

sediment record and hence their data, and continue to approach the subject in a rigorous and quantitative way<sup>5,10</sup>.

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## Effects of Expected Global Climate Change on Marine Faunas

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G.N. Somero

*Anthropogenically induced global climate change is likely to have a major impact on marine ecosystems, affecting both biodiversity and productivity. These changes will, in turn, have a large impact on humankind's interactions with the sea. By examining the effects of past climate changes on the ocean, as well as by determining how shifts in physical parameters of the ocean may affect physiology, biochemistry and community interactions, scientists are beginning to explore the possible effects of global climate change on marine biota.*

Intensive study of the possible effects of global warming on terrestrial ecosystems over the last decade has led to a preliminary consensus on the likely influence

of climate change on temperature and precipitation, and in turn on agriculture, forestry and terrestrial biodiversity on a global scale<sup>1</sup>. Marine ecosystems have not been considered to the same extent, and thus there is little predictive ability regarding the effects of global climate change on marine biota<sup>2–4</sup>.

Marine ecosystems yield 53 million tonnes (t) of food per year, and another 22 t is annually reduced to meal and oil<sup>5</sup>. Marine fisheries directly employ eight to ten million people, and support many more through food processing and distribution, equipment manufacture and repair, and other ancillary activities. Furthermore, in a number

of developing countries, fisheries provide a large fraction of the average daily protein intake<sup>5</sup>, making food sources from the sea difficult to replace. For these reasons, developing an adequate understanding of the effects of global climate change on the marine ecosystem is imperative.

This review combines predictions derived from atmosphere–ocean modeling with descriptions of the effects of both paleoclimatological temperature change and more recent transitory climatic effects such as El Niño to offer a synoptic view of the expected effects of global warming on the ocean ecosystem.

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## Physical effects

### *Predictions from modeling*

A lack of knowledge about how projected anthropogenic increases in radiatively active gases such as CO<sub>2</sub> will interact with the ocean remains the major obstacle to predictions of the manner and extent that ocean temperature, current patterns, and stratification will be affected by global change<sup>3,6</sup>. The best estimations of climate change effects on the ocean derive from general circulation models (GCMs), the most advanced of which combine atmospheric simulations with oceans containing complex descriptions of thermohaline mixing<sup>7</sup>. While GCMs offer the best forecasts of physical changes in the ocean, further refinements are needed to overcome present limitations. These include low resolution and oversimplification of geographical features<sup>6,8</sup>, unrealistic descriptions of climatologically important processes such as thermohaline mixing<sup>6,9</sup> and cloud cover<sup>7</sup>, exclusion of biological and chemical processes that affect CO<sub>2</sub> flux on longer time scales<sup>6,9</sup>, and the inability to run coupled oceanic-atmospheric GCMs synchronously without *ad hoc* correction factors<sup>7</sup>. Furthermore, GCMs can provide no information on small-scale short-lived physical changes in the upper 200 m of the ocean, where most marine organisms occur.

Despite these restrictions, GCMs do make a number of practical global-scale predictions, which biologists can use to forecast how climate change may affect marine communities. A commonly cited scenario is that a doubling of CO<sub>2</sub> from preindustrial levels will result in an increase in atmospheric temperatures of 2–4°C at the Equator, and 6–9°C at higher latitudes (50–70 degrees latitude north and south)<sup>10</sup>. In comparison, the Intergovernmental Panel on Climate Change recently has predicted<sup>11</sup> that global mean surface temperature change will lie in the range of 1.5–4.5°C. Although there are disparities among predictions of absolute temperature change, there is agreement that these changes will directly affect the oceans through latitudinal and vertical shifts in water temperature<sup>10</sup>, and will indirectly influence currents and mix-

ing through changes in atmospheric wind patterns and velocities<sup>9</sup> and storm track patterns<sup>12</sup>. However, it may not be possible accurately to predict regional temperature changes from these global-scale forecasts. For example, Bakun<sup>13</sup> suggests that global warming may decrease surface water temperatures along the west coast of the USA as a result of an increase in wind-driven upwelling.

Other predicted global-scale changes include increased precipitation around the equator and at high latitudes, which will cause the salinity (and thus density) of the mixed layer in these areas to decrease<sup>14</sup>. Reduced salinity, coupled with a reduction in wind-driven mixing due to smaller latitudinal temperature differences, will lead to increased mixed-layer stability at higher latitudes<sup>1</sup>. Also, because dissolved CO<sub>2</sub> (and consequently H<sub>2</sub>CO<sub>3</sub>) in the ocean will increase, the pH of surface waters is expected to drop by 0.3 (corresponding to a doubling of H<sup>+</sup> ions)<sup>12</sup>. Finally, sea level is expected to rise approximately 0.5 m by the year 2100 (Ref. 15) as a result of thermal expansion of sea water and increased ice melt; this may lead to a drastic reduction in size and biodiversity of coastal habitats<sup>16</sup>. While each of these physical changes can be expected to impact on marine biological processes, we will focus on two major factors: temperature change and increased mixed-layer stability.

### *Predictions by analogy*

In addition to modeling, global change effects can also be examined through analogy with past climate fluctuations. Climatic instability is the rule rather than the exception in the Earth's history, and the effects of longer-term climatic shifts on the ocean are often revealed in sediment cores. Using such cores, Romine<sup>17</sup> determined distributions of eastern Pacific radiolarian assemblages over the last 127 000 years, and correlated these with modern distributions to infer climatically driven movement of water masses. From the altered positions of these water masses, she deduced that during the last glacial period, from 36 000 to 18 000 years BP, trade winds were more

intense than at present, and that the northeast trade winds shifted to the south during periods of ice sheet growth. During periods of warming, the northern subtropical water mass and its associated fauna in the eastern Pacific moved northward.

Romine also found an interglacial reduction in productivity along the west coast of the Americas, from which she inferred a decrease in upwelling due to diminished wind stress. This is in accord with Müller and Erlenkeuser<sup>18</sup>, who found sedimentary evidence for increased upwelling during glacial stages. Their results indicate that primary production off north-west Africa during these periods was 2–3 times greater than it is presently. They concluded that this was 'the result of intensified upwelling as a response to a general increase in atmospheric and oceanic circulation'.

Extrapolation of these findings to the question of future global warming suggests that the latitudinal temperature gradient will decrease, and this will cause a reduction in the strength of the subtropical gyres; a concomitant shift in the trade winds will produce a poleward displacement in sub-equatorial water masses. It is also likely that reductions in wind stress will diminish upwelling.

The causes and timescales of previous climatic fluctuations are, however, different from the predicted anthropogenic change<sup>13</sup>. Thus, direct extrapolation may not be entirely accurate. Furthermore, the above data relate to glacial-interglacial changes, as opposed to the expected change from an interglacial to an 'enhanced interglacial'<sup>19</sup>.

The El Niño phenomenon is another more transient shift in ocean circulation, also caused by fluctuations in trade wind strength. During these events, warm nutrient-poor subtropical waters flood poleward along western continental margins, affecting the indigenous temperate and even subarctic marine communities. The inhabitants of these ecosystems experience two major stressors: increased competition from subtropical forms migrating with the inflowing warm water, and reduced resources resulting from a decrease in nutrient levels<sup>20,21</sup>.

During the 1982–83 El Niño, one of the most severe recorded, water

temperatures off California increased by over 2°C in both summer and winter<sup>22</sup>. This brought a massive influx of subtropical species; at least 13 were collected significantly farther north than their previously recorded range, while 18 species of invertebrates and 38 species of vertebrates were reported to have increased in abundance in the northern parts of their ranges during this time<sup>23</sup>. The influx of warm subtropical waters also reduced nutrients in the mixed layer, causing a massive decline in primary productivity. Zooplankton biomass, an indirect measure of primary productivity, was lower in 1982–83 than during any previous recorded year off California<sup>22</sup>; reduced zooplankton stocks were also recorded as far north as British Columbia<sup>23</sup>. Similarly, during past Benguela Niños (events climatically analogous to El Niños but occurring off the west coast of southern Africa), primary productivity has fallen by more than two-thirds<sup>3</sup>, thereby seriously affecting each level of the trophic chain from zooplankton to sea birds.

The effects of these stresses are economic as well as ecological. During the 1982–83 El Niño there was a large decline in coastal fisheries catches; fish catch per unit effort off California was reduced by almost 20% (Ref. 24), and the overall cost to North American fishermen was between \$200 million and \$270 million<sup>12</sup>.

In summary, both paleoclimatological and El Niño data suggest that anthropogenically induced warming may be accompanied by a diminution of trade wind intensity, a reduction in wind-driven upwelling and a poleward shift of sub-equatorial water masses and their resident biota. All of these changes will potentially lead to a decrease in biological productivity, especially along western continental margins.

#### The upper Pleistocene north-east Pacific as a global change model

Temperature change associated with the last glacial period, at a maximum 18 000 years ago, was responsible for displacement of marine species and whole communities latitudinally on the western margin of the North American continent. Moore *et al.*<sup>25</sup>, using coccolith, foraminiferan, diatom and radio-

larian core data, compared sea surface temperatures (SSTs) 18 000 years ago with SSTs at present. They showed that SSTs off southern California and Baja California at that time were 2°C cooler during the summer and over 4°C cooler during the winter than they are now (Fig. 1).

These temperature shifts profoundly influenced the biota of the California Current. Hubbs<sup>26</sup> showed that in historic times there have been shifts in the northern distribution of fishes on the California coast associated with warmer climatic conditions. Further, he suggested that the presence of a number of northern relict species in the upper Gulf of California was the result of Pleistocene cooling – which drove species south – and subsequent warming – which trapped them in the Gulf as they moved north. Present<sup>27</sup> supported this hypothesis with a list of 32 species thought to have such disjunct distributions.

Addicott<sup>28</sup>, who examined late Pleistocene mollusk assemblages in central California and Oregon, found conclusive evidence that marine biogeographic provinces were further south during this time. However, his evidence suggests that temperature changes were not so great south of Point Conception. Addicott felt that the southward shift of biotic communities was partly due to direct climatic cooling of temperate and sub-arctic surface waters, but was also affected by increased upwelling north of Point Conception. This explained the large southern shift in the cool temperate Oregonian province, which was greatly affected by upwelling, and the smaller shift in the warm temperate Californian province south of Point Conception (Fig. 2).

From comparisons of central Californian Upper Pleistocene assemblages with modern homologs, Addicott also determined that water temperatures during this period were approximately 2°C cooler in the summer and 4°C cooler during the winter than at present. The level of agreement between Addicott's Upper Pleistocene winter and summer temperature estimates and those of Moore *et al.* is gratifying, considering the inherent uncertainties in each technique – Moore's

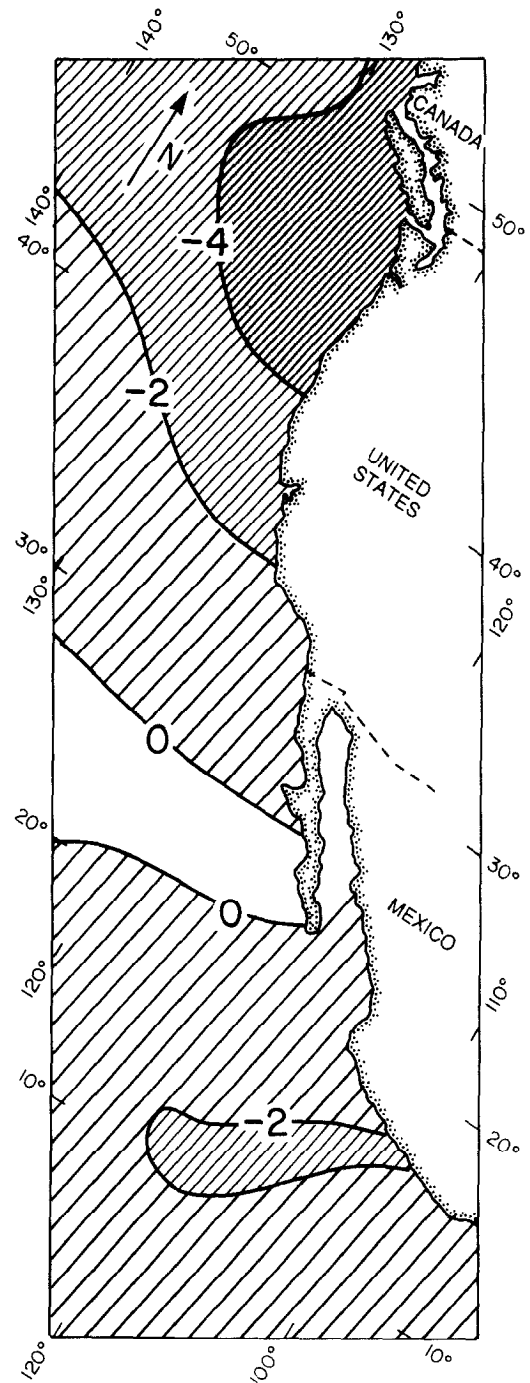


Fig. 1. Difference between February sea surface temperatures 18 000 BP and February sea surface temperatures at present on the west coast of North America. The tongue of cold water west of Mexico is due to the Tehuantepec upwelling. From Ref. 25, with permission.

data are limited by low resolution, while Addicott's temperature values apply only to the narrow intertidal–subtidal zone.

To summarize, Moore's core data, Hubbs' fish data and Addicott's mollusk data all indicate that water temperatures along the western coast of North America were significantly cooler during the late Pleistocene, and that biogeographic regimes moved south as a result. Subsequent warming caused a northward shift in species ranges; an additional warming may be expected to cause these ranges to shift further.

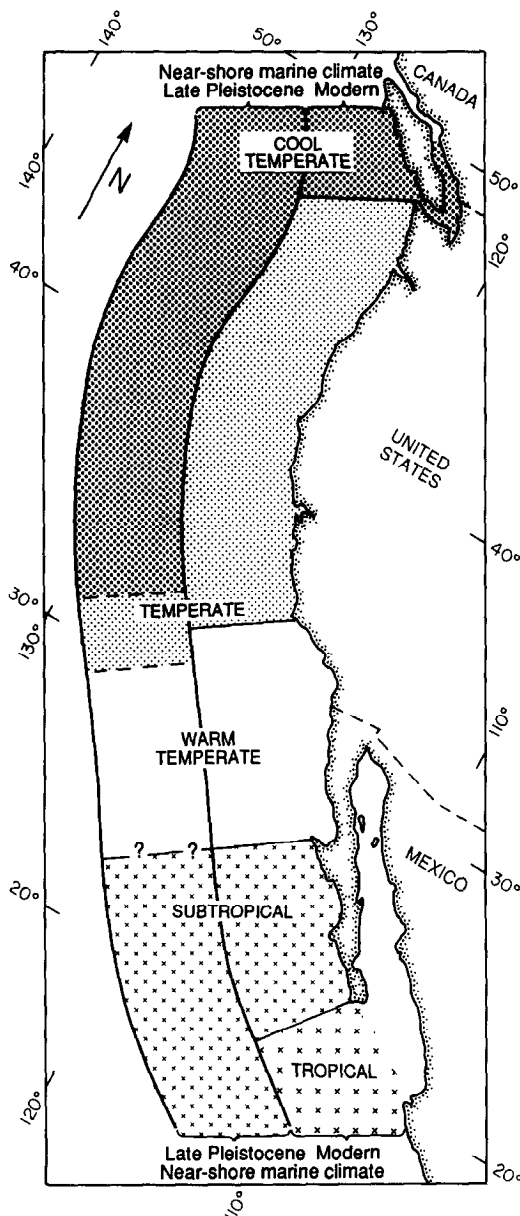


Fig. 2. Positions of biogeographic provinces on the west coast of North America currently and during the upper Pleistocene. From Ref. 28, with permission.

### Biological effects

#### Temperature effects

As temperatures change, not all populations will necessarily shift their ranges in response. Those that do stay in place may either adapt genetically or live under suboptimal conditions. Because most marine organisms are ectotherms whose body temperatures differ little from ambient temperature, pervasive adaptations at the physiological and biochemical level will be required among those that do not alter their ranges in order to cope with environmental warming. If climate changes are not too extreme, phenotypic adjustments may provide marine species an adequate means of dealing with environmental warming. These are likely to include changes in concentrations of enzymes of energy metabolism to compensate for temperature-

induced changes in metabolic rate<sup>29</sup>; shifts in the phospholipid composition of cellular membranes to affect retention of optimal membrane fluidity ('homeoviscous adaptation')<sup>29</sup>; and adjustments in concentrations of heat shock proteins to protect the cellular metabolic apparatus from heat damage<sup>30</sup>. These acclimatizations may allow species to survive in their current habitats despite an increase in ambient temperature.

Even though the physiological properties discussed above are highly plastic and can be modified to compensate for changes in temperature, other traits, notably protein thermal stability and thermal optima for function, are under rigid genetic control and cannot be modified through phenotypic adjustments. A sufficiently large shift in temperature will therefore cause these genetically fixed, nonacclimatizable traits to become dysfunctional. Thus, as temperature changes, it is likely that such traits will be altered by selection acting on genetic variability present in populations. That is, as temperature increases, genotypes from warmer areas of a species' range will gain a selective advantage over those from cooler areas. The presence of genetic variability within the species will thus allow some level of adaptation to changing temperatures.

Although data on this important process are sparse, studies of homologous forms of enzymes in fishes and invertebrates that are adapted to different thermal regimes suggest that changes in average habitat temperature of only a few degrees Celsius are sufficient to favor selection for adaptive differences in protein structure and function. Comparisons of lactate dehydrogenase (LDH) homologs of congeneric barracudas (genus *Sphyraena*) from tropical, subtropical and temperate regions showed the LDHs of species that varied in average habitat temperature by only 3–8°C were adaptively different in kinetic properties ( $K_m$  and  $k_{cat}$  values)<sup>31</sup>. Comparisons of LDH and other enzymes of latitudinally distinct populations of the eurythermal fish *Fundulus heteroclitus*, as well as studies of malate dehydrogenases of the archaeo-gastropod genus

*Haliotis* (abalone), also support the hypothesis that temperature differences of only a few degrees Celsius are adequate to favor adaptive modification in proteins<sup>32</sup>. Thus, groups occurring over a wide thermal range will generally have a broad pool of genetic variability from which to draw. However, if temperature change exceeds the thermal limit of the most warm-adapted genotypes in these taxa, then natural selection acting on population genetic variability will be ineffective in maintaining proteins with adequate thermal traits.

As temperatures exceed this threshold, adaptation will be possible solely through evolutionary processes such as amino acid substitution. From sequence analyses of barracuda LDHs, it appears that only a small number of amino acid substitutions, perhaps no more than one percent of primary structure, are sufficient to induce temperature-adaptive changes in these proteins. Nonetheless, with a unit evolutionary period (the time required for a one percent change in sequence) of approximately 13 million years<sup>33</sup>, LDHs and other proteins that evolve slowly may be unable to adapt with sufficient speed to compensate for predicted global warming.

Results from comparative protein biochemistry suggest three important methods of coping with temperature change. First, modest changes in climate due to global warming may induce physiological acclimatization without requiring alterations in genotype. Second, larger climate changes may confront organisms with temperatures at which their proteins no longer have optimal structural and functional properties. In this case, natural selection may favor the genotypes already present in the species which are more warm-adapted than those predominating before the climatic change. Third, as temperature change exceeds the ability of any existing genotype to cope, alterations in amino acid sequence may be necessary to allow survival of the species in its original habitat. Because of the slow rate of evolution in certain enzymes, genetically fixed, non-plastic features such as protein sequence may be of overriding importance in establishing the limits of thermal tolerance.

Species are not adapted to a particular absolute temperature, but to a certain range of temperatures. Accordingly, some species, such as polar fishes, are markedly stenothermal while others, including many temperate estuarine forms, are extremely eurythermal<sup>34</sup>. The extent to which each species can acclimatize to changing temperature – that is, its level of eurythermy – will play a role in determining how its range will be shifted or constricted, and how it will cope with new competitive pressures. Thus, the ability of each species to survive in the face of environmental temperature change is strongly dependent on that species' past thermal adaptations<sup>35</sup>. Temperature shifts will usually favor species more closely adapted to the new thermal regime (often immigrants), and will give eurytherms an advantage over stenotherms. Furthermore, indigenous stenotherms may be adversely affected by synergistic interactions between temperature increase and other climatically related physical changes such as increased suspended sediment load, short-wave radiation and salinity. Consequently, organisms adapted to a broader thermal range, including many temperate neritic forms, will gain an advantage over presumably more stenothermal subarctic and arctic forms. However, if water temperatures also become more equable in temperate areas, these forms may in turn face competition from the influx of a tropical biota; this occurred at the end of the Pleistocene, and probably resulted in a loss of biomass and diversity as some biogeographic ranges were compressed (see Fig. 2).

Redistribution as a result of thermal change will not be possible for all marine communities, however. Species may be restricted to suboptimal ranges because of geographical barriers. They may also be kept from shifting into thermally suitable areas, even in the absence of geographical barriers, owing to a lack of necessary physical resources such as appropriate substrate, nutrient levels or nursery grounds for larvae. Corals, a special case, will be greatly affected by an increase in SSTs because so many species currently exist close to

their upper thermal tolerances<sup>36</sup>. The severity and frequency of coral bleaching events has increased markedly over the last two decades, perhaps in response to warming<sup>37</sup>, and a predicted increase in SST of 1–2°C in the next 50 years will have significant effects on many coral species<sup>16</sup>. Regardless of taxon, restriction to suboptimal ranges may induce habitat reduction or even extinction through physiological stresses and competition from immigrants.

Distributional shifts in response to increased temperature may not necessarily be latitudinal, but may include vertical displacements to deeper, cooler waters<sup>1,26</sup>. Many marine species occur in shallow water, or even intertidally, in the cooler reaches of their ranges, but are found progressively deeper near the warmer limits of their distributions. In an analogous manner, as temperatures change in response to anthropogenic warming, the current shallow water populations of these species may retreat into cooler deep waters. Such submergence in response to global warming, however, may disrupt community-wide trophic interactions, including loss of prey species or introduction of competitors. It may also reduce the population size of the migrant group, because deeper waters will not support the same biomass as more productive surface waters.

Finally, temperature shifts may affect species through disruption of larval stages. Because most larvae are planktonic, their transport and dispersal by currents will be affected as the latter are strengthened or weakened by climate change. This will have a deleterious effect if individuals metamorphose far from appropriate substrate or feeding grounds. Also, spawning by many species occurs in synchrony with phytoplankton blooms, thus assuring food resources for growing larvae. As temperature and wind patterns alter the timing or location of both spawning and blooms, the synchrony critical to successful recruitment of future populations may be compromised<sup>12</sup>.

The above arguments indicate that reductions in absolute numbers, biomass or primary productivity of marine species due to climate change may become

common, and will have negative impacts both ecologically and economically. In certain areas, though, the opposite may occur. Increased temperature will raise metabolic rates, and if the organism's thermal maximum for growth is not exceeded – and sufficient nutrients are present – may lead to faster maturation and increased fecundity. Higher temperatures, especially when coupled with higher CO<sub>2</sub> levels, may also increase primary productivity. However, nutrient levels are subject to constraints that act locally, such as vertical mixing and terrestrial run-off. Thus, areas where these processes are expected to remain influential after global warming, including areas of continental shelf at high latitudes, are most likely to experience increased productivity.

#### Stratification effects

Stratification will be affected by global changes in parameters that directly alter mixed-layer stability (e.g. temperatures, wind stress and precipitation) as well as by local and regional influences such as submarine topography, terrestrial run-off and sea ice.

Increases in mixed-layer stability can, like temperature, have both positive and negative effects on marine biota. In some locations primary productivity is limited by vertical mixing due to wind stress and upwelling, which advects phytoplankton from surface waters. For example, Dickson *et al.*<sup>38</sup> have shown that changes in wind patterns in the North Sea lead to changes in timing and magnitude of phytoplankton blooms. They correlated weather data with productivity measurements from 1950 to 1980, and found that an increase in northerly wind stress during the spring months leads to a decrease in productivity, probably due to advection of phytoplankton below critical depth. Lange *et al.*<sup>39</sup> studied the relationship between diatom biomass and strength of upwelling off the California coast and found that as the California current, and thus upwelling and mixing, decreased in strength from 1954 to the present, the amount of diatom production also decreased.

Strong surface layer mixing can also reduce the number of planktonic

larvae surviving to metamorphosis. In areas where strong mixing is presently a limiting factor, an increased mixed layer stability resulting from climatic change will increase primary productivity and thus biomass of the community. Alternatively, areas presently having the level of mixing needed to bring nutrients into the mixed layer without advecting away too much of the planktonic community will be adversely affected by a climatically induced stability which reduces the surface concentration of nutrients<sup>1</sup>. The interaction among dinoflagellates, diatoms and trophic-chain length is one example of the effects of changes in mixed-layer stability. Because diatoms are larger than dinoflagellates, they form the base of a shorter, more efficient trophic ladder to economically valuable fish stocks. However, dinoflagellates are motile, whereas diatoms are not. Thus, in areas where vertical mixing occurs at low levels, dinoflagellates are more common because diatoms tend to sink away from the sunlit surface waters<sup>40</sup>. It follows that, in these areas, if mixed layer instability is moderately increased, diatoms will predominate and productivity will climb. Alternatively, as is predicted in most oceanic GCMs, an expansion of the stable mixed layer at higher latitudes will lead to a predominance of dinoflagellates, more trophic levels and reduced total biomass<sup>12</sup>.

It should be noted that the physical processes and interactions controlling primary production in the ocean are not well understood and the above scenarios cannot take into account all possible effects of climatic change. For example, while a moderate increase in mixed-layer stability may lead to maintenance of phytoplankton above critical depth, it may also lead to a decrease in mixing of nutrients from deeper waters. The result these competing factors will have on total primary productivity cannot be known without more accurate models which take into account idiosyncrasies of local environments.

# Conclusion

To predict more accurately how physical modifications in the ocean associated with global climate

change will affect marine biota, a number of improvements in GCMs are necessary. Neither the nature of vertical ocean circulation nor climatic effects such as cloud cover and heat transport are adequately understood. Also, the ability to realistically couple models of ocean and atmosphere must be improved to produce valid forecasts of climatic change.

This is not to say that biologists need only wait for physical modelers to produce more accurate predictions; there are many poorly understood biological processes which will influence in unknown ways the responses of the marine biota to global climate change. These include the extent of phenotypic plasticity, as well as the genetic variability available to species as they adapt to climate change; the effect of loss or constriction of susceptible and perhaps keystone species on community structure; and the role changes in geographic distribution will play in larval recruitment, foraging, competition and predator-prey relationships.

Although this list of physical and biological uncertainties is daunting and by no means complete, it is no excuse for inaction on the part of the scientific community. The ramifications of climate change on terrestrial and, as outlined in this review, marine biota are great. Thus, we cannot afford the luxury of waiting for near-certainty in our physical or biological predictions before we study their economic and ecological consequences.

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During the late 1960s and early 1970s the accumulating evidence of magnetic orientation forced the conclusion that the orientation of migratory birds and homing pigeons is based upon multiple stimuli. 'Cue-conflict experiments' have provided a powerful means of asking how these directional cues relate one to another. The weight of evidence suggests that in short-term orientation decision making, magnetic cues take precedence over stars, and visual information at sunset overrides both these stimuli. Recent experiments point to polarized skylight patterns as the relevant cue in dusk orientation. Although cue-conflict experiments have now been performed on a diversity of species, generalizations are weakened because of differences in experimental design, in the cues examined and in our ability to manipulate those cues. There remains a need for carefully designed comparative studies.

Until about twenty years ago, the general consensus was that compass orientation in birds was based on a unitary mechanism: night migrants relied upon a star compass, and diurnal migrants and homing pigeons used a time-compensated sun compass. Evidence from radar surveillance that migratory birds were often well oriented when flying under solid overcast skies, and evidence from lab studies that several species possessed a magnetic compass and that visual stimuli at sunset influenced the orientation of obligate night migrants, forced a sea change in thinking about this problem. The notion that we were searching for *the* mechanism of orientation was replaced by the hypothesis that birds possess interrelated back-up orientation systems, a view codified in seminal reviews by Keeton<sup>1</sup> and Emlen<sup>2</sup>.

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## Orientation Cues Used by Migratory Birds: A Review of Cue-Conflict Experiments

Kenneth P. Able

There is now substantial evidence that migratory birds use the earth's magnetic field, stars, patterns of polarized skylight and perhaps the sun as sources of compass information<sup>3</sup>. The existence of multiple orientation capabilities raises interesting questions; at the same time it imposes substantial problems in the design of experiments. Many early experiments confused necessary and sufficient conditions for orientation: given multiple capabilities, the persistence of orientation in the absence of a given stimulus does not demonstrate that the stimulus may not be used when present. The bird may simply have switched to some other cue.

Exploration of the hierarchical relationship among orientation cues in migratory birds has involved two approaches: (1) the development of orientation behavior in young birds has been studied by manipulating the experience of hand-raised birds during the first months of life<sup>4</sup>; and (2) the orientation of mature birds has been examined in 'cue-conflict' experiments. It is this latter paradigm that I examine here.

### Cue-conflict experimental design

As in most experimental studies of migratory orientation, cue-conflict experiments depend upon the fact that migratory birds exhibit oriented hopping when placed in circular cages of several types<sup>5</sup>. The general cue-conflict paradigm consists of presenting a bird (usually simul-

taneously) with two or more relevant orientation cues. One or more of the directional cues is then manipulated and the bird's orientation is monitored for any change. From a series of such experiments, one attempts to infer the hierarchy among the orientation stimuli. A typical experiment might involve placing an orientation cage surrounded by electric coils outdoors under the clear night sky. In this situation, a bird in the cage will have access to two known orientation cues, the stars and the magnetic field. The coils can be used to shift the direction of magnetic North so that magnetic compass directions differ from those indicated by the stars. If, compared to controls tested in an unshifted magnetic field, the birds experiencing the cue conflict changed direction as predicted by the magnetic field shift, one would conclude that in this situation magnetic orientation took precedence over orientation by the stars.

The ability of this approach to reveal insights into the behavior that would occur under natural conditions depends on the degree to which experimenters can create and manipulate the putative stimuli used in orientation. Some of the relevant cues are more amenable than others to realistic manipulation. It is, for example, technically straightforward to produce artificial magnetic fields that precisely mimic that of the earth. On the other hand, manipulations of visual orientation