynchus* dolphins are 5–10 times longer (150–600 μs) and roughly half the bandwidth (10–20 kHz) of bottlenose dolphin clicks, and their sound pressure levels range between 150 and 170 dB re 1 μPa at 1 m—several orders of magnitude weaker than the loudest bottlenose dolphin clicks (for *Phocoena phocoena*: Møhl & Andersen 1973; Kamminga & Wiersma 1981; Amundin 1991; for *Phocoenoides dalli*: Hatakeyama & Soeda 1990; for *Cephalorhynchus commersonii*: Kamminga & Wiersma 1982; Evans *et al.* 1988; for *C. hectori*: Dawson & Thorpe 1990). Bottlenose dolphins may produce echolocation clicks with spectral peaks well below 100 kHz, but porpoise and *Cephalorhynchus* clicks tend to have peaks above 100 kHz. Ketten (1994, 2000) describes porpoises and *Cephalorhynchus* as having inner ears that are specialized for high-frequency audition (> 100 kHz). Variability in the echolocation signals and hearing specializations of odontocetes suggests caution in assuming that all species process sonar sounds the same way as bottlenose dolphins do.

6.4.2 Do sperm whales echolocate?

Sperm whales produce click sounds that many biologists think are used for echolocation. However, unlike dolphins, sperm whales have not been kept in captivity for long enough to allow experimental demonstration of echolocation. We know that when sperm whales dive and forage, they tend to produce long series of click sounds with relatively invariant ICIs of 0.5–2.0 s (Whitehead & Weilgart 1990, 1991). As sperm whales start a dive, they often begin these clicks as they reach depths of 150–300 m (Papastavrou *et al.* 1989). Recordings of particularly loud sperm whale clicks often include reverberation from the sea floor (Fig. 6.9), so it is likely that sperm whales hear echoes if they approach the bottom during a dive. Sperm whales are large

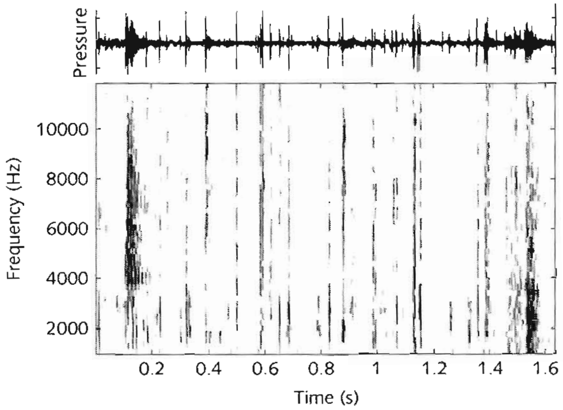


Fig. 6.9 Spectrogram of a slow click from a sperm whale, *Physeter macrocephalus*, in waters near the island of Dominica in the Caribbean. The direct arrival of the click is visible on the left of the spectrogram, and an echo of the click reflecting off the sea floor is visible on the right of the spectrogram at 1.5 s. The shorter clicks in the middle of the spectrogram are regular clicks from sperm whales. (From data courtesy of William Watkins.)

(up to 45 t) and dive rapidly (1–2 m/s) (Papastavrou *et al.* 1989; Watkins *et al.* 1993). If sperm whales could not detect proximity to the bottom, there would be a risk of collision. One way to test whether sperm whales use clicks to detect the sea floor assumes that sperm whales follow eqn 6.4 and produce a click after hearing the bottom echo from the previous click. As a sperm whale dives, the distance between the whale and the sea floor decreases; this means that the round trip travel time to the bottom should decrease. If the repetition rate of these clicks is correlated with the round trip travel time, then the repetition rate should increase as the whale dives, a prediction for which Gordon *et al.* (1992) and Gordon and Tyack (2002) found supportive evidence.

Sperm whales may also detect their squid prey in the deep dark ocean using echolocation (Backus & Schevill 1966; Gordon 1987; Whitehead & Weilgart 1990). Sperm whales feed on squid at depths of 400 m or more during dives that typically last 40–50 min (Papastavrou *et al.* 1989). During these dives, sperm whales produce clicks with a pattern that Gordon (1987), Gordon *et al.* (1992) and Jaquet *et al.* (1999) interpret as consistent with detecting prey. On the other hand, Watkins (1980) argues that sperm whale clicks are not well suited to echolocation of prey. For example, the clicks of sperm whales are lower in frequency, longer in duration and have been thought to be much less directional than the high-frequency clicks of dolphins. However, Møhl *et al.* (2000) report suggestive evidence that sperm whale clicks may be much more directional than has been thought, with properties better suited to echolocation. Clearly, more careful work is needed to determine whether and how sperm whales use echo information to detect prey or locate targets.

6.4.3 Can odontocetes stun or injure prey with loud sounds?

An original theory of how dolphins may use sound that has appealed to the popular press is the 'acoustic stunning hypothesis' of Norris and Møhl (1983). These investigators reviewed evidence that odontocetes can produce sounds with very high sound pressure levels such as the 220+ dB bottlenose dolphin clicks discussed above. However, these high-frequency clicks have a very rapid rise time and only achieve such high source levels for several microseconds, so the total energy delivered by the signal is comparable to the less intense, longer sounds produced by many cetaceans (Au 1993). Sperm whales and dolphins also produce intense lower frequency clicks, with durations of tens of milliseconds. There are few reliable calibrated estimates of the source level of these sounds, so it is difficult to analyse their possible acoustic effects. Norris and Møhl (1983) review observations that fish being preyed upon by dolphins may appear disorientated or incapacitated. They propose that this debilitation is caused by exposure to the intense, pulsed sounds of odontocetes. However, there are other explanations for the fish behaviour, such as low levels of oxygen in dense fish schools (Würsig 1986). Testing the acoustic stunning hypothesis requires exposing fish to sounds of odontocetes where the received level at the fish is measured with a calibrated hydrophone, coupled with subsequent behavioural and anatomical testing of the fish subjects. Until this kind of carefully controlled experiment is conducted, 'acoustic stunning' must remain in the 'interesting but untested' category of theories.

6.4.4 Low-frequency echolocation

The only echolocation system that has been demonstrated in cetaceans involves the use of high-frequency clicks by small odontocetes. These animals clearly have evolved a highly specialized system for echolocation. However, sound may be used to explore the environment even among cetaceans that are not specialized for high-frequency echolocation. Norris (1967, 1969), Payne and Webb (1971) and Thompson *et al.* (1979) have all suggested that whales might be able to sense echoes of low-frequency vocalizations from distant bathymetric features to orientate or navigate. Migrating bowhead whales (*Balaena mysticetus*) appear to use echoes from their calls to detect ice obstacles (Clark 1989; George *et al.* 1989). Ellison *et al.* (1987) used acoustic models to show that deep-keeled ice may produce strong echoes from the low-frequency calls of migrating bowhead whales, and they suggest that bowhead whales may use these echoes to sense and avoid deep ice.

6.4.5 The chequered history of research on seal echolocation

Pinnipeds are readily available for experiments in a captive setting, and the excitement about dolphin echolocation stimulated studies of echolocation in pinnipeds. The first papers published on this topic (Poulter 1963a, 1963b, 1966) presented evidence for echolocation in the California sea lion. In response, Schusterman (1967) and Schevill (1968) published papers arguing that Poulter's conclusions were not justified by his data. Undeterred, Poulter & Del Carlo (1971) published a paper confidently entitled 'Echo ranging signals: sonar of the Steller sea lion, *Eumetopias jubata*'. An independent group followed up on this work a decade later, publishing a paper entitled 'Evidence that seals may use echolocation' (Renouf & Davis 1982). Wartzok *et al.* (1984) published a rebuttal questioning whether this evidence was convincing enough to force a reassessment of earlier studies that found no experimental evidence for echolocation in seals (Evans & Haugen 1963; Schusterman 1967; Oliver 1978; Scronce & Ridgway 1980). Publication of a paper on a topic such as echolocation in marine mammals will usually stimulate studies that attempt to replicate the finding. In the case of dolphin echolocation, the findings were confirmed by more careful experimental designs, but in the case of echolocation by pinnipeds, most studies have failed to replicate the results or found flaws in the design of the experiments.

6.5 COMMUNICATION

6.5.1 Introduction

The etymological root of 'communicate' means 'to share', and communication can be defined as 'any sharing of information . . . between individual animals' (Smith 1977, p. 11). Social behaviour and social structure establish the selective pressures that shape and maintain characteristics of signals and signalling behaviour (Evans & Bastian 1969; Green & Marler 1979; McKinney 1992). Communication is almost always framed as a process in which a sender transmits information to a receiver via a signal (Owings & Morton 1998). In studying any communicative exchange, it is important to consider the costs and benefits of the information transfer to both sender and receiver. Some authors limit the term 'true communication' to exchanges of information that benefit both the signaller and the receiver (Smith 1977). When communication benefits the signaller at a cost to the receiver, it has been termed 'manipulation' (Dawkins & Krebs 1978; Krebs & Davies 1993). Signals that benefit the signaller through true communication or manipulation may become evolutionarily specialized as displays. When communication benefits a receiver at a cost to the signaller, this may be called 'eavesdropping' (Bradbury & Vehrencamp 1998) or 'interception' (Myrberg 1981). Unintentional cues that may inform a receiver at a cost to the signaller are unlikely to evolve into ritualized displays; rather selection would favour decreasing the signalling value of the cue, making it more cryptic. As was discussed in Section 6.2.1, signals form a continuum from highly ritualized displays to subtle incidental cues. Much information used by communicating animals comes from the context of the interaction, from cues such as scents or markings used in individual recognition, or from simple unritualized behaviours such as intention movements of advance or retreat. A biologist analysing a communicative interaction cannot just focus on the most obvious display, but must attend to all of these sources of information.

Wilson (1975, p. 111) argues that communication has occurred when a signal changes the probabilities of subsequent behaviour in a receiver. This is a behavioural interpretation of the formal definition of communication used in information theory, where a signal is described as providing a receiver with information that reduces uncertainty (although it may be misleading information in the case of manipulation) and allows the receiver to make decisions. Wilson's (1975) definition cannot provide a practical criterion for assessing whether communication occurs in a particular interaction between animals. Communication in animals is not limited to situations where one signal alters the probabilities of the subsequent response from one receiver. A female songbird may listen to thousands of songs from many males before choosing a mate. A young songbird listening to a song may alter an auditory template that will only be expressed in the following year. Even when an animal shows no obvious response to a communicative exchange, students of animal cognition may be able to design tests to indicate that an animal has learned from it. It makes little sense to argue that communication occurred only after the test was given. We favour adopting a more cognitive perspective on these issues, in which the information from the signal detected by the receiver is viewed as communication, whether or not it has elicited immediate behavioural responses.

6.5.2 Structure, function, adaptation and phylogeny in acoustic signals

> *'All scientists use models, whether they realize it or not' (James & McCulloch 1985, p. 44).*

Textbook descriptions of research on animal communication may describe a simple sequential process in which a display is described, the social context in which the display is produced and responses of receivers are analysed, and finally the function is inferred. In practice, however, communicative sounds are seldom differentiated by quantitative analysis of acoustic measurements alone, but are often described using a combination of qualitative information on acoustic structure and social uses. For example, if a fieldworker hears calls that sound similar when her study animal sees a predator, then she might call these 'alarm' calls. This becomes a problem if researchers are not explicit about the interaction between descriptive and functional analyses. For this reason, it is usually recommended for ethologists to use one set of terms for descriptive analyses of displays and different terms to refer to the assumed function (Martin & Bateson 1993).

Two main questions trouble researchers as they describe repertoires: 'How many kinds of calls are there?' and 'What do the calls mean?' There is no single answer to these questions. The first question is based on the erroneous assumption that one can always define a unique set of calls based upon acoustic structure. This is not always the case; the number of call types recognizable on structural grounds depends upon how fine or coarse a level of description is used (e.g. how many variables are used). In turn, this is set by the nature of the investigation; in studies of phylogeny or adaptation, 'one needs behavioural events that strike an optimum between being diverse enough to reveal change and conservative enough to expose relationships' (Barlow 1992, p. 368). Some workers have used multivariate methods such as cluster analysis to help determine repertoire size. However, cluster analyses depend upon which acoustic variables and which clustering algorithm are selected, so the analytical results (including the hierarchical nature of most clustering applications) may reflect the subjective choices of researchers (Sneath & Sokal 1973; Miller 1979, 1988; de Queiroz & Good 1997; Janik 1999).

The second question is complicated because there may not be a one-to-one correlation between call type and function. For example, when a territorial male songbird sings a song, the song may have different functions depending upon the potential audience: females, other territorial males or young males. The songs of some songbirds appear to be interchangeable; in this case, different songs may have the same functional role (Smith 1996). If single call types can have multiple functions, and if multiple call types can have the same function in the same species (Altmann 1967; Smith 1977, 1997; Green & Marler 1979), then it is clearly necessary to separate the structural description of calls from the functional interpretation.

6.5.2.1 From calls to repertoires: acoustic structure across scales

Descriptions and physical analyses of acoustic signals are integral parts of comprehensive ethograms. Many invaluable 'first accounts' of vocalizations placed communicative sounds in a few convenient categories, described in terms of both acoustic structure and social context, and presented as representative spectrograms (Bartholomew & Collias 1962; Schevill & Watkins 1965; Schevill *et al.* 1966; Peterson & Bartholomew 1969; Ray *et al.* 1969; Stirling & Warneke 1971; Lisitsina 1973; Stirling 1973). Early workers did not have the advantage of digital computers and a range of quantitative techniques for analysis and interpretation (Watkins 1967b; Marler 1969; Beecher 1988; Beeman 1998; Stoddard 1998). These quantitative techniques of acoustic analysis enable a more explicit acoustic analysis separated from the functional context that may colour the interpretations of the human observer.

Traditionally, the starting point for structural description of a species' acoustic repertoire has been the identification of signalling acts at a low level, such as the vocal classes shown in Fig. 6.10.

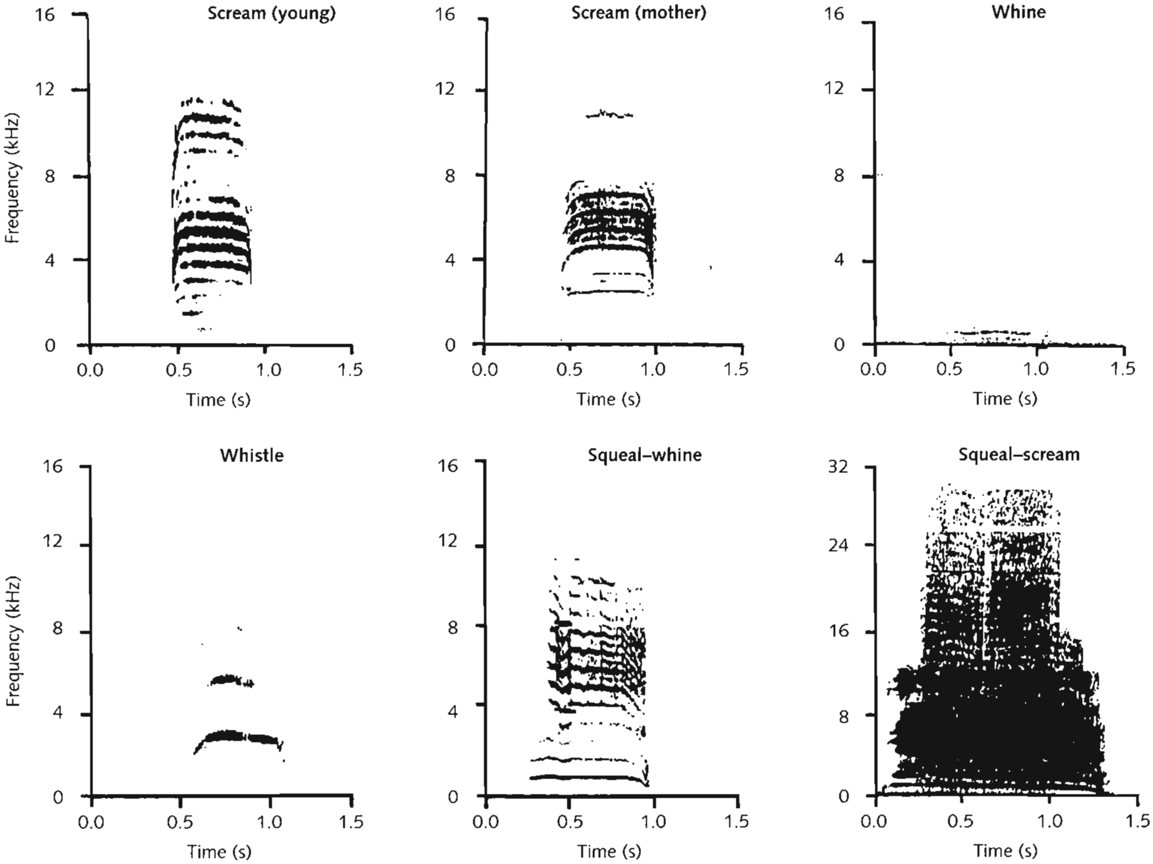


Fig. 6.10 Part of the vocal repertoire of the sea otter (*Enhydra lutris*), shown as spectrograms. The 'scream' call (upper left two spectrograms) could be considered as a single call type; the 'whine' often merges into 'squeal–whine', so these may illustrate variation in signal form within a single broadly defined call type. (From McShane *et al.* 1995.)

The vocalizations of some animals appear to fall into easily distinguishable general categories, such as the pulses and tonal whistles of dolphins. However, the decision of what comprises the smallest unit for this low-level repertoire of signal units (Smith 1986, p. 316) is seldom discussed in detail, and this decision can strongly influence later results. For example, does one count an individual dolphin pulse or train of pulses as the basic unit? There are likely to be hundreds more pulses than trains, so counts of the calls would be significantly affected by this choice. Some dolphin whistles are composed of subunits that may be separated by gaps of silence. Caldwell *et al.* (1990) called these subunits 'loops'. When individual dolphins are isolated, they often produce an individually distinctive whistle with a stereotyped initial loop, a variable number of repetitions of a central loop, followed by a terminal loop. Others studying dolphin whistles may split whistles whenever there is a moment of silence (McCowan & Reiss 1995). This seemingly minor change can lead to very different conclusions about whistles. McCowan and Reiss (1995) analysed as whistles what Caldwell *et al.* (1990) would have called loops, and concluded that there were few individually distinctive whistles in a group of captive dolphins.

The reason for this problem regarding lumping or splitting the basic unit of vocalization is that many species have repertoires of patterned combinations of signal units (Smith 1986, p. 324). This has traditionally been recognized for bird song, where the basic unit of vocalization, the song, is made up of a sequence of individual sounds (often termed syllables). Examples of patterned sequences in marine mammals include the underwater songs of Weddell seals (Green & Burton 1988; Morrice *et al.* 1994) and humpback whales (Payne & McVay 1971). Patterned displays may also combine optical and acoustic components, such as air-bladder displays of male hooded seals (Fig. 6.7) or the jaw-clap display of bottlenose dolphins (Overstrom 1983). These patterned combinations of signal units are governed by organizational rules (Smith 1986, 1991b) such as those reviewed by Hailman *et al.* (1985). Patterned combinations need not be elaborate; in Hawaiian monk seals (*Monachus schauinslandi*) a common airborne threat vocalization is a series of bubble sounds followed by a guttural expiration (Miller & Job 1992). These patterned combinations of low-level signal units need not be separated by silence, but little research has analysed the issue of whether individual utterances of animals are made up of 'chunks' that may be recombined in different patterns.

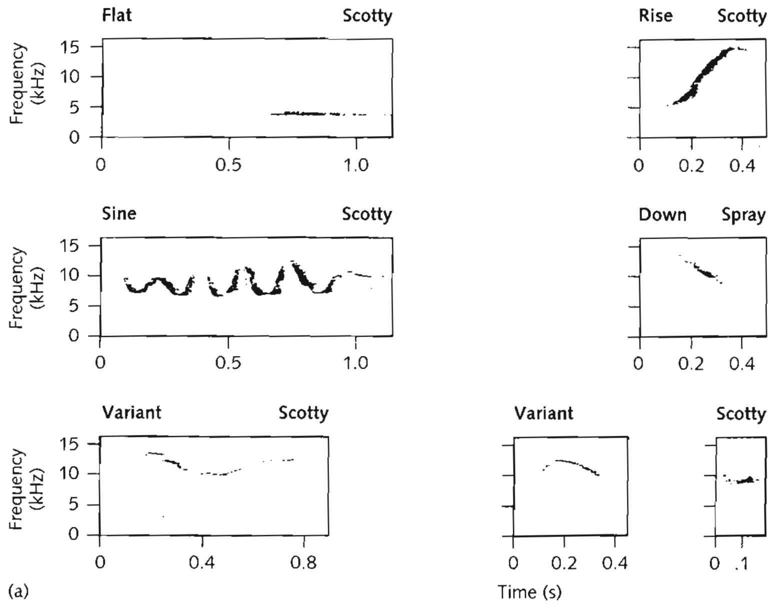


Fig. 6.11 (a) Spectrograms of whistles from bottlenose dolphins (*Tursiops truncatus*) arranged in acoustically distinct categories. (Adapted from Tyack 1986.) (*continued*)

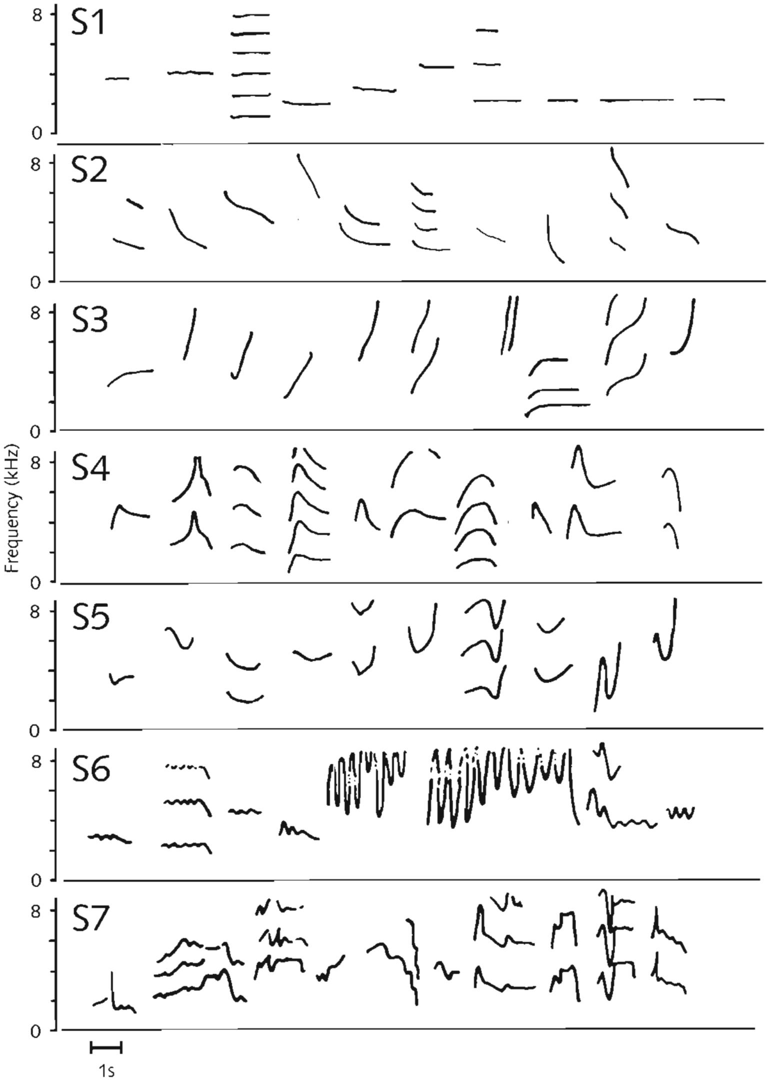


Fig. 6.11 (*cont'd*) (b) Contours from pilot whales (*Globicephala melas*) arranged as a graded series. (Adapted from Weilgart & Whitehead 1990.)

Most analyses of animal sounds tend to focus on categorizing vocalizations into discrete categories. Another way to approach repertoire description is to describe variations of signal form across signal units (Smith 1986, p. 317). Following this approach, variation could be described in acoustic features such as presence, number or distribution of harmonic structures; frequency or amplitude modulation; presence of broadband noise, biphonation or subharmonics; and rate of vocalization. Such acoustic qualities can vary substantially across repetitions of a single display type. Viewed in this way, the 'squeal' and 'squeal–whine' of the sea otter may be variations on a single class of signal, as the former often merges into the latter (Fig. 6.10) (McShane *et al.* 1995). The dolphin whistles illustrated in Fig. 6.11a separate whistles with downward, flat or upward frequency modulation as discrete categories. However, as Taruski (1979), Weilgart and Whitehead (1990) and others have noted, odontocete whistles can also be viewed as a continuum of changing frequency modulation (Fig. 6.11b). When whistles can be attributed to an individual, each individual may produce series of whistles that are very similar in some acoustic features (contour of the loops) and variable in others (such as number of loops, duration, etc.). In this context, the stereotyped features may carry information useful for individual recognition, while the other features may carry other information. Variation in signal form greatly increases the information available in a communication system; the importance of variation in form has been well stated by Hailman and Ficken (1996, p. 141): 'apparent types of vocalizations do carry information, but the details, and in some cases perhaps the most important information, lies in the variations on a type'. Brownlee and Norris (1994, p. 180) make this point for dolphin whistles: 'Variations in how whistles are emitted can carry graded . . . information about emotional state, level of alertness, hierarchy, the presence of food or danger . . . the modulation or temporal patterning of the whistles allows transmission of a variety of context-specific information. . . . Such a signal system can be modulated in intensity, frequency, and frequency pattern through time to produce a complex system of great potential information-carrying capacity . . .'.

Not only can an individual animal produce a sequence of signals, but two or more animals may have repertoires of formalized interactions (Smith 1986, p. 325). Examples are vocal interchanges between mothers and their offspring, boundary displays between territorial male otariids, precopulatory and copulatory behaviour between males and females, and so on (Gentry 1975; Lisitsina 1981; Miller 1991). Formalized interactions can involve a call and response of several signals between two animals over a few seconds, but they can involve more than two parties, and can involve more signals over a longer time. For example, Brownlee and Norris (1994, p. 182) suggest that spinner dolphins (*Stenella longirostris*) monitor whistle rates across an entire school over periods of a few minutes to an hour or more as they swim in a zig-zag path in order to time the behavioural transition from inshore resting to travelling offshore to feed: 'We interpret the fluctuating occurrence of contagious whistles during zig-zag swimming as partially social facilitation, with dolphins testing each other's alertness until the school is primed for its transit out to sea.'

6.5.2.2 Social functions and functional analysis

How we view the 'meaning' or 'function' of a display depends upon which model of animal communication we adopt. Researchers studying animal communication may employ widely differing models with different assumptions and descriptive/analytical approaches (for example, compare the linguistic model used by Evans & Bastian (1969) to more behavioural ecological models such as those used by Miller (1991) and Tyack (1999) for marine mammals). Our language biases and constrains our interpretations of what communication is for, how it functions and how it is structured (Golani 1992). 'Alarm' calls, 'dialect', and 'call type' are examples of widely (and casually!) used language in animal communication research that bias research programmes from conceptualization and data collection through to data analysis and interpretation.

Calls used by mothers and pups of otariids can serve as an example of how interpretation can be embedded in the name of a call. After fasting while nursing their pup for a week or two following birth, otariid females begin a cycle of alternately feeding offshore and nursing the pup on land. When females return from their marine feeding trips, they and their pups need to find one another, and do so initially through loud vocalizations; females also tend to return to where they and their pups habitually nurse, and pups tend to return there in anticipation of their mothers' return. Vocalizations used by females and pups in this circumstance are commonly referred to as 'pup attraction calls' and 'female attraction calls', respectively (Fig. 6.8b). Confusingly, 'pup attraction calls' can mean 'calls used by pups to attract females', and 'female attraction calls' can mean 'calls used by females to attract pups'. Another problem with these terms is that they define the calls in terms of context rather than structure, and this assumes that there is a one-to-one mapping of this particular context onto a specific call with one specific function (Lisitsina 1988; Insley 1996; Fernández-Juricic *et al.* 1999; Phillips & Stirling 2000, 2001). Interestingly, the vocalizations in question are very similar in structure to a call type used by territorial males variously termed roar, full threat call, etc. (E.H. Miller & A.V. Phillips, unpublished

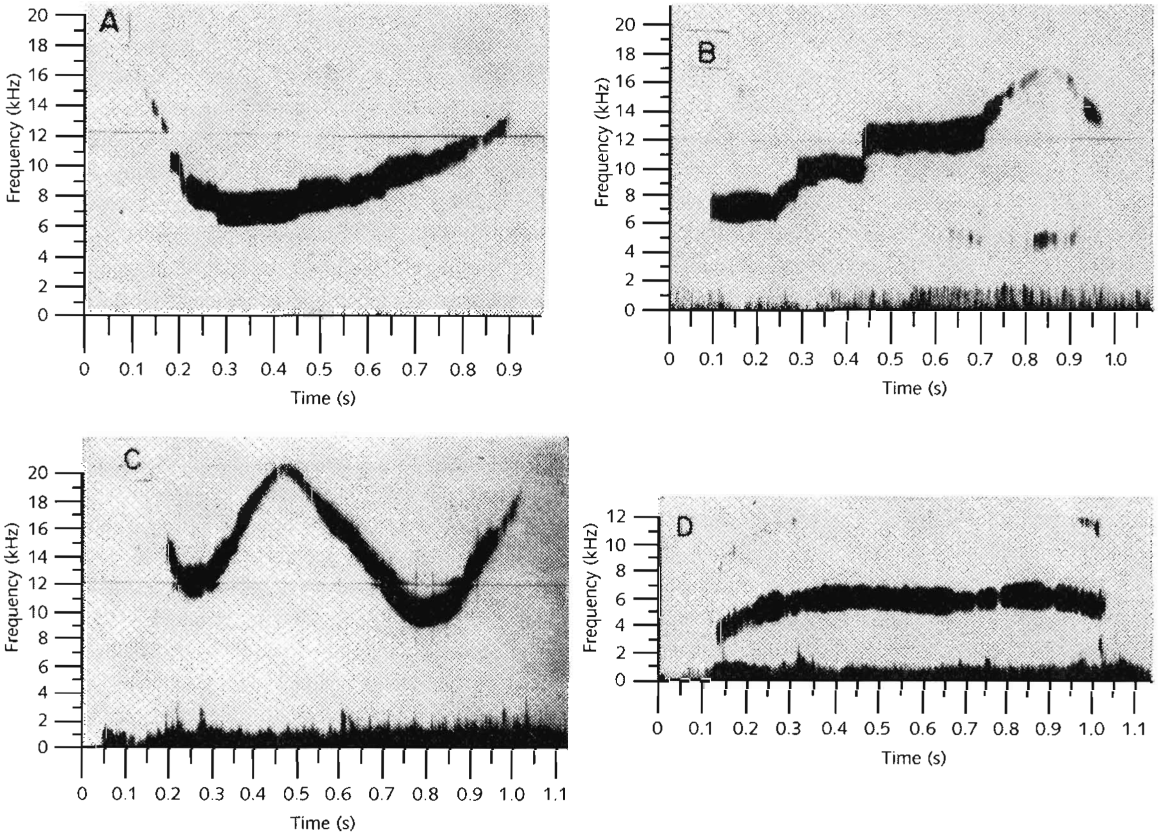
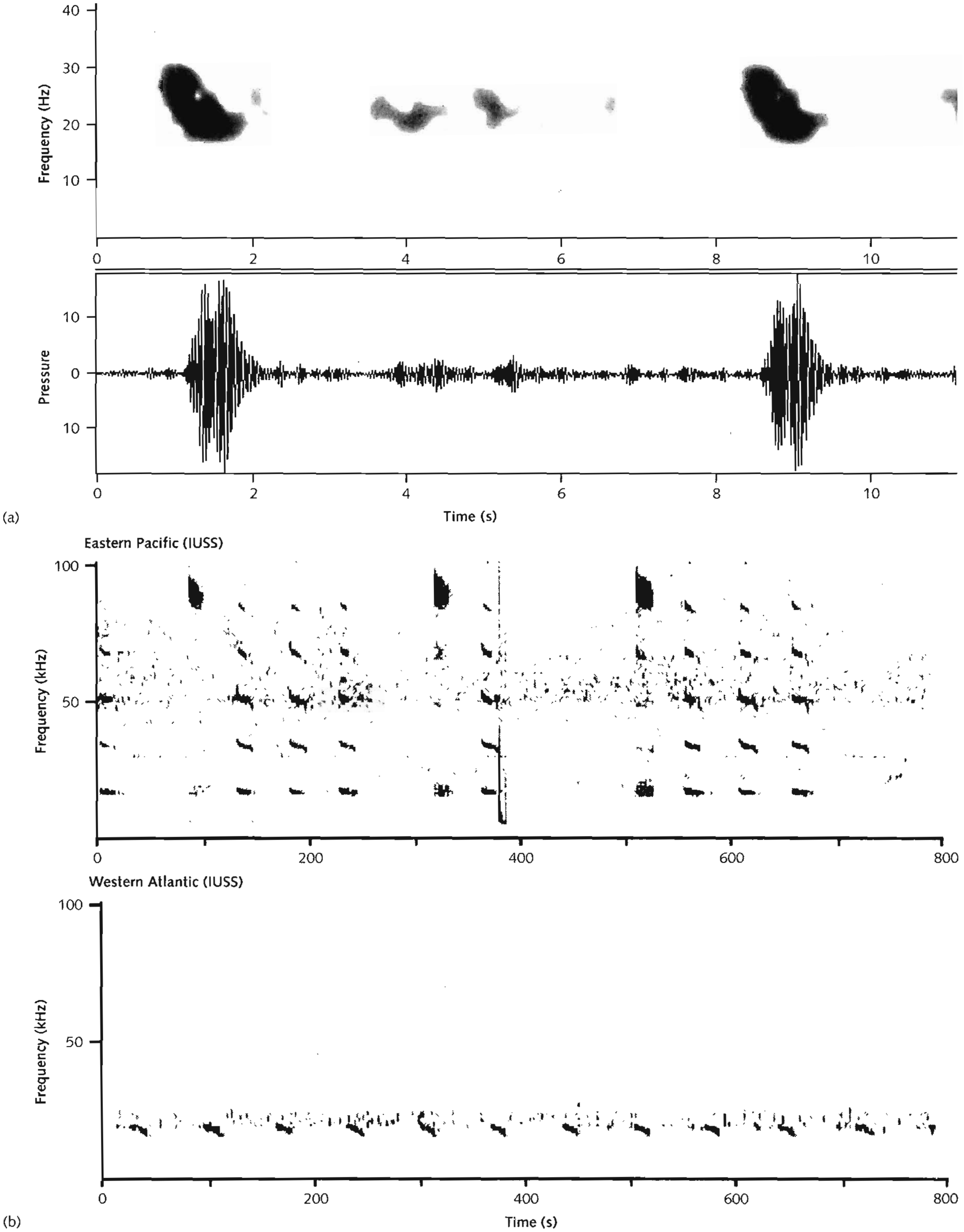


Fig. 6.12 Contours and spectrograms of signature whistles recorded from different captive common dolphins (*Delphinus delphis*). (From Caldwell & Caldwell 1968.)

data). Why should the calls be so similar in structure? The answer may be that the calls of females, pups and males are the same in terms of the kinds of behavioural information made available to receivers. That information could simply be 'I am seeking interaction or am willing to interact', with information about location (e.g. in the case of territorial males, or of females and pups reuniting), and from non-behavioural messages in the vocalization also used by the receiver in selecting an appropriate response. For example, sex, age or body size may be indicated by frequency and spectral features; individuality may be reflected in a unique combination of acoustic features, and so on (St Clair Hill *et al.* 2001).

Another example of problems with mixing functional and descriptive terms involves dolphin whistles. Early descriptions of dolphin whistles often used recorded whistles when animals were harmed by the human observers—these whistles were called 'distress whistles' (e.g. Lilly 1963; Busnel & Dziedzic 1968). Caldwell and Caldwell (1965, 1968) noted that in their recordings of captive dolphins, each individual dolphin tended to produce an individually distinctive whistle, which they termed a 'signature whistle' (Fig. 6.12). More recent observations suggest that wild and captive dolphins tend to produce these 'signature whistles' when they are isolated (Janik & Slater 1998) or involuntarily restrained by humans (Sayigh *et al.* 1990), so many of the so-called 'distress whistles' are likely to have been the individually distinctive 'signature whistle' of those individuals (Caldwell *et al.* 1990). Many ethological studies of communication assume that their goal should be to define a repertoire of species-specific


40
30
20
10
Frequency (Hz)
0
2
4
6
8
10
Pressure
10
0
10
0
2
4
6
8
10
Time (s)
(a)
Eastern Pacific (IUSS)
100
50
Frequency (kHz)
0
200
400
600
800
Western Atlantic (IUSS)
100
50
Frequency (kHz)
0
200
400
600
800
Time (s)
(b)

calls that are shared within an age–sex class. However, recordings from isolated dolphins suggest a different pattern where individuals have highly distinctive whistles. Rather than being defined using acoustic information independent from knowledge of who made the call, signature whistles are defined operationally as a highly stereotyped and individually distinctive whistle typically made by some dolphins when isolated. As with the seal calls, dolphins may use similar whistles in a variety of social contexts (mother–young, male pair, etc.) to make similar information available to a partner, often maintaining contact and expressing willingness to interact.

Many studies of communication in marine mammals provide general correlations of vocal production and broad behavioural states, such as feeding, travelling, socializing and resting. Bengtson and Fitzgerald (1985) found strong correlations between rates of vocalization and general behavioural categories of West Indian manatees. Hoelzel and Osborne (1986) and Ford (1989) found that both rates and types of vocalizations in killer whales varied as a function of behavioural context. The patterns of click production are very different when sperm whales are socializing near the surface or feeding while diving (Whitehead & Weilgart 1991). These coarse analyses can help identify whether a particular call is more probably involved in behavioural states such as feeding versus travelling, but more fine-grained analyses are required to tease apart the pattern of signal and response by which short-range communication can mediate short-term social interactions. Fine-grained analyses require techniques for identifying which individual animal makes each display (e.g. Burgess *et al.* 1998; Miller & Tyack 1998) and requires following the behaviour of an individual signaller and potential receivers over time. Fine-grained analyses of marine mammal displays have been conducted for communication in air between pinnipeds (e.g. Trillmich 1981) and for agonistic interactions of dolphins (Overstrom 1983; Samuels & Gifford 1997).

Details of adaptive 'design features' may vary interspecifically because of differences in environment, effective range or intended receivers. There is an important difference in the functional analysis of signals evolved for communication over long versus short ranges. Inferring the function of vocalizations is relatively simple for long-distance signals but can be very difficult for those used over short distances. The reasons are simple: long-range signals are adapted in form and pattern of delivery to withstand degradation and attenuation, and little information outside the signal itself is available to recipients. Thus long-distance signals are typically loud, stereotyped, spectrally simple, long, repetitive and temporally patterned (e.g. repeated rhythmically or with strong sequential ordering). All of these features describe the sequences of low-frequency calls produced by finback and blue whales during the breeding season (Fig. 6.13) (Cummings & Thompson 1971; Edds 1982; Watkins *et al.* 1987; Tyack & Clark 2000). We do not know the effective range of these calls for whales, but humans can easily detect these calls at ranges of hundreds of kilometres (Tyack & Clark 2000). Long-range signals may be adapted to reach different classes of recipients over different distances (Terhune & Ronald 1986). For example, the underwater songs of male Weddell seals and the airborne roars of territorial male otariids communicate over shorter distances to females than to competing males, because the females to whom a sound may be directed tend to be closer than the nearest adult males.

Most research on acoustic communication focuses on loud specialized signals that have evolved for long-range communication. Our knowledge and understanding of short-range sounds are severely limited but cues and soft vocalizations that evolved for short transmission distances are likely to be important in group-living or gregarious species. Short-range

Fig. 6.13 (*opposite*) Spectrograms of low-frequency calls of finback (*Balaenoptera physalus*) and blue (*Balaenoptera musculus*) whales. (a) Waveform and spectrogram illustrating two low-frequency (nominally 20 Hz) pulses of finback whales recorded in the North Atlantic. The direct arrivals of pulses are visible at 1–2 s and 9–10 s, and echoes from reverberation of the first pulse are visible between 4 s and 5 s. (b) Low-frequency calls from blue whales recorded from different ocean basins using arrays of US navy hydrophones mounted on the sea floor in the eastern North Pacific and western North Atlantic. There are systematic differences in the calls from the different oceans. The Pacific call has a 90 Hz unit that is absent from the Atlantic calls, and the lower frequency components of the Pacific and Atlantic calls have different rhythmic patterns. (From Tyack & Clark 2000.)

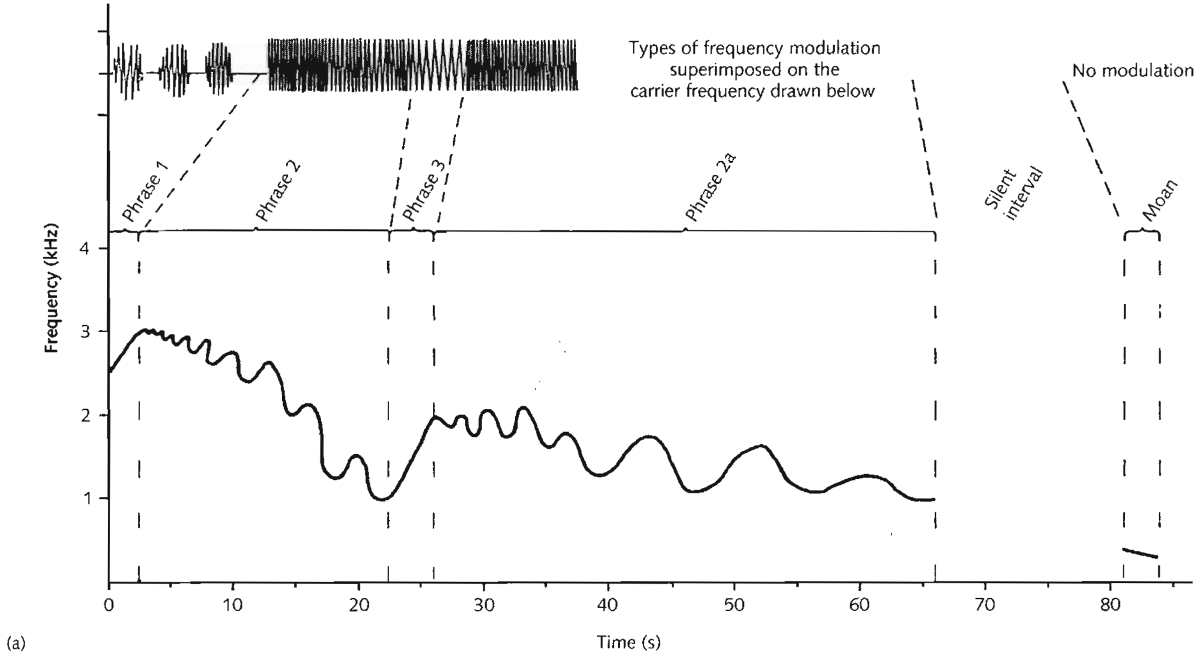
signals are altered little by the physical environment, and so can be acoustically more complex and can encode much information through subtle variation in acoustic structure. Short-range communication is often multimodal; non-acoustic information about the signaller is often directly available to recipients nearby. Recipients can use this information outside the signal itself when appraising a signal's meaning —information such as a signaller's distance and orientation, the presence or proximity of other animals, knowledge of the individual identity of the signaller and past experience with the signaller, etc. The adaptive functions of short-range sounds can be difficult to assess because their proximate effects are often subtle and varied; they are often accompanied by optical, chemical or tactile information; they include many sounds produced in the course of other activities; and their significance to receivers is greatly affected by information outside the sounds themselves (Smith 1977, 1997; Cheney & Seyfarth 1990; Hauser 1996; Bradbury & Vehrencamp 1998). Some short range signals are produced almost continuously; variation in these tonic signals may communicate about a calling animal's state (Schleidt 1973). The bark vocalization of territorial male otariids and chuff vocalization of polar bears are examples of tonic signalling (Wemmer *et al.* 1976; Peters 1984; Miller 1991).

Long-range signals are often selected to be loud, stereotyped and simple, but paradoxically many long-distance signals are shaped by sexual selection, which often promotes signal diversification and complexity (Andersson 1994; Bradbury & Vehrencamp 1998). Thus males must often be under selection to produce effective long-range signals that are poorly designed for long-range transmission! One way to solve this paradox is to make a signal contrast with the ambient environment. In many species of seal and several species of whale, males are known to repeat songs during the breeding season. This regular repetition of songs may make them easier to detect in random noise. If the receiver detects a pattern of expected repetition, it can more reliably detect songs in noise. Harp seals produce vocalizations that contrast with ambient noise not only by repetition, but also by increasing amplitude, frequency and pulse rate over the course of each call (Watkins & Schevill 1979; Terhune *et al.* 1987; Terhune 1994). Signal complexity can be increased by changing successive repetitions in some predictable way. The songs of Weddell seals and humpback whales follow syntactical rules for ordering different types of elements (Payne & McVay 1971; Guinee *et al.* 1983; Morrice *et al.* 1994). Gradual changes in acoustic structure within long songs, termed 'drift' by Andrew (1969) and Lemon (1975) and 'progressive change' by Payne *et al.* (1983), enable directions and rates of change to be readily tracked by recipients (Fig. 6.14) (Marler & Tenaza 1977; Payne *et al.* 1983; Payne & Payne 1985).

6.5.2.3 *Evolution of acoustic signals: from variation to phylogeny*

Genetically based phenotypic variation within populations is a prerequisite for population differentiation and ultimately for speciation (see Chapter 11). Therefore, the description and measurement of natural variations provide important information for evolutionary studies. The vocalizations of most non-human terrestrial mammals have acoustic features that appear to be influenced primarily by genetic factors. Some marine mammalogists have advocated using vocalizations as an indicator of population structure (Payne & Guinee 1983). However, many marine mammals can learn to imitate acoustic models in their environment (Janik & Slater 1997), so one must be careful in selecting features from vocalizations for evolutionary studies. Few measures of acoustic variation exist for marine mammal vocalizations, but a general trend seems to be toward greater variation in temporal than in frequency variables (Miller 1986, 1991).

Important components of variation within populations include sex, individuality, age, size and social context. Differences in vocalizations between the sexes of marine mammals are pronounced for the sperm whale, in which adult males have a head and spermaceti organ much larger than adult females (Nishiwaki *et al.* 1963). An unusual kind of click, called a 'slow click' by Weilgart and Whitehead (1988), is reportedly only produced by adult males. Female Amazonian manatees are reported to have higher frequency calls than males (R.S. Sousa Lima, personal communication). If these differences between sounds of adult males and females stem



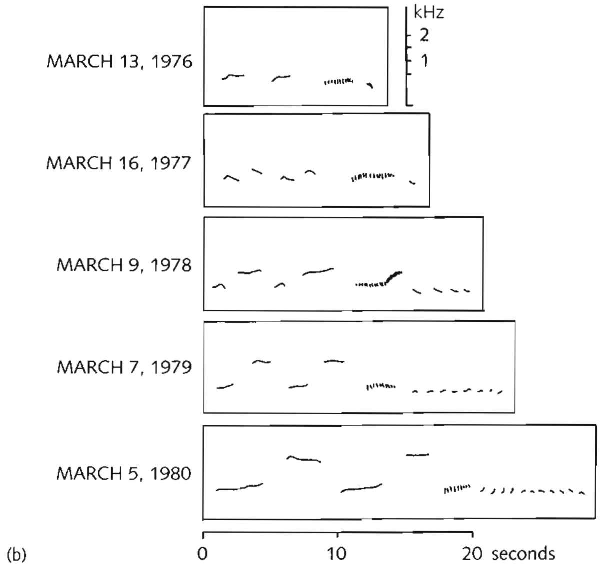


Fig. 6.14 Song repetition, syntax and gradual changes ('drift') within songs of the bearded seal (*Erignathus barbatus*) and humpback whale (*Megaptera novaeangliae*). These features of song are typical of reproductive advertisement displays in marine mammals, and may be adaptations to assist receivers to accurately receive a complex long-distance signal. (a) The song of the bearded seal exhibits syntactical organization in the initial bursts of frequency modulation (FM; phrase 1) of the carrier frequency, continuous but varying FM (phrase 2), slower but regular FM (phrase 3), etc. The song also undergoes progressive changes (sometimes with slow reversals) internally over its course, e.g. in carrier frequency (depicted in the schematic representation of a spectrogram, below). (From Ray *et al.* 1969.) (b) Each row represents a phrase from one theme of a humpback whale's song. This phrase is repeated a variable number of times before the whale switches to a different theme. Each row illustrates a typical phrase from each of 5 years in the songs of humpback whales in Hawaiian waters, showing progressive changes in the song over periods of years. (From Payne *et al.* 1983.)

from differences in the sound-producing organs, then they are likely to be good candidates for phylogenetic analyses. Long-distance underwater displays used to attract mates are restricted to males in most species studied to date, for example humpback whales (Glockner 1983; Baker *et al.* 1991; Palsbøll *et al.* 1992), bearded and Weddell seals and walruses (Section 6.3.2.1). Female Weddell seals do not produce all of the vocalizations produced by males (Thomas & Kuechle 1982), but where both sexes produce the same class of sounds, almost no sexual differences have been reported.

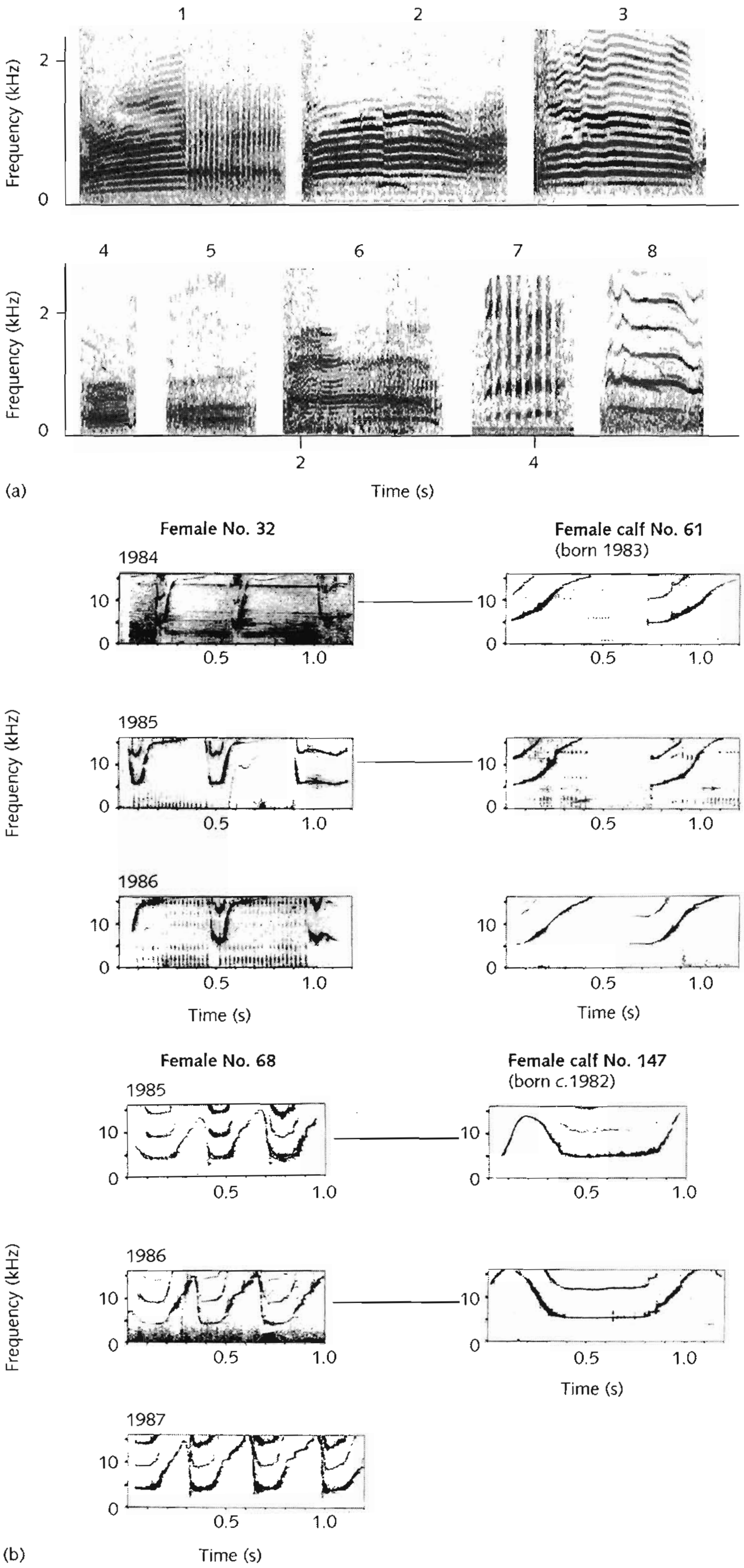


Fig. 6.15 Individuality is nearly universal in acoustic structure. (a) Spectrograms of South American sea lion (*Otaria flavescens*): primary call from three mothers (1–3); and grunts from two females (4, 5), a primary call from a yearling (6), and primary calls from two pups (7, 8). (From Fernández-Juricic *et al.* 1999.) (b) Individually distinctive whistles from two adult female bottlenose dolphins (*Tursiops truncatus*) and their daughters recorded in several different years. (From Sayigh *et al.* 1990.)

Numerous studies report individual differences in the vocalizations of marine mammals, some of which are known to persist over years (Fig. 6.15) (Sandegren 1976; Shipley *et al.* 1981; Trillmich 1981; Stirling *et al.* 1987; Caldwell *et al.* 1990; Sayigh *et al.* 1990; Fernández-Juricic *et al.* 1999; Insley 2000; Phillips & Stirling 2000; Sanvito & Galimberti 2000b; St Clair Hill *et al.* 2001). There are slight differences in the vocal tracts of different individuals, and these differences lead to individually distinctive characteristics that are called 'voice cues' among terrestrial animals. However, these involuntarily distinctive vocal characteristics may be less distinctive in underwater than in airborne vocalizations (Tyack 1999). As mammals dive, gases in the vocal tract halve in volume for every doubling of pressure. These depth-induced changes in the volume and shape of the vocal tract are likely to outweigh the subtle developmental differences that lead to differences in voice. For example, the whistles of a beluga whale recorded at different depths show strong differences in their frequency spectra (Ridgway 1997). If there is a functional need for diving animals to have individually distinctive calls, they may be unable to use voice cues and may need to create distinctive calls by learning to modify acoustic features under voluntary control, such as the frequency modulation of whistles. Janik and Slater (1997) and Tyack (1999) argue that this may have provided an important selection pressure for vocal learning in marine mammals.

Evidence from closely related species of birds suggests that animals evolve systems for parent–offspring recognition if the ecological setting involves a sufficient risk of providing care to the wrong offspring or of withholding care from the correct one (Loesche *et al.* 1991). Job *et al.* (1995), McCulloch and Boness (2000), Phillips and Stirling (2000) and Insley (1992, 2000, 2001) have studied vocal individuality in pinnipeds on the basis of predictions from this model. Insley (1992) predicted that the calls of female northern fur seals would be more individually different from one another than those of female northern elephant seals, because in the former species females and pups separate repeatedly and must reunite largely on the basis of vocalizations. His prediction was met.

Effects of size and age on acoustic structure are largely caused by variation in the anatomy of sound production in mammals, and account for a substantial proportion of natural variation. Little attention has been paid to the effects of development on the acoustic structure of vocalizations in bears and pinnipeds (Rasa 1971; Shipley *et al.* 1986). In spite of limited study, marine mammals stand out among non-human mammals in the extent to which vocal learning may play a role in vocal development (Janik & Slater 1997; Tyack & Sayigh 1997). Male Weddell seals lengthen some underwater vocalizations in response to conspecific vocalizations (Terhune *et al.* 1994b). The strongest evidence of modification of pinniped vocalization resulting from exposure to auditory models stems from Hoover, a common seal raised by humans, who started to imitate speech sounds with a Maine accent as he reached sexual maturity (Ralls *et al.* 1985). There is similar evidence that odontocete cetaceans can imitate novel man-made sounds (beluga whale: Eaton 1979; bottlenose dolphin: Evans 1967; Caldwell & Caldwell 1972b; Herman 1980; Richards *et al.* 1984).

Population differentiation in signals can result from genetic divergence or cultural divergence, or both (Lynch 1996). The term 'dialect' generally refers to the latter. Killer whales in the Puget Sound area have repertoires of stereotyped calls that are distinctive for each matrilineal group (Ford 1989); these have been called dialects, although the groups may be sympatric. These killer whale calls are generally thought to be learned, with enough copying error so that the longer groups have been separated, the less similarity there is between call repertoires (Ford 1991). Based on observed geographical differences alone, it is impossible to infer whether these group-distinctive call repertoires are rooted in genetic or cultural change, but acoustic divergence in the face of high gene flow or independent evidence of vocal learning make the latter more likely. Because geographical differentiation can result from either or both processes, one cannot infer population or stock discreteness solely from geographical differences in vocalizations; additional information on dispersal or development, or experimental studies are also required (James 1991).

Studies on geographical variation in marine mammal vocalizations have focused on the songs of humpback whales and a few species of pinnipeds. The underwater songs of rutting male Weddell seals, bearded seals, harp seals, leopard seals (*Hydrurga leptonyx*) and walruses vary geographically, as do some long-distance vocal displays of elephant seals (Le Boeuf & Peterson 1969; Le Boeuf & Petrinovich 1975; Ray & Watkins 1975; Stirling *et al.* 1983, 1987; Thomas & Stirling 1983; Thomas *et al.* 1988; Morrice *et al.* 1994; Terhune 1994; Rogers *et al.* 1995; Thomas & Golladay 1995; Pahl *et al.* 1997; Perry & Terhune 1999; Sanvito & Galimberti 2000b). The best documented and most striking geographical patterns are in Weddell seals, which show distinctly different call types in different parts of their range and show some evidence of geographical variation even on a small spatial scale.

There is strong evidence for geographical and temporal variation in the songs of humpback whales (Helweg *et al.* 1998). Guinee *et al.* (1983) tracked changes over 1–2 years in the songs of a small number of individual whales, and found that the song of each whale was more similar to other whales recorded at the same time than to its own song from a different year. This verifies that individual whales modify their songs to match the current version. The convergence of songs from different whales sung during the same period, coupled with progressive and pervasive changes in songs over time, provide evidence that geographical variation in humpback songs reflects cultural change (Payne *et al.* 1983).

Acoustic characters measured from vocalizations are candidates for characters that will show informative patterns of ancestry and descent, but few systematic or phylogenetic studies of vocalizations in related species have been carried out for marine mammals. These studies are complicated by the clear evidence for vocal learning in odontocetes, mysticetes and pinnipeds. On the other hand, most other mammals (especially non-human terrestrial mammals) appear to inherit pattern generators for stereotyped vocal output, and will develop the species-typical repertoire with little or no auditory input from conspecific individuals (Janik & Slater 1997). A species-typical vocalization that develops independently of exposure must represent a highly coordinated set of inherited traits involving central pattern generators, and neural control of vocal and respiratory musculature and of the sound-production apparatus. Such a complex and coordinated system may evolve relatively slowly, especially for acoustic features closely tied to the sound-production apparatus. These kinds of features are therefore likely to be informative about higher level phylogenetic relationships. Other features such as the sequential patterning of sound units may evolve more rapidly and thus be more useful for phylogenetic studies at the population or species level. Stirling (1971) described vocalizations of several species of southern hemisphere fur seals and Miller and Phillips (2001) addressed evolutionary conservatism of vocalizations in *Arctocephalus* plus the northern fur seal. These studies suggest that evolutionary conservatism is likely to be found in general purpose signals that are shared by different classes of senders and receivers; these will often be short-range signals (Moynihan 1973; Fernández-Juricic *et al.* 1999). In contrast, sexually selected displays, like long-distance broadcast displays of whales and rutting male pinnipeds, are likeliest to evolve most quickly. Improving knowledge of phylogenetic relationships will permit explicit tests of evolutionary rates and trends in acoustic communication of marine mammals (Brooks & McLennan 1991; Ford 1991; Irwin 1996; Prum 1997). To do so will require more quantitative acoustic analyses of the similarity of calls than are currently typically performed, and more comprehensive descriptions of repertoire structure and signalling behaviour.

6.6 CONCLUSIONS

6.6.1 Gaps in our knowledge

We know a lot about the diversity of sounds produced by marine mammals and have a detailed understanding of how captive dolphins echolocate on artificial targets, but lack knowledge in many areas:

1 Functional anatomy of sound-producing and sound-filtering structures; mechanisms of sound production.

2 Acoustic perception (including categorization of natural sounds).

3 Use of echolocation by odontocetes in the wild (what are the targets for which this ability evolved?).

4 Use of low-frequency sounds to orientate in and explore the environment.
5 Vocal development and vocal learning.
6 Functional analyses of vocalizations and vocal behaviour; the behavioural significance of variation in acoustic displays.
7 Social recognition through vocalizations.

All these areas present opportunities for future research. Recent advances in electronics and signal processing enable quantitative analysis of vocal repertoires and enable techniques for field identification of who is vocalizing, and for relating vocal behaviour to social interaction.

As researchers develop larger databases of animal sounds with associated information, there is an increasing need for recordings and data to be made available for other research purposes (Kroodsma *et al.* 1996; Bradbury *et al.* 1999). In the pioneering studies on marine mammal bioacoustics, sounds were recorded on magnetic tapes that are deteriorating. Since many marine mammal populations have vocal repertoires that may change over time, these early recordings can be extremely valuable. It can also be very expensive to go to sea, and much research depends upon serendipitous circumstances that can be difficult to duplicate. Many recordings obtained in this work have aesthetic and scientific value well beyond the use made by any one investigator. The effort to develop techniques for categorizing marine mammal sounds would also benefit enormously from some standardized sets of recorded sounds, so the different techniques could be evaluated with the same set of stimuli. Bradbury *et al.* (1999) and Kroodsma *et al.* (1996) argue for the development of systematic collections of archived marine mammal sounds that are readily accessible to scientists and to the general public.

6.6.2 The importance of scale in marine mammal communication and echolocation

The oceans have few boundaries, on scales from molecules or micrometres to oceanic basins or megametres. Even simple ocean processes such as diffusion may be important over temporal scales from milliseconds to millenia. Thus it is a commonplace of oceanography that one must be explicit about the spatial and temporal scales over which one is analysing data. When students think of animal communication, they often imagine one animal sending one signal to a recipient a few metres away that responds within seconds. Yet the adaptive significance of many activities, such as feeding and reproduction, accumulate over the lifetime of an animal. There are many cases where the short-term cost of an interaction, say male–male competition for dominance in a breeding system, looms large on short temporal scales, and is only outweighed by the long-term benefit of increased access to females. When one analyses the function(s) of animal calls, it is critical to think carefully about which temporal scales are relevant, both for costs and benefits. We have pointed out examples from dolphin whistles and humpback song where the simple act of categorizing calls depends upon choice of temporal scales, a choice that is seldom discussed explicitly. These choices may have profound influences upon our results, and we should think carefully about our reasons for choosing one particular scale for an analysis. We also need to think about the spatial scales that are appropriate for solving particular problems. For example, an echolocating dolphin uses high-frequency clicks to detect an obstacle or prey at a range of 1–100 m. Most baleen whales migrate thousands of kilometres on an annual basis. Unlike dolphin echolocation, which functions well for detecting small targets within 100 m, baleen whales face problems of orienting over hundreds of kilometres, problems that would be better addressed with low-frequency signals.

6.6.3 Importance of bioacoustic research to conservation

Many marine mammal populations were heavily exploited over the past centuries (see Chapter 14). Some, such as the Steller sea cow (*Hydrodamalis gigas*) were driven extinct, and others, such as the northern right whale (*Eubalaena glacialis*), have poor prospects of surviving another century (Caswell *et al.* 1999). For decades it has been recognized that there is an urgent need to monitor the populations of marine mammals. Where pinnipeds congregate on a few breeding beaches, it may be easy to monitor their populations, but many marine mammals are dispersed in the oceans. All marine mammals must surface to breathe, so many census techniques rely upon sighting animals from ships or airplanes. Yet most marine mammals at sea are only visible at the surface for 1–10% of the time, so it is difficult to count them efficiently or accurately. Other techniques that rely upon sighting animals can track individuals by photographing natural markings and can use mark-recapture techniques to estimate population size. This approach can be useful for small localized populations, but can suffer from sighting biases.

Acoustic monitoring of the vocalizations of marine mammals has proven to be a useful tool for estimating the distribution and abundance of some species. For example, Clark *et al.* (1996) spent more than a decade tracking vocalizations of bowhead whales migrating past Point Barrow, Alaska, and these acoustic detections yielded much higher population estimates than visual detections from the same area. Ships may combine a visual survey with using an array of hydrophones to detect and locate vocalizing whales (Norris *et al.* 1999). These acoustic data can in some circumstances be used exactly as visual sightings, with much higher detection rates for animals such as sperm whales (Leaper *et al.* 1992).

An appreciation for the amazing ways in which marine mammals have adapted to make use of the acoustic properties of the ocean can help us to appreciate that man-made noise in the sea may present a conservation problem for marine mammals. Over the past century, the acoustic environment of the sea has changed with the advent of motorized shipping, underwater explosives and the development of sound sources such as sonars, air guns, etc. (Richardson *et al.* 1995). Any or all of these sources of noise might interfere with how marine mammals use sound in the sea (Richardson *et al.* 1995), so noise pollution might have serious short- and long-term impacts on activity budgets, communication, echolocation, feeding and social structure in marine mammals.

The study of how marine mammals use sound is not just fascinating in its own right as basic research, but it also is important for protecting these animals and encouraging the recovery of endangered populations.

REFERENCES

Abe, H., Hasegawa, Y. & Wada, K. (1977) A note on the air-sac of ribbon seal. *Scientific Reports of the Whales Research Institute* 29, 129–135.

Altmann, S.A. (1967) The structure of primate social communication. In: *Social Communication among Primates* (S.A. Altmann, ed.), pp. 325–362. University of Chicago Press, Chicago, IL.

Amundin, M. (1991) *Sound production in odontocetes with emphasis on the harbour porpoise, Phocoena phocoena.* PhD Thesis, University of Stockholm, Stockholm, Sweden.

Amundin, M. & Andersen, S.H. (1983) Bony nares air pressure and nasal plug muscle activity during click production in the harbour porpoise, *Phocoena phocoena*, and the bottlenosed dolphin, *Tursiops truncatus. Journal of Experimental Biology* **105**, 275–282.

Anderson, P.K. & Barclay, R.M.R. (1995) Acoustic signals of solitary dugongs: physical characteristics and behavioral correlates. *Journal of Mammalogy* 76, 1226–1237.

Andersson, M. (1994) *Sexual Selection.* Princeton University Press, Princeton, NJ.

Andrew, R.J. (1963) Trends apparent in the evolution of vocalization in the Old World monkeys and apes. *Symposia of the Zoological Society of London* **10**, 89–101.

Andrew, R.J. (1969) The effects of testosterone on avian vocalizations. In: *Bird Vocalizations: Their Relation to Current Problems in Biology and Psychology* (R.A. Hinde, ed.), pp. 97–130. Cambridge University Press, Cambridge, UK.

Andrew, R.J. (1972) The information potentially available in mammal displays. In: *Non-Verbal Communication* (R.A. Hinde, ed.), pp. 179–206. Cambridge University Press, Cambridge, UK.

Andrew, R.J. (1976) Use of formants in the grunts of baboons and other nonhuman primates. *Annals of the New York Academy of Sciences* **280**, 673–693.

Aroyan, J.L. (1996) *Three-dimensional numerical simulation of biosonar signal emission and reception in the common dolphin.* PhD Thesis, University of California at Santa Cruz, Santa Cruz, CA.

Aroyan, J.L., Cranford, T.W., Kent, J. & Norris, K.S. (1992) Computer modeling of acoustic beam formation in *Delphinus delphis. Journal of the Acoustical Society of America* **92**, 2539–2545.

Aroyan, J.L., McDonald, M.A., Webb, S.C. *et al.* (2000) Acoustic models of sound production and propagation. In: *Hearing in Whales and Dolphins* (A.N. Popper, R.H. Fay & W.W.L. Au, eds), pp. 409–469. Springer-Verlag, New York.

Au, W.W.L. (1993) *The Sonar of Dolphins.* Springer-Verlag, New York.

Au, W.W.L. (2001) Echolocation. In: *Encyclopedia of Marine Mammals* (W.F. Perrin, B. Würsig & H.G.M. Thewissen, eds), pp. 358–367. Academic Press, San Diego.

Backus, R. & Schevill, W.E. (1966) *Physeter* clicks. In: *Whales, Dolphins, and Porpoises* (K.S. Norris, ed.), pp. 510–528. University of California Press, Berkeley, CA.

Bain, D.E. (1992) Multi-scale communication by vertebrates. In: *Marine Mammal Sensory Systems* (J.A. Thomas, K.A. Kastelein & A.Ya. Supin, eds), pp. 601–629. Plenum Press, New York.

Baker, C.S., Lambertsen, R.H., Weinrich, M.T. *et al.* (1991) Molecular genetic identification of the sex of humpback whales (*Megaptera novaeangliae*). In: *Genetic Ecology of Whales and Dolphins* (A.R. Hoelzel, ed.), pp. 105–111. Reports of the International Whaling Commission Special Issue No. 13. International Whaling Commission, Cambridge, UK.

Ballard, K.A. & Kovacs, K.M. (1995) The acoustic repertoire of hooded seals (*Cystophora cristata*). *Canadian Journal of Zoology* 73, 1362–1374.

Barlow, G.W. (1992) Is the mobility gradient suitable for general application? *Behavioral and Brain Sciences* **15**, 267–268.

Bartholomew, G.A. & Collias, N.E. (1962) The role of vocalization in the social behaviour of the northern elephant seal. *Animal Behaviour* **10**, 7–14.

Beecher, M.D. (1988) Spectrographic analysis of animal vocalizations: implications of the 'uncertainty principle'. *Bioacoustics* **1**, 187–208.

Beeman, K. (1998) Digital signal analysis, editing, and synthesis. In: *Animal Acoustic Communication: Sound Analysis and Research Methods* (S.L. Hopp, M.J. Owren & C.S. Evans, eds), pp. 59–103. Springer-Verlag, Berlin.

Beer, C.G. (1982) Conceptual issues in the study of communication. In: *Acoustic Communication in Birds, Vol. 2: Song Learning and its Consequences* (D.E. Kroodsma & E.H. Miller, eds), pp. 279–310. Academic Press, New York.

Bengtson, J.L. & Fitzgerald, S.M. (1985) Potential role of vocalizations in West Indian manatees. *Journal of Mammalogy* **66**, 816–819.

Berland, B. (1958) The hood of the hooded seal, *Cystophora cristata* Erxl. *Nature* **182**, 408–409.

Berland, B. (1966) The hood and its extrusible balloon in the hooded seal—*Cystophora cristata* Erxl. *Norsk Polarinstitutt, Årbok, Oslo* **1965**, 95–102.

Boness, D.J. & James, H. (1979) Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Zoology* **188**, 477–500.

Bradbury, J.W. & Vehrencamp, S.L. (1998) *Principles of Animal Communication.* Sinauer Associates Inc., Sunderland, MA.

Bradbury, J., Budney, G.F., Stemple, D.W. & Kroodsma, D.E. (1999) Organizing and archiving private collections of tape recordings. *Animal Behaviour* **57**, 1343–1344.

Brauer, R.W., Jennings, R.A. & Poulter, T.C. (1966) The effect of substituting helium and oxygen for air on the vocalization of the California sea lion, *Zalophus californianus.* In: *Proceedings of the Third Annual Conference on Biological Sonar and Diving Mammals* (T.C. Poulter, ed.), pp. 68–72. Stanford Research Institute, Fremont, California.

Brooks, D.R. & McLennan, D.A. (1991) *Phylogeny, Ecology, and Behavior. A Research Program in Comparative Biology.* University of Chicago Press, Chicago, IL.

Brownlee, S.M. & Norris, K.S. (1994) The acoustic domain. *The Hawaiian Spinner Dolphin* (K.S. Norris, B. Würsig, R.S. Wells & M. Würsig, eds), pp. 161–185. University of California Press, Berkeley, CA.

Bryden, M.M. & Felts, W.J.L. (1974) Quantitative anatomical observations on the skeletal and muscular systems of four species of Antarctic seals. *Journal of Anatomy* **118**, 589–600.

Burgess, W.C., Tyack, P.L., LeBoeuf, B.J. & Costa, D.P. (1998) A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Deep-Sea Research* **45**, 1327–1351.

Burns, J.J. (1981a) Bearded seal *Erignathus barbatus* Erxleben, 1777. In: *Handbook of Marine Mammals, Vol 2: Seals* (S.H. Ridgway & R.J. Harrison, eds), pp. 145–170. Academic Press, London.

Burns, J.J. (1981b) Ribbon seal *Phoca fasciata* Zimmermann, 1783. In: *Handbook of Marine Mammals, Vol 2: Seals* (S.H. Ridgway & R.J. Harrison, eds), pp. 89–109. Academic Press, London.

Busnel, R.-G. & Dziedzic, A. (1968) Etude des signaux acoustiques associé à des situations détresse chez certain cétacés odontocètes. *Annales de l'Institut Océanographique, Monaco* **46**, 109–144.

Caldwell, D.K. & Caldwell, M.C. (1972a) *The World of the Bottlenose Dolphin.* Lippincott, Philadelphia.

Caldwell, M.C. & Caldwell, D.K. (1965) Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature* **207**, 434–435.

Caldwell, M.C. & Caldwell, D.K. (1968) Vocalizations of naïve captive dolphins in small groups. *Science* **159**, 1121–1123.

Caldwell, M.C. & Caldwell, D.K. (1972b) Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. *Cetology* **9**, 1–8.

Caldwell, M.C., Caldwell, D.K. & Tyack, P.L. (1990) A review of the signature whistle hypothesis for the Atlantic bottlenose dolphin, *Tursiops truncatus.* In: *The Bottlenose Dolphin: Recent Progress in Research* (S. Leatherwood & R. Reeves, eds), pp. 199–234. Academic Press, San Diego.

Calkins, D. & Lent, P.C. (1975) Territoriality and mating behavior in Prince William Sound sea otters. *Journal of Mammalogy* **56**, 528–529.

Caswell, H., Fujiwara, M. & Breault, S. (1999) Declining survival probability threatens the North Atlantic right whale. *Proceedings of the National Academy of Science, USA* **96**, 3308–3313.

Cheney, D.L. & Seyfarth, R.M. (1990) *How Monkeys See the World: Inside the Mind of Another Species.* University of Chicago Press, Chicago, IL.

Cherry, C. (1978) *On Human Communication: a Review, a Survey, and a Criticism.* MIT Press, Cambridge, MA.

Chiasson, R.B. (1955) *The morphology of the Alaskan fur seal.* PhD Thesis, Stanford University, Stanford, CA.

Clark, C.W. (1989) The use of bowhead whale call tracks based on call characteristics as an independent means of determining tracking parameters. *Reports of the International Whaling Commission* **39**, 111–113.

Clark, C.W., Charif, R., Mitchell, S. & Colby, J. (1996) Distribution and behavior of the bowhead whale, *Balaena mysticetus*, based on analysis of acoustic data collected during the 1993 spring migration off Point Barrow, Alaska. *Reports of the International Whaling Commission* **46**, 541–552.

Cranford, T.W. (1992) *Functional morphology of the odontocete forehead: implications for sound generation.* PhD Thesis, University of California at Santa Cruz, Santa Cruz, CA.

Cranford, T.W. (1999) The sperm whale's nose: sexual selection on a grand scale? *Marine Mammal Science* **15**, 1133–1157.

Cranford, T.W. (2000) In search of impulse sound sources in odontocetes. In: *Hearing in Whales and Dolphins* (A.N. Popper, R.H. Fay & W.W.L. Au, eds), pp. 109–155. Springer Verlag, New York.

Cranford, T.W., Amundin, M. & Norris, K.S. (1996) Functional morphology and homology in the odontocete nasal complex: implications for sound generation. *Journal of Morphology* **228**, 223–285.

Cummings, W. & Thompson, P.O. (1971) Underwater sounds from the blue whale, *Balaenoptera musculus. Journal of the Acoustical Society of America* **50**, 1193–1198.

Dawkins, R. & Krebs, J.R. (1978) Animal signals: information or manipulation. In: *Behavioural Ecology: an Evolutionary Approach* (J.R. Krebs & N.B. Davies, eds), pp. 282–309. Sinauer Associates, Sunderland, MA.

Dawson, S. & Thorpe, C.W. (1990) A quantitative analysis of the sounds of Hector's dolphin. *Ethology* **86**, 131–145.

de Queiroz, K. & Good, D.A. (1997) Phenetic clustering in biology: a critique. *Quarterly Review of Biology* **72**, 3–30.

Dormer, K.J. (1979) Mechanism of sound production and air recycling in delphinids: cineradiographic evidence. *Journal of the Acoustical Society of America* **65**, 229–239.

Dorst, J. (1973) Appareil respiratoire. In: *Traité de Zoologie, Vol 16: Mammifères, Splanchnologie* (J. Anthony, L. Arvy, J. Dorst, M. Gabe, R. Weill & P. Zeitoun, eds), pp. 484–600. Masson, Paris.

Eaton, R.L. (1979) A beluga whale imitates human speech. *Carnivore* **2**, 22–23.

Edds, P.L. (1982) Vocalizations of the blue whale, *Balaenoptera musculus*, in the St Lawrence River. *Journal of Mammalogy* **63**, 345–347.

Ellison, W.T., Clark, C.W. & Bishop, G.C. (1987) Potential use of surface reverberation by bowhead whales, *Balaena mysticetus*, in under-ice navigation. *Reports of the International Whaling Commission* **37**, 329–332.

Evans, H.E. (1993) *Miller's Anatomy of the Dog.* W.B. Saunders, Philadelphia, PA.

Evans, W.E. (1967) Vocalization among marine mammals. In: *Marine Bioacoustics* (W.N. Tavolga, ed.), Vol. 2, pp. 159–186. Pergamon Press, Oxford.

Evans, W.E. & Bastian, J. (1969) Marine mammal communication: social and ecological factors. In: *The Biology of Marine Mammals* (H.T. Andersen, ed.), pp. 425–475. Academic Press, New York.

Evans, W.E. & Haugen, R. (1963) An experimental study of echolocation ability of a California sea lion, *Zalophus californianus* (Lesson). *Bulletin of the Southern California Academy of Sciences* **62**, 165–175.

Evans, W.E. & Maderson, P.F.A. (1973) Mechanisms of sound production in delphinid cetaceans: a review and some anatomical considerations. *American Zoologist* **13**, 1205–1213.

Evans, W.E., Awbrey, F.T. & Hackbarth, H. (1988) High frequency pulse produced by free ranging Commerson's dolphin *Cephalorhynchus commersonii* compared with those of phocoenids. *Reports of the International Whaling Commission Special Issue* 9, 173–181.

Fay, F.H. (1960) Structure and function of the pharyngeal pouches of the walrus (*Odobenus rosmarus* L.). *Mammalia* **24**, 361–371.

Fay, F.H. (1982) *Ecology and biology of the Pacific Walrus, Odobenus rosmarus divergens Illiger.* North American Fauna No. 74. US Department of the Interior, Fish and Wildlife Service, Washington, DC.

Fay, F.H., Ray, G.C. & Kibal'chich, A.A. (1984) Timing and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus* Illiger. In: *Soviet–American Cooperative Research on Marine Mammals, Vol. 1: Pinnipeds* (F.H. Fay & G.A. Fedoseev, eds), pp. 89–99. NOAA Technical Report NMFS No. 12. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Washington, DC.

Fee, M.S., Shraiman, B., Pesaran, B. & Mitra, P.P. (1998) The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. *Nature* **395**, 67–71.

Fernández-Juricic, E., Campagna, C., Enriquez, V. & Ortiz, C.L. (1999) Vocal communication and individual variation in breeding South American sea lions. *Behaviour* **136**, 495–517.

Fitch, W.T. (1997) Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America* **102**, 1213–1222.

Ford, J.K.B. (1989) Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology* **67**, 727–745.

Ford, J.K.B. (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology* **69**, 1454–1483.

Gailey-Phipps, J.J. (1984) *Acoustic communication and behavior of the spotted seal (Phoca largha).* PhD Thesis, Johns Hopkins University, Baltimore, MD.

Gentry, R.L. (1975) Comparative social behavior of eared seals. *Rapports et Procès-Verbaux Des Réunions, Conseil International Pour l'Exploration de la Mer* **169**, 188–194.

George, J.C., Clark, C., Carroll, G.M. & Ellison, W.T. (1989) Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, spring 1985. *Arctic* **42**, 24–30.

Glockner, D.A. (1983) Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. In: *Communication and Behavior of Whales* (R. Payne, ed.), pp. 447–464. Westview Press, Boulder, CO.

Golani, I. (1992) A mobility gradient in the organization of vertebrate movement: the perception of movement through symbolic language. *Behavioral and Brain Sciences* **15**, 249–266.

Goold, J.C. & Jones, S.E. (1995) Time and frequency domain characteristics of sperm whale clicks. *Journal of the Acoustical Society of America* **98**, 1279–1291.

Gordon, J.C.D. (1987) *Behaviour and ecology of sperm whales off Sri Lanka*. PhD Thesis, University of Cambridge, Cambridge, UK.

Gordon, J.C.D. (1991) Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. *Journal of Zoology* **224**, 301–314.

Gordon, J.C.D., Leaper, R., Hartley, F.G. & Chappell, O. (1992) Effects of whale watching vessels on the surface and underwater acoustic behaviour of sperm whales off Kaikoura New Zealand. *New Zealand Department of Conservation, Science and Research Series* **52**, 64.

Gordon, J. & Tyack, P.L. (2002) Sounds and cetaceans. In: *Marine Mammals: Biology and Conservation* (P.G.H. Evans & J.A. Raga, eds), pp. 139–196. Kluwer Academic/Plenum Press, New York.

Green, K. & Burton, H.R. (1988) Do Weddell seals sing? *Polar Biology* **8**, 165–166.

Green, S. & Marler, P. (1979) The analysis of animal communication. In: *Handbook of Behavioral Neurobiology, Vol 3: Social Behavior and Communication* (P. Marler & J.G. Vandenberghe, eds), pp. 73–158. Plenum Press, New York.

Griffin, D.R. (1958) *Listening in the Dark*. Yale University Press, New Haven. (Reprint edition, 1974. Dover Publications, New York.)

Guinee, L., Chu, K. & Dorsey, E.M. (1983) Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). In: *Communication and Behavior of Whales* (R. Payne, ed.), pp. 59–80. Westview Press, Boulder, CO.

Hailman, J.P. & Ficken, M.S. (1996) Comparative analysis of vocal repertoires, with reference to chickadees. In: *Ecology and Evolution of Acoustic Communication in Birds* (D.E. Kroodsma & E.H. Miller, eds), pp. 136–159. Comstock Publishing Associates, Ithaca, NY.

Hailman, J.P., Ficken, M.S. & Ficken, R.W. (1985) The 'chick-a-dee' calls of *Parus atricapillus*: a recombinant system of animal communication compared with written English. *Semiotica* **56**, 191–224.

Hanggi, E.B. & Schusterman, R.J. (1992) Underwater acoustical displays by male harbour seals (*Phoca vitulina*): initial results. In: *Marine Mammal Sensory Systems* (J.A. Thomas, R.A. Kastelein & A.Y. Supin, eds), pp. 449–457. Plenum Press, New York.

Hanggi, E.B. & Schusterman, R.J. (1994) Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*. *Animal Behaviour* **48**, 1275–1283.

Hartman, D.S. (1971) *Behavior and ecology of the Florida manatee, Trichechus manatus latirostris (Harlan), at Crystal River, Citrus County*. PhD Thesis, Cornell University, Ithaca, NY.

Hatakeyama, Y. & Soeda, H. (1990) Studies on echolocation of porpoises taken in salmon gillnet fisheries. In: *Sensory Abilities of Cetaceans* (J.A. Thomas & R. Kastelein, eds), pp. 269–281. Plenum Press, New York.

Hauser, M.D. (1996) *The Evolution of Communication*. MIT Press, Cambridge, MA.

Helweg, D.A., Cato, D.H., Jenkins, P.F., Garrigue, C. & McCauley, R.D. (1998) Geographic variation in South Pacific humpback whale songs. *Behaviour* **135**, 1–27.

Herman, L.M. (1980) Cognitive characteristics of dolphins. In: *Cetacean Behavior: Mechanisms and Functions* (L.M. Herman, ed.), pp. 363–429. Wiley-Interscience, New York.

Herzing, D.L. (1996) Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals* 22, 61–79.

Hewer, H.R. (1974) *British Seals*. William Collins & Sons, Glasgow, UK.

Hoelzel, A.R. & Osborne, R.W. (1986) Killer whale call characteristics: implications for cooperative foraging. In: *Behavioral Ecology of Killer Whales* (B.C. Kirkevold & J.S. Lockhard, eds), pp. 373–403. Alan R. Liss, New York.

Hunter, J. (1787) Observations on the structure and oeconomy of whales. *Philosophical Transactions* 77, 371–450.

Insley, S.J. (1992) Mother–offspring separation and acoustic stereotypy: a comparison of call morphology in two species of pinnipeds. *Behaviour* **120**, 103–122.

Insley, S.J. (2000) Long-term vocal recognition in the northern fur seal. *Nature* **406**, 404–405.

Insley, S.J. (2001) Mother–offspring vocal recognition in northern fur seals is mutual not asymmetrical. *Animal Behaviour* **61**, 129–137.

Irwin, R.E. (1996) The phylogenetic content of avian courtship display and song evolution. In: *Phylogenies and the Comparative Method in Animal Behavior* (E.P. Martins, ed.), pp. 234–252. Oxford University Press, New York.

James, F.C. (1991) Complementary descriptive and experimental studies of clinal variation in birds. *American Zoologist* **31**, 694–706.

James, F.C. & McCulloch, C.E. (1985) Data analysis and the design of experiments in ornithology. In: *Current Ornithology* (R.F. Johnston, ed.), pp. 1–63. Plenum Publishing, New York.

Janik, V.M. (1999) Pitfalls in the categorization of behavior: a comparison of dolphin whistle categorization methods. *Animal Behavior* **57**, 133–143.

Janik, V.M. & Slater, P.J.B. (1997) Vocal learning in mammals. *Advances in the Study of Behavior* **26**, 59–99.

Janik, V.M. & Slater, P.J.B. (1998) Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour* **56**, 829–838.

Jaquet, N., Dawson, S., Slooten, E. & Douglas, L. (1999) Sperm whale vocal behavior: why do they click? In: *Abstracts, Thirteenth Biennial Conference on the Biology of Marine Mammals*, pp. 89–90. Society for Marine Mammalogy, Lawrence, KA.

Job, D.A., Boness, D.J. & Francis, J.M. (1995) Individual variation in nursing vocalizations of Hawaiian monk seal pups, *Monachus schauinslandi* (Phocidae, Pinnipedia), and lack of maternal recognition. *Canadian Journal of Zoology* **73**, 975–983.

Kaiser, H.E. (1974) *Morphology of the Sirenia. A Macroscopic and X-ray Atlas of the Osteology of Recent Species.* S. Karger, Basel.

Kamminga, C. & Wiersma, H. (1981) Investigations on cetacean sonar II. Acoustical similarities and differences in odontocete sonar signals. *Aquatic Mammals* **8**, 41–62.

Kamminga, C. & Wiersma, H. (1982) Investigations on cetacean sonar V. The true nature of the sonar sound of *Cephalorhynchus commersonii. Aquatic Mammals* **9**, 95–104.

Kastak, D. & Schusterman, R.J. (1998) Low-frequency amphibious hearing in pinnipeds: methods, measurements, noise, and ecology. *Journal of the Acoustical Society of America* **103**, 2216–2228.

Kastelein, R.A., Dubbeldam, J.L. & de Bakker, M.A.G. (1997) The anatomy of the walrus head (*Odobenus rosmarus*). Part 5: the tongue and its function in walrus ecology. *Aquatic Mammals* **23**, 29–47.

Kastelein, R.A., Postma, J. & Verboom, W.C. (1995) Airborne vocalizations of Pacific walrus pups (*Odobenus rosmarus divergens*). In: *Sensory Systems of Aquatic Mammals* (R.A. Kastelein, J.A. Thomas & P.E. Nachtigall, eds), pp. 265–285. De Spil, Woerden, the Netherlands.

Kelemen, G. (1963) Comparative anatomy and performance of the vocal organ in vertebrates. In: *Acoustic Behaviour of Animals* (R.-G. Busnel, ed.), pp. 489–521. Elsevier, Amsterdam.

Kenyon, K.W. (1969) *The Sea Otter in the Eastern Pacific Ocean.* North American Fauna No. 68. US Department of the Interior, Fish and Wildlife Service, Washington, DC.

Ketten, D.R. (1994) Functional analyses of whale ears: adaptations for underwater hearing. *IEEE Proceedings in Underwater Acoustics* **1**, 264–270.

Ketten, D.R. (1997) Structure and function in whale ears. *Bioacoustics* **8**, 103–135.

Ketten, D.R. (2000) Cetacean ears. In: *Hearing in Whales and Dolphins* (A.N. Popper, R.H. Fay & W.W.L. Au, eds), pp. 43–108. Springer Verlag, New York.

King, J.E. (1972) On the laryngeal skeletons of the leopard seal, *Hydrurga leptonyx*, and the Ross seal, *Ommatophoca rossi. Mammalia* **36**, 146–156.

King, J.E. (1983) *Seals of the World.* Cornell University Press, Ithaca, NY.

Klump, G.M. & Shalter, M.D. (1984) Acoustic behaviour of birds and mammals in the predator context. I Factors affecting the structure of alarm signals; II The functional significance and evolution of alarm signals. *Zeitschrift für Tierpsychologie* **66**, 189–226.

Kooyman, G.L. (1981) Leopard seal *Hydrurga leptonyx* Blainville, 1820. In: *Handbook of Marine Mammals, Vol 2: Seals* (S.H. Ridgway & R.J. Harrison, eds), pp. 261–274. Academic Press, London.

Kooyman, G.L. & Andersen, H.T. (1969) Deep diving. In: *The Biology of Marine Mammals* (H.T. Andersen, ed.), pp. 65–94. Academic Press, New York.

Kooyman, G.L., Hammond, D.D. & Schroeder, J.P. (1970) Bronchograms and tracheograms of seals under pressure. *Science* **169**, 82–84.

Kovacs, K.M. & Lavigne, D.M. (1986) *Cystophora cristata. Mammalian Species* **258**, 1–9.

Krebs, J.R. & Davies, N.B. (1993) *An Introduction to Behavioural Ecology.* Blackwell Scientific Publications, Oxford.

Kroodsma, D.E., Budney, G.F., Grotke, R.W. *et al.* (1996) Natural sound archives: guidance for recordists and a request for cooperation. In: *Ecology and Evolution of Acoustic Communication in Birds* (D.E. Kroodsma & E.H. Miller, eds), pp. 474–486. Comstock Publishing Associates, Ithaca, NY.

Lavigne, D.M. & Kovacs, K.M. (1988) *Harps and Hoods: Ice-breeding Seals of the Northwest Atlantic.* University of Waterloo Press, Waterloo, Ontario.

Lawrence, B. & Schevill, W.E. (1956) The functional anatomy of the delphinid nose. *Bulletin of the Museum of Comparative Zoology, Harvard* **114**, 103–151.

Le Boeuf, B.J. & Peterson, R.S. (1969) Dialects in elephant seals. *Science* **166**, 1655–1656.

Le Boeuf, B.J. & Petrinovich, L.F. (1974) Elephant seals: interspecific comparisons of vocal and reproductive behavior. *Mammalia* **38**, 16–32.

Le Boeuf, B.J. & Petrinovich, L.F. (1975) Elephant seal dialects: are they reliable? *Rapports et Proces-Verbaux des Réunions, Conseil International pur l'Exploration de la Mer* **169**, 213–218.

Leaper, R., Chappell, O. & Gordon, J.C.D. (1992) The development of practical techniques for surveying sperm whale populations acoustically. *Reports of the International Whaling Commission* **42**, 549–560.

Lemon, R.E. (1975) How birds develop song dialects. *Condor* **77**, 385–406.

Levenson, C. (1972) *Characteristics of Sounds Produced by Humpback Whales (Megaptera novaeangliae).* NAVOCEANO Technical Note No. 7700-6-72. Naval Oceanographic Office, Washington, DC.

Lieberman, P. (1984) *The Biology and Evolution of Language.* Harvard University Press, Cambridge, MA.

Lilly, J.C. (1963) Distress call of the bottlenose dolphin: stimuli and evoked behavioral responses. *Science* **139**, 116–118.

Lisitsina, T.Y. (1973) The behavior and acoustical signals of the northern fur seal *Callorhinus ursinus* on the rookery. *Zoologicheskii Zhurnal* **52**, 1220–1228 (in Russian).

Lisitsina, T.Y. (1981) Structure of the breeding grounds and the social behavior of the eared seals (Otariidae). In: *Ecology, Population Structure and Infraspecific Communication Processes in Mammals* (N.P. Naumov & V.E. Sokolov, eds), pp. 99–150. Nauka, Moscow.

Lisitsina, T.Y. (1988) Situation-dependent changes of sound signals of females and the young of *Callorhinus ursinus* (Pinnipedia, Otariidae). *Zoologicheskii Zhurnal* 67, 274–286 (in Russian).

Loesche, P., Stoddard, P.K., Higgins, B.J. & Beecher, M.D. (1991) Signature versus perceptual adaptations for individual vocal recognition in swallows. *Behaviour* **118**, 15–25.

Lynch, A. (1996) The population memetics of birdsong. In: *Ecology and Evolution of Acoustic Communication in Birds* (D.E. Kroodsma & E.H. Miller, eds), pp. 181–197. Comstock Publishing Associates, Ithaca, NY.

McCowan, B. (1995) A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (Delphinidae, *Tursiops truncatus*). *Ethology* **100**, 177–193.

McCowan, B. & Reiss, D. (1995) Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae, *Tursiops truncatus*): a reevaluation of the signature whistle hypothesis. *Ethology* **100**, 193–209.

MacKay, R.S. & Liaw, C. (1981) Dolphin vocalization mechanisms. *Science* **212**, 676–678.

McKinney, F. (1992) Courtship, pair formation, and signal systems. In: *Ecology and Management of Breeding Waterfowl* (B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu, eds), pp. 214–250. University of Minnesota Press, Minneapolis, MN.

McShane, L.J., Estes, J.A., Riedman, M.L. & Staedler, M.M. (1995) Repertoire, structure, and individual variation of vocalizations in the sea otter. *Journal of Mammalogy* 76, 414–427.

Marler, P. (1969) Tonal quality of bird vocalizations. In: *Bird Vocalizations: their Relations to Current Problems in Biology and Psychology* (R.A. Hinde, ed.), pp. 5–18. Cambridge University Press, Cambridge.

Marler, P. & Tenaza, R. (1977) Signaling behavior of apes with special reference to vocalization. In: *How Animals Communicate* (T.A. Sebeok, ed.), pp. 965–1033. University of Indiana, Bloomington, IN.

Marlow, B.J. (1975) The comparative behaviour of the Australasian sea lions *Neophoca cinerea* and *Phocarctos hookeri* (Pinnipedia: Otariidae). *Mammalia* **39**, 159–230.

Martin, P. & Bateson, P. (1993) *Measuring Behaviour. An Introductory Guide*, 2nd edn. Cambridge University Press, Cambridge, UK.

McCulloch, S. & Boness, D.J. (2000) Mother–pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada. *Journal of Zoology* **251**, 449–455.

Merdsoy, B.R., Curtsinger, W.R. & Renouf, D. (1976) *Preliminary Underwater Observations of the Breeding Behavior of the Harp Seal (Pagophilus groenlandicus)*. NTIS, ACMRR/MM/SC118. FAO Advisory Committee on Marine Resources Research, Bergen, Norway.

Miller, E.H. (1975) Walrus ethology. I. The social role of tusks and applications of multidimensional scaling. *Canadian Journal of Zoology* **53**, 590–613.

Miller, E.H. (1979) An approach to the analysis of graded vocalizations of birds. *Behavioral and Neural Biology* **27**, 25–38.

Miller, E.H. (1985) Airborne acoustic communication in the walrus *Odobenus rosmarus*. *National Geographic Research* **1**, 124–145.

Miller, E.H. (1986) Components of variation in nuptial calls of the least sandpiper (*Calidris minutilla*; Aves, Scolopacidae). *Systematic Zoology* **35**, 400–413.

Miller, E.H. (1988) Description of bird behavior for comparative purposes. In: *Current Ornithology* (R.F. Johnston, ed.), Vol. 5, pp. 347–394. Plenum Press, New York.

Miller, E.H. (1991) Communication in pinnipeds, with special reference to non-acoustic communication. In: *The Behaviour of Pinnipeds* (D. Renouf, ed.), pp. 128–235. Chapman & Hall, London.

Miller, E.H. & Boness, D.J. (1983) Summer behavior of Atlantic walruses *Odobenus rosmarus rosmarus* (L.) at Coats Island, N.W.T. (Canada). *Zeitschrift für Säugetierkunde* **48**, 298–313.

Miller, E.H. & Job, D.A. (1992) Airborne acoustic communication in the Hawaiian monk seal, *Monachus schauinslandi*. In: *Marine Mammal Sensory Systems* (J.A. Thomas, R.A. Kastelein & A.Y. Supin, eds), pp. 485–531. Plenum Press, New York.

Miller, E.H. & Murray, A.V. (1995) Structure, complexity, and organization of vocalizations in harp seal (*Phoca groenlandica*) pups. In: *Sensory Systems of Aquatic Mammals* (R.A. Kastelein, J.A. Thomas & P.E. Nachtigall, eds), pp. 237–264. De Spil, Woerden, the Netherlands.

Miller, P.J. & Tyack, P.L. (1998) A small towed beamforming array to identify resident killer whales (*Orcinus orca*) concurrent with focal behavioral observations. *Deep-Sea Research* **45**, 1389–1405.

Miller, P.J. & Phillips, A.V. (2001) *Sexual selection and vocal evolution in fur seals and sea lions (Carnivora Otariidae)*. Unpublished manuscript.

Miller, L.A., Pristed, J., Møhl, B. & Surlykke, A. (1995) The click-sounds of narwhals (*Monodon monoceros*) in Inglefield Bay, Northwest Greenland. *Marine Mammal Science* **11** (4), 491–502.

Møhl, B. & Andersen, S. (1973) Echolocation: high frequency component in the click of the harbour porpoise (*Phocoena phocoena* L.). *Journal of the Acoustical Society of America* **54**, 1368–1372.

Møhl, B., Terhune, J.M. & Ronald, K. (1975) Underwater calls of the harp seal, *Pagophilus groenlandicus*. *Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer* **169**, 533–543.

Møhl, B., Wahlberg, M., Madsen, P.T., Miller, L.A., Surlykke, A. (2000) Sperm whale clicks: directionality and source level revisited. *Journal of the Acoustical Society of America* **107**, 638–648.

Mohr, E. (1963) Beiträge zur Naturgeschichte der Klappmütze, *Cystophora cristata* Erxl. 1777. *Zeitschrift für Säugetierkunde* **28**, 65–84.

Morrice, M.G., Burton, H.R. & Green, K. (1994) Microgeographic variation and songs in the underwater vocalisation repertoire of the Weddell seal (*Leptonychotes weddellii*) from the Vestfold Hills, Antarctica. *Polar Biology* **14**, 441–446.

Moynihan, M. (1970) Control, suppression, decay, disappearance and replacement of displays. *Journal of Theoretical Biology* **29**, 85–112.

Moynihan, M. (1973) The evolution of behavior and the role of behavior in evolution. *Breviora (Museum of Comparative Zoology)* **415**, 1–29.

Murchison, A.E. (1980) Detection range and range resolution of echolocating bottlenose porpoise (*Tursiops truncatus*). In: *Animal Sonar Systems* (R.-G. Busnel & J.F. Fish, eds), pp. 43–70. Plenum, New York.

Murie, J. (1874) Researches upon the anatomy of the Pinnipedia. Part III. Descriptive anatomy of the sea-lion (*Otaria jubata*). *Transactions of the Zoological Society of London* **8**, 501–582.

Myrberg Jr, A.A. (1981) Sound communication and interception in fishes. In: *Hearing and Sound Communication in Fishes* (W.N. Tavolga, A.N. Popper & R.R. Fay, eds), pp. 395–425. Springer-Verlag, New York.

Nachtigall, P.E., Lemonds, D.W. & Roitblat, H.L. (2000) Psychoacoustic studies of dolphin and whale hearing. In: *Hearing in Whales and Dolphins* (A.N. Popper, R.H. Fay & W.W.L. Au, eds), pp. 330–363. Springer-Verlag, New York.

Negus, V.E. (1949) *The Comparative Anatomy and Physiology of the Larynx*. Heinemann, London.

Nishiwaki, M., Ohsumi, S. & Maeda, Y. (1963) Change of form in the sperm whale accompanied with growth. *Scientific Reports of the Whales Research Institute Tokyo* **17**, 1–4.

Norris, K.S. (1967) Some observations on the migration and orientation of marine mammals. In: *Animal Orientation and Navigation* (R.M. Storm, ed.), pp. 101–125. Oregon State University Press, Corvallis, OR.

Norris, K.S. (1969) The echolocation of marine mammals. In: *The Biology of Marine Mammals* (H.T. Andersen, ed.), pp. 391–423. Academic Press, New York.

Norris, K.S. & Harvey, G.W. (1972) A theory for the function of the spermaceti organ of the sperm whale. In: *Animal Orientation and Navigation* (S.R. Galler, K. Schmidt-Koenig, G.J. Jacobs, R.E. Belleville, eds), p. 262. NASA Special Publication, Washington DC.

Norris, K.S. & Møhl, B. (1983) Can odontocetes debilitate prey with sound? *American Naturalist* **122**, 85–104.

Norris, K.S., Prescott, J.H., Asa-Dorian, P.V. & Perkins, P. (1961) An experimental demonstration of echolocation behavior in the porpoise, *Tursiops truncatus* (Montagu). *Biological Bulletin* **120**, 163–176.

Norris, T.F., McDonald, M. & Barlow, J. (1999) Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *Journal of the Acoustical Society of America* **106**, 506–514.

Nowicki, S. (1987) Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. *Nature* **325**, 53–55.

Odend'hal, S. (1966) The anatomy of the larynx of the California sea lion (*Zalophus californianus*). In: *Proceedings of the Third Annual Conference on Biological Sonar and Diving Mammals* (T.C. Poulter, ed.), pp. 55–67. Stanford Research Institute, Fremont, CA.

Oliver, G.W. (1978) Navigation in mazes by a gray seal, *Halichoerus grypus* (Fabricius). *Behaviour* 67, 97–114.

Overstrom, N.A. (1983) Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). *Zoo Biology* **2**, 93–103.

Owings, D.H. & Morton, E.S. (1998) *Animal Vocal Communication: a New Approach*. Cambridge University Press, Cambridge, UK.

Pahl, B.C., Terhune, J.M. & Burton, H.R. (1997) Repertoire and geographic variation in underwater vocalisations of Weddell seals (*Leptonychotes weddellii*, Pinnipedia: Phocidae) at the Vestfold Hills, Antarctica. *Australian Journal of Zoology* **45**, 171–187.

Palsbøll, P.J., Vader, A., Bakke, I. & El-Gewely, M.R. (1992) Determination of gender in cetaceans by the polymerase chain reaction. *Canadian Journal of Zoology* **70**, 2166–2170.

Papastavrou, V., Smith, S.C. & Whitehead, H. (1989) Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Canadian Journal of Zoology* 67, 839–846.

Payne, K. & Payne, R. (1985) Large scale changes over 19 years in the songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie* **68**, 89–114.

Payne, K.B., Tyack, P. & Payne, R.S. (1983) Progressive changes in the songs of humpback whales. In: *Communication and Behavior of Whales* (R. Payne, ed.), pp. 9–59. Westview Press, Boulder, CO.

Payne, R.S. & Guinee, L.N. (1983) Humpback whale (*Megaptera novaeangliae*) songs as an indicator of 'stocks'. In: *Communication and Behavior of Whales* (R. Payne, ed.), pp. 333–358. Westview Press, Boulder, CO.

Payne, R.S. & McVay, S. (1971) Songs of humpback whales. *Science* **173**, 585–597.

Payne, R.S. & Webb, D. (1971) Orientation by means of long range acoustic signalling in baleen whales. *Annals of the New York Academy of Sciences* **188**, 110–141.

Perry, E.A. & Terhune, J.M. (1999) Variation of harp seal (*Pagophilus groenlandicus*) underwater vocalizations among three breeding locations. *Journal of Zoology, London* **249**, 181–186.

Peters, G. (1978) Einige Beobachtungen zur Lautgebung der Bären—Bioakustische Untersuchungen im Zoologischen garten. *Zeitschrift Des Kölner Zoo* **21**, 45–51.

Peters, G. (1984) On the structure of friendly close range vocalizations in terrestrial carnivores (Mammalia: Carnivora: Fissipedia). *Zeitschrift für Säugetierkunde* **49**, 157–182.

Peterson, R.S. & Bartholomew, G.A. (1969) Airborne vocal communication in the California sea lion *Zalophus californianus. Animal Behaviour* **17**, 17–24.

Phillips, A.V. & Stirling, I. (2000) Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis. Marine Mammal Science* **16**, 592–616.

Phillips, A.V. & Stirling, I. (2001) Vocal repertoire of South American fur seals, *Arctocephalus australis*: structure, function and context. *Canadian Journal of Zoology* 79, 420–437.

Piérard, J. (1965) La cavité sous-cricoïdienne (antrum subcricoideum) de l'otarie de Steller (*Eumetopias jubata* Schreber). *Mammalia* **29**, 429–431.

Piérard, J. (1969) Le larynx du phoque de Weddell (*Leptonychotes weddelli*, Lesson, 1826). *Canadian Journal of Zoology* **47**, 77–87.

Pierce, J.R. (1983) *The Science of Musical Sound*. Scientific American Books, New York.

Popov, L.A. (1961) Materials to the general morphology of *Cystophora cristata*, Erxl. of Greenland Sea. *Trudy Soveshchaniya Po Ekologii I Promyslu Morskikh Mlekopitayushchikh* (E.N. Pavlovskiy & S.E. Kleinenberg, eds), pp. 180–191. Izdatel'stvo Akademii Nauk SSR, Moscow.

Poulter, T.C. (1963a) Sonar signals of the sea lion. *Science* **139**, 753–755.

Poulter, T.C. (1963b) The sonar of the sea lion. *IEEE Transactions in Ultrasonic Engineering* **10**, 109–111.

Poulter, T.C. (1965) Location of the point of origin of the vocalization of the California sea lion, *Zalophus californianus*. In: *Proceedings of the Second Annual Conference on Biological Sonar and Diving Mammals* (T.C. Poulter, ed.), pp. 41–48. Stanford Research Institute, Fremont, CA.

Poulter, T.C. (1966) The use of active sonar by the California sea lion, *Zalophus californianus. Journal of Auditory Research* **6**, 165–173.

Poulter, T.C. & Del Carlo, D.G. (1971) Echo ranging signals: sonar of the Steller sea lion, *Eumetopias jubata. Journal of Auditory Research* **11**, 43–52.

Prum, R.O. (1997) Phylogenetic tests of alternative intersexual selection mechanisms: trait macroevolution in a polygynous clade (Aves: Pipridae). *American Naturalist* **149**, 668–692.

Purves, P.E. (1966) Anatomical and experimental observations on the cetacean sonar system. In: *Animal Sonar Systems* (R.-G. Busnel, ed.), pp. 197–269. Laboratoire de Physiologie Acoustique, Jouy-en-Josas, France.

Purves, P.E. & Pilleri, G. (1973) Observations on the ear, nose, and throat and eye of *Platanista indi. Investigations on Cetacea* **5**, 13–57.

Purves, P.E. & Pilleri, G. (1983) *Echolocation in Whales and Dolphins*. Academic Press, London.

Ralls, K., Fiorelli, P. & Gish, S. (1985) Vocalizations and vocal mimicry in captive harbour seals, *Phoca vitulina. Canadian Journal of Zoology* **63**, 1050–1056.

Rasa, O.A.E. (1971) Social interaction and object manipulation in weaned pups of the northern elephant seal *Mirounga angustirostris. Zeitschrift für Tierpsychologie* **29**, 82–102.

Ray, G.C. (1981) Ross seal *Ommatophoca rossi* Gray, 1844. In: *Handbook of Marine Mammals, Vol 2: Seals* (S.H. Ridgway & R.J. Harrison, eds), pp. 237–260. Academic Press, London.

Ray, G.C. & Watkins, W.A. (1975) Social function of underwater sounds in the walrus *Odobenus rosmarus. Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer* **169**, 524–526.

Ray, G.C., Watkins, W.A. & Burns, J.J. (1969) The underwater song of *Erignathus* (bearded seal). *Zoologica (New York)* **54**, 79–83.

Reeves, R.R. & Ling, J.K. (1981) Hooded seal *Cystophora cristata* Erxleben, 1777. In: *Handbook of Marine Mammals, Vol 2: Seals* (S.H. Ridgway & R.J. Harrison, eds), pp. 171–194. Academic Press, London.

Reeves, R.R., Stewart, B.S. & Leatherwood, S. (1992) *The Sierra Club Handbook of Seals and Sirenians*. Sierra Club Books San Francisco, CA.

Reidenberg, J.S. & Laitmann, J.T. (1988) Existence of vocal folds in the larynx of odontoceti (toothed whales). *Anatomical Record* **221**, 886–891.

Renouf, D. & Davis, M.B. (1982) Evidence that seals may use echolocation. *Nature* **300**, 635–637.

Richards, D.G., Wolz, J.P. & Herman, L.M. (1984) Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus. Journal of Comparative Psychology* **98**, 10–28.

Richardson, W.J., Greene Jr, C.R., Malme, C.I. & Thomson, D.H. (1995) *Marine Mammals and Noise*. Academic Press, New York.

Ridgway, S. (1997) First audiogram for marine mammals in the open ocean and at depth: hearing and whistling by two white whales down to 30 atmospheres. *Journal of the Acoustical Society of America* **101**, 3136 (abstract).

Ridgway, S.H., Carder, D.A., Green, R.F. *et al.* (1980) Electromyographic and pressure events in the nasolaryngeal system of dolphins during sound production. In: *Animal Sonar Systems* (R.G. Busnel & J.F. Fish, eds), pp. 239–250. Plenum Publishing, New York.

Rogers, T., Cato, D.H. & Bryden, M.M. (1995) Underwater vocal repertoire of the leopard seal (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. In: *Sensory Systems of Aquatic Mammals* (R.A. Kastelein, J.A. Thomas & P.E. Nachtigall, eds), pp. 223–236. De Spil, Woerden, the Netherlands.

Rossing, T.D. (1990) *The Science of Sound*, 2nd edn. Addison-Wesley, Reading, MA.

Rubin, P. & Vatikiotis-Bateson, E. (1998) Measuring and modeling speech: production. In: *Animal Acoustic Communication: Sound Analysis and Research Methods* (S.L. Hopp, M.J. Owren & C.S. Evans, eds), pp. 251–290. Springer-Verlag, Berlin.

Samuels, A. & Gifford, T. (1997) A quantitative assessment of dominance relations among bottlenose dolphins. *Marine Mammal Science* **13**, 70–99.

Sandegren, F.E. (1976) Agonistic behavior in the male northern elephant seal. *Behaviour* **57**, 136–158.

Sanvito, S. & Galimberti, F. (2000a) Bioacoustics of southern elephant seals. I. Acoustic structure of male aggressive vocalizations. *Bioacoustics* **10**, 259–282.

Sanvito, S. & Galimberti, F. (2000b) Bioacoustics of southern elephant seals. II. Individual and geographic variation in male aggressive vocalizations. *Bioacoustics* **10**, 287–307.

Sayigh, L.S., Tyack, P.L., Wells, R.S. & Scott, M.D. (1990) Signature whistles of free-ranging bottlenose dolphins, *Tursiops truncatus*: stability and mother–offspring comparisons. *Behavioral Ecology and Sociobiology* **26**, 247–260.

Schevill, W.E. (1968) Sea lion echo ranging? *Journal of the Acoustical Society of America* **43**, 1458–1459.

Schevill, W.E. & Watkins, W.A. (1965) Underwater calls of *Leptonychotes* (Weddell seal). *Zoologica* **50**, 45–46.

Schevill, W.E., Watkins, W.A. & Ray, C. (1966) Analysis of underwater *Odobenus* calls with remarks on the development and function of the pharyngeal pouches. *Zoologica (New York)* **51**, 103–106.

Schleidt, W.M. (1973) Tonic communication: continual effects of discrete signs in animal communication systems. *Journal of Theoretical Biology* **42**, 359–386.

Schneider, R. (1962) Vergleichende Untersuchungen am Kehlkopf der Robben (Mammalia, Carnivora, Pinnipedia). *Jahrbuch Morphologisches* **103**, 177–262.

Schneider, R. (1963) Morphologische Anpassungserscheinungen am Kehlkopf einiger aquatiler Säugetiere. *Zeitschrift für Säugetierkunde* **28**, 257–267.

Schneider, R. (1964) Der Larynx der Säugetiere. *Handbuch der Zoologie* Band **8**, Lieferung **35**, 7(**5**), 1–128.

Schusterman, R.J. (1967) Perception and determinants of underwater vocalization in the California sea lion. In: *Animal Sonar Systems* (R.-G. Busnel, ed.), pp. 535–617, Laboratoire de Physiologie Acoustique, Jouy-en-Josas, France.

Schusterman, R.J. (1977) Temporal patterning in sea lion barking (*Zalophus californianus*). *Behavioral Biology* **20**, 404–408.

Scronce, B.L. & Ridgway, S.H. (1980) Grey seal, *Halichoerus*: echolocation not demonstrated. In: *Animal Sonar Systems* (R.-G. Busnel & J. Fish, eds), pp. 991–993, Plenum Press, London.

Shipley, C., Hines, M. & Buchwald, J.S. (1981) Individual differences in threat calls of northern elephant seal bulls. *Animal Behaviour* **29**, 12–19.

Shipley, C., Hines, M. & Buchwald, J.S. (1986) Vocalizations of northern elephant seal bulls: development of adult call characteristics during puberty. *Journal of Mammalogy* 67, 526–536.

Shipley, C., Carterette, E.C. & Buchwald, J.S. (1991) The effects of articulation on the acoustical structure of feline vocalizations. *Journal of the Acoustical Society of America* **89**, 902–909.

Shipley, C., Stewart, B.S. & Bass, J. (1992) Seismic communication in northern elephant seals. In: *Marine Mammal Sensory Systems* (J.A. Thomas, R.A. Kastelein & A.Y. Supin, eds), pp. 553–562. Plenum Press, New York.

Sleptsov, M.M. (1940) On adaptations of pinnipeds to swimming. *Zoologicheskii Zhurnal* **19**, 379–386 (in Russian).

Slijper, E.J. (1979) *Whales*, 2nd edn. Cornell University Press, Ithaca, NY.

Smith, W.J. (1977) *The Behavior of Communicating: an Ethological Approach*. Harvard University Press, Cambridge, MA.

Smith, W.J. (1986) Signaling behavior: contributions of different repertoires. In: *Dolphin Cognition and Behavior: a Comparative Approach* (R.J. Schusterman, J.A. Thomas & F.G. Wood, eds), pp. 315–330. Lawrence Erlbaum Associates, Hillsdale, NJ.

Smith, W.J. (1991a) Animal communication and the study of cognition. In: *Cognitive Ethology: the Minds of Other Animals* (C.A. Ristau, ed.), pp. 209–230. Lawrence Erlbaum Associates, Hillsdale, NJ.

Smith, W.J. (1991b) Singing is based on two markedly different kinds of signaling. *Journal of Theoretical Biology* **152**, 241–253.

Smith, W.J. (1996) Using interactive playback to study how songs and singing contribute to communication about behavior. In: *Ecology and Evolution of Acoustic Communication in Birds* (D.E. Kroodsma & E.H. Miller, eds), pp. 377–397. Comstock Publishing Associates, Ithaca, NY.

Smith, W.J. (1997) The behavior of communicating, after twenty years. In: *Perspectives in Ethology, Vol. 12: Communication* (D.H. Owings, M.D. Beecher & N.S. Thompson, eds), pp. 7–53. Plenum Press, New York.

Sneath, P.H.A. & Sokal, R.R. (1973) *Numerical Taxonomy: the Principles and Practice of Numerical Classification*. W.H. Freeman, San Francisco, CA.

Sokolov, A.S., Kosygin, G.M. & Shustov, A.P. (1970) Structure of lungs and trachea of Bering Sea pinnipeds. In: *Pinnipeds of the North Pacific* (English translation of *Vsesoyuznyi Nauchno-Issledovatel'skii Institut Morskogo Rybnogo Khozyaistva I Okeanografii (VINRO), Vol. 68 (1968)*) (V.A. Arsen'ev & K.I. Panin, eds), pp. 250–262. Israel Program for Scientific Translations, Jerusalem, Israel.

St Clair Hill, M., Ferguson, J.W.H., Bester, M.N. & Kerley, G.I.H. (2001) Preliminary comparison of calls of the hybridizing fur seals *Arctocephalus tropicalis* and *A. gazella*. *African Zoology* 36, 45–53.

Stirling, I. (1971) Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson) II. Adult females and pups. *Australian Journal of Zoology* **19**, 267–273.

Stirling, I. (1973) Vocalization in the ringed seal (*Phoca hispida*). *Journal of the Fisheries Research Board of Canada* **30**, 1592–1594.

Stirling, I. & Warneke, R.M. (1971) Implications of a comparison of the airborne vocalizations and some aspects of the behaviour of the two Australian fur seals, *Arctocephalus* spp., on the evolution and present taxonomy of the genus. *Australian Journal of Zoology* **19**, 227–241.

Stirling, I., Calvert, W. & Cleator, H. (1983) Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the high arctic. *Arctic* 36, 262–274.

Stirling, I., Calvert, W. & Spencer, C. (1987) Evidence of stereotyped underwater vocalizations of male Atlantic walruses (*Odobenus rosmarus rosmarus*). *Canadian Journal of Zoology* **65**, 2311–2321.

Stoddard, P.K. (1998) Application of filters in bioacoustics. In: *Animal Acoustic Communication: Sound Analysis and Research Methods* (S.L. Hopp, M.J. Owren & C.S. Evans, eds), pp. 105–127. Springer-Verlag, Berlin.

Taruski, A.G. (1979) The whistle repertoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. In: *Behavior of Marine Animals, Vol 3: Cetaceans* (H.E. Winn & B.L. Olla, eds), pp. 345–368. Plenum Press, New York.

Terhune, J.M. (1994) Geographical variation of harp seal underwater vocalizations. *Canadian Journal of Zoology* 72, 892–897.

Terhune, J.M. & Ronald, K. (1973) Some hooded seal (*Cystophora cristata*) sounds in March. *Canadian Journal of Zoology* **51**, 319–321.

Terhune, J.M. & Ronald, K. (1986) Distant and near-range functions of harp seal underwater calls. *Canadian Journal of Zoology* **64**, 1065–1070.

Terhune, J.M., MacGowan, G., Underhill, L. & Ronald, K. (1987) Repetitive rates of harp seal underwater vocalizations. *Canadian Journal of Zoology* **65**, 2119–2120.

Terhune, J.M., Burton, H. & Green, K. (1994a) Weddell seal in-air call sequences made with closed mouths. *Polar Biology* **14**, 117–122.

Terhune, J.M., Grandmaitre, N.C., Burton, H.R. & Green, K. (1994b) Weddell seals lengthen many underwater calls in response to conspecific vocalizations. *Bioacoustics* **5**, 223–226.

Thomas, J.A. & Golladay, C.L. (1995) Geographic variation in leopard seal (*Hydrurga leptonyx*) underwater vocalizations. In: *Sensory Systems of Aquatic Mammals* (R.A. Kastelein, J.A. Thomas & P.E. Nachtigall, eds), pp. 201–221. De Spil, Woerden, the Netherlands.

Thomas, J.A. & Kuechle, V.B. (1982) Quantitative analysis of Weddell seal (*Leptonychotes weddelli*) underwater vocalizations at McMurdo Sound, Antarctica. *Journal of the Acoustic Society of America* 72, 1730–1738.

Thomas, J.A. & Stirling, I. (1983) Geographic variation in the underwater vocalizations of Weddell seals (*Leptonychotes weddelli*) from Palmer Peninsula and McMurdo Sound, Antarctica. *Canadian Journal of Zoology* **61**, 2203–2212.

Thomas, J.A., Puddicombe, R.A., George, M. & Lewis, D. (1988) Variations in underwater vocalizations of Weddell seals (*Leptonychotes weddelli*) at the Vestfold Hills as a measure of breeding population discreteness. *Hydrobiologia* **165**, 279–284.

Thompson, P.O., Cummings, W.C. & Ha, S.J. (1986) Sounds, source levels, and associated behavior of humpback whales, southeast Alaska. *Journal of the Acoustic Society of America* **80**, 735–740.

Thompson, T.J., Winn, H.E. & Perkins, P.J. (1979) Mysticete sounds. In: *Behavior of Marine Animals, Vol. 3: Cetaceans* (H.E. Winn & B.L. Olla, eds.), pp. 403–431. Plenum Press, New York.

Trillmich, F. (1981) Mutual mother–pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. *Behaviour* **78**, 21–42.

Turl, C.W. & Penner, R.H. (1989) Differences in echolocation click patterns of the beluga *(Delphinapterus leucas)* and the bottlenosed dolphin (*Tursiops truncatus*). *Journal of the Acoustical Society of America* **86** (2), 497–502.

Tyack, P. (1986) Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? *Behavioral Ecology and Sociobiology* **18**, 251–257.

Tyack, P. (1991) Use of a telemetry device to identify which dolphin produces a sound. In: *Dolphin Societies: Discoveries and Puzzles* (K. Pryor & K.S. Norris, eds.), pp. 319–344. University of California Press, Berkeley, CA.

Tyack, P.L. (1997) Studying how cetaceans use sound to explore their environment. *Perspectives in Ethology, Vol. 12. Communication* (D.H. Owings, M.D. Beecher & N.S. Thompson, eds), pp. 251–297. Plenum Press, New York.

Tyack, P.L. (1999) *Functional Aspects of Cetacean Communication.* In: *Cetacean Societies: Field Studies of Whales and Dolphins* (J. Mann, R. Connor, P.L. Tyack & H. Whitehead, eds), pp. 270–307, University of Chicago Press, Chicago, IL.

Tyack, P.L. & Clark, C.W. (2000) Communication and acoustic behavior of dolphins and whales. In: *Hearing in Whales and Dolphins* (A.N. Popper, R.H. Fay & W.W.L. Au, eds), pp. 156–224. Springer-Verlag, New York.

Tyack, P.L. & Sayigh, L.S. (1997) Vocal learning in cetaceans. In: *Social Influences on Vocal Development* (C.T. Snowdon & M. Hausberger, eds), pp. 208–233. Cambridge University Press, Cambridge, UK.

Tyack, P.L. & Whitehead, H. (1983) Male competition in large groups of wintering humpback whales. *Behaviour* **83**, 132–154.

Urick, R.J. (1983) *Principles of Underwater Sound*, 3rd edn. McGraw-Hill, New York.

Verboom, W.C. & Kastelein, R.A. (1995) Rutting whistles of a male Pacific walrus (*Odobenus rosmarus divergens*). In: *Sensory Systems of Aquatic Mammals* (R.A. Kastelein, J.A. Thomas & P.E. Nachtigall, eds), pp. 287–298. De Spil, Woerden, the Netherlands.

Wartzok, D., Schusterman, R.J. & Gailey-Phipps, J. (1984) Seal echolocation? *Nature* **308**, 753.

Watkins, W.A. (1967a) Air-borne sounds of the humpback whale, *Megaptera novaeangliae*. *Journal of Mammalogy* **48**, 573–578.

Watkins, W.A. (1967b) The harmonic interval: fact or artifact in spectral analysis of pulse trains. In: *Marine Bio-Acoustics* (W.N. Tavolga, ed.), Vol. 2, pp. 15–42. Pergamon Press, London.

Watkins, W.A. (1980) Acoustics and the behavior of sperm whales. In: *Animal Sonar Systems* (R.-G. Busnel & J.F. Fish, eds), pp. 283–290. Plenum Press, New York.

Watkins, W.A. (1981) Activities and underwater sounds of fin whales. *Scientific Reports of the Whales Research Institute* **33**, 83–117.

Watkins, W.A. & Schevill, W.E. (1976) Right whale feeding and baleen rattle. *Journal of Mammalogy* 57, 58–66.

Watkins, W.A. & Schevill, W.E. (1979) Distinctive characteristics of underwater calls of the harp seal, *Phoca groenlandica*, during the breeding season. *Journal of the Acoustical Society of America* **66**, 983–988.

Watkins, W.A. & Wartzok, D. (1985) Sensory biophysics of marine mammals. *Marine Mammal Science* **1**, 219–260.

Watkins, W.A., Tyack, P., Moore, K.E. & Bird, J.E. (1987) The 20-Hz signals of finback whales (*Balaenoptera physalus*). *Journal of the Acoustical Society of America* **82**, 1901–1912.

Watkins, W.A., Daher, M.A., Fristrup, K.M., Howald, T.J. & di Sciara, G.N. (1993) Sperm whales tagged with transponders and tracked underwater by sonar. *Marine Mammal Science* 9, 55–67.

Weilgart, L. & Whitehead, H. (1988) Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology* 66, 1931–1937.

Weilgart, L.S. & Whitehead, H. (1990) Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behavioral Ecology and Sociobiology* **26**, 399–402.

Wemmer, C., Von Ebers, M. & Scow, K. (1976) An analysis of the chuffing vocalization in the polar bear (*Ursus maritimus*). *Journal of Zoology, London* **180**, 425–439.

Whitehead, H. & Weilgart, L. (1990) Click rates from sperm whales. *Journal of the Acoustical Society of America* **87**, 1798–1806.

Whitehead, H. & Weilgart, L. (1991) Patterns of visually observable behavior and vocalizations in groups of female sperm whales. *Behaviour* **118**, 275–296.

Wilden, I., Herzel, H., Peters, G. & Tembrock, G. (1998) Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics* **9**, 171–196.

Wilson, E.O. (1975) *Sociobiology*. Harvard University Press, Cambridge, MA.

Winn, H.E. & Schneider, J. (1977) Communication in sireniens [*sic*], sea otters, and pinnipeds. In: *How Animals Communicate* (T.A. Sebeok, ed.), pp. 809–840. Indiana University Press, Bloomington, IN.

Würsig, B. (1986) Delphinid foraging strategies. In: *Dolphin Cognition and Behavior: a Comparative Approach* (R.J. Schusterman, J.A. Thomas & F.G. Wood, eds), pp. 347–359. Lawrence Erlbaum Associates, Hillsdale, NJ.