

Culture and conservation of non-humans with reference to whales and dolphins: review and new directions

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Abstract

There is increasing evidence that culture is an important determinant of behavior in some non-human species including great apes and cetaceans (whales and dolphins). In some cases, there may be repercussions for population biology and conservation. Rapidly evolving “horizontal” cultures, transmitted largely within generations, may help animals deal with anthropogenic change and even allow them to exploit it, sometimes with negative consequences for both the animals and humans. In contrast, stable “vertical” or “oblique” cultures, transmitted principally between generations, may impede adaptation to environmental change, and confound range recovery, reintroductions and translocations. Conformist stable cultures can lead to maladaptive behavior, which may be mistaken for the results of anthropogenic threats. They can also structure populations into sympatric sub-populations with distinctive cultural variants. Such structuring is common among cetaceans, among which sympatric sub-populations may face different anthropogenic threats or respond to the same threat in different ways. We suggest that non-human culture should be integrated into conservation biology when considering populations with such attributes, and also more generally by refining definitions of evolutionarily significant units and considering how cultural attributes may change our perspectives of non-humans.

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1. Introduction

“Conservation”, when applied to humans, almost always refers to valued cultural attributes: to art forms, architecture, languages or “ways of life”. For instance, the organization Cultural Survival (2002) declares “The diversity of cultures around the world is increasingly endangered. This diversity constitutes the wealth of all humanity. We have more than a moral obligation to respect and promote cultural diversity—it is in our interest.”

For all other forms of life conservation has been tightly focused on genetic diversity. We are going to suggest that in some circumstances, for some species, culture should be integrated into conservation biology.

We will take most of our examples from cetaceans. However, many of our arguments apply to other non-human species for which culture seems important (see Sutherland, 1998). For instance, culture has begun to be considered in the conservation of chimpanzees, *Pan troglodytes*, (Goodall, 1994; McGrew, 2003) and elephants, Elephantidae, (McComb et al., 2001).

Culture has been defined in many varied ways (e.g., Munding, 1980). The definition that we prefer is “information or behavior – shared by a population or subpopulation – which is acquired from conspecifics through some form of social learning” (Rendell and Whitehead, 2001a). Here, “population” could include the whole species, and “subpopulation” any subdivision of a population which contains at least a few individuals in each set. This definition has four important elements: that culture affects behavior and thus phenotypes; that it is a group phenomenon; that it is transmitted from

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individual to individual and so, like genes, is an inheritance system (Boyd and Richerson, 1985); and that the transmission is through some form of social learning (see Whiten and Ham, 1992 for definitions of social learning). Our definition is similar to that used by most of those who study culture in other non-humans (e.g., Slater, 2001; Laland and Hoppitt, 2003; McGrew, 2003), cultural theorists (e.g., Boyd and Richerson, 1996), and some social scientists (Cronk, 1999). However, some psychologists restrict culture to transmission only through imitation and teaching (Galef, 1992), a restriction that we and others contest (Whiten and Ham, 1992; Boesch, 2001; Rendell and Whitehead, 2001a; Laland and Hoppitt, 2003), and there are anthropologists and other social scientists who use completely different definitions including elements such as “shared values” (e.g., Ingold, 2001), which cannot currently be applied to non-humans.

Culture, as conceived by us and many others, has some similarities with genetic inheritance. It can mutate and evolve, is subject to the natural selection of both cultural variants and culture-bearers, and often leads to adaptive behavior. However, there are some important differences (see Boyd and Richerson, 1985): individuals can receive culture from a range of donors in addition to their parents; they can choose which culture to adopt; and their own experiences and behavior can influence the form of culture that is transmitted to other individuals, so acquired characters can be inherited. A consequence is that culture can affect behavioral and population biology, and thus conservation issues, in ways that are importantly different from those traditionally expected from a model that only includes genetic inheritance.

Culture is very varied, and this variation has implications for its interactions with conservation. For instance, contrasts have often been drawn between “horizontal” cultures, where transmission is between members of the same generation, and “vertical” or “oblique” cultures where animals learn behavior from parents or other members of previous generations (Cavalli-Sforza et al., 1982). Horizontal cultural transmission can be highly effective in quickly changing population behavior in adaptive ways, an example being the rapid decrease in the use of certain chemicals by humans once they are shown to be toxic. Conversely, vertical cultures, like some religions, can be highly conservative and can constrain adaptive responses to environmental change.

Using our definition of culture, or any similar one, culture is quite common among animals, especially those that are more cognitively advanced (Boyd and Richerson, 1996). However, in most of the species possessing recognized cultural capacities, only a small proportion of behavior seems to be determined by social learning, and much of this may be functionally neutral,

as has been argued for songbirds (Slater, 1986; although see Grant and Grant, 1996). Generally, in these cases, it seems unlikely that culture will be an important factor in population biology or conservation. In contrast, among the great apes and cetaceans, and perhaps in a few other groups (other primates, elephants, bats and parrots are good candidates; see de Waal and Tyack, 2003), social learning likely determines a large proportion of behavior, including functionally important behavior such as foraging (McGrew, 1992; Whiten et al., 1999; Rendell and Whitehead, 2001b; van Schaik et al., 2003). In these species, culture can affect fitness and population biology in important ways, and so, we argue, have a potential bearing on conservation biology. This is especially the case when the form that culture takes leads to discrete, behaviorally differentiated population segments that can possess quite distinct ecological roles. Luck et al. (2003) argue that population diversity, especially in terms of the range of ecosystem services provided, should be an important element of population and conservation biology. Culture can provide such population diversity.

We will primarily use the cetaceans, whales and dolphins, to make our case. Cetaceans have been studied less thoroughly than the great apes, and less is known of their behavior. However, primatologists have acknowledged that cetaceans have behavior, social learning skills and cultural capacities which appear at least as advanced as those of the non-human great apes (Dunbar, 2001; Whiten, 2001). Furthermore, the cetacean culture that is emerging from current studies includes a feature that is not known among non-human great apes and that has particular significance for conservation: stable, sympatric, culturally determined groups within populations.

We will briefly summarize the evidence for culture in whales and dolphins, and then show how different forms of culture can have consequences for conservation biology. We provide few solid prescriptions for dealing with these consequences but rather seek to highlight issues that may require further consideration in cultural species.

2. Cetacean culture

There are about 70 species of whale and dolphin. They are diverse, ranging in size from 1.4 m animals, such as Hector's dolphins, *Cephalorhynchus hectori*, to the 30 m blue whale, *Balaenoptera musculus*, in diet from zooplankton to the large whales themselves, and in habitat from tropical rivers to the deep Antarctic Ocean. In only four species have more than a very few papers on social behavior in the wild been published (Connor et al., 1998): the humpback whale, *Megaptera novaeangliae*, the sperm whale, *Physeter macrocephalus*, the orca or killer whale, *Orcinus orca*, and the bottlenose dol-

phin, *Tursiops* spp. Even for these species, there is much that we do not know. In captivity, knowledge of behavior is even more taxonomically concentrated, with almost all behavioral research using the bottlenose dolphin.

Despite difficulties in studying the behavior of the whales and dolphins, and, compared to primates and songbirds, a lack of knowledge on behavior, communication and social structure, there is strong evidence for cetacean cultures in the four best studied species (Rendell and Whitehead, 2001b), and some most interesting speculations for some of the others (for instance on spinner dolphins, *Stenella longirostris*, Norris, 1994). Sophisticated social learning abilities exist, at least in bottlenose dolphins and orcas (Boran and Heimlich, 1999). Of the several types of social learning which have been recognized (e.g., Whiten and Ham, 1992), imitation is often singled out as being particularly significant for the promulgation of culture (e.g., Galef, 1992; Boyd and Richerson, 1996 but see Laland and Hoppitt, 2003). The bottlenose dolphin can imitate both vocally and non-vocally and has been shown to understand the broad concept of imitation (Herman and Pack, 2001). Some consider it the most sophisticated non-human imitator (e.g., Whiten, 2001).

This social learning seems to have led to culture, of various types. Among the baleen whales (suborder Mysticeti), there are several known cases of horizontally transmitted cultures (Rendell and Whitehead, 2001b). The best understood horizontal culture of cetaceans is the mating song of the male humpback whale. At any time during the winter breeding season, all the males in any ocean sing more or less the same elaborate song, but this communal song evolves over months and years (Payne, 1999). Songs in different oceans at any time are different but follow the same general syntactical and evolutionary rules.

Horizontal cultures are also found in the suborder Odontoceti, the toothed whales and dolphins. An example is the “dead-salmon carrying” fad of the well-studied “southern resident”, fish-eating, orcas of the Puget Sound area of the northeast Pacific. It began with a female in K-Pod carrying around a dead salmon in 1987, spread to the other two pods in the southern resident community over a 5–6 week period and then stopped (R. Osborne, personal observation). It was noted a few times the following summer, and then never again.

Probably more significant from the conservation perspective are vertically or obliquely transmitted cultures. Populations of all the well-studied odontocetes are culturally structured and subpopulations with distinct cultural trait groups are often sympatric. Among the bottlenose dolphins of Shark Bay, Western Australia, there are at least four distinctive foraging specializations, at least some of which are likely transmitted ver-

tically from mother to daughter (Connor, 2001; Mann, 2001; Mann and Sargeant, 2003). Similar population structure by foraging specializations is found in other dolphin communities, for instance in cases of human-dolphin fishing co-operatives. In Brazil there are at least two cases where some, but not all, bottlenose dolphins in a community have a long-standing and complex cooperative relationship with local fishers which is almost certainly vertically transmitted between generations of both dolphins and fishers (Simões-Lopes et al., 1998).

The population of orcas off the west coast of Canada is clearly structured at a number of hierarchical levels, and much of this structuring seems to be cultural. At the highest level, different “types” of orca (“residents” and “transients”) are sympatric, but show sufficient differences in feeding behavior, vocalizations, social systems, morphology, and genetics that they may be incipient species (Baird, 2000). It has been suggested that this division was originally cultural (Baird, 2000). At lower levels, “communities”, “clans” and “pods” of orcas may differ in vocalizations, foraging behavior and social behavior, but often have overlapping ranges (Ford et al., 1999). The complex, stable and sympatric vocal and behavioral cultures of orca groups have no known parallel outside humans (Rendell and Whitehead, 2001b). The closest analog is with the sperm whale, whose society is also arranged into a multi-level hierarchy, at least two levels of which may support cultural differences among sympatric groups: the approximately 10-member “social units” and ocean-wide “clans” with thousands of members each (Rendell and Whitehead, 2003; Whitehead, 2003).

Some of the attributions of culture to behavioral differences between segments of cetacean populations which are mentioned in this paper are not fully proven and have been contested (see commentaries on Rendell and Whitehead, 2001b). For instance, there is a segment of the scientific community which is unwilling to ascribe culture to a species without experimental proof of social learning (e.g., Galef, 1992). Among cetaceans this is impossible for the larger whales, only exists for the bottlenose dolphin (see above), and, even here, the apparently cultural characteristics of wild populations of this species have not been experimentally tested in the laboratory. However, there are many reasons for questioning such a restriction for culture, including the observation that transmission mechanisms for most human culture have not been experimentally tested in the laboratory (Boesch, 2001; Rendell and Whitehead, 2001a). In all the cases of cetacean behavioral differences cited below, we believe that the evidence strongly points to culture rather than alternative genetic, environmental or ontogenetic causes (Rendell and Whitehead, 2001a).

The emerging picture, then, is that whale and dolphin behavior is strongly affected by culture. The culture comes in a range of forms, from high-turnover

horizontal cultures of the baleen whales to the stable vertical cultures that structure odontocete populations. Cetacean cultural behavior includes vocalizations, foraging and ranging behavior, and social norms, but, in contrast to chimpanzees and orangutans, *Pongo* spp., there is little evidence of material cultures (Rendell and Whitehead, 2001b).

3. Horizontal cultures and conservation

3.1. Dealing with environmental change

It has been suggested several times that a principal adaptive advantage of culture in humans is to navigate environmental change (e.g., Boyd and Richerson, 1985; Laland et al., 1996): if animals can learn from each other they can adapt to changing environments more quickly than if each individual must learn the optimal behavior independently, and much more quickly than is possible with natural selection of genetically determined behavior. Thus species with cultural capacities possess a potential advantage when environments change, even if they themselves are the agents of the change. Humans, the supreme cultural animals, are exemplars of ecological success in changing environments. But there are other cases of species with cultural capacities which have become dominant in their habitats: elephants (Laws, 1970), a number of bird species including starlings, *Sturnus vulgaris*, (West et al., 2003) and several species of cetaceans, including the sperm whale which seems to dominate much of the mesopelagic ecosystem (Clarke, 1977). Each of these species, probably at least partially because of their social learning skills, has shown adaptation to human-caused environmental change, including crop-raiding by elephants (Osborn, 2002), the colonization of North America by European starlings following European humans (West et al., 2003), and fish-stealing by sperm whales (see below).

Thus, as humans change ecosystems, species with the capacity for horizontal transmission of adaptive behavior may be better placed to survive.

3.2. Exploiting anthropogenic change

Exploitation of new opportunities can also lead to trouble. Elephants raid farmers' fields, exploiting anthropogenic developments with negative consequences for both the farmers and elephants (Douglas-Hamilton et al., 2001). Observations by wildlife managers and scientists suggest that crop-raiding may be learned by elephants from other elephants (Osborn, 2002), explaining the speedy spread and widespread nature of the phenomenon.

Cetaceans too. In several areas of the world, cetaceans have learned to remove fish from fishing gear, and

given the rapid spread of the behavior within populations, there is little doubt that social learning is responsible for at least some of the recruitment to the population of fish-stealers. Examples include orcas and/or sperm whales taking fish from long-lines in the fisheries for Patagonian tooth-fish, *Dissostichus eleginoides*, off the southern parts of South America, bluenose, *Hyperoglyphe antarchia*, off New Zealand, halibut, *Hippoglossus stenolepis*, and sablefish, *Anoplopoma fimbria*, near Alaska (e.g., Yano and Dahlheim, 1995; Ashford et al., 1996; National Marine Fisheries Service, 1998; Nolan et al., 2000).

One quite well-studied example is the spread of long-line depredation by killer whales from Prince William Sound (PWS) to the inland waterways of southeast Alaska. "Resident" (fish-eating) killer whales in PWS have been taking fish from long-lines since the early 1980s if not earlier, but this behavior was not reported in Southeast Alaskan waters until the mid 1990s, when one of the two "resident" pods (AF) in the area was observed stealing fish (M. Dahlheim, pers. comm.). AF visited PWS during the 1980s, associating with PWS pods known to take fish from long-lines (although AF was not observed taking fish from longlines in PWS). The other Southeast Alaskan "resident" pod, AG, rarely visited PWS and was not observed with the fish-eating PWS pods before 1992, and has not been observed taking fish from long-lines in southeast Alaska (Matkin et al., 1997; M. Dahlheim, pers. comm.). The inference is that pod AF learned the behavior from the PWS pods.

In many of these cases of crop-raiding by elephants and fish-stealing by whales the animals suffer hostile repercussions from angry farmers and fishers including shooting and calls for culls. If elephants and cetaceans did not learn so well from other elephants and cetaceans, it seems highly likely that these problems would be much less severe.

4. Vertical, and oblique, cultures and conservation

Vertical, and oblique, cultures are passed between generations and can be stable over many generations, particularly if enhanced by conformity, the imperative "to do the done thing" (Richerson and Boyd, 1998). Vertical cultures can influence genetic evolution (Laland, 1992; Grant and Grant, 1996; Whitehead, 1999) and may structure populations (e.g., Nettle, 1999; Rendell and Whitehead, 2003).

4.1. Cultural conservatism

While rapidly evolving horizontal cultures may make a species more able to adapt to environmental change, stable vertical cultures can have the opposite effect. They

may inhibit the adaptive responses that stimulus-response behavior, individual learning and innovation would normally produce (although to a lesser extent than overriding genetic determination). For example, if, due to cultural traditions, orcas continued to use areas of their habitat despite excessive vessel traffic, sewage, or underwater noise, their adherence to tradition could potentially over-ride what would otherwise be avoidance of noxious environmental conditions (Osborne, 1999).

For cetaceans perhaps the most important aspect of this cultural conservatism relates to the reestablishment of a species in an ecological niche following extirpation due to whaling. Most large whale populations were enormously reduced by commercial whaling which began hundreds of years ago but reached its peak during the 1960s (Clapham et al., 1999). These populations are now virtually protected from whaling so that recovery is expected, and in some cases apparent. However, while reasonable, and sometimes growing, population densities are found in some areas, other traditionally important habitat remains deserted. There are several documented examples of this including the North Atlantic right whales, *Eubalaena glacialis*. Centuries of whaling reduced the population to perhaps a few tens of animals in early 20th Century, but there was some recovery so now a few hundred animals are found in the western North Atlantic, and the animals are fairly common in a few areas such as the entrance to the Bay of Fundy (Katona and Kraus, 1999). However, right whales are currently almost entirely absent from Labrador waters where Basque whalers caught tens of thousands of animals during the 16th and 17th Centuries (Katona and Kraus, 1999). Oceanic climate change may play some role in this lack of recovery, but it is perhaps more plausible that the whalers, by killing the Labrador animals, also destroyed the cultural knowledge of how to use Labrador waters. While we can document the end of traditional use of a habitat, whaling probably removed other cultural knowledge from populations, and this loss likely inhibits their recovery.

4.2. Maladaptive behavior

More fundamentally, cultural evolution has a greater potential to lead to maladaptive behavior than genetic evolution or individual learning (Boyd and Richerson, 1985). This is particularly the case for conformist cultures in which individuals actively adopt the most common cultural variants in their experience. Conformist cultures can be particularly stable, and lead to strong group identification and cultural group selection (Richerson and Boyd, 1998). This process is a leading candidate for explaining genetically maladaptive behavior by humans (Boyd and Richerson, 1985), such as religiously prescribed fertility limitations, or the eating

of dead relatives' brains. Conformist cultural evolution can also potentially result in maladaptive behavior in non-humans. This can lead to the appearance of conservation problems, where no anthropogenic threat is actually operating.

For example, on 27 July 2002, 55 pilot whales, *Globicephala melas*, stranded on the beaches of Cape Cod, Massachusetts. Despite being refloated and pointed out to sea, they came back and eventually all died. Mass death on a tourist beach does not fit with our conception of well-adapted wild animals. The public and press assumed there was a conservation problem, and started making links. An August 5 2002 article in the *Toronto Star* was headlined "Is new sonar driving whales ashore?" We can be fairly confident that the mass stranding on Cape Cod had no connection to the recently developed military low-frequency sonar. Although military sonars do kill whales, and mass strandings of some species are closely linked with naval activities (Balcomb and Claridge, 2001; Jepson et al., 2003), there were none operating near Cape Cod in late July 2002, and mass strandings of pilot whales have been fairly commonplace in places like Cape Cod for at least centuries (Sergeant, 1982).

So, why do pilot whales behave so obviously non-adaptively if it is not the result of an anthropogenic threat? There has been much speculation (e.g., Simmonds, 1997) but no clear answer, and we have suggested that mass strandings of cetaceans may be linked to conformist cultures (Rendell and Whitehead, 2001b). In this scenario, healthy animals run up on the beaches and die at least partially because the culturally transmitted imperative to remain with the group holds sway over the individual's survival instinct. Although culture has not been studied in pilot whales, they seem to have social structures with similar general attributes to orcas and sperm whales (Heimlich-Boran, 1993; Ottensmeyer and Whitehead, 2003), the types that seem to promote conformist cultures.

The implication is that for cetaceans, like humans, strange, and apparently maladaptive, behavior, may be a product of cultural evolution and not a result of anthropogenic changes to their environment, especially if it is a group phenomenon. Thus not all weird behavior indicates a conservation problem, although some, such as mass strandings of several whale species simultaneously, does (Balcomb and Claridge, 2001; Jepson et al., 2003).

4.3. Reintroduction and translocation

Culture interacts with conservation in the introduction of captive animals into the wild and the forced movement of animals between areas (Sutherland, 1998). Reintroductions and translocations are important conservation tools in some circumstances, and culture will

affect their success. The principal issues are whether the animals possess the knowledge to survive and breed in their new habitat.

Cultural aspects undoubtedly affect the success of cetacean reintroductions (see, e.g., Wells et al., 1998), but reintroduction is not generally considered an important tool in cetacean conservation (e.g., Reeves and Mead, 1999). Translocations from the highly impacted Yangtze River to a protected oxbow have been attempted in attempts to save the critically endangered baiji (*Lipotes vexillifer*), but these were not successful (Zhang et al., 2003). Cultural aspects may have had a role in this. Translocations of finless porpoises (*Neophocaena phocaenoides*) between the same two habitats have been successful (Ding et al., 2000). This contrast may partially result from differences in the role of cultural knowledge in the two species.

4.4. Sympatric cultural variants

Conservation biology is complicated by population subdivisions. Anthropogenic threats may affect the different segments in different ways leading to multiple responses. The situation is particularly complex when the population segments are sympatric. In non-territorial cultural species, these types of population division may easily arise, and be reinforced by conformism. A terrestrial example is the elephant in which sympatric groups may respond differently to threats based upon levels of cultural knowledge within the group, as indicated by the age of the group's matriarch (McComb et al., 2001). This study emphasized the importance for population persistence of maintaining cultural knowledge within different segments of a structured population under anthropogenic threat.

In the ocean territoriality is much less prevalent than on land, leaving more opportunities for sympatric socially learned behavioral variants within species. A well-studied example is the sea otter, *Enhydra lutris*, in which individuals that share habitat have distinctive foraging styles, which are learned from their mothers, and so may possess distinctive ecological roles (Estes et al., 2003). Among cetaceans, sympatric groups often have distinctive behavioral repertoires resulting from vertical cultural transmission and apparently rendered stable by conformism, a situation which has a range of conservation ramifications. Culturally discrete sub-populations in the same habitat may face different conservation threats, or may respond to the same threat in different ways.

In Moreton Bay, Australia, bottlenose dolphins regularly feed from trawler discards (Chilvers and Corkeron, 2001). Among the several hundred dolphins that use Moreton Bay, two sympatric communities have been recognized, one of which generally feeds with trawlers, and the other of which never does (Chilvers and Cork-

eron, 2001). Although they live in the same area, dolphins from the two communities rarely interact socially, except possibly for some mating (Chilvers and Corkeron, 2001). It may become necessary to restrict trawling to safeguard the resources, peneaid prawns. How will this affect the trawler dolphins? Other impacts, such as the effects of pollutants run-off into sea-grass beds, may primarily affect the non-trawler dolphins (Chilvers and Corkeron, 2001), so the conservation issues are difficult.

Similar conundrums are emerging for other species. For instance, dusky dolphins (*Lagenorhynchus obscurus*) near the Kaikoura Canyon, New Zealand, feed at night on mesopelagic fishes and squid (Würsig et al., 1989). A subset of those animals, and habitually the same every year, travel about 160 km north to the Marlborough Sounds in winter and there feed in the day on near-surface schooling fishes (K.J. Benoit-Bird, B. Würsig and C.J. McFadden submitted). Traveling to Marlborough Sounds is thought to be culturally transmitted (B. Würsig, pers. comm.). The Marlborough Sound users are now facing increasingly choked bays due to extensive mussel farm development in the Marlborough Sounds area, and the dolphins do not use areas with mussel farms (Markowitz et al., 2004).

Off the Galápagos Islands, most female and immature sperm whales are from either the "Regular" clan or the "Plus-one" clan (Rendell and Whitehead, 2003). Groups from these clans differ not only in the predominant types of "coda" vocalizations they make, which give the clans their name, but also in movement patterns and habitat use (Whitehead and Rendell, 2004). "Regular" groups tend to have convoluted tracks close to the islands whereas the "Plus-one" groups move in straighter lines further offshore. The Galápagos Islands, like the entire eastern tropical Pacific, is strongly affected by the El-Niño/Southern (ENSO) Oscillation ocean climate phenomenon (Arntz, 1986). In warm, ENSO, conditions the sperm whales off the Galápagos Islands have dramatically reduced feeding success (Smith and Whitehead, 1993). However, ENSO seems to affect the clans to different extents. In 1989, a normal cool year, groups of the "Regular" clan had much higher feeding success (as indicated by defecation rates) than those of the "Plus-one" clan, whereas in the difficult ENSO conditions of 1987, it was the "Plus-one" clan that did better (Whitehead and Rendell, 2004). As global climate change will probably increase the frequency of ENSO conditions, and make the general ocean climate more like those of an ENSO (e.g., Stott et al., 2002), it seems likely that the clans will be differentially adapted to dealing with the effects of global warming. The clans are distinguished culturally, not genetically, (Rendell and Whitehead, 2003), so that cultural diversity may be more significant than genetic diversity in equipping sperm whales to deal with coming changes to the ocean climate.

In orcas, too, sympatric culturally distinguished groupings face different conservation threats. For instance, off southern Vancouver Island, fish-eating “residents” are found in the same waters as mammal-eating “transients”. The residents are threatened by declines in salmon stocks and by rampant whale-watching (Osborne, 1999; Trites and Barrett-Lennard, 2001; Erbe, 2002; NOAA, 2002), while for transients extreme concentrations of pollutants linked to their high trophic level (Ross et al., 2000) are probably the major concern.

4.5. *Sympatric cultural variants and evolutionarily significant units*

These situations, in which sympatric culturally distinct populations have characteristic conservation issues, or may respond differently to threats, indicate the importance of preserving both genetic and cultural diversity (Sutherland, 1998). For instance, in the case of the sperm whales, the “Plus-one” clan’s cultural complex may be vital as the ocean climate warms.

Conservation is often believed to be promoted through considering the status of populations below the sub-species level, sometimes called “evolutionarily significant units” (ESUs). A consensus definition of ESU has yet to be achieved, and the practice of assigning them is very much under development. We can now add a further twist to this difficult issue: should culture be considered in the determination of ESUs?

Geographically distinct cultures could be used as part of the process of dividing populations, so that, for example, chimpanzee populations in different parts of Africa might be assigned to different ESUs based upon cultural similarity (Whiten et al., 2001) as well as geographic and genetic proximity. The situation becomes more difficult when population segments overlap geographically and genetically, but are clearly distinguishable based upon culturally transmitted behavior.

A controversial case that contains strong cultural undercurrents is that of the “southern resident” orcas. The southern resident community contains about 80 fish-eating orcas whose range straddles the US-Canadian border. The population has been declining since 1995, but the reasons for this are unclear (NOAA, 2002). The southern residents are sympatric with the mammal-eating “transient” orcas, and share some of their range with the “northern resident community” which also eat fish. There are about 200 northern residents, and although they seem less threatened than the southern residents, their population has also started to decline recently (Trites and Barrett-Lennard, 2001). There is little mating between the northern and southern residents, and they are genetically distinct (Barrett-Lennard, 2000). However, genetic divergence is small, just one base pair in the control region of the mitochondrial genome and $F_{ST} = 0.144$ using 11 microsatellite loci

(Barrett-Lennard, 2000). The principal, and probably fundamental, differences between the communities are cultural. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) reviewed orca status in 2001, and divided the orcas into “nationally significant populations” assigning a status of “Endangered” (the highest risk category available for an extant population) to the southern residents, “Threatened” to the northern residents, and “Threatened” to the transients (www.cosewic.gc.ca). In contrast, the US National Marine Fisheries Service (NMFS) in 2002 refused a petition to declare the southern residents “Endangered”, listing them only as “Depleted” as they were not considered a “distinct population segment” but were “part of the general killer whale population in the North Pacific, which is considered healthy” (NOAA, 2002; NOAA Press release 02-076; <http://www.nwr.noaa.gov/mmammals/whales/srkwnews.pdf>). Supporting this decision, NMFS noted that the northern and southern residents use similar habitat types, that loss of the southern residents would not necessarily result in a gap in the species’ range, and that the genetic differences between the northern and southern residents is small (NOAA, 2002). NMFS also considered “pod-specific traits, such as acoustic repertoire, that have been described by some biologists as ‘cultural’” but concluded “that there was insufficient evidence to indicate whether these ‘cultural’ traits were inherited or learned, and thus whether they truly signify an evolutionarily important trait” (NOAA, 2002). This reasoning is confused, as cultural traits must be learned and may or may not also be inherited between generations. However, the implication seems to be that traits acquired through learning are not evolutionarily important, and, thus, in apparent contrast to the Canadian listing agency (COSEWIC), NMFS specifically appears to disregard culture in this listing decision.

Where do these practices stand in the light of the evolving theory of ESUs? There have been many approaches to defining ESUs (Fraser and Bernatchez, 2001), but the focus is on genetic separation, not cultural differences. In the definitions of Dizon et al. (1992), Moritz (1994) and Fraser and Bernatchez (2001), ESUs are delineated entirely on the basis of information and inferences about gene flow and differences in allele distributions. There are some broader approaches which do not specifically mention genes in the basic definition. Waples (1991) and O’Brien and Mayr (1991), extending the biological species concept, consider ESUs as population subsets that are substantially reproductively isolated. However, “reproduction” is of genes not cultural variants. One definition of ESU that, on the surface, appears to allow cultural entities to be listed *per se*, comes from the cladistic approach of Vogler and DeSalle (1994) in which ESUs are discriminated using characters which cluster individuals or populations to

the exclusion of other such clusters. Such characters must be heritable, which admits many culturally determined attributes. However characters must also “define phylogenetic (i.e., genetically separated) lineages” (Vogler and DeSalle, 1994), and so we are back to genes again.

The emphasis on genetic patterns and processes, or restrictions to reproductively isolated population segments, would probably rule out ESU designation for most known instances of the culturally determined segregation of a sympatric population, such as the Moreton Bay bottlenose dolphins and sperm whale clans. In contrast, the “types” and communities of orcas are largely reproductively isolated, and show genetic differences (Barrett-Lennard, 2000), allowing potential discrimination into ESUs under several of the criteria.

Fundamentally we are trying to conserve biodiversity, which may be defined as the “full variety of life on Earth” (Takacs, 1996). A large part of this variety is heritable phenotypic variation. The mechanism by which information is transferred between generations is of secondary significance. There are several mechanisms by which information which determines phenotypes may be transferred between generations, of which genetics is much the most significant, and culture the clear runner up (Maynard Smith, 1989). Definitions of the ESU which are neutral as to transmission mechanisms could easily be derived from current proposals. For instance, Fraser and Bernatchez’s (2001) “lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level (lineage) of the species” could become a “lineage demonstrating highly restricted flow of information that determines phenotypes from other such lineages within the higher organizational level (lineage) of the species”.

Such an approach would lead to “cultural ESU’s” only very rarely: both a large and functionally important part of the behavior of animals would have to be due to social learning, and there would need to be little cultural exchange between population segments, despite the segments sharing geographical ranges and most functionally important genes. In most species cultural variants are either geographically or genetically discrete or of little functional importance, but orcas would probably qualify, and maybe sperm whales and elephants. We believe that preserving significant cultural variants in such species is an important part of conserving the species itself.

5. Conclusion

We have heard arguments that if we are at the stage of conserving non-human cultures, then the real conservation battles have already been won. We disagree. For a range of non-human animals, culture is a vital

determinant of phenotype, and so how the animals interact with humans and our cultural artifacts. Thus, culture should be an integral element of the conservation biology of these species.

Cultural organisms do not behave like those for which culture has little significance. Clearly maladaptive behavior is often taken as a sign of a threat to individuals or populations, but genetically maladaptive behavior is to be expected in conformist cultures. In cultural societies, individuals with important cultural knowledge may have population significance far in excess of their reproductive capacities (McComb et al., 2001), and populations may be structured in significant ways by cultural knowledge and cultural habit. As we hope we have shown, these mean that conservation takes on an additional dimension. This is manifestly recognized for humans, but we should also consider culture in the conservation of other species – in individual cases by noting how cultural diversity interacts with anthropogenic threats, as well as perhaps more systematically by adding the potential for culture to our concepts of ESUs and other staples of conservation biology.

It has been suggested that the recognition of culture in other animals should affect our perception of them (Fox, 2001). Cultural Survival (2002) believes that there is a “moral obligation” to conserve human cultural diversity. So, in addition to considering culture as a part of the mix of biological attributes that affects how organisms interact with anthropogenic threats, perhaps culture should also be inserted into the roots of our conservation biology: why we wish to conserve organisms, and what we wish to conserve about them. These questions are difficult, and perhaps beyond the scope of most practicing conservation biologists. However, this does not mean that the implications of non-human cultures should just be left to the ethicists: non-human culture is not just “chimpanzees/dolphins/elephants reading poetry”, it is the source of survival skills fundamental to the daily lives of these animals.

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References

- Arntz, W.E., 1986. The two faces of El Niño 1982–83. *Meeresforschung* 31, 1–46.

- Ashford, J.R., Rubilar, P.S., Martin, A.R., 1996. Interactions between cetaceans and longline fishery operations around South Georgia. *Marine Mammal Science* 12, 452–456.
- Baird, R.W., 2000. The killer whale – foraging specializations and group hunting. In: Mann, J., Connor, R.C., Tyack, P., Whitehead, H. (Eds.), *Cetacean Societies*. University of Chicago Press, Chicago, pp. 127–153.
- Balcomb, K.C., Claridge, D.E., 2001. A mass stranding of cetaceans caused by naval sonar in the Bahamas. *Bahamas Journal of Science* 5, 2–12.
- Barrett-Lennard, L., 2000. Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. Ph.D. Dissertation, University of British Columbia, Vancouver.
- Boesch, C., 2001. Sacrileges are welcome in science! Opening a discussion about culture in animals. *Behavioral and Brain Sciences* 24, 327–328.
- Boran, J.R., Heimlich, S.L., 1999. Social Learning in Cetaceans: hunting, hearing and hierarchies. *Symposia of the Zoological Society, London* 73, 282–307.
- Boyd, R., Richerson, P.J., 1996. Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy* 88, 77–93.
- Boyd, R., Richerson, P., 1985. *Culture and the Evolutionary Process*. Chicago University Press, Chicago.
- Cavalli-Sforza, L.L., Feldman, M.W., Chen, K.H., Dornbusch, S.M., 1982. Theory and observation in cultural transmission. *Science* 218, 19–27.
- Chilvers, B.L., Corkeron, P.J., 2001. Trawling and bottlenose dolphins' social structure. *Proceedings of the Royal Society of London* B268, 1901–1905.
- Clapham, P.J., Young, S.B., Brownell, R.L.J., 1999. Baleen whales: conservation issues and the status of the most endangered populations. *Mammal Review* 29, 35–60.
- Clarke, M.R., 1977. Beaks, nets and numbers. *Symposia of the Zoological Society, London* 38, 89–126.
- Connor, R.C., 2001. Individual foraging specializations in marine mammals: culture and ecology. *Behavioral and Brain Sciences* 24, 329–330.
- Connor, R.C., Mann, J., Tyack, P.L., Whitehead, H., 1998. Social evolution in toothed whales. *Trends in Ecology and Evolution* 13, 228–232.
- Cronk, L., 1999. *That complex whole: culture and the evolution of human behavior*. Westview Press, Boulder, CO.
- Cultural Survival, 2002. *Annual Report 2001–2002. Celebrating 30 years of Cultural Survival*. Cultural Survival, Cambridge, MA.
- de Waal, F.B.M., Tyack, P.L., 2003. *Animal social complexity: intelligence, culture, and individualized societies*. Harvard University Press, Cambridge, MA.
- Ding, W., Renjun, L., Zhang, X., Jian, Y., Wei, Z., Zhao, Q., Wang, X., 2000. Status and conservation of the Yangtze finless porpoise. In: Reeves, R.R., Smith, B.D., Kasuya, T. (Eds.), *Biology and Conservation of Freshwater Cetaceans in Asia*. IUCN Species Survival Commission, Gland, Switzerland, pp. 81–85.
- Dizon, A.E., Lockyer, C., Perrin, W.F., Demaster, D.P., Sisson, J., 1992. Rethinking the stock concept. *Conservation Biology* 6, 24–36.
- Douglas-Hamilton, I., Barnes, R.F.W., Shoshani, H., Williams, A.C., Johnsingh, A.J.T., 2001. Elephants. In: Macdonald, D. (Ed.), *The new encyclopedia of mammals*. Oxford University Press, Oxford, UK, pp. 436–445.
- Dunbar, R.I.M., 2001. Do how do they do it? *Behavioral and Brain Sciences* 24, 332–333.
- Erbe, C., 2002. Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. *Marine Mammal Science* 18, 394–418.
- Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., Lyon, B.E., 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology* 72, 144–155.
- Ford, J.K.B., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S., Balcomb, K.C., 1999. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76, 1456–1471.
- Fox, M.A., 2001. Cetacean culture: philosophical implications. *Behavioral and Brain Sciences* 24, 333–334.
- Fraser, D.J., Bernatchez, L., 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Molecular Ecology* 10, 2741–2752.
- Galef, B.G., 1992. The question of animal culture. *Human Nature* 3, 157–178.
- Goodall, J., 1994. Postscript – conservation and the future of chimpanzee and bonobo research in Africa. In: Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., Heltne, P.G. (Eds.), *Chimpanzee Cultures*. Harvard University Press, Cambridge, MA, pp. 397–404.
- Grant, B.R., Grant, P.R., 1996. Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution* 50, 2471–2487.
- Heimlich-Boran, J.R., 1993. Social organization of the short-finned pilot whale *Globicephala macrorhynchus*, with special reference to the comparative social ecology of delphinids. Ph.D. Dissertation, Cambridge University, Cambridge, UK.
- Herman, L.M., Pack, A.A., 2001. Laboratory evidence for cultural transmission mechanisms. *Behavioral and Brain Sciences* 24, 335–336.
- Ingold, T., 2001. The use and abuse of ethnography. *Behavioral and Brain Sciences* 24, 337.
- Jepson, P.D., Arbelo, M., Deaville, R., Patterson, I.A., Castro, P., Degollada, E., Ross, H.M., Herráez, P., Pocknell, A.M., Rodríguez, F., Howiell, F.E., Espinosa, A., Reid, R.J., Jaber, J.R., Martin, V., Cunningham, A.A., Fernández, A., 2003. Gas bubble lesions in stranded cetaceans. *Nature* 425, 575–576.
- Katona, S.K., Kraus, S., 1999. Efforts to conserve the North Atlantic right whale. In: Twiss, J.R., Reeves, R.R. (Eds.), *Conservation and Management of Marine Mammals*. Smithsonian Institution Press, Washington, DC, pp. 311–331.
- Laland, K.N., 1992. A theoretical investigation of the role of social transmission in evolution. *Ethology and Sociobiology* 13, 87–113.
- Laland, K.N., Hoppitt, W., 2003. Do animals have culture? *Evolutionary Anthropology* 12, 150–159.
- Laland, K.N., Richerson, P.J., Boyd, R., 1996. Developing a theory of animal social learning. In: Heyes, C.M., Galef, B.G.J. (Eds.), *Social Learning in Animals: The Roots of Culture*. Academic Press, San Diego, CA, pp. 129–154.
- Laws, R.M., 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21, 1–15.
- Luck, G.W., Daily, G.C., Ehrlich, P.R., 2003. Population diversity and ecosystem services. *Trends in Ecology and Evolution* 18, 331–336.
- Mann, J., 2001. Cetacean culture: definitions and evidence. *Behavioral and Brain Sciences* 24, 343.
- Mann, J., Sargeant, B., 2003. Like mother, like calf: the ontogeny of foraging traditions in wild Indian ocean bottlenose dolphins (*Tursiops* sp.). In: Fragaszy, D.M., Perry, S. (Eds.), *The biology of traditions; models and evidence*. Cambridge University Press, Cambridge, UK, pp. 236–266.
- Markowitz, T.M., Harlin, A.D., Würsig, B., McFadden, C.J., 2004. Dusky dolphin foraging habitat: overlap with aquaculture in New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14, 133–149.
- Matkin, C.O., Matkin, D.R., Ellis, G.M., Saulitis, E., McSweeney, D., 1997. Movements of resident killer whales in southeastern Alaska and Prince William Sound, Alaska. *Marine Mammal Science* 13, 469–475.
- Maynard Smith, J., 1989. *Evolutionary Genetics*. Oxford University Press, Oxford, UK.

- McComb, K., Moss, C., Durant, S.M., Baker, L., Sayialel, S., 2001. Matriarchs as repositories of social knowledge in African elephants. *Science* 292, 491–494.
- McGrew, W.C., 2003. Ten dispatches from the chimpanzee culture wars. Intelligence, culture, and individualized societies. In: de Waal, F.B.M., Tyack, P.L. (Eds.), *Animal Social Complexity*. Harvard University Press, Cambridge, MA.
- McGrew, W.C., 1992. Chimpanzee material culture: implications for human evolution. Cambridge University Press, Cambridge, UK.
- Moritz, C., 1994. Defining 'evolutionary significant units' for conservation. *Trends in Ecology and Evolution* 9, 373–375.
- Mundinger, P.C., 1980. Animal cultures and a general theory of cultural evolution. *Ethology and Sociobiology* 1, 183–223.
- National Marine Fisheries Service, 1998. Sperm whale (*Physeter macrocephalus*): North Pacific stock, Stock Assessment Report, pp. 111–114.
- Nettle, D., 1999. Language variation and the evolution of societies. In: Dunbar, R.I.M., Knight, C., Power, C. (Eds.), *The Evolution of Culture*. Rutgers University Press, Piscataway, NJ, pp. 214–227.
- NOAA, 2002. Status Review under the Endangered Species Act: Southern Resident Killer Whales (*Orcinus orca*), NOAA Technical Memorandum NMFS-NWAFSC-54, Seattle, WA.
- Nolan, C.P., Liddle, G.M., Elliot, J., 2000. Interactions between killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) with a longline fishing vessel. *Marine Mammal Science* 16, 658–664.
- Norris, K.S., 1994. Comparative view of cetacean social ecology, culture, and evolution. In: Norris, K.S., Würsig, B., Wells, R.S., Würsig, M. (Eds.), *The Hawaiian Spinner Dolphin*. University of California Press, Berkeley, CA, pp. 301–344.
- O'Brien, S.J., Mayr, E., 1991. Species hybridization and protection of endangered animals. *Science* 253, 251–252.
- Osborn, F.V., 2002. *Capsicum oleoresin* as an elephant repellent: field trials in the communal lands of Zimbabwe. *Journal of Wildlife Management* 66, 674–677.
- Osborne, R.W., 1999. A historical ecology of Salish Sea resident killer whales (*Orcinus orca*): with implications for management. Ph.D. Dissertation, University of Victoria, Victoria, British Columbia.
- Ottensmeyer, C.A., Whitehead, H., 2003. Behavioural evidence for social units in long-finned pilot whales. *Canadian Journal of Zoology* 81, 1327–1338.
- Payne, K., 1999. The progressively changing songs of humpback whales: a window on the creative process in a wild animal. In: Wallin, N.L., Merker, B., Brown, S. (Eds.), *The Origins of Music*. MIT Press, Cambridge, MA, pp. 135–150.
- Reeves, R.R., Mead, J.G., 1999. Marine mammals in captivity. In: Twiss, J.R., Reeves, R.R. (Eds.), *Conservation and Management of Marine Mammals*. Smithsonian Institution Press, Washington, DC, pp. 412–436.
- Rendell, L., Whitehead, H., 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society of London B* 270, 225–231.
- Rendell, L., Whitehead, H., 2001a. Cetacean culture: still afloat after the first naval engagement of the culture wars. *Behavioral and Brain Sciences* 24, 360–373.
- Rendell, L., Whitehead, H., 2001b. Culture in whales and dolphins. *Behavioral and Brain Sciences* 24, 309–324.
- Richerson, P.J., Boyd, R., 1998. The evolution of human ultrasociality. In: Eibl-Eibesfeldt, I., Salter, F.K. (Eds.), *Indoctrinability, Ideology and Warfare*. Berghahn Books, London, pp. 71–95.
- Ross, P.S., Ellis, G.M., Ikononou, M.G., Barrett-Lennard, L.G., Addison, R.F., 2000. High PCB concentrations in free-ranging Pacific killer whales (*Orcinus orca*): effects of age, sex and dietary preference. *Marine Pollution Bulletin* 40, 504–515.
- Sergeant, D.E., 1982. Mass strandings of toothed whales (Odontoceti) as a population phenomenon. *Scientific Reports of the Whales Research Institute* 34, 1–47.
- Simmonds, M.P., 1997. The meaning of cetacean strandings. *Bulletin Institut Royal de Sciences Naturelles de Belgique Biologie* 67 (Suppl.), 29–34.
- Simões-Lopes, P.C., Fabián, M.E., Menegheti, J.O., 1998. Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. *Revista Brasileira de Zoologia* 15, 709–726.
- Slater, P.J.B., 2001. There's CULTURE and Culture. *Behavioral and Brain Sciences* 24, 356–357.
- Slater, P.J.B., 1986. The cultural transmission of bird song. *Trends in Ecology and Evolution* 1, 94–97.
- Smith, S.C., Whitehead, H., 1993. Variations in the feeding success and behaviour of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. *Canadian Journal of Zoology* 71, 1991–1996.
- Stott, L., Poulsen, C., Lund, S., Thunell, R., 2002. Super ENSO and global climatic oscillations at millennial time scales. *Science* 297, 222–226.
- Sutherland, W.J., 1998. The importance of behavioural studies in conservation biology. *Animal Behaviour* 56, 801–809.
- Takacs, D., 1996. *The Idea of Biodiversity: Philosophies of Paradise*. John Hopkins University Press, Baltimore, MD.
- Trites, A.W., Barrett-Lennard, L.G., 2001. COSEWIC status report on killer whales (*Orcinus orca*), Committee on the Status of Endangered Wildlife in Canada. Ottawa.
- van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S., Merrill, M., 2003. Orangutan cultures and the evolution of material culture. *Science* 299, 102–105.
- Vogler, A.P., DeSalle, R., 1994. Diagnosing units of conservation management. *Conservation Biology* 8, 354–363.
- Waples, R.S., 1991. Pacific salmon, *Oncorhynchus* spp. and the definition of 'species' under the Endangered Species Act. *Marine Fisheries Review* 53, 11–22.
- Wells, R.S., Bassos-Hull, K., Norris, K.S., 1998. Experimental return to the wild of two bottlenose dolphins. *Marine Mammal Science* 14, 51–71.
- West, M.J., King, A.P., White, D.J., 2003. Discovering culture in birds: the role of learning and development. In: de Waal, F.B.M., Tyack, P.L. (Eds.), *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*. Harvard University Press, Cambridge, MA, pp. 470–492.
- Whitehead, H., 2003. *Sperm Whales: Social Evolution in the Ocean*. University of Chicago Press, Chicago, IL.
- Whitehead, H., 1999. Culture and genetic evolution in whales. *Science* 284, 2055a.
- Whitehead, H., Rendell, L., 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *Journal of Animal Ecology* 73, 190–196.
- Whiten, A., 2001. Imitation and cultural transmission in apes and cetaceans. *Behavioral and Brain Sciences* 24, 359–360.
- Whiten, A., Ham, R., 1992. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behavior* 21, 239–283.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 2001. Charting cultural variation in chimpanzees. *Behaviour* 138, 1481–1516.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. *Nature* 399, 682–685.
- Würsig, B., Würsig, M., Cipriano, F., 1989. Dolphins in different worlds. *Oceanus* 32, 71–75.

Yano, K., Dahlheim, M.E., 1995. Killer whale, *Orcinus orca*, depredation on long-line catches of bottomfish in the southeastern Bering Sea and adjacent waters. *Fishery Bulletin US* 93, 355–372.

Zhang, X., Wang, D., Liu, R., Wei, Z., Hua, Y., Wang, Y., Chen, Z., Wang, L., 2003. The Yangtze river dolphin or baiji (*Lipotes vexillifer*): population status and conservation issues in the Yangtze River, China. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13, 51–64.