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Reports of the Taxonomic Sub-Groups: Mysticetes[1]

Interface of social learning and culture with conservation in baleen whales

Abstract

Culture, defined as information or behaviours shared within a group and acquired from conspecifics through some form of social learning, acts as a second inheritance system which has important implications for conservation efforts. Understanding the influence of social learning and culture in animal's lives is essential to planning and predicting outcomes of conservation actions. Culture plays a significant role in cetaceans' lives, and some of the best evidence for social learning has come from baleen whales (mysticetes). An essential first step in a conservation framework is to identify key indicators of social learning in well-studied species which could be applied to other more elusive species. The Convention on the Conservation of Migratory Species of Wild Animals (CMS), an international treaty operating under the UN Environment Programme (UNEP), has recently integrated animal culture into their management framework. Here, as part of the UNEP CMS framework, we first evaluate key evidence for social learning and culture in baleen whales using case studies. We then provide key indicators by behavioural context to assist in identifying potential cases of social learning which may be useful in future conservation assessment and management frameworks.

1. Introduction

Conservation approaches and decision-making have the key goal of maintaining genetic and phenotypic diversity to ensure long-term persistence and adaptive potential of populations [1]. One phenotypic difference within and among populations can be behaviour [2,3]. Behavioural differences are often known to arise and be maintained through social learning. This has led to the increasing recognition of social learning and resultant culture as important factors that may impact the viability and structure of populations and influence animals' responses to conservation strategies [4,5]. Social learning is defined as any learning process that is facilitated by the observation of, or interaction with, another animal or its products [5–8]. Information or behaviours learnt through social learning can flow in various directions: vertically from parents to offspring; obliquely from older often unrelated individuals to younger individuals; and horizontally between peers [9]. From the building blocks of social learning, information may transmit through groups, creating local behaviours that persist over generations and time as traditions [5]. Culture is defined here, following others, as information or behaviours shared within a group and acquired from

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conspecifics by some form of social learning [4–6,10,11]. Cultures can therefore include traditions, especially those that involve a large proportion of a population, as well as rapidly changing behaviours that are being updated by social learning. Social learning and culture can occur across a diversity of contexts, from mate choice to foraging to migration routes [12–15], and multiple cultural traits may be present within a population or species [16]. For example, humpback whales (*Megaptera novaeangliae*) can maintain multiple independently evolving cultural traits within a population as they display song (vocal) culture, migratory culture, and socially learnt foraging traditions [16–19]. These baleen whales are one of the best studied cetaceans, but many other baleen whale species also display various socially learnt behaviours.

Here, we explore different case studies of social learning and cultural transmission in baleen whales by behavioural context. These case studies allow us to elucidate potential indicators for such behaviours in less well studied species and evaluate the strength of evidence for incorporating social learning and culture into conservation management across baleen whales. Previous publications have made the case that social learning and animal culture have important implications for conservation, through the interface of behaviour with vital rates, habitat use and responses to conservation measures [4,5]. Social learning can be a cause, consequence or marker of demography, vital rates, population genetic structure, phenotypic diversity and ecological niche separation [5,20,21]. We acknowledge, however, that ‘gold standard’ evidence involving controlled field or laboratory experiments are not always possible or potentially ethical in endangered and elusive species such as baleen whales. Instead, we rely on observed or inferred (correlative) patterns of behavioural expression to infer the presence of cultural processes and apply the precautionary principle [5,22]. This paper forms part of an UNEP CMS working group initiative on the conservation implications of animal culture. Below we explore evidence by behavioural context to elucidate social learning and cultural traditions across the baleen whales and important conservation implications of such behaviour.

2. Migratory traditions

a) Right whale migratory culture - North Atlantic right whales (NARW)

Cultural aspects of the movement and foraging ecology of North Atlantic right whales (NARW), *Eubalaena glacialis*, are poorly considered, yet understanding them will be important for their conservation. Baleen whales’ foraging movements cover substantial portions of ocean basins, and can be culturally driven (e.g., see below, [23]). NARW calves remain with their mother for around a year and appear to learn about foraging sites during this time [24].

In recent years, the distribution of NARW along the east coast of North America has changed [25], with the species abandoning at least one foraging site, the Bay of Fundy. At the same time, NARW have occupied two apparently new foraging sites, in the waters off southern New England, USA [26–28] and in the Gulf of St Lawrence [29,30]. Both ‘new’ sites were used by NARW historically [27,31], but were not used by many individuals until recently. The southern New England site appears to be used by many individuals, and this usage has increased in recent years [26,27]. On the other hand, the Gulf of St Lawrence is used by a very specific cohort of the same individuals, numbering a little under half of the species [30]. Most of these whales moved into the Gulf after 2015 [29]. Females observed in the Gulf are now more likely to calve than those that do not feed there [32]. As the poor reproductive success of NARW is a substantial contributor to their current decline [33], the survival and fecundity of these Gulf- using individuals is particularly important.

The oceanographic drivers of recent broad-scale changes in NARW foraging patterns are well understood [34]. Yet NARW's primary prey, *Calanus finmarchicus*, ranges across the North Atlantic from the coast of New England in the southwest to at least the north of Norway [35]. NARW's current abundance is just over 300 [36], but prior to whaling was 10,000 – 20,000 [37]. NARW do not occupy a substantial part of their former range (e.g., [38]), although some individuals have been observed making occasional forays to these areas (e.g., [39]). Their abundance is now so reduced that their density in much of their former range must be more than an order of magnitude less than it once was. That being so, the effect of this reduced density is that they will be extremely rare, and often absent from much of their former range. Biological oceanography explains the details of small-scale movements of NARW once they are in a foraging area [40,41]. An important question for NARW conservation is why do individual whales choose to use the foraging areas that they do? Understanding this will require a better understanding of the cultural factors underpinning NARW decisions driving their movements at large spatial scales. Given the conservation challenges posed by NARW's movements into these two new areas, and their likely distributional changes in response to further marine ecosystem disruption in the face of climate alteration [34,35,42], this area of research requires more consideration than it has received to date.

b) Right whale migratory culture – Southern right whales (SRW)

As with NARW, southern right whales (SRW), *Eubalaena australis*, appear to transmit preferences in migratory destinations from mother to offspring in the first year of life [15,43]. This traditional knowledge of migratory habitats is hypothesised to shape both SRW and NARW habitat use and recovery after exploitation, but, in the case of SRW, on a circumpolar scale allowing large-scale processes to be gleaned.

Prior to whaling, there were ~120,000 SRW spread across 12 wintering grounds [44]. The strength of connection between wintering grounds and mid- to high-latitude Southern Hemisphere foraging areas varied, and this geographic arrangement and varied connectivity created a kind of migratory network [44,45]. When whaling extirpated SRW using a specific migratory habitat, this led to the loss of the knowledge of the area as a good migratory destination. This loss of 'cultural memory', exacerbated by the removal of neighbouring populations and low density, means that once-inhabited areas are unlikely to be recolonized on a timeframe relevant to management (i.e., decades; [46]). On a circumpolar scale, this has led to a patchwork of recovery, with some wintering grounds recovering while others remain remnant or potentially extirpated (e.g., Chile-Peru and mainland New Zealand; see [45] for a recent review). As with the NARW, SRW appear to modify their foraging habitat use in response to climate change [47], while the same questions surrounding underlying mechanisms for this change remain unanswered.

The common traits of maternally-directed learning of migratory destinations and long-term site fidelity in *Eubalaena* are also present in humpback whales [17], and are likely to be shared with other baleen whale species. Furthermore, *Eubalaena* also appear to display some behavioural flexibility, shown by their ability to shift foraging grounds in response to changes in prey abundance. The mechanism(s) underpinning such shifts are poorly understood, as highlighted above in the NARW, but one potential factor is social learning of new migratory destinations.

c) Blue whale migratory memory

Blue whales, *Balaenoptera musculus*, use spatial memory to enhance the performance of their foraging migrations in the eastern North Pacific Ocean [23]. Spatial memory can play an important role in animal migration by allowing migrating animals to make movement decisions using information beyond their immediate perceptual ranges and to forecast future conditions based on experiences of past conditions [48,49]. Spatial memory can also improve efficiency of movement, for example, by facilitating navigation to high-quality forage patches [50,51] or stopover sites [52]. As a result of these benefits, memory is expected to be favored in organisms such as blue whales that are long-lived, which can have extended periods of learning, and in environments that have predictable variation.

By comparing ten years of satellite tracking from blue whales' northward migrations into the California Current Ecosystem with the timing of the spring bloom in prey availability, blue whale movements were found to closely match the long-term average phenology of prey availability, rather than contemporaneous conditions [23]. In addition, the same study found that blue whales foraged in locations that were highly predictable year-to-year and had high long-term productivity. These results indicate that blue whales use memory to time their northward migrations to exploit shifting hotspots of predictable and high-quality resources in the dynamic ocean environment. Because the timing of productivity in the California Current Ecosystem has significant interannual variability and habitat patches are highly dynamic [53], blue whales are thought to maximize their resource gain during migration by targeting predictable foraging areas, a strategy that should favor memory. This conclusion is supported by another study which found that over an 11-year period, blue whales consistently arrived in Monterey Bay, CA during time periods when prey availability was more predictable relative to time periods of higher but more variable prey availability [54].

While the above evidence demonstrates that spatial memory plays an important role in long-distance blue whale migrations, blue whales likely also fine-tune their movements at finer spatial scales in response to local, proximate conditions to locate individual prey patches. Moreover, another recent study found that the same blue whale population responds dynamically to oceanographic conditions in real-time to initiate their southward migrations to tropical breeding areas [55]. Thus, blue whale movements during migration are likely driven by a combination of scale-dependent internal (e.g., memory, perception, energetic state) and external (resource availability, social environment) factors. The extent this migratory behaviour is influenced by social learning and/or by individual experiences is unclear. However, blue whales likely have the capacity for social learning; blue whales sing population-specific songs (creating vocal dialects) with recent evidence suggesting some plasticity in the display [56,57]. Further research is required to tease apart the influence of social learning in the migratory and vocal behaviour of blue whales.

3. Foraging behaviours and traditions

a) Socially learned foraging tactics in humpback whales

Baleen whales exhibit a range of foraging tactics, but little is known of their development. A notable exception is the spread of lobtail feeding observed among the Gulf of Maine, USA humpback whales [16]. This is a behavioural sequence consisting of an individual hitting the water's surface with the fluke several times (known as 'lobtailing'), followed by a circular dive in the immediate area during which the individual produces bubbles to form a bubble-net, then a surface lunge within the bubble-net during which the whale gapes and engulfs shoals of prey [16,58,59]. The lobtail feeding strategy emerged following a local crash in the herring population, and population peaks of sand lance, leading to a shift in prey availability [60]. Over time, the behaviour spread to nearly 40% of the identified population. The strength of the evidence for social transmission in this behaviour is based on a number of factors. Firstly, its sample size was particularly robust (653 individuals) and restricted to individuals with at least 20 resightings (as opposed to the typical five resights [61]). Secondly, the study period covered nearly three decades and included the apparent introduction or innovation of lobtail feeding into the population. Finally, when network diffusion models of the spread included social learning, they were several orders of magnitude more supported than equivalent models without a social learning term. The case of lobtail feeding therefore illustrates strong evidence of horizontal cultural transmission being a key factor in the spread of a foraging behaviour across a population with ecological consequences in terms of prey selection.

In addition to the specific example of lobtail feeding, humpback whales show a high degree of plasticity in their foraging tactics [62] indicating significant potential for additional instances of social learning to emerge from ongoing research. These tactics include lunging [63], the use of bubbles [64] or body parts to corral prey [65], or scooping prey from the substrate [66]. Several of these behaviours involve coordination between multiple individuals, making a social component obligatory to their effective use. For example, synchronized lunge feeding occurs among large groups on the southeast Alaskan feeding grounds [62], while pairs or small groups of whales in the Gulf of Maine will engage in coordinated bottom-side roll feeding [66,67] and varieties of bubble-net feeding [68]. Coordination in a few of these strategies is thought to occur through accompanying contact foraging calls [67]. A specific example of emerging evidence for other socially learned tactics is the ‘trap feeding’ innovation observed off the coast of British Colombia [65]. This tactic involves an individual remaining at or near the surface with their mouth open and either spinning or utilizing their pectoral fins to push prey towards their mouth. Models of trap feeding suggest that both social associations and residence (which often correlates with social contact) may contribute to the observed spread, both of which factor into cultural transmission.

Humpbacks also appear to adapt and innovate their foraging tactics in response to surrounding environmental conditions. Instances of bubble-net feeding in the Gulf of Maine follow the movement of mobile prey patches [69], while lunge feeding rates decline with water temperature on the east Antarctic feeding grounds [70]. This illustrates where the intersection between social learning and conservation can occur within the context of foraging behaviour. Social learning is likely to be a key factor in the ability of this species to respond and adapt to environmental change through their plasticity in foraging techniques. Further, since these responses often involved specialisation, they could have significant downstream ecological effects on targeted prey. The clear importance of foraging culture in humpback whales and its relationship with both their ecology and their environment emphasizes the need to understand the role of foraging culture across baleen whale species.

b) Bryde’s whale foraging behaviours

The Bryde’s whale, *Balaenoptera edeni*, similar to humpback whales but unlike many other baleen whales, demonstrate behavioural plasticity in foraging behaviours, prey types and depths within and between regions [71]. Like other baleen whales, they typically lunge-feed by engulfing a large volume of water and filtering out prey but they can prey switch and change their foraging strategy depending on whether they are feeding on fish or zooplankton. In the Hauraki Gulf, Aotearoa/New Zealand, they use a chin-slapping tactic to aggregate zooplankton before rapidly turning on their side to engulf prey. In contrast, the same individuals will switch strategy and lunge at speed directly underneath fish prey [72]. There is a learned component to these behaviours with mothers observed chin-slapping and their calf then lunging through the aggregated zooplankton prey [72]. In the Gulf of Thailand, by contrast, Bryde’s whales remain almost stationary at the sea surface while fish spill into their wide-open mouth. This distinctive and commonly observed behaviour known as ‘tread-water feeding’ has been observed in adults and calves with the calf alongside their presumed mother learning this foraging behaviour [73]. Another recently described specialisation revealed Bryde’s whales undertake high-speed chases near the seabed to catch low density schools of fish in nearshore South African waters [74].

Whilst not highly social whales, Bryde’s may aggregate around prey patches where these behavioural specialisations are most likely transmitted either through direct observation of other adults or passed from mothers to calves. The high level of local specialisation in behaviours throughout the world may make these populations vulnerable to disturbance. For the populations where individuals may switch prey types, water depths and foraging strategies suggest a suite of learned behaviours to ensure their energetic demands are met. The range of atypical behaviours that Bryde’s whales use and the description of new local specialisations requires further examination of how these novel behaviours eventuate and how they are transmitted within populations. The above foraging case studies suggest that social learning may play a role in foraging ecology across multiple other species of baleen whale.

3. Vocal dialects and song culture

a) Humpback whale song culture

The songs of humpback whales are recognised as one of the strongest and clearest cases for social learning and resultant vocal culture in any species of animal [4,6,75,76]. Like many other baleen whales, humpback whales migrate annually between high latitude summer feeding areas and low latitude winter breeding areas (e.g., [77,78]). On migration as well as on the breeding grounds, male humpback whales produce complex, highly structured songs primarily during the breeding season [79]. Songs consist of a continuous string of vocalisations. Each song usually contains four to eight ‘themes’ usually sung in a consistent order, with each theme consisting of repeats of a particular ‘phrase’. The phrases themselves are comprised of sequences of sounds arranged in a specific pattern. Each phrase usually contains from one to five different sound types. Phrases usually last ten to fifteen seconds, while a theme may last from less than a minute to several minutes, and a song cycle (*i.e.*, all themes sung at least once) for around five to twenty minutes.

The song, however, is not just complex and hierarchical in structure. It is also shared among all the males in any particular population, so that males use the same sounds arranged into the same phrase types and resultant themes. Even more extraordinarily, however, the pattern of the song changes within the population over time, but all or most singers update their songs so as to maintain concurrent song matching [18]. The rate of song change is variable, but large-scale changes or ‘evolutions’ in songs generally occur over a few years although ‘revolutionary’ song changes, where entire new songs from a neighbouring population can enter and spread through a population, may occur over as little as a few months within a single singing season [75]. Song revolutions and shared song among different ocean basins occur within Southern Hemisphere populations [76], where the open Southern Ocean allows for mixing of individuals from different populations on the feeding grounds. This likely allows for songs to be transmitted between populations either via changes in individual migratory destinations or through shared migratory corridors as whales leave the feeding areas [80,81]. Most records of song revolutions come from the South Pacific Ocean [76,82,83], but recently a song revolution was documented in the South Atlantic (Brazil) [84,85], supporting evidence for a ‘Southern Ocean Exchange’ [80,86], which would allow a full circumpolar exchange of song. Thus far, there is no evidence of a song revolution occurring in the Northern Hemisphere.

Regardless of revolution or evolution, change is rapid even compared with the songs of most birds (e.g., white-throated sparrows, *Zonotrichia albicolis*; [87]). The only conceivable way in which this complex vocal display can be shared within (and between) populations but change so rapidly over time is through social learning, with each singer constantly listening to the songs of others and updating their own songs accordingly. Although the process itself is largely hidden from us due to the difficultly in studying individual whales over the necessary time spans, the products of this process, the songs themselves, tell a startlingly clear story of social learning and emergent culture, each population having, at any time, its own population-wide vocal display.

b) Acoustic behaviour in the bowhead whale

Among baleen whales, only humpback and bowhead whales (*Balaena mysticetus*) sing complex songs that change within and between years in a population. Like humpback whales, singing in bowhead whales occurs seasonally and it is presumed to be a male display, although this remains unconfirmed. However, unlike humpback whales, bowhead whales sing dozens of distinctly different song types within a single breeding season and this behaviour occurs under sea ice during the polar night (i.e., during the boreal winter) [88]. Each song bout consists of a 45 s – 2 min long phrase repeated over and over for many hours with time gaps of several seconds to a few minutes between songs [89]. Song types appear roughly sequentially over a season being heard for a few days or weeks and then not again within the breeding season or in following years, as far as we know. Data from multiple years and two populations of bowhead whales suggest that the notes used to compose songs change completely between years, driving song variability [88,90]. The recording of overlapping, distinctly different songs suggests that not all individuals in a population sing the same song at the same time [91,92]. The question arises as to whether each whale has their own song, whether there is song sharing among some individuals in a population, and whether individuals switch songs within a season and between years. Preliminary evidence suggests that some whales produce very similar songs, and these are recorded close in time (within days to at most weeks) while others do not [93]. What has yet to be explored is whether population-level differences in singing behaviour or song composition exist in the four different, geographically isolated populations of bowhead whales.

Bowhead whales can mimic the sounds of ice, other species living in the ice (e.g., beluga whales, *Delphinapterus leucas*, and bearded seals, *Erignathus barbatus*), and can create completely novel sounds and combinations of sounds. This includes the ability to produce two distinct sounds at once [94–96]. Counter-calling, in which migrating whales produce repeated “signature calls” in response to other swimming whales producing different signals, is perhaps the clearest example of bowhead whales exchanging information [97,98]. Although most counter callers maintained their signature call, in some instances, calling bowhead whales were heard to switch to the call type of another migrating whale which might be a form of acoustic mimicry [97]. The great level of flexibility in bowhead whale acoustic behavior indicates the capacity for learning and adaptation, suggesting that these variations in acoustic behavior might represent a form of culture [99].

4. Key indicators and conservation implications of social learning

Climate change and other anthropogenic impacts have placed many ecosystems and the animals within them under great pressure. In times of rapid change, adaptability is vital and for any species, the ability to adapt relies on variation (whether genetic or behavioural plasticity). While most conservation efforts to date have focused on preserving variation through genetics, the other major source of variability available to a species is via socially learned behaviours. These can vary from scales of familial groups to entire populations where they can result in cultures, i.e. behavioural differences within and between populations that are learnt socially.

As highlighted above, there are likely multiple facets to social learning and cultural behaviours in baleen whales. Where behaviours are not homogenous across a population or species, understanding the phenotypic variation of individuals and groups is essential for effective conservation management [4,5]. Such heterogeneity may create differences in vital rates and fitness of individuals across a population [14,100]. Adaptive behaviours may spread quickly when assisted by social learning, such as the exploitation of a new food source or habitat. It is also important to know whether a cultural trait is adaptive or not. In killer whales (*Orcinus orca*), for example, the cultural conservatism around diet in some populations has led to substantial declines in abundance [101]). While in others, novel learned foraging behaviours have spread and increased efficiency but may have their own conservation issues (e.g. human-wildlife conflicts from foraging around fishing gear) [102,103]. Expression of socially learnt behaviours can provide resilience, but identifying how to incorporate this information into conservation measures is challenging and likely situation specific. There is never a one- size-fits-all solution. As outlined in Brakes et al. [5], these endeavours are "intended to help guide practitioners towards 'future-proofing' populations by conserving both cultural variation and the capacity for innovation and social learning to maximize the resilience of vulnerable populations."

But how do we weight evidence and generalise this knowledge to those elusive species for which we have a paucity of information? Evidence from baleen whales does not involve controlled field or laboratory experiments, as these are not currently possible or potentially ethical. Instead, it relies on behavioural observation and, where needed, we infer the presence of cultural processes and apply the precautionary principle following Brakes et al., among others [5,22]. From our case studies, we highlight potential key indicators of social learning and culture, and how such learning might interface with various behavioural contexts (Table 1). Importantly, multiple, independently evolving traditions within a population may be present which stem from different behavioural contexts.

In the context of migratory traditions, we see fidelity to migratory terminals that is likely socially learnt, but we also see variation when individuals move to other feeding or breeding areas. There is an underlying behavioural conservancy but also variance that is likely adaptive. Apart from gene flow between populations, this may also lead to the 'rediscovery' of some previous breeding areas (e.g., the mainland of New Zealand for southern right whales, or Fiji for humpback whales). While good evidence for this is not yet available in these long-lived, slowly recovering species, the role that variance may play in conservation and recovery is clear.

Aside from cultural patterns in the use of feeding grounds, foraging behaviours themselves can be cultural. As shown above, humpback whales display a high degree of plasticity in their foraging tactics [62]. This indicates significant potential for additional instances of social learning to emerge from ongoing research following in the footsteps of lobtail feeding in the Gulf of Maine, the best-studied example to date. Foraging plasticity and change in behaviour within a population can be seen as strong potential indicators of social learning and should be examined further. The plasticity in foraging tactics of Bryde's whales is an excellent case in point.

Shared, rapidly changing song dialects are strong indicators of social learning in the context of vocal communication. Both humpback and bowhead whales display vocal plasticity and rapid change that cannot be explained without social learning. Other baleen whale species display song population dialects composed of less complex vocal repertoires. This provides weak evidence for social learning contributing to vocal behaviour(s) where song has been described. Social calls have been less well studied in most species but may also provide evidence of dialects. Whether or not the patterns of songs are adaptive is not known. If song patterns provide some indication of fitness, however, the patterns, although ephemeral in humpback and bowhead whales, have an important function beyond just being able to sing.

From this evidence, we provide species specific recommendations for the inclusion of social learning (and culture) into conservation decisions (Table 2). We hope this effort will assist both scientists and conservation practitioners along with policy makers in embedding animal culture and social learning into conservation policy and practice.

Table 1. Potential indicators of social learning and culture in baleen whales and how such learning might interface with various behavioural contexts. a) Does current evidence suggest or support the potential for a role of social learning and culture, by major behavioural contexts? Yes (Y), No Evidence (NE), or Unknown (UN). Evidence for potential social learning can be Vertical (V), Maternally directed (MD) (a special case within vertical), Oblique (O), Horizontal (H) or Unknown (UN). b) Is there variation in any of the behavioural contexts within or between populations? Yes (Y), No (N), or Unknown (UN). And are any of these variations persistent? (timescale: days, weeks, months, years, decades, centauries)? n/a = single population present. All = site fidelity, migratory, foraging, and communication all present. Popn = population.

	a) Potential indicators of social learning/culture				b) Variation and persistence of behaviour					
Species	Site fidelity	Migration	Foraging	Communication	Variation in behavioural trait within popn	Is this persistent?	Variation in behavioural trait between popn	Is this persistent?	Potential for social learning	References
Balaenidae										
Balaena mysticetus	Y (MD)	Y (MD)	Y (H?)	Y (H?)	Y (song, migration)	Y (weeks-decades)	Y (migratory, song)	Y (weeks-decades)	Y (MD, H?)	[88,89,104]
Eubalaena australis	Y (MD, H)	Y (MD)	Y (H)	NE	Y (migration, foraging)	Y (centuries)	Y (migratory)	Y (centuries)	Y (MD, H)	[105]
Eubalaena glacialis	Y (MD, H)	Y (MD, H)	NE	Y (UN)	Y (migration)	Y (centuries)	n/a	n/a	Y (MD, H)	[106]
Eubalaena japonica	Y (MD, H)	Y (MD)	NE	Y (UN)	Y (UN)	Y (UN)	Y (UN)	Y (UN)	Y (MD, H)	[107]
Balaenopteridae										
Balaenoptera acutorostrata	Y (UN)	Y (MD)	Y (UN)	Y (UN)	Y (foraging, song)	Y (UN)	Y (migration, song)	Y (UN)	Y (MD)	[108,109]
Balaenoptera bonaerensis	UN	Y (UN)	Y (UN)	Y (H)	UN	UN	UN	UN	UN	[110]
Balaenoptera borealis	Y (MD)	Y (MD)	UN	Y (UN)	Y (migration)	Y (years)	UN	UN	Y (MD)	[111,112]
Balaenoptera edeni	Y (UN)	Y (MD)	Y (MD, H)	UN	Y (foraging)	Y (decades)	Y (migration, foraging)	Y (decades)	Y (MD, H)	[71–73,113]
Balaenoptera musculus	Y (MD?)	Y (UN)	UN	Y (H)	Y (song)	Y (decades)	Y (song)	Y (decades)	Y (MD?, H)	[56]
Balaenoptera omurai	Y (UN)	UN	UN	Y (H)	Y (song)	UN	Y (song)	UN	Y (H)	[114]
Balaenoptera physalus	Y (MD?)	Y (MD?)	UN	Y (H)	Y (migration)	Y (UN)	Y (migration, song)	Y (years-decades)	Y (MD?, H)	[115,116]
Balaenoptera ricei	Y (UN)	N	UN	NE	N	N	n/a	n/a	UN	
Megaptera novaeangliae	Y (MD)	Y (MD)	Y (H)	Y (H)	Y (foraging, song)	Y (decades)	Y (all)	Y (years-decades)	Y (MD, H)	[16,17,76,84–86]
Neobalaenidae										
Caperea marginata	UN	UN	UN	UN	UN	UN	UN	UN	UN	
Eschrichtiidae										
Eschrichtius robustus	Y (MD)	Y (MD, H)	NE	NE	Y (migration)	Y (centuries)	Y (migratory)	Y (centuries)	Y (MD, H)	[117,118]

Table 2. Recommendations of inclusion of social learning (and culture) in conservation decisions based on current evidence (from Table 1). The weight of evidence: Strong (S); Weak (W); No Evidence (NE); Unknown (UN). Priority for integration into conservation management is primarily based on IUCN listings [119]; multiple listings may be present if there are IUCN, IWC or Nationally recognised subpopulations: Critically Endangered (CR); Endangered (EN); Vulnerable (VU); Near Threatened (NT); Least Concern (LC); Data Deficient (DD).

Species	**Common name**	**Evidence for inclusion in conservation decisions**			**Priority (IUCN Red List)**
		Migration	**Foraging**	**Communication**	
Balaenidae					
Balaena mysticetus	Bowhead whale	W	W	S	LC
Eubalaena australis	Southern right whale (SRW)	S	W	NE	LC (EN: subpopns.)
Eubalaena glacialis	North Atlantic right whale (NARW)	S	NE	W	CR
Eubalaena japonica	North Pacific right whale	W	NE	W	EN
Balaenopteridae					
Balaenoptera acutorostrata	Common minke whale	S	W	W	LC
Balaenoptera bonaerensis	Antarctic minke whale	W	W	W	NT
Balaenoptera borealis	Sei whale	W	UN	W	EN
Balaenoptera edeni	Bryde’s whale	S	S	UN	LC
Balaenoptera musculus	Blue whale	S	UN	S	EN
Balaenoptera omurai	Omura’s whale	UN	UN	W	DD
Balaenoptera physalus	Fin whale	W	UN	W	VU
Balaenoptera ricei	Rice’s whale	NE	UN	NE	CR
Megaptera novaeangliae	Humpback whale	S	S	S	LC (EN: subpopns.)
Neobalaenidae					
Caperea marginata	Pygmy right whale	UN	UN	UN	LC
Eschrichtiidae					
Eschrichtius robustus	Gray whale	S	NE	NE	LC

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Authors' contributions

E.C.G., E.L.C., P.C. and M.J.N co-wrote the manuscript and developed ideas for the tables, with core writing contributions from B.A., J.A.A., R.C., L.R., R.S.S-L., and K.S. All co-authors provided feedback and approved the final manuscript.

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