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The potential impacts of global climate change on marine protected areas

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Contents

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Abstract

The potential effects of global climate change on marine protected areas do not appear to have been addressed in the literature. This paper examines the literature on protected areas, conservation biology, marine ecology, oceanography, and climate change, and reviews some of the relevant differences between marine and terrestrial environments. Frameworks and classifications systems used in protected area design are discussed. Finally, a framework that summarizes some of the important oceanographic processes and their links to the food chain are reviewed. Species abundance and distribution are expected to change as a result of global climate change, potentially compromising the efficacy of marine protected areas as biodiversity conservation tools. This review suggests the need for: further interdisciplinary research and the use of linked models; an increase in marine protected areas for biodiversity conservation and as research sites for teasing apart fishing effects from climate effects; a temporally responsive approach to siting new marine protected areas, shifting their locations if necessary; and large-scale ecosystem/integrated management approaches to address the competing uses of the oceans and boundary-less threats such as global climate change and pollution.

Introduction

There is scientific consensus that global warming is real (Schneider, 1993) and that one of the factors forcing climate change is the anthropogenic addition of greenhouse gases to the atmosphere (Houghton et al., 2001). Scientists have utilized models referred to as general circulation models to examine the physical and chemical interactions between the oceans, atmosphere, biota, ice, and land at a large scale (Root and

Schneider, 1993). General circulation models project future climate by comparing simulations with and without changes in concentration of greenhouse gases such as carbon dioxide (CO_2). Many such models have examined a likely scenario of a doubling of CO_2 over 100 years, and found an increase in temperature of 1.5–4.5 °C. This rate of increase would exceed any seen in the last 10,000 years (Houghton et al., 1996). Although the global average surface temperature increased during the 20th century by 0.6 °C ± 0.2 °C (Houghton et al., 2001), warming is not occurring in all regions of the globe, thus the projected change in climatic conditions will be referred to in this paper as global climate change.

Studies on global climate change and the marine environment have concentrated on the 'biological pump,' or the ocean's role in sequestering carbon dioxide (e.g., Berger et al., 1989; Denman et al., 1996; Mann and Lazier, 1996). Few published papers in recent years examine global climate change and its effects on marine ecosystems, and there is limited mention of marine protected areas in the context of global climate change. This paper examines and anticipates how global climate change might affect the distribution and abundance of species. Will the features upon which marine protected area site selections are based potentially shift in location with the impacts of global climate change?

The rate of loss of biodiversity has been identified by many authors as cause for alarm (Bedward et al., 1992; Norse, 1993; Walker, 1995). Protected areas and parks have been used as tools for biodiversity conservation for some time. The theory and practice have evolved from focusing on individual protected areas to networks of protected areas that consider the surrounding environment or the 'matrix' (Crow and Gustafson, 1997) and sufficient connections or corridors between the areas (Noss and Cooperrider, 1994; Noss, 1995). Although the development of marine protected areas and their conceptual frameworks lag those for the terrestrial environment by approximately a century (Norse, 1993; Day and Roff, 2000), there has been increasing attention paid to the need for networks of no-take reserves and representative marine conservation networks.

Protected areas were created largely as a response to anthropogenic disturbance, yet one of the largest scale anthropogenic disturbances, global climate change, is only now being considered in the context of protected areas. Solomon (1994) noted that most parks are designed assuming environmental stability and have goals to preserve specific biotic communities in perpetuity. Scott and Suffling (2000) recently conducted a study using general circulation models to examine four climate change scenarios of carbon dioxide doubling in 100 years. They estimated that only approximately one quarter of the current parks would remain in the same unit of classification system (ecoclimatic provinces (Rizzo and Wiken, 1992) or vegetation formations (Lenihan and Neilson, 1995)). Scott and Suffling state: "Climate change represents an unprecedented challenge for Parks Canada ... {It is} simultaneously a threat and opportunity to different species and ecological communities within the national parks system ... Current ecological communities will begin to disassemble and 're-sort' into new assemblages. The dynamic biogeography brought about by global climate change will effectively alter the 'rules' of ecological conservation."

This paper reviews some of the relevant and current thinking on protected areas, conservation biology, marine ecology, and climate change literature, and investigates whether and how static notions of protected area designation, which originated in the terrestrial environment, are appropriate for the marine environment, or even on land, given the anticipated impacts of global climate change over the next 100 years. The relative dynamism of the marine environment is emphasized, for example, how masses of water containing biological communities can shift in location over relatively short time scales (decadal or less) (Mann and Lazier, 1996; Thomson and Galbraith, 2001). This review focuses mainly on bottom-up oceanographic processes as controls or drivers of species' distribution and abundance in the pelagic marine environment. Bottom-up processes cause physical forcing of biological processes through impacts on primary production (Longhurst, 1998). Species at the top of trophic structures exert strong controls on ecosystems, and will be affected by global climate change in complex ways (Ray et al., 1992). These top down processes are also likely to be important (Ray et al., 1992) and will need to be addressed by others in the future. In this paper, marine and terrestrial environments are compared to highlight fundamental differences, and then frameworks and classification of protected areas are reviewed. Finally, a conceptual framework is presented which serves as a basis for discussion of some of the likely impacts of global climate change on pelagic biodiversity.

Key differences between terrestrial and marine environments

The marine environment differs from the terrestrial environment in a number of fundamental ways relevant to the anticipated effects of global climate change on marine protected areas. The key differences in the environments stem from the characteristics of the medium which holds or contains most of the respective biodiversity. In the terrestrial environment, most biodiversity lives at the interface of the geological substrate and the air. Most marine biodiversity lives in a liquid medium, water, which is 60 times more viscous and 850 times denser than air (Norse, 1993). The density of water provides buoyancy, which allows for active swimmers, or nekton, to spend most of their time in the water column, compared to "temporary aero-nekton" such as birds, bats and dragonflies (Norse, 1993).

A related result of these large differences in viscosity and density is that large supporting structures, characteristic of terrestrial plants such as trees, are not necessary in marine environments (Steele, 1985; Norse, 1993). Tiny single-celled plants, the phytoplankton, can therefore be primary producers while remaining suspended in the water column for some time, depending on their size and water movements (Day and Roff, 2000). Planktonic primary and secondary production along with reproductive propagules and nutrients are transported by water movements such as currents and upwelling. This degree of mobility of key ecosystem components has no parallel in the terrestrial environment even though there is some wind transport of reproductive propagules in the terrestrial environment (Strathmann, 1985; Norse, 1993); thus, Day and Roff (2000) referred to the pelagic realm as a qualitatively unique environment. Most marine species of fish and invertebrates have pelagic larval stages (Roughgarden et al., 1988), and a much larger proportion of marine species than terrestrial species disperse before they attain the adult phase (Strathmann, 1985; Norse, 1993). A pelagic life history permits even sessile species to disperse long distances to habitats that are less densely populated (Strathmann, 1985).

Pelagic life history stages may disperse actively or passively. In either case, dispersal can be further facilitated by the relative absence of physical barriers to vertical and horizontal migration in the marine environment (Hamner, 1988). Oceans are interconnected while many landmasses are not (Norse, 1993). Thus, on average, marine species have larger ranges and sometimes dispersal spans huge geographic distances (Allison et al., 1998).

Terrestrial ecologists generally study land as a two-dimensional, horizontal mosaic (García-Moliner et al., 1993). This is related to the far greater depth of the inhabited ocean compared to the terrestrial biosphere (almost 4,000 m compared to an average of 20 m respectively) (Norse, 1993). García-Moliner et al. (1993) contrast the terrestrial concept of a "patch" as two-dimensional and discontinuous with the "patchiness" of "spatio-temporal scales of water movement" in pelagic environments. In the latter case, the combination of fluid dynamics and primary producers and herbivores with very short generation times means that in areas of higher concentrations of nutrients, patches of plankton can be formed, exploited, and dispersed in short time scales. Longhurst (1998) refers to this as the "fierce coupling" of the marine environment. Phytoplankton concentrations can shift by kilometers from day to day and complicate attempts to draw fixed boundaries around marine biogeographic provinces (Norse, 1993). The rapid response time and mobility of plankton within currents is in stark contrast to the turnover rate of a forest, comprising the longest-lived terrestrial organisms; thus, the ability of forests to respond and move with ambient temperature change is orders of magnitude slower (Davis, 1989; Steele, 1991). Changes in nutrient supply as a result of global climate change might elicit marine biological responses on a time-scale of decades rather than centuries (Denman et al., 1996).

Finally, the greater heat capacity of water than that of air means that sudden temperature changes, such as occur on land, do not occur. (Steele, 1985). As a result, marine species that inhabit more stable environments such as the tropics may live close to their upper thermal limit (Ray et al., 1992; Norse, 1993). Therefore, even small increases in temperature as a result of global climate change could significantly affect these and other stenothermal species.

Protected area networks: Frameworks and brief review

Government agencies have particular mandates that influence the determination of the goals and criteria for selection and design of marine protected areas (Day and Roff, 2000). Marine protected areas can be directed at conserving overall biodiversity or at some portion of biodiversity (such as commercial fish species or endangered species). If the key goal is the conservation of biodiversity as a whole, the current approach is generally the development of "representative" protected areas (Noss and Cooperrider, 1994; Hummel 1995; Interim Marine and Coastal Regionalisation for Australia Technical Group, 1998; Day and Roff, 2000). Systems of protected areas are representative if they "sample the full range of environmental gradients, or habitat types, at a given scale" (Day and Roff, 2000) or "encompass the range of regional variation in species or natural environments" (Bedward et al., 1992). Day and Roff (2000) note the need for a "systematic, science-based framework within which to choose marine protected areas and assess progress toward a representative system." They contrast this to *ad hoc* approaches to site selection based on local biological characteristics or scenic features (Day and Roff, 2000). Protected areas have also been focused on saving specific "glamour species" (Scott et al., 1993). Many authors note that a species-specific approach to protecting endangered species is costly and does not protect the myriad of other species, habitats in which they live, nor the ecological processes on which they depend (Belbin, 1993; Scott et al., 1993; Walker, 1995; Day and Roff, 2000).

Scientists in the areas of biogeography and vegetation analysis have developed frameworks to classify terrestrial ecosystems (Westhoff and van der Maarel, 1980; Meidinger and Pojar, 1991) as have marine scientists and oceanographers (Harper et al., 1993; Interim Marine and Coastal Regionalisation for Australia Technical Group, 1998; Longhurst, 1998; Zacharias et al., 1998; Day and Roff, 2000). Protected areas researchers have in turn utilized, adapted or created new classification systems to assist in the process of identification of representative areas, habitat types, and communities. The assumption is that key abiotic and biotic variables "control" the distribution of animal and plant species (Belbin, 1993) and, furthermore, that species assemblages can be predicted on the basis of these features (Noss, 1995; Day and Roff, 2000).

These schemes divide the natural environment into units of particular ecosystems, habitat types, or other features. For example, cluster analysis has been used to identify zones of relatively high similarity, as was done by Belbin (1993). The Nature Conservancy (TNC) created a "coarse and fine filter" approach to capture different levels of biodiversity: community-level and species-level inventories, respectively (Noss, 1987). The coarse filter employs classifications for plant and natural communities. Natural communities are habitat-based and may combine species, substrate, soil, and other features, e.g., pine rockland and mesic flatwoods in Florida (Noss, 1987). According to TNC, species such as narrow endemics or wide-ranging mammals, which are not included with the coarse filter can be caught in the fine filter (Noss, 1987). Gap analysis is a related method that combines layers of data using a Geographic Information System (specifically vegetation types and various indicator species) and uses the notion of representative ecosystem units (Scott et al., 1993).

World Wildlife Fund Canada (WWF) has proposed that a classification framework of "enduring features" such as topographic relief and the origin and texture of parent materials and soil (Peterson and Peterson, 1991) should be the basis for representation of Canadian natural regions in a protected area network (Noss, 1995). The assumption is that these features are more stable in their distribution than vegetation and other biotic elements, and yet reflect biological features. Similarly, Day and Roff (2000), in a report for WWF, have created a hierarchical classification for marine conservation that uses enduring and recurrent geophysical and oceanographic features. Other systems have used a combination of biological and physical attributes to create hierarchies of classification (Harper et al., 1993; Interim Marine and Coastal Regionalisation for Australia Technical Group, 1998; Zacharias et al., 1998) for use in the designation of representative marine protected areas.

Additional levels of information, criteria and decision rules are generally part of determining representative protected areas. These facilitate the actual selection of units or portions of the units for incorporation into a representative protected area network, and help to ensure a more complete coverage of biodiversity. They are essentially a "fine filter" even where this terminology is not used, as in Day and Roff (2000). Any features or criteria proposed for selection of single marine protected area could also be used as a fine filter in a representative network. Marine examples include spawning or feeding areas of particular species, areas containing high biodiversity, rare or endangered species or their habitat, and areas of high productivity (Fisheries and Oceans Canada and B.C. Land Use Coordination Office, 1998).

Bedward et al. (1992) developed a computer program, CODA (Conservation Options and Decision Analysis), which is interactive and utilizes iterative selection algorithms to create alternative reserve configurations. Targets and objectives are set that reflect the priorities of those participating in the exercise. An example might be to represent each rare species and significant community in at least three catchments. The example in their paper utilizes two types of data: environmental domains (a kind of representative classification unit) and known locations of species and plant communities of particular significance (essentially coarse and fine filters). CODA is an interesting and useful tool because of its explicitness, simplicity, and flexibility.

Some of the elements and approaches to protected area design are conceptualized in Figure 1. A spectrum of approaches to protected areas is given, ranging from representative marine protected area frameworks that utilize classification schemes and physical data only, through frameworks that combine biological and physical data using indicator species, to individual marine protected areas that are focused on particular species. Note that "coarse" and "fine" filter refer to assumptions about the relationship between environmental variables or indicators, and species' biology. At the coarse level, which can be applied over a range of spatial scales, we assume that environmental variables dictate species' distribution, and at the fine level we acknowledge that reality is more complex. Frameworks that focus exclusively at either end of the spectrum will probably not effectively accomplish biodiversity conservation.

These frameworks are applied under the assumption that critical biological determinants of species distribution will not change over the short-term (Solomon, 1994). Furthermore, protected areas currently have static boundaries, presumably to accommodate political and social systems or the necessity for user groups to identify boundaries and in so doing, obey existing regulations. Global climate change appears to challenge these static perspectives within a human time-scale, i.e., 50–100 years (Scott and Suffling, 2000).

Hunter et al. (1988) noted that biological communities are ephemeral. Palaeoecological research has shown that range contractions of various plant taxa were highly individualistic during past climatic changes. With the predicted rates of climate changes, communities will disassemble and species will shift their ranges at different rates (Peters and Darling, 1985; Hunter et al., 1988). Thus, the assumption that communities are tightly co-evolved units is clearly challenged (Hunter et al., 1988). Hunter et al. (1988) suggest that in using a coarse-filter approach, physical variables and environments should be the main focus, rather than the distribution of modern communities. WWF's approach using enduring and recurrent features attempts to address these concerns.

In Day and Roff's (2000) marine classification, "recurrent oceanographic features or processes" are defined as those that "may reoccur in a predictable fashion in the same geographical area." However, several of the criteria (other than slope and benthic substrate) are enduring or recurrent, in that areas with these characteristics may continue to exist, but not in the same geographical location. These include temperature, amount of sea-ice cover, and degree of vertical stratification. As further discussed in the next section, the marine environment will respond more rapidly to global climate change than will the terrestrial; thus Day and Roff's (2000) seascapes will actually shift in location as both global climate change and marine protected area planning continue to unfold. The framework actually has built-in responsiveness to environmental change.

Methods of exploring potential impacts of global climate change

Several methods of exploring possible impacts of climate change in the pelagic marine environment include historical analogy (Murawski, 1993), including palaeoecological data (e.g., Baumgartner et al., 1992); the use of recent data (generally less than 100-year old datasets: the "short-term data" of Rastetter (1996) and "the observed record" of Easterling et al. (2000)); modeling (DeAngelis and Cushman, 1990); or a combination of these approaches (Frank et al., 1990). It is worth noting that the tool kit chosen depends to some extent on the researchers' expertise or available data. Murawski (1993), for example, had bottom-trawl survey data dating back to 1967, which allowed him to examine the distribution of fish with changes in sea temperature and to attempt to extrapolate to potential impacts of global climate change.

In recent years, studies have examined inter-annual and inter-decadal climate variability and elaborated the complex connections between ocean, atmosphere, climate, and effects on productivity of marine systems (Graham, 1994; Francis et al., 1998; Sugimoto and Tadokoro, 1998; Chavez et al., 1999). Periods of climate variability can be used as short-term data

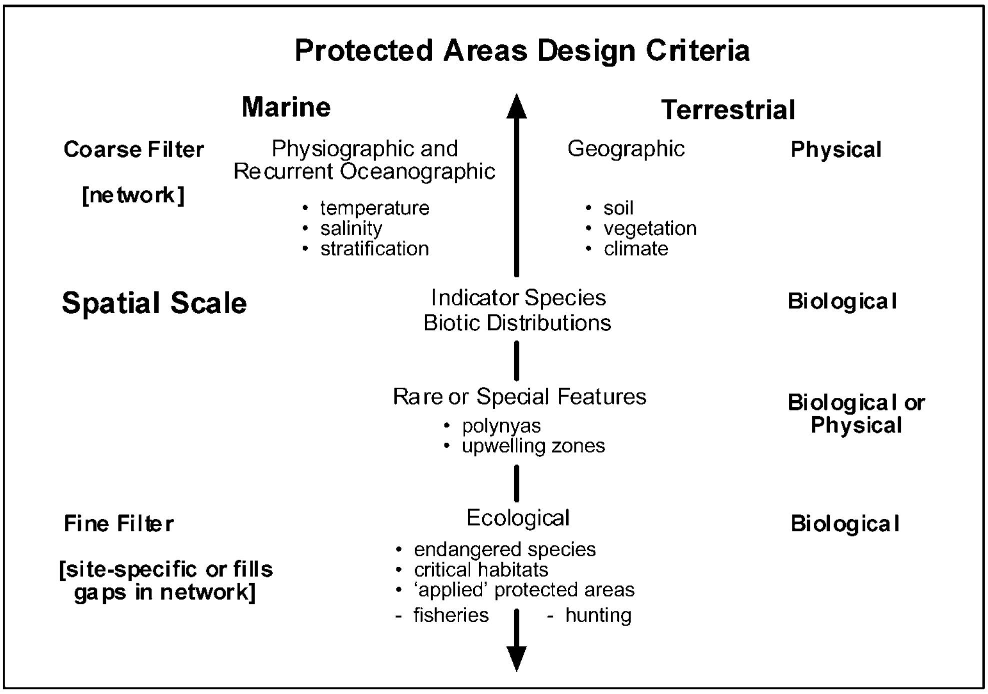

Figure 1. A schematic summarizing various approaches and criteria for selection of protected area sites and networks is shown: a continuum from mainly physical, large scale, coarse filter approaches to network design, to mainly biological smaller scale, fine filter approaches to site selection.

(Rastetter, 1996) to investigate local or regional impacts of global climate change. The El Niño-Southern Oscillation phenomenon is complex, and clearly summarized in Mann and Lazier (1996). Changes in pressure between the eastern and western sides of the Pacific Ocean basin cause abrupt warming of sea-surface temperature, among other changes. Upwelling still occurs but the water is much warmer and lower in nutrients; thus a sharp decline occurs in productivity and biomass at all trophic levels (Ray et al., 1992; Mann and Lazier, 1996). The term "regime" describes a multiyear set of ocean conditions, reflected in periods of linked recruitment patterns of fish populations or physical variables (Beamish et al., 1999). The term "regime shift" refers to a synchronous change in these conditions. Although this term was not used by Frank et al. (1990), they referred to decadal warming and cooling periods in the northwest Atlantic Ocean. Hill (1995) noted that the 50-year-old warming trend in the California Current provides an opportunity to study how global climate change may affect marine ecosystems. El Niño-Southern Oscillation and regime shifts occur on shorter time scales: inter-annual and decadal, respectively, and the factors that drive them differ considerably from global climate change; thus caution must be exercised in making predictions by using trends based on these phenomena (Bakun, 1990; Rastetter, 1996). In fact, there is evidence that decadal-scale fluctuations pre-date anthropogenic global warming (Baumgartner et al., 1992). It is therefore necessary to distinguish signals related to global warming from other kinds of variability, whether inter-annual or decadal, or changes induced by fishing (Frank et al., 1990; Paine, 1993; Easterling et al., 2000). Frank et al. (1990) noted that the effects of global climate change on large-scale climatic fluctuations such as El Niño-Southern Oscillation are unclear. Barry et al. (1995) atributed the establishment of typically southern species in a more northern site of the California coast to El Niño-Southern Oscillation events acting in conjunction with global climate change.

Hinch et al. (1995) coupled simulation results from a general circulation model to a simplified mixed-layer ocean model to examine secondary production, salmon growth, and energetics. Tynan and DeMaster (1997) used an approach which combined short-term physical data with predictions from general circulation models to suggest that trends of decreasing extent of sea ice and warming in the past 20-30 years in the Arctic may be a result of global climate change. Frank et al. (1990) typify this combined approach, used in most biological papers on the subject. Specifically, Wright et al. (1986), a team of physical oceanographers, had utilized outputs from general circulation model models to predict the most likely scenarios of oceanographic conditions in the Canadian northwest Atlantic. Frank et al. (1990) combined these scenarios with published findings on the effects of temperature and related changes in marine biota to outline the most probable impacts on fisheries. Their paper reviews a large number of studies that showed direct and indirect relationships of climate on physical and biological processes.

Global climate change impacts on biodiversity and ocean processes

A framework that summarizes some of the major pathways of impacts of global climate change on marine biota is presented in Figure 2. A review of selected literature pertinent to this framework is followed by a discussion of currents and retention. This framework is based on oceanographic processes that cause physical forcing of biological processes (Longhurst, 1998). Bakun (1996) refers to a "fundamental triad," three types of oceanographic processes that provide habitats for coastal pelagic fishes: enrichment, retention, and concentration processes. Nutrients are necessary for phytoplankton production and are made available through various types of turbulent or mixing processes that occur in upwelling, or tidally-influenced, areas or fronts. (Fronts are zones where two masses of water come together, and in doing so, generate and concentrate high productivity. Shelf-tidal fronts are the zone where tidally mixed waters meet stratified waters (Mann and Lazier, 1996).) Larvae need to be retained, generally by currents, at locations where conditions such as food and temperature are suitable. Finally, food needs to be concentrated enough for feeding to be efficient.

Primary production and water column stability

Figure 2 focuses mainly on the factors that influence primary production and, therefore, the rest of the food chain, i.e., enrichment processes as well as the concentration processes of frontal formation and water column stability. Arrows show the direction of influence of one factor on another. Although feedbacks occur (e.g., Denman et al., 1996) and are important in understanding global carbon fixation, they are not considered here since they add a level of complexity that researchers have not yet examined in a marine ecological/global climate change context. The signs (+/−) indicate the correlation or general tendency between the two factors: for example, when the temperature of the atmosphere increases, the temperature of the ocean increases, especially the surface layer, and this results in increased water column stability. Similarly, any process that increases freshwater at the surface (runoff or the melting of sea ice) will increase water column stability. In both cases, the mechanism is increased buoyancy of the surface layer; therefore, more wind or other causes of mixing will be required to disturb the vertical stratification of the water column. Generally, in order for phytoplankton production to increase, events that cause mixing, and therefore make nutrients available, must be followed by stabilization of the water column. This permits more plankton cells to be retained in the upper, lit portion of the water column or euphotic zone (it also concentrates them, facilitating their consumption by zooplankton). If high turbulence was to continue, algal cells would be mixed throughout a deeper layer, beyond the reach of sunlight (Mann and Lazier, 1996). Conversely, if stratification continues too long, nutrients in the euphotic zone become depleted.

One of the key patterns emerging from Figure 2 is that climate change, through a number of pathways, may increase water column stability and potentially decrease productivity through reduced nutrient availability. A paper on the California Current demonstrated the link between a moderate surface warming of approximately 1.5 °C since 1951 and a major decline (80%) in zooplankton biomass (Roemmich and McGowan, 1995), also citing related steep declines in populations of sea birds (Veit et al., 1996). It is not clear whether the warming is anthropogenic or part of interdecadal fluctuations (Roemmich and McGowan, 1995). In El Niño years, reduced zooplankton abundance leads to a major reduction in the abundance of young-of-the-year rockfish species (Ralston as cited in Hill (1995)). Roemmich and McGowan (1995) caution that global climate change-caused increases in stratification could be "devastating."

Wright et al. (1986) utilized outputs of researchers' general circulation models to predict a combina-

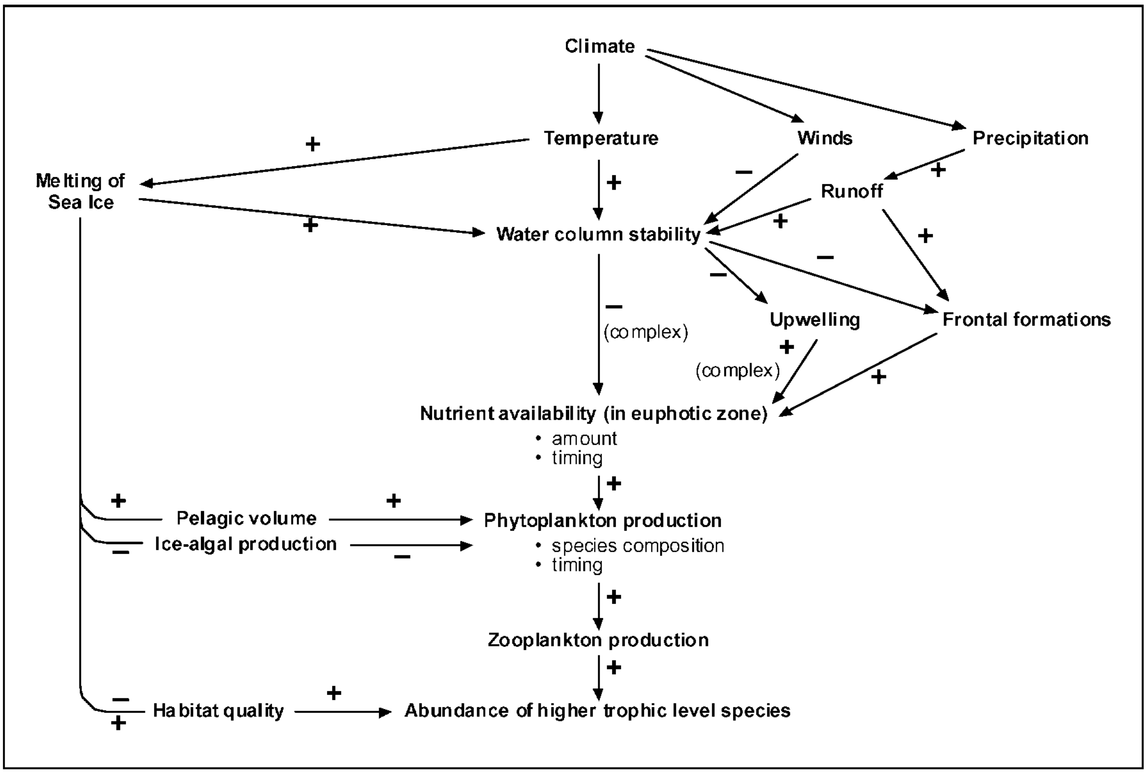

Figure 2. The variable effects of climate on oceanographic processes and production are shown. Signs (+/–) indicate the correlation between any two factors.

tion of reduced winds, increased temperature, and increased precipitation in the northwest Atlantic in response to global climate change. Frank et al. (1990) used their results and further predicted that reduced salinity (from increased runoff) would result in increased vertical stratification, with the following consequences: generally reduced productivity and a related decrease in biomass of cod stocks (Sutcliffe et al., 1983); and a shift in the location of shelf-tidal fronts toward the coast, with reduction in their area, and related productivity. Herring stocks may also be reduced (Frank et al., 1990) since their mean abundance is positively correlated with the size of well-mixed areas such as shelf-tidal fronts (Iles and Sinclair, 1982). Hunt et al. (2001) have reported evidence of a long-term southward shift in the position of the Sub-Antarctic Front and postulate related impacts on plankton and higher trophic levels in the vicinity of the Prince Edward Islands.

In the past 20–30 years, the extent of sea ice has decreased in the Arctic Ocean coincident with warming trends (Tynan and DeMaster, 1997). An increased fresh layer, possibly of warmer temperature, may have similar effects on water column stratification as described above. Thus, the notion that ice-free waters will result in increased productivity (Mann and Lazier, 1996; Figure 2) seems doubtful.

If winds increase under global climate change, water column stability may decrease. Bakun (1990) predicted that alongshore winds will intensify, as a result of adjacent lands heating and the relative increase in the heat differential between land and ocean. Upwelling and productivity should increase as a result. However, Roemmich and McGowan (1995), using data on the California Current, showed that upwelling was reduced even though alongshore winds increased. Therefore, as Figure 2 shows, effects of global climate change are complex and depend on relative magnitudes of a number of drivers. Hsieh and Boer (1992) showed through a coupled general circulation model, that mid-latitude continents did not follow Bakun's (1990) scenario. They demonstrated instead that winds in most parts of the world will generally weaken and so too will open ocean upwelling, while coastal upwelling will not be enhanced. Global biological productivity is predicted to decrease. Wright et al. (1986) also predicted a reduction in wind stress over the entire northwest Atlantic of about 10%. Frank et al. (1990) suggested that production may decrease as a result with subsequent impacts on larval fish.

Relationships stemming from "water-column stability" are more complex than the signs in Figure 2 would imply. If climate change causes a shift in the timing of water column mixing or stratification, this can ripple throughout the food web. For example, warming is likely to increase the duration of seasonal stratification (waters will stratify earlier in the spring and mix later in the fall) such that phytoplankton composition will shift from a predominance of diatoms to dinoflagellates (Frank et al., 1990). This could increase the length of foodwebs and decrease energy available for fish production (Frank et al., 1990). Furthermore, turbulent mixing is not always positive. A dome-shaped relationship has been found between wind-generated turbulence and larval mortality (Cury and Roy, 1989). Some intermediate level is optimum, since too much turbulence interferes with feeding ability (Rothschild and Osborn, 1988; MacKenzie et al., 1994) and too little stifles primary production (Figure 2). Dickson et al. (1988) demonstrated how a 30-year increase in northerly winds was associated with a decline of phytoplankton and zooplankton near the British Isles, but was linked to an increase in upwelling intensity along the Iberian west coast.

The melting of sea ice has additional impacts on marine ecosystems (Figure 2). Marine mammal species such as seals require a variety of particular ice conditions for pupping, molting, feeding, breathing, and movements on or under ice. Changes in the qualities of ice have ramifications for species abundance and distributions (Tynan and DeMaster, 1997). Whale species such as narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*) (both Monodontidae) in the Arctic (Tynan and DeMaster, 1997) and blue (*Balaenoptera musculus*), fin (*B. physalus*), humpback (*Megaptera novaeangliae*) and minke (*B. acutorostrata*) (all Balaenidae) in the Antarctic either feed at or frequent ice edges (de la Mare, 1997). Ice has associated algae and zooplankton, the latter feeding arctic cod (*Boreogadus saida*; Gadidae), which is a pivotal species in the arctic food web (Tynan and DeMaster, 1997). The nature of sea ice aggregates arctic cod, which may be critical for the foraging success of cod predators. Tynan and DeMaster (1997) concluded that a reduction in the extent of sea ice may alter the seasonal distributions, geographic ranges, patterns of migration, nutritional status, reproductive success, and ultimately the abundance and stock structure of some marine mammal species (Figure 2). Hofmann and Powell (1998) reviewed a complex interaction between Antarctic krill (*Euphausia superba*), salps (*Salpa thompsoni*), and sea ice in which long ice cover duration and large ice extent result in high krill recruitment rate.

Direct and indirect effects of temperature

The simplest and most widely recognized direct effect of temperature change is that mobile species will "track" their preferred temperatures and redistribute themselves or change their migration routes and timing (Rose and Leggett, 1988; Frank et al., 1990; Ray et al., 1992; Murawski, 1993; Tynan and DeMaster, 1997). Frank et al. (1990) summarized shifts in the abundance and distribution of species in the northwest Atlantic: during the warming trend of the 1940s, there was a northward shift of several species including mackerel (*Scomber scombrus*; Scombridae) and menhaden (*Brevoortia tyrannus*; Clupeidae), and during the cooling trend of the 1960s, several others retracted their range southwards while dogfish (*Squalus acanthias*; Squalidae) and capelin (*Mallotus villosus*; Osmeridae) extended their migrations southward. The Gulf of Maine may serve as an indicator of potential warming because it is a transition zone for several fish faunas.

Temperature also directly affects metabolic rate: for example, it increases growth rates in fish and invertebrates, reduces incubation times of eggs, and has a number of other physiological effects. Ray et al. (1992) reviewed a variety of temperature effects on marine populations and physiology in considerable detail. Indirect effects of predicted decreases in primary and secondary production (Figure 2) would slow growth rates, affecting: ability to compete; ability to escape predators; size at age; fecundity; spawning date; duration of spawning; and consequently mortality and reproductive rate (Ford, 1982; Frank et al., 1990; Ray et al., 1992). Warmer water in 1983 resulted in a "moving forward" of peak abundances of ctenophores, which then competed with haddock (*Melanogramms aeglefinus*; Gadidae) larvae, resulting in the lowest year-class on record (Frank, 1986).

Currents and retention

Currently there is not as much literature addressing the effects of changes in currents on biota at a regional or local scale. Because currents are influenced by runoff, winds, temperature, and salinity, there are likely to be significant changes in current patterns and strength with global climate change (Ray et al., 1992). Migration of adults of some species is expected to be affected in terms of energy expenditure (DeAngelis and Cushman, 1990) and orientation related to cues that current speed and direction may provide (Rose and Leggett, 1988). Larval dispersal, and conversely retention, is a function of water movement in the form of currents and eddies. Larvae and other zooplankton may be passively transported into or out of areas favorable in terms of food supply or temperature, or they may use swimming or other active capacity such as vertical migration to enter the "right" currents (Iles and Sinclair, 1982; Provenzano et al., 1983; Fortier and Leggett, 1984; Cowen et al., 2000). However, if currents change in direction or depth, then larval behaviors that were previously adaptive may no longer be so. Iles and Sinclair (1982) noted that the integrity of herring larval retention areas might vary considerably from year to year, in relation to current patterns. Roughgarden et al. (1988) hypothesized that during intervals of stronger upwelling, related to increased winds, water movements could carry larval barnacles sufficiently offshore so as to negatively impact settlement. Bailey et al. (1999) described how an anomalous weather event affected current patterns and consequently larval transport, noting also that climate change may influence the frequency or timing of such anomalies.

At a large spatial scale, the Gulf Stream is likely to decrease in strength, and the Labrador Current to increase, with global climate change (Frank et al., 1990). The former change will likely decrease the formation of warm core rings: these have been linked to poor year-classes of groundfish species because they sweep larvae off the shelf, which is their characteristic habitat (Myers and Drinkwater, 1989). As a result, Frank et al. (1990) suggested a greater probability of strong annual recruitment in groundfish stocks south of 45° N. However, the interaction of various mechanisms influencing recruitment are complex (Figure 2). Squid will likely decrease in abundance in eastern Canada for the same reason because they are thought to be carried from the southeastern USA by the Gulf Stream and onto the Scotian shelf by warm core rings (Frank et al., 1990).

It is often assumed that marine populations are 'open': larvae disperse widely and populations are well-connected (Cowen et al., 2000). However, Cowen et al. (2000) concluded from a modeling exercise of larval fish dispersal that, given larval behaviors and estimated mortality rates, larval retention near local populations may be of great importance. If conditions change in a species' historical range as a result of global climate change, larval dispersal to new, suitable areas will depend on a match between currents with "appropriate" biophysical characteristics (passively or actively selected) and life history characteristics such as larval duration.

Discussion

Temporal and regional variability in climate are associated with global climate change yet models are limited in their simulation of regional climate conditions (Schneider, 1993; Easterling et al., 2000). Large-scale multi-decadal trends in primary production have been detected and may be related to global climate change. For example, phytoplankton biomass in the northeast Atlantic and the North Sea north of 59° N has decreased since 1948 and may be associated with the spread of unusually cold Arctic waters (Reid et al., 1998). Total chlorophyll *a* has increased in the water column during the summer since 1968 in association with increased winter winds and decreased sea surface temperature in the central North Pacific ocean (Venrick et al., 1987). The kinds of impacts that these and other potential changes will have at local levels on particular species is highly uncertain. In terms of marine protected areas, the issues or species of concern will depend on the objectives for the network or protected area and particulars of geographic location. For these reasons, this review paper suggests general comments and a framework for other investigators to build upon.

Animals and plants have evolved life histories that are cued to important natural cycles or processes on which they depend. Global climate change is likely to newly synchronize or desynchronize the timing of critical life history events (Frank et al., 1990). Any changes in timing or characteristics of these cycles or events will challenge some species' ability to adapt and favor others. Tynan and DeMaster (1997) noted that gray whales may benefit from reduced ice in the Arctic, while the nonuniformity of predicted changes means that some locations will experience more ice formation. Opportunistic species may adjust by shifting diets, as gannets (*Sula bassana*; Sulidae) did with a shift from warm- to cold-water fish species in the 1990s in the northwest Atlantic (Montevecchi and Myers, 1997). Wider-ranging species may leave the area, and local species may decline in abundance in response to reduced productivity, as was the case with seabirds in the California Current in the 1990s (Oedekoven et al., 2001). Barry et al. (1995) demonstrated at Hopkins Marine Station that invertebrate species' ranges shifted northward, consistent with increases in shoreline temperatures over a 60-year period. However, Easterling et al. (2000) cited examples of range shifts and local extinctions of species which may be responding to the increase in extreme weather events linked to global climate change rather than mean climatological values.

Natural selection acts rapidly to eliminate "unworkable" patterns (Bakun, 1996). Species with short generation times, and sufficient genetic variability may be able to adapt *in the evolutionary sense* to the changing conditions associated with global climate change. However, many species' success will depend on their ability to disperse to new, favourable habitats. Ray et al. (1992) and Steele (1991) noted that extinctions are less likely in marine environments as a result of the mobility, large ranges, high fecundity, and short generation times of primary producers, and the wider dispersal ability, and rapid growth rates of most marine organisms. These generalizations may be true relative to the terrestrial environment; however, the interaction of fishing pressure, unfavourable ocean conditions, and limited dispersal of some species (Cowen et al., 2000; Warner et al., 2000) warrants precaution in marine protected area and marine conservation planning.

The changes in oceanographic and biological processes and conditions triggered by global climate change will cause changes in abundance and distribution of many species, and consequently in biodiversity. Specifically, oceanographic features such as fronts, which are important feeding grounds, may shift in location. The strengthening of vertical stratification may greatly influence production. Currents may shift in location and strength but there is limited literature investigating this in a marine ecological context. Furthermore, there is little understanding of how species richness affects or is affected by primary production (Ray et al., 1992).

Large uncertainties exist in the atmospheric models, as well as in the oceanographic scenarios used to examine potential responses of marine life to global climate change (Frank et al., 1990). Thus, this area of research is a "highly speculative exercise" (Frank et al, 1990) where the magnitudes and even the direction of change is uncertain (Mann and Lazier, 1996). However, as Rastetter (1996) and Schneider (1993) noted, we need to use and continue to develop these models because our options are limited and time is pressing. The rate of global climate change is an important factor, as is the geographic variability of climate change, especially expressed at the regional scale. Several authors have expressed the utility of using linked models to understand processes at the meso-scale (Roughgarden et al., 1988) and regional scales (Root and Schneider, 1993; Tynan and DeMaster, 1997). DeAngelis and Cushman (1990) recommend linking a variety of types of models to investigate global climate change and fisheries. They use a diagram of causal chains, or envirogram (rather like Figure 2 here), to identify the most influential links for modeling purposes. To complement the modeling, further basic research is needed (Ray and Grassle, 1991), especially over broad geographic and long temporal scales (Quinn and Karr, 1993; Root and Schneider, 1993). Long-term quantitative studies on community structure are essential because shifts in structure "represent an integrated response to longer-term climate change superimposed on the effects of shorter term factors" (Barry et al., 1995). Given the lack of available and relevant long-term datasets, novel datasets such as whaling records (de la Mare, 1997) and archives (Magnusson, 1995; Yasuda et al., 1999) should be encouraged and utilized in time-series analyses. A research agenda must take into account that marine species interact with their environment over a hierarchy of scales (Mann and Lazier, 1996; Hofmann and Powell, 1998), and both top-down and bottom-up (Ray et al., 1992) processes are likely to be important depending on scale and context.

Conclusions

Since many governments and agencies are in the process of creating frameworks for marine protected area networks (e.g., Fisheries and Oceans Canada and Land Use Coordination Office BC, 1998), it is a strategic time to consider the potential effects of global climate change in research and policy agendas.

Where possible, researchers should collaborate across disciplines to create linked, relevant models. The framework presented here (Figure 2) can be used as a basis to build a model for a particular region, and input likely conditions such as wind speeds, levels of precipitation, and runoff. An area such as the Gulf of Maine would be a good candidate for further research because it will likely respond relatively rapidly to global climate change, has been relatively well-researched, and is currently the focus of marine protected area attention (Brody, 1998). Modeling experiments using the CODA approach for siting networks of protected areas (Bedward et al., 1992), combined with other linked models, may be a promising endeavor. Specifically, potential future conditions of climate, habitat, and biodiversity could be modeled, and then some percentage of the network could be placed in units defined by these conditions, rather than the present ones.

In terms of a policy agenda for marine conservation, this review suggests a deliberately two-pronged approach. A network of protected areas based on current or potential future conditions may help to conserve biodiversity, protect particular endangered populations or critical habitats, and play a role as a hedge against rapid anthropogenic changes (Graham, 1988; Querol, 1993; Allison et al., 1998). Given the relative lack of "highly protected" marine protected areas compared to terrestrial environments (e.g., 0.2–1.25% and 10.5% by area, respectively in British Columbia, Canada, (Zacharias and Howes, 1998)), a continued push for their increase is essential for conservation of marine biological diversity, and as critical study sites to permit teasing apart human impacts, such as fishing and development, from the effects of global climate change. The latter rationale has not received sufficient emphasis. Both coarse- and fine-filter approaches are worthwhile, depending on site-specific or network goals. However, it must be recognized that communities will disassemble (Peters and Darling, 1985): some species will move and others may not be able to adapt. The research outlined above may assist us in anticipating where it may or may not be worthwhile investing particular types of conservation efforts. More "purposely manipulative" strategies may be required, given the expected rates of change associated with global climate change (Quinn and Karr, 1993). There is also a need to consider flexible boundaries (Peters and Darling, 1985) if shifts of particular features and species appear to be occurring, for example, polynyas, or ice-free zones, which are critical habitats for many marine mammal species. Fisheries managers already utilize closed areas for varying time periods as a management tool. Thus the creation of some "shorter"-term protected areas that are reassessed and relocated in light of global climate change may be an option.

The second prong and long-term approach is to protect sufficiently large areas that are close enough to permit the reshuffling of species which will occur. Leopold (1966) noted: "To keep every cog and wheel is the first precaution of intelligent tinkering." In the marine context of global climate change, this translates to a precautionary approach that maintains or improves the health of current marine biological communities. This large-scale protection would best occur within holistic management models such as integrated coastal zone, ecosystem, and multiple use management (Norse, 1993; Grumbine, 1994; Leadbitter et al., 1999). These planning frameworks are more appropriate for addressing boundaryless threats including pollutants, introduced species, disease and global climate change (Allison et al., 1998). Continued demand for goods and services, against a backdrop of declining primary production and changes in biodiversity (Denman et al., 1996), provides further strong rationale for improved, holistic management. Examples of large protected areas zoned for multiple use include the Great Barrier Reef Marine Park, National Marine Conservation Areas (currently under legislative review in Canada), and biosphere reserves (Kenchington and Agardy, 1990; Allison et al., 1998).

An important aspect of the ecosystem approach to management is recognizing the fragmentation of institutions and disciplines and addressing it through interdisiciplinary cooperation and research (Norse, 1993; Quinn and Karr, 1993; Yaffee, 1997). Schneider (1993) has recommended that climatologists work with ecologists "to produce information {on global climate change} useful to the development of conservation strategies." In a similar vein, it is recommended that marine ecologists who tend to focus on smaller-scales (Roughgarden et al., 1988; Pimm, 1991; Schneider, 1993; Rosenzweig, 1995) work with both physical and biological oceanographers to develop a cross-scale research agenda to examine potential effects of global climate change on marine biota.

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