A Review of the Scientific Justification for Maintaining Cetaceans in Captivity

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CONTENTS

Summary

1. Increasingly, zoos and marine parks are arguing that research is an important part of their role and that knowledge acquired in this way is essential for conserving cetaceans in the wild. This report reviews the research that has been conducted on whales and dolphins in captivity. It documents the information that has been gathered on haematology and blood chemistry; disease; physiology; experimental psychology and cognition; behaviour; reproduction; captive breeding; and environmental protection. The report questions the relevance of these studies to free-living whales and dolphins, their conservation and the justification for experiments on captive animals.

2. Normal ranges for haematology and blood biochemistry have been established for the majority of commonly held whales and dolphins. Whilst these data are useful for monitoring the health of captive animals, their relevance to free-living animals is limited because captivity leads to alterations in basic haematology and blood biochemistry. In addition, considerable individual variation exists in haematology and blood biochemistry such that individual baselines are needed to interpret their significance and this is not feasible for wild animals.

3. Some similarities exist between the types of disease seen in captive and wild cetaceans. Bacterial pneumonia is an important cause of morbidity and mortality in both categories. However, important differences exist which make captive animals a poor model for disease in free-ranging populations. For example, captive animals do not carry a parasite burden as they are routinely treated with anthelmintics. In contrast, parasitic disease is ubiquitous in wild cetaceans. In addition, knowledge from captive studies of disease has given little insight into the recent outbreaks of morbillivirus disease and large scale mortality of some species of dolphins.

4. Exercise and respiratory physiology has been studied using animals trained to undertake tasks in a pool or to accompany boats to sea. Whilst these have provided interesting knowledge about comparative physiology, they have been limited by the physical dimensions of pools (precluding studies on diving) together with the relatively sedentary life style and abnormal diet of captive animals. If such data were to be used uncritically in management programmes, it could be misleading.

5. Experimental psychology and cognition has dominated the research agenda on captive cetaceans. Bottlenose dolphins have been the primary species for these studies because of their relatively small size and ease with which they can be trained. Research on the visual, auditory and echolocation systems has been driven, in large part, by the US Navy's interest in the application of such knowledge to improving underwater detection systems. These studies have revealed that dolphins have extensive cognitive abilities and sophisticated sensory systems for exploring their environment. However, the extrapolation of this information to conservation issues, such as entanglement in nets, is limited by the barren acoustical and visual environment of captivity. This is further constrained by the large element of learning that takes place in the use of these senses. Learning in captivity may give a false impression of animals' abilities in the wild.

6. The social organisation of animals in captivity is controlled by dominance hierarchies. In contrast, the situation in natural environments is more dynamic and aggressive behaviours are much less a feature of the description of free-living cetaceans. Confinement also results in stereotyped behaviours such as uni-directional circling of the pool. Studies of the behaviour of wild animals have been used to improve the conditions of animals kept in captivity by indicating appropriate group size and sex composition. However, studies of behaviour in captivity do not seem to have the potential to improve the conservation of wild cetaceans in the same way as they are too artificial.

7. Zoos and marine parks have improved their survival and breeding records for some species such as the bottlenose dolphin and orca. Other species, such as the river dolphins, have extremely poor survival records in captivity. Basic reproductive data on calving intervals and age at sexual maturity has been obtained for some species. It would be dangerous to apply this information directly to the conservation and management of wild populations as it may overestimate their reproductive capacities. Feeding has a marked effect on these parameters and the unnatural composition and idealised nature of zoo diets mean that animals may be growing more quickly and reproducing earlier and more frequently than in the natural environment.

8. The captive bred populations which exist to date cannot be considered as self-sustaining populations. No scientifically based plans to conserve genetic diversity exist. If a plan were to be designed to maintain 90% of the genetic diversity of the original population over 200 years this could require several thousands of animals to be kept. Rather than having any such justifiable target, breeding programmes have consciously and unconsciously selected for an a captivity adapted population which may soon be better thought of as 'domesticated'.

9. It has been suggested that the knowledge gained from species which breed well in captivity could be used in developing captive breeding plans for endangered species such as the baiji. However, species behave very differently in captivity and what is appropriate to one species may be misleading for others. Comparing the rather robust bottlenose dolphin to the shy baiji may prove counterproductive. Understanding a species' ecology and behaviour in the wild to shape conservation efforts will provide more relevant knowledge.

10. Some research has been conducted which aspires to be directly relevant to addressing environmental harm including oil pollution and entanglement in fishing gear. The effects of oil pollution have been studied on captive bottlenose dolphins which show that there is little physical evidence of harm but that animals try to avoid oil sheens if possible. This has been interpreted as meaning oil spills are of little significance to dolphins. However, such information may be of little use to the policy maker who should know of the considerable harm that oil spills have on other wildlife.

11. Experiments to attempt to reduce the problem of entanglement in fishing gear have taken place. The extent to which porpoises can detect nets of different thickness and whether they can be deterred using sound or reflectors has been investigated,

for example.   Noise as a deterrent shows the most promise but the same sorts of experiments have been conducted directly in the wild. These studies are obviously more realistic and have also detected effects on prey, something not identified in laboratory studies.

12. The report concludes that the physically restricted conditions of captivity, together with animals' behaviour being learnt in a unnatural environment, the small numbers of highly trained animals involved and the changing genetic basis of the captive cetacean population means that the scientific basis for captive animals acting as a models of wild animals is in increasing doubt. The increased sophistication of studies on free-living animals and the greater relevance of data from those studies further throws the justification for research on captive cetaceans into doubt.

1. Introduction

Cetaceans have been held in captivity since the 1860s (Defran & Pryor, 1980) and since that time around 35 different species have been kept with varying levels of success. The five most commonly held species are listed in Table 1.1. The bottlenose dolphin (*Tursiops truncatus*) has long been the most commonly held species, mainly because it combines performance trainability with an ability to tolerate captivity to a certain extent. In contrast, some other species such as the Amazon river dolphin or boto (*Inia geoffrensis*) and the baiji (*Lipotes vexillifer*) tolerate captivity poorly and do not perform aerial behaviours attractive to visitors, therefore, very few individuals of this species are now kept in captivity. Although others such as the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) have been difficult to maintain in captivity, their dramatic aerial activity has encouraged zoos to continue to keep them. The largest species in captivity is the killer whale or orca (*Orcinus orca*) its size, dramatic markings and trainability make it an ideal performance animal from the perspective of the captivity industry.

While trainability, appearance and tolerability of captivity have clearly driven the development of the zoo industry in this area, voyeuristic entertainment has become a less acceptable justification for captivity in the 1990s as concerns for animal welfare and the environment have increased. Increasingly, therefore, zoos and marine parks have argued that research is an important part of their role and justifies keeping cetaceans in captivity and conducting experiments with them. They claim that this research will help us understand cetaceans better and therefore be able to protect them in their natural environments.

For example, Pryor & Norris (1991) have said:

> "captive animals offer us understanding that cannot be acquired at a distance, and such understanding is fundamental to caring about cetaceans."

This report reviews the research that has been undertaken on captive cetaceans and questions the usefulness of research data from experiments on captive animals to the conservation of whales and dolphins in the wild.

There is a great deal of research published which relates only to the husbandry of animals in captivity. For example, their capture (Dudok van Heel., 1986), training (Abel, 1986; Defran & Pryor, 1980) and water quality requirements (Manton, 1986). This research is not considered in this report because it does not have any conservation value and cannot be argued to have. This report considers the fundamental areas of research, including basic physiology, disease, psychology, and reproduction together with work which is conservation related by definition such as on fisheries by-catch.

Table 1.1: Species of cetaceans most commonly kept in captivity (after Defran & Pryor, 1980).

Common name	Species
Bottlenose dolphin	*Tursiops truncatus*
Orca	*Orcinus orca*
Beluga	*Delphinapterus leucas*
False killer whales	*Pseudorca crassicans*
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*
Common dolphin	*Delphinus delphis*
Pilot whale	*Globicephala sp*
Hawaiian spinner dolphin	*Stenella longirostris*
Rough-toothed dolphin	*Steno bredanensis*
Boto	*Inia geoffrensis*

2. Haematology and Blood Chemistry

Establishing normal parameters for cetacean haematology and blood chemistry has long been a goal of research with captive animals. Over the years the justification for the research has expanded from determining baseline levels from which to assess the health of animals in captivity to being able 'to diagnose disease problems in wild populations' (Cornell *et al* ., 1988). However, as discussed in detail below, the relevance and application of haematology and blood chemistry data collected from captive animals to wild animals is questionable. Among other things, considerable individual variation exists (Bossart & Dierauf, 1990) and differences between wild and captive individuals of the same species have been detected (e.g. Asper *et al.,* 1990; St. Aubin & Geraci, 1989a).

Another focus of haematology and blood chemistry studies has been to find a quantitative measure of stress in cetaceans (Dierauf, 1990). Many animals have been placed under severely stressful conditions in the search for this goal and the experiments have resulted in the death of at least two bottlenose dolphins (Thompson & Geraci, 1986) and a 10-25% loss of body weight in several belugas (St. Aubin & Geraci, 1988; St. Aubin & Geraci, 1989a). Whether such studies contribute to the conservation of wild cetaceans is considered below.

Comparative haematology and blood chemistry has also been used to identify adaptive changes in cetaceans. For example, to understand how cetaceans are able to make frequent, prolonged dives to great depths and to survive in the hyper-osmotic environment of the sea.

Haematology

A haematology profile measures the numbers of red and white blood cells together with their physical characteristics. Table 2.1 gives the main parameters measured

together with the type of health information they can provide. Bossart and Dierauf (1990) have reviewed the reviewed the literature on haematology in cetaceans and its interpretation. All the major species which are kept in captivity now have published normal ranges for haematology, including orca (Cornell, 1983), beluga (Cornell *et al*., 1988), harbour porpoise (Kastelein *et al*., 1997a) and bottlenose dolphin (Asper *et al*., 1990). Some haematological values have also been reported for river dolphins kept in captivity (Ridgeway *et al*., 1989; Zhimei & Daoquan, 1989), but the information is too insufficient for normal ranges to be known with confidence.

Although normal ranges have been established for some species they have to be used with caution for two main reasons. Firstly, significant individual variation in haematology has been recorded in the beluga (Cornell *et al*., 1988), harbour porpoise (Kastelein *et al*., 1997a) and orca (Cornell, 1983) which has led Bossart and Dierauf (1990) to conclude that:

> "..individual baselines must be established for each animal in one's care before being confident that any particular value is abnormal. In delphinid hemograms, white blood cell (WBC) indices can vary between animals of the same species as well as from those listed in the literature. A WBC count that appears to fall within a normal literature range for that species may, if previous hemograms dictate, actually be a significant leukocytosis for the individual dolphin."

Therefore, there are limitations to any potential use of haematology data in investigating disease in wild animals because of the need to know what is normal for any one individual. Before firm conclusions could be drawn, there would need to be repeated sampling from an individual or, at least, extensive sampling from the population to gain some idea of the normal range. Neither approach would be practical in the field.

Secondly, the small amount of data that is available shows that captivity itself also affects haematology. Wild bottlenose dolphins have significantly higher white blood cell (WBC) counts, a lower percentage of neutrophils and a higher percentage of eosinophils than captive dolphins (Asper *et al*., 1990). Beluga whales showed a progressive decline in packed cell volume and haemoglobin during a 10 week period in captivity which was attributed to a reduced oxygen demand as a result of the imposed period of relative inactivity (St. Aubin & Geraci, 1989a). The whales also had a decrease then increase in WBC, associated initially with a fall in eosinophil and lymphocyte numbers, followed by an increase in neutrophils. The lower total WBC and eosinophil levels recorded in captive animals are thought to be associated with a reduced exposure to infection and particularly to parasitism (Asper *et al*.,1990). However, reductions in eosinophil levels are also associated with stress and this may, account for short term reductions after capture (St. Aubin & Geraci, 1989a).

Comparative haematology studies have shown that there has been considerable

evolution in red blood cell parameters to facilitate diving behaviour. Red blood cells are much larger in cetaceans than terrestrial mammals to increase oxygen carrying capacity and packed cell volume (PCV) is greater as a result (Bossart & Dierauf, 1990). Haemaglobin, PCV and RBC is higher in offshore than coastal bottlenose dolphins (Duffield, 1990) which may reflect different physiological demands.

Blood chemistry

Studies of blood chemistry involve measurement of the chemical components in serum or plasma - the non-cellular part of blood. This includes a wide range of electrolytes, enzymes and hormones. Reproductive hormones are considered in section 7. The other most frequently measured parameters are shown in Table 2.2 together with an indication of their clinical significance. However, clinical significance is much less well understood for many of the blood chemistry measurements than haematology.

Bossart and Dierauf (1990) have reviewed the literature on serum chemistry in cetaceans and its interpretation. Blood chemistry measurements have been conducted on all the major species which are kept in captivity, including orca (Cornell, 1983), beluga (Cornell et al., 1988), harbour porpoise (Andersen, 1968; Kastelein et al., 1990; Kastelein et al ., 1997a) and bottlenose dolphin (Asper et al., 1990). Some, less detailed data is also available on river dolphins (Ridgeway et al., 1989; Zhimei & Daoquan, 1989).

As with haematology, the extrapolation of 'normal' values for captive dolphins to wild animals is not completely straightforward although the extent of any differences is difficult to estimate because of the limited studies on wild animals. However, the artificial diets of captive animals clearly affect some aspects of their blood chemistry. Levels of blood urea nitrogen (BUN) are related to the protein content of the diet and cholesterol and triglyceride levels are affected by the fat content. BUN levels were lower in captive bottlenose dolphins than in wild dolphins and cholesterol and triglyceride levels higher (Asper et al., 1990). The levels of triglyceride rose and cholesterol level fluctuated in beluga whales kept in captivity for 10 weeks and fed on oil-rich herring rather then their normal diet of decapod crustaceans (St. Aubin & Geraci, 1989).

Another difference between wild and captive species has been detected in circulating levels of the thyroid hormones; thyroxine (T3) and triiodothyronine (T4). In free living belugas, there are seasonal variations in T3 and T4, with levels significantly higher in the summer than in the winter (St.Aubin & Geraci, 1989b). This seasonal variation is not seen in captive belugas which is attributed to their relatively constant environment. In harbour seals, similar seasonal changes in T3 and T4 have been recorded and are thought to be associated with the preservation of fat in cold waters (Renouf & Noseworthy, 1991) as thyroid hormones are important in the regulation of metabolic activity. St. Aubin et al., (1996b) did not detect seasonal variation in T3 and T4 levels in wild bottlenose dolphins, but found that levels of total and free T4 and

free T3 were higher in wild females compared to 'semi-domesticted' (kept in natural sea water enclosures at the Naval Command, Control and Surveillance Center Laboratories) animals. The authors thought the difference may be due to effects of reproduction and lactation.

In captive killer whales, Cornell (1983) has detected individual differences in clinical chemistry according to their place of origin. Pacific orcas had lower lactic dehydrogenase (LDH) activity than Atlantic animals. Older male animals had higher BUN and creatinine than others and young orcas had higher glucose and lower total protein levels than mature animals. Again, it was concluded that establishing an individual's normal profile was important for interpretation.

Stress, discussed in the next section, can have a very dramatic effect on some serum chemical constituents, adding to difficulties of interpretation because both wild and captive animals may be stressed during sampling.

Table 2.1: Commonly measured haematology parameters and an outline of their clinical significance.

PARAMETER	CLINICAL SIGNIFICANCE
Total red blood cell count (RBC)	Decreased in anaemia and poor nutrition Increased in dehydration
Haematocrit or packed cell volume (PCV)	Decreased in anaemia and poor nutrition Increased in dehydration
Haemoglobin concentration (Hb)	Decreased in anaemia and malabsorbtion
Mean corpuscular volume (MCV)	May increase or decrease in different types of anaemia
Mean corpuscular haemoglobin concentration (MCHC)	May increase or decrease in different types of anaemia
Blood smear	To identify if immature or abnormal RBCs are present as found in different types of anaemia
Total white blood cell count (WBC)	Elevated by stress and bacterial infection
Neutrophils	Elevated by stress and bacterial infection Decreased by overwhelming bacterial infections and toxaemia
Lymphocytes	Increased in viral infections Decreased by stress
Monocytes	Increased in chronic inflammatory conditions
Eosinophils	Increased in parasite infections Decreased by stress
Basophils	Rarely seen, significance unclear
Bands or immature neutrophils	Increased in infections

Table 2.2 The most commonly measured blood chemistry parameters and an indications of their clinical significance.

PARAMETER	CLINICAL SIGNIFICANCE
Liver associated enzymes	
Aspartate aminotransferase (AST)	Elevations in liver and muscle damage
Alanine amino transferase (ALT)	Elevations in liver and muscle damage
Gamma glutamyl transpeptidase (GGT)	Elevation in liver diseases
Alkaline phosphatase (ALP)	Elevation in liver diseases and during normal growth
Bilirubin:	
Direct	Elevations in obstructive liver disease
Indirect	Elevation in haemolysis and pre-hepatic disease
Creatine kinase (CK)	Elevated with cardiac or skeletal muscle damage - e.g. handling or transport
Blood urea nitrogen (BUN)	Elevated with kidney disease, may be reduced with liver damage
Creatinine	Elevated in kidney disease
Lactic dehydrogenase (LDH)	Increased in general cell damage
Glucose	Increased in stress and diabetes mellitus
Triglyceride	Deceased with prolonged fasting
Cholesterol	Increased in hypothyroidism and diabetes mellitus, decreased with malabsorbtion and starvation
Total Protein	Increased in dehydration, decreased in starvation and malabsorbtion
Albumin	Increased in dehydration, decreased in malnutrition and liver or kidney disease
Globulin	Increased in some immune system diseases
Electrolytes: Sodium, Potassium, Chloride, Phosphorus	Electrolyte levels give an indication of the operation of a variety of homeostatic mechanisms in the body.

The effects of stress on haematology and blood chemistry

The response from scientists to questions about the welfare of animals in captivity, has been to search for an 'objective' measure of stress. "Being able to define and measure marine mammal stress has taken on new importance by offering a defensible way of assessing animal well being" (Dierauf, 1990). The underlying assumption is that stress must cause a measurable change in some physiological parameter and that, if no measurable change exists, an animal is not stressed.

Captive cetaceans have been put through some unquestionably stressful situations in experimental studies. The main changes identified have been in plasma cortisol,

thyroid hormone, aldosterone and eosinophils. Dosing a bottlenose dolphin with carbon tetrachloride and keeping it on the move for 72 hours without food until it became 'visibly irritated and unusually aggressive' caused small changes in creatinine kinase, glucose and potassium (Geraci & Medway, 1973).

Three bottlenose dolphins were chased for up to 3 hours before capture and blood sampling (Thompson & Geraci, 1986). Cortisol and aldosterone levels were elevated and eosinophil numbers reduced. Even animals used to having blood samples taken showed a stress response in terms of raised cortisol and aldersterone levels. The conclusion was that eosinophil numbers were the best measure of stress. Two dolphins used in the study died 2-5 days after being given adrenocorticotrophic hormone (ACTH) to mimic natural stress.

Another study involved removing six beluga whales from the wild and holding them in two 8.2m diameter pools for 10 weeks during which time four lost 15-25% of their body weight (St. Aubin & Geraci, 1988; St. Aubin & Geraci, 1989a).   Plasma levels of T3 and T4 were reduced and remained low throughout the study period.   There were short term (one week duration) reductions in eosinophil and lymphocyte numbers and increased levels of aldosterone cortisol, glucose, iron, potassium, creatinine kinase, aspartate amino transferase and gamma glutamyl transpeptidase.

Many other, similar studies have been undertaken, and these were reviewed by Dierauf (1990). Although these studies may prove useful clinically for treating cetaceans in captivity and possibly stranded animals, it is difficult to envisage their relevance to understanding the biology of wild populations.

Conclusions

Studies of haematology and blood chemistry are undoubtedly useful for monitoring and treating animals held in captivity as they provide basic information about a range of body systems. 'Normal' ranges for haematology and some serum or plasma chemicals are now relatively well known for several species. However, because individual differences exist, captivity results in changes as animals adapt to the new environment and sub-populations of a species may have different levels of some components, their value in conservation terms is less clear.

> "Studies on captured wild specimens have yielded seemingly ideal data, but these do not always correlate with the data from captive animals. Captivity demands physiological adjustments that can be reflected in blood values" (Medway & Geraci, 1986).

An additional problem is that it is usually impractical to collect samples from wild animals. Stranded animals may be sampled and the results used in an evaluation of

their likelihood of survival, but for others this is not the case. Although some populations of free-living bottlenose dolphins are routinely captured and sampled (e.g. Asper *et al*., 1990), this only gives data on a few small populations - most cannot be sampled in this way.

Although understanding stress seems to be a potentially useful goal, the confusion, for a free-living animal, between the stress of capture and any other stress seems intrinsically difficult to unravel. In their study of bottlenose dolphins and stress, Thompson and Geraci (1986) found there was a maximal stress response measured in circulating cortisol levels which was not exceeded even if the experimental stress period was extended. Perhaps the problem here is that the search for a quantitative measure of stress in this way is misplaced, especially as stress is such a diverse concept and may not be so easily defined chemically. Acute and chronic stress, for example, may produce different effects and although finding a measurable physiological stress response may be productive in certain situations (Dierauf, 1990), it may prove difficult to unravel the subtle effects of long-term low level stress.

3. Disease

The literature on diseases in cetaceans which originates from captive animals, is largely a series of case reports and reviews of the illnesses which occur. It is difficult to know how representative disease in captive animals is when applied to free-living animals. Data on disease in wild animals comes mainly from stranded animals, many of which are already dead, and even the extent to which live stranded animals represent the whole disease spectrum is unclear.

However, there are indications that important differences exist between captive and wild animals in the diseases seen although there are also some similarities. In addition, when outbreaks of disease have occurred in wild cetaceans, the literature on disease in captive animals does not appear to have been very helpful in their investigation. This section briefly reviews the main differences in the diseases of captive and wild cetaceans and considers the extent to which knowledge from captive animals has helped address disease problems in wild populations.

Infectious diseases

In captive animals, bacterial pneumonia is considered the most common cause of death in dolphins (Sweeney, 1986a) and orcas (Greenwood & Taylor, 1985). Pneumonia is also one of the most common causes of death in wild, stranded animals. In dolphins from British waters, bacterial pneumonia was a common finding (Baker, 1992a). In harbour porpoises, parasites were a more frequent cause of bronchopneumonia than bacteria although bacterial pneumonia was one of the more common causes of death (Baker & Martin, 1992a). Therefore, bacterial pneumonia seems to be a common problem for both captive and wild cetaceans (Dunn, 1990).

Systemic mycotic infections have been recorded in both captive and free-living animals involving organisms such as *Nocardia*, *Candida* and *Aspergillus* although

they occur much less frequently than bacterial infections (for a review see Dunn, 1990; Sweeney, 1986a). However, candidiasis seems to be a particular problem for captive cetaceans and has been the cause of illness or death of a wide range of species including bottlenose dolphin, beluga whale, harbour porpoise (Dunn, 1982) and orca (Greenwood & Taylor, 1985). It is thought that conditions in captivity place cetaceans at special risk of *Candidia* infections (Greenwood & Taylor, 1985) and that other illnesses or stress may predispose individual animals to developing disease (Dunn, 1982). Mycotic dermatitis with *Fusarium* has also been recorded in captive cetaceans where predisposing factors were suggested to be long term antibiotic therapy or other situations which compromise immune function (Frasca *et al*., 1996).

Infectious skin diseases have been recorded in both free-living and captive species (Sweeney, 1986a). Viral infections with pox and herpes viruses were found to be common in animals stranded in British waters (Baker, 1992b). Infections with *Erysipelothirx rusopathiae* are also reported in captive cetaceans associated with skin lesions and septicimia (e.g. Calle *et al*., 1993).

Parasitic disease

One of the most obvious differences between disease in captive and wild cetaceans is in the incidence and importance of parasites. Parasite burdens are ubiquitous in free-living animals and when animals are captured for exhibition, they inevitably carry a wide array of endo- and ectoparasites (Dailey, 1986). However, animals in captivity are treated with anthelmintics and parasite burdens decline quickly. Even without treatment, levels of parasites decline, which has been postulated to be associated with the changed diet and lowered exposure (Dailey, 1986).

Although parasitic infections in free-living cetaceans will not inevitably cause disease, they are likely to contribute to morbidity and mortality and this is well recorded (e.g. Baker & Martin, 1992). Therefore, studies of captive animals are unlikely to contribute to understanding this dimension of disease in wild animals.

Other diseases

Gastric ulceration is one commonly reported condition in both captive and wild cetaceans (Sweeney, 1986b). In captive cetaceans, treatment for gastric ulceration with antacids and cimetidine is common (Sweeney, 1986b; Stoskopf, 1990). However, although gastric ulceration has clear clinical significance in captive animals, there is less evidence to suggest it is so in free-living cetaceans.

Epizootics in wild populations

The recent emergence of eptizootics, caused by morbilliviruses, leading to large scale mortalities in striped dolphins in the Mediterranean and bottlenose dolphins on the east coast of the United States is well documented (e.g. Duigan *et al*, 1996; Simmonds & Mayer, 1997). Although these outbreaks of disease may have had a major impact on the affected populations, studies on captive whales or dolphins had not warned of the possibility or contributed significantly to understanding the events. The main preoccupation of scientists involved with captive populations is the risk that is posed to animals in captivity if infected cetaceans are introduced and the risks of

reintroduction of captive animals to the wild (Brill & Freidl, 1993; St.Aubin *et al*., 1996a).

Conclusions

Data on disease incidence in captive cetaceans is obviously important for their care and clinical treatment. How such information helps us understand disease in free-living animals is much less certain. Parasites do not feature as causes of disease in captive animals as routine treatment is used. Some diseases, such as candidiasis and gastric ulceration, may be more prevalent or of greater importance in captivity than in the wild.

In particular, studies of disease in captive animals have not helped in understanding some of the most visible marine mammal mortality events in recent years. Therefore, from a conservation perspective, there seems little value gained from disease studies on captive animals.

4. Physiology

Basic physiological studies aim to understand the physical functioning of an animal. The majority of physiological studies with captive cetaceans have been conducted on bottlenose dolphins because of their relatively small size and the ease with which they can be trained. For such studies dolphins have to be trained to undertake certain specific research tasks (such as, in swimming studies, pushing against a load) and more generally useful behaviours such as presenting their flukes for blood sampling or urinating on command.

Many physiological studies have been conducted at the Naval Ocean Systems Center (NOSC) in Hawaii (e.g. Williams *et al*., 1992; Williams *et al* 1993., Pabst *et al*., 1995) which reflects the US Navy's long term interest in dolphins.   The Navy is particularly interested in the echolocation and acoustic abilities of dolphins, knowledge which they feel may be applied to improve underwater detection methods (see section 5 on Experimental Psychology and Cognition). They have also been interested in the hydrodynamics of dolphins and whether they have special adaptations which make them more efficient in the water and which could be used to improve ship technology (Ridgeway & Carder, 1990).

Physiological experiments on harbour porpoises have also been conducted at the Harderwijk Marine Mammal Park in the Netherlands using animals in a rehabilitation programme (e.g. Kastelein *et al.,* 1997b; 1997e).

Swimming and diving

At the NOSC, bottlenose dolphins are kept in open-water floating pens and trained to accompany boats on open-water swimming sessions. In other research centres,

dolphins are trained to swim at certain speeds in their normal enclosures (e.g. Fish, 1993).

Studies of exercising bottlenose dolphins have shown that they have energetic profiles which are similar to those in sedentary terrestrial mammals but have a lower energy cost of swimming than other aquatic mammals (Williams *et al*., 1993). It has also been demonstrated that bottlenose dolphins can conserve energy while travelling by wave-riding and bow-riding on boats (Williams *et al*., 1992) confirming behavioural studies on free-living animals (Shane *et al*., 1986). The pressure sensitive skin folding identified by Ridgeway & Carder (1990) following electroencaphalogram and electromyrogram studies of dolphins using skin microvibrations was thought to enhance dolphins' swimming potential relative to other species. However, other studies of energy expended during swimming trials in captivity have shown that although bottlenose dolphins are 'well adapted for efficient high-performance swimming, [they] show no unusual hydrodynamic performance' (Fish, 1993).

The NOSC studies have also demonstrated that bottlenose dolphins have an effective counter-current heat exchange mechanism which keeps the testicles of male animals cool during exercise even though they are located between two major muscles of locomotion (Pabst *et al*., 1995).

Diving is obviously an important dimension of the physiological adaptations of cetaceans to the marine environment. However, there have been few studies of this aspect, mainly because of the physical limitations imposed by captivity. Those studies which have been carried out are now around 25 years old (e.g. Ridgeway *et al*., 1969; Ridgeway & Howard, 1979). However, with the development of miniaturised radio and acoustic telemetry systems and time-depth recorders, studies of diving behaviour is now being conducted using free-living cetaceans such as harbour porpoises (Westgate *et al.,* 1995) which is revealing the depths and frequency of dives.

Research on the respiratory physiology of species other than bottlenose dolphins in captivity has been much less sophisticated. For example, in juvenile harbour porpoises measurements of peak inspiratory flow rate and tidal volume have been made with animals out of the water (Kastelein *et al* ., 1997e). Considerable individual variation was seen and the authors acknowledged that the experimental conditions could not be considered representative of the natural environment.

Energetics and nutrition

Having some understanding of energetics and nutrition is important for feeding cetaceans in captivity. The literature has been extensively reviewed by Worthy (1990). Data from captive cetaceans is sparse and most research was conducted in the 1970s and does not appear to be a feature of research effort today although studies of food intake and growth (Kastelein *et al* ., 1997b) and the passage time of food in harbour porpoises (Kastelein *et al* ., 1997c) has been reported recently. However, growth rates in captive animals may differ from those in the wild where food availability may be restricted at times.

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Knowledge of cetacean energy requirements can also be used to calculate the amount of food consumed in the wild. This in turn can be used to develop multi-species models of the marine environment. The data from captive studies does not appear to have been used directly in this way. For example, the Norwegians, who are developing multi-species models of the Barents Sea, have used data from minke whales killed during commercial and scientific whaling (Bogstad *et al.,* 1995).

Conclusions

Physiological studies can give interesting insights into the way in which cetaceans are adapted to their marine existence. This knowledge enriches our understanding of these animals and provides interesting comparative data. However, it seems to have little obvious practical application in the conservation of animals in the wild. In particular, studies of nutrition and energetics are likely to be poor predictors of the performance of wild animals because of the sedentary life style of captive animals and their consequent lack of basic fitness and abnormal diet.

5. Experimental Psychology and Cognition

Research effort into the visual, hearing and echolocation abilities of cetaceans has been enormous and continuing. The majority of this work has taken place in the United States and Russia. The cetacean sonar system has held particular fascination for researchers, driven, in part, by the US Navy's interest in its potential application to improving underwater detection systems. Bottlenose dolphins have again been the preferred research animal and they have learnt complicated techniques to allow researchers to determine, for example, whether they can detect different shapes and in how many dimensions. These experiments usually rely upon operant conditioning where a correct response is rewarded with food and is used in its simplest form to train performance behaviours. Adaptations include the 'go, no-go' technique. For example, in experiments on taste the dolphin is trained to place its mouth on a bite plate just above the water. Two solutions are dribbled into the mouth which are the same (e.g. water followed by water) or different (e.g. water followed by sugar solution). When they are the same, the animal must stay at the bite plate, if they are different it must go back into the water. Another version, forced choice, is to train a dolphin to press one of two plates depending on whether two objects are the same or different (see Moore, 1991 for description). Using such techniques, researchers have investigate the cognitive abilities of dolphins.

All of these studies use animals which have undergone considerable training and therefore the numbers of animals used in any one experiment is usually low and only general conclusions can be drawn from the behaviour of individual animals.

Hearing and the processing of auditory information

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The hearing sensitivities of many species of cetacean have been determined through experimental studies with captive dolphins and individual deficiencies have been identified (Ridgeway & Carder, 1997). Both behavioural and electrophysiological audiograms have been used to investigate hearing with bottlenose dolphins and orcas being the most extensively studied (for a review see Richardson *et al*., 1995). These studies have shown that most cetaceans have good hearing in the 60-120 kHz range with high-frequency hearing being particularly acute. A few species, such as the harbour porpoise and the Indus river dolphin, have hearing ranges which extend to 130kHz and the difference has been attributed to the low-visibility environments they inhabit (Wood & Evans, 1980). Table 5.1 gives the hearing ranges and echolocation of the main species kept in captivity.

In 1991, Louis Herman (Herman, 1991) reviewed the work on audition in dolphins by his group at the NOSC in Hawaii and others. These studies have shown that dolphins have an excellent auditory memory and ability to mimic sounds. Dolphins are also able to understand sentences conveyed in 'a simple, artificial acoustical language' (Herman, 1991). For example dolphins can differentiate between auditory instructions such as "take the surfboard to the frisbee" and "take the frisbee to the surfboard". As a result the information processing skills in this sensory system were considered equal to the visual processing skills of non-human primates.

Table 5.1 The hearing sensitivities and echolocation properties of some of the main species kept in captivity (after Richardson *et al*., 1995; Wood & Evans, 1980).

| Species | Echolocation | | Hearing | |
	Pulse type	Peak frequency (kHz)	Range (kHz)	Peak sensitivity (kHz)
Bottlenose dolphin	pulse: 10-200 μsec	110-130	75-150	20-80
Killer whale	pulse: 0.5-1.5msec	12-25	0.5-31	15
Harbour porpoise	pulse: 40-200 μsec	110-150	1-150	8, 32, 64
Beluga	pulse: 20-100 μsec	40-60; 100-120	1-123	60-65

Echolocation

The echolocation abilities of cetaceans are impressive. It is hoped that understanding the dolphin's sonar system may help develop better ways to study the oceans, improve navigational tools and reduce cetacean entanglement in fishing nets (Moore, 1991).

In his 1991 review of echolocation research, Moore (1991) described what was known about the frequency and amplitude of echolocation signals and how it has been demonstrated that dolphins can exert voluntary control over them. There are

differences between species in the frequency and peak energy emission characteristics of their echolocation signals (see Table 5.1). Some species such as the harbour porpoise and Dall's porpoise produce very high frequency echolocation signals compared to other species (Hatakeyama & Soeda, 1990) although the ecological significance of such differences is unclear. The echolocation signals produced by harbour porpoises have been described in detail following studies with animals in a rehabilitation unit (Verboom & Kastelein, 1995; 1997; Goodson *et al.*, 1995; Kastelein *et al.*,1995c).

Early studies established that much echolocation behaviour is learnt. When species such as the common and whitesided dolphin, used to swimming in clear waters, were placed in turbid water, they hit the sides of the pool until, over a period of days, they learn to depend less on vision and more on echolocation (see Wood & Evans, 1980).

Dolphins can use echolocation to discriminate between objects based on size, shape, material composition and combinations of these. Studies with blindfolded dolphins have shown they can use echoic information to derive complex shape information although they have difficulty matching aspect dependent targets (such as cubes or pyramids) at different orientations (Pack & Herman, 1995; Helwg *et al.*, 1996a; 1996b). Studies have also shown that dolphins have near perfect intersensory recognition of complex 3-D objects which suggest "that what a dolphin "sees" through echolocation is functionally similar to what it sees through vision" (Pack & Herman, 1995). Other studies have confirmed these findings and shown that visual and echoic information can be combined to increase accuracy (Harley *et al.*, 1996).

Oceanic conditions have been shown to affect the performance of long-range target detection by a false killer whale (Turl & Thomas, 1992) indicating the probable importance of environment in echolocation ability. Studies with a harbour porpoise (Kastelein *et al.*, 1997d) showed it was also able to distinguish between targets buried up to 7cm deep in sand, suggesting echolocation may be used to identify the position of benthic prey.

Because dolphins' abilities are much superior to conventional sonar systems, researchers are developing and evaluating artificial neural networks in an effort to mimic the dolphins abilities (see e.g. Au, 1994; Au *et al*., 1995a). Although these systems are gradually being improved they have not yet proved themselves in complex situations. Dolphins have also been used to determine their own acoustic reflectivity to help in use of sonar systems (Au, 1996). The echolocating abilities of other species held in captivity such as the beluga whale (Au *et al.*, 1987) and the false killer whale (Au *et al.,* 1995b) have also been investigated but much less intensively.

Vision

For a long period, vision was thought rather unimportant to dolphins, particularly as initial studies suggested that it was rather difficult for dolphins to distinguish visually between shapes. Later it became clear that methodological problems had resulted in misleading information being generated and that dolphins have good vision in air and water (see Herman, 1991 for review). The difficulties animals adapted to clear water

had when placed in turbid water also confirms the functional importance of vision (Wood & Evans, 1980).

Bottlenose dolphins appear to have sophisticated systems for processing visual information. They can understand visual questions and report on whether objects are present or absent in a tank and take visual cues and signals from gestures of trainers. They are also able to integrate visual information with information from other senses such as echoic (see above) and proprioceptive (Herman, 1991).

Communication

As well as echolocation 'clicks', cetaceans also produce whistles and other noises to communicate and these are thought to be important in maintaining social relationships. Captive bottlenose dolphins are again the main research animal but studies have also been conducted with other species such as orca and harbour porpoise.

Most studies have involved describing the sounds produced and their frequency, with less emphasis being placed on how these relate to behaviour. Studies of the whistles of bottlenose dolphins have shown that they tend to have an individual repertoire of whistles, that they can imitate others' whistles and that vocal learning takes place (Caldwell *et al* ., 1990; Tyack, 1991; McCown & Reiss, 1995). Cetaceans are one of the very few non-human mammals in which vocal learning has been recorded (McCown & Reiss, 1995).

Early studies had suggested that bottlenose dolphins had a 'signature whistle' which was produced over 90% of the time and established a dolphin's identity for others. This is now disputed and the evidence for it thought to be a result of recordings being taken from isolated animals often out of the water (Tyack, 1990). Animals kept in social groups have a much greater diversity of whistle production which also includes mimicking the whistles of others in the group suggesting that whistles play a role in social communication more complex than simply identifying an individual (Tyack, 1990; McCown & Reiss, 1995).

It is now well recognised that captivity and artificial conditions cause changes in the sounds produced by cetaceans. The repertoire of whistles produced by a bottlenose

dolphin kept with one other animal which then died was very different after two years of isolation (Tyack, 1990). A dolphin isolated for seven years lost his signature whistle and produced a whole range of whistles which seemed to be imitations of the sounds played to him in the experiments he was involved in. The authors (Caldwell *et al*., 1990) concluded "This observation alerts us to the potential differences between the whistle of long-term captive animals subjected to many sounds versus those in a relatively normal acoustic environment".

Differences between the sounds produced by captive and free-living orcas have also been described (Morton *et al*., 1986; Bain, 1986). A captive juvenile Bryde's whale produced different sounds than free-ranging pairs of the same species (Edds *et al*., 1993).

These differences between free-living and captive animals in the sounds they produce, the effects of captivity and especially social isolation, throw into question the usefulness and relevance of studies of sound production by captive cetaceans.

Consciousness

At the Earthtrust laboratories in Hawaii, a series of experiments have been conducted with bottlenose dolphins that have a rather different perspective. It is being investigated whether dolphins have a sense of 'self-awareness' (Marten & Psarakos, 1995). In these studies the reactions of dolphins to real-time video recordings of themselves are compared to playbacks and their reactions to strange dolphins in neighbouring pens. The results suggest that dolphins can recognise themselves in a mirror, and not simply as another member of the species - a psychological test of self-awareness.

Other research on the consciousness of bottlenose dolphins has taken place at Dolphin Research Center (Marathon, Florida) (Smith *et al*., 1995) and has involved comparative studies of dolphin and human reactions in uncertain situations. In these studies there was behavioural evidence that the animal was conscious that it was uncertain in some of the difficult tasks presented. These findings were considered important in reassessing the extent to which animals are thought to be self-aware and because animals may be able to teach more about human self-awareness.

Conclusions

Most experimental psychology studies have built on the training techniques used for exhibitions. They have built a picture of the bottlenose dolphin in particular, as an animal with extensive cognitive abilities and a sophisticated sensory system for exploring its environment. However, there are constraints on the usefulness of data from captivity. Some of the problems include the barren acoustic and visual nature of the majority of captive environments and assessing the relevance of studies involving a few highly trained individual animals.

Data on hearing, echolocation and vision may prove to help reduce entanglement in

fishing nets and this is considered in more detail in section 8. But foraging behaviour, for example, takes place in a complex and changing environment. Sea conditions and the physical nature of the sea bed are two of the factors which may influence audition, echolocation and vision. The emphasis of sensory studies has not been on these dimensions but has been focused on understanding cetaceans' echolocation abilities to harness them for use in developing sonar systems for use by humans.

Studies of consciousness may help us understand cetaceans in relation to man and possibly, thereby, increase our respect for them, develop willingness to protect them and their environments. However, the techniques for doing this probably only scrape the surface of understanding and the problems of communication and interpretation are enormous. Finding tests of whether animals are self-aware are as much exercises in how well we can train animals to understand what we want them to do as much, if not more than, what we learn about their conscious processes.

Fascinating as the data from captive studies of cognition and consciousness may seem, it may be fulfilling humans' needs rather than those of the animals concerned. Whether this justifies the imposition of captivity and experimentation remains in question.

6. Behaviour

A great deal of behavioural work undertaken in dolphinaria has been concerned with how to train whales and dolphins to undertake certain tasks (e.g. Defran & Pryor, 1980). These have primarily been for display purposes but also for management such as blood and urine sampling (see sections 2 and 5). Training techniques rely on operant conditioning where a reward is given for the correct behaviour and none given if the wrong behaviour is performed. This has no obvious relevance to the behaviour of cetaceans in their natural habitats and is not considered in detail here.

However, there have been studies of 'normal' behaviour of animals in captivity when they are interacting with each other rather than their trainers. What insight this has given and how it relates to studies conducted on wild animals is therefore the focus of this section. The most recent claims of such research are that they allow the development of quantitative techniques which have been absent or are less easy to apply in natural settings (Östman, 1991; Samuels & Gifford, 1997). Therefore, the extent to which quantification relies upon captivity studies and to what degree research on wild populations suffers from a lack of quantification is addressed.

Social structure

Shane *et al.,* (1986) have reviewed and compared the social structure of free-ranging and captive bottlenose dolphins. One of the problems in this area of research is that the group composition of captive animals is imposed by the conditions of captivity. The small size of groups held and the limitations of pool sizes mean that the establishment of sub-groups, for example, is severely limited. In captivity, social organisation of bottlenose dolphins is controlled by male dominance. In contrast the situation in natural environments is much more dynamic, with adult males forming small groups based on age and sex. Adult and sub-adult males are rarely seen

together, and females form groups in which there is prolonged association, for 3-6 years, between females and their calves (see Shane *et al*., 1986).

The aggressive behaviour, such as chasing, threats and ramming, seen in captive bottlenose dolphins establishing dominance (Samuels & Gifford, 1997) is much less of a feature in descriptions of behaviour in free-ranging animals. There may, of course, be hierarchies based on dominance among sub-groups of wild animals which change over time as they do in captivity (Östman, 1991; Samuels & Gifford, 1997).

Samuels & Gifford (1997) suggest that past observations on wild dolphins may have been misleading because non-quantitative studies may have highlighted the obvious aggressive behaviour of males and discounted the more subtle agonistic behaviours responsible for maintaining hierarchies in female groups. They propose that quantitative studies based on captivity could improve understanding of wild populations. However, quantification of behaviour in the wild which pre-selects for behaviours previously identified in captivity may impose a bias which is equally misleading.

Activity patterns

Studies on the activity of a range of species in captivity have centred on describing the types of behaviour seen including sexual behaviour, birth and rearing (e.g. Shane *et al*., 1986; Cockcroft & Ross, 1990; McCown & Reiss, 1991; Reccia & Tyack, 1991); aggression as described above, and general activity levels (Shane *et al*., 1986). Because of the restricted nature of captivity there is a lack of information about foraging behaviour and response to predators.

The amount of travelling behaviour that dolphins in captivity can undertake is, obviously, determined by the size of their pool. Pool size has been shown to influence aggression which is increased when bottlenose dolphins are more closely confined and the amount of time spent milling and travelling is reduced (Bassos & Wells, 1996). When the same dolphins used in this study were released to the wild they spent considerably more time travelling than when in captivity (Bassos, 1993 cited in Bassos & Wells, 1996). Harbour porpoises swim faster and dive more frequently in larger outdoor floating pens that when confined in smaller pools (Kastelein & Staal, 1997). Bottlenose dolphins and harbour porpoises kept in pools also tend to circle the pool in one direction especially if kept in isolation (Kastelein & Staal, 1997; Sobel *et al*., 1994). Social contact decreases stereotyped behaviour but animals may circle the pool together.

Studies of females and calves have given information on suckling frequency and growth rates (e.g. Cheal & Gales, 1991; Cockcroft & Ross, 1990; Joseph *et al*., 1987) and maternal behaviour including discipline (Cockfroft & Ross, 1990; McCown & Reiss, 1991).

There are data about interactions between humans and dolphins in 'swim with the dolphin' programmes in captivity compared to those with free-living animals (Frohoff & Packard, 1995). The behaviour of the dolphins was very different in these two

situations. The behaviour of captive dolphins was mainly directed and reinforced by humans whereas the behaviour of free-ranging dolphins consisted mainly of interactions between the dolphins themselves and was initiated and controlled by them.

Conclusions

The conditions imposed by captivity clearly have effects on social structure (which is imposed) and general behaviour. Size of pool is one of the most important factors influencing the expression of behaviour. These constraints mean that the relevance of behavioural studies on captive animals to free-living animals always remains in doubt. In fact it is one area where studies of free-living animals are more useful to establishing basic requirements for captive animals than visa versa. Bassos & Wells (1997) have pointed to the relevance of their long-term studies of free-living bottlenose dolphins in improving the conditions of captive animals. Gygax (1997) has even suggested that behavioural research on free-living animals is more important than research on captive animals in this context. Those working with captive animals also recognise the primary importance of understanding the social structure and behaviour of wild animals to improve conditions (Laule & Desmond, 1991).

7. Reproduction and Captive Breeding

The survival times and reproductive success rates of institutions keeping cetaceans has become central to the debate concerning the acceptability of captivity. Reproductive success has become equated, in some circles, with adequate husbandry (see Ames, 1991). Maintaining self-perpetuating populations is becoming a justification in itself as a preservation strategy for populations as well as reducing the need to take animals from the wild.

For example it is argued that through captive breeding and research….

"..it is possible to establish normal gestational periods, calving intervals, and infant growth rates and colour changes with age, all of which are applicable to the natural history and management … but are difficult to document in the wild. Such births demonstrate that it is possible to propagate new species successfully if knowledge gained from other species is used as a starting point. Finally, such births demonstrate that zoos and marine zoological parks are no longer merely consumers of wild animals, but are capable of establishing self sustaining populations for study and, in some cases, eventual release to the natural environment" (Joseph *et al*., 1987).

Research on survival and reproduction is, therefore, becoming more intensive because of the central political role it plays in the justification for captivity. Only research on environmental problems facing free-living cetaceans (see section 8) can be used with the same apparent moral force by proponents of captivity. This section reviews the research which has been undertaken on survival and reproduction and the argument which is being made for captivity as a means to ensure the continued survival of some species.

Survival in Captivity

Survival of all the main species maintained in captivity has improved in the past decade (Small & DeMaster, 1995a). However, there appears to be no central inventory of captive cetaceans world wide, their survival and reproductive success but long-term studies of some populations are beginning to be published using US data from the Marine Mammal Inventory Report (MMIR) (DeMaster& Drevenak, 1988; Small & DeMaster, 1995a) and other censuses (Duffield & Wells, 1991; Duffield & Miller, 1988). The acclimation time for bottlenose dolphins to captivity has been estimated to be 35 days as mortality rates before that time are higher than afterwards (Small & DeMaster, 1995b) and this period is excluded from some studies (Small & DeMaster, 1995a).

Because there are too few calves of some species in captivity, such as belugas, it is impossible to determine age-specific differences in survival for all species (Small & DeMaster, 1995a). The differences in age distribution of captive and wild populations also interferes with comparisons (Duffield & Wells, 1991; DeMaster & Drevenak, 1988) as the average age in captivity is lower that that in the wild. The trend for some institutions to keep single sex groups of bottlenose dolphins to reduce the numbers of births in captivity also affects reproductive statistics (Duffield & Wells, 1991).

However, some conclusions have been drawn from studies conducted to date. Small and Demaster (1995a) found that the calf mortality of captive bottlenose dolphins and orcas was significantly higher than those in the wild. There were also significant differences between marine parks in the survival times of bottlenose dolphin adults and calves. Duffield and Wells (1991) compared captive bottlenose dolphin census data in the US and Canada with data from a long-term study of free-living bottlenose dolphins in Sarasota. They found maximum longevity to be similar in both populations, but a higher crude birth rate, fecundity recruitment rate and mortality rates in the captive group.

Although the survival statistics for species such as the bottlenose dolphin seem good, this is certainly not true for all species. Some species seem particularly susceptible to the stress of captivity and do not do well. This includes the Amazon river dolphin whose average longevity in captivity in the United States has been estimated to be 32.6 months (Caldwell *et al*., 1989). Short life span was attributed, in part to *Inia* being aggressive when held in groups in captivity and stress associated diseases caused by transportation and captivity. The Yangtze river dolphin, the baiji, has also not fared well in captivity and only one adult male is held at an aquarium in China. Two other baiji captured at a later date also subsequently died (Kaiya & Xingduan, 1991). The baiji appear to be shy animals and less able to adapt to captivity than the bottlenose dolphin. When a female baiji was transferred into a semi-natural reserve she died within months (Anon, 1997).

Breeding in Captivity

The success rates of breeding some species of cetaceans in captivity have increased over the past decade reducing the need to take animals from the wild, although this still takes place. One hundred and twenty two bottlenose dolphin calves were born in captivity between 1983 and 1990 (Ames, 1991) and 11 killer whale calves have been born in captivity in North America up to 1993 (Duffield *et al*., 1995). Goals of breeding programmes are not always clear although at one research institute, the Naval Ocean Systems Center (NOSC), it is:

> "..to breed and raise "in house" …dolphins, ensuring healthy animals with desirable characteristics, including trainability, adaptability to captivity, and known breeding lineage" (Schroeder, 1990b).

Although bottlenose dolphins in particular appear to be breeding well in captivity, they were not thought to have reached self-sustaining status in 1991 (Duffield & Wells, 1991), but it is thought they are now kept in sufficient numbers (around 336 in the US and Canada in 1992) that a self-sustaining zoological population could be established (Duffield & Shell, 1994). Twenty nine percent of bottlenose dolphins in captivity in the US and Canada were captive born in 1992 (Duffield & Shell, 1994). The requirements for a self-sustaining population are considered further below.

Other species which have conceived and given birth in captivity include orcas (Duffield & Miller, 1988), white sided dolphins (Hudson & Ramirez, 1996), beluga whales (Russel *et al*., 1997), and Commerson's dolphin (Joseph *et al*., 1987).

Studies of the reproductive cycle have been used to estimate age at sexual maturity and calving interval of orcas (Duffield & Miller, 1988; Duffield *et al*., 1995), and bottlenose dolphins (Cornell *et al*., 1987; Schroeder, 1990a). Nutrition is likely to be linked to age at sexual maturity and calving interval as it is in many other species which limits how these values could be used in a management or conservation context.

Advanced reproductive technologies (ART) (Robuck *et al*., 1994) are now being applied to bottlenose dolphins. This includes techniques such as synchronisation and induction of ovulation and artificial insemination using frozen semen. The justification given for using such techniques is two fold (Robuck *et al*., 1994). Firstly, to develop techniques using a successfully breeding group so that they could be used in the management of endangered species. Secondly, to facilitate gene flow between animals in isolated institutions through the use of artificial insemination.

Levels of circulating hormones have been measured to describe the oestrus cycle in bottlenose dolphins and orcas. Serum progesterone levels are used as indicators of pregnancy in the bottlenose dolphin (Cornell *et al*., 1987; Schroeder, 1990a) and orca (Duffield *et al*., 1995). Levels of ovarian hormone levels and their metabolites in urine

are used to monitor the oestrus cycle in orcas (Duffield *et al*., 1995). Measurements of serum testosterone levels in male bottlenose dolphins have been used to follow the onset of sexual maturity and to identify periods when animals are most fertile (Schroeder, 1990a; Robeck *et al*., 1994).

At the NOSC artificial insemination following induction of ovulation has been attempted on five occasions in which two animals conceived but spontaneously aborted (Schroeder,1990b; Schroeder & Keller, 1990). However, natural fertilisation following induction of ovulation using pregnant mare serum gonadotrophin followed by human chorionic gonadotrophin has resulted in live births (Schroeder, 1990b). Embryo transfer does not seem to have been used on cetaceans to date (Robuck *et al*., 1994). Cloning is another technique which is now being proposed as a conservation technique for endangered mammalian species (Ryder & Benirschke, 1997). It may be considered for cetaceans but has not been applied yet.

Although sub-populations of both bottlenose dolphins and orcas have been described that show evidence of genetic isolation, these do not appear to have been kept separate in captive breeding programmes. For example, mitochondrial DNA (mtDNA) analysis shows distinctive differences between Atlantic and Pacific forms suggesting divergence as a result of population separation following bio-geographic events (Dowling & Brown, 1993). There are haematological, genetic and physical differences between onshore and offshore forms of bottlenose dolphins which are apparently of genetic origin (Duffield, 1990; Curry *et* al., 1998; Hohn *et al*., 1998). However, Pacific and Atlantic forms of bottlenose dolphins have been included in the same breeding programmes (Cornell *et al*., 1987). Similarly for orcas, differences in mtDNA exist between North Pacific and North Atlantic orcas and differences exist between the so-called 'transient' and resident groups of orcas off Vancouver Island (Hoelzel, 1991). Again, Pacific and Atlantic animals have been mated in captive breeding programmes (Duffield & Miller, 1988).

Conclusions - Captive Breeding as a Conservation Tool?

All the research on reproduction using captive animals is clearly relevant to the successful breeding of animals in captivity. It is important to understand growth rates and normal calf behaviour to monitor health of new born animals. Knowing the most fertile periods will help determine when to introduce males to females with the best chances of success. However, the highly controlled environment of the aquarium is a long way from that of the ocean. Food availability, whether a suitable mate is present at the correct time and general health are just three of many factors likely to influence calving intervals, for example. Values that are established in captivity would have to be very carefully verified in the wild if they were to be applied in management regimes, otherwise mistakes could be made in predictions about how well a population could grow in size in following, for example, an outbreak of disease.

However, captive breeding programmes are said to have three other benefits:

1. as captive populations increase they will become self sustaining and remove the need to take more animals from the wild.

2. the information from cetaceans bred in captivity can be applied to help more endangered species.
3. captive bred populations may be necessary to preserve endangered species.

Whilst these benefits sound valid and laudable, they are not unequivocally so.

Self sustaining populations

Zoos and marine parks also promote captive breeding as a way of reducing and finally eliminating the need to take animals from the wild. Although there has been a reduction in the numbers of animals being taken into captivity, if the genetic health of the captive population is to be maintained it may require the introduction of new genetic material into the gene pool. This is because cetaceans are kept in small isolated groups and transport between them can be both expensive and dangerous. Some degree of inbreeding depression is considered inevitable in captive populations (Arnold, 1995).

The issue of what number of animals needs to be kept to maintain a population in captivity is difficult to calculate and depends on the goals of the programme. When dealing with small numbers, the need to maintain the genetic health of a population is one such goal. One widely supported aim of captive breeding is to ensure 90% of the genetic variation of the original wild population over a 200 year period (Soulé *et al.*, 1986). The intention of such a goal is to ensure sufficient variation remains in a population for it to be able to respond to gradually changing habitats. Any captive population of cetaceans will never be able to be anything other than small because of the physical problems of housing a large population

Genetic diversity (GD) is used as a measure of genetic variation and this will decline over time in a closed population if no new variation is introduced by mutation or new individuals (Lacy, 1995). The effective population size, Ne, is the term used in designing captive breeding programmes. Ne is the size of an idealised population which has the same intergenerational variance in GD as the wild population. However, the number Ne does not equal the total number in a population, it is usually less than that number because in a real population mating is not random or sex ratios equal (Lacy, 1985). Therefore the total population size will have to be larger than the calculated Ne to reach the goal of maintaining 90% of the original genetic variation over 200 years. Exactly how much larger the population would have to be is a matter of judgement. However Ne may only be 10-25% of the total population size (Foose *et al.*, 1995). Therefore even for a species with a relatively long generational time, like cetaceans, and an Ne as low as 500 (as has been recommended for the Asian Rhino (see Foose *et al.*, 1995)), could require a total captive population of between 2,500 to 5,000. Even when maintaining a defined sub-population with an Ne of 10, a total population of 25-100 of each group would be needed. Because aquariums are widely spaced and complete co-operation between institutes might be difficult to achieve, the

total number required for a cetacean population will be greater than in situations where movement and cross breeding is easy. Advanced reproductive technologies are being explored for use with bottlenose dolphins to avoid inbreeding depression and to create self-sustaining populations. However, their use in most other species is severely restricted because the most important requirement is a group of animals which already breeds well in captivity (Robuck *et al*., 1994). Techniques such as artificial insemination have yet to result in a live birth in any captive cetacean.

However, for those species which have been bred in captivity to date, perhaps the most pertinent question is 'what population would be sustained?' The considerable mixing of bottlenose dolphins of different origins, in both regional and local terms means that a hybrid population has been established (see above). The position may be reached where no further introductions of animals is needed to maintain numbers or genetic diversity but in research terms these would be a semi-domesticated population of performing animals of questionable relevance to wild populations.

There appears to be no co-ordinated, scientifically defined (in terms of maintenance of GD) plans for breeding bottlenose dolphins or orcas in captivity. Therefore the scientific defence of captive breeding in terms of a self-sustaining population appears rather flimsy.

Preserving endangered species

One of the emerging research aspirations with captive cetaceans is to be able to develop techniques to maintain endangered species in captivity. The species for which this is most promoted is the Yangtse river dolphin or baiji. Numbers of this dolphin are thought to have dwindled to less than 300 as a result of habitat destruction, disturbance and pollution (Perrin & Brownell, 1989). Experience with this species in captivity has been limited and has had little success but is hoped that knowledge from other species such as the bottlenose dolphin could be applied to the baiji.

In wild populations not threatened with extinction, ecological and demographic factors are considered more important that genetic factors. However, for small populations on the verge of extinction genetic factors become much more important (Lande, 1995). Ralls (1989) considered that a successful breeding programme for the baiji would require an Ne of 20-25 animals and that 200-300 animals would need to be the final population size at the end of the 200 years. It is unclear what the total foundation population in captivity or semi-captivity would have to be to establish this effective population but it could range from 80 to 250 based on Ne being 10-25% of total population (Foose *et al.,* 1995).

However, only one male baiji survives in captivity in China, all other captured animals dying with months. Therefore the big hurdle for this population is to achieve 'Stage One' of Ralls (1989) programme - 'Achieving routine breeding in semi-captivity'. Because there has been no progress on this front in the nine years since this article was published and numbers of baiji have probably declined even further, the outlook

appears bleak. Given the extremely poor performance of baiji in captivity to date, capturing any number of them may simply hasten their demise and efforts may be better placed at preserving their natural habitat and gaining better insight into their ecology in the wild. Advanced reproductive technologies give no hope until a well established captive breeding population exists (Robuck *et al*., 1994).

The problems faced by the baiji may also be reproduced with other species. Given the space requirements for keeping cetaceans, is it realistic to consider captive breeding as an effective preservation strategy? The resources needed would be enormous. Keeping three or four animals in captivity to breed is not a scientifically justifiable strategy unless the long term goals of genetic conservation have been set and an assessment made as to whether they are plausible. Little such analysis has been undertaken. Concurrently, the ultimate aim in preserving an endangered species would be to eventually restock the population in the wild. Considering the difficulties discussed, practical conservation measures in the wild should be the recommended preservation strategy for endangered species.

There can be no justification for maintaining bottlenose dolphins or killer whales, for example, on these grounds as wild populations of these species are not in a dramatic decline.

Learning from other species

How relevant are studies on captive cetaceans which are breeding well in captivity to breeding endangered cetaceans? This is proposed as an important justification for breeding bottlenose dolphins for example. Ridgeway *et al* (1989) have considered the lessons from breeding bottlenose dolphins that could be applied to the baiji.   Most of these relate to basic husbandry and emphasise the need to understand the specific ecology of the baiji. Because river dolphins in particular have proved much less easy to maintain in captivity than some other species of cetacean, knowledge of bottlenose dolphins may be of only marginal help and could be misleading.

Conclusions

When considering the cetacean breeding programmes which have taken place in zoos and marine parks, it is difficult to come to any other conclusion than justifications based on preservation are nothing more than *post hoc* excuses for what has been, in reality, an *ad hoc* process. There have been no goals set in terms of the preservation of genetic diversity and its definition for a self-sustaining population. The mixing of genetically different populations means that the strategy pursued to date has been misplaced and ruled out the possibility of reintroduction. Conscious and unconscious selection will have resulted in a group of animals being bred which may be successful in captivity but not good models of the wild population.

Designing conservation strategies based on maintaining habitats has the potential to avoid these pitfalls. The genetic diversity conserved with such an approach may better equip animal populations to deal with changing conditions.

8. Environmental Protection

Another reason for conducting research on captive cetaceans is that it may help develop methods or policies to protect wild animals from environmental harm caused by humans. Oil pollution and entanglement in fishing gear have been the areas where most research on captive cetaceans has been undertaken. To a lesser extent there has been research on the effects of noise and investigations of immune function which may be relevant to pollution studies but these have not been a primary concern. What research has been undertaken on oil and entanglement and to what extent the data can be used to protect wild cetaceans is the subject of this section.

Oil Pollution

Oil pollution is perhaps the most visible form of degradation of the marine environment. Oil spills are not obviously associated with mortalities of cetaceans in the same way they are with birds and sea otters, leading some to the conclusion 'there is no gripping evidence that oil contamination has been responsible for the death of a cetacean' (Geraci, 1990). Because, on the one hand, some whales and dolphins have been seen swimming and feeding in oil slicks, and on the other hand, other evidence showed that some animals avoided oil, experiments were designed to test whether bottlenose dolphins could detect oil and avoid it.

These studies showed that dolphins can detect films of oil depending on their thickness and whether they are mixed with water (which improved detection). It was concluded that dolphins should be able to detect thick films near the source of a spill but not thin films further away (Geraci *et al*., 1983). Further studies showed that dolphins actively avoided a controlled oil spill and showed a marked startle responses when they surfaced through it (Smith *et al*., 1983). By conducting experiments at night it was possible to demonstrate that animals use mainly visual clues to detect oil but their response to it relies on their tactile sense (St. Aubin *et al*., 1985).

The same group of researchers tested the sensitivity of dolphins skins to applications of crude oil. They demonstrated that they were relatively resistant and much more so than human skin and concluded 'that in real life contact with oil would be less harmful than we and others had proposed' (Geraci, 1990).

Thus following research on captive bottlenose dolphins the opinion appears to be that although dolphins clearly dislike being in oil, that it doesn't do them much, if any, harm.   It is not clear why intense dislike and startle responses do not constitute evidence of harm, but this probably reflects a bias by the researchers in their choice of measures of harm towards those that are expressed as physical ill effects that they can quantify.

Entanglement in Fishing Gear

Entanglement and drowning in fishing gear is now thought to be one of the most important causes of death in cetaceans associated with human activities. Porpoises have been particularly affected, with one, the vaquita (*Phocoena sinus*) being threatened with extinction as a result (Jefferson & Curry, 1994). These losses have led to questions being asked about why cetaceans are not able to detect fishing gear and avoid it and whether changes to the design of nets could make them easier for whales and dolphins to detect. Many experiments to investigate these questions are now being conducted on animals in captivity. The echolocation and other sensory studies which have been conducted in captivity (see section 5) are also relevant to this subject as they have revealed the ways in which cetaceans explore their environments.

Based on studies of vision and echolocation it has been shown that gill nets are of poor visibility and their low acoustic target strength means they are difficult for animals' sonar systems to detect (Au & Jones, 1991). In contrast pelagic trawl nets should be visually detectable (Kastelein *et al*., 1997f) but animals still become entangled. There are also differences between species in how well they detect nets. Japanese studies (Hatekayama *et al*., 1986, cited in Verboom & Kastelein, 1995) showed that beluga whales could detect gill nets at a distance of 5.5 metres 50% of the time. For harbour porpoises the 50% detection distance was only 1-2 metres.

A lot of work in this area has taken place at the Harderwijk Marine Mammal Park in the Netherlands using harbour porpoises. They have studied the responses of rehabilitated harbour porpoises to ropes (Kastelein *et al*., 1995a), showing that 13mm diameter nylon ropes could be detected and avoided but that in the presence of live fish the ropes (placed horizontally across the pool) were not avoided so frequently. Using nylon mesh nets of different mesh sizes, they have been able to demonstrate that harbour porpoises could learn to detect and avoid nets suspended in their pools (Kastelein *et al*., 1995b). Their ability to detect nets was much better in light than dark. However, in the variety of situations they tested an animal became entangled at least once.

Other studies with harbour porpoises in Japan (Hatakeyama & Soeda, 1990) have suggested that the wave form characteristics of the harbour porpoise echolocation clicks make them less able to detect gill nets than some other species such as Dall's porpoise. These studies together with basic knowledge of required target strengths for different species to detect nets could be used to help design reflectors to make nets more 'visible' to cetaceans.

Efforts to prevent entanglement have also involved generating noises to deter animals which have had to use knowledge of cetacean hearing to choose sounds which will fall

within their hearing range. Dutch researchers have studied the response of harbour porpoises to various noises (Kastelein *et al*., 1997f; 1997g). Broad band sweeps were most effective in changing the porpoise's behaviour and were effective in encouraging the porpoise to swim through net meshes she would not normally pass. This was to investigate whether such noise would encourage an animal to escape from the sides of a trawl net. 'Pingers' on nets caused Commerson's dolphins (*Cephalorhynchus commersonii*) to show attempts at dramatic avoidance (although they were unable to do this as they were confined in a pool) including leaping out of the water and aggressive acts toward each other (Anderson *et al*., 1998).

These studies in captivity may give some indication of work to pursue with wild animals. However, the acoustic and visual nature of the captive environment mean that only limited conclusions may be drawn from such studies. For example, there will be a great deal of reverberation from the walls of pens; ambient sound levels are much lower than at sea; and the distractions of fish and other cetaceans is absent. What works in practice is always going to be the important question.

Conclusions

Although research on captive animals with relevance to environmental threats may give clues to other work to pursue it may be of limited value. For example, the way in which evidence on the effects of oil spills on captive bottlenose dolphins has been collected and presented may have subtle but significant effects on environmental protection which may not be to the benefit of wildlife. Firstly, the importance of oil spills may be reduced in policy makers eyes because bottlenose dolphins show no evidence of harm. Secondly, there can be little doubt of the harmful effects on many other species of animals whatever the definitions of harm, which make the experiments on captive animals difficult to justify.

In the case of entanglement, concentrating on technical efforts to get whales and dolphins to avoid nets may divert attention from other issues at stake. Studies with Commerson's dolphins in captivity showed extreme aggression and avoidance reactions to 'pingers' placed on test nets (Anderson *et al*., 1998). If all gill nets and trawls carry such devices, what effect will this have on food availability when large productive areas of the seas are rendered 'no-go areas'? There is also the question of whether the pointers to productive actions are likely to be the most effective in the complex environment of the oceans because a false impression of effectiveness may have been given. Studies have been conducted in the wild with harbour porpoises (e.g. Kraus *et al*., 1997) which have demonstrated that such work is feasible and may make a better contribution to avoiding the problem of entanglement.

9. Discussion and Conclusions

The most important issue which is raised by this report is the extent to which captive animals are an adequate model of the wild population. A second important issue identified is whether any knowledge, whilst interesting to humans, is an end which justifies captivity and experimentation.

The factors which affect the answers to these questions, across all the fields of research, include the impact of the physical conditions of captivity, the nature of the captive population and the availability of alternative methods to collect data.

Physical conditions of captivity

The physical fact of confinement has profound effects on many aspects of cetacean physiology and ecology. Basic haematology and biochemistry parameters are altered for several reasons including the stress of captivity, routine medication such as worming and diet (see sections 2 & 3). Shallow pools and restricted areas for travel mean that adaptive changes associated with the physiological requirements of diving and foraging may be lost (see section 4).

Behaviour is also profoundly affected by captivity (see section 5). Social organisation is determined by the institutions involved. Stereotyped behaviour is a common occurrence, mainly evidenced by uni-directional circular swimming patterns. Hierarchies based on dominance are the norm rather than the more fluid pattern of social organisation seen in wild animals. Animals in captivity are often highly trained and much of their behaviour is directed. They do not have to forage for food, rather successful foraging becomes associated with ability to learn the appropriate tricks or experimental protocol.

Much social behaviour and communication skills are learnt as are other techniques such as echolocation (see section 6). Animals in captivity will learn a range of behaviours and skills needed to survive in marine parks and these may be very different from those needed to be successful in the wild. This is likely to be an increasing problem for researchers using captive born animals.

The environment in captivity is also very static, unaffected by changing weather conditions and prey availability. Investigating the bland environment of the pool will be very different from the complex environment of the oceans. Experimental conditions tend to be controlled even further, changing one parameter at a time to find cause effect relationships which may hide of neglect the possibility of complex cause effect chains. Even basic reproductive data on calving intervals and fecundity may not be relevant to wild populations because changing environmental conditions and food availability will affect reproductive potential (see section 8).

Therefore the physical nature of the captive environment will have a profound influence on the quality and relevance of insights which the research can provide. Ironically it is only by conducting studies on wild animals and making comparative assessments that the value of captive studies be assessed. Inevitably this raises the question of whether the studies could not more appropriately be carried out in the wild.

What population does the captive population represent?

Not only does the physical nature of the captive population distance them from their wild counterparts but so does their genetic makeup. Captive populations are mainly an *ad hoc* collection of animals. Pacific and Atlantic forms of bottlenose dolphins and orcas have been mixed and mated. Individuals have been taken from different sub-populations with different ranges and behaviours. This mixture is now forming the basis of the breeding population with the hope of its becoming self-sustaining (see Section 8).

This begs the question of what exactly does the captive population represent in relation to the wild population? Where would the offspring of the breeding programme fit in the marine environment? The crude genetic diversity of captive animals out-crossed with those from different forms or groups may have increased but what conservation value does this have? The answer may be 'very little' as the domestication and mixed parentage of captive animals increases. Conscious and inadvertent selection for success in captivity add to the problems.

Thus as one committed researcher (Pryor, 1991) has commented:

> "The dolphin, primarily the bottlenose dolphin, may well prove to be the newest large animal in our history to accept domestication".

However, the domestication of the bottlenose dolphin undermines its scientific justification as a model of the wild population.

Furthermore, inside this rather selective group of animals in captivity, only certain individuals participate in experiments, because they have to be highly trained to do so and the investment in time and money means limited numbers are involved. Many of the cognition studies involve one or two animals and the same applies to other areas of research. Only one animal was used in the Dutch studies of the harbour porpoise to determine the effects of sounds and responses to nets (Kastelein *et al* 1997f; 1997g). Only two animals were used in their earlier studies of entanglement (Kastelein *et al*., 1995), both of which were juveniles when brought into captivity and which may have had much to learn about echolocation. Therefore, whether data comes from a representative sample is very questionable.

Another related question is whether a representative of one cetacean species can be used as a model for others? Although basic conditions of care such as those relating to standards of water quality may be relevant to many species much important information may well be species specific. Species behave very differently in captivity (Defran & Pryor, 1980), in ways related to their particular biology and ecology. Therefore extrapolating from one species to another should only be undertaken with great caution, understanding that it might be misleading and potentially damaging.

Availability of data on wild populations.

Our ability to conduct research on wild populations is increasing rapidly. Some of this

is invasive in some respects, such as the use of satellite tagging and time depth recorders, but does not impose the same restrictions that captivity does. Long-term behavioural studies of different populations of cetaceans are providing data which gives important insights into social organisation and activity. Through this kind of understanding conditions in captivity have been improved.

Studies in the wild have thrown up questions that would not have arisen in captive studies. For example, in their studies of the use of acoustic alarms to reduce by-catch of harbour porpoises (Kraus *et al*., 1997) not only was entanglement reduced by the use of alarms, but the types of prey in the nets also changed. The noise from the alarm may have been affecting the fish rather than the porpoises, reducing by-catch that way or it may have been a combination of effects. A net alarm which deters fish as well as cetaceans is unlikely to find favour with fishers.

Techniques for use in the wild have become increasingly sophisticated. Visual sonar, radio and satellite tracking are becoming routine allowing much more information to be collected than was possible in the past. Because of the complexities of the natural environment such research may prove more directly relevant to conservation of wild species.

Useful knowledge?

The shortcomings of the captive environment, the unnatural nature of the captive population, the lack of a representative sample and our improving ability to study animals in their natural environment all undermine the case for research on captive dolphins being directly relevant to conservation of wild populations.

However, it is not possible to argue that research on captive animals has taught us nothing. The studies of cetacean sensory systems have revealed a great deal about the physical nature of the echolocation signals, audition and vision and animal's cognition. Some ways in which these may help in social communication between cetaceans and how they make sense of the world have been identified (Herman, 1991) but the interpretation of laboratory data has relied heavily upon studies on free-living animals. The usefulness of experimental studies to conservation may have been limited because they have rarely had an ecological perspective from the start. Studies have been concerned mainly with the finer points of animals ability to discriminate between shapes and materials such as spheres and triangles and steel and iron. These may be ideal studies if you are seeking to improve underwater sonar detection systems required to identify and track ships but when it comes to understanding foraging techniques and entanglement in fishing gear they are of less obvious relevance.

Limited scientific justification for captive whale and dolphin research

Proponents of captive research often suggest that criticism of it is based on emotional responses to animals in captivity. Yet this report has shown that on scientific grounds

the justification is debatable. It is interesting that although researchers may denigrate critics on the grounds of anthropomorphism, they often engage in the same kind of discourse. One has talked about an animal who worked hard to understand complicated training routines and what was required of him as 'a true professional' who 'appears to enjoy the work' (Moore, 1991). Bottlenose dolphins have been termed 'willing, even dedicated co-workers in extremely complex research tasks' (Pryor, 1991). It has been argued that dolphins prefer captivity to the oceans (Kirtland & Stringer, 1995; Pryor, 1991) without thought about why this maybe and whether captivity has equipped animals with any real choice. Therefore, the researchers, like their critics, have relationships with whales and dolphins which influence their opinions, and their science is not isolated from their emotional and social reactions.

At best a judgement about the relevance of research with captive cetaceans to conservation of wild animals has to be highly qualified. Such research may give clues to the situation in the wild but the irony is that confirmation and interpretation through research on free-living animals will be needed. The rather belated justification for captivity as scientific research tool to understand and thereby conserve free-living whales and dolphins is therefore largely a political, opportunistic response to changing public opinion about zoos and marine parks. When the knowledge gained is measured against value to conservation it is seen to be lacking. Defending captivity on the basis of scientific research is, therefore, rather dubious.

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