

VIEWPOINT

Marine protected areas and ocean basin management

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ABSTRACT

1. All reserve designs must be guided by an understanding of natural history and habitat variability.

2. Differences in scale and predictability set aside highly dynamic pelagic systems from terrestrial and nearshore ecosystems, where wildlife reserves were first implemented. Yet, as in static systems, many pelagic species use predictable habitats to breed and forage. Marine protected areas (MPAs) could be designed to protect these foraging and breeding aggregations.

3. Understanding the physical mechanisms that influence the formation and persistence of these aggregations is essential in order to define and implement pelagic protected areas. We classify pelagic habitats according to their dynamics and predictability into three categories: static, persistent and ephemeral features.

4. While traditional designs are effective in static habitats, many important pelagic habitats are neither fixed nor predictable. Thus, pelagic protected areas will require dynamic boundaries and extensive buffers.

5. In addition, the protection of far-ranging pelagic vertebrates will require dynamic MPAs defined by the extent and location of large-scale oceanographic features.

6. Recent technological advances and our ability to implement large-scale conservation actions will facilitate the implementation of pelagic protected areas.

7. The establishment of pelagic MPAs should include enforcement, research and monitoring programmes to evaluate design effectiveness.

8. Ultimately, society will need a holistic management scheme for entire ocean basins. Such overarching management will rely on many innovative tools, including the judicious use of pelagic MPAs.

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KEY WORDS: fronts; highly migratory species; marine protected area (MPA); migration routes; ocean basin conservation; pelagic conservation; seamounts

INTRODUCTION

Once viewed as the ultimate wilderness, it is increasingly apparent that the oceans have been heavily affected by human activities. The most serious impacts result from the diverse perturbations of fishing, including the consumption of 25–35% of the primary production from upwelling and temperate continental shelves, the virtual removal of the top of coastal and pelagic food webs, the gross depletion

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of target stocks, and the massive wastage of bycatch (Alverson *et al.*, 1994; Dayton *et al.*, 1995; Pauly and Christensen, 1995; Pauly *et al.*, 1998).

Jean Baptiste Lamarck and Thomas Huxley considered marine organisms immune to extinction because they were so plentiful and productive. This notion reflects the widespread belief of the 18th and 19th centuries that inexhaustible ocean resources would never be depleted by human activities. In recent years, however, the mounting number of extinctions and local extirpations suggests that the risk of extinction in marine systems is greater than we have assumed (Brander, 1981; Carlton, 1993; Casey and Myers, 1998). Currently, threatened pelagic species include invertebrates, teleosts, elasmobranchs, marine turtles, seabirds, pinnipeds and cetaceans (Safina, 1995; Croxall and Gales, 1997; Roberts and Hawkins, 1999). In the face of continued habitat degradation and mounting fishing pressure, this list is certain to increase in the future.

One of the most pragmatic approaches to ocean conservation is to establish marine protected areas (hereafter referred to as MPAs). Because the term MPA has been applied to many different concepts, we use the expression in the generic sense to include a variety of management tactics. MPAs have been widely proposed to protect estuarine and coastal systems, fisheries resources, critical habitats of endangered species and parks for public enjoyment (Ray, 1976; Agardy, 1994; Murray *et al.*, 1999). Often, the result is a complicated patchwork of coastal sanctuaries, ecological reserves, refuges, national marine sanctuaries and marine parks designed to meet disparate objectives and subject to different regulations. In California, for example, 103 MPAs with 12 different denominations had been established by 1997 (McArdle, 1997).

While most discussions of MPAs have focused on nearshore habitats, such as intertidal communities and coral reefs, protected areas have rarely been considered in pelagic conservation. Throughout this paper, 'pelagic' refers to species, processes and ecosystems that occur in the water-column and are not attached to the substrate. However, pelagic and benthic systems are coupled, and many water-column properties arise from the interactions of currents with features of the sea floor. Our use of the term 'pelagic' does not involve political considerations, merely function and structure. Thus, 'pelagic' species inhabit continental shelves, 200-mile Economic Exclusive Zones, and the 'high seas' beyond national boundaries.

MPAs have not been used in pelagic conservation due to the open and dynamic nature of the high seas, which inhibit MPA design and enforcement (Robinson, 1992; De Fontaubert *et al.*, 1996; Boersma and Parrish, 1999). Traditionally, pelagic systems are managed with single-species approaches, and conservation relies on the improvement of regulations (e.g. quota enforcement and size restrictions) and the modification of fishing gear (e.g. pingers and tori lines). Many of these regulations are dependent upon accurate scientific knowledge of the life history, migratory patterns and influence of environmental variability on population dynamics of the target species. Such information is difficult to obtain, and is rarely available for commercially unimportant species (e.g. bycatch). The failure of single-species management is exemplified by the overfished status of fish stocks worldwide, and by the pervasive ecosystem-level impacts of bycatch (Dayton *et al.*, 1995; Pauly *et al.*, 1998).

This paper is designed to stimulate discussion and research on the implementation of pelagic protected areas. We believe that the conservation of far-ranging pelagic species, both targeted and killed incidentally by fishing, represents the most pressing problem; hence, we focus our review on the conservation of the large vertebrates (fish, birds, turtles and mammals). Here, we highlight those habitat features that might be used to identify and implement MPAs to protect these far-ranging species. We hope to build on the paper by Mills and Carlton (1998), with full understanding that meaningful conservation efforts can only succeed with the support of an international consensus based on an appreciation of oceanographic and biological processes.

We hope the world community will respond to this growing crisis with the innovative integrated management of entire ocean basins. Such management might be modelled after other successful international agreements, such as the Convention for the Conservation of Antarctic Marine Living

Resources (CCAMLR) or the International Whaling Commission (IWC). These agreements are far beyond the scope of this paper. Our intention is to argue that in principle large-scale reserves can be applied to the highly dynamic marine habitat, and can offer important tools for such ocean basin management.

GENERAL CONSIDERATION OF PELAGIC SYSTEMS

For all systems, reserve designs must relate to both the ecology (e.g. habitats, habits and migrations) and the life history (e.g. mode of reproduction, ontogenetic habitat changes and social system) of the relevant species, as well as the inherent variability of their habitats (e.g. disturbances, oceanographic regimes and climatic change) (Ray and McCormick-Ray, 1993; Russ and Alcala, 1998; Boersma and Parrish, 1999).

Pelagic systems are inherently different from terrestrial landscapes where wildlife reserves were first implemented. Terrestrial and marine ecosystems differ in the ecological constraints shaping life, in the processes responsible for pattern, and in the dominant scales of physical and biological variability (Smith, 1978; Steele, 1985). The distributions of pelagic species are largely dictated by the intricacies of water flow, and by the coupling of physical and biological processes that promote the growth and retention of planktonic populations (Haury *et al.*, 1978; Steele, 1978; McGowan and Walker, 1985). These, in turn, are mediated by physical forcing dominated by large scales of time and space, between seasons and decades and tens to thousands of kilometres (meso to mega scales; Stommel, 1963; Smith, 1978; Denman, 1994). The dynamic nature of pelagic systems and the prevalence of variability over large scales blur the linkages between physical and biological processes, spreading biotic interactions over spatial scales that greatly exceed those prevalent in terrestrial systems (Vinogradov, 1981; Steele, 1985; Jaquet *et al.*, 1996).

In spite of these intrinsic differences, some design issues and objectives of pelagic protected areas are similar to those in nearshore and terrestrial systems. Similarities exist where properties of pelagic systems derive from physical features that are geographically fixed or predictable, and when the objective is to protect a static habitat (e.g. seamounts, mangroves or salt marshes), or a relatively sedentary species (e.g. orange roughy, *Hoplostethus atlanticus*). Conversely, important differences arise from the unique, dynamic properties of many pelagic systems. In particular, the issues of scale and predictability, which in turn drive the extreme mobility exhibited by many pelagic species, will require new approaches and concepts before effective pelagic MPAs can be implemented.

The simplest scenario involves protecting sedentary species or well-defined, geographically fixed habitats with static protected areas (Agardy, 1994; Boersma and Parrish, 1999; Probert, 1999). However, even in terrestrial systems, static protected areas have failed in cases where threatened species were highly-mobile or migratory, because impacts outside of the protected areas were not mitigated or adequately understood (Robbins *et al.*, 1989; Boersma and Parrish, 1999). In pelagic systems, where many species range over thousands of kilometres, and where migration routes are dynamic and poorly understood, the conservation of highly-mobile and migratory species remains a most serious challenge.

The emperor penguin (*Aptenodytes forsteri*) exemplifies the challenges posed by the conservation of highly migratory pelagic species (Figure 1). After dispersing from their colonies, adult emperor penguins remain within the Ross Sea. On the other hand, fledglings venture north of the 60th parallel, the boundary defined by the Antarctic Treaty to protect Antarctic living resources (Kooyman *et al.*, 1996). Pelagic species forage far from their breeding areas and do not respect arbitrary boundaries imposed by managers. Moreover, many pelagic predators, including pinnipeds, penguins, sharks and albatrosses, have complex foraging strategies involving the segregation of different genders and age classes at sea (Strasburg, 1958; Prince *et al.*, 1992; Steward and DeLong, 1995; Kooyman *et al.*, 1996). Thus, rigid designs based on politics or convenience will likely lead to ineffective protected areas. Conversely, the boundaries of effective pelagic MPAs will have to be guided by an understanding of natural history and habitat variability.

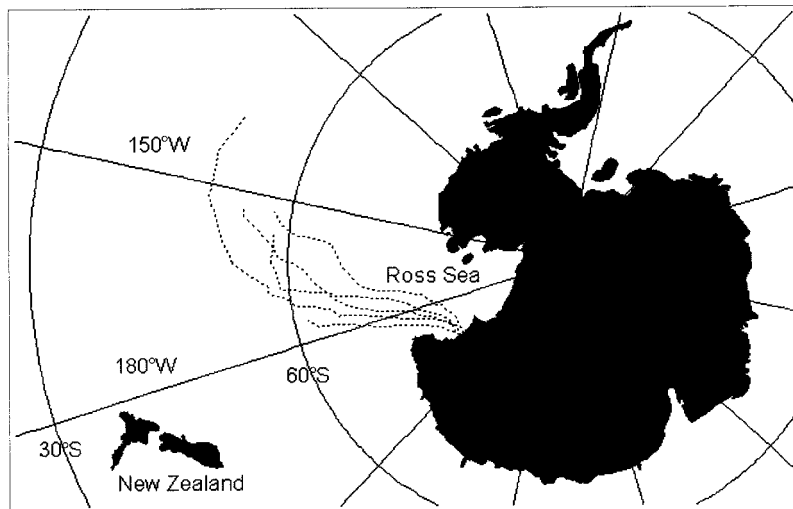


Figure 1. An understanding of natural history is vital to delineate effective pelagic protected areas. Fledging emperor penguins (hatched lines) disperse north of 60°S, the boundary defined by the Antarctic Treaty to protect them (December–March, 1995–1996). Redrawn from Kooyman *et al.* (1996).

The discussion of pelagic MPAs below includes both geographically restricted regions, which can be important feeding or breeding grounds for marine predators, and larger oceanographic features at the scale of entire ocean basins. This distinction is important because networks of isolated MPAs can protect species in a given time and place, but most pelagic predators are far-ranging. Thus, effective pelagic conservation will require consideration and protection of entire migration routes.

APPLYING MPA CONCEPTS TO PELAGIC SYSTEMS

Pelagic systems represent a vast and featureless landscape to our untrained eyes. Nevertheless, pelagic species are not distributed randomly. Instead, their patchy distributions are influenced by patterns of productivity and prey abundance, which are, in turn, driven by physical forcing at multiple scales (Haury *et al.*, 1978; Hunt and Schneider, 1987; Denman, 1994).

The transition from weekly-moving planktonic to actively-moving nektonic organisms introduces additional MPA design complications because behaviour becomes an increasingly important determinant of species distributions (Weber *et al.*, 1986; Hunt and Schneider, 1987). Physical processes drive the timing and magnitude of primary production (Holligan, 1981; Owen, 1981; LeFevre, 1986), and influence the distribution of planktonic organisms (Haury *et al.*, 1978; Wolanski and Hamner, 1988; Franks, 1992). Conversely, large and mobile pelagic vertebrates are often decoupled from the underlying physical structure because they can regulate their position with respect to the water flow (Denman, 1994; Schneider, 1994). The distributions of marine predators and their prey may also be decoupled at small spatial scales as a result of predator avoidance behaviour (e.g. Logerwell and Heargreaves, 1996), the existence of prey refuges (e.g. Rose and Leggett, 1990), the inability of predators to profitably exploit small patches (e.g. Piatt, 1990), and the failure to detect (e.g. Logerwell *et al.*, 1998) and to aggregate at small and ephemeral prey patches (e.g. Obst, 1985).

Yet, in spite of the potential decoupling between physical processes and nekton dispersion, there is strong evidence that physical forcing does influence the distribution of pelagic vertebrates at multiple

scales. Over ocean basins (thousands of kilometres), the ranges of nektonic species frequently mirror large-scale oceanographic domains and current systems known to influence primary productivity and plankton biogeography (Sund *et al.*, 1981; Ballance *et al.*, 1997; Brodeur *et al.*, 1999). At finer scales (tens to hundreds of kilometres), nekton distributions are likely mediated by the dispersion and availability of prey (Hunt and Schneider, 1987; Rose and Leggett, 1990; Hunt *et al.*, 1999). Cetaceans, seabirds and large predatory fish exploit predictable regions of enhanced productivity and prey aggregation associated with bathymetric gradients, water mass boundaries and upwelling plumes (Sund *et al.*, 1981; Fiedler *et al.*, 1998; Hunt *et al.*, 1998).

Knowledge of the dynamics and the scales of the processes responsible for the formation of these important habitat features is essential to define and implement pelagic protected areas. In particular, the degree to which habitat features reoccur, the amount of time they persist, and how much their location and extent vary in time and space will determine the feasibility of pelagic MPAs. We have classified habitat features into three categories according to their predictability and dynamics: static bathymetric, persistent hydrographic and ephemeral hydrographic features. These represent progressively more difficult systems for the implementation of MPAs. For these three types of habitat features, we describe the scales of the relevant physical forcing functions, provide evidence of their biological effects, and discuss possible management options to define and implement MPAs. We direct the readers to the extensive reviews by Owen (1981), Robinson (1983), Boehlert and Genin (1987), Roden (1987), Schneider (1991), Olson *et al.* (1994), and Hunt *et al.* (1999) for a more thorough discussion of physical–biological interactions in marine systems.

Static bathymetric features

Many pelagic predators aggregate at static bathymetric features, such as reefs, shelf breaks, submarine canyons, seamounts and in the lee (downstream) of islands. Irregularities of the sea floor often alter water flow above them, enhance mixing, and promote upwelling of nutrient-rich waters. In turn, increased turbulence and water-column mixing promote localized production and the aggregation of planktonic prey at secondary convergence zones, persistent eddies and fronts (Thompson and Wolanski, 1984; Simpson and Tett, 1986; Wolanski and Hamner, 1988). In addition to promoting and retaining elevated localized production, bathymetric features can also enhance foraging opportunities for predators by concentrating and making prey accessible. For instance, turbulent flow over banks and along passes often drives zooplankton into surface waters and concentrates vertically migrating organisms into subsurface patches, which are readily exploited by near-surface predators (Simard *et al.*, 1986; Hunt *et al.*, 1998, 1999).

Shelf breaks and submarine canyons also constitute important foraging habitats for pelagic vertebrates, including seabirds, pinnipeds, cetaceans, salmon and swordfish. These marine predators exploit elevated primary production and high standing stocks of zooplankton, fish and squid in the vicinity of shelf breaks (Fournier *et al.*, 1979; Simard *et al.*, 1986; Springer *et al.*, 1996). Two mechanisms have been invoked to explain prey aggregations at shelf breaks: first, high primary production stimulates the localized production of higher trophic levels; and second, shelf break fronts aggregate prey produced elsewhere (Schneider, 1991; Springer *et al.*, 1996). In addition, there is evidence that shallow shelves and ledges adjacent to deep-water areas trap vertically-migrating zooplankton in shallow waters, where it is accessible to diving predators (Schoenherr, 1991; Hunt *et al.*, 1996; Fiedler *et al.*, 1998).

Even though most examples of bathymetric physical forcing originate from coastal waters (Doty and Oguri, 1956; Hunt *et al.*, 1998), there is mounting evidence that similar mechanisms are at play in offshore systems. Obstacles such as islands and guyots interact with ocean currents and promote water-column mixing, which in turn stimulates primary production. In addition, eddies and stationary vortices, called Taylor columns, stimulate primary production in the vicinity of guyots by bringing cold, nutrient-rich

water closer to the surface (Boehlert and Genin, 1987; Roden, 1987; Comeau *et al.*, 1995). The closed circulation associated with these features likely retains the enhanced local production in the vicinity of seamounts (Uda and Ishino, 1958; Boehlert and Genin, 1987). In turn, much of this localized production is transferred to resident predators, such as euphausiids and rockfishes (Genin *et al.*, 1988; Haury *et al.*, 1995; Koslow, 1997), which in turn support dense aggregations of mobile predators, including seabirds, tuna and marine mammals (Sund *et al.*, 1981; Ensor and Shaughnessy, 1990; Haney *et al.*, 1995).

In summary, seamounts represent areas of high production and important foraging grounds of predictable prey aggregation. In addition, the ecological significance of seamounts is underscored by evidence that, oftentimes, they constitute the mating and spawning areas of far-ranging pelagic species. For example, despite its vast range, pelagic armorhead (*Pentaceros wheeleri*) spawning in the north Pacific is restricted to seamounts along the southern Emperor–northern Hawaiian Ridge between 29° and 35° latitude north (Boehlert and Sasaki, 1988). Similarly, there is evidence that far-ranging species, such as the scalloped hammerhead (*Sphyrna lewini*), aggregate in the vicinity of seamounts (Klimley, 1993). Predictable mating aggregations of wide-ranging pelagic species are susceptible to destructive pulse fisheries, which frequently also heavily damage slow-growing resident fish and invertebrate communities (Dayton *et al.*, 1995; Koslow, 1997; Koslow and Gowlett-Holmes, 1998).

Persistent hydrographic features

Persistent hydrographic features, such as currents and frontal systems, represent some of the best known oceanographic patterns (Franklin, 1786; Sverdrup *et al.*, 1942; Favourite *et al.*, 1976). Fronts have long been recognized as regions of elevated biological activity in continental shelves, where seabirds, marine mammals and tunas aggregate to exploit prey concentrations supported by elevated production and retention at convergences (Laurs *et al.*, 1984; Briggs *et al.*, 1988; Hunt *et al.*, 1996). Similarly, oceanic fronts and water mass boundaries are important features of the circulation, biogeography and ecology of the world's oceans (Sverdrup *et al.*, 1942; Fager and McGowan, 1963; Laurs and Lynn, 1991).

In pelagic systems, changes in the types and abundances of marine organisms often occur at persistent fronts, where waters of different temperature and salinity meet (Sund *et al.*, 1981; Gould and Piatt, 1993; Brodeur *et al.*, 1999). Moreover, persistent hydrographic features constitute important foraging areas of predictable primary production and prey aggregation (Ogi, 1984; Laurs and Lynn, 1991; Gong *et al.*, 1993). The high predictability and the persistence of oceanic fronts make them ideal signposts and highways, delineating the migratory routes of pelagic species in otherwise featureless landscapes (Olson and Podesta, 1987; Yoder *et al.*, 1994; Morreale *et al.*, 1996; Table 1).

Table 1. Spatial predictability of the frontal regions defining the transition zone in the subarctic North Pacific

Oceanographic survey				Feature predictability			
Latitude (range)	Longitude (range)	Months	Years	Front	Mean latitude	Spatial variability	References
39°–48°N	170°E	July	1981–1986	SFZ	43°N	50 km	Roden (1991)
39°–48°N	175.5°E	July	1981–1986	SFZ	43°N	150 km	Roden (1991)
38.5°–47.5°N	175.5°E	July	1978–1991	SFZ	42.5°–45°N	2.5° latitude	Ignell <i>et al.</i> (1995)
35°–47°N	155°E–145°W	May–December	1984–1990	SFZ	43°–45°N	2° latitude	Yatsu <i>et al.</i> (1993)
38.5°–47.5°N	175.5°E	July	1978–1991	SAB	38.5°–42°N	3.5° latitude	Ignell <i>et al.</i> (1995)
35°–47°N	155°E–145°W	May–December	1984–1990	SAB	40°–42°N	2° latitude	Yatsu <i>et al.</i> (1993)

The subarctic frontal zone (SFZ) separates subarctic proper and transition zone waters, and the subarctic boundary (SAB) separates transition zone and subtropical waters.

In the North Pacific, a narrow (40°–44°N) region of strong temperature and salinity gradients, termed the Transition Domain, is of particular biological importance (Fager and McGowan, 1963; Lynn, 1986; Roden, 1991). The fronts delineating the extent of this oceanographic domain delimit the ranges of subarctic and subtropical species, and influence the distribution of far-ranging fish, seabirds and marine mammals (Laurs and Lynn, 1991; McKinnell and Waddell, 1993; Ignell *et al.*, 1995). These frontal zones contain the highest standing stocks of micronekton (small squids, small fishes and crustaceans) in the North Pacific during the boreal spring and summer (Aron, 1962; Shimazaki, 1986; Percy, 1991). The total fish and squid biomass caught at standardized drifnet sampling stations tripled from 100–300 kg in subtropical and subarctic waters, north and south of the Transition Domain, to 300–1200 kg within the waters of the Transition Domain (Shimazaki, 1986). These predictable prey aggregations are, in turn, exploited by a variety of far-ranging predators which migrate into subarctic waters seasonally (Mishima, 1981; Ogi, 1984; Yatsu *et al.*, 1993).

Nevertheless, the significance of the Transition Domain goes beyond the abundance and diversity of its fauna. This region represents a vital foraging habitat and migratory route for many species, including valuable fisheries resources (salmonids and albacore tuna *Thunnus alalunga*), and vulnerable non-target species (albatrosses, shearwaters, sharks and turtles) (Table 2). Moreover, many cosmopolitan squid, fish, mammals, birds and the endangered loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) turtles migrate across the Transition Domain following the North Pacific current (Laurs and Lynn, 1991; Weatherall *et al.*, 1993; Springer *et al.*, 1999).

Perhaps the most significant ecological role of the Transition Domain is as a breeding and nursery ground for far-ranging organisms. Many pelagic species, such as squids and sharks, segregate according to age and sex, with the larger and more fecund individuals venturing farther north into the colder, more productive subarctic Pacific (Strasburg, 1958; Mishima, 1981; Sinclair, 1991; Murata and Hayase, 1993). For instance, blue shark (*Prionace glauca*) catches north of 40°N consist exclusively of large females, whereas younger individuals of both genders are caught in waters to the south (Strasburg, 1958). Similarly, neon flying squid (*Ommastrephes bartrami*) seasonal migration patterns differ between genders and across body size, with the larger females ranging farther north (Sinclair, 1991).

The Transition Domain also represents a nursery for the juveniles of far-ranging species during their first years at sea. For instance, the summer migration route of albacore tuna between the spawning areas in the western Pacific and North America runs through the Transition Domain (Laurs and Lynn, 1991). Juveniles between 1–4 years of age were incidentally taken in squid drifnets as they migrated through the Transition Domain (Bartoo *et al.*, 1993; Yatsu *et al.*, 1993). Similarly, Gould and Piatt (1993) reported that 79 and 88% of all sooty (*Puffinus griseus*) and short-tailed (*P. tenuirostris*) shearwaters recovered from gillnets during the 1980s were immature birds commuting to the Bering Sea and the subarctic North Pacific. Similar age composition data for tufted (*Lunda cirrhata*) and horned (*Fratercula corniculata*) puffins suggest that the Transition Domain represents an important wintering area for seabirds breeding in the North Pacific (Gould *et al.*, 1982). In addition, analyses of bycatch and telemetry data have revealed that this region is a nursery for juvenile northern fur seals (*Callorhinus ursinus*) from the Asian and Pribilof stocks (Baba *et al.*, 1993; Buckland *et al.*, 1993; Yatsu *et al.*, 1993).

Oceanic fronts, like the ones defining the North Pacific Transition Domain, support high densities of marine predators and their prey (Aron, 1962; Ogi, 1984; Percy, 1991; Springer *et al.*, 1999). Fishing fleets, too, are attracted to these frontal zones, owing to improved fishing conditions (Gong *et al.*, 1993; Murata and Hayase, 1993). Thus, relatively small geographic areas often concentrate much of the pelagic fishing effort and associated ecological impacts, such as tar and plastic pollution, bycatch, and ghost fishing by lost and abandoned gear (Dahlberg and Day, 1985; Galt, 1985; Bartoo *et al.*, 1993). The ecological significance of oceanic frontal features and their susceptibility to intense fishing activities and habitat degradation underscore the need to establish pelagic MPAs.

Table 2. Habitats of selected North Pacific pelagic vertebrates during summer (June–September)

Species	Water masses/Domains	Range SST (°C)	Core habitat SST (°C)	References
Chinook salmon	SAW	7–10	Subarctic boundary	McKinnell and Waddell (1993), Yatsu <i>et al.</i> (1993)
Chum salmon	SAW	2.5–11	Subarctic boundary	McKinnell and Waddell (1993), Yatsu <i>et al.</i> (1993)
Coho salmon	SAW	7–12	Subarctic boundary	McKinnell and Waddell (1993), Yatsu <i>et al.</i> (1993)
Pink salmon	SAW	3–11	Subarctic boundary	McKinnell and Waddell (1993), Yatsu <i>et al.</i> (1993)
Sockeye salmon	SAW	2.5–9	Subarctic boundary	McKinnell and Waddell (1993), Yatsu <i>et al.</i> (1993)
Dall's porpoise	SAW/SFZ/TRD	<17	Transition domain	Miyashita (1993), Yatsu <i>et al.</i> (1993)
Northern fur seal	SAW/SFZ/TRD	<17	Transition domain	Baba <i>et al.</i> (1993), Buckland <i>et al.</i> (1993)
Eight-armed squid	SAW/SFZ/TRD	8–15	Transition domain	McKinnell and Waddell (1993), Yatsu <i>et al.</i> (1993)
Sooty shearwater	SAW/SFZ/TRD/STR	<19	Subarctic boundary (12–10)	Ogi (1984), Gould and Piatt (1993)
Laysan albatross	SAW/SFZ/TRD/STR	11–20	Transition domain	Gould and Piatt (1993), Springer <i>et al.</i> (1999)
Black-footed albatross	SAW/SFZ/TRD/STR	7–20	Transition domain	Gould and Piatt (1993), Springer <i>et al.</i> (1999)
Pacific saury	SAW/SFZ/TRD/STR	7–20	Subarctic boundary (10.5–12.5)	Ogi (1984), Yatsu <i>et al.</i> (1993)
Blue shark	SAW/SFZ/TRD/STR	8–20	Transition domain (11–16)	Strasburg (1958), Nakano <i>et al.</i> (1985)
Boreal chub-hook squid	SAW/SFZ/TRD/STR	6–15	Transition domain	McKinnell and Waddell (1993), Yatsu <i>et al.</i> (1993)
Salmon shark	SAW/SFZ/TRD	4–11	Transition domain	McKinnell and Waddell (1993), Yatsu <i>et al.</i> (1993)
Pacific white-sided dolphin	SFZ/TRD/STR	11–18	Transition domain	Buckland <i>et al.</i> (1993), Miyashita (1993)
Neon flying squid	SFZ/TRD/STR	10–20	Subtropical front (18–20)	Gong <i>et al.</i> (1993), Yatsu <i>et al.</i> (1993)
Leatherback turtle	SAW/TRD/STR	12–20, 15–18		Weatherall <i>et al.</i> (1993), Yatsu <i>et al.</i> (1993)
Northern right whale dolphin	TRD/STR	12–18	Transition domain	Buckland <i>et al.</i> (1993), Miyashita (1993)
Albacore tuna	TRD/STR	14–20	Transition domain (11–16)	Laurs and Lynn (1991), Kimura <i>et al.</i> (1997)

Range describes surface temperature (SST) conditions inhabited by the various species within subtropical–subarctic waters.

Core habitat refers to the narrower range of sea surface temperature and to the hydrographic features where fisheries catches and sightings are concentrated.

SAW: subarctic water mass; SFZ: subarctic frontal zone; TRD: transition domain; STR: subtropical water mass.

Ephemeral hydrographic features

A network of isolated pelagic protected areas could protect species associated with predictable bathymetric and hydrographic features. However, other ecologically important marine environments are neither fixed in space nor persistent. A variety of physical forcing mechanisms, including upwelling, eddies and filaments generate ephemeral fronts responsible for enhanced production and convergence (Franks, 1992; Larson *et al.*, 1994; Olson *et al.*, 1994). Unlike the persistent features described above, ephemeral hydrographic features are defined by short-lived gradients in water properties. These features vanish once they mix with the surrounding waters. However, highly-mobile pelagic species find and exploit ephemeral fronts while they persist (Laurs *et al.*, 1977; Briggs *et al.*, 1988). Fishermen also understand the significance of these features, which, despite their small extent and short duration, support high catches of valuable species, including tunas, salmonids and billfishes (Laurs *et al.*, 1984; Ignell and Murphy, 1993; Podesta *et al.*, 1993). The need to protect ephemeral hydrographic features is underscored by evidence that these restricted areas represent important habitats of enhanced biological activity, as well as rich fishing grounds, where fisheries catches and bycatch are often concentrated (Uda and Ishino, 1958; Podesta *et al.*, 1993).

Upwelling forcing is one of the best-understood processes responsible for transient gradients in water properties. Upwelling replenishes surface nutrients and enhances primary production by vertically transporting cool, nutrient-rich water to the surface. Upwelling is temporally predictable and occurs seasonally in response to favourable wind conditions. Throughout the season of favourable winds, upwelling episodes can persist from days to weeks (Traganza *et al.*, 1981; Wing *et al.*, 1995). Plumes of recently-upwelled water may extend for tens of kilometres across the shelf and for hundreds of kilometres in the along-shore direction (Mooers and Robinson, 1984; Briggs *et al.*, 1988). Strong gradients in physical and biological properties separate the cool, salty, nutrient-rich upwelling plumes from warmer, fresher, nutrient-poor waters offshore. A variety of pelagic predators, including seabirds, marine mammals and tunas, feed on the neuston, zooplankton and larval fish aggregated at the convergence zones and fronts that delineate upwelling plumes (Laurs *et al.*, 1977; Briggs *et al.*, 1988; Larson *et al.*, 1994).

The interaction of upwelled water with the dominant flow gives rise to ephemeral fronts and eddies disjunct from upwelling centres. For example, off the west coast of North America, large volumes of upwelled water are transported offshore by high-speed jets of cool and productive water. These filaments are thin and elongated features, in the order of 50 km wide and up to several hundreds of kilometres long, which intrude into warmer and nutrient-poor offshore waters. The resulting temperature and ocean colour fronts frequently persist for a few weeks (Traganza *et al.*, 1981; Mooers and Robinson, 1984; Strub *et al.*, 1991). Pelagic predators find and exploit these ephemeral and highly dynamic features before they disintegrate. Off central California, for instance, albacore aggregate along the edge of warm-water filaments intruding into the cooler coastal water, and in the vicinity of cold-water jets advecting offshore (Laurs *et al.*, 1984).

Short-lived fronts are also created along the edges of eddies. These are highly dynamic and ephemeral features formed as a result of flow instabilities along current edges and bathymetric obstacles (Royer, 1978; Owen, 1980, 1981). The dynamic nature and the persistence of eddies make them important habitat features capable of enhancing and retaining primary and secondary production (The Ring Group, 1981; Backus and Craddock, 1982; Olson and Backus, 1985). Eddies are large, conspicuous, and long-lived hydrographic features, with diameters in the order of tens to hundreds of kilometres, and lifespans of up to several months (Owen, 1980, 1981; Robinson, 1983). Their rotation (vorticity) creates secondary flow features, including high-speed peripheral jets, areas of upwelling and downwelling, and convergence zones. Cold-core (anticyclonic) eddies are characterized by the doming of isopycnals and upwelling of nutrient-rich waters at the centre, and by downwelling and retention along the periphery (Schmidt and Vastano, 1976; Owen, 1981). Upwelling within cold-core rings supports enhanced primary production, which is, in turn, exploited by a variety of predators, including seabirds and fish (The Ring Group, 1981; Yoder *et al.*, 1981; Haney, 1986). Conversely, the aggregation of marine predators and their prey within warm-core (cyclonic) eddies

is mediated by convergence and downwelling at their core (Schmidt and Vastano, 1975; Olson and Backus, 1985; Griffin, 1999). Overall, the significance of eddies as habitat features is underscored by evidence that regions where permanent (Costa Rica Dome, Blackburn *et al.*, 1970; Fiedler *et al.*, 1991), and transient (Oyashio–Kuroshio confluence, Uda and Ishino, 1958; Ignell and Murphy, 1993) eddies predictably occur are characterized by elevated primary production, high zooplankton biomass, and the aggregation of pelagic fishes, seabirds and marine mammals.

In addition to coastal upwelling and eddies, wind forcing, deep convection and buoyancy fluxes can create small-scale fronts and convergence zones (Weller, 1985; Olson *et al.*, 1994). These features promote patchiness by aggregating floating objects and weakly-swimming zooplankton (Alldredge, 1982; Hamner and Schneider, 1986). Although the ecological significance of these ephemeral fronts is poorly understood, they appear to constitute important nurseries and foraging habitats for many pelagic species, including sea turtles and billfishes (Carr, 1987; Podesta *et al.*, 1993).

DESIGN RECOMMENDATIONS FOR PELAGIC MPAS

MPAs could conceivably be designed to protect important breeding and foraging grounds associated with three generic types of pelagic habitats: bathymetrically static, hydrographically persistent, and hydrographically ephemeral features. Pelagic protected areas could adopt the ‘core–buffer’ zonation model devised for biosphere reserves, whereby a patchwork of ‘core’, ‘buffer’ and ‘transition’ areas with distinct functional roles and levels of protection are integrated to achieve multiple research, conservation and development goals (Batisse, 1982, 1993; Ray and McCormick-Ray, 1993). Pelagic MPAs based on the ‘core–buffer’ model have already been implemented to protect benthic communities and species inhabiting bathymetrically-defined static habitats (Koslow and Gowlett-Holmes, 1998; Hooker *et al.*, 1999). However, the increasingly dynamic and unpredictable nature of hydrographic features will require more complicated MPA designs.

The simplest scenario entails static MPAs designed to protect geographically fixed and easily discernible bathymetric features, defined by isobaths on a chart. For instance, a small-scale (40 × 40 km) MPA could be designed to protect the diverse cetacean assemblage inhabiting the Gully, a submarine canyon in the Nova Scotian shelf (Figure 2). A fully protected ‘core’ area delineated by the extent of the 200 m and 2000 m isobaths would exclude oil and gas exploitation, boat traffic and fishing. ‘Buffers’ surrounding the ‘core’ area could then be used to protect cetaceans from other ‘low-impact’ activities, such as noise pollution from seismic exploration. This MPA would require year-round enforcement to protect the resident northern bottlenose whale (*Hyperoodon ampullatus*) population and 11 other seasonally-occurring cetaceans (Hooker *et al.*, 1999).

Static protected areas cannot track the dynamic features that many pelagic predators exploit. Thus, one of the most important design modifications necessary to implement effective pelagic MPAs is the use of flexible boundaries, defined by the properties of the water-column. Predictable associations among species’ distributions and easily measurable ocean properties, such as temperature and chlorophyll concentrations, could be used to delineate potential areas of suitable habitat and likely concentration (Smith *et al.*, 1986; Ignell *et al.*, 1995; Polovina *et al.*, 2000).

Large-scale protected areas can be defined on the basis of water mass properties. Particularly, ocean temperature is an ideal variable to delineate dynamic MPA boundaries because it determines, to a great extent, the ranges of pelagic organisms, and it can be readily monitored at sea and remotely from space. In addition, because oceanographers and fisheries biologists already define species ranges on the basis of water temperature, the thermal preferences of many marine predators are already well known (Mikol, 1997; Table 2). Furthermore, fishing fleets already use commercially available analyses of oceanographic conditions to pinpoint profitable fishing areas associated with eddies and frontal zones (Laurs *et al.*, 1984;

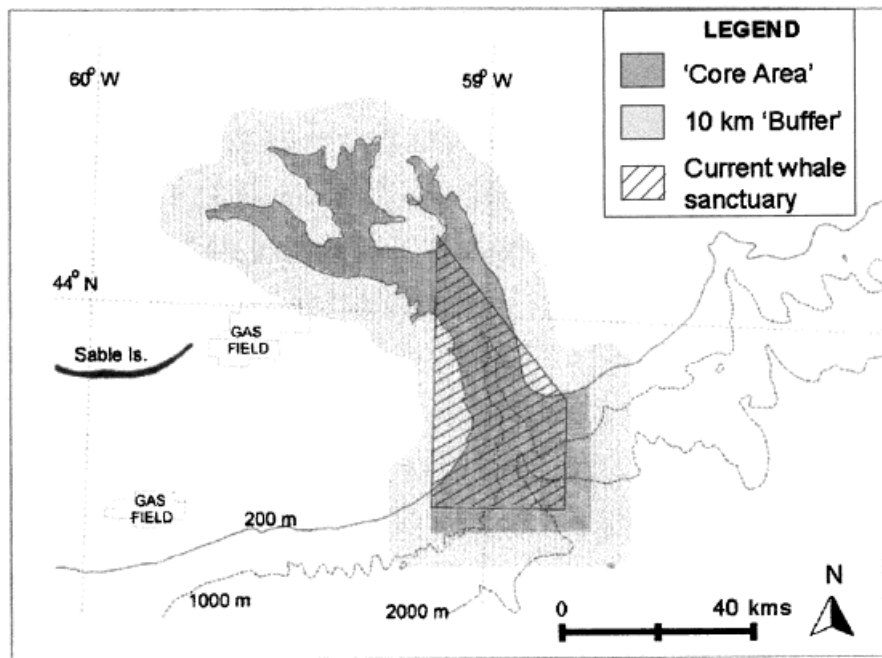


Figure 2. Example of a static MPA around the Gully, off Nova Scotia. The rigid design of the current 'whale sanctuary' contrasts with a bathymetrically defined MPA concept based on a 'core' area delineated by the 200 m and 2000 m isobaths, and a surrounding 10 km 'buffer'. Redrawn from Hooker *et al.* (1999).

Mikol, 1997). For example, the 15°C isotherm defines the southern range limit of North Pacific salmonids (Ignell *et al.*, 1995), while high catches of albacore tuna frequently occur in the vicinity of the 13.9°C thermal front (Mikol, 1997).

The same simple temperature measurements that have been used to pinpoint profitable fishing areas in the past (Laurs *et al.*, 1984; Mikol, 1997), could help define pelagic protected areas in the future. For example, an MPA designed to protect the albacore tuna migration route across the North Pacific Transition Domain could exclude fishing from that species' preferred range of water temperature (11°–16°C; Table 2). Similar regulations have already been used to manage high-seas fisheries in the North Pacific. For instance, during the 1980s, the Japanese large-mesh and squid drifnet fisheries were regulated using a system of seasonal area closures designed to mitigate salmonid bycatch and conflicts between coastal and longline fisheries targeting tunas (Nagao *et al.*, 1993; Nakano *et al.*, 1993). These regulations defined seasonal area closures based on an understanding of the habitat preferences and the seasonal occurrence of threatened non-target species. For instance, to minimize salmonid bycatch, drifnet fisheries were excluded from subarctic waters. This was achieved by restricting fishing effort to the south of a latitudinal boundary, which followed the northward migration of the subarctic boundary and ranged from 40°N (June and December) to 46°N (July) (Nagao *et al.*, 1993; Nakano *et al.*, 1993).

Yet, many pelagic predators exploit habitats that are neither defined by static nor temporally persistent features. The protection of pelagic species that exploit ephemeral hydrographic features, such as eddies and fronts, is inherently difficult because these are dynamic features defined by short-lived gradients in water properties. Eddies, filaments and upwelling plumes drift away, embedded in the dominant flow, age as the water properties change, and finally disappear when the property gradients defining them vanish. Even though these are ephemeral features, they are relatively predictable in space (within tens to hundreds of kilometres), and somewhat (at least seasonally) predictable in time. For example, along eastern

boundary currents, upwelling plumes originate from specific sites, often anchored on coastal points and capes (Traganza *et al.*, 1981; Huyer, 1983; Strub *et al.*, 1991). Jets and squirts also occur at predictable localities offshore from upwelling centres (Traganza *et al.*, 1981; Mooers and Robinson, 1984; Strub *et al.*, 1991). Similarly, regions of strong eddy activity are not uniformly distributed across ocean basins (Roden, 1987; Fu and Cheney, 1995). Eddies are repeatedly spun from meandering currents, forced by wind-driven upwelling, and created downstream from islands, banks and guyots (Barkley, 1968; Bernstein *et al.*, 1977; Owen, 1980). Off California, for instance, semi-permanent eddies are commonplace downstream from the Point Conception and the Point Sur upwelling centres (Huyer, 1983; Haury *et al.*, 1986). In particular, the southern California eddy (SCE) constitutes the most predictable mesoscale feature off California. This is a large (> 200 km diameter) and highly predictable cyclonic eddy, which occurs persistently off southern California between July and January, and periodically between February and May (Wyllie, 1966; Owen, 1980; Figure 3). The fact that many of these ephemeral hydrographic features are somewhat predictable in space, makes it possible to consider 'core' and 'buffer' approaches to the design of MPAs. In each case, geographically fixed (e.g. seamount) and temporally persistent (e.g. water mass boundary) features could be used to delineate 'core' areas defined by the average extent of potential habitats, while 'buffers' could be defined by the variability about those mean conditions.

Extensive 'buffers' will be necessary to reconcile the dynamic water-column properties, and the diffuse physical–biological interactions in pelagic systems with effective MPA designs. 'Buffers' surrounding areas of 'core' habitat would help MPAs accommodate the physical mechanisms that decouple foraging aggregations from the bathymetric and hydrographic features ultimately responsible for water-column mixing and elevated production. For instance, the shedding of Taylor columns and the propagation of trapped eddies likely decouple regions of elevated production and dense prey aggregations from seamounts (Barkley, 1972; Royer, 1978; Cheney *et al.*, 1980). There are also pragmatic reasons to utilize the 'buffer' concept. For example, conditions at the sea surface are often decoupled from the subsurface properties influencing the distribution of pelagic organisms (Murata and Hayase, 1993; Brill, 1994). For instance, the physical and biological signatures of fronts may extend up to several tens of kilometres from the location of their surface expression (e.g. surface isotherms) (Owen, 1981; Franks, 1992). In addition, when predators aggregate at frontal features, they form patches that often match the spatial scales of the front (e.g. Rossby radius, Briggs *et al.*, 1988; Schneider *et al.*, 1990). In fact, even MPAs designed to protect benthic communities and sedentary mating aggregations may benefit from 'buffers' around a bathymetrically-defined 'core' habitat. 'Buffers' have been suggested to mitigate certain far-reaching

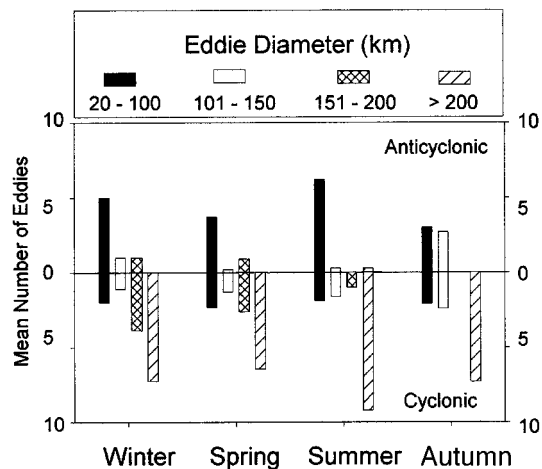


Figure 3. Average 10-year incidence of eddies off southern California (31°–35° N) from the coast to 300 nautical miles offshore (1949–1965). Eddies are characterized by type (cyclonic or anticyclonic) and by size (diameter). Data from Owen (1980).

human activities, and to maintain the linkages between benthic communities and water-column processes (Koslow and Gowlett-Holmes, 1998; Hooker *et al.*, 1999; Probert, 1999).

The understanding of the water mass preferences of marine predators could be used to delineate potential habitats suitable for protection. These areas could then be protected using dynamic MPAs based on the seasonal or permanent closure of large regions (hundreds to thousands of squared kilometres). For instance, off central California, MPAs designed to protect the cool upwelling plumes where cetaceans and seabirds forage could restrict fishing activities to warm waters above a prescribed temperature threshold (Smith *et al.*, 1986; Briggs *et al.*, 1988). Ultimately, MPA designs would be guided by an understanding of the physical forcing mechanisms (e.g. upwelling favourable winds), and of natural history (e.g. seasonal occurrence off California). Pragmatically, such regulations would be communicated to fishing fleets using simple descriptions of the temporal (e.g. months) and spatial (e.g. temperature range) extent of the fishery closures.

The familiar problems of displaced effort and enforcement that complicate nearshore MPAs occur in the pelagic realm as well. For example, shifting fishing activities into less productive areas may actually increase the overall effort. Without reducing effort, any aerial restriction may merely intensify the impacts outside of the MPA by shifting the fishing pressure into adjacent areas. Thus, managers should anticipate the likely ecosystem-level consequences of pelagic MPAs before they are implemented. Narrowly-focused single-species management plans may merely reduce the bycatch of a threatened or popular species at the expense of other taxa. For instance, efforts to protect Eastern Pacific dolphins by setting tuna nets on logs have increased shark bycatch (Hall, 1998). Similarly, setting long-lines at night to protect threatened albatrosses has led to higher bycatch of nocturnal white-chinned petrels (*Procellaria aequinoctialis*) (Weimerskirch *et al.*, 1999).

Another obvious roadblock inhibiting the establishment of pelagic protected areas is the inability to enforce dynamic MPA boundaries in the high seas. Enforcement actions could be based on the ability to determine the location of fishing vessels equipped with transponders, and to survey real-time ocean properties over large-scales using satellite remote sensing (Bernstein *et al.*, 1977; Smith *et al.*, 1986; Fu and Cheney, 1995).

OCEAN BASIN MANAGEMENT

Ultimately, society will need a holistic management scheme for entire ocean basins. Such overarching management will depend upon the use of many innovative tools, including the judicious implementation of MPAs. Clearly there are no all-serving management techniques because the scaling is so variable. Steele (1978) and Denman (1994) selected the dimensions of patches and the ambits of species as appropriate spatio-temporal scales for the study of pelagic systems. Similarly, the scales of ocean management can be defined by foraging/breeding aggregations, and the ranges of the vulnerable populations and species (Prince *et al.*, 1992; Ray and McCormick-Ray, 1993; Saunders and McFarlane, 1997). However, there is a great deal of uncertainty in this approach because the ambits of pelagic organisms range in the order of tens, hundreds and thousands of kilometres for plankton, small nektonic organisms (forage fish and squid) and large nekton (seabirds, cetaceans and tunas), respectively (Hauray *et al.*, 1978; Steele, 1978; Hunt and Schneider, 1987). Basin-wide MPAs might be required to protect far-ranging species, such as the wandering albatross (*Diomedea exulans*), the sperm whale (*Physeter macrocephalus*) and the leatherback turtle.

Our inability to protect far-ranging species is particularly problematic in oceanic systems, where highly-mobile vertebrates range across entire ocean basins (Eckert and Sarti, 1997; Spear and Ainley, 1999; Weimerskirch *et al.*, 1999). In spite of the recognition for the need to link isolated MPAs into networks (Ogden, 1997; Ray, 1999), the design of protected oceanic corridors remains a daunting challenge because migration routes are dynamic and often poorly understood (Laurs and Lynn, 1991; Resendiz *et al.*, 1997; Spear and Ainley, 1999). In fact, even when predictable migratory pathways do exist, it would be impossible

to set aside movement corridors for all threatened species. This line of thought has led to the conclusion that large MPAs should encompass a large proportion (50–90%) of the total suitable habitat (Mills and Carlton, 1998; Boersma and Parrish, 1999).

MPAs designed to protect specific foraging and mating grounds could mitigate certain forms of habitat degradation (e.g. oil spills, noise pollution and changing disturbance regimes), and mortality (e.g. bycatch and boat strikes). It is unlikely, however, that a network of isolated MPAs would grant far-ranging species protection because impacts outside of the protected areas would not be properly mitigated (Kooyman *et al.*, 1996; Eckert and Sarti, 1997; Boersma and Parrish, 1999). Thus, the foraging ranges and the migration routes of pelagic species are also relevant for the design of pelagic protected areas.

The ineffectiveness of isolated MPAs and our inability to protect vast networks of movement corridors represent major roadblocks to pelagic conservation. Yet, since the ocean is the habitat of many highly endangered pelagic vertebrates, conservation and management measures must seek solutions at comparable large scales (Prince *et al.*, 1992; Eckert and Sarti, 1997; Weimerskirch *et al.*, 1999). In particular, it is our contention that pelagic MPA designs must scale up the protection of isolated habitat features and protect large-scale features of the global ocean.

An example of potential basin-wide management tactics for the North Pacific would focus on the ecological importance of the North Pacific Transition Domain. The Transition Domain supports a rich and diverse fauna, comprising cosmopolitan, subarctic and subtropical visitors, as well as endemic transitional species (Fager and McGowan, 1963; McKinnell and Waddell, 1993; Yatsu *et al.*, 1993). At least 40 species of seabirds, 18 cetaceans, two pinnipeds, three sea turtles, five squids, four sharks and 24 bony fishes, including economically valuable salmonids and tunas, occur at some time of the year in the Transition Domain (Brodeur *et al.*, 1999; Springer *et al.*, 1999; Table 2). A large-scale, dynamic MPA delineated by the location of sea surface isotherms could be used to protect commercially valuable and non-target pelagic species during their transpacific migration across the Transition Domain (Figure 4).

However, most of these species also migrate extensively throughout the basin, often following the currents that form the North Pacific gyre (Morreale *et al.*, 1996; Spear and Ainley, 1999; Polovina *et al.*, 2000). Protection within the North Pacific Transition Domain will be ineffective if these same species

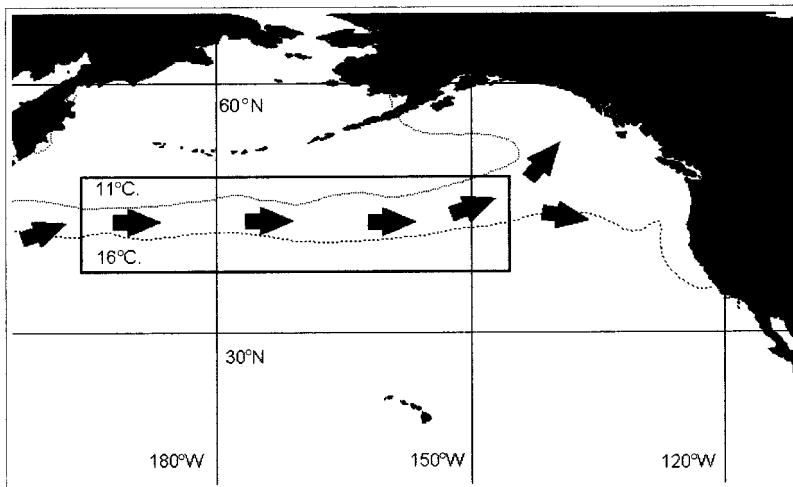


Figure 4. Example of a dynamic, large-scale MPA defined by sea surface temperature isotherms delineating the North Pacific Transition Domain (16–11°C). Isotherms during July 1998 provide a static snapshot of otherwise dynamic frontal features. Arrows indicate the flow of the North Pacific current and the likely migration route of albacore tuna across the basin. Trimmed 1° SST monthly mean data courtesy of the Pacific Fisheries Environmental Laboratory (<http://www.pfeg.noaa.gov/>).

experience significantly higher mortality during the remainder of their migratory cycles from displaced fishing effort. Traditional corridors tend to be idiosyncratic for specific species, and in any case, are impossible here. One solution might be a single protected area, in the form of a ring encompassing the mid-section of the currents forming the North Pacific gyre, that might protect species throughout their migratory ranges (Figure 5). In such a design, any given cross-section of the broad migratory routes will have a 'safe' path through which at least some individuals can migrate unharmed.

Thus, dynamic MPAs could be designed to protect large hydrographic features of the global ocean. The permanent fronts defining water mass boundaries and current systems constitute ideal features for the design of large-scale pelagic MPAs due to their predictability (Table 1). In particular, the strong concordance between nekton species assemblages and water-column properties provides an effective foundation for the design of large-scale dynamic MPAs defined by water properties (Table 2).

The establishment of dynamic MPAs designed to protect pelagic migration routes in the North Pacific would represent an ecosystem management approach to the conservation of both pelagic vertebrates and fisheries resources. Such large-scale MPA concepts would address immediate conservation goals by granting protection to breeding aggregations (e.g. neon flying squid), mature and fecund individuals (e.g. blue sharks, leatherback turtles and salmonids), and juveniles (e.g. fur seals, shearwaters and albacore tuna) of threatened and economically-important far-ranging species. In addition, longer-term conservation goals would be addressed by protecting large-scale ocean features critical to many other pelagic species. Thus, this multi-species approach would represent a proactive and precautionary conservation umbrella designed to protect fisheries resources and pelagic vertebrates before they became endangered (Mangel *et al.*, 1996; Dayton, 1998).

We support the protection of substantial areas of ecologically important and persistent hydrographic features, such as fronts, boundary currents and gyres, to ensure the long-term conservation of pelagic species and fishery resources. Here, we have focused on the North Pacific Transition Domain. However, similar design concepts could be applied to other equally important regions of the world's ocean, such as the Bering Sea green belt, the Costa Rica dome, the equatorial convergence, the Oyashio–Kuroshio confluence, the Antarctic polar front, and the California current.

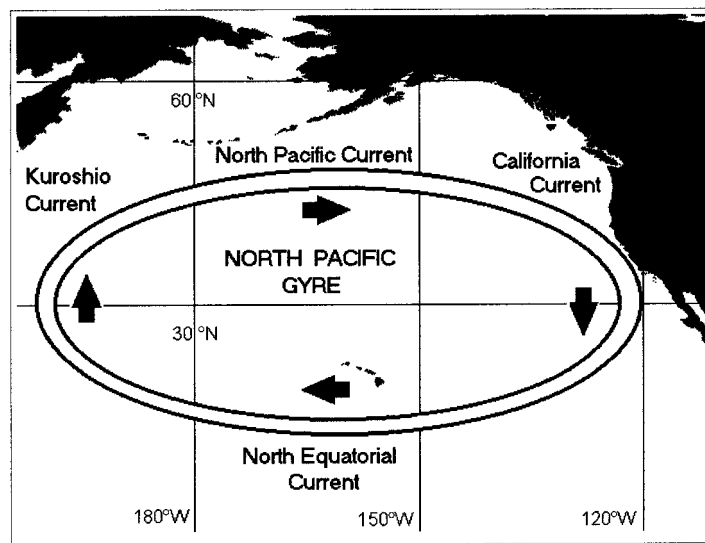


Figure 5. Schematic of a large-scale pelagic MPA encompassing the average location of the currents forming the North Pacific gyre. Arrows indicate the direction of water flow around the basin, and the likely migration route of many far-ranging pelagic vertebrates.

Technological roadblocks have inhibited implementation of large-scale conservation measures in the world's oceans. Recent advances (e.g. global positioning systems, large-scale monitoring of ocean conditions using satellite remote sensing, remote detection and monitoring of vessels using acoustic and satellite technologies) will facilitate the implementation, enforcement and evaluation of pelagic MPAs. Similarly, the ability to implement conservation actions at the necessary large scales may open the door to the design of large-scale pelagic protected areas (e.g. highly migratory and straddling stocks agreement (Aqorau and Bergin, 1998); bycatch mitigation plans (FAO, 1997); international pelagic species conservation plans (FAO, 1998); United Nations drifnet resolution (United Nations, 1991)).

Clearly, this approach relies on political will which is not yet apparent. However, it represents the safest way to ensure the long-term conservation of pelagic vertebrates and fisheries resources, given the constraints of (1) imperfect knowledge of the habitats of all threatened pelagic species, (2) limited ability to establish MPAs specifically designed to protect every single threatened species, and (3) the realization that the processes responsible for the aggregation of pelagic vertebrates at isolated features may change in the future, particularly in light of changing global climate. Our basic objective is to demonstrate that, despite the many large uncertainties regarding ocean processes, the scientific information is presently available to implement sweeping environmental reform that can protect our oceanic heritage, if only humanity can find the political willpower to proceed.

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REFERENCES

- Agardy MT. 1994. Advances in marine conservation: the role of marine protected areas. *Trends in Ecology and Evolution* **9**: 267–270.
- Allredge AL. 1982. Aggregation of spawning appendicularians in surface windrows. *Bulletin of Marine Science* **32**: 250–254.
- Alverson DL, Freeberg MH, Pope JG, Murawski SA. 1994. A global assessment of fisheries bycatch and discards. In *FAO Fisheries Technical Paper*, No. 339. FAO: Rome.
- Aqorau T, Bergin A. 1998. The UN Fish Stocks Agreement—a new era for international cooperation to conserve tuna in the central western Pacific. *Ocean Development and International Law* **29**: 21–42.
- Aron W. 1962. The distribution of animals in the eastern North Pacific and its relationship to physical and chemical conditions. *Journal Fisheries Research Board of Canada* **19**: 271–314.
- Baba N, Kiyota M, Hatanaka H, Nitta A. 1993. Biological information and mortality of northern fur seals (*Callorhinus ursinus*) by the high seas Japanese squid drifnet fishery. *International North Pacific Fisheries Commission Bulletin* **53**: 461–472.
- Backus RH, Craddock JE. 1982. Mesopelagic fishes in Gulf Stream cold core rings. *Journal of Marine Research* **40**(Supplement): 1–20.
- Ballance LT, Pitman RL, Reilly SB. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* **78**: 1502–1518.
- Barkley RA. 1968. The Kuroshio–Oyashio front as a compound vortex street. *Journal of Marine Research* **26**: 83–104.
- Barkley RA. 1972. Johnston Atoll's wake. *Journal of Marine Research* **30**: 201–216.
- Bartoo N, Holts D, Brown C. 1993. Evidence of interactions between high seas drifnet fisheries and the North American Troll Fishery for albacore. *International North Pacific Fisheries Commission Bulletin* **53**: 367–380.
- Batisse M. 1982. The biosphere reserve: a tool for environmental conservation and management. *Environmental Conservation* **9**: 101–111.
- Batisse M. 1993. Development and implementation of the biosphere reserve concept and its applicability to coastal regions. In *Application of the Biosphere Reserve Concept to Coastal Marine Areas: Papers Presented at the*

- UNESCO/IUCN San Francisco Workshop of 14–20 August 1989, Price A, Humphrey S (eds). IUCN: Gland, Switzerland; 1–11.
- Bernstein RL, Breaker L, Whritner R. 1977. California current eddy formation: ship, air, and satellite results. *Science* **195**: 353–359.
- Blackburn M, Laurs RM, Owen RW, Zeitzschel B. 1970. Seasonal and areal changes in standing stocks of phytoplankton, and micronekton in the eastern tropical Pacific. *Marine Biology* **7**: 14–31.
- Boehlert GW, Genin A. 1987. A review of the effects of seamounts on biological processes. In *Seamounts, Islands and Atolls*, Geophysical Monograph 43, Keating BH, Fryer P, Batiza R, Boehlert GW (eds). American Geophysical Union: Washington, DC; 319–334.
- Boehlert GW, Sasaki T. 1988. Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean. *Fishery Bulletin* **86**: 453–465.
- Boersma PD, Parrish JK. 1999. Limiting abuse: marine protected areas, a limited solution. *Ecological Economics* **31**: 287–304.
- Brander K. 1981. Disappearance of common skate *Raja batis* from the Irish Sea. *Nature* **290**: 48–49.
- Briggs KT, Ainley DG, Spear LB, Adams PB, Smith SE. 1988. Distribution and diet of Cassin's auklet and common murre in relation to central California upwellings. *Proceedings of the International Ornithological Congress* **19**: 983–990.
- Brill RW. 1994. A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessment. *Fisheries Oceanography* **3**: 204–216.
- Brodere R, McKinnell S, Nagasawa K, Percy W, Radchenko V, Tagaki S. 1999. Epipelagic nekton of the North Pacific subarctic and Transition Zones. *Progress in Oceanography* **43**: 365–397.
- Buckland ST, Cattanch KL, Hobbs RC. 1993. Abundance estimates of Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise and northern fur seal in the North Pacific. *International North Pacific Fisheries Commission Bulletin* **53**: 387–407.
- Carlton JT. 1993. Neoextinctions of marine invertebrates. *American Zoologist* **33**: 499–509.
- Carr A. 1987. New perspective in the development of the pelagic stage of sea turtle development. *Conservation Biology* **1**: 103–121.
- Casey JM, Myers RA. 1998. Near extinction of a large, widely distributed fish. *Science* **281**: 690–692.
- Cheney RE, Richardson PL, Nagasawa K. 1980. Tracking a Kuroshio ring with a free drifting buoy. *Deep-Sea Research* **27**: 641–654.
- Comeau LA, Vezina AF, Bourgeois M, Juniper SK. 1995. Relationship between phytoplankton production and the physical structure near Cobb Seamount, Northeast Pacific. *Deep-Sea Research* **42**: 993–1005.
- Croxall JP, Gales R. 1997. An assessment of the conservation status of albatrosses. In *Albatross Biology and Conservation*, Robertson G, Gales R (eds). Surrey Beatty and Sons Ltd: Chipping Norton; 46–65.
- Dahlberg ML, Day RH. 1985. Observations of man-made objects on the surface of the North Pacific. In *Proceedings of the Workshop on the Fate and Impact of Marine Debris*, 27–29 November 1984, Honolulu, Hawaii, Shomura RS, Yoshida HO (eds). NOAA-TM-NMFS-SWFC-54, US Department of Commerce, NOAA Technical Memorandum, NMFS: Honolulu, HI; 198–212.
- Dayton PK. 1998. Reversal of the burden of proof in fisheries management. *Science* **279**: 821–822.
- Dayton PK, Thrush SF, Agardy MT, Hofman RJ. 1995. Viewpoint environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**: 205–232.
- De Fontaubert AC, Downes DR, Agardy TS. 1996. *Biodiversity in the Seas: Implementating the Convention of Biological Diversity in Marine and Coastal Habitats*. World Conservation Union: Washington, DC.
- Denman KL. 1994. Scale-determining biological–physical interactions in oceanic food webs. In *Aquatic Ecology: Scale, Pattern and Process*, Giller PS, Hildrew AG, Raffaelli DG (eds). Blackwell Scientific: Oxford; 377–402.
- Doty MS, Oguri M. 1956. The island mass effect. *Journal of the International Council for the Exploration of the Sea* **22**: 33–37.
- Eckert SA, Sarti L. 1997. Distant fisheries implicated in the loss of the World's largest leatherback nesting population. *Marine Turtle Newsletter* **78**: 2–7.
- Ensor PH, Shaughnessy PD. 1990. Fur seals over the Kerguelen Plateau and elsewhere in the southern Ocean. *Polar Biology* **10**: 481–483.
- Fager EW, McGowan JA. 1963. Zooplankton species groups in the North Pacific. *Science* **140**: 453–460.
- FAO. 1997. Implementation of the code of conduct for responsible fisheries and other instruments. Food and Agriculture Organization Fisheries Department, DM/SW/97/5. <http://www.fao.org/fi/agreem/codecond/ficonde.asp> [27 Sept. 2000].
- FAO. 1998. The international plan of action for the conservation and management of sharks. Food and Agriculture Organization Fisheries Department. <http://www.fao.org/fi/ipa/manage.asp> [27 Sept. 2000].

- Favourite F, Dodimead AJ, Nasu K. 1976. Oceanography of the subarctic Pacific region. *International North Pacific Fisheries Commission Bulletin* **33**: 1–187.
- Fiedler PC, Philbrick V, Chavez F. 1991. Oceanic upwelling and productivity in the eastern Tropical Pacific. *Limnology and Oceanography* **36**: 1834–1850.
- Fiedler PC, Reilly SB, Hewitt RP, Demer D, Philbrick VA, Smith S, Armstrong W, Croll DA, Tershy BR, Mate BR. 1998. Blue whale habitat and prey in the California Channel Islands. *Deep-Sea Research* **45**: 1781–1801.
- Franklin B. 1786. A letter from Dr. Benjamin Franklin to Mr. Alphonsus le Roy . . . containing sundry maritime observations. *Transactions of the American Philosophical Society* **2**: 294–329.
- Franks PJS. 1992. Swim or sink: accumulation of biomass at fronts. *Marine Ecology Progress Series* **82**: 1–12.
- Fournier RO, Van Det M, Wilson JS, Hargreaves NB. 1979. Influence of the shelf-break off Nova Scotia on phytoplankton standing stock in winter. *Journal of the Fisheries Board of Canada* **36**: 1228–1237.
- Fu LL, Cheney RE. 1995. Application of satellite altimetry to ocean circulation studies: 1987–1994. *Reviews of Geophysics* **33** (Suppl.): 213–223.
- Galt JA. 1985. Oceanographic factors affecting the predictability of drifting objects at sea. In *Proceedings of the Workshop on the Fate and Impact of Marine Debris*, 27–29 November 1984, Honolulu, Hawaii, Shomura RS, Yoshida HO (eds). NOAA-TM-NMFS-SWFC-54, US Department of Commerce, NOAA Technical Memorandum, NMFS: Honolulu, HI; 497–507.
- Genin A, Haury L, Greenblatt P. 1988. Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. *Deep-Sea Research* **35**: 151–175.
- Gong Y, Kim S, An DH. 1993. Abundance of neon flying squid in relation to oceanographic conditions in the North Pacific. *International North Pacific Fisheries Commission Bulletin* **53**: 191–204.
- Gould PJ, Forsell DJ, Lensink CJ. 1982. Pelagic distribution and abundance of seabirds in the Gulf of Alaska and eastern Bering Sea. FWS/OBS-82/84, US Department of Interior, Fish and Wildlife Service, Washington, DC.
- Gould PJ, Piatt JF. 1993. Seabirds of the central North Pacific. In *The Status, Ecology, and Conservation of Marine Birds of the North Pacific*, Vermeer K, Briggs KT, Morgan KH, Siegel-Causey D (eds). Canadian Wildlife Service: Ottawa; 27–38.
- Griffin RB. 1999. Sperm whale distributions and community ecology associated with a warm-core ring off Georges Bank. *Marine Mammal Science* **15**: 33–51.
- Hall MA. 1998. An ecological view of the tuna-dolphin problem: impacts and trade-offs. *Reviews in Fish Biology and Fisheries* **8**: 1–34.
- Hamner WH, Schneider DC. 1986. Regularly spaced rows of medusae in the Bering Sea: role of Langmuir circulation. *Limnology and Oceanography* **31**: 171–177.
- Haney JC. 1986. Seabird aggregation at Gulf Stream frontal eddies. *Marine Ecology Progress Series* **28**: 279–285.
- Haney JC, Haury LR, Mullineaux LS, Fey CL. 1995. Sea-bird aggregation at a deep North Pacific seamount. *Marine Biology* **123**: 1–9.
- Haury LR, Fey C, Hobday A, Genin A. 1995. Copepod carcasses in the ocean. I. Over seamounts. *Marine Ecology Progress Series* **123**: 57–63.
- Haury LR, Mc Gowan JA, Wiebe PH. 1978. Patterns and processes in the time-space scales of plankton distributions. In *Spatial Patterns in Plankton Communities*, Steele JH (ed.). Plenum Press: New York; 277–327.
- Haury LR, Simpson JJ, Pelaez J. 1986. Biological significance of a recurrent eddy off Point Conception, California. *Journal of Geophysical Research* **91**(C11): 12937–12956.
- Holligan PM. 1981. Biological implications of fronts on the north-west European continental shelf. *Philosophical Transactions of the Royal Society of London* **302**: 547–562.
- Hooker SK, Whitehead H, Gowans S. 1999. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology* **13**: 592–602.
- Hunt GL Jr, Schneider DC. 1987. Scale dependent processes in the physical and biological environment of seabirds. In *The Feeding Ecology of Seabirds and their Role in Marine Ecosystems*, Croxall JP (ed.). Cambridge University Press: Cambridge; 7–41.
- Hunt GL Jr, Coyle KO, Hoffman S, Decker MB, Flint EN. 1996. Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. *Marine Ecology Progress Series* **141**: 1–11.
- Hunt GL Jr, Russell RW, Coyle KO, Weingartner T. 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series* **167**: 241–259.
- Hunt GL, Mehlum F, Russell RW, Irons D, Decker MB, Becker PH. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. *Proceedings of the International Ornithological Congress* **22**: 2040–2056.
- Huyer A. 1983. Coastal upwelling in the California current system. *Progress in Oceanography* **12**: 259–284.
- Ignell SE, Murphy JM. 1993. Salmonid spatial patterns near the North Pacific subarctic frontal zone. *International North Pacific Fisheries Commission Bulletin* **53**: 253–271.

- Ignell SE, Carlson SR, Rumbaugh RA. 1995. Variability in frontal boundaries, temperatures, and the ranges of species and pelagic marine communities along 175°30'E, 1978–9191. In *Climate Change and Northern Fish Populations*, Canadian Special Publication in Fisheries and Aquatic Sciences, vol. 121, Beamish RJ (ed.). National Research Council: Ottawa; 667–674.
- Jaquet N, Whitehead H, Lewis M. 1996. Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. *Marine Ecology Progress Series* **145**: 1–10.
- Kimura S, Nakai M, Sugimoto T. 1997. Migration of albacore, *Thunnus alalunga*, in the North Pacific Ocean in relation to large oceanic phenomena. *Fisheries Oceanography* **6**: 51–57.
- Klimley AP. 1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biology* **117**: 1–22.
- Koslow JA. 1997. Seamounts and the ecology of deep-sea fisheries. *American Scientist* **85**: 168–176.
- Koslow JA, Gowlett-Holmes K. 1998. The seamount fauna off southern Tasmania: benthic communities, their conservation and impacts of trawling. Final Report to Environment Australia and the Fisheries Research Development Corporation, FRDC Project 95/058.
- Kooyman GL, Kooyman TG, Horning M, Kooyman CA. 1996. Penguin dispersal after fledging. *Nature* **383**: 397.
- Larson RJ, Lenarz WH, Ralston S. 1994. The distribution of pelagic juvenile rockfish of the genus *Sebastes* in the upwelling region off central California. *California Cooperative Oceanic Fisheries Investigations Reports* **35**: 175–219.
- Lauris RM, Yuen HSH, Johnson JH. 1977. Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. *Fishery Bulletin* **75**: 347–355.
- Lauris RM, Fiedler PC, Montgomery DR. 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Research* **31**: 1085–1099.
- Lauris RM, Lynn RJ. 1991. North Pacific albacore ecology and oceanography. In *Biology, Oceanography, and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone: Papers from the North Pacific Transition Zone Workshop*, 9–11 May 1988, Wetherall JA (ed.). NMFS 105, US Department of Commerce, NOAA Technical Report, NMFS: Springfield, VA; 69–87.
- LeFevre J. 1986. Aspects of the biology of frontal systems. *Advances in Marine Biology* **23**: 163–299.
- Logerwell EA, Hearnreaves NB. 1996. The distribution of sea birds relative to their fish prey off Vancouver Island—opposing results at large and small spatial scales. *Fisheries Oceanography* **5**: 163–175.
- Logerwell EA, Hewitt RP, Demer DA. 1998. Scale-dependent patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. *Ecography* **21**: 212–223.
- Lynn RJ. 1986. The subarctic and northern subtropical fronts in the eastern North Pacific Ocean in spring. *Journal of Physical Oceanography* **16**: 209–222.
- Mangel M, Talbot LM, Meffe GK, Agardy MT, Alverson DL, Barlow J, Botkin DB, Budowski G, Clark T, Cooke J, Crozier RH, Dayton PK, Elder DL, Fowler CW, Funtowicz S, Giske J, Hofman RJ, Holt SJ, Kellert SR, Kimball LA, Ludwig D, Magnusson K, Malayang BS III, Mann C, Norse EA, Northridge SP, Perrin WF, Perrings C, Peterman RM, Rabb GB, Regier HA, Reynolds JE III, Sherman K, Sissenwine MP, Smith TD, Starfield A, Taylor RJ, Tillman MF, Toft C, Twiss JR Jr, Wilen J, Young TP. 1996. Principles for the conservation of wild living resources. *Ecological Applications* **6**: 338–362.
- McArdle DB. 1997. *California Marine Protected Areas*. Sea Grant College Program: La Jolla, CA.
- McGowan JA, Walker PW. 1985. Dominance and diversity maintenance in an oceanic ecosystem. *Ecological Monographs* **55**: 103–118.
- McKinnell S, Waddell B. 1993. Associations of species caught in the Japanese large scale pelagic squid drifnet fishery in the central North Pacific Ocean: 1988–1990. *International North Pacific Fisheries Commission Bulletin* **53**: 91–146.
- Mikol B. 1997. Temperature directed fishing: how to reduce bycatch and increase productivity. Marine Advisory Bulletin No. 48, Alaska Seagrant College Program, University of Alaska, Fairbanks.
- Mills CE, Carlton JT. 1998. Rationale for a system of international reserves for the open ocean. *Conservation Biology* **12**: 244–247.
- Mishima S. 1981. On the passing over of subtropical fishes to the subarctic region in the summer season. *Bulletin of the Faculty of Fisheries Hokkaido University*, Special Volume: 61–71.
- Miyashita T. 1993. Distribution and abundance of some dolphins taken in the North Pacific drifnet fisheries. *International North Pacific Fisheries Commission Bulletin* **53**: 435–450.
- Mooers CNK, Robinson AR. 1984. Turbulent jets and eddies in the California current and inferred cross-shore transport. *Science* **223**: 51–53.
- Morreale SJ, Standora EA, Spotila JR, Paladino FV. 1996. Migration corridor for sea turtles. *Nature* **384**: 319–320.
- Murata M, Hayase S. 1993. Life history and biological information on flying squid (*Ommastrephes bartramii*) in the North Pacific Ocean. *International North Pacific Fisheries Commission Bulletin* **53**: 147–182.

- Murray SN, Ambrose RF, Bonshack JA, Botsford LW, Carr MH, Davis GE, Dayton PK, Gotshall D, Gunderson DR, Hixon MA, Lubchenco J, Mangel M, MacCall A, McArdle DA, Ogden JC, Roughgarden J, Starr RM, Tegner MJ, Yoklavich M. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries* **24**(11): 11–25.
- Nagao K, Ota S, Hirono J. 1993. Regulation of the Japanese high seas drifnet fisheries. *International North Pacific Fisheries Commission Bulletin* **53**: 39–44.
- Nakano H, Makiyama M, Shimazaki K. 1985. Distribution and biological characteristics of the blue shark in the central North Pacific. *Bulletin of the Faculty of Fisheries Hokkaido University* **36**: 99–113.
- Nakano H, Okada K, Watanabe Y, Uosaki K. 1993. Outline of the large-mesh drifnet fishery of Japan. *International North Pacific Fisheries Commission Bulletin* **53**: 25–37.
- Obst BS. 1985. Densities of Antarctic seabirds at sea and the presence of the krill *Euphausia superba*. *The Auk* **102**: 540–549.
- Ogden JC. 1997. Marine managers look upstream for connections. *Science* **278**: 1414–1415.
- Ogi H. 1984. Feeding ecology of the sooty shearwater in the western subarctic North Pacific Ocean. In *Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships*, Nettleship DN, Sanger GA, Springer PF (eds). Canadian Wildlife Service: Ottawa; 78–84.
- Olson DB, Backus RH. 1985. The concentration of organisms at fronts: a cold-water fish and a warm-core ring. *Journal of Marine Research* **43**: 113–137.
- Olson DB, Hitchcock GL, Mariano AJ, Ashjan CJ, Peng G, Nero RW, Podesta GP. 1994. Life on the edge: marine life and fronts. *Oceanography* **7**(2): 52–60.
- Olson DB, Podesta GP. 1987. Oceanic fronts as pathways in the sea. In *Signposts in the Sea*, Herrnkind WF, Thistle AB (eds). Florida State University: Tallahassee; 1–15.
- Owen RW. 1980. Eddies of the California current system: physical and ecological characteristics. In *The California Islands: Proceedings of a Multidisciplinary Symposium*, Power DM (ed.). Santa Barbara Museum of Natural History: Santa Barbara, CA; 237–263.
- Owen RW. 1981. Fronts and eddies in the sea: mechanisms, interactions and biological effects. In *Analysis of Marine Ecosystems*, Longhurst AR (ed.). Academic Press: New York; 197–231.
- Pauly D, Christensen V. 1995. Primary production required to sustain global fisheries. *Nature* **374**: 255–257.
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. 1998. Fishing down marine food webs. *Science* **279**: 860–863.
- Pearcy WG. 1991. Biology of the transition region. In *Biology, Oceanography, and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone: Papers from the North Pacific Transition Zone Workshop*, 9–11 May 1988, Honolulu, Hawaii, Wetherall JA (ed.). NMFS 105, US Department of Commerce, NOAA Technical Report, NMFS: Springfield, VA; 39–55.
- Piatt JF. 1990. The aggregative response of common murre and Atlantic puffins to schools of capelin. *Studies in Avian Biology* **14**: 36–51.
- Podesta GP, Browder JA, Hoey JJ. 1993. Exploring the association between swordfish catch rates and thermal fronts on US longline grounds in the western North Atlantic. *Continental Shelf Research* **13**: 253–277.
- Polovina JJ, Kobayashi DR, Parker DM, Seki MP, Balazs GH. 2000. Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fisheries Oceanography* **9**: 1–13.
- Prince PA, Wood AG, Barton T, Croxall JP. 1992. Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the south Atlantic. *Antarctic Science* **4**: 31–36.
- Probert PK. 1999. Seamounts, sanctuaries and sustainability: moving towards deep-sea conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**: 601–605.
- Ray GC. 1976. Critical marine habitats: definition, description, criteria and guidelines for identification and management. In *An International Conference on Marine Parks and Reserves, Tokyo, Japan*. IUCN: Morges, Switzerland; 15–59.
- Ray CG. 1999. Coastal-marine protected areas: agonies of choice. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**: 607–614.
- Ray GC, McCormick-Ray MG. 1993. Challenges for biosphere reserves in coastal marine realms: representing ecological scales. In *Application of the Biosphere Reserve Concept to Coastal Marine Areas: Papers Presented at the UNESCO/IUCN San Francisco Workshop of 14–20 August 1989*, Price A, Humphrey S (eds). IUCN: Gland, Switzerland; 13–20.
- Resendiz A, Resendiz B, Nichols WJ, Seminoff JA, Kamezaki N. 1997. First confirmed east–west transpacific movement of a loggerhead sea turtle, *Caretta caretta*, released in Baja California, Mexico. *Pacific Science* **52**: 151–153.

- Robbins CS, Sauer JR, Greenberg RS, Droege S. 1989. Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Sciences* **86**: 7658–7862.
- Roberts CM, Hawkins JP. 1999. Extinction risk in the sea. *Trends in Ecology and Evolution* **14**: 241–246.
- Robinson AR. 1983. Overview and summary of eddy science. In *Eddies in Marine Science*, Robinson AR (ed.). Springer-Verlag: New York; 3–15.
- Robinson GA. 1992. Benguela upwelling: how does it affect South Africa's conservation philosophy? In *Benguela Trophic Functioning*, South African Journal of Marine Science **12**, Payne AIL, Brink KH, Mann KH, Hilborn R (eds). Sea Fisheries Institute: Cape Town; 1063–1067.
- Roden GI. 1987. Effect of seamounts and seamount chains on ocean circulation and thermohaline structure. In *Seamounts, Islands and Atolls*, Geophysical Monograph **43**, Keating BH, Fryer P, Batiza R, Boehlert GW (eds). American Geophysical Union: Washington, DC; 335–354.
- Roden GI. 1991. Subarctic-subtropical transition zone of the North Pacific: large scale aspects and mesoscale structure. In *Biology, Oceanography, and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone: Papers from the North Pacific Transition Zone Workshop*, 9–11 May 1988, Honolulu, Hawaii, Wetherall JA (ed.). NMFS 105, US Department of Commerce, NOAA Technical Report, NMFS: Springfield, VA; 1–38.
- Rose GA, Leggett WC. 1990. The importance of scale to predator prey spatial correlations—an example of Atlantic fishes. *Ecology* **71**: 33–43.
- Royer TC. 1978. Ocean eddies generated by seamounts in the North Pacific. *Science* **199**: 1063–1064.
- Russ GR, Alcalá AC. 1998. Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. *Coral Reefs* **17**: 399–416.
- Safina C. 1995. The world's imperiled fish. *Scientific American* **273**: 46–53.
- Saunders MW, McFarlane GA. 1997. Observations of the spawning distribution and biology of offshore Pacific hake (*Merluccius productus*). *California Cooperative of Oceanic Fisheries Investigations Reports* **38**: 147–157.
- Schmidtz JE, Vastano AC. 1975. Entrainment and diffusion in a Gulf Stream cyclonic ring. *Journal of Physical Oceanography* **5**: 93–97.
- Schmidtz JE, Vastano AC. 1976. On entrainment and diffusion in a Gulf of Mexico anticyclonic ring. *Journal of Physical Oceanography* **6**: 399–402.
- Schneider DC. 1991. The role of fluid dynamics in the ecology of marine birds. *Oceanography Marine Biology Annual Reviews* **29**: 487–521.
- Schneider DC. 1994. Scale-dependent patterns and species interactions in marine nekton. In *Aquatic Ecology: Scale, Pattern and Process*, Giller PS, Hildrew AG, Raffaelli DG (eds). Blackwell Scientific: Oxford; 441–467.
- Schneider DC, Pierotti R, Threlfall W. 1990. Alcid patchiness and flight direction near a colony in eastern Newfoundland. *Studies in Avian Biology* **14**: 23–35.
- Shimazaki K. 1986. Distribution of the pelagic fish community around the subarctic boundary in the North Pacific Ocean. *International North Pacific Fisheries Commission Bulletin* **47**: 247–264.
- Schoenherr JR. 1991. Blue whales feeding on high concentrations of euphausiids around Monterey submarine canyon. *Canadian Journal of Zoology* **69**: 583–594.
- Simard Y, de Ladurantaye R, Therriault JC. 1986. Aggregation of euphausiids along a coastal shelf upwelling environment. *Marine Ecology Progress Series* **32**: 203–215.
- Simpson JH, Tett PB. 1986. Island stirring effects on phytoplankton growth. In *Tidal Mixing and Plankton Dynamics*, Bowman MJ, Yentsch CM, Peterson WT (eds). Springer-Verlag: Berlin; 41–76.
- Sinclair EH. 1991. Review of the biology and distribution of the neon flying squid (*Ommastrephes bartrami*) in the North Pacific Ocean. In *Biology, Oceanography, and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone: Papers From the North Pacific Transition Zone Workshop*, 9–11 May 1988, Honolulu, Hawaii, Wetherall JA (ed.). NMFS 105, US Department of Commerce, NOAA Technical Report, NMFS: Springfield, VA; 57–67.
- Smith PE. 1978. Biological effects of ocean variability: time and space scales of biological response. *Journal of the International Council for the Exploration of the Sea* **173**: 117–127.
- Smith RC, Dustan P, Au D, Dunlap EA. 1986. Distribution of cetaceans and sea-surface chlorophyll concentrations in the California current. *Marine Biology* **91**: 385–402.
- Spear LB, Ainley DG. 1999. Migration routes of sooty shearwaters in the Pacific Ocean. *The Condor* **101**: 205–218.
- Springer AM, McRoy CP, Flint MV. 1996. The Bering Sea green belt: shelf-edge processes and ecosystem production. *Fisheries Oceanography* **5**: 205–223.
- Springer AM, Piatt JF, Shuntov VP, Van Vliet GB. 1999. Marine birds and mammals of the Pacific subarctic gyres. *Progress in Oceanography* **43**: 443–487.
- Steele JH. 1978. Some comments on plankton patches. In *Spatial Patterns in Plankton Communities*, Steele JH (ed.). Plenum Press: New York; 1–20.
- Steele JH. 1985. A comparison of marine and terrestrial ecological systems. *Nature* **313**: 355–358.

- Steward BS, DeLong RL. 1995. Double migrations of the northern elephant seal, *Mirounga angustirostris*. *Journal of Mammalogy* **76**: 196–205.
- Stommel H. 1963. Varieties of oceanographic experience. *Science* **139**: 572–575.
- Strasburg DW. 1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. *Fishery Bulletin* **58**: 335–361.
- Strub TP, Kosro PM, Huyer A. 1991. The nature of cold filaments in the California current system. *Journal of Geophysical Research* **92**: 14743–14768.
- Sund PN, Blackburn M, Williams F. 1981. Tunas and their environment in the Pacific: a review. *Oceanography and Marine Biology Annual Reviews* **19**: 443–512.
- Sverdrup HU, Johnson MJ, Fleming RH. 1942. *The Oceans: Their Physics, Chemistry and General Biology*. Prentice Hall: Englewood Cliffs, NJ.
- The Ring Group. 1981. Gulf Stream cold-core rings: their physical, chemistry and biology. *Science* **212**: 1091–1100.
- Thompson RE, Wolanski E. 1984. Tidal period upwelling within Raine Island entrance, Great Barrier Reef. *Journal of Marine Research* **42**: 787–808.
- Traganza ED, Conrad JC, Breaker LC. 1981. Satellite observations of a cyclonic upwelling system and giant plume in the California current. In *Coastal Upwelling*, Richards FA (ed.). American Geophysical Union: Washington, DC; 228–241.
- Uda M, Ishino M. 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. *Journal of Tokyo University of Fisheries* **44**: 105–129.
- United Nations. 1991. General Assembly resolution calling for a moratorium on drift-net fishing, 20 December 1991, Resolution 46/215.
- Vinogradov ME. 1981. Ecosystems of equatorial upwellings. In *Analysis of Marine Ecosystems*, Longhurst AR (ed.). Academic Press: London; 69–93.
- Weatherall JA, Balazs GH, Tokunaga RA, Yong MYY. 1993. Bycatch of marine turtles in north Pacific high-seas drifnet fisheries and impacts on the stocks. *International North Pacific Fisheries Commission Bulletin* **53**: 519–538.
- Weber LH, El-Sayed SZ, Hampton I. 1986. The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean south of Africa. *Deep-Sea Research* **33**: 1327–1343.
- Weimerskirch H, Catard A, Prince PA, Chérel Y, Croxall JP. 1999. Foraging white-chinned petrels *Procellaria aequinoctialis* at risk: from the tropics to Antarctica. *Biological Conservation* **86**: 273–275.
- Weller R. 1985. Three dimensional flow in the ocean. *Science* **227**: 1552–1556.
- Wing SR, Botsford LW, Largier JL, Morgan LE. 1995. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. *Marine Ecology Progress Series* **128**: 199–211.
- Wolanski E, Hamner WH. 1988. Topographically controlled fronts in the ocean and their biological importance. *Science* **241**: 177–181.
- Wyllie J. 1966. Geostrophic flow of the California current at the surface and at 200 meters. In *California Cooperative Oceanic Fisheries Investigations Atlas*, vol. 4.
- Yatsu A, Shimada H, Murata M. 1993. Distributions of epipelagic fishes, squids, marine mammals, seabirds and sea turtles in the central North Pacific. *International North Pacific Fisheries Commission Bulletin* **53**: 111–146.
- Yoder JA, Ackleson SG, Barber RT, Flamens P, Balch WM. 1994. A line in the sea. *Nature* **371**: 689–692.
- Yoder JA, Atkinson LP, Lee TN, Kim HH, McLain CR. 1981. Role of Gulf Stream frontal eddies in forming phytoplankton patches on the outer southeast shelf. *Limnology and Oceanography* **26**: 1103–1110.