

---

## Culture and traditions in vocal communication of cetaceans: a review (Cetartiodactyla: Cetacea)

---

Adéla ZVĚŘINOVÁ, Olga ŠIMKOVÁ & Eva LANDOVÁ

Department of Zoology, Faculty of Science, Charles University, Viničná 7,  
CZ–128 44 Praha 2, Czech Republic

received on 21 January 2022

**Abstract.** Vocal communication is the main mean of communication for cetaceans and some species developed vocal culture and traditions. They are maintained through both production and contextual learning, used to acquire two types of sounds: signature calls and songs. Signature calls are present only in species living in stable groups or fission-fusion society. They are used as an identification tool to maintain cohesion and contact with conspecifics. Songs are present in most baleen whales, but only humpback and bowhead whales change within and between seasons. They use vocal learning to conform to one type used by all individuals. Vocal learning is also employed during vocal development in ontogenesis, together with maturation. The existence of social groups in other species together with the lack of research suggest that traditions are more widespread among cetaceans than is currently known.

**Key words.** Whales and dolphins, vocal communication, vocal learning, cultural transmission, vocal traditions, signature calls.

### INTRODUCTION

Defining culture is not a straightforward task since many definitions can be found in literature, and scientists tend to differ in their preference for them. However, it is generally accepted that culture includes transmission of one or more behavioural aspects among individuals, resulting in a group sharing such trait. Traditions, i.e., accumulative culture, are those behaviours (that one individual could not invent by itself) shared from generation to generation (BOYD & RICHERSON 1996). Cetaceans are one of the few taxa with documented traditions.

Transmission of behaviours that form a culture or a tradition is enabled through social learning and observation (BOYD & RICHERSON 1996). There are three types, based on the individuals included: vertical, horizontal, oblique. Vertical transmission takes place between a parent and offspring, horizontal among age peers and oblique between an individual and a member of the older generation that is not a parent (CAVALLI SFORZA & FELDMAN 1981). In cetaceans, these transmissions are known from various behavioural aspects (such as feeding strategies), including vocalisations (RENDELL & WHITEHEAD 2001).

In vocal communication, apart from learning when to produce a signal, some species also learn how to produce it. These two main types of vocal learning are labelled contextual and production, consecutively. Production learning is the modification of sounds based on experience with conspecifics, resulting in (dis)similar sounds to the model. Contextual learning means

---

doi: 10.37520/lynx.2023.015

using sounds in new contexts based on experience (JANIK & SLATER 1997). In short, during production learning, the sound itself is modified, whereas in contextual it is not.

Vocal traditions of cetaceans are established through both types (JANIK & SLATER 1997). Depending on the type of vocal signal, they are used to either acquire a signal or conform to one common version of it.

## CULTURES IN THE CETACEAN WORLD

### Song of baleen whales

The song of the humpback whale (*Megaptera novaeangliae*) is a classic example of horizontal cultural transmission (Fig. 1). It is a highly rhythmic, complex, fixed sequence of various sounds of both low and high frequency (WINN & WINN 1978). It is hierarchically structured: from subunits to units, making up phrases that are part of themes (PAYNE & MCVAY 1971, WINN & WINN 1978). The song is characteristic by its ever-changing nature that is maintained through vocal learning (PAYNE & PAYNE 1985, ERIKSEN et al. 2005). Segmentation (i.e. replacing one theme with a new, similar-sounding one) is used to bring new parts into the repertoire resulting in the creation of temporary hybrid songs before establishing a completely new one (GARLAND et al. 2017).

The changes can be labelled as cultural evolution and revolution (NOAD et al. 2000). Cultural evolution is the constant change within and between years in a population song (PAYNE & PAYNE 1985). At the start of a new season, it resembles the old song, before alteration or replacement of some parts takes place (PAYNE & PAYNE 1985, ERIKSEN et al. 2005). In the end, the song is different from those of previous seasons, though some units may prevail in upcoming years (PAYNE & PAYNE 1985). The longer the seasons are apart from each other, the more different the songs are (ERIKSEN et al. 2005) and old song types or themes are never brought back (PAYNE & PAYNE 1985, ERIKSEN et al. 2005).

Despite the constant changes, little variety (except the song duration and precise configuration of units) is seen among individuals of one population in one year. All males in one population culturally conform to singing the same song at any given time (PAYNE & MCVAY 1971, WINN & WINN 1978, PAYNE & PAYNE 1985). It is also important to note that although it changes

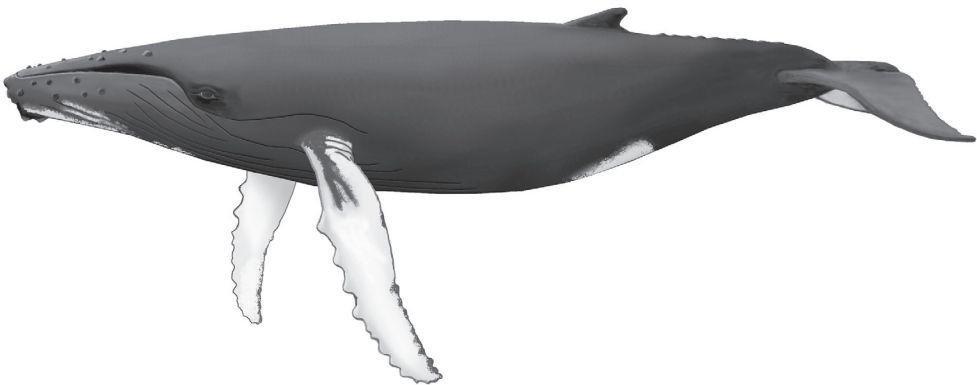


Fig. 1. Humpback whale (*Megaptera novaeangliae*). Original by O. ŠIMKOVÁ.

frequently, it does so only within a fixed framework of the sequence of themes and temporal characteristics (PAYNE & McVAY 1971, PAYNE & PAYNE 1985).

Revolution describes a situation when a certain song type is completely replaced by another one in a short time. The new type comes from a different population and can be present with the old and intermediate type, before completely taking over (NOAD et al. 2000). Transmission of song types across populations can be explained by movement of a couple of individuals to different areas (NOAD et al. 2000), singing on shared feeding grounds (GARLAND et al. 2013) or migration route (OWEN et al. 2019). One example of a vast horizontal cultural transmission was described in the southern Pacific, where one song type transferred from the east-Australian population to others in the eastern direction. The song appeared in the consecutive areas 1–2 years apart (GARLAND et al. 2011). The question of why it is changing remains to be answered.

The song of the bowhead whale (*Balaena mysticetus*) is much akin to the humpback's one: the structure (i.e., the number of phrases and their structure, length of the song) changes every year (suggested by CUMMINGS & HOLLIDAY 1987, confirmed by DELARUE et al. 2009) and the components are either completely new or similar to those of the previous years. All whales also sing an identical version of the song, showing no variation in any characteristics (DELARUE et al. 2009, TERVO et al. 2011). Apart from changing between years, the song also changes within a season, evolving from a primitive version to a complex one (DELARUE et al. 2009), therefore more than one type of song can be present in one season (STAFFORD et al. 2008, TERVO et al. 2009, 2011). All this indicates horizontal cultural transmission occurring in bowhead whales (DELARUE et al. 2009).

## Vocal clans of sperm whales

Sperm whales (*Physeter macrocephalus*) live in social units that form a vocal clan based on their similar coda repertoire (Fig. 2). Codas are short sequences of clicks, usually about 1 second long (WATKINS & SCHEVILL 1977, WATKINS 1980) and appear in clusters, often in the form of exchange between more whales (WATKINS & SCHEVILL 1977, MOORE et al. 1993, WEILGART & WHITEHEAD 1993). There are many different stereotyped types of codas, differing in their pattern, i.e., the number of clicks and intervals between them (WATKINS & SCHEVILL 1977, WATKINS 1980, MOORE et al. 1993, WEILGART & WHITEHEAD 1993). They are produced mainly by females and young whales in social units (MARCoux et al. 2006) during resting and socialising periods (WHITEHEAD & WEILGART 1991, RENDELL & WHITEHEAD 2003) and when meeting other groups (WATKINS & SCHEVILL 1977, WATKINS 1980).

The repertoire is maintained on a clan level, forming dialects within a population (RENDELL & WHITEHEAD 2003). No clans share a repertoire, even though one type of coda, the 5R coda, has been found in more clans (WEILGART & WHITEHEAD 1993, GERO et al. 2016b, OLIVEIRA et al. 2016). However, it seems to contain individual identity, as it shows high individual variability (GERO et al. 2016b), especially in the inter-click intervals and inter-pulse intervals (OLIVEIRA et al. 2016). Also, it often initiates an exchange (WEILGART & WHITEHEAD 1993) and belongs to the most common coda types (GERO et al. 2016a, OLIVEIRA et al. 2016).

Units within a clan can differ in their repertoires. However, there is only little distinction between them, and they have at least two shared types covering more than 10% (GERO et al. 2016b). For example, 1+1+3 coda was found in all units of only one vocal clan near the Dominica Island, as one of the most common types (GERO et al. 2016a). It is stereotyped across all units, even in calf repertoires, therefore likely used as a clan identification coda (GERO et al.

2016b). Individuals in a unit also differ in the usage proportions of coda types and may produce some distinctively (GERO et al. 2016b) but all types are shared and the most common compose over 75% of the unit repertoire (RENDELL & WHITEHEAD 2004). Overall, there is a tendency for convergence both at unit and clan level, being one of the biggest reasons for homogenised repertoire (KONRAD et al. 2018).

The repertoire dialects are stable for years (WEILGART & WHITEHEAD 1997, GERO et al. 2016b), conserved in matrilineal units, even after splitting (WEILGART & WHITEHEAD 1997, WHITEHEAD et al. 1998). They are culturally transmitted through social learning, resulting in variations and dialects (RENDELL & WHITEHEAD 2003, 2004, AMORIM et al. 2020). The repertoire is learned by young whales from their mothers and other older members of the unit (WEILGART & WHITEHEAD 1997, RENDELL et al. 2012, KONRAD et al. 2018). The codas of calves and juveniles are generally less stereotyped and stable than those of adults (WATKINS et al. 1988). They also produce more coda types and some shared types more frequently (GERO et al. 2016b). The younger the calf, the more variable click sequences it produces, which only increase in stability,

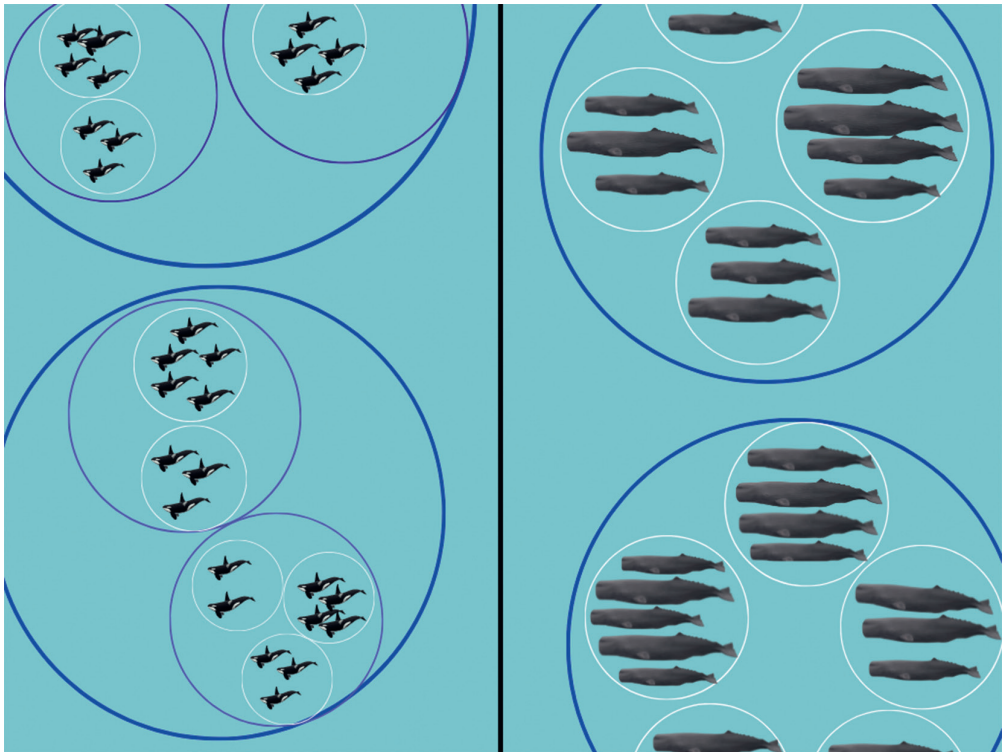


Fig. 2. Comparison of social structure of killer and sperm whales. Based on information from BIGG et al. (1990), FORD (1991) and RENDELL & WHITEHEAD (1993). Circles represent different social groups: white maternal units, purple pods, and blue vocal clans. Sizes and numbers of both individuals and groups are only illustrative. Original by A. ZVĚŘINOVÁ.

stereotypy, and complexity with age (WATKINS et al. 1988), gradually crystallising into their natal unit repertoire (GERO et al. 2016b).

Horizontal transmission has been suggested to occur between units within a clan (KONRAD et al. 2018), but also between clans, when females switch, although it happens very rarely (RENDELL et al. 2012).

The presence of dialects can be explained neither by environmental conditions nor genetics. Firstly, some vocal clans are sympatric, inhabiting the same area, and they all have a distinct repertoire (RENDELL & WHITEHEAD 2003, AMORIM et al. 2020). Secondly, intra-clan mtDNA haplotype sharing does not occur more often than inter-clan, and haplotypes are shared among clans (RENDELL & WHITEHEAD 2003, RENDELL et al. 2012). It is true, however, that maternally related units, meaning with common dominant mtDNA haplotypes, have more similar coda repertoires. This is easily explained by the parallelism of learning and inheriting genetics from the mother (WHITEHEAD et al. 1998).

### Killer whale pulsed calls dialects

Pod-specific pulsed calls of killer whales or orcas (*Orcinus orca*) are also culturally transmitted. It is known that orcas are vocal production learners, capable of imitation and copying various sounds (FOOTE et al. 2006), even out of their usual repertoire (ABRAMSON et al. 2018). In one cross-fostering experiment with bottlenose dolphin and orca, the orca produced significantly more whistles and clicks (typical of bottlenose dolphin) than wild orcas normally do (MUSSEY et al. 2014). In another experiment, juvenile males produced calls of an adult male after he was introduced into the pool (CRANCE et al. 2014). Therefore, it is not surprising that orcas learn their pod-specific pulsed calls repertoire (FORD 1989, MILLER & BAIN 2000, FOOTE et al. 2006, FILATOVA & MILLER 2015).

They are learned by calves mainly from their mothers (FORD & FISHER 1983, FORD 1991, DEECKE et al. 2010) but also from other maternal relatives, members of a matriline (YURK et al. 2002). After birth, the production of family-specific calls increases significantly for about 14 days, enhancing the calf's recognition of those calls and thus maintaining spatial proximity with matriline members (WEISS et al. 2006).

The social system of orcas starts with a maternal unit (MU) – a family of mother and her offspring up to four generations. Related MUs form a pod, and pods belong to a vocal clan (BIGG et al. 1990), distinct in its repertoire. Vocal clans are likely to have a common maternal ancestor (FORD 1991, YURK et al. 2002); and form dialects within a community (Fig. 2).

Dialects within a clan develop due to differences in repertoire between MUs accumulated over time (MILLER & BAIN 2000): when a pod/MU splits, the repertoire starts to diverge, evolving independently. The mechanisms that lead to the unique repertoires include innovation, cultural drift, and vertical and selection learning (FORD 1991, YURK et al. 2002).

In contrast to the sperm whale, orcas' MUs/pods with the most similar repertoire are the most recently split (FORD 1991), or closely related, as repertoire similarity correlates with relatedness (YURK et al. 2002, DEECKE et al. 2010). The more closely related MUs are, the more similar their repertoire is, even if they do not preferentially associate with each other. That means orcas use selection learning, choosing who to learn call types from (DEECKE et al. 2010). Even though rarely, imitation of calls from other clans occurs (FORD 1991, WEISS et al. 2011), but they are never transferred into the repertoire (FORD 1991), further proving selection learning, as even though orcas copy sounds from more whales, they only learn and sustain the ones from family.

Horizontal transmission seems to be also present in orca societies. Firstly, parallel changes in one vocal type were found between two matriline, in a form of vocal matching, which implies learning between matriline within a pod (DEECKE et al. 2000). Secondly, community-specific stereotyped whistle types are learned throughout the life of adult whales when an association between clans occurs, possibly functioning as a community-level recognition signal (RIESCH et al. 2006).

The complex repertoires of killer whales likely exist due to their social structure (FORD 1991), increasing the efficiency of intra-pod communication and maintaining its cohesion (FORD 1989).

### Bottlenose dolphin signature whistles

The bottlenose dolphins (*Tursiops truncatus*) (Fig. 3) use both production and contextual learning to acquire their individually specific signature whistles (JANIK 2013). Signature whistles are individual-specific, stereotyped whistles, distinct with their contour, first described by CALDWELL & CALDWELL (1965). They remain stable over years (CALDWELL et al. 1989, DOS SANTOS et al. 2005), even though some parameters, such as intensity, duration, and repetition, change slightly depending on stress or excitement levels (CALDWELL et al. 1989, ESCH et al. 2009). The development of a signature whistle takes 1–2 years. Once it is learned, it remains stable for long years (ESCH et al. 2009).

Calves mimic and incorporate sounds from their natal environment and surroundings into their repertoire (FRIPP et al. 2005), as they learn from both related and unrelated conspecifics within their community (MCCOWAN & REISS 1995, FRIPP et al. 2005). On average, there are six adult models with similar whistles, although it is unknown if calves learn from all or only some



Fig. 3. Bottlenose dolphin (*Tursiops truncatus*). Photo by O. ŠIMKOVÁ.



of them (FRIPP et al. 2005). Association and whistle copying were not found to be correlated (MCCOWAN & REISS 1995), though FRIPP et al. (2005) noted that the six models were dolphins who spend the least amount of time with the studied calves.

Males seem to have similar whistles to their mothers more often than females do, which can be explained by the different life histories of the sexes. Males disperse, while females stay close to their matriline, which puts forward a need for a distinct type (SAYIGH et al. 1990, 1995). Calves are also able to learn sounds from other species, such as humans: captive dolphin calve whistles are much flatter and of lower frequency than their wild counterparts, reminiscent of trainers' whistle sounds (MIKSIS et al. 2002).

Learning continues throughout dolphin life in adulthood, as they mimic other signature whistles (TYACK 1986, KING et al. 2013) to address the individual (KING & JANIK 2013), developing an association between a specific whistle and a dolphin (CALDWELL et al. 1989, KING & JANIK 2013). Copies of such whistles are similar in contour to the original, however differ in frequency parameters. It was suggested the sound is altered at will, as a form of identification of the copying dolphin (KING et al. 2013). Signature whistle matching occurs mainly between closely associated animals (KING et al. 2013).

Another example is the convergence of whistles in a male alliance reported by SMOLKER & PEPPER (1999). They noted that the three males gradually altered their repertoire, losing individual whistles and replacing them with a shared contour. Over time, they were indistinguishable from each other. However, KING et al. (2018) found distinctive signature whistles in male alliances, noting they play a central role in such a group formation.

### Other possibilities of vocal learning

Apart from the species mentioned above, which also happen to be the most studied ones, vocal learning has been hinted in other cetacean species. In one cross-fostering experiment, Risso's dolphin (*Grampus griseus*) produced whistles very alike those of the bottlenose dolphins, which were rarely found in wild conspecifics. It shows that they use models to learn from during whistle development (FAVARO et al. 2016).

Belugas (*Delphinapterus leucas*) are capable of imitating and copying sounds they hear (Fig. 4). They do so spontaneously, and can even mimic unnatural, computer-made sounds they have never encountered before (MURAYAMA et al. 2014). The studies by VERGARA & BARRETT-LENNARD (2008) and MISHIMA et al. (2015) both suggested a presence of a signature call. Though the calls were different in each study, both were found to be gradually learned by calves, until they reached a stereotypy and the call no longer changed.

Other studies show that signature sounds may also be present in other species (CALDWELL & CALDWELL 1968, HERZING 1996, SHAPIRO 2006, MARCOUX et al. 2012): narwhal (*Monodon monoceros*), Atlantic spotted dolphin (*Stenella frontalis*), and common dolphin (*Delphinus delphis*). Also, researchers who have had the opportunity to study calf vocal development all found the calf sounds to be different from the adult ones (CALDWELL et al. 1989, EDDS et al. 1993, ZOIDIS et al. 2008, PARKS et al. 2011, FIGUEIREDO & SIMÃO 2014, DOMBROSKI et al. 2016). Maturation is one of the main factors driving the development, due to physiological advancements as well as different behavioural needs and motivations (ROOT-GUTTERIDGE et al. 2018, INDECK et al. 2020), though there are likely more mechanisms contributing to it (EDDS et al. 1993, FIGUEIREDO & SIMÃO 2014). Some noted that vocal learning is one of them (MCCOWAN & REISS 1995, VERGARA & BARRETT-LENNARD 2008). Unfortunately, right now, due to the lack

of studies, it is impossible to say how big of a portion of the cetacean repertoire is learned and what part is determined genetically.

## CONCLUSIONS

Based on a review of the available literature, it is apparent that cetacean species that use vocal learning produce one of two signal types: signature calls or songs. Signature calls are learned through vertical and oblique transmission, especially during the early vocal development and when learning to recognise the calls of other individuals in a community. They are either individual-specific in species with fission-fusion society, such as dolphins, or group-specific in species living in stable groups, such as maternal units of orcas and sperm whales and adult male alliances of bottlenose dolphins (SMOLKER & PEPPER 1999). Since signature calls were suggested to be present in more species, and vocal learning is essential for their acquisition, it is quite likely the incidence is higher.

Humpback and bowhead whales use vocal learning through horizontal transmission to conform to one type of song. Although songs are found in more baleen whale repertoires, which raises the question of vocal learning being present in other singing species, only the humpback whale and bowhead whale songs are complex and constantly changing. Also, they form big aggregations during the breeding season (when the song is mostly heard). If any of these factors influence the need for vocal learning is speculative.

Working with the available data, a possible conclusion would be that vocal learning is present only in species with signature calls or complex songs. However, the fact that in all four *most studied* species of cetaceans (that is sperm whale, killer whale, humpback whale, and bottlenose dolphin) vocal learning functions in acquiring a repertoire, arises a question if more species use it.

On top of that, signature calls were hinted in more cetacean species, meaning they are very likely to use vocal learning to form their repertoire. Even though there is currently no empirical evidence to support this statement, it is important to note there is a serious lack of research focusing on vocal learning (and behavioural context of vocalisation in general), in cetaceans. Evidence was mostly found only in bottlenose dolphin, as it is commonly held captive, where experiments are relatively easily conducted. The other studies were predominantly observational. Therefore, the possibility of a higher incidence of vocal learning in cetaceans cannot be ruled out with certainty.



Fig. 4. Beluga (*Delphinapterus leucas*). Original by O. ŠIMKOVÁ.



## REFERENCES

- ABRAMSON J. Z., HERNÁNDEZ-LLOREDA M. V., GARCÍA L., COLMENARES F., ABOITIZ F. & CALL J., 2018: Imitation of novel conspecific and human speech sounds in the killer whale (*Orcinus orca*). *Proceedings of the Royal Society B: Biological Sciences*, **285**(20172171): 1–10.
- AMORIM T. O. S., RENDELL L., DI TULLIO J., SECCHI E. R., CASTRO F. R. & ANDRIOLO A., 2020: Coda repertoire and vocal clans of sperm whales in the western Atlantic Ocean. *Deep-Sea Research Part I: Oceanographic Research Papers*, **160**(103254): 1–8.
- BIGG M. A., OLESIUK P. F., ELLIS G. M., FORD J. K. B. & BALCOMB K. C., 1990: Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission*, **12**: 383–405.
- BOYD R. & RICHERSON P. J., 1996: Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, **88**: 77–93.
- CALDWELL M. C. & CALDWELL D. K., 1965: Individualized whistle contours in bottle-nosed dolphins (*Tursiops truncatus*). *Nature*, **207**: 434–435.
- CALDWELL M. C. & CALDWELL D. K., 1968: Vocalization of naive captive dolphins in small groups. *Science*, **159**: 1121–1123.
- CALDWELL M. C., CALDWELL D. K. & TYACK P., 1989: Review of the Signature-Whistle Hypothesis for the Atlantic bottlenose dolphin. Pp. 199–234. In: LEATHERWOOD S. & REEVES R. R. (eds.): *The Bottlenose Dolphin*. Academic Press, Cambridge, 653 pp.
- CAVALLI-SFORZA L. L. & FELDMAN M. W., 1981: *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton University Press, Princeton, 388 pp.
- CRANCE J. L., BOWLES A. E. & GARVER A., 2014: Evidence for vocal learning in juvenile male killer whales, *Orcinus orca*, from an adventitious cross-socializing experiment. *Journal of Experimental Biology*, **217**: 1229–1237.
- CUMMINGS W. C. & HOLLIDAY D. V., 1987: Sounds and source levels from bowhead whales off Pt. Barrow, Alaska. *Journal of the Acoustical Society of America*, **82**: 814–821.
- DEECKE V. B., FORD J. K. B. & SPONG P., 2000: Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *Animal Behaviour*, **60**: 629–638.
- DEECKE V. B., BARRETT-LENNARD L. G., SPONG P. & FORD J. K. B., 2010: The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*). *Naturwissenschaften*, **97**: 513–518.
- DELARUE J., LAURINOLLI M. & MARTIN B., 2009: Bowhead whale (*Balaena mysticetus*) songs in the Chukchi Sea between October 2007 and May 2008. *Journal of the Acoustical Society of America*, **126**: 3319–3328.
- DOMBROSKI J. R. G., PARKS S. E., GROCH K. R., FLORES P. A. C. & SOUSA-LIMA R. S., 2016: Vocalizations produced by southern right whale (*Eubalaena australis*) mother-calf pairs in a calving ground off Brazil. *Journal of the Acoustical Society of America*, **140**: 1850–1857.
- DOS SANTOS M. E., LOURO S., COUCHINHO M. & BRITO C., 2005: Whistles of bottlenose dolphins (*Tursiops truncatus*) in the Sado Estuary, Portugal: Characteristics, production rates, and long-term contour stability. *Aquatic Mammals*, **31**: 453–462.
- EDDS P. L., ODELL D. K. & TERSHY B. R., 1993: Vocalisations of a captive juvenile and free-ranging adult-calf pairs of Bryde's whales, *Balaenoptera edeni*. *Marine Mammal Science*, **9**: 269–284.
- ERIKSEN N., MILLER L. A., TOUGAARD J. & HELWEG D. A., 2005: Cultural change in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. *Behaviour*, **142**: 305–328.
- ESCH H. C., SAYIGH L. S., BLUM J. E. & WELLS R. S., 2009: Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *Journal of Mammalogy*, **90**: 638–650.
- FAVARO L., NEVES S., FURLATI S., PESSANI D., MARTIN V. & JANIK V. M., 2016: Evidence suggests vocal production learning in a cross-fostered Risso's dolphin (*Grampus griseus*). *Animal Cognition*, **19**: 847–853.
- FIGUEIREDO L. D. & SIMÃO S. M., 2014: Bryde's whale (*Balaenoptera edeni*) vocalizations from southeast Brazil. *Aquatic Mammals*, **40**: 225–231.

- FILATOVA O. A. & MILLER P. J. O., 2015: An agent-based model of dialect evolution in killer whales. *Journal of Theoretical Biology*, **373**: 82–91.
- FOOTE A. D., GRIFFIN R. M., HOWITT D., LARSSON L., MILLER P. J. O. & HOELZEL A. R., 2006: Killer whales are capable of vocal learning. *Biology Letters*, **2**: 509–512.
- FORD J. K. B., 1989: Acoustic behaviour 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.
- FORD J. K. B. & FISHER H. D., 1983: Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia. Pp. 129–161. In: PAYNE R. (ed.): *Communication and Behavior of Whales*. Westview Press, Boulder, xii+643 pp.
- FRIPP D., OWEN C., QUINTANA-RIZZO E., SHAPIRO A., BUCKSTAFF K., JANKOWSKI K., WELLS R. & TYACK P., 2005: Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition*, **8**: 17–26.
- GARLAND E. C., GOLDIZEN A. W., REKDAHL M. L., CONSTANTINE R., GARRIGUE C., HAUSER N. D., POOLE M. M., ROBBINS J. & NOAD M. J., 2011: Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology*, **21**: 687–691.
- GARLAND E. C., GEDAMKE J., REKDAHL M. L., NOAD M. J., GARRIGUE C. & GALES N., 2013: Humpback whale song on the Southern Ocean feeding grounds: Implications for cultural transmission. *Public Library of Science One*, **8**(11; e79422): 1–9.
- GARLAND E. C., RENDELL L., LAMONI L., POOLE M. M. & NOAD M. J., 2017: Song hybridization events during revolutionary song change provide insights into cultural transmission in humpback whales. *Proceedings of the National Academy of Sciences of the United States of America*, **114**: 7822–7829.
- GERO S., BÖTTCHER A., WHITEHEAD H. & MADSEN P. T., 2016a: Socially segregated, sympatric sperm whale clans in the Atlantic Ocean. *Royal Society Open Science*, **3**(160061): 1–10.
- GERO S., WHITEHEAD H. & RENDELL L., 2016b: Individual, unit and vocal clan level identity cues in sperm whale codas. *Royal Society Open Science*, **3**(150372): 1–12.
- HERZING D., 1996: Vocalizations and associated underwater behaviour of free-ranging Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals*, **22**: 61–79.
- INDECK K. L., GIROLA E., TORTEROTOT M., NOAD M. J. & DUNLOP R. A., 2020: Adult female-calf acoustic communication signals in migrating east Australian humpback whales. *Bioacoustics*, **30**: 341–365.
- JANIK V. M., 2013: Cognitive skills in bottlenose dolphin communication. *Trends in Cognitive Sciences*, **17**: 157–159.
- JANIK V. M. & SLATER P. J. B., 1997: Vocal learning in mammals. *Advances in the Study of Behavior*, **26**: 59–99.
- KING S. L. & JANIK V. M., 2013: Bottlenose dolphins can use learned vocal labels to address each other. *Proceedings of the National Academy of Sciences of the United States of America*, **110**: 13216–13221.
- KING S. L., SAYIGH L. S., WELLS R. S., FELLNER W. & JANIK V. M., 2013: Vocal copying of individually distinctive signature whistles in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, **280**: 1–9.
- KING S. L., FRIEDMAN W. R., ALLEN S. J., GERBER L., JENSEN F. H., WITTEWIT S., CONNOR R. C. & KRÜTZEN M., 2018: Bottlenose dolphins retain individual vocal labels in multi-level alliances. *Current Biology*, **28**: 1993–1999.
- KONRAD C. M., FRASIER T. R., RENDELL L., WHITEHEAD H. & GERO S., 2018: Kinship and association do not explain vocal repertoire variation among individual sperm whales or social units. *Animal Behaviour*, **145**: 131–140.
- MARCOUX M., WHITEHEAD H. & RENDELL L., 2006: Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology*, **84**: 609–614.
- MARCOUX M., AUGER-MÉTHÉ M. & HUMPHRIES M. M., 2012: Variability and context specificity of narwhal (*Monodon monoceros*) whistles and pulsed calls. *Marine Mammal Science*, **28**: 649–665.

- McCOWAN B. & REISS D., 1995: Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): Role of learning. *Journal of Comparative Psychology*, **109**: 242–260.
- MIKSIK J. L., TYACK P. L. & BUCK J. R., 2002: Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. *Journal of the Acoustical Society of America*, **112**: 728–739.
- MILLER P. J. O. & BAIN D. E., 2000: Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, **60**: 617–628.
- MISHIMA Y., MORISAKA T., ITOH M., MATSUO I., SAKAGUCHI A. & MIYAMOTO Y., 2015: Individuality embedded in the isolation calls of captive beluga whales (*Delphinapterus leucas*). *Zoological Letters*, **1**(27): 1–13.
- MOORE K. E., WATKINS W. A. & TYACK P. L., 1993: Pattern similarity in shared codas from sperm whales (*Physeter catodon*). *Marine Mammal Science*, **9**: 1–9.
- MURAYAMA T., IJIMA S., KATSUMATA H. & ARAI K., 2014: Vocal imitation of human speech, synthetic sounds and beluga sounds, by a beluga (*Delphinapterus leucas*). *International Journal of Comparative Psychology*, **27**: 369–384.
- MUSSER W. B., BOWLES A. E., GREBNER D. M. & CRANCE J. L., 2014: Differences in acoustic features of vocalizations produced by killer whales cross-socialized with bottlenose dolphins. *Journal of the Acoustical Society of America*, **136**: 1990–2002.
- NOAD M. J., CATO D. H., BRYDEN M. M., JENNER M.-N. & JENNER K. C. S., 2000: Cultural revolution in whale songs. *Nature*, **408**: 537–537.
- OLIVEIRA C., WAHLBERG M., SILVA M. A., JOHNSON M., ANTUNES R., WISNIEWSKA D. M., FAIS A., GONÇALVES J. & MADSEN P. T., 2016: Sperm whale codas may encode individuality as well as clan identity. *Journal of the Acoustical Society of America*, **139**: 2860–2869.
- OWEN C., RENDELL L., CONSTANTINE R., NOAD M. J., ALLEN J., ANDREWS O., GARRIGUE C., POOLE M. M., DONNELLY D., HAUSER N. & GARLAND E. C., 2019: Migratory convergence facilitates cultural transmission of humpback whale song. *Royal Society Open Science*, **6**(190337): 1–15.
- PARKS S. E., SEARBY A., CÉLÉRIER A., JOHNSON M. P., NOWACEK D. P. & TYACK P. L., 2011: Sound production behavior of individual North Atlantic right whales: Implications for passive acoustic monitoring. *Endangered Species Research*, **15**: 63–76.
- PAYNE R. S. & McVAY S., 1971: Songs of humpback whales. *Science*, **173**: 585–597.
- PAYNE R. & PAYNE K., 1985: Large scale changes over 19 years in songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie*, **68**: 89–114.
- RENDELL L. & WHITEHEAD H., 2001: Culture in whales. *Behavioral and Brain Sciences*, **24**: 309–382.
- RENDELL L. E. & WHITEHEAD H., 2003: Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society B: Biological Sciences*, **270**: 225–231.
- RENDELL L. & WHITEHEAD H., 2004: Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurement. *Animal Behaviour*, **67**: 865–874.
- RENDELL L., MESNICK S. L., DALEBOUT M. L., BURTENSHAW J. & WHITEHEAD H., 2012: Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? *Behavior Genetics*, **42**: 332–343.
- RIESCH R., FORD J. K. B. & THOMSEN F., 2006: Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia. *Animal Behaviour*, **71**: 79–91.
- ROOT-GUTTERIDGE H., CUSANO D. A., SHIU Y., NOWACEK D. P., VAN PARIJS S. M. & PARKS S. E., 2018: A lifetime of changing calls: North Atlantic right whales, *Eubalaena glacialis*, refine call production as they age. *Animal Behaviour*, **137**: 21–34.
- 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.
- SAYIGH L. S., TYACK P. L., WELLS R. S., SCOTT M. D. & IRVINE A. B., 1995: Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, **36**: 171–177.

- SHAPIRO A. D., 2006: Preliminary evidence for signature vocalizations among free-ranging narwhals (*Monodon monoceros*). *Journal of the Acoustical Society of America*, **120**: 1695–1705.
- SMOLKER R. & PEPPER J. W., 1999: Whistle convergence among allied male bottlenose dolphins (*Delphinidae*, *Tursiops* sp.). *Ethology*, **105**: 595–617.
- STAFFORD K. M., MOORE S. E., LAIDRE K. L. & HEIDE-JØRGENSEN M. P., 2008: Bowhead whale springtime song off West Greenland. *Journal of the Acoustical Society of America*, **124**: 3315–3323.
- TERVO O. M., PARKS S. E. & MILLER L. A., 2009: Seasonal changes in the vocal behavior of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western-Greenland. *Journal of the Acoustical Society of America*, **126**: 1570–1580.
- TERVO O. M., PARKS S. E., CHRISTOFFERSEN M. F., MILLER L. A. & KRISTENSEN R. M., 2011: Annual changes in the winter song of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland. *Marine Mammal Science*, **27**: 241–252.
- TYACK P., 1986: Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? *Behavioral Ecology and Sociobiology*, **18**: 251–257.
- VERGARA V. & BARRETT-LENNARD L. G., 2008: Vocal development in a beluga calf (*Delphinapterus leucas*). *Aquatic Mammals*, **34**: 123–143.
- WATKINS W. A., 1980: Acoustics and the behavior of sperm whales. Pp. 283–290. In: BUSNEL R. G. & FISH J. F. (eds.): *Animal Sonar Systems. NATO Advanced Study Institutes Series*, 28. Plenum Press, New York, xxiv+1135 pp.
- WATKINS W. A. & SCHEVILL W. E., 1977: Sperm whale codas. *Journal of the Acoustical Society of America*, **62**: 1485–1490.
- WATKINS W. A., MOORE K. E., CLARK C. W. & DAHLHEIM M. E., 1988: The sounds of sperm whale calves. Pp. 99–107. In: NACHTIGAL P. E. & MOORE P. W. B. (eds.): *Animal Sonar. NATO Advanced Study Institutes Series*, 156. Springer, Boston, xv+862 pp.
- WEILGART L. & WHITEHEAD H., 1993: Coda communication by sperm whales (*Physeter macrocephalus*) off the Galapagos Islands. *Canadian Journal of Zoology*, **71**: 744–752.
- WEILGART L. & WHITEHEAD H., 1997: Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, **40**: 277–285.
- WEISS B. M., LADICH F., SPONG P. & SYMONDS H., 2006: Vocal behavior of resident killer whale matriline with newborn calves: The role of family signatures. *Journal of the Acoustical Society of America*, **119**: 627–635.
- WEISS B. M., SYMONDS H., SPONG P. & LADICH F., 2011: Call sharing across vocal clans of killer whales: Evidence for vocal imitation? *Marine Mammal Science*, **27**(2): E1–E13.
- WHITEHEAD H. & WEILGART L., 1991: Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour*, **118**: 275–296.
- WHITEHEAD H., DILLON M., DUFAULT S., WEILGART L. & WRIGHT J., 1998: Non-geographically based population structure of south pacific sperm whales: Dialects, fluke-markings and genetics. *Journal of Animal Ecology*, **67**: 253–262.
- WINN H. E. & WINN L. K., 1978: The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Marine Biology*, **47**: 97–114.
- YURK H., BARRETT-LENNARD L., FORD J. K. B. & MATKIN C. O., 2002: Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, **63**: 1103–1119.
- ZOIDIS A. M., SMULTEA M. A., FRANKEL A. S., HOPKINS J. L., DAY A., MCFARLAND A. S., WHITTG A. D. & FERTL D., 2008: Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii. *Journal of the Acoustical Society of America*, **123**: 1737–1746.