INTO THE BRAINS OF WHALES.

For copyright reasons we cannot publish the final article on the WDCS website. Thus the following document is a penultimate pre-print version of the paper that has since been published in ***Applied Animal Behaviour Science* 100 (103-116)** in October 2006. The conclusions and information presented in this version are the same as in the final one.

The final article can be obtained for a fee from the publishers: journal home page: http://www.elsevier.com/wps/find/journaldescription.cws_home/503301/description#description

or go to http://www.elsevier.com/wps/find/homepage.cws_home and follow the links.

Into the Brains of Whales.

Mark P. Simmonds,

Whale and Dolphin Conservation Society,
Brookfield House,
St. Paul's Street,
Chippenham, Wiltshire
SN 15 1LJ

Phone UK +44 1249 449 500 Fax +44 1249 449 501
Email mark.simmonds@wdcs.org

Abstract

Whilst studies on cetaceans have focused on a few populations of just a few species, various complex behaviours and social structures that support the notion that cetaceans should be regarded as intelligent animals have been revealed. The evidence to support this is reviewed here and is best developed for some odontocete species, although recent studies on minke whales show that the behaviour of baleen whales may be more complex than previously thought. As one consequence of high intelligence, the potential impacts of whaling and other removals may be far greater than they appear and a new approach to the conservation of these species – which takes into account their intelligence, societies, culture and potential to suffer - is advocated.

Key words: Cetaceans, Dolphins, Whales, Intelligence, Culture, Conservation, Welfare, Management

Introduction.

The mammalian order Cetacea includes over 80 known species of whales, dolphins and porpoises and popularly believed to contain some of the most intelligent animals. Although research on cetacean social systems lags some three decades behind equivalent work on primates (Connor *et al*., 1998), new research and expert analyses of research and behaviour (e.g. Whitehead, 2003; Mann *et al*., 2000; Connor *et al*., 1998) mean that, whilst acknowledging the limitations of our present understanding, we can now engage in a well informed consideration of cetacean intelligence, society and culture and attempt to relate our conclusions to urgent conservation and welfare issues.

However, there are a number of significant methodological difficulties involved in evaluating cetacean intelligence. Lusseau and Newman (2004) noted that "animal social networks are substantially harder to study than networks of human beings because they do not give interviews or fill out questionnaires…". Consequently, information must be gained by direct observation of individuals and their interactions with conspecifics. However, when studying marine mammals, the practical difficulties and expense involved in observational work are considerable, including the fact that individuals tend to be wide-ranging, fast moving and, in the case of several species, also very deep-diving. This has lead to the development of stringent photo-identification techniques which in recent years have provided an important insight into cetacean social networks. A further complication is the degree to which the cetacean behaviour observable at the sea surface reflects their activities more generally. This is especially true of the deep divers such as the beaked whales of the family Ziiphidae or the cachalots (or sperm whales), *Physeter macrocephalus*, which spend so much of their time in the depths. In the case of the latter in particular, studies at the surface are now being combined with sophisticated acoustic techniques which enable the animals to be monitored underwater, including monitoring particular individuals (Whitehead, 2003).

Another tier of complexity is provided by the likelihood that physically proximate individuals, apparently operating as a distinct group, may actually be in acoustic contact with other more distant animals creating a larger, dispersed social unit that is far more difficult to study. Janik (2000a) recently calculated that wild common bottlenose dolphin, *Tursiops truncatus*, whistles in the Moray Firth, Scotland, could be discernable 20-25 km away (in water of 10m depth and with a sea state of zero). The larger, louder whales may be in contact across entire ocean basins. In fact, cetaceans predominantly perceive their world using sound and remarkable hearing abilities; a distinction that makes comparison with primates difficult.

Another methodological issue is the anatomical differences between cetaceans and primates. Goold and Goold in *The Animal Mind* (1994) commented "… privately many primatologists (and publicly a few) concede that they assume that their subjects are to some degree self aware. In part this may arise not because primates are so much smarter than others species, but because it is easier for humans to read primate gestures and emotional expressions than the equivalents in, say, beavers or dolphins. It is also easier for us to empathize with behavioural responses to situations that could touch our own lives." Thus they highlight the possibility that our interpretation of cetacean behaviour might be hampered by a lack of empathy which could also have significant implications for conservation priorities and welfare issues.

In terms of behavioural interpretation, the physical differences between primates and cetaceans are significant. For example, whilst the arrangement of bones in the cetacean forelimb is similar to our own, the phalanges are encased within a flipper, which acts as an aqua-foil for lift and steering. Thus they lack the manipulative abilities of primates and cannot gesture or point with the same facility. Similarly, the musculature of their heads prohibits facial expressions, although a few species such as the beluga, *Delphinapterus leucas*, have some 'facial' mobility.

From their work on primates, Russon and Bard (1996) identified the following signs of intelligence: problem solving by insight; tool use/manufacture; imitation; sense of self; pedagogy and culture. This paper reviews the recent key literature and results concerning relevant cetacean attributes in these key areas and, additionally, considers some evidence that suggests emotional responses in cetaceans. It is also worth commenting at the outset that two evolutionary pressures on cetaceans are likely to have resulted in the development of high cognitive functioning: firstly the patchy un-predictable prey resources that they tend to exploit (Rendall and Whitehead, 2001) and, secondly, the cognitive demands of living in complexly bonded social groups (Dunbar, 2003).

Brain Development and Cetacean Senses

The size and complexity of the brain has long been used as a basic indicator of intelligence. The only animal group that rivals the primates in this regard is the cetaceans (Marino *et al.*, 2004). In fact, amongst the odontocetes (the toothed cetaceans), some relative brain sizes challenge the hominid mammalian line and arise from a substantial increase in encephalization apparent during the Oligocene (Marino, 2002). The relative cerebellum size is greater in some dolphins than in any of the primates, including humans (Marino *et al.*, 2000). The larger whales have large bodies as an adaptation to their ecological niches - including some organs such as the acoustic lens in the head of cachalots and their thick layer of blubber that require little nervous control - and this may explain why they fare less well if brain size is compared to body size (Parsons *et al.*, 2003).

Brain development in cetaceans has been related to acoustic signal ‘processing needs’. Most cetaceans are active ‘echolocators’, producing high frequency clicks to investigate the world around them (Simmonds *et al.*, 2004), these and the non-echolocators may also use ambient sounds to help them navigate (Clark cited in Carey, 2005). The full alacrity of cetacean hearing across the entire order is still not clear but some notion of their high sensitivity has been known since the early 1950s when it was shown that dolphins would respond with sound signals to a single BB shot (air rifle pellet) dropped into their pool (Benjamin and Bruce, 1982). In open waters, bottlenose dolphins can detect the presence of a water-filled sphere of diameter 7.6cm over distances of up to 110m (Au and Snyder, 1980).

Modern cetaceans have been evolving separately from their closest living relatives for at least 52 million years and from the primates for 92 million years. Marino *et al.* (2004) challenge the notion that the single remaining human lineage pruned down from a "bushier tree" of relatives means that several species of highly encephalised animals cannot co-exist. In fact, their review of the fossil record and extant species shows that multiple highly-encephalised delphinoids coexist today and have done so for at least 15 million years.

Examples of Intelligent Behaviours.

Brain size and comparative development is, at best, only an indicator of intelligence and a better way to access intelligence may be to look at behaviour, including communication skills. Captive cetaceans, especially bottlenose dolphins and orcas, *Orcinus orca*, have successfully been taught to repeat a wide range of actions. In fact, bottlenose dolphins modify taught behaviours and invent new ones (Norris, 2002). They appear to make their play more complex and difficult over time, arguably a ‘hallmark of intelligence’ and innovative play is also known in wild dolphins (figure 1).

The bottlenose dolphin can imitate both vocally and non-vocally and is considered by some to be the most sophisticated non-human imitator (e.g. Whitten, 2001). Herman (cited in Norris, 2002) suggests that the extensive vocal and behavioural mimicry of the dolphins is “a seemingly unique combination of abilities among non-human animals” and notes that dolphins can copy behaviours and sounds without extensive repetition or training. Behavioural fads have also been seen to spread spontaneously among captives.

Bottlenose dolphins have also shown that they can learn and generalise a variety of reporting tasks. This includes reporting on named objects in their environment; reporting on the behaviour of others (including other dolphins, humans and seals) by mimicry; and reporting their own behaviour (Mercado *et al.*, 1998). From their experiments, Mercado *et al.* (1998) suggest that dolphins can ‘flexibly access memories of their recent actions’ that are of sufficient detail for re-enactment. For example, bottlenose dolphins will ‘point’ at objects to guide humans to them. They do this by stopping their forward progress, often less than two metres from an object, aligning their anterior-posterior axis for a few seconds and then alternating head direction between the object and the trainer (Xitco *et al.*, 2004). These pointing behaviours are affected by the degree of attentiveness of the experimenters, and do not occur with humans absent.

Despite their lack of fingers and thumbs, both wild and captive dolphins may spontaneously manipulate objects. There is one well-documented use of tools in a wild Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, population which occurs in Shark Bay, Australia. The animals (almost exclusively females) are often seen carrying sponges on the ends of their beaks probably to protect them whilst they forage in the sediments on the seafloor where spiny sea urchins might otherwise cause puncture wounds (Smolker *et al*., 1997).

Another example of manipulation involves the bubbles that dolphins produce underwater. Breathing is a voluntary activity in cetaceans and the bubbles may be released in streams, clouds or as single bubble-rings. Although the physics that create these doughnut-shaped bubble formations are well understood (a bubble bigger than two centres in diameter tends to become a ring because of pressure differences between the top and bottom), the production of stable rings probably requires practice, expertise and forethought (McCowan *et al.*, 2000). Dolphins manipulate their bubble-rings by forming vortices around them, causing them to flip, turn vertically or fuse. McCowan *et al.* (2000) concluded that this form of manipulation was consistent with at least ‘low level planning’ prior to bubble production, again implying self-monitoring. They also report anecdotal evidence that young dolphins learn to produce rings from their mothers.

Self-Awareness.

Hart and Karmel (1996) identify the following behaviours as evidence of self-awareness: linguistic markers such as recalling personal memories; linguistic self-referencing (rare but known in language-trained apes); cognitive behavioural markers, particularly mirror self referencing based on marks on face (shown by apes); imitation; and emotional markers – divided into self conscious emotions (e.g. guilt, shame, embarrassment or pride) and empathy (e.g. helping a wounded individual).

Until recently, only humans and great apes had shown convincing evidence of mirror-self recognition but similar test have also been applied to bottlenose dolphins with unequivocal results (Reiss and Marino, 2001). Two captive animals exposed to reflective surfaces used them to investigate marks placed on various parts of their bodies by orientating themselves appropriately at the reflective surfaces. The dolphins did not display any attempts at social behaviour towards their mirror images and spent more time at the mirrors when marked than when sham-marked (where the marking process was repeated but without leaving a mark). One dolphin, when marked for the first and only time on the tongue, swam straight to a mirror and engaged in a mouth opening and closing sequence never before exhibited by this individual. Interestingly, and unlike chimpanzees, they showed no interest in the artificial marks placed on each other. Reiss and Marino (2001) suggest that this may be because dolphins, unlike primates, do not groom. The previous apparent confinement of self-recognition to man and apes has naturally generated interest in its relationship to higher levels of abstract psychological self-awareness. In humans, the ability to recognise oneself does not emerge reliably until about18-24 months of age. This dolphin study now indicates that this ability is not limited to the primate line of evolution.

Emotional responses may be an indicator of higher cognitive functions. However, Frohoff (2000) warns of the significant interspecies communication problems in interpreting cetacean emotions. For example, she reports that she has often seen captive dolphins exhibiting what were to her blatant indications of stress or aggression while interacting with human visitors, but that these signals are usually misunderstood or ignored. Nonetheless, various emotions (in addition to stress and aggression) have been attributed to cetacean behaviour. For example, two male orcas appeared to exhibit grief after the body of an older female was found dead. The circumstances giving rise to this observation are extremely rare as cetacean corpses are typically lost at sea. In life, the female was always accompanied by two younger males, believed to be her sons. These animals had been monitored since the 1970s and, uniquely, for a day or two after the dead body was found, in mid-November 1990, the two sons swam together but without contact with any other orcas, visiting again and again the places that their mother had passed in the last few days of her life. Rose (2000a), an experienced orca researcher, who reported this event, commented that their steady swimming retracing the mother's movements seemed expressive of grief. Both orcas are still alive, still swimming side by side and whilst now they do occasionally socialise with others, they are still often seen alone.

Other emotions proposed for cetaceans include parental love, as exhibited by orcas (Rose, 2000b), and prolonged grieving following the loss of a calf (Herzing, 2000a). Herzing

(2000b), a renown field biologist, also identifies ‘joy’ in the long term subjects of her work, the Atlantic spotted dolphins, *Stenella frontalis*, living off the Bahamas. Whilst these accounts of emotions might be dismissed because they are anecdotal or unproven, the fact that they are provided by experienced field scientists who have studied these animals for many years.

Frohoff (2000) reports that the altruistic behaviour sometimes shown to people by dolphins (for example, saving swimmers from drowning) is actually inconsistent; for example, whilst she has witnessed a small group of wild spotted dolphins deliberately go to help a nearby swimmer in distress (an action that has also been reported by others (Simmonds, 2003)), on another occasion she was ‘abandoned’ by a group of wild dolphins and left in the presence of a twelve-foot bull shark. Frohoff comments that such inconsistency indicates that “the emotional life of dolphins is probably as multifaceted and colourful as our own, and our appreciation of them needs to encompass their full range of emotional expression – not just the parts that we find attractive”.

One interesting example of an angry response from a dolphin is recounted by Schusterman (2000) and relates to the efforts to teach captive bottlenose dolphins artificial language in Hawaii. A female dolphin had just been given a series of gestural signals. When she didn’t respond correctly she was given ‘negative feedback’ and a moment later responded by grabbing a large plastic pipe floating nearby and hurling it at the trainer, missing the young lady’s head by inches. Cartilidge (pers comm.) reports a similar event when an ‘angry’ dolphin deliberately threw the spiny-part of a fish which injured its trainer's hand when he instinctively grabbed the missile. In fact, from his experience, Cartilidge (pers comm.) reports that in his experience captive cetaceans often behaved in an emotional (frustrated or angry manner) when given negative feedback.

Language.

Cetaceans are certainly amongst the most vocal of animals. However, the question of whether they have language has proved vexing. It was probably John Lilly in the 1960s who first speculated in favour of a dolphin language, although most biologists remain sceptical (Norris, 2002). Nevertheless, various lines of research support this notion, including attempts to teach dolphins artificial languages, thereby indicating that their mental capacities are adequate to such a task. Such studies, at the University of Hawaii, have shown that dolphins can acquire an artificial language including concepts of grammar and syntax (Norris, 2002). Gould and Gould (1994) commented that whilst the vocabulary taught to dolphins is relatively small (about three dozen words), their ability to decode 5 word sentences is "remarkable".

Several authors have proposed that bottlenose dolphins have distinctive 'signature whistles' that are specific to individuals and which also provide evidence of the significance of vocal mimicry in the wild. In a study of wild Scottish common bottlenose dolphins, Janik (2000b) found that these signals were copied and repeated by conspecifics that were out of visual contact, suggesting that they address each other individually, using learned sound patterns. Other researchers have challenged such a straight-forward signature whistle hypothesis (McCowan and Reiss, 2001) but there is agreement that bottlenose dolphins have a large whistle repertoire that changes substantially during the animals' development and that sequences of whistles could contain considerable information. McCowan and Reiss (2001) also noted that infant dolphins babble sequences of whistles that become more organised as they mature.

Research into cetacean communication may have been hampered by an exclusive focus on those calls that are most easily audible to humans, rather than their full range of vocalisations. This approach ignores the potential of their higher frequency 'clicks' to convey information (as well a primarily being a tool for echolocation)(Simmonds, 2004). Secondly, the captive conditions where most studies have been made may affect their communications by creating an inappropriate acoustic environment or not offering contact with conspecifics with common 'language'. There is also a general lack of adequate appreciation of both non-verbal signals and of the context of communications.

Wild cetaceans also have many dramatic natural behaviours that have no obvious purpose, such as breaching and tail-slapping, but which may have a communicatory function. Certainly the noise of a tail-slap or breach would be a more significant sound source underwater. Bubblestreams have also recently been suggested as having a role in communication (Fripp, 2005).

As with human languages, a particular emitted sound could have one meaning in one context – say during a co-ordinated feeding activity – and another during a different one, such as breeding behaviour. The meaning of the sound might also be further modified by posture of the emitter (or even the intended recipient) or the order of events during which it is created.

In the wild, in addition to the studies on bottlenose dolphin whistles, wild orca communications have also been studied in some detail. In British Columbia, matrilineal groups of resident orcas have 7-17 identified call types that vary amongst pods and the pods all have distinctive features in their call repertoires, creating ‘dialects’ (Ford, 2002).

Until we can monitor all possible sources of signals and the context in which they are made – which will require some very sophisticated underwater research – the issue of language will probably remain unproven. However, it is clear that many cetaceans live in co-operative societies in which they co-ordinate many of their activities, including predation, and their calls (which at the very least have the potential to convey considerable information) and other signals are important in this.

Group Living

“During the summer of 1977, thirty false killer whales (*Pseudorca crassidens*), floated in the shallows of the dry Tortugas for three days… A large male in the centre of the group lay on his side, bleeding from his right ear. When a shark swam by, the whales flailed their tails. Individuals became agitated when people separated the whales to return them to deeper water but became calm once back in physical contact with other whales.

Despite the risk of stranding and growing blisters from exposure to the sun, the group stayed together and did not leave until the male died on the third day" (Connor, 2000). Connor (2000) used this incident to illustrate the remarkably strong dependence of cetaceans on group living. This ranges from orcas which are regarded as living in the "most stable groups known among mammals" (Connor, 2000) to individuals, which whilst not appearing to live in stable groups, regularly join with others for particular activities, such as feeding (e.g. humpback whales, *Megaptera novaeangliae*) or migration (e.g. gray whales, *Eschrichtius robustus*). In between these strategies lie the flexible 'fission-fusion' societies of the bottlenose dolphins, in which individuals associate in small groups which change composition on a regular basis (sometimes daily or even hourly).

Connor (2000) emphasises that no other group of mammals has evolved in an environment so devoid of refuges from predators. Consequently, many species, especially the smaller open ocean dwellers, have "nothing to hide behind but each other". Not only will this factor have significantly shaped the societies of cetaceans but it will undoubtedly have bearing on the nature of their intelligence.

Connor *et al.*, 1998 report that two contrasting results emerge from comparisons of the better known odontocetes with terrestrial mammals, both convergent and divergent strategies. There are remarkable convergences between the social systems of cachalots and bottlenose dolphins and terrestrial species - particularly elephants and chimpanzees, respectively. However, studies on orcas and Baird's beaked whales, *Berardius bairdii*, reveal novel social solutions related to aquatic living. For example, the fact that neither male nor female orcas disperse from the groups that they were born into in some populations does not seem to have a terrestrial equivalent. Connor *et al.* (1998) suggest that it is the low cost of travel at sea for these superbly streamlined animals that allows them to range widely enough to ensure that different orca pods meet adequately often to allow breeding to occur effectively. In fact bottlenose dolphins and orcas represent two ends of a spectrum of cetacean social strategies: The first living in highly flexible 'fission-fusion societies' and the second exhibiting stable relationships that last years and sometimes life-times.

Whilst, the mating system of bottlenose dolphins has been ridiculously sensationalised by some in the media as 'gang rape', male competition is a common component of many mammal mating systems. It is taken to a particularly sophisticated level in some (but not all) bottlenose dolphin populations, where males form 'nested' levels of allegiances to sequester females in reproductive condition (Krutzen *et al.*, 2004). Allegiances within social groups are comparatively rare in mammals. In fact, bottlenose dolphins are the only species other than humans wherein the males have been shown to form two levels of nested alliance formation within a social group. They also have two strategies in this regard: the first consists of small long-term alliances (the longest lasting of which was observed for 17 years). These pairs or trios of males control access to individual females in reproductive condition. Teams of two or more of these first order alliances may co-operate to attack other allegiances or defend such attacks themselves.

The second strategy is where the first order alliances are more labile and exist within a stable second-order alliance or 'super-alliance' within which the males frequently switch their alliance partners. Connor *et al*. (2001) found that whilst the shifting make-up of alliances invited the hypothesis that members treated each other as interchangeable resources, there are strong preferences and avoidances at play. In addition, Krutzen *et al.* (2003) have shown that the animals following the first strategy tend to be more closely related than by chance and, in the second strategy, the males in the group are not closely related. From a recent study of paternity conducted on the well-researched bottlenose dolphins of Shark Bay, Western Australia, it appears that these co-operative strategies are successful, although calves are also fathered by males without alliance partners (Krutzen *et al.*, 2004).

Another form of co-operative behaviour was recently reported for common bottlenose dolphins in Cedar Key, Florida (Gazda *et al*., 2004). Dolphins hunting in a group have two types of specialisations: the 'driver dolphins' (which are consistently the same individuals in the two groups studied) herd fish towards the 'barrier dolphins'. Group hunting with a division of role and individual specialisation is very rare and Gazda *et al.* (2004) report that it has only been previously recorded from a study of co-ordinated group hunts in lions, *Panthera leo*.

Lusseau and Newman (2004) recently applied a new tool to the study of dolphin populations revealing further complexity. They applied techniques developed for the analysis of human social networks to the well-studied social network of the 62 Indo-

Pacific bottlenose dolphins, *Tursiops aduncus*, of Doubtful Sound, New Zealand. In addition to identifying various sub-groupings within the population, this technique identified what they termed ‘broker dolphins’ that acted as links between sub-communities. These ‘brokers’ played a crucial role in the social cohesion of the community as a whole.

There have been few studies of the societies of baleen whales. The humpback whale is the best studied baleen species but research has to a significant extent focused on male mating strategies (prompted by the whale’s complex calls), foraging ecology and life history (Clapham, 2000). Connor (2000) comments that “although baleen whales appear to lack the stable social groups that are common among odontocetes, several observations suggest that long-term bonds might be more common than is commonly thought to be the case.” Alongside other factors he notes the potential for long distance communication in these species.

In the case of the minke whales (the commercial whalers currently favoured target species) very little is known of their behaviour. However, there is one place where one population of minke whales on the Great Barrier Reef in Australia is proving tractable to long-term study, including recognition and monitoring of individuals. This population of dwarf minke whales - regarded as an undescribed sub-species of the northern minke whale (i.e. *Balaenoptera acutorostrata* sp.) – is being studied with the help of local whale watching operations (Birtles and Arnold, 2002 and Birtles *et al.*, 2002). Known adult females return on an annual basis to within metres of where they were previously seen.

Known individuals have also been regularly seen together in a style that at least emulates the fission-fusion society of some dolphins. Overall, these six tonne animals are reported to be remarkably inquisitive and sociable, and a range of repeated behaviours have been identified for them: bubble streaming and blasting; rolling over in the water, white belly up; and jaw gapping and jaw clapping (Arnold and Birtles, 2002). Moreover, whilst these minke whales, like all the other baleen species, lack the system of air sacs in the forehead region used by toothed whales to produce sounds, they are far from mute. Their sounds probably come from the larynx region (although they also lack vocal cords) and are in the 10-9,400 Hz range (so for the most part audible to us) including a mechanical sounding call that has three rapid pulses and a longer trailing note. They also produce sounds that are described as grunts, moans and belches.

Culture.

There is an emerging but compelling argument that some cetacean species exhibit "culture", specifically "information or behaviour - shared by a population or subpopulation - which is acquired from conspecifics through some form of social learning" (Rendall and Whitehead, 2001). In this case, the definition of "population" is taken to include the whole species and "subpopulation" refers to any sub-division of a population which contains at least a few individuals. Culture has a widespread cross-generational effect on behaviour and, therefore, on phenotypes and population biology. Like genes, it is also an inheritance system and affects phylogeny (for a fuller discussion see Whitehead *et al.*, 2004).

The evidence for culture in cetaceans includes experimental studies on bottlenose dolphins showing that they have sophisticated social learning abilities, including motor and vocal imitation; observational evidence for imitation and teaching in orcas and also some other whale species; cultural transmission in several species – notably the complex and stable call dialects and behavioural (foraging patterns and techniques) cultures of sympatric orcas; group based cultures in cachalots , including distinctive dialects; and, the song of male humpback whales – where all males on any breeding ground sing the same song, which evolves over months and years (Whitehead, 2002). Sympatric groups within a particular cetacean population can also exhibit different cultural traits. For example, within the population of bottlenose dolphins in Shark Bay, Western Australia, they are least four distinctive foraging specialisations, at least some of which are likely to be transmitted from mother to calf. Indeed, this has recently been shown to be the case for sponge-bearing (Krutzen *et al*., 2005). Similar divisions within populations according to foraging specialisations are found in other dolphin communities, including cases of human-dolphin fishing co-operation (Simmonds, 2004) Another example could be the high-risk stranding-feeding behaviour exhibited by the orcas of one population in Patagonia: a behaviour which is clearly learnt by the calves from older animals – and where a mistake could prove lethal (Simmonds, 2004).

The populations of orcas off the west coast of Canada have various hierarchical divisions and much of this structuring appears cultural. The primary division is between resident orcas and transients, which are sympatric but show differences in feeding behaviour, vocalisations, social systems, morphology, and genetics. They may, in fact, be incipient species, although the original division between them was essentially cultural (Baird, 2000). The complex, stable and sympatric vocal and behavioural cultures of orca groups have being suggested as being more advanced than those exhibited by chimpanzees (Norris, 2002) and as having no parallel other than within human society (Rendell and Whitehead, 2001).

Cachalots also have significant divisions in their societies which recent research has started to unravel (Whitehead 2003). These large, deep-diving, click-producing whales share their ranges with several thousand others of their own species and females and young form groups of around 20-30 individuals that travel together and coordinate their activities. These groups often consist of two or more social units which are long term companions interacting over years. Certain sets of catchalot social units possess very similar coda (click pattern) repertoires and these units, termed “clans”, are believed to represent cultural variants (Whitehead, 2003). There are some 4-5 clans found across the North Pacific and each spans many thousands of kilometres and probably consists of tens of thousands of animals. Whitehead (2003) notes that the clans are not perfectly matrilineal and there is one record of an individual that swapped clans.

The notion of culture within cetaceans has been challenged. The original keystone paper by Rendell and Whitehead appeared together with 39 written commentaries, some strongly critical and some supportive (Norris, 2002). This led to a lengthy debate within the literature. More recently, Whitehead *et al.* (2004) have commented that in cultural societies, individuals with important cultural knowledge may have a population significance far in excess of their reproductive capacity. Most large whale populations were enormously reduced by commercial whaling (which peaked during the 1960s) but, whilst some recovery is apparent in certain areas, in some other traditionally important habitat areas there is none. It is therefore plausible that the whalers destroyed not just numerous individuals but also the cultural knowledge that they harbour relating to how to exploit certain habitats and areas. Thus, Whitehead *et al*. (2004) suggest “non- human culture” should be integrated into conservation biology.

Conclusions

The issue of cetacean intelligence has been very controversial in the last few decades and the enthusiasm of some popular authors for promoting cetaceans as highly intelligent in the 1960s arguably caused a counter-productive back-lash (Samuels and Tyack, 2000); with sceptics highlighting lack of rigorous scientific proof, reliance on anecdotal information and failure to separate instinct from intelligence. Gaskin underpinned his very thoughtful – and still widely cited - criticism by asking “two basic questions:
1) Is there any real social structure in cetacean populations?
2) Do cetaceans have highly developed social behaviour?” (Gaskin, 1982).

We now have the benefit of more than two decades of further and increasingly sophisticated research which has shown relationships and behaviours that were hinted at in Gaskin's day. I therefore propose that the answer to Gaskin's two primary questions is now, for some species at least, an unequivocal 'yes'.

The emerging body of evidence for the advanced cognitive abilities of some cetaceans is outlined in table 1. and, if we accept this perspective, the next question is how should this knowledge affect our interactions with these animals? Our primary interactions are broadly summarised in figure 2. and to this can be added some statistics, for example:

- It has been estimated that some 200,000 cetaceans are killed annually in fishing nets (Read *et al*., 2003);
- The last available data for Japanese whaling reveal that only 40.2% of animals die 'instantaneously' (Brakes and Fisher, 2004) - similar statistics from other hunts are presented in table 2; and
- "A blue whale, which lives 100 years, that was born in 1940, today has had his acoustic bubble shrunken from 1,000 miles to 100 miles because of noise pollution" (Clark in Carey, 2005).

There is not room here to fully explore the relationship between the intelligence of these animals and the conservation and welfare matters that affect them, but it is clear that deaths in hunts and fishing nets may often be prolonged and painful and also significantly affect more members of the population than just the animals killed. It is also clear that we are having a widespread impact on their environment. Our relationship with these animals therefore needs to move to a new paradigm. What were previously regarded as 'living marine resources' – and typically widespread species distributed across an inexhaustible sea - should now be recognised as unique individuals, communities, societies and cultures and valued as such.

Acknowledgements.

Grateful thanks to Nicola Kemp, Charlie Phillips, Doug Cartilidge (who was a dolphin trainer in the 1970s), Phillipa Brakes, Sue Fisher, Steve Isaac and Alastair Birtles for their insights and their comments on an earlier draft. Whilst the author has drawn on information gleaned from experiments on captive dolphins, he wishes to make it clear that he does not believe cetaceans should be held in captivity, nor that these experimental studies justify this.

References

Baird, R.W. 2000. The killer whale – foraging specialisations and group hunting. In: Mann, J., Connor, R.C., Tyack, P., Whitehead, H. (Eds). Cetacean Societies. University of Chicago Press, Chicago, pp. 127-153.

Benjamin, L. T., Bruce, D. 1982. From a bottle-fed chimp to a bottlenose dolphin: a contemporary appraisal of Winthrop Kellog.

Birtles, A., Arnold, P. 2002. Dwarf minke whales in the Great Barrier Reef – current state of knowledge. CRC Reef Brochure. CRC Research Centre Ltd., Townsville Australia. Available at: http://www.reef.crc.org.au/publications/brochures/index.html

Birtles, R.A., P.W. Arnold, Dunstan, A. 2002. Commercial swim programmes with dwarf minke whales of the Northern Great Barrier Reef, Australia: Some characteristics of encounters with management implications. Australian Mammalogy 24: 23-38.

Brakes P., Fisher, S. 2004. Commercial and Aboriginal Subsistence Whaling. Chapter 6 in Brakes, P., Butterworth, A., Simmonds, M. and Lymbery, P. 2004 (Eds). Troubled Waters – a review of the welfare implications of modern whaling activities. World Society for the Protection of Animals, London. Available at www.wspa-international.org

Carey, B. 2005. Noise pollution disrupts whale communication. MSNBC news 20/2/2005: at: http://www.msnbc.msn.com/id/7003587/

Clapham, P.J. 2000. The Humpback Whale – seasonal feeding and breeding in a baleen whale. In Mann, J., Connor, R.C. Tyack, P.L. and Whitehead, H. 2000. [Eds] Cetacean Societies: field studies of dolphins and whales. The University of Chicago Press, Chicago, USA. PP 173-196

Connor, R.C. 2000. Group living in whales and dolphins. In Mann, J., Connor, R.C. Tyack, P.L., Whitehead, H., 2000. [Eds] Cetacean Societies: field studies of dolphins and whales. The University of Chicago Press, Chicago, USA Pp 199- 218

Connor, R.C., Heithaus, M.R., Barre, L.M., 2001. Complex social structure, alliance, stability and mating access in a bottlenose dolphin 'super-alliance'. Proc. R. Soc. Lond. B 268: 263-267.

Connor, R.C., Mann, J., Tyack, P.L., Whitehead, H., 1998. Social evolution in toothed whales. Trends in Ecology and Evolution 13: 228-232.

Dunbar, R.I.M., 2003. The Social Brain: mind language and society in evolutionary perspective. Annu. Rev. Anthropol. 32: 163-81.

Ford, J.K.B., 2002. Dialects In Mann, J., Connor, R.C. Tyack, P.L., Whitehead, H., 2000. [eds] Cetacean Societies: field studies of dolphins and whales. The University of Chicago Press, Chicago, USA.

Fripp, D., 2005. Bubblestream whistles are not representative of a bottlenose dolphin's vocal repertoire. Marine Mammal Science 21: 29-44

Frohoff, T. 2000. The Dolphin's Smile. In: Berkoff, M. [Ed] The Smile of the Dolphin. Discovery Books, London.

Gaskin, D.E, 1982. The ecology of whales and dolphins. Heinemann, London and Exeter.

Gazda, S.K., Connor, R.C., Edgar, R.K., Cox, F., 2004. A division with role specialization in group-hunting bottlenose dolphins (Tursiops truncatus) off Cedar Key, Florida. Proc.R.Soc.B. 272(1559):135-140

Goold, J.L., Goold, C.G., 1994. The Animal Mind. Scientific Anerican Library, New York.

Hart, D., Karmel, M.P., 1996. Self awareness and self-knowledge in humans, apes and monkeys. In Russon, A.E., Bard, K.A., and Parker, S.T. (Editors) Reaching into the thought – The minds of great apes. Cambridge University Press.

Herzing, D.L., 2000a. A trail of grief. In: Berkoff, M. [Editor] The Smile of the Dolphin. Discovery Books, London.

Herzing, D.L., 2000b. The pleasure of their company. In: Berkoff, M. [Editor] The Smile of the Dolphin. Discovery Books, London.

Janik, V., 2000a. Source levels and the estimated active space of bottlenose dolphin (Tursiops truncatus) whistles in the Moray Firth, Scotland. J Comp Physiol A 186: 673-680.

Janik, V., 2000b. Whistle matching in wild bottlenose dolphins Science 289: 1355-1357.

Krutzen, M., Barre, L.M., Connor, R.C., Mann, J., Sherwin, W.B. 2004. ‘Oh father: where art thou?’ – Paternity assessment in an open fission-fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. Molecular Ecology: 13: 1975-1990

Krutzen, M., Mann, J., Heithaus, M.R., Connor, R.C., Bejder, L. and Sherwin, W.B. 2005. Cultural transmission of tool use in bottlenose dolphins. PNAS 102: 8939-8943

Lonsdale, J. 2000. Bottlenose Dolphin Kill - Futo Port, Shizuoka, Japan**,** 14th October 1999. Environmental Investigation Agency unpublished briefing prepared for the UK government. 7 pages.

Lusseau, D., Newman, M.E.J., 2004. Identifying the role that animals play in their social networks. Proc. R. Soc. Lond. B (Suppl.) 271: S477-S481

Marino, L. 2002. Brain Size Evolution. In Perrin, W.F., Wursig, B. and Thewissen, J.G.M. [Eds] 2002. Encyclopedia of Marine Mammals. Academic Press, San Diego, USA. Pp: 158-162.

Marino, L., Rilling, J.K., Lin, S.K., Ridgway, S.H. 2000. Relative volume of the cerebellum in dolphins and comparison with anthropoid primates. Brains, Behaviour and Evolution. 56(4) 204-211

Marino, L., McShea, D.W., M.D. Uhen. 2004. Origin and evolution large brains in toothed whales. The Anatomical Record Part A 81A: 1-9

McCowan, B., Marino, L, Vanve, E., Walke, L., Reiss, D., 2000. Bubble ring play of bottlenose dolphins (Tursiops truncatus): implications for cognition. Journal of Comparative Psychology 114: 98-106.

Mercado III, E., Murray, S.O, Uyeyama, R.K., Pack, A.A. and Herman, L.M. 1998. Memory for recent actions in the bottlenose dolphin (*Tursiops truncatus*): repetition of arbitrary behaviours using an abstract rule. Animal Learning and Behaviour 26(2): 210-218.

Mann, J., Connor, R.C., Tyack, P. and Whitehead, H. 2000. Cetacean Societies – Field Studies of Dolphins and Whales. The University of Chicago Press, Chicago and London

Norris S. 2002. Creatures of culture? Making the case for cultural systems in whales and dolphins. Bioscience 52: 9-14.

McCowan XXXand Reiss D.,. 2001. The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalisations. Animal Behaviour 62: 1151-1162

Parsons, E.C.M., Rose, N.A. and Simmonds, M.P. 2004. Whales – individuals, societies and cultures. Chapter 4 in Brakes, P., Butterworth, A., Simmonds, M. and Lymbery, P. 2004 (editors). Troubled Waters – a review of the welfare implications of modern whaling activities. World Society for the Protection of Animals, London. Available at www.wspa-international.org

Read, A.J., Drinker, P., Northridge, S. 2003. By-catches of marine mammals in US fisheries and a first attempt to estimate the magnitude of global marine mammal by-catch. Paper submitted to the Scientific Committee of the International Whaling Commission SC/55/BC. 12 pages.

Reiss, D. and Marino, L. 2001. Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. PNAS 98: 5937-5942

Rendall, L. and Whitehead, H. 2001. Culture in whales and dolphins. Behavioural and brain sciences, 24: 309-324.

Rose, N.A. 2000a. A death in the family. In: Berkoff, M. [Editor] The Smile of the Dolphin. Discovery Books, London.

Rose, N.A. 2000b. Giving a little latitude. In: Berkoff, M. [Editor] The Smile of the Dolphin. Discovery Books, London.

Russon, A.E. and K.A. Bard. 1996. Exploring the minds of great apes: Issues and controversies. In Russon, A.E., Bard, K.A., and Parker, S.T. (Editors) Reaching into the thought – The minds of great apes. Cambridge University Press.

Samuels, A and Tyack, P. 2000. Flukeprints – a history of studying cetacean societies. In (eds) Mann, J., Connor, R.C., Tyack, P. and Whitehead, H. 2000. Cetacean Societies – Field Studies of Dolphins and Whales. The University of Chicago Press, Chicago and London. .

Schusterman, R.J. 2000. Pitching a fit. In: Berkoff, M. [Editor] The Smile of the Dolphin. Discovery Books, London.

Simmonds, M.P. 2004. Whales and Dolphins of the World. New Holland Publishers Ltd., London, UK.

Simmonds, M.P., Dolman, S. D., Weilgart, L. 2004. Oceans of Noise 2004. Whale and Dolphin Conservation Society, Chippenham, UK. Available at: http://www.wdcs.org/dan/publishing.nsf/allweb/48A0C8D9C559FA0680256D2B004027D4

Smolker, R., Richards, A., Connor, R., Mann, J. and Berggren, P. 1997. Sponge-carrying by dolphins (Delphinidae, *Tursiops* sp.)- A foraging specialisation involving tool use. Ethology, 103: 454-465.

Whitehead, H. 2002. Culture in whales and dolphins. In Perrin, W.F., Wursig, B. and Thewissen, J.G.M. [Editors] 2002. Encyclopedia of Marine Mammals. Academic Press, San Diego, USA.

Whitehead, H. 2003. Sperm whales: social evolution in the ocean. University of Chicago Press, Chicago, USA.

Whitehead, H., Rendall, L., Osbourne, R.W. and Wursig, B. 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new direction. J. Biological Conservation 120: 431-441.

Whitten, A. 2001 Imitation and cultural transmission in apes and cetaceans. Behav. Brain Sci. 24: 359-60.

Xitco, M.J., Gory, J.D., Kuczaj II, S.A. 2004. Dolphin pointing is linked to the attentional behaviour of a receiver. Anim Cogn (2004) 7: 231-238

Table 1. A summary of evidence for higher cognitive functioning in cetaceans.

---

i. High level of encephalisation, including very well developed cerebellum in many species

ii. Long lives and long periods of parental care (evidence of post-reproductive care-givers) – exploiters of typically patchy and unpredictable prey

iii. Ability to learn complex behaviours and solve problems

iv. Ability to improvise/innovate

v. Tool use (but not tool manufacture)

vi. Vocal and behavioural imitation

vii. Ability to learn artificial languages (limited vocabulary but understand grammar and syntax)

viii. Many species exhibit closely co-ordinated behaviours

ix. Many species have complex social interactions

x. Evidence of self awareness, awareness of others, including emotional responses

xi. Cultural transmission of information

Table 2. Examples of recent whaling data based on information provided to the International Whaling Commission (from Brakes and Fisher, 2004). TTD = Time to death.
.

Nation concerned /species	Year	Number killed	% died immediately	Average TTD	Max TTD (minutes)	Number struck but lost
Norwegian Minke whales	2001 2002	552 634	79.7 80.7	145 seconds 141 seconds	90 90	10 1
Japan Minke whales	2001/2002 2002/2003	440 440	33.0 40.2	203 seconds 157 seconds	No data No data	No data No data
Russian Federation Gray whales	2002	131	-	32 minutes	56	-
Russian Federation Bowhead whales	2002	2	-	41 minutes	53	1
US (Alaskan Innuit hunt) Bowheads	2002	39	-	-	-	11
Greenland (West) Minke whales	2002	131	5.3	16 minutes	300	5
Greenland (East) Minke whales	2002	10	0	21 minutes	90	0
Greenland Fin Whales	2002	13	7.7	9 minutes	25	0

Figure 1.

Common bottlenose dolphin in the Moray Firth, Scotland, playing with seaweed – a frequently observed behaviour of this particular individual (Phillips, pers. comm.). Photocredit: Charlie Phillips.

Figure 2

The Consequences of human activities in the marine environment for cetaceans.