

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/228351576>

Potential effects of climate change on marine mammals

Chapter *in* Oceanography and marine biology · June 2007

CITATIONS

91

READS

477

11 authors, including:



M. Begoña Santos

Instituto Español de Oceanografía

161 PUBLICATIONS 2,826 CITATIONS

SEE PROFILE



Graham John Pierce

University of Aberdeen

351 PUBLICATIONS 8,045 CITATIONS

SEE PROFILE



Humphrey Q. P. Crick

Natural England

96 PUBLICATIONS 4,083 CITATIONS

SEE PROFILE



Robert Anthony Robinson

British Trust for Ornithology

106 PUBLICATIONS 2,967 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Social transformations of marine social-ecological systems [View project](#)



Small scale fisheries and the EU zero discard policy [View project](#)

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

J.A. LEARMONTH¹, C.D. MACLEOD¹, M.B. SANTOS^{1,2},
G.J. PIERCE¹, H.Q.P. CRICK³ & R.A. ROBINSON³

¹*School of Biological Sciences [Zoology], University of Aberdeen,
Tillydrone Avenue, Aberdeen, AB24 2TZ, U.K.*

E-mail: j.a.learmonth@abdn.ac.uk

²*Instituto Español de Oceanografía, Centro Costero de Vigo,
Cabo Estay, Canido, 36200 Vigo, Spain*

³*British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, U.K.*

Abstract Predicted impacts of climate change on the marine environment include an increase in temperature, a rise in sea levels and a decrease in sea-ice cover. These impacts will occur at local, regional and larger scales. The potential impacts of climate change on marine mammals can be direct, such as the effects of reduced sea ice and rising sea levels on seal haul-out sites, or species tracking a specific range of water temperatures in which they can physically survive. Indirect effects of climate change include changes in prey availability affecting distribution, abundance and migration patterns, community structure, susceptibility to disease and contaminants. Ultimately, these will impact on the reproductive success and survival of marine mammals and, hence, have consequences for populations. Marine mammal species, which have restricted geographical distributions with little or no opportunity for range expansion in response to climate change, may be particularly vulnerable to the effects of climate change. The potential effects of climate change on marine mammals have a number of implications for their conservation and highlight several areas requiring further research.

Introduction

The Earth's climate is changing (IPCC 2001a). The global average land and sea surface temperature has increased over the twentieth century and precipitation has increased over the same period, particularly over mid- and high-latitudes. These changes have had secondary impacts. For example, as temperatures have increased the extent of ice cover has decreased and global sea level has risen. Such changes are evident from the global network of climate instruments and, over a longer timescale, from the use of historical proxies such as tree rings or ice cores. The causes of such changes are open to debate, but most of the observed warming over the last 50 yr has probably been due to increased CO₂ emissions, and these increases are likely to continue (e.g., Hulme et al. 2002, EEA 2004).

Global climate change will affect the physical, biological and biogeochemical characteristics of the oceans and coasts. Known or predicted large-scale and regional impacts of climate change on the marine environment include an increase in temperature, a rise in sea levels, and changes in ocean circulation, sea-ice cover, salinity, CO₂ concentrations, pH, rainfall patterns, storm frequency, wind speed, wave conditions and climate patterns (FRS 1998, Hansen et al. 2001, IPCC 2001a, Sear et al. 2001, Hulme et al. 2002, FRS 2003, ICES 2004).

Climate change is likely to present a major challenge to the world's wildlife, and to impact overall levels of biodiversity. Changing climate has already had a number of impacts on wildlife, across a range of taxa, and these impacts are set to increase unless suitable mitigation measures are taken (Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, EEA 2004, Parmesan & Galbraith 2004).

The effect of climate change on the marine environment has the potential to have, and in some cases has already had, a considerable impact on marine ecosystems and species. These effects could include changes in abundance, distribution, timing and range of migration, community structure, the presence and species composition of competitors and/or predators, prey availability and distribution, timing of breeding, reproductive success and, ultimately, survival (IWC 1997, Tynan & DeMaster 1997, Harwood 2001, Würsig et al. 2002). While some species may increase in abundance or range, climate change will increase the risk of extinction of other more vulnerable species. The geographical extent of the damage or loss, and the number of systems affected, will increase with the magnitude and rate of climate change (IPCC 2001a).

Uncertainties about the nature and degree of future climate change make it impossible to know exactly how weather, ocean circulation and biological productivity will be affected (for example, Weaver & Zwiers 2000). Effects on the marine environment are especially difficult to predict because of the complex interactions between ocean processes and climate and will vary greatly between areas. Therefore, predictions of the effects on species and populations are highly speculative (Würsig et al. 2002). The impacts of climate change will reflect the timing and geographic scale of the changes, as well as on the longevity, generation time and geographic distribution of the species (Würsig et al. 2002). For example, large but 'slow' (in the order of decades or centuries) shifts in the climate have occurred throughout the Earth's history, and these have driven the evolution of adaptive characteristics, within-species variations, population discreteness and extinctions (Würsig et al. 2002).

There have been several recent papers linking the effects of climate change to marine mammals (e.g., Ferguson et al. 2005, MacLeod et al. 2005). The present paper reviews current information on the observed and predicted changes in climate and their potential impacts, direct and indirect, on marine mammals. Examples of observed effects are given for mysticetes (baleen whales), odontocetes (toothed whales, dolphins and porpoises), pinnipeds (seals, sea lions and walrus), sirenians (manatee and dugong) and the polar bear (*Ursus maritimus*), based on published accounts and reports. Many of the indirect effects of climate change on marine mammals will be through changes in prey availability; therefore potential effects of climate change on prey species, such as fish, cephalopods and plankton are also reviewed.

Range of marine mammals

Marine mammals are found in just about all ocean habitats, as well as several rivers and inland seas. In the open ocean, marine mammals may be thought of as 'surface dwellers', that spend most of their lives within about 200 m of the surface, 'deep divers', that routinely dive to depths below 500 m for short periods of time, or 'deep dwellers' that spend much of their time at depths below 500 m. Several species are semipelagic; occurring in areas between shallow and deep water, often at the edge of the continental shelf or some other underwater feature. Many marine mammals are coastal, with baleen whales, odontocetes, pinnipeds and sirenians all having coastal representatives (Würsig 2002).

A species' distribution is affected by a combination of demographic, evolutionary, ecological, habitat-related and anthropogenic factors although, in general, prey availability is likely to be particularly critical (Forcada 2002). Species habitat preferences are generally thought to be related to the distribution of preferred prey, which in turn are often determined by physical oceanographic features. Therefore, the habitat preferences of marine mammals are often defined by physical and chemical characteristics of the water, which define water masses and current boundaries where

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

prey accumulates. For example some species, such as Heaviside's (*Cephalorhynchus heavisidii*), Commerson's (*C. commersonii*) and Peale's (*Lagenorhynchus australis*) dolphins, are associated with cold-water currents, and blue whales (*Balaenoptera musculus*) are often found in areas of cool upwelling waters (Forcada 2002, LeDuc 2002). Therefore, although marine mammals are observed widely across the world's oceans, distribution within the overall range is often patchy, with some areas being used more frequently than others. These 'preferred' areas or 'critical habitats' are probably particularly important for survival and reproduction, and it is changes to these areas that are most likely to affect the distribution and abundance of marine mammals (Harwood 2001).

While the fine-scale distribution of marine mammal species may be related to oceanographic features and conditions through their effects on prey distribution, the regional or global ranges of marine mammal species are often related to water temperature (Table 1). For example, bowhead whales (*Balaena mysticetus*) and narwhals (*Monodon monoceros*) are found only in Arctic waters, Atlantic white-beaked dolphins (*Lagenorhynchus albirostris*) are only found in cold temperate waters, and species such as spinner (*Stenella longirostris*) and pantropical spotted (*S. attenuata*) dolphins are restricted to tropical waters (Mann et al. 2000). A species' range may be limited in some cases because it is not adapted for living in certain environments. For example, tropical delphinids may not range into higher latitudes due to limitations on their abilities to thermoregulate in colder water or find food in different habitats. Competition, either from closely related species or from ecologically similar species, may also exclude a species from a particular region in which it could otherwise survive (i.e., competitive exclusion) (Forcada 2002). However, whether the relationship between the range of many marine mammal species and water temperature is direct, with species only being able to survive within specific temperature ranges, or indirect with temperature affecting competitive abilities of ecologically similar species, is unknown in most cases.

Within a species range, there may be regular changes in areas of occurrence as their biological and ecological requirements change (Forcada 2002). Of these changes, the most common are seasonal migrations. Migration can be described as "the seasonal movement between two geographic locations that is related to the reproductive cycle, changes in temperature, and prey availability" (Forcada 2002) or "the persistent movement between two destinations" (Cockeron & Connor 1999). The Bonn Convention on the Conservation of Migratory Species of Wild Animals (1979) (CMS) is an important instrument in the management of migratory species. It defines a migratory species as "the entire population or any geographically separate part of the population of any species or lower taxon of wild animals, a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries".

The basic driving forces for migration are ecological and biogeographic factors, like seasonality, spatiotemporal distributions of resources, habitats, predation and competition (Alerstam et al. 2003). The triggers for migration may relate to changes in day length but, as the timing of migrations can vary from year to year, prey abundance may also be an important factor, and temperature and sea-ice formation can also be influential (Stern 2002).

Most baleen whales (mysticetes), such as blue, grey (*Eschrichtius robustus*), fin (*Balaenoptera physalus*), sei (*B. borealis*), northern and southern right whales (*Balaena glacialis* and *B. australis*) and humpback whales (*Megaptera novaeangliae*), undertake long seasonal migrations between tropical calving grounds in winter and high latitude feeding grounds in summer. For example, grey whales are highly migratory with an annual migration covering up to 15,000–20,000 km between summer feeding grounds in Arctic or subarctic waters and winter breeding grounds in temperate or subtropical southern waters (Jones & Swartz 2002). Bowhead whales also migrate but their longitudinal movements are equal to or greater than their latitudinal movements and they never leave Arctic waters. The migration or seasonal movements of Bryde's (*Balaenoptera edeni*) and minke whales (*B. acutorostrata*) are often less well defined and less predictable than those of other migratory baleen whales (Forcada 2002).

Table 1 Species range (breeding site for pinnipeds), IUCN status and potential effects of climate change on the range of cetaceans, pinnipeds, sirenians and other marine mammal species

Family and species name	Common name	Species range (breeding site for pinnipeds)	IUCN status	Potential effects of climate change on species range
Mysticeti		Baleen Whales		
Balaenidae				
<i>Balaena mysticetus</i>	Bowhead whale	N Hemisphere: Arctic waters, circumpolar	LR:cd	↓
<i>Balaena glacialis</i>	Northern right whale	N Atlantic & Pacific: subpolar to tropical	EN (D)	?↓
<i>Balaena australis</i>	Southern right whale	S Hemisphere: Antarctic to temperate	LR:cd	?↓
Neobalaenidae				
<i>Caperea marginata</i>	Pygmy right whale	S Hemisphere: circumpolar, cold temperate		?↓
Eschrichtiidae				
<i>Eschrichtius robustus</i>	Grey whale	N Pacific: warm temperate to arctic	LR:cd	?
Balaenopteridae				
<i>Megaptera novaeangliae</i>	Humpback whale	Worldwide: cold temperate/polar to tropical	VA (A)	?
<i>Balaenoptera acutorostrata</i>	Minke whale ¹	Worldwide: polar to tropical	LR:nt	?
<i>Balaenoptera bonaerensis</i>	Antarctic minke whale ¹	S Hemisphere: polar to tropical	LR:cd	?
<i>Balaenoptera edeni/brydei</i>	Bryde's whale	Worldwide: warm temperate to tropical	DD	
<i>Balaenoptera borealis</i>	Sei whale	Worldwide: cold temperate to tropical	EN (A)	?
<i>Balaenoptera physalus</i>	Fin whale	Worldwide: polar to tropical	EN (A)	?
<i>Balaenoptera musculus</i>	Blue whale	Worldwide: polar to tropical	EN (A)	?
Odontoceti		Toothed Whales		
Physeteridae				
<i>Physeter macrocephalus</i>	Sperm whale	Worldwide: polar to tropical	VU (A)	?
Kogiidae				
<i>Kogia breviceps</i>	Pygmy sperm whale	Worldwide: warm temperate to tropical	DD	↑
<i>Kogia sima</i>	Dwarf sperm whale	Worldwide: warm temperate to tropical		↑
Ziphiidae				
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	Worldwide: cold temperate to tropical	DD	?
<i>Berardius arnuxii</i>	Arnoux's beaked whale	S Hemisphere: circumpolar, polar to subtropical	LR:cd	?
<i>Berardius bairdii</i>	Baird's beaked whale	N Pacific: polar to subtropical	LR:cd	?

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

Table 1 (continued) Species range (breeding site for pinnipeds), IUCN status and potential effects of climate change on the range of cetaceans, pinnipeds, sirenians and other marine mammal species

Family and species name	Common name	Species range (breeding site for pinnipeds)	IUCN status	Potential effects of climate change on species range
<i>Tasmacetus shepherdi</i>	Shepherd's beaked whale	S Hemisphere: warm temperate to subpolar	DD	?
<i>Indopacetus pacificus</i>	Longman's beaked whale	Indian Ocean and Pacific: tropical waters	DD	?
<i>Hyperoodon ampullatus</i>	Northern bottlenose whale	N Atlantic: arctic to cold temperate waters	LR:cd	↓
<i>Hyperoodon planiformis</i>	Southern bottlenose whale	S Hemisphere: circumpolar, Antarctic to temperate	LR:cd	?
<i>Mesoplodon hectori</i>	Hector's beaked whale	S Hemisphere: cold temperate to subtropical	DD	?
<i>Mesoplodon mirus</i>	True's beaked whale	Worldwide: warm temperate to subtropical	DD	?↑
<i>Mesoplodon europaeus</i>	Gervais' beaked whale	Atlantic: warm temperate to tropical	DD	?↑
<i>Mesoplodon bidens</i>	Sowerby's beaked whale	N Atlantic: subpolar to warm temperate	DD	?
<i>Mesoplodon grayi</i>	Gray's beaked whale	S Hemisphere: cold to warm temperate	DD	?
<i>Mesoplodon peruvianus</i>	Pygmy beaked whale	SE and NE Pacific: cold temperate to tropical	DD	?
<i>Mesoplodon bowdoini</i>	Andrew's beaked whale	S Hemisphere: cold temperate to subtropical	DD	?
<i>Mesoplodon carlhubbsi</i>	Hubbs' beaked whale	N Pacific: cold temperate to subtropical	DD	?
<i>Mesoplodon ginkgodens</i>	Ginkgo-toothed beaked whale	N Pacific and Indian Ocean: temperate to tropical	DD	?
<i>Mesoplodon stejnegeri</i>	Stejneger's beaked whale	N Pacific: warm temperate to subpolar	DD	?
<i>Mesoplodon layardii</i>	Strap-toothed beaked whale	S Hemisphere: polar to subtropical	DD	?
<i>Mesoplodon densirostris</i>	Blainville's beaked whale	Worldwide: warm temperate to tropical	DD	?
<i>Mesoplodon traversii</i>	Spade-toothed whale	Unknown possibly S Pacific: cold temperate to subtropical		?↑
<i>Mesoplodon perrini</i>	Perrin's beaked whale	Unknown possibly NE Pacific: warm temperate to subtropical		?
Platanistidae				
<i>Platanista gangetica</i>	Ganges river dolphin	India, Nepal, Bhutan and Bangladesh: freshwater only	EN (A)	↓
Iniidae				
<i>Inia geoffrensis</i>	Boto	Peru, Ecuador, Brazil, Bolivia, Venézuela, Colombia: freshwater only	VU (A)	↓

Table 1 (continued) Species range (breeding site for pinnipeds), IUCN status and potential effects of climate change on the range of cetaceans, pinnipeds, sirenians and other marine mammal species

Family and species name	Common name	Species range (breeding site for pinnipeds)	IUCN status	Potential effects of climate change on species range
Lipotidae				
<i>Lipotes vexillifer</i>	Baiji	China: freshwater only	CR (ACD)	↓
Pontoporiidae				
<i>Pontoporia blainvillei</i>	Franciscana	Brazil to Argentina: coastal waters from Doce River	DD	↓
Monodontidae				
<i>Delphinapterus leucas</i>	Beluga or white whale	Circumpolar in arctic seas: arctic to cold temperate	VU (A)	↓
<i>Monodon monoceros</i>	Narwhal	Arctic Ocean	DD	↓
Delphinidae				
<i>Cephalorhynchus commersonii</i>	Commerson's dolphin	S America, Falkland and Kerguelen islands: coastal, subpolar to cold temperate	DD	↓
<i>Cephalorhynchus eutropia</i>	Chilean dolphin	S South America: coastal, subpolar to warm temperate	DD	?
<i>Cephalorhynchus heavisidii</i>	Heaviside's dolphin	SW Africa: cold to warm temperate	DD	?
<i>Cephalorhynchus hectori</i>	Hector's dolphin	New Zealand: coastal waters, cold to warm temperate	EN (AC)	↓
<i>Steno bredanensis</i>	Rough-toothed dolphin	Worldwide: warm temperate to tropical	DD	?
<i>Sousa teuszii</i>	Atlantic hump-backed dolphin	SE Atlantic: coastal and river mouths, subtropical to tropical	DD	?
<i>Sousa plumbea</i>	Indian hump-backed dolphin	Indian Ocean: coastal, subtropical to tropical		?
<i>Sousa chinensis</i>	Indo-pacific hump-backed dolphin	Indian Ocean: coastal and rivers, tropical	DD	?
<i>Sotalia fluviatilis</i>	Tucuxi	SW Atlantic: coastal, estuaries and rivers, tropical	DD	↓
<i>Tursiops aduncus</i>	Bottlenose dolphin	Indian and Pacific Ocean: coastal, tropical	DD	?
<i>Tursiops truncatus</i>	Bottlenose dolphin	Worldwide: cold temperate to tropical	DD	↑
<i>Stenella attenuata</i>	Pantropical spotted dolphin	Worldwide: tropical	LR:cd	?↑
<i>Stenella frontalis</i>	Atlantic spotted dolphin	Atlantic Ocean: subtropical to tropical	DD	?↑
<i>Stenella longirostris</i>	Spinner dolphin	Worldwide: tropical	LR:cd	?↑
<i>Stenella clymene</i>	Clymene dolphin	Atlantic Ocean: tropical	DD	?
<i>Stenella coeruleoalba</i>	Striped dolphin	Worldwide: cold temperate to tropical	LR:cd	?↑

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

Table 1 (continued) Species range (breeding site for pinnipeds), IUCN status and potential effects of climate change on the range of cetaceans, pinnipeds, sirenians and other marine mammal species

Family and species name	Common name	Species range (breeding site for pinnipeds)	IUCN status	Potential effects of climate change on species range
<i>Delphinus delphis</i>	Short-beaked common dolphin ²	Worldwide: temperate and tropical		?↑
<i>Delphinus capensis</i>	Long-beaked common dolphin ²	Worldwide: subtropical		?↑
<i>Delphinus tropicalis</i>	Arabian common dolphin ²	Arabian Sea: coastal waters, tropical		?
<i>Lagenodelphis hosei</i>	Fraser's dolphin	Worldwide: warm temperate to tropical	DD	?↑
<i>Lagenorhynchus albirostris</i>	White-beaked dolphin	N Atlantic: cold temperate		
<i>Lagenorhynchus acutus</i>	Atlantic white-sided dolphin	N Atlantic: subpolar to warm temperate		?↓
<i>Lagenorhynchus obliquidens</i>	Pacific white-sided dolphin	N Pacific: cold temperate to subtropical		?↓
<i>Lagenorhynchus obscurus</i>	Dusky dolphin	S Hemisphere: cold to warm temperate	DD	?↓
<i>Lagenorhynchus australis</i>	Peale's dolphin	S America: subpolar to warm temperate	DD	?
<i>Lagenorhynchus cruiger</i>	Hourglass dolphin	S Hemisphere: polar to warm temperate		?↓
<i>Lissodelphis borealis</i>	N. right whale dolphin	N Pacific: subpolar to subtropical		?
<i>Lissodelphis peronii</i>	S. right whale dolphin	S Hemisphere: polar to subtropical	DD	?
<i>Grampus griseus</i>	Risso's dolphin	Worldwide: cold temperate to tropical	DD	?
<i>Peponocephala electra</i>	Melon-headed whale	Worldwide: tropical		?↑
<i>Feresa attenuata</i>	Pygmy killer whale	Worldwide: tropical to warm temperate		?↑
<i>Pseudorca crassidens</i>	False killer whale	Worldwide: warm temperate to tropical		?↑
<i>Orcinus orca</i>	Killer whale, orca	Worldwide: polar to tropical	LR:cd	?
<i>Globicephala melas</i>	Long-finned pilot whale	Worldwide (ex N Pacific): polar to warm temperate		?
<i>Globicephala macrorhynchus</i>	Short-finned pilot whale	Worldwide: tropical to subtropical	LR:cd	?↑
<i>Orcella brevirostris</i>	Irrawaddy dolphin	SE Asia, N Australia and Papua New Guinea: tropical coastal waters and estuaries	DD	↓
Phocoenidae				
<i>Neophocaena phocaenoides</i>	Finless porpoise	Indo-Pacific: warm temperate to tropical	DD	?
<i>Phocoena phocoena</i>	Harbour porpoise	N Pacific and N Atlantic: subpolar to cold temperate	VU (A)	?↓

Table 1 (continued) Species range (breeding site for pinnipeds), IUCN status and potential effects of climate change on the range of cetaceans, pinnipeds, sirenians and other marine mammal species

Family and species name	Common name	Species range (breeding site for pinnipeds)	IUCN status	Potential effects of climate change on species range
<i>Phocoena sinus</i>	Vaquita	Gulf of California: subtropical	CR (C)	↓
<i>Phocoena spinipinnis</i>	Burmeister porpoise	S America: coastal cold temperate to subtropical	DD	?
<i>Phocoena dioptrica</i>	Spectacled porpoise	S Hemisphere: polar to cold temperate	DD	?↓
<i>Phocoenoides dalli</i>	Dall's porpoise	N Pacific: subpolar to temperate	LR:cd	?
Otariidae				
<i>Artocephalus pusillus</i>	Cape fur seal	S Africa and S Australia: warm temperate (land)		?
<i>Artocephalus gazelle</i>	Antarctic fur seal	S Hemisphere (excluding SE Pacific): polar to subpolar		?↓
<i>Artocephalus tropicalis</i>	Subantarctic fur seal	S Hemisphere (excluding SE Pacific): high temperate		?
<i>Artocephalus townsendi</i>	Guadalupe fur sea	NE Pacific: warm temperate to tropical (land)	VU (D)	?
<i>Artocephalus philippii</i>	Juan Fernández fur seal	West coast of South America, Chile: temperate (land)	VU (D)	?
<i>Artocephalus forsteri</i>	New Zealand fur seal	S Australia and New Zealand: temperate (land)		?
<i>Artocephalus australis</i>	South American fur seal	S America and Falklands: subpolar to temperate (land)		?
<i>Artocephalus galapagoensis</i>	Galápagos fur seal	Galápagos Islands: equatorial (land)	VU (A)	?↓
<i>Callorhinus ursinus</i>	Northern fur seal	N Pacific and Bering Sea: subpolar to temperate (land)	VU (A)	?
<i>Zalophus californianus</i>	California sea lion	NE Pacific: warm temperate to tropical (land)		?
<i>Zalophus wollebaeki</i>	Galápagos sea lion	Galápagos Islands: equatorial (land)	VU (A)	?↓
<i>Eumetopias jubatus</i>	Steller sea lion	N Pacific: subpolar to cold temperate (land)	EN (A)	?↓
<i>Neophoca cinera</i>	Australian sea lion	SE Indian Ocean, S and SW Australia: temperate (land)		?
<i>Phocartos hookeri</i>	New Zealand sea lion	SW Pacific, NZ: subpolar to cold temperate (land)	VU (D)	?
<i>Otaria flavescens</i>	South American sea lion	S America and Falklands: polar to subtropical (land)		?
Odobenidae				
<i>Odobenus rosmarus</i>	Walrus	Arctic Ocean and adjoining seas		?↓
Phocidae				
<i>Ergnathus barbatus</i>	Bearded seal	Arctic (pack ice)		?↓
<i>Phoca vitulina</i>	Harbour seal	N Hemisphere: subpolar to warm temperate (land)		?

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

Table 1 (continued) Species range (breeding site for pinnipeds), IUCN status and potential effects of climate change on the range of cetaceans, pinnipeds, sirenians and other marine mammal species

Family and species name	Common name	Species range (breeding site for pinnipeds)	IUCN status	Potential effects of climate change on species range
<i>Phoca largha</i>	Spotted seal	N Pacific, Chukchi Sea: polar (pack ice)		?↓
<i>Pusa hispida</i>	Ringed seal	Arctic regions, Baltic Sea: (fast ice)		?↓
<i>Pusa caspica</i>	Caspian seal	Caspian Sea: polar to subpolar (fast ice)	VU (B)	?↓
<i>Pusa sibirica</i>	Baikal seal	Lake Baikal, Siberia: polar to subpolar (fast ice)	LR:nt	?↓
<i>Halichoerus grypus</i>	Grey seal	N Atlantic: subpolar to cold temperate (land, ice)		?↓
<i>Histiophoca fasciata</i>	Ribbon seal	N Pacific: polar (pack ice)		?↓
<i>Pagophilus groenlandicus</i>	Harp seal	N Atlantic: polar to cold temperate (pack ice)		?↓
<i>Cystophora cristata</i>	Hooded seal	N Atlantic: polar to cold temperate (pack ice)		?↓
<i>Monachus monachus</i>	Mediterranean monk seal	Med. Sea, Black Sea, NW African coast: subtropical (land)	CR (C)	?↓
<i>Monachus schauinslandi</i>	Hawaiian monk seal	Hawaiian Islands: tropical (land)	EN (C)	?
<i>Mirounga leonina</i>	Southern elephant seal	Subantarctic, Antarctic, southern S. America (land)		?↓
<i>Mirounga angustirostris</i>	Northern elephant seal	N Pacific: subpolar to subtropical (land)		?↓
<i>Leptonychotes weddellii</i>	Weddell seal	Antarctic (fast ice)		?↓
<i>Ommatophoca rossii</i>	Ross seal	Antarctic (fast ice)		?↓
<i>Lobodon carcinophaga</i>	Crabeater seal	Antarctic (pack ice)		?↓
<i>Hydrurga leptonyx</i>	Leopard seal	Antarctic (pack ice)		?
Trichechidae				
<i>Trichechus manatus</i>	Caribbean manatee	Florida, Caribbean (marine and freshwater)	VU (A)	?↑
<i>T. m. latirostris</i>	Florida manatee	Florida peninsula, occasionally as far south as Bahamas		
<i>T. m. manatus</i>	Antillean manatee	Mainland coast from Mexico to Venezuela, and Brazil including the Greater and Lesser Antilles		
<i>Trichechus senegalensis</i>	African manatee	West Africa (marine and freshwater)	VU (A)	?
<i>Trichechus inunguis</i>	Amazon manatee	Amazon river (marine and freshwater)	VU (A)	?
Dugongidae				
<i>Dugong dugon</i>	Dugong	Indian and western Pacific oceans (marine)	VU (A)	?

Table 1 (continued) Species range (breeding site for pinnipeds), IUCN status and potential effects of climate change on the range of cetaceans, pinnipeds, sirenians and other marine mammal species

Family and species name	Common name	Species range (breeding site for pinnipeds)	IUCN status	Potential effects of climate change on species range
Ursidae				
<i>Ursus maritimus</i>	Polar bear	Arctic	LR:cd	?↓
Mustelidae				
<i>Enhydra lutris</i>	Sea otter	Canada, U.S., Mexico, Japan, Russian Federation (terrestrial, marine)	EN (A)	?
<i>Lontra felina</i>	Marine otter	Argentina, Chile, Peru (terrestrial, freshwater, marine)	EN (A)	?
<i>Lutra lutra</i>	Common otter	Worldwide (terrestrial, freshwater, marine)	NT	?

Notes: ↑ indicates a possible increase in range, ↓ indicates a possible decrease in range and ? indicates effects on range are unknown.

IUCN status: (CR = critically endangered; EN = endangered; VU = vulnerable; A = declining population, B = small distribution and decline or fluctuation, C = small population size and decline, D = very small or restricted); NT = near threatened; LR:cd = low risk, conservation dependent; LR:nt = low risk, near threatened; DD = data deficient.

1. Minke whale: several authors refer to two species of minke whale — the Antarctic minke whale (*B. bonaerensis*) and the dwarf minke whale (*B. acutorostrata*) — however, in the context of this review both are referred to as minke whales.
2. Common dolphins: three species of common dolphins have been identified — the short-beaked common dolphin (*D. delphis*), the long-beaked common dolphin (*D. capensis*) and the Arabian common dolphin (*D. tropicalis*) — however, in the context of this review all are referred to as common dolphins due to the overlap in distribution of *D. delphis* and *D. capensis*.

Source: Based on Ridgeway & Harrison 1985, Rice 1998, Mann et al. 2000, Perrin et al. 2002, Reid et al. 2003b, IUCN 2004, Kaschner 2004.

Baleen whale migrations have generally been regarded as a response to the need to feed in colder waters and reproduce in warmer waters. Explanations for such long-range migrations have included (i) direct benefits to the calf, for example, increase in survival in calm, warm waters, (ii) relict from times when continents were closer together, (iii) the possible ability of some species to supplement their food supply with plankton encountered on migration or on calving grounds, (iv) reducing the risk of killer whale predation of new born calves in low latitudes and (v) species with a large body size (and lower mass specific metabolic rates) are able to make the long migrations that allow them to take advantage of warmer, and predator-free, waters (Bannister 2002, Stern 2002).

The movements of odontocetes (toothed whales) vary more in scale depending on geographic range and species. For example, some sperm whales (*Physeter macrocephalus*) undertake long seasonal migrations similar to those of baleen whales, between high-latitude feeding grounds and warmer water breeding areas, although this is probably quite unusual in odontocetes (Whitehead 2002). Large seasonal movements often occur in oceanic odontocetes, for example, *Stenella* species and common dolphins (*Delphinus delphis*). Coastal bottlenose dolphins (*Tursiops truncatus*) exhibit

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

a full spectrum of movements, including seasonal migrations, year-round home ranges, periodic residency and occasional long-range movements (Wells & Scott 2002). Bottlenose dolphins living at the high-latitude or cold-water extremes of the species' range may migrate seasonally, for example, along the Atlantic coast of the U.S. (Wells & Scott 2002). North-south and inshore-offshore seasonal movements have been observed in several odontocete species, including harbour porpoise (*Phocoena phocoena*) (Northridge et al. 1995, Anderson et al. 2001, Bjørge & Tolley 2002).

Dispersal and migration is common in several pinniped species. Sea lion species, such as the California sea lion (*Zalophus californianus*), tend to live in warmer areas where food resources are more constant and there is less dispersal from breeding sites. However, Phocidae species (true seals) that live in higher latitudes, which are more dependent on ice cover and/or seasonally changing prey, tend to have a wider dispersal. For example, northern and southern elephant seals (*Mirounga angustirostris* and *M. leonina*) spend between 8 and 10 months at sea each year, with long-distance migrations from breeding and moulting sites to feeding areas (Forcada 2002). Polar bears undertake seasonal migrations, and these long-range movements are generally related to ice cover and seal distribution (Forcada 2002). Sirenians, such as manatees (*Trichechus manatus*), also embark on seasonal movements. For example in Florida, where water temperature is a major determinant factor (Reynolds & Powell 2002).

Migration and the range of marine mammal species have evolved within constantly changing environmental conditions. Species have adapted to historic changes in climate. However, many of these changes, such as the retreat of the polar front in the Pleistocene, occurred at a rate that allowed species to adapt. Although marine mammals are capable of adapting to environmental changes, it is unclear if they will be able to adapt at the rate of climate change predicted in the near future (Stern 2002).

Wild species have three basic possible responses to climate change: (i) change geographical distribution to track environmental changes; (ii) remain in the same place but change to match the new environment, through either plastic response, such as shifts in phenology (for example timing of growth, breeding, etc.) or genetic response, such as an increase in the proportion of heat tolerant individuals; or (iii) extinction (IPCC 2001a).

Climate change

Future changes in the global climate are difficult to predict. The climate system is made up of a number of components: the atmosphere, oceans, land surface, cryosphere (ice areas) and biosphere (including human influences). Each of these systems is the result of a large array of drivers and climate is a result of complex interactions between each of the components. The only way to make quantitative predictions about future changes in climate is through the use of Global Climate Models (GCM) which simulate future climates given an emissions scenario and a mathematical representation of climate processes. Currently, there are hundreds of climate scenarios described in the literature. These scenarios, which cover both global and regional areas, have been developed for a variety of purposes and consider a large range of possible emission levels and other factors. Currently, the most extensively used scenarios, and those referred to in this review, are compiled by the Intergovernmental Panel on Climate Change (IPCC) in its Third Assessment Report (IPCC 2001b).

The observed and predicted effects of global climate change vary between areas. Examples from the U.K. and surrounding waters have been included as an indication of these changes, as there is a long-time series for climate data and there have been intense efforts to predict future changes. The predicted changes for the U.K. are based on the U.K. Climate Impacts Program (UKCIP) scenarios, which provide the most comprehensive assessment of climate change impacts in the U.K. (Hulme et al. 2002).

Changes in temperature

Globally the average surface temperature (the average of near surface air temperature over land and sea surface temperature) has increased over the twentieth century by $0.6 \pm 0.2^{\circ}\text{C}$, with an increase of $0.4\text{--}0.7^{\circ}\text{C}$ in marine air temperature and a $0.4\text{--}0.8^{\circ}\text{C}$ increase in sea-surface temperature since the late-nineteenth century (IPCC 2001b). The global ocean heat content has increased significantly since the late 1950s, with more than half of the increase occurring in the upper 300 m of the ocean, this is equivalent to a rate of temperature increase in this layer of about $0.04^{\circ}\text{C}/\text{decade}$ (IPCC 2001b). The globally averaged surface (sea and land) temperature is projected to increase by $1.4\text{--}5.8^{\circ}\text{C}$ over the period 1990–2100 (IPCC 2001b). Projections indicate that the warming would vary by region (IPCC 2001a).

In most areas of the North Atlantic during 2003, temperature in the upper water layers remained higher than the long-term average, with new records set in several regions (ICES 2004). Over the northern North Sea, average air temperatures have risen by 0.8°C since 1960. Since 1995, winter sea temperatures in Scottish coastal waters have been warming faster than summer ones, resulting in a smaller annual range each year. Winter seabed temperatures at fishing grounds in the North Sea show a long-term warming trend since the 1970s. Over the last 30 yr, Scottish offshore waters have also warmed by between 1 and 1.5°C . In oceanic waters at the edge of the U.K.'s continental shelf there has been a steady rise in temperature over the past 100 yr (FRS 1998, 2003). There has been an overall warming of U.K. coastal waters, with an increase in annually averaged temperature of about 0.6°C over the past 70–100 years, with a substantial increase over the last 20 yr (Hulme et al. 2002). Climate change scenarios for the U.K. predict that the annual temperature across the U.K. may rise by between 2 and 3.5°C by the 2080s. The temperature of U.K. coastal waters will also increase, although not as rapidly as over land. Offshore waters in the English Channel may warm in summer by between 2 and 4°C over the same period (Hulme et al. 2002).

Changes in sea levels

Tide gauge data show that global average sea level rose between 0.1 and 0.2 m during the twentieth century (IPCC 2001b). Global mean sea level is projected to rise by 0.09–0.88 m between 1990 and 2100. The geographical distribution of sea-level changes results from interactions between factors such as the geographical variation in thermal expansion, and changes in salinity, winds and ocean circulation. Therefore the range of regional variation is substantial compared with the global average sea level rise (IPCC 2001b).

Climate change scenarios for the U.K. predict that by the 2080s sea levels may be between 2 cm below and 58 cm above the current level in western Scotland and between 26 and 86 cm above the current level in southeast England, depending on the climate change scenario and effects of land movements. Extreme sea levels, occurring through combinations of high tides, sea-level rise and changes in winds, are also predicted to become more frequent at many U.K. coastal locations (Hulme et al. 2002).

A rise in sea level is likely to affect most coastal habitats, although the extent will vary with location and type of coastal habitat. Many coastal areas are already experiencing increased levels of sea flooding, accelerated coastal erosion and seawater intrusion into freshwater sources and these processes will increase with climate change and rises in sea levels (IPCC 2001a). Low-latitude tropical and subtropical coastlines are highly susceptible to climate change impacts (IPCC 2001a).

Changes in ocean circulation

In the Arctic, as temperature increases, more freshwater from melting snow and ice will be released into the North Atlantic, through the Fram Strait between northeastern Greenland and Svalbard. This

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

could exert a strong influence on salinity in the North Atlantic, shift the Gulf Stream current, and even affect upwelling related to the Great Ocean Conveyor Belt current system (Tynan & DeMaster 1997, Marotzke 2000).

Most models show a weakening of the ocean thermohaline circulation, which will lead to a reduction of heat transport into high latitudes of the Northern Hemisphere. The current projections using climate models do not exhibit a complete shutdown of the thermohaline circulation by 2100. Beyond 2100, the thermohaline circulation could completely, and possibly irreversibly, shut down in either hemisphere (IPCC 2001b). Climate change scenarios predict a weakening of the Gulf Stream during the twenty-first century, perhaps by as much as 25% by 2100, although a shutdown of the Gulf Stream is not predicted in any climate models (Hulme et al. 2002). Shifts in the locations of fronts and upwellings are also expected as the climate changes, but are difficult to predict.

Changes in sea-ice extent

There has been a retreat of sea-ice extent in the Arctic spring and summer by about 10–15% since the 1950s. It is likely that there has been about a 40% decline in Arctic sea-ice thickness during the late summer to early autumn in recent decades and a slower decline in winter sea-ice thickness (IPCC 2001b). In the Northern Hemisphere snow cover and sea-ice extent are projected to decrease further (IPCC 2001b). Over the past 100–150 yr, observations show that there has probably been a reduction of about two weeks in the annual duration of lake and river ice in the mid to high latitudes of the Northern Hemisphere (IPCC 2001b). The sea-ice extent in Antarctica appears to be more stable, with no readily apparent relationship between decadal changes in Antarctic temperatures and sea-ice extent since 1973 (IPCC 2001b). However, the Antarctic Peninsula ice shelves have retreated over the last century, resulting in the collapse of the Prince Gustav and parts of the Larsen ice shelves in 1995 (Vaughan & Doake 1996, IPCC 2001b).

Changes in salinity

Changes in salinity may occur as a result of increased evaporation with increased temperature and changes in ocean circulation. There may also be more localised changes in salinity as a result of changes in precipitation and associated river input and land run-off or the melting of ice sheets.

In most areas of the North Atlantic during 2003, salinity in the upper layers remained higher than the long-term average, with new records set in several regions (ICES 2004). The salinity of Scottish oceanic waters has generally increased, with values approaching the highest recorded over the past 100 yr. This may indicate the arrival of warmer, more saline waters from further south in the Atlantic (FRS 1998). In southern North Sea fishing areas (e.g., German Bight), there is an apparent trend of decreasing salinity at the sea bed in winter, which may be linked to freshwater inputs from rivers around the coast (FRS 2003). Inshore waters off the northeast of Scotland have experienced a decrease in salinity in the past 5 yr (FRS 2003).

Changes in CO₂ concentrations and pH

The atmospheric concentration of carbon dioxide (CO₂) has increased by 31% since 1750. The rate of increase over the past century is unprecedented during the past 20,000 yr, with the present atmospheric CO₂ increase being caused by anthropogenic emissions of CO₂ (IPCC 2001b). The oceans absorb CO₂ from the atmosphere and in the past 200 yr the oceans have absorbed approximately half of the CO₂ produced by fossil fuel burning and cement production (Royal Society 2005). The uptake of anthropogenic CO₂ by the oceans will continue to increase with increasing atmospheric CO₂ concentrations. However, warming will reduce the solubility of CO₂ and increased

temperatures will also increase vertical stratification (decreasing mixing between ocean layers), which will also reduce CO₂ uptake by the oceans (IPCC 2001b, Royal Society 2005).

Increasing atmospheric CO₂ concentration has no significant fertilisation effect on marine biological productivity, but it decreases pH (IPCC 2001b). It is estimated that this uptake of CO₂ has led to a reduction in the pH of surface waters by 0.1 units, which is the equivalent to a 30% increase in the concentration of hydrogen ions. Surface waters (<100 m) which are slightly alkaline (average pH is about 8.2) are becoming more acidic (Royal Society 2005). The average pH of the oceans is estimated to fall by 0.5 units (equivalent to a three-fold increase in the concentration of hydrogen ions) by the year 2100 if global emissions of CO₂ continue to rise at current levels (Royal Society 2005). The scale of the changes may vary regionally, affecting the magnitude of biological effects (Royal Society 2005).

Changes in rainfall patterns

In the Northern Hemisphere it is very likely that precipitation has increased by 0.5–1% per decade in the twentieth century over most mid and high latitude land areas, and it is likely that rainfall has increased by 0.2–0.3% per decade over the tropical land areas (10°N–10°S) (IPCC 2001b). In the mid and high latitudes of the Northern Hemisphere over the latter half of the twentieth century, there has probably been a 2–4% increase in the frequency of heavy precipitation events (IPCC 2001b). Global average precipitation is projected to increase during the twenty-first century, with regional increases and decreases (IPCC 2001b). More intense precipitation events are very likely over many areas (IPCC 2001b).

For example, throughout the U.K., winters over the last 200 yr have become wetter relative to summers, with a larger proportion of winter precipitation in all regions falling on heavy rainfall days compared to 50 yr ago (Hulme et al. 2002). Climate change scenarios for the U.K. predict that winter precipitation will increase, with increases ranging from 10–35% by the 2080s. The pattern for summer precipitation is reversed, with almost the whole of the U.K. becoming drier (Hulme et al. 2002).

Changes in storm frequency, wind speed and wave conditions

Climate change is likely to affect local weather conditions in a number of ways. For example, there is a greater frequency in the formation of hurricanes and typhoons when water temperatures are 28°C or above, and so the general warming of oceans may lead to changes in the frequency or strength of such weather events (IPCC 2001a).

Climate change may also affect local weather in general rather than just the occurrence of specific types of weather events. For example, over the northern North Sea average wind speeds have become 2 knots faster since 1960 (FRS 1998). Waves in the North Sea have increased in size, by about 20 cm every 10 yr, as a result of increase in the average wind speed (FRS 1998). Around the U.K. coastline there was an apparent increase in average wave height of 10–15% between the 1980s and 1990s. The roughening wave climate over the last 40 yr is likely to result from a change in the strength of the North Atlantic Oscillation (NAO) (Hulme et al. 2002). In the last decade the U.K. has also experienced an increase in the frequency of gales, although this is not unprecedented in the historic record as gale frequencies are also related to the NAO (Hulme et al. 2002).

Changes in climate patterns

Large-scale patterns of climate variability, such as the El Niño-Southern Oscillation (ENSO) and the NAO, account for major variations in weather and climate around the world and have been

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

shown to affect marine species and fish stocks, through both direct and indirect pathways (Stenseth et al. 2002). The effects of short-term events such as El Niño and NAO can provide valuable insight into the potential effects of climate change.

The El Niño-Southern Oscillation (ENSO)

Fluctuations in tropical Pacific sea-surface temperature are related to the occurrence of El Niño events, during which the equatorial surface waters warm considerably from the International Date Line to the west coast of South America. The Southern Oscillation is a global-scale 'see-saw' in atmospheric mass, involving exchanges of air between the Eastern and Western hemispheres centred in tropical and subtropical latitudes. Warm ENSO events are those in which both a negative Southern Oscillation and an El Niño occur together. Different phases of the ENSO shift the location of the heaviest tropical rainfall, and these changes in the heating of the atmosphere distort the flow of air over thousands of kilometres, producing anomalous cold and warm regions (Stenseth et al. 2002).

Warm episodes of the ENSO phenomenon (which affects regional variations of precipitation and temperature over much of the tropics, subtropics and some mid-latitude areas and can affect the incidence and severity of hurricanes and typhoons) have been more frequent, persistent and intense since the mid-1970s, compared with the previous 100 yr (IPCC 2001b). Even with little or no change in El Niño amplitude, global warming is likely to lead to greater extremes of drying and heavy rainfall and to increase the risk of droughts and floods that occur with El Niño events in many different regions (IPCC 2001b).

It is possible that overall climate change will have some similar effects to short-term El Niño events, although the effects of global climate change could be more gradual and more subtle. Potential changes in the frequency, intensity and persistence of climate extremes (e.g., heat waves, heavy precipitation and drought) associated with the ENSO could emerge as key determinants of future impacts and vulnerability (IPCC 2001a).

The North Atlantic Oscillation (NAO)

The North Atlantic Oscillation is a north-south alteration in atmospheric mass between the subtropical atmospheric high-pressure centre over the Azores and the atmospheric subpolar low-pressure centre over Iceland. It determines the strength of the westerly winds blowing across the North Atlantic Ocean between 40 and 60°N. Variability in the direction and magnitude of the westerlies is responsible for fluctuations in winter temperatures and the balance of precipitation and evaporation across the Atlantic and the adjoining landmasses. During positive phases of the NAO, the westerly winds are strengthened and moved northward, causing increased precipitation and temperatures over northern Europe and the southeastern U.S. and dry anomalies in the Mediterranean region (Planque & Taylor 1998, Stenseth et al. 2002). Climate change scenarios suggest the North Atlantic Oscillation will tend to become more positive in the future, resulting in more wet, windy, mild winters (Hulme et al. 2002).

Impacts of climate change on marine mammals

The potential impacts of climate change on marine mammals can be (i) direct, such as the effects of reduced sea ice and rising sea levels on seal haul-out sites or a species tracking a specific range of water temperatures in which they can physically survive, and (ii) indirect, such as the potential impacts on reproductive success through effects on the distribution and abundance of prey or the structure of prey communities at specific locations.

Effects of changes in temperature

Direct effects

The most likely direct effects of changes in water temperature on marine mammals are shifts in species ranges as species track preferred or required temperature conditions. Baleen whales are less likely to be directly affected by changes in temperature, compared to other marine mammals, because of their mobility and thermoregulatory ability, although calves may be more susceptible than adults (IWC 1997). The majority of baleen whales, such as the blue, grey, humpback and fin whales, migrate large distances and experience temperature variations between their polar feeding grounds and tropical breeding grounds. However, several species have a more restricted distribution, for example, bowhead whales which are found only in the polar waters of the Arctic and may be uniquely heat intolerant (IWC 1997, Bannister 2002).

Toothed whales (odontocetes) are more likely to be directly affected by changes in water temperature than baleen whales, as in general they are much smaller and several species are limited in the range of water temperatures that they inhabit. For example, belugas (*Delphinapterus leucas*) are restricted to polar and cold temperate waters in Arctic seas. As water temperatures change, species that inhabit specific ranges of water temperature would be expected to shift their geographic ranges to track preferred or required temperature conditions. However, for several species there may be physical limits to their ability to change their geographic range. For example, the endangered vaquita (*Phocoena sinus*), whose distribution is limited to the warm waters at the northern end of the Gulf of California, and river dolphins, baiji (*Lipotes vexillifer*), Ganges river dolphin (*Platanista gangetica*), Boto (*Inia geoffrensis*) and tucuxi (*Sotalia fluviatilis*), may be particularly vulnerable. Some individuals within a population may also be more susceptible than others, for example finless porpoise (*Neophocaena phocaenoides*) calves (IWC 1997). Increased variation in sea temperature, especially in coastal areas, may also be important: for example, a mass mortality of bottlenose dolphins in the Gulf of Mexico has been linked to an unusual cold-water event (IWC 1997).

Changes in water temperature will also directly affect pinnipeds and sirenians. For example, the distribution of the manatee is influenced by temperature, with waters colder than 20°C increasing the manatees' susceptibility to cold stress and cold-induced mortality. Therefore an increase in sea temperature (i.e., extension of 20°C isotherm) could lead to a possible increase in range directly related to changes in temperature (Reynolds & Powell 2002, Würsig et al. 2002).

Indirect effects

The direct and indirect effects of climate change on prey species can in turn have several indirect effects on marine mammals, including changes in distribution, abundance and migration, community structure, susceptibility to disease and contaminants, and reproductive success. Climate change may also indirectly affect marine mammal species through competition with other marine mammals.

Changes in distribution, abundance and migration

Marine mammals in general and baleen whales in particular, require dense patches of prey, such as crustaceans (copepods, euphausiids or krill, amphipods, shrimp), cephalopods (squid) and schooling fish. Therefore, the distribution, abundance and migration of baleen whales reflects the distribution, abundance and movements of these dense prey patches, which have in turn been linked to oceanographic features including fronts, eddies and primary productivity. These features, and hence the formation of dense prey patches, can be affected by several factors including temperature. Thus, the distribution of feeding whales, such as North Atlantic right whales, can be predicted from surface temperature and bathymetric variables, such as depth and slope, due to their effects on prey distribution.

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

Changes in plankton distribution, abundance and composition are related to ocean climate, including temperature (Southward et al. 1995; Planque & Taylor 1998; Ducrotoy 1999; Heath et al. 1999a,b; Edwards et al. 2001, 2002; Beare et al. 2002; Beaugrand 2003; Reid et al. 2003a; Edwards & Richardson 2004; Moline et al. 2004). For example, in the northeastern North Atlantic Ocean and adjacent seas there have been recent shifts in all copepod assemblages, with a northward extension of more than 10° in latitude of warm-water species associated with a decrease in the number of colder-water species. These changes reflect regional increases in sea-surface temperature (Beaugrand & Reid 2003). Therefore marine mammals and their prey that depend on plankton species may be affected by these shifts in distribution.

The distribution, abundance and migration of odontocetes are also strongly influenced by prey distribution, for example, in the Gulf of Maine/Georges Bank, northeast America, shifts in cetacean distributions and abundance relate to trends in fish abundance (Kenney et al. 1996). In the Faroe Islands where there is a long history (catch statistics are available for almost 300 yr) of traditional drive harvest of long-finned pilot whales (*Globicephala melas*), peaks in catch rates are correlated with periods of warmer temperatures and the occurrence of their main prey, the pelagic squid *Todarodes sagittatus*. The occurrence of pelagic squid may be influenced by temperature directly, or indirectly through effects on hydrography or productivity, which in turn, influences the distribution and abundance of the pilot whales (Bjørge 2002).

Temperature can directly affect the embryonic development, age of sexual maturity, timing of spawning, growth and survival of most fish and cephalopod species (for example, Boyle 1983). The distribution, abundance and migration of several fish and cephalopod species are also related to temperature, including whiting (*Merlangius merlangus*), herring (*Clupea harengus*), veined squid (*Loligo forbesi*) and Patagonian long-fin squid (*L. gahi*) (Sims et al. 2001, Zheng et al. 2002, Pierce & Boyle 2003, Arkhipkin et al. 2004, Sissener & Bjørndal 2005). The distributions of both exploited species, such as Atlantic cod (*Gadus morhua*) and common sole (*Solea solea*), and nonexploited species in the North Sea have responded markedly to recent increases in sea temperature, with distributions of nearly two-thirds of species shifting in mean latitude and/or depth over the past 25 yr (Perry et al. 2005). An increase in the abundance of several warm-water species, including anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the North Sea and North Atlantic, also correspond to recent increases in temperature (Stebbing et al. 2002, Beare et al. 2004a,b). These shifts in prey species are likely to affect the distribution of marine mammal species.

For example, changes in species distribution have been related to increases in temperature indirectly through the effects on prey. During the 1982–83 El Niño event, near-shore bottlenose dolphins expanded their range from southern to central California and have stayed in the new northern range well after the warming event subsided in the mid-1980s. It is believed that movement of prey, rather than water temperature itself, may have caused the range expansion (Wells et al. 1990, Wells & Scott 2002). Bottlenose dolphins off the northeast coast of Scotland are at the northern limit of their distribution. There is evidence of a recent range expansion, the causes of which are unknown, but may be related to changes in prey abundance and/or distribution (Wilson et al. 2004). A recent expansion in range of fur seals in the subantarctic Indian Ocean has been related to climate and its effects on prey. For example, the re-establishment of Antarctic fur seals (*Arctocephalus gazelle*) on Heard Island in the past 50 yr coincides with warmer temperature, glacier recession and hypothesised improved food supplies (Shaughnessy & Green 1998).

Changes in community structure

Shifts in the range of a species may be a response to climate change directly or indirectly as a result of changes in prey distribution or availability, and/or interactions with other species (Davis et al. 1998). Changes in the cetacean community of northwest Scotland have been related to recent

ocean warming. There has been a decline in the relative frequencies of strandings and sightings of white-beaked dolphins, a colder-water species and a relative increase in strandings and sightings of common dolphins, a warmer-water species (MacLeod et al. 2005). These results suggest a possible range expansion of common dolphins and a decrease in range of white-beaked dolphins, which may be due to the direct effects of changes in temperature or indirect effects, such as competitive exclusion. This has potentially serious implications for white-beaked dolphins, which are generally found in cold water less than 200 m deep around northwest Europe, as their ability to respond to climate change by tracking suitable habitat may be restricted, due to the lack of suitable shelf waters further north. This may lead to a decline in abundance or its distribution becoming fragmented (MacLeod et al. 2005).

Climate-related changes in cetacean community structure have also been associated with El Niño events. During the 1982–83 El Niño, near-bottom spawning market squid (*Loligo opalescens*) and short-finned pilot whales (*Globicephala macrorhynchus*), which normally feed on the squid, were absent from the southern California area (Shane 1994). The absence of pilot whales was followed several years later by an influx of Risso's dolphins (*Grampus griseus*) feeding on the returned market squid. The Risso's dolphins may have taken advantage of the temporarily vacant niche left by the pilot whales, apparently as a result of the El Niño event (Shane 1995).

Effects on reproductive success

Changes in temperature, through the effects on prey availability, can have potentially serious impacts on the reproductive success of marine mammals. For example, a decrease in North Atlantic right whale calf survival has been related to the effects of climate variability on prey abundance (Greene & Pershing 2004). Female fin whales, in years of great food abundance at the summer feeding grounds, might produce a calf in consecutive years, whereas in poor years the cycle can be extended to 3 yr. In female fin whales, there appears to be a close correlation between food abundance, body fat condition and fecundity (Lockyer 1986). It is thought that ovulation is suppressed if a certain threshold level of body weight or fat is not attained (Boyd et al. 1999). Similar strategies have also been observed in terrestrial animals, for example red deer (*Cervus elaphus*) (e.g., Hamilton & Blaxter 1980). Calving intervals and the sex ratios of calves of humpback whales have been related to maternal condition: females in a 'superior' condition had a calving interval of 3 or more years and the sex ratio of their calves was biased toward males (Wiley & Clapham 1993).

Observations of sea-surface temperature and the abundance of sperm whale calves near the Galapagos Islands suggest that females have a lower rate of conception after periods of warm sea-surface temperature, usually caused by ENSO events. Although the relationship between increased sea-surface temperature and the abundance of calves is tentative, it is supported by poor foraging success of females and immature sperm whales during warm conditions when primary productivity is suppressed (Whitehead 1997). Therefore, any increase in temperature as a result of global warming and/or the frequency and duration of El Niño events could have serious implications for populations such as sperm whales in the Galápagos Islands (Whitehead 1997).

Differences in reproductive success have also been related to prey availability in odontocetes, pinnipeds and sirenians. For example, in harbour porpoise from the Bay of Fundy, changes in the growth and age of sexual maturity have been linked to changes in prey availability (Read & Gaskin 1990). In Antarctic fur seals the duration of pregnancy is longer and birth takes place later in years associated with reduced prey availability (Boyd 1996). Reproductive failure, especially in the form of high juvenile mortality, affected several seal colonies, including Galápagos fur seals (*Arctocephalus galapagoensis*), during the major El Niño year of 1982. This massive recruitment failure was attributed to shifts in prey distribution, as at least some lethal and sublethal effects were linked to starvation (Würsig et al. 2002). In sirenians there appears to be considerable potential plasticity of

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

life-history parameters in response to food availability, with food shortages probably causing sirenians to reproduce later and less often (Boyd et al. 1999).

Breeding in many species may be timed to coincide with maximum abundance of suitable prey, either for the lactating mother or the calf at weaning, so that any changes in the environmental conditions which determine prey abundance may cause a mismatch in synchrony between predator and prey, either in time or location. Migratory species that travel long distances between feeding and breeding areas may be particularly vulnerable to mismatching.

The uncoupling of phenological relationships has important implications for trophic interactions, altering food-web structures and leading to changes in the ecosystem. The recruitment success of higher marine trophic levels is highly dependent on synchronization with plankton production. Observations indicate that the marine pelagic community responds to climate changes, and that the level of response differs throughout the community and seasonal cycle. These differences in response have led to a mismatch between successive trophic levels and a change in synchrony of timing between primary, secondary and tertiary production (Edwards & Richardson 2004). The link between climate change and the cascade effects on trophic levels has been observed in phytoplankton, zooplankton and salmon (*Salmo salar*) in the northeast Atlantic, with predicted temperature increases expected to result in a decline in the abundance of salmon returning to home waters (Beaugrand & Reid 2003). The growth and survival of cod larvae (*Gadus morhua*) depends on synchronous production with their main prey, the early stages of zooplankton (Stenseth et al. 2002). The decline in cod recruitment in the North Sea has been linked to rising temperatures affecting the plankton ecosystem (O'Brien et al. 2000, Beaugrand et al. 2003). Changes due to mismatches in the food chain and the effects on prey species are likely to have serious implications for marine mammals.

Increased susceptibility to disease, contaminants and other potential causes of death

Increased susceptibility to disease, starvation and the exposure to contaminants have been related to changes in prey type or reduced prey availability (Thompson et al. 1997, Geraci et al. 1999, Geraci & Lounsbury 2002, Würsig et al. 2002). For example, marked interannual variations in food availability, diet composition and body condition of harbour seals (*Phoca vitulina*) were associated with physiological responses, such as differences in haematological parameters. Differences observed in leukocyte counts could have resulted from immuno-suppression, for example because of differences in prey nutrient or contaminant levels (Thompson et al. 1997).

Insufficient prey availability results in the use of blubber reserves and the associated mobilisation of any accumulated contaminants, such as organochlorines, organobromines and polyaromatic hydrocarbons (Aguilar et al. 1999, Reijnders & Aguilar 2002). The majority of persistent organic pollutants and toxic elements have the potential to cause immune, reproductive and endocrine disrupting effects (Helle et al. 1976, Fuller & Hobson 1986, Reijnders 1986, Aguilar & Borrell 1994, de Swart et al. 1994, Kuiken et al. 1994, Jepson et al. 1999, Ross et al. 2000, Hoffman et al. 2001).

The frequency and severity of toxic algal blooms are likely to increase as a result of nutrient enrichment (increased rainfall and runoff) and increased temperature. Fatal poisonings have occurred in cetaceans, pinnipeds and manatees (Geraci et al. 1989, 1999; Hernández et al. 1998; Scholin et al. 2000; Domingo et al. 2002; Geraci & Lounsbury 2002; Gilmartin & Forcada 2002). Changes in precipitation, pH, water temperature, wind, dissolved CO₂ and salinity can affect water quality in estuarine and marine waters and some marine disease organisms and algal species are strongly influenced by one or more of these factors. Climate change has the potential to increase pathogen development and survival rates, disease transmission, and host susceptibility (Harvell et al. 2002).

Higher temperatures may also stress organisms, increasing their susceptibility to some diseases, especially if they are at the upper end of their thermal tolerance (Lafferty et al. 2004). Climate

change is expected to affect the range and migratory patterns of many marine mammals, which in turn could lead to a spread of viruses and the introduction of novel pathogens. In the past two decades there has been an apparent increase in large-scale mortality events such as morbillivirus infections, which caused massive die-offs of striped dolphins (*Stenella coeruleoalba*) in the Mediterranean Sea and seals in Europe, although the actual causes are not fully understood (Kennedy et al. 1992, Aguilar & Raga 1993, Cebrian 1995, Kennedy 1996, Geraci et al. 1999, Harvell et al. 1999, Kennedy 1999, Van Bresseem et al. 2001, Domingo et al. 2002, Geraci & Lounsbury 2002).

Effects of rising sea levels

Direct effects

Cetaceans, both baleen whales and odontocetes, are unlikely to be directly affected by rises in sea levels, although important habitats for coastal species and species that require coastal bays and lagoons for breeding, such as grey and humpback whales, could be affected (IWC 1997).

Pinniped haul-out sites for breeding, nurseries and resting are likely to be directly affected. For example, rising sea levels could eliminate already scarce haul-out sites of the Mediterranean monk seal (*Monachus monachus*), especially by the flooding of caves that provide the only refuges for some groups (Harwood 2001, Würsig et al. 2002).

Indirect effects

The construction of sea-wall defences and protective measures for coastal habitats against increasing sea levels could potentially impact coastal marine species and possibly interfere with migration routes. For example, in Florida between 1974 and 1996 about 4% of manatee deaths were due to crushing and drowning in flood gates or canal locks (Reynolds & Powell 2002). Dams and other structures have also obstructed the normal migration routes of manatees along rivers in South America and West Africa (Reynolds & Powell 2002).

Effects of changes in ocean currents

Direct effects

The range of marine mammals that are associated with oceanic fronts, such as the Antarctic convergence in the Southern Ocean, could be directly affected by changes in ocean currents and the positions of associated fronts. In the Southern Ocean, the Antarctic convergence, an oceanic front between cold southern polar waters and northern temperate waters, is an important physical feature that defines the normal southern extent of the distributions of most tropical and temperate marine mammals. The ocean temperature can change by as much as 10°C across the Antarctic convergence, which may only be a few miles across (Boyd 2002). The segregation of male and female sperm whales is associated with the Antarctic convergence, with only male sperm whales found within the Southern Ocean during summer, and females and young males remaining north of the polar front throughout the year (Boyd 2002).

Indirect effects

Changes in ocean mixing, deep water production and coastal upwelling will have profound impacts on the status, sustainability, productivity and biodiversity of the coastal zone and marine ecosystem (IPCC 2001a). Changes in ocean currents will directly affect the distribution, abundance and migration of plankton, many fish and cephalopod species (for example, Planque & Taylor 1998, Waluda et al. 2001, Walther et al. 2002), which in turn will affect marine mammals. For example, in the Barents

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

Sea fluctuations in the influx of Atlantic water affects the location of the polar front and water temperature. This influences the distribution and species composition of the primary and secondary production, with subsequent effects on the distribution and diet of minke whales (Bjørge 2002).

Effects of a decrease in sea-ice cover

Direct effects

Seals that rely on ice for breeding are likely to suffer considerable habitat loss with a decrease in sea-ice extent. Particularly vulnerable may be species that are confined to inland seas and lakes, such as the Caspian seal (*Phoca caspica*), the Baikal seal (*Phoca siberica*), and subspecies of the ringed seal (*Phoca hispida lagodensis* and *P. h. saimensis*), which will be limited in their ability to track the receding ice cover (Harwood 2001).

During the breeding season, the ice on which pinnipeds haul out must be thick enough and persist long enough for completion of the critical stages of birth, feeding of the pups, and in many cases, completion of their annual moult (Burns 2002). Ice characteristics can affect the distribution and activity patterns of pinnipeds, with pack ice (i.e., large pieces of ice, which vary from a few metres to several hundred metres in diameter, that are not attached to land) offering a more constant substratum than fast ice (i.e., ice that is attached to the land), which is highly variable with season (breeding sites of pinnipeds are given in Table 1). For pinnipeds that reproduce on fast ice, the duration of lactation and rearing of their young strongly depends on ice conditions (Forcada 2002). Ringed seals, bearded seals (*Ergnathus barbatus*) and walruses (*Odobenus rosmarus*), which rely on suitable ice substrate for resting, pupping and moulting, may be particularly vulnerable to changes in sea-ice extent (Tynan & DeMaster 1997). For example, earlier spring breakup of ice together with lower snow depths suggest a continued low pup survival of ringed seals in western Hudson Bay (Ferguson et al. 2005).

Polar bears require ice as a solid substratum on which to hunt and rear their offspring. The distribution of polar bears is probably a function of the distribution of ice conditions that allow them to hunt and travel most efficiently, especially in areas of ice floes, between foraging areas and areas where they give birth and rear their young. Therefore, any changes in the extent and type of ice cover are expected to affect the distributions, foraging and reproductive success of polar bears (Tynan & DeMaster 1997, Forcada 2002). In western Hudson Bay there has been a significant decline in the condition of adult male and female polar bears, along with an overall decline in the proportion of independent yearling cubs between 1981 and 1998, during which period the breakup of the sea ice had been occurring earlier, causing the bears to come ashore in poorer condition (Stirling et al. 1999).

Open-water areas, such as annual recurring polynyas (areas within the pack ice that are almost always clear of ice), driven by upwelling or wind, variable shore leads or cracks, or tidal- and wind-driven openings in the sea ice, are critical for several marine mammal species, such as walrus, belugas, narwhals and bowhead whales (Heide-Jørgensen & Laidre 2004). Although global warming has reduced sea-ice formation in the Arctic this trend is not uniform and any changes in the timing and distribution of these important open water areas will have direct and severe implications for the marine mammals dependent on them (Tynan & DeMaster 1997, Heide-Jørgensen & Laidre 2004, Laidre & Heide-Jørgensen 2005).

Indirect effects

Changes in the extent and concentration of sea ice may alter the seasonal distribution, geographic ranges, patterns of migration, nutritional status, reproductive success, and ultimately the abundance and stock structure of species associated with the ice edge, such as plankton, fish, crustaceans and marine mammals (Tynan & DeMaster 1997). Melting ice sheets in the Arctic will reduce ocean

salinities, which in turn may cause highly variable shifts in the distribution and biomass of major constituents of Arctic food webs. These changes in the distribution and abundance of prey will affect more mobile species such as the bowhead whales, belugas and narwhals, as well as resident or sedentary species, such as pinnipeds and polar bears (Tynan & DeMaster 1997, Laidre et al. 2004). For example, periods of decline in the production of ringed seals, and consequently polar bears, have been linked with ice conditions, possibly as a result of a reduction in regional productivity causing poor nutritional condition in the seals (Tynan & DeMaster 1997).

Large baleen whale species that undertake long distance migrations from tropical breeding grounds to high-latitude feeding grounds close to the ice edge may be at risk as the polar ice caps retreat. The longer migration paths that will be required will increase the costs of movement and reduce the duration of the feeding season (Stern 2002). Species, such as the grey whale, that use the Arctic for summer feeding grounds are likely to experience disruptions in the timing and distribution of their food sources (Tynan & DeMaster 1997). Migratory species within the Arctic will also be affected, for example, the migration of belugas and narwhals is linked to the spring production of ice algae and ice-edge productivity (Tynan & DeMaster 1997). Warming in the Arctic will cause changes in species compositions, with a tendency for poleward shifts in species assemblages and loss of some polar species (Tynan & DeMaster 1997).

In the Southern Ocean, climate change is likely to produce long-term, perhaps irreversible, changes in the physical oceanography and ecology. Projected reductions in sea-ice extent will alter under-ice biota and the spring bloom in the sea-ice marginal zone and will cause profound impacts to all levels in the food chain, from algae to krill to whales (e.g., Fraser & Hofmann 2003). Marine mammals which have life histories that tie them to specific breeding sites, such as Weddell (*Lep-tonychotes weddellii*), Ross (*Ommatophoca rossii*) and crabeater (*Lobodon carcinophaga*) seals, will be severely affected by shifts in their foraging habitats and migration of prey species associated with a decrease in sea-ice extent. For example, growth and survival of seal pups are directly influenced by krill abundance. Warming could reduce the extent of pack ice in the Antarctic and thus affect the distribution and abundance of krill. Declining krill abundance in the region of the Antarctic Peninsula during the 1990s has been linked to low winter sea-ice extent (Boyd 2002, Fraser & Hofmann 2003).

Effects of changes in salinity

Direct effects

The salinity of the surface waters of the open ocean varies between 32 practical salinity units (psu) in the subarctic Pacific to 37 psu in subtropical gyres. At the coastal and polar limits of the ocean and in marginal seas, processes such as local precipitation and evaporation, river runoff and ice formation can result in salinities of less than 10 and greater than 40 psu. Many marine mammals have adapted to tolerate variations in salinity (Fiedler 2002).

However, populations of bottlenose dolphins from areas of low water temperature and low salinity have been found to exhibit higher skin lesion prevalence and severity. It is thought that such conditions may impact on the epidermal integrity or produce more general physiological stress, potentially making the animals more vulnerable to natural infections or anthropogenic factors (Wilson et al. 1999). This indicates that variations in environmental factors can have an important effect on disease in marine mammals.

Indirect effects

Changes in salinity, for example, with changes in river inputs/runoff and melting ice, will influence the distribution and abundance of prey through effects on stratification of the water column and circulation and possibly also due to limited salinity tolerance. For example, most cephalopods are

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

particularly sensitive to changes in salinity (Boyle 1983, Fiedler 2002). Shifts in the phytoplankton community structure, from diatoms to cryptophytes, in the near-shore coastal waters along the Antarctic Peninsula have been linked to glacial melt-water runoff and reduced surface water salinity. This shift in phytoplankton community structure directly affects the zooplankton assemblage. Antarctic krill do not graze efficiently on cryptophytes due to their small size, and an increase in the relative abundance of cryptophytes will cause a shift in the spatial distribution of krill. This in turn will affect higher trophic levels in the food web as krill is an important prey for several seabird and marine mammal species (Moline et al. 2004).

Effects of changes in CO₂ concentrations and pH

Direct effects

Carbon dioxide accumulating in the atmosphere permeates into ocean surface layers, where it may impact on marine animals (Pörtner et al. 2004). The direct effects of increased CO₂ concentrations and associated decrease in pH on marine mammals are unknown.

Indirect effects

Increased levels of CO₂ have important implications for large marine animals that do not breathe air (i.e., the prey of marine mammals) as increased CO₂ will acidify the body tissues and fluids (hypercapnia) and affect the ability of blood to carry oxygen. Changes in CO₂ levels and pH are likely to affect metabolic function and therefore growth and reproduction of water breathing animals (Pörtner et al. 2004, Royal Society 2005). Sensitivity is highest in ommastrephid squids, such as *Illex illecebrosus*, which are characterised by a high metabolic rate and extremely pH-sensitive blood oxygen transportation. In comparison to squid, fish are better protected from CO₂ effects as they have a lower metabolic rates and higher capacities to compensate for CO₂-induced pH disturbances (Pörtner et al. 2004). In general, the number of species suffering from acute CO₂ toxicity will be limited. However, although individuals in a population may be tolerant over a short period, it is impossible to determine the long-term effects of changes in CO₂ levels and pH on individuals and populations (Pörtner et al. 2004).

Effects of changes in rainfall patterns

Direct effects

More intense precipitation events and flash floods will result in increased runoff. Thus, increased nutrient inputs into coastal waters, combined with an increase in water temperatures could cause an increase in toxic algal blooms and eutrophication (see section above on increased susceptibility to diseases and other causes of death).

Indirect effects

The effects of eutrophication play an important role in phytoplankton seasonal and community dynamics in the southern North Sea (Edwards et al. 2001). Changes associated with changes in rainfall patterns, for example, a decrease in salinity in coastal waters, will affect the distribution and abundance of prey species. Increased runoff as a result of increased precipitation may also cause an increase in inputs of pollutants, including sewage, with potential effects on coastal marine mammal and prey species.

Changes in rainfall patterns are likely to lead to an increased demand for fresh water in some areas, resulting in the regulation of water flow through the use of dams and dredging. These are major barriers to the migration of river dolphins. Such activities have already created small isolated populations and rendered some areas of otherwise suitable habitat completely inaccessible. Flood control will result in loss of shallow water habitats that are often used extensively during rainy seasons (Harwood 2001).

Effects of changes in storm frequency, wind speed and wave conditions

Direct effects

Changes in prevailing ocean wave height and directions and storm waves and surges can be expected to have serious impacts on coasts as they will be superimposed on increasing sea levels (IPCC 2001a). Pinniped haul-out sites for breeding and nurseries are likely to be vulnerable to any changes in storm frequency and wave conditions, for example, the Mediterranean monk seal, which is reliant on a small number of caves or narrow beaches for breeding (Harwood 2001, Würsig et al. 2002).

Indirect effects

Coastal ecosystems such as coral reefs and atolls, salt marshes and mangrove forests, and submerged aquatic vegetation will be directly impacted by any changes in storm frequency and intensity (IPCC 2001a). These areas are important nursery grounds for many fish and invertebrate species, and therefore the prey of marine mammals.

Effects of changes in climate patterns

Direct effects

Changes in climate patterns, such as El Niño events, have been linked directly and indirectly to massive die-offs and shifts in distribution of plankton, fishes (such as anchovy), seabirds and marine mammals (Stenseth et al. 2002).

Indirect effects

The predicted increase in frequency of warm events associated with the ENSO, would result in a decline in plankton biomass and fish larvae abundance, adversely impacting fish recruitment patterns and spatial distribution of fish stocks, with subsequent effects on marine mammals, seabirds and ocean biodiversity (IPCC 2001a, Stenseth et al. 2002).

The indirect effects associated with El Niño events on marine mammal species are mostly related to changes in prey availability and include (i) changes in community structure, for example, after the 1982–83 El Niño short-finned pilot whales appeared to be replaced by Risso's dolphins (Shane 1994, 1995), (ii) changes in species ranges, for example, the range expansion of bottlenose dolphins along the Californian coast during and after the 1982–83 El Niño event (Wells et al. 1990), and (iii) effects on reproduction, for example, reduced fecundity or calf survival in sperm whales of the eastern tropical Pacific during and after an El Niño event in the late 1980s (Whitehead 1997), and high juvenile mortality in seal colonies, such as Galapagos fur seals during the El Niño year of 1982 (Würsig et al. 2002). There is also some indirect evidence for environmental effects on reproduction in female dusky dolphins (*Lagenorhynchus obscurus*) during the 1982–83 El Niño event off Peru. The deposition of poorly calcified dentinal growth layer groups in the teeth of

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

pregnant and lactating females during the period of El Niño and reduced prey availability, indicated nutritional stress (Manzanilla 1989, Boyd et al. 1999).

The NAO can influence, directly and indirectly, the recruitment, growth, distribution, abundance and survival of several fish, cephalopod and plankton species (Stenseth et al. 2002). For example, changes in sea temperatures driven by NAO variations have been linked to cod recruitment off Labrador and Newfoundland, and in the Barents Sea (Stenseth et al. 2002). The temporal and spatial population dynamics of *Calanus finmarchicus* and *C. helgolandicus* have been linked to the NAO (Planque & Taylor 1998, Beare et al. 2002, Stenseth et al. 2002, Beaugrand & Ibanez 2004). Early stages of *Calanus* species are the main prey for larvae and early juveniles of many fish species throughout the North Atlantic and thus influence fish recruitment success and consequently the size of fish populations (Stenseth et al. 2002, Walther et al. 2002). These changes in prey abundance and distribution as a result of the NAO are likely to have direct and indirect effects on marine mammal species in the North Atlantic.

In addition to ENSO and NAO variability, the persistence of multi-year climate-ocean regimes and switches from one regime to another have been recognised, with changes in recruitment patterns of fish populations linked to such switches (IPCC 2001a). Similarly, survival of marine mammals and seabirds is also affected by interannual and longer-term variability in several oceanographic and atmospheric properties and processes, especially in high latitudes (IPCC 2001a).

Conservation and legislation related to marine mammals

The conservation status of marine mammals is provided by the World Conservation Union (IUCN), which maintains a red list of threatened species and provides advice to organisations such as International Whaling Commission (IWC) and Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In the most recent Red List (IUCN 2004) (listed in Table 1), six of the 28 cetacean species for which sufficient data were available are considered endangered, five species are listed as vulnerable and two species, the vaquita and baiji, are critically endangered; 14 of the 15 species that are listed as low risk are conservation dependent and one is listed as near threatened. Nearly 60% of the 67 cetacean species included in the IUCN red list are classed as being 'data deficient', indicating that a lack of scientific knowledge is a major barrier to the conservation of cetacean populations. Seven of the 11 pinniped species listed in the IUCN red list are classed as vulnerable, two as endangered and one, the Mediterranean monk seal, as critically endangered. All four sirenian species are listed as vulnerable, both the sea otter and marine otter are endangered and polar bears are conservation dependent.

Marine mammals are subjected to various threats and pressures throughout their range, including incidental catch in fisheries, boat strikes, prey depletion, pollution (including heavy metals, organochlorine compounds, oil and sewage), habitat disturbance and degradation; algal blooms, noise pollution, introduction of exotic species and pathogens, marine debris and climate change (Perrin et al. 2002, Evans & Raga 2001).

International conservation conventions and institutions that relate to marine mammals include the IWC, which was created in 1946 following the International Convention for the Regulation of Whaling. Formerly devoted to the regulation of whaling, the IWC has increasingly become involved in the preservation and recovery of cetacean populations. In 1996 the IWC sponsored a workshop on climate change and cetaceans (IWC 1997).

The Convention on the Conservation of Migratory Species of Wild Animals (CMS or Bonn Convention) is an international treaty that provides a mechanism for regional conservation agreements. This has led to the Agreement on the Conservation of Small Cetaceans of the Baltic and North Sea (ASCOBANS) and the Agreement on the Conservation of Small Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ASCOBAMS). ASCOBANS carried out a

multinational abundance survey of cetaceans in 1994 throughout the Baltic and North Sea (Hammond et al. 2002) and another survey was carried out in 2005.

Marine mammals are also protected under conservation acts such as the Marine Mammal Protection Act in the U.S. and the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). Protected or management areas intended, at least in part, to benefit marine mammals have been established in several areas, for example, the Biosphere Reserve in the upper Gulf of Mexico to protect the vaquita and the Hawaiian Island Humpback Whale Sanctuary (for further examples see Reeves 2002).

Implications of climate change for the management and conservation of marine mammals

Management and conservation measures need to take into account the potential changes in range and changing requirements of marine mammals. The adverse effects on breeding habitat may be reduced by creating protected areas for the remaining habitat, if this can be identified. However, the main method for adapting to change in the wider environment will be to manage human impacts on the resources required by marine mammal species through some form of ecosystem-based management. The European Marine Strategy proposes the management of all human activities in the sea based on three central features: an Ecosystem Approach, Integrated Management and a Regional Focus for the coordination and delivery of management programmes.

One way to protect marine mammals would be to designate marine protected areas ('no-take zones') for the prey of marine mammals as well as marine mammal species. However, the ideal location of such areas is likely to change over time, and this will require different legislation than currently used. For example, there needs to be a degree of flexibility in the establishment of protected areas for marine mammals, such as Special Areas of Conservation (SAC), to take into account the potential shift in range and needs of marine mammals resulting from climate change (e.g., Wilson et al. 2004 and MacLeod et al. 2005).

However, protective and conservation measures will not be able to solve many of the problems faced by marine mammals as a result of climate change and therefore the mitigation of greenhouse gases to prevent temperature increase and the associated changes in climate may be the only solution.

Knowledge gaps and future research

Marine mammals are large, long-lived warm-blooded animals that show considerable behavioural plasticity. This plasticity allows many species to respond to environmental changes within a single generation and these species are unlikely to be affected physiologically by moderate changes in the physical characteristics of their environment. Their apparent reliance on behavioural responses to environmental changes, some of which can be transmitted culturally, means that low genetic diversity, which has been demonstrated for some species, does not necessarily affect their ability to respond to such changes. However, the limits to this plasticity are not known.

One of the greatest threats to marine mammals probably comes from changes in their food resources, as a result of climate change. Many prey species such as fish, cephalopods and plankton appear to rely on, and are influenced by, particular sets of environmental conditions. Any changes in the geographic distribution of these conditions as a result of climate change will affect the abundance and distribution of prey species. This will ultimately affect the availability of these prey to marine mammals, which in turn would affect their distribution and migration, and could have serious consequences for reproduction and survival. More information is required to determine the potential impact of climate change on the timing and extent of population movements, distribution,

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

abundance, recruitment, and species composition of prey. The theoretical basis for identifying and tracking areas where the prey of marine mammals should be protected is limited, and more information is required on the factors affecting prey availability and prey quality.

Future data needs include the continued monitoring or establishment of long-term stranding and sightings records of marine mammals, especially in areas at the northern and southern limits of the range of the species. The range of migratory and resident species can be very sensitive to climate and individuals can show an immediate response, for example, in their migratory destinations. Therefore, as with climatic data, a long time series is required to distinguish year-to-year variation from long-term trends (IPCC 2001a, Walther et al. 2002). These data are needed to (i) detect changes in the community structure, abundance or distribution of species, (ii) compare with long-term records of other marine species such as plankton, fish, cephalopods and environmental variables and (iii) detect any changes in cause of death (i.e., the presence of 'new' diseases, etc.).

The establishment of regular marine mammal monitoring programmes in areas where information is limited, especially areas that are known or thought to be important for breeding and/or feeding and on migration routes, is essential. The regionally distinctive effects of climate change make it difficult to predict the potential impacts on most species; therefore more information is required on a regional scale to determine critical habitat and diet. This is especially true for populations that are already under threat: those with reduced abundance due to past whaling, by-catch and/or pollutants and restricted to a limited distribution and/or dependent on critical habitats for breeding or feeding. More information is required for species, such as beaked whales (Ziphiidae), for which very little is known about their distribution, abundance, migration and diet, and for which, therefore, the potential effects of climate change or any other potential threat are difficult to predict.

In general, more information and research is needed on the direct effects of temperature change on marine mammals; the potential impacts of changes in salinity, pH and CO₂; habitat use and requirements for almost all species; competitive interactions between marine mammal species, and the effects of climate change on the spread and prevalence of diseases. The effects of climate change are unlikely to be isolated and therefore further information is required on the potential effects of synergetic interactions, for example, the effects of changes in prey availability combined with the effects of increased stress due to changes in temperature, etc. To understand the impacts of climate change on marine mammal species and populations, we also need to take into account other threats and pressures, such as habitat degradation/destruction, by-catch, pollution, noise, etc., already faced by many marine mammals. Currently there has been very little done to model/predict future climate change scenarios in relation to their potential effects and impacts on marine mammals.

Summary of the potential effects of climate change on marine mammals

Direct effects of changes in temperature include shifts in species ranges; some may expand and some may contract. However, species with restricted ranges, for example, polar species, the vaquita and river dolphins, may be particularly vulnerable. More information is needed on potential direct physiological effects of increased temperature on marine mammals and the possible implications.

Indirect effects of changes in temperature include the effects of climate change on prey availability affecting the distribution, abundance and migration, community structure, susceptibility to disease and contaminants, reproductive success, and, ultimately, the survival of marine mammal species. Changes in the range and abundance of competitors and predators will also affect marine mammals to varying degrees depending on the species and location. Management and conservation measures need to take into account the potential changes in species' range by creating protected areas for the remaining and predicted habitat.

Rising sea levels will directly affect pinniped haul-out sites. The Mediterranean monk seal may be particularly vulnerable as it is reliant on a small number of caves or narrow beaches for breeding and these sites could easily be destroyed or rendered unusable by rising sea levels and increased storm frequency. Remaining breeding sites, as well as potentially suitable breeding sites as conditions change, need to be protected. The construction of protective barriers for coastal habitats, against rising sea levels, could have several implications for coastal marine mammals, including habitat degradation, effects on prey, direct mortality and obstruction to migration. Detailed environmental impact assessments are required that take into account the current and possible future impacts on marine mammals.

Changes in ocean currents, upwellings and fronts could affect the distribution of marine mammals either directly, especially if the limits to their range are defined by the boundary between two water masses, or indirectly as a result of changes in the distribution and occurrence of prey associated with currents, upwellings and fronts. Protective measures could include flexible no-take zones that follow changes in prey distribution rather than fixed areas.

Marine mammals, particularly those that rely on ice or the environment close to the ice edge, are vulnerable to the direct effects of a decrease in sea-ice cover. Seals and polar bears that rely on ice for breeding are likely to suffer considerable habitat loss. Large baleen whale species that undertake long-distance migrations from tropical breeding grounds to high-latitude feeding grounds close to the ice edge may be at risk as the polar ice caps retreat. The longer migration paths that will be required will increase the costs of movement and reduce the duration of the feeding season. Changes in sea extent and salinity will affect all species associated with the ice edge, either directly or indirectly through spatial and/or temporal changes in prey availability.

The potential effects and impacts of changes in salinity, pH and CO₂ on marine mammals are not fully understood and require further research, although prey species — especially cephalopods — may be particularly sensitive. Changes in rainfall patterns and increased runoff, as well as changes in temperature, salinity, pH and CO₂, could increase toxic algal blooms. Fatalities due to toxic algal blooms have occurred in cetacean, pinniped and manatee species. Improving water management and control of discharges could help to elevate the potential risks of increased eutrophication and toxic algal blooms.

The greatest threat to marine mammals probably comes from changes in their food resources as a result of climate change. For example, many species appear to rely on particular sets of environmental conditions to concentrate their prey. If climate change affects the geographic distribution of these oceanographic conditions, this could ultimately have serious consequences for marine mammal reproduction and survival.

For populations that are already under threat (e.g., from low numbers due to past whaling, severely affected by by-catch and/or pollutants, restricted to a limited distribution dependent on critical habitats for breeding or feeding), the effects (direct and/or indirect) of climate change may be more important.

Acknowledgements

The work for this review was carried out as part of the Climate Change and Migratory Species Report for DEFRA Research Contract CR0302. Thanks also go to John Harwood (SMRU) who provided useful comments and suggestions on an early draft of the report and to other colleagues who participated in discussions on the effects of climate change at the project workshop in Cambridge, 2005.

References

- Aguilar, A. & Borrell, A. 1994. Abnormally high polychlorinated biphenyl levels in striped dolphins (*Stenella coeruleoalba*) affected by the 1990–1992 Mediterranean epizootic. *The Science of the Total Environment* **154**, 237–247.
- Aguilar, A., Borrell, A. & Pastor, T. 1999. Biological factors affecting variability of persistent pollutant levels in cetaceans. In *Chemical Pollutants and Cetaceans*, Special Issue 1, P.J.H. Reijnders et al. (eds). Cambridge: International Whaling Commission, 83–116.
- Aguilar, A. & Raga, J.A. 1993. The striped dolphin epizootic in the Mediterranean Sea. *Ambio* **22**, 524–528.
- Alerstam, T., Hedenström, A. & Åkesson, S. 2003. Long-distance migration: evolution and determinants. *Oikos* **103**, 247–260.
- Anderson, L.W., Ruzzante, D.E., Walton, M., Berggren, P., Bjørge, A. & Lockyer, C.H. 2001. Conservation genetics of harbour porpoises, *Phocoena phocoena*, in eastern and central North Atlantic. *Conservation Genetics* **2**, 309–324.
- Arkhipkin, A.I., Grzebielec, R., Sirotka, A.M., Remeslo, A.V., Polishchuk, I.A. & Middleton, D.A.J. 2004. The influence of seasonal environmental changes on the ontogenetic migrations of the squid *Loligo gahi* on the Falkland shelf. *Fisheries Oceanography* **13**, 1–9.
- Bannister, J.L. 2002. Baleen whales. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 62–72.
- Beare, D.J., Batten, S., Edwards, M. & Reid, D.G. 2002. Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. *Journal of Sea Research* **48**, 29–49.
- Beare, D.J., Burns, F., Greig, T., Jones, E.G., Peach, K., Kienzle, M., McKenzie, E. & Reid, D.G. 2004a. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. *Marine Ecology Progress Series* **284**, 269–278.
- Beare, D.J., Burns, F., Jones, E., Peach, K., Portilla, E., Greig, T., McKenzie, E. & Reid, D.G. 2004b. An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biology* **10**, 1209–1213.
- Beaugrand, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fisheries Oceanography* **12**, 270–283.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S. & Reid, P.C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature* **426**, 661–664.
- Beaugrand, G. & Ibanez, F. 2004. Monitoring marine plankton ecosystems II: long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. *Marine Ecology Progress Series* **284**, 35–47.
- Beaugrand, G. & Reid, P.C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* **9**, 801–817.
- Bjørge, A. 2002. How persistent are marine mammal habitats in an ocean of variability? In *Marine Mammals: Biology and Conservation*, P.G.H. Evans & J.A. Raga (eds). New York: Kluwer Academic/Plenum Publishers, 63–91.
- Bjørge, A. & Tolley, K.A. 2002. Harbour Porpoise. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 549–551.
- Boyd, I.L. 1996. Individual variation in the duration of pregnancy and birth date in Antarctic fur seals: the role of environment, age, and sex of foetus. *Journal of Mammalogy* **77**, 124–133.
- Boyd, I.L. 2002. Antarctic marine mammals. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 30–36.
- Boyd, I.L., Lockyer, C. & Marsh, H.D. 1999. Reproduction in marine mammals. In *Biology of Marine Mammals*, J.E. Reynolds III. & S.A. Rommel (eds). Washington, D.C.: Smithsonian Institution Press, 218–286.
- Boyle, P.R. (ed.). 1983. *Cephalopod Life Cycles*. London: Academic Press.
- Burns, J.J. 2002. Arctic marine mammals. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 39–45.
- Cebrian, D. 1995. The striped dolphin *Stenella coeruleoalba* epizootic in Greece, 1991–1992. *Biological Conservation* **74**, 143–145.

- Cockeron, P.J. & Connor, R.C. 1999. Why do baleen whales migrate? *Marine Mammal Science* **15**, 1228–1245.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783–786.
- de Swart, R.L., Ross, P.S., Vedder, L.J., Timmerman, H.H., Heisterkamp, S., Van Loveren, H., Vos, J.G., Reijnders, P.J.H. & Osterhaus, A.D.M.E. 1994. Impairment of immune function in harbour seals (*Phoca vitulina*) feeding on fish from polluted water. *Ambio* **23**, 155–159.
- Domingo, M., Kennedy, S. & Van Bresseem, M. 2002. Marine mammal mass mortalities. In *Marine Mammals: Biology and Conservation*, P.G.H. Evans & J.A. Raga (eds). New York: Kluwer Academic/Plenum Publishers, 425–456.
- Ducrotoy, J.P. 1999. Indications of change in the marine flora of the North Sea in the 1990s. *Marine Pollution Bulletin* **38**, 646–654.
- Edwards, M., Beaugrand, G., Reid, P.C., Rowden, A.A. & Jones, M.B. 2002. Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series* **239**, 1–10.
- Edwards, M., Reid, P. & Planque, B. 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES Journal of Marine Science* **58**, 39–49.
- Edwards, M. & Richardson, A.J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881–884.
- EEA. 2004. Impacts of Europe's changing climate. Copenhagen: European Environment Agency.
- Evans, P.G.H. & Raga, J.A. (eds). 2001. *Marine Mammals Biology and Conservation*. New York: Kluwer Academic/Plenum Publishers, 630 pp.
- Ferguson, S.H., Stirling, I. & McLoughlin, P. 2005. Climate change and ringed seals (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* **21**, 121–135.
- Fiedler, P.C. 2002. Ocean Environment. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 824–830.
- Forcada, J. 2002. Distribution. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 327–333.
- Fraser, W.R. & Hofmann, E.E. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series* **265**, 1–15.
- FRS 1998. Scottish Ocean Climate Status Report 1998. Report No. 9/99. Aberdeen, U.K.: Fisheries Research Services, 11 pp.
- FRS 2003. Scottish Ocean Climate Status Report 2000–2001. Report No. 05/03. Aberdeen, U.K.: Fisheries Research Services, 20 pp.
- Fuller, G.B. & Hobson, W.C. 1986. Effects of PCBs on reproduction in mammals. In *PCBs and the Environment*, II, J.S. Waid (ed.). Boca Raton, FL: CRC Press, 101–125.
- Geraci, J.R., Andersen, D.M., Timperi, R.J., St. Aubin, D.J., Early, G.A., Prescott, J.H. & Mayo, C.A. 1989. Humpback whales fatally poisoned by dinoflagellate toxin. *Canadian Journal of Fisheries and Aquatic Sciences*. **46**, 1895–1898.
- Geraci, J.R., Harwood, J. & Lounsbury, V.J. 1999. Marine mammal die-offs. In *Conservation and Management of Marine Mammals*, J.R. Twiss Jr. & R.R. Reeves (eds). Washington, D.C.: Smithsonian Institution Press, 367–395.
- Geraci, J.R. & Lounsbury, V. 2002. Marine mammal health: holding the balance in an ever changing sea. In *Marine Mammals: Biology and Conservation*, P.G.H. Evans & J.A. Raga (eds). New York: Kluwer Academic/Plenum Publishers, 365–384.
- Gilmartin, W.G. & Forcada, J. 2002. Monk seals. In *Encyclopedia of Marine Mammals*, W.F. Perrin. et al. (eds). San Diego: Academic Press, 756–759.
- Greene, C.H. & Pershing, A.J. 2004. Climate and the conservation biology of North Atlantic right whales: the right whale at the wrong time? *Frontiers in Ecology and the Environment* **2**, 29–34.
- Hamilton, W.J. & Blaxter, K.L. 1980. Reproduction in farmed red deer 1: hind and stag fertility. *Journal of Agricultural Science* **95**, 261–273.
- Hammond, P.S., Berggren, P., Benke, H., Borchers, D.L., Collet, A., Heide-Jorgensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F. & Oien, N. 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology* **39**, 361–376.

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

- Hansen, B., Turrell, W.R. & Østerhus, S. 2001. Decreasing overflow from the Nordic seas into the Atlantic Ocean through the Faroe Bank channel since 1950. *Nature* **411**, 927–930.
- Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., Grimes, D.J., Hofmann, E.E., Lipp, E.K., Osterhaus, A.D.M.E., Overstreet, R.M., Porter, J.W., Smith, G.W. & Vasta, G.R. 1999. Emerging marine diseases — climate links and anthropogenic factors. *Science* **285**, 1503–1510.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S. & Samuel, M.D. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* **296**, 2158–2162.
- Harwood, J. 2001. Marine mammals and their environment in the twenty-first century. *Journal of Mammalogy* **82**, 630–640.
- Heath, M.R., Adams, R.D., Brown, F., Dunn, J., Fraser, S., Hay, S.J., Kelly, M.C., Macdonald, E.M., Robertson, M. R., Robertson, S. & Wilson, C. 1999a. Plankton monitoring off the east coast of Scotland in 1997 and 1998. Report No. 13/99. Aberdeen, U.K.: Fisheries Research Services, 32 pp.
- Heath, M.R., Beare, D.J., Dunn, J., Fraser, J.G., Hay, S.J. & Turrell, W.R. 1999b. Monitoring the effects of climate change — overwintering abundance of *Calanus finmarchicus* in the Faroe-Shetland Channel. Report No. 14/99. Aberdeen, U.K.: Fisheries Research Services, 24 pp.
- Heide-Jørgensen, M.P. & Laidre, K.L. 2004. Declining extent of open-water refugia for top predators in Baffin Bay and adjacent waters. *Ambio* **33**, 487–494.
- Helle, E., Olsson, M. & Jensen, S. 1976. PCB levels correlated with pathological changes in seal uteri. *Ambio* **5**, 261–263.
- Hernández, M., Robinson, I., Aguilar, A., González, L.M., López-Jurado, L.F., Reyero, M.I., Cacho, E., Franco, J., López-Rodas, V. & Costas, E. 1998. Did algal toxins cause monk seal mortality? *Nature* **393**, 28.
- Hoffman, D., Rattner, B. A., Scheunert, I. & Korte, F. 2001. Environmental Contaminants. In *Ecotoxicology of Wild Mammals*, R.F. Shore & B.A. Rattner (eds), Chichester, England: John Wiley & Sons Ltd., 1–48.
- Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Lowe, J., Murphy, J.M., Hassell, D., Boorman, P., McDonald, R. & Hill, S. 2002. Climate change scenarios for the United Kingdom: the UKCIP02 scientific report. Norwich: Tyndall Centre for Climate Change Research, 120 pp.
- ICES. 2004. The Annual ICES Ocean Climate Status Summary 2003/2004. Report No. 269. Copenhagen: International Council for the Exploration of the Sea, 32 pp.
- IPCC. 2001a. *Climate Change 2001: Impacts, Adaptation and Vulnerability*. Cambridge: Cambridge University Press, 1032 pp.
- IPCC. 2001b. *Climate Change 2001: The Scientific Basis*. Cambridge: Cambridge University Press, 881 pp.
- IUCN. 2004. Red list of threatened species. www.redlist.org. [Date accessed: December 2004]
- IWC. 1997. Report of the IWC workshop on climate change and cetaceans. *Report of the International Whaling Commission* **47**, 293–313.
- Jepson, P.D., Bennett, P.M., Allchin, C.R., Law, R.J., Kuiken, T., Baker, J.R., Rogan, E. & Kirkwood, J.K. 1999. Investigating potential associations between chronic exposure to polychlorinated biphenyls and infectious disease mortality in harbour porpoises from England and Wales. *The Science of the Total Environment* **243/244**, 339–348.
- Jones, M.L. & Swartz, S.L. 2002. Gray whale. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 524–536.
- Kaschner, K. 2004. *Modelling and mapping resource overlap between marine mammals and fisheries on a global scale*. PhD, Alber-Lubwigs-Universität, Freiburg, Germany.
- Kennedy, S. 1996. Infectious diseases of cetacean populations. In *The Conservation of Whales and Dolphins*, M.P. Simmonds & J.D. Hutchinson (eds). Chichester, U.K.: John Wiley & Sons, 333–353.
- Kennedy, S. 1999. Morbilliviral infections in marine mammals. In *Chemical Pollutants and Cetaceans*, Special Issue 1, P.J.H. Reijnders et al. (eds). Cambridge: International Whaling Commission, 267–273.
- Kennedy, S., Kuiken, T., Ross, H.M., McAliskey, M., Moffett, D., McNiven, C.M. & Carole, M. 1992. Morbillivirus infection in two common porpoises (*Phocoena phocoena*) from the coasts of England and Scotland. *Veterinary Record* **131**, 286–290.
- Kenney, R.D., Payne, M., Heinemann, D.W. & Winn, H.E. 1996. Shifts in Northeast shelf cetacean distributions relative to trends in Gulf of Maine/Georges Bank finfish abundance. In *The Northeast Shelf Ecosystem: Assessment, Sustainability and Management*, K. Sherman et al. (eds). Cambridge, MA: Blackwell Science, 169–196.

- Kuiken, T., Bennett, M.E., Allchin, C.R., Kirkwood, J.K., Baker, J., Lockyer, C., Walton, M. & Sheldrick, M.C. 1994. PCBs, cause of death and body condition in harbour porpoises (*Phocoena phocoena*) from British waters. *Aquatic Toxicology* **28**, 13–28.
- Lafferty, K.D., Porter, J.W. & Ford, S.E. 2004. Are diseases increasing in the ocean? *Annual Review of Ecology and Systematics*. **35**, 31–54.
- Laidre, K.L. & Heide-Jørgensen, M.P. 2005. Arctic sea ice trends and narwhal vulnerability. *Biological Conservation* **121**, 509–517.
- Laidre, K.L., Heide-Jørgensen, M.P., Logdson, M.L., Hobbs, R.C., Heagerty, P., Dietz, R., Jørgensen, O.A. & Treble, M.A. 2004. Seasonal narwhal habitat associations in the high Arctic. *Marine Biology* **145**, 821–831.
- LeDuc, R. 2002. Biogeography. In *Encyclopedia of Marine Mammals*, W.F. Perrin. et al. (eds). San Diego: Academic Press, 99–103.
- Lockyer, C.H. 1986. Body fat condition in Northeast Atlantic fin whales, *Balaenoptera physalus*, and its relationship with reproduction and food resource. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 142–147.
- MacLeod, C.D., Bannon, S.M., Pierce, G.J., Schweder, C.S., Learmonth, J.A., Herman, J.S. & Reid, R.J. 2005. Climate change and the cetacean community of north-west Scotland. *Biological Conservation* **124**, 477–483.
- Mann, J., Connor, R.C., Tyack, P.L. & Whitehead, H. (eds). 2000. In *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago: The University of Chicago Press, 415 pp.
- Manzanilla, S.R. 1989. The 1982–1983 El Niño event recorded in dentinal growth layers in teeth of Peruvian dusky dolphins (*Lagenorhynchus obscurus*). *Canadian Journal of Zoology* **67**, 2120–2125.
- Marotzke, J. 2000. Abrupt climate change and thermohaline circulation: mechanisms and predictability. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 1347–1350.
- Moline, M.A., Claustre, H., Frazer, T.K., Schofield, O. & Vernet, M. 2004. Alterations of the food web along the Antarctic Peninsula in response to a regional warming trend. *Global Change Biology* **10**, 1973–1980.
- Northridge, S.P., Tasker, M.L., Webb, A. & Williams, J.M. 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena*), white-beaked dolphins (*Lagenorhynchus albirostris*) and minke whales (*Balaenoptera acutorostrata*) around the British Isles. *ICES Journal of Marine Science* **52**, 55–66.
- O'Brien, C.M., Fox, C.J., Planque, B. & Casey, J. 2000. Climate variability and North Sea cod. *Nature* **404**, 142.
- Parnesan, C. & Galbraith, H. 2004. Observed impacts of global climate change in the U.S. Arlington, VA: Pew Center on Global Climate Change.
- Parnesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- Perrin, W.F., Würsig, B. & Thewissen, J.G.M. (eds). 2002. *Encyclopedia of Marine Mammals*. San Diego: Academic Press, 1414 pp.
- Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. 2005. Climate change and distribution shifts in marine fishes. *Science* **308**, 937.
- Planque, B. & Taylor, A.H. 1998. Long-term changes in zooplankton and the climate of the North Atlantic. *ICES Journal of Marine Science* **55**, 644–654.
- Pörtner, H.O., Langenbuch, M. & Reipschläger, A. 2004. Biological impact of elevated ocean CO₂ concentrations: lessons from animal physiology and earth history. *Journal of Oceanography* **60**, 705–718.
- Read, A. & Gaskin, D.E. 1990. Changes in growth and reproduction of Harbour porpoises, *Phocoena phocoena*, from the Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 2158–2163.
- Reeves, R.R. 2002. Conservation efforts. In *Encyclopedia of Marine Mammals*, W.F. Perrin. et al. (eds). San Diego: Academic Press, 276–297.
- Reid, D.G., Edwards, M., Beaugrand, G., Skogen, M. & Stevens, D. 2003a. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fisheries Oceanography* **12**, 260–269.
- Reid, J.B., Evans, P.G.H. & Northridge, S.P. (eds). 2003b. *Atlas of Cetacean Distribution in North-west European Waters*. Peterborough: Joint Nature Conservation Committee, 75 pp.

POTENTIAL EFFECTS OF CLIMATE CHANGE ON MARINE MAMMALS

- Reijnders, P.J.H. & Aguilar, A. 2002. Pollution and marine mammals. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 948–957.
- Reijnders, P.J.H. 1986. Reproductive failure in common seals feeding on fish from polluted coastal waters. *Nature* **324**, 456–467.
- Reynolds, J.E. & Powell, J.A. 2002. Manatees. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 709–720.
- Rice, D.W. 1998. *Marine Mammals of the World: Systematics and Distribution*. The Society of Marine Mammalogy, Special Publication No. 4.
- Ridgeway, S.H. & Harrison, R. (eds). 1985. *Handbook of Marine Mammals. Volume 3: The Sirenians and Baleen Whales*. London: Academic Press.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. 2003. Fingerprints of global warming on plants and animals. *Nature* **421**, 57–60.
- Ross, P.S., Vos, J.G., Birnbaum, L.S. & Osterhaus, A.D.M.E. 2000. PCBs are a health risk for humans and wildlife. *Science* **289**, 1878–1879.
- Royal Society. 2005. Ocean acidification due to increasing atmospheric carbon dioxide. Policy Document 12/05. London: The Royal Society, 60 pp.
- Scholin, C.A., Gulland, F., Doucette, G.J., Benson, S., Busman, M., Chavez, F.P., Cordaro, J., DeLong, R., De Vogelaere, A., Harvey, J., Haulena, M., Lefebvre, K., Lipscomb, T., Loscutoff, S., Lowenstine, L.J., Marin III, R., Miller, P.E., McLellan, W.A., Moeller, P.D.R., Powell, C.L., Rowles, T., Silvagni, P., Silver, M., Spraker, T., Trainer, V. & Van Dolah, F.M. 2000. Mortality of sea lions along the central California coast linked to a toxic diatom bloom. *Nature* **403**, 80–84.
- Sear, C., Hulme, M., Adger, N. & Brown, K. 2001. The impacts of global climate change of the UK overseas territories. Norwich: Tyndall Centre for Climate Change Research, 49 pp.
- Shane, S.H. 1994. Occurrence and habitat use of marine mammals at Santa Catalina Island, California from 1983–91. *Bulletin Southern California Academy of Sciences* **93**, 13–29.
- Shane, S.H. 1995. Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, California, USA. *Marine Ecology Progress Series* **123**, 5–11.
- Shaughnessy, P.D. & Green, K. 1998. Continued increase in the population of Antarctic fur seals, *Arctocephalus gazella*, at Heard Island, Southern Ocean. *Marine Mammal Science* **14**, 384–389.
- Sims, D.W., Genner, M.J., Southward, A.J. & Hawkins, S.J. 2001. Timing of squid migration reflects North Atlantic climate variability. *Proceedings of the Royal Society of London, B Biological Sciences* **268**, 2607–2611.
- Sissener, E.H. & Bjørndal, T. 2005. Climate change and the migratory pattern for Norwegian spring-spawning herring — implications for management. *Marine Policy* **29**, 299–309.
- Southward, A.J., Hawkins, S.J. & Burrows, M.T. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology* **20**, 127–155.
- Stebbing, A.R.D., Turk, S.M.T., Wheeler, A. & Clarke, K.R. 2002. Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960–2001). *Journal of the Marine Biological Association of the United Kingdom* **82**, 177–180.
- Stenseth, N., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S. & Lima, M. 2002. Ecological effects of climate fluctuations. *Science* **297**, 1292–1296.
- Stern, S.J. 2002. Migration and movement patterns. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 742–750.
- Stirling, I., Lunn, N.J. & Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climate change. *Arctic* **52**, 294–306.
- Thompson, P.M., Tollit, D.J., Corpe, H.M., Reid, R.J. & Ross, H.M. 1997. Changes in haematological parameters in relation to prey switching in a wild population of harbour seals. *Functional Ecology* **11**, 743–750.
- Tynan, C.T. & DeMaster, D.P. 1997. Observations and predictions of Arctic climatic change: potential effects on marine mammals. *Arctic* **50**, 308–322.

- Van Bresseem, M.F., Van Waerebeek, K., Jepson, P.D., Raga, J.A., Duignan, P.J., Nielsen, O., Di Benedetto, A.P., Siciliano, S., Ramos, R., Kant, W., Peddemors, V., Kinoshita, R., Ross, P.S., López-Fernandez, A., Evans, K., Crespo, E. & Barrett, T. 2001. An insight into the epidemiology of dolphin morbillivirus worldwide. *Veterinary Microbiology* **81**, 287–304.
- Vaughan, D.G. & Doake, C.S.M. 1996. Recent atmospheric warming and retreat of ice shelves on the Antarctic Peninsula. *Nature* **379**, 328–331.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**, 389–395.
- Waluda, C.M., Rodhouse, P.G., Podestá, G.P., Trathan, P.N. & Pierce, G.J. 2001. Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. *Marine Biology* **139**, 671–679.
- Weaver, A.J. & Zwiers, F.W. 2000. Uncertainty in climate change. *Nature* **407**, 571–572.
- Wells, R.S., Hansen, L.J., Baldrige, A., Dohl, T.P., Kelly, D.L. & Defran, R.H. 1990. Northward extension of the range of bottlenose dolphins along the California coast. In *The Bottlenose Dolphin*, S. Leatherwood & R.R. Reeves (eds). San Diego: Academic Press, 421–431.
- Wells, R.S. & Scott, M.D. 2002. Bottlenose dolphins. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 122–128.
- Whitehead, H. 1997. Sea surface temperature and the abundance of sperm whale calves off the Galápagos Islands: implications for the effects of global warming. *Report of the International Whaling Commission* **47**, 941–944.
- Whitehead, H. 2002. Sperm whale. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego, Academic Press, 1165–1172.
- Wiley, D.N. & Clapham, P.J. 1993. Does maternal condition affect the sex ratio of offspring in humpback whales? *Animal Behaviour* **46**, 321–324.
- Wilson, B., Arnold, H., Bearzi, G., Fortuna, C.M., Gaspar, R., Ingram, S., Liret, C., Pribanic, S., Read, A.J., Ridoux, V., Schneider, K., Urian, K.W., Wells, R.S., Wood, C., Thompson, P.M. & Hammond, P.S. 1999. Epidermal diseases in bottlenose dolphins: impacts of natural and anthropogenic factors. *Proceedings of the Royal Society of London, B Biological Sciences* **266**, 1077–1083.
- Wilson, B., Reid, R. J., Grellier, K., Thompson, P.M. & Hammond, P.S. 2004. Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. *Animal Conservation* **7**, 331–338.
- Würsig, B. 2002. Ecology, Overview. In *Encyclopedia of Marine Mammals*, W.F. Perrin et al. (eds). San Diego: Academic Press, 367–370.
- Würsig, B., Reeves, R.R. & Ortega-Ortiz, J.G. 2002. Global climate change and marine mammals. In *Marine Mammals: Biology and Conservation*, P.G.H. Evans & J.A. Raga (eds). New York: Kluwer Academic/Plenum Publishers, 589–608.
- Zheng, X., Pierce, G.J., Reid, D.G. & Jolliffe, I.T. 2002. Does the North Atlantic current affect spatial distribution of whiting? Testing environmental hypotheses using statistical and GIS techniques. *ICES Journal of Marine Science* **59**, 239–253.