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Making protected area networks effective for marine top predators

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ABSTRACT: The design of ecological networks of marine protected areas (MPAs) is generally based on the identification of areas of high abundance for species of conservation concern or focal biodiversity targets. We discuss the applicability of this approach to marine top predators and contend that the design of comprehensive and effective MPA networks requires the following 7 principles: (1) the use of wildlife-habitat modelling and spatial mapping approaches to develop testable model predictions of species distribution and abundance; (2) the incorporation of life-history and behavioural data into the development of these predictive habitat models; (3) the explicit assessment of threats in the design and monitoring process for single- or multi-species MPAs; (4) the serious consideration of dynamic MPA designs to encompass species which use well-defined but spatially dynamic ocean features; (5) the integration of demographic assessment in MPA planning, allowing provision of advice to policy makers, ranging from no to full protection; (6) the clear articulation of management and monitoring plans allowing retrospective evaluation of MPA effectiveness; and (7) the adoption of an adaptive management approach, essential in the light of ongoing and anticipated ecosystem changes and species range shifts in response to climate change.

KEY WORDS: Marine Protected Areas · Marine reserves · Reserve networks · Top predators · Marine mammals · Marine birds · Marine turtles · Predatory fish

INTRODUCTION

How to implement space-based management for marine top predators is not obvious. However, the potential value of marine protected areas (MPAs) as tools for pelagic conservation is slowly becoming recognised, as many of the criticisms leveled against them have been countered by conceptual advances (e.g. the advent of integrated marine zoning schemes for the high seas), the development of novel technologies for effective protected area management and monitoring (e.g. real-time tracking of protected species and dynamic habitats), and the growing political will to implement large-scale management actions (e.g. international collaboration to combat illegal-unreported-unregulated fisheries on the high seas; Crowder & Norse 2008, Howell et al. 2008, Game et al. 2009). Here we consider some of the continuing challenges to the

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design, implementation and management of networks of protected areas for the conservation of marine top predators and their habitats.

Management for these ocean travellers, such as far-ranging marine mammals, sea turtles and sea birds, requires measures at scales relevant to their spatial ambits and life-history requirements. In particular, ecology-centred MPA networks need to include design criteria, management goals and monitoring programmes capable of incorporating the complex life history characteristics of these species, the dynamics of their oceanic habitats and the vast scope of detrimental human activities. This integrated perspective requires spatially explicit information on the dispersion and overlap of critical habitats and threats in space and time, and a mechanistic understanding of the physical and biological processes underlying any associations.

DEFINITION OF AN MPA NETWORK

The International Union for Conservation of Nature (IUCN-WCPA 2008, p. 12) defines an MPA network as: 'a collection of individual MPAs or reserves operating cooperatively and synergistically, at various spatial scales and with a range of protection levels that are designed to meet objectives that a single reserve cannot achieve'. However, because multiple meanings of this term have been applied to MPAs, including scientific and social considerations, there is some confusion concerning the methods for designing and evaluating MPA networks. Physical networks defined on the basis of scientific principles can focus on single species, multiple-species, and habitat or management criteria, alone or in combination.

(1) Networks involving single-species management aim to promote species survival by maximising adequacy and connectivity (for a glossary of terms, see Table 1), through inclusion of multiple life-history stages and the maintenance of site-specific (e.g. local abundance, population age structure) and network-wide (e.g. genetic structure, population range, population abundance) characteristics of the focal species. Thus, a network may include multiple sites intended to protect organisms at several life history stages (e.g. a breeding site and a feeding site used by the same individuals). Additionally, designs based on replicated sites can enhance resilience by providing redundancy (insurance against localised disasters). While the notion of protecting species throughout their range is not new, and has been applied in terrestrial ecosystems to protect migratory and far-ranging species (Luthin 1987, Shimazaki et al. 2004, White 2009, Rabinowitz & Zeller 2010), its application in the marine

Table 1. Glossary of relevant terms

Adaptive management	The application of feedback loops, enabling activities to be assessed and modified on the basis of experience. Advocates a cyclical approach, based on managing with what we know now, but building rigorous assessment, evaluation and improvement into a continuous process, thus avoiding management paralysis resulting from insufficient information and developing resilient management systems capable of dealing with changing conditions.
Adequacy	Sufficient protection (e.g. appropriate size, spacing, and shape for spatially explicit management) to ensure that management goals are attained (e.g. ensure viability of populations and systems), despite varying conditions.
Complementarity	Conservation areas should complement one another in terms of the features they contain (species, communities, habitats), and each should be as different as possible from the others until important or valued features are adequately represented (Margules & Sarkar 2007)
Connectivity	Describes linkages between life-history stages across a species' range, or between different habitats connected by the transfer of organisms, matter or energy amongst them.
Gap analysis	Identifies matches and mismatches in area coverage between threats, protected areas and valuable ecological resources, to identify highly valued species and habitats, or important ecological features, left unprotected or especially susceptible to threats. Facilitates the prioritisation of protective measures and the improvement of the representativeness and effectiveness of protected areas.
Redundancy	The protection of replicates of important resources to provide insurance against mismanagement or catastrophes.
Representation	Ensures coverage of the full range of biodiversity, especially rare and threatened species, within a hierarchy based on widely accepted specific habitat classifications (e.g. shelf, slope, deep water) and biogeographic domains (e.g. eco-regions; Spalding et al. 2007)
Resilience	Ability to withstand high degrees of chronic stress (e.g. commercial exploitation, winter storms, El Niño events) as well as catastrophic events (e.g. oil spills, hurricanes), whether arising from natural disturbance or human activities

environment is a work in progress (Inchausti & Weimerskirch 2002, Wilson et al. 2004, Hawkes et al. 2006, Shillinger et al. 2008). The advent of novel approaches (such as migration mapping through satellite and geolocation tracking, or the identification of individuals through tagging and unique markings) is facilitating the design of MPA networks aimed at protecting migratory species (Palumbi et al. 2003). Frequently, single-species approaches are legally mandated due to the protected status of a species (e.g. creation of Special Areas of Conservation for protected marine mammals, via the European Union's Natura 2000 directive). Protective measures for a protected species often involve restrictions on specific types of human activity (e.g. fishing, shipping), backed by substantial political will and support for monitoring and enforcement. A good example is the establishment of a marine reserve including a specific boat-exclusion zone for protection of loggerhead sea turtle *Caretta caretta* nesting areas at Zakynthos, Greece (Zbinden et al. 2007, Schofield et al. 2009).

(2) Networks involving multi-species management generally aim to protect biodiversity targets by maximising complementarity and representation, and often employ bio-physical mapping to identify representative ecological areas needing protection. Increasingly, a novel approach is being used in scenarios with poor or incomplete data. Rather than simply mapping species distributions using direct (e.g. tracking data, surveys) or indirect (e.g. bycatch) data, the identification of ecological proxies for important ocean processes and structures (e.g. upwelling, frontal systems) can be used as target areas for additional research (Worm et al. 2003). In general, MPA networks for single species tend to be reactive (based on detrimental conservation status of a particular species; Slooten et al. 2006a), whereas those for multiple species are more proactive, and often involve precautionary measures aimed at precluding (or at least curtailing) potentially detrimental activities before they begin (pre-empting a fishery or prohibiting exploitation of seabed mineral resources; Campagna et al. 2007). However, monitoring and evaluation of the network goals and performance can be very difficult in this multi-species approach, particularly given the presence of multiple indirect ecosystem-level responses from either bottom-up or top-down processes (Mangel & Hofman 1999, Zacharias et al. 2006).

(3) Habitat-based MPA networks are designed to fulfil a set of habitat protection requirements (e.g. to encompass a given percentage of that habitat's areal extent within a given jurisdiction or biogeographic domain). In this respect, such a network may have little biological linkage between protected spaces, since the criteria used to select these targets (e.g. 20 % of the marine habitat) are not based on widely applicable ecological principles, but are driven by biogeographic structural classifications (e.g. seafloor features or benthic sediment types) which are often not well suited to pelagic species and oceanic systems (Agardy 1994). As a result, these networks may protect representative ecological structures within a biogeographic domain (a submarine canyon, a shelf-break area, a seamount, an estuary), which together do not encompass the life cycle of any one organism. Thus, the usefulness of protected area designation to the biota may be compromised in instances when MPA networks are designed without a solid underlying ecological foundation and a coherent conservation mandate. In particular, the ecosystem-wide 'umbrella' benefits of these MPA networks may be overestimated, without having the conceptual or monitoring framework to quantify their magnitude.

(4) Alternatively, MPA networks may seek to achieve socio-political goals (maintain social and economic links between sites, harmonise monitoring and management approaches throughout the range of a species, maximise cost-effectiveness or capacity building). Laudable as such other goals of MPA networks may be, we focus in this review on the ecological objectives of protective measures, rather than on the ancillary socio-political benefits of MPA implementation and management. At the same time, we recognise that social and political factors in the management of human activities in protected areas frame the problem of conservation prioritisation and can function as critical constraints on any analysis (Sala et al. 2002, Charles & Wilson 2009).

Several software programmes have become available recently to aid in the systematic planning and prioritisation of protected areas, including single- and multi-species networks, depending on the ecological, habitat, social and economic weightings assigned in the mapping process. These include Marxan, C-Plan, Zonation and ConsNet, which can be explored further in other publications or websites (Carwardine et al. 2007, Moilanen 2007, Ciarleglio et al. 2009). Use of such tools with the best available scientific data and expert knowledge should allow the establishment of large-scale networks of MPAs which meet the physical and ecological needs of wide-ranging species and accommodate the management practices of multiple countries or stakeholders.

SCIENCE-BASED DESIGN

MPAs are often established prior to an objective science-based analysis, invoking the precautionary principle (i.e. that absence of information is insufficient reason to delay undertaking conservation measures). Lack of information is often due to a paucity of data (if appropriate technology or funding is unavailable). Ultimately, however, the incorporation of science-based design and objectives into protected area designation and adaptive management is the only prudent approach (Carr & Raimondi 1999).

Because prioritisation of protected areas can be achieved at several levels, as described in the previous section, this process may need to account for the objectives of both single- and multi-species management, the threats species are facing, and the related socio-economic costs and benefits. Science-based design of protected areas relies on quantitative spatial prioritisation, allowing explicit and repeatable formulation (Moilanen et al. 2009). This quantitative framework helps promote the monitoring and evaluation of progress toward the conservation goals embedded within the design criteria.

Data requirements and analytical tools

The crux of the design process for marine mammals, birds and turtles is the creation of spatial maps documenting species distributions and — if possible — species abundance. Understanding the mechanistic relationships that underlie the documented associations between populations and their habitats provides the predictive power to anticipate species patterns and habitat preferences (Elith & Leathwick 2009). Such power is particularly crucial when the protected species cue on dynamic features — such as frontal systems and water masses — which change location, shape and size over time (Hyrenbach et al. 2000). Species mapping methods range from the basic portrayal of presence/absence data, to the incorporation of measures of abundance (relative abundance including survey effort, or absolute abundance using line transect data from systematically designed surveys) and modelling techniques to generate density surfaces of species incidence (presence/absence) and abundance (Box 1; see also Matthiopoulos & Aarts 2010). The quality of model results can be highly variable, depending on the type of survey conducted (Matthiopoulos & Aarts 2010).

It is important to consider the inherent biases and limitations of data sources and survey design. Ideally, available information would include data on the distribution of individuals throughout their life cycle, thus allowing the MPA network design to encompass important breeding grounds, foraging areas and movement corridors (Hooker & Gerber 2004). Unfortunately, this is rarely the case. Instead, MPA network designs are often based on disjunct data from multiple areas and different time periods (seasons or years). Furthermore, the merging of different types of surveys (e.g. aerial versus shipboard) and the integration of disparate types of observations (e.g. tracking versus surveys) are critical concerns (Hyrenbach et al. 2006).

While the integration of multiple sparse datasets often constitutes the best available science for rare and endangered species (e.g. Karnovsky et al. 2005), the inherent biases of this patchwork approach should be considered and, if possible, tested by contrasting the model results from the individual datasets and approaches (Louzao et al. 2009). In addition to contrasting habitat use patterns derived from tracking the movements of individuals or from surveying their aggregations (Hyrenbach et al. 2006), novel conceptual approaches may be required to merge disparate datasets. Particularly promising avenues involve the hierarchical delineation of habitats ('species range' versus 'core areas'; Louzao et al. 2006) and the development of predictions with distinct time horizons (*a priori* 'seasonal climatologies' updated by recent observations; Redfern et al. 2006).

Model results delineating the habitat of migratory species that do not travel in large groups during the entire life cycle (such as shearwaters, albatrosses, sea turtles, or large whales) are likely to underestimate the importance of migratory pathways in comparison to the wintering and summering grounds. Any analysis that employs the probability of encounter, the residency time or the density of organisms as a metric of 'importance' would likely select large portions of the winter and summer habitat for protection, before selecting the migratory routes for inclusion in an MPA network. Yet, the pulsing or pulsating flow of migrating organisms along these movement corridors (high numbers of animals moving through a small area, such as grey whales *Eschrichtius robustus* migrating between Baja California, Mexico, and Alaska, USA) means that severe impacts on the population could result from even small-scale events that overlap spatially and temporally with the migratory pathway (e.g. an oil spill, bycatch in coastal gillnets).

Because all parts of a species' habitat (i.e. all areas where it occurs) are not of equal value to the population, it cannot be assumed that areas of high animal incidence or abundance ('hotspots') automatically constitute 'critical habitat', although it may be reasonable, and precautionary, to take this as a default assumption in the absence of evidence to indicate otherwise. The obverse is that low animal densities in a given portion of the species' range do not necessarily signify low importance (e.g. migration corridors in which animals spend little time but without which their movements would be severely compromised). In order to correctly assess critical habitat, information on ecology (encompassing life history, behaviour, Box 1. Spatial mapping of species

Many of the tools established to help designate protected areas rely on spatial mapping of the species of concern. Such maps may vary in their detail depending on how the distribution data are obtained, the ancillary environmental data collected and the modelling methods used to integrate and interpret these disparate datasets.

Sightings data

Much marine predator data is collected in the form of 'sightings', representing observations of animals or groups of animals in space (Evans & Hammond 2004). Such sightings data may allow the generation of presence-only maps of occupancy (e.g. for strandings and incidental sightings) when there is no design and no record of search effort. However, data on where animals were observed can only be related to study area usage by incorporating knowledge of where animals were not. Thus search effort is required to provide a measure of relative or absolute density and to provide information on habitat selection. The best way to achieve this is through a proper survey design for line transects with, whenever possible, equal coverage probability across the study area (Buckland et al. 2002).

Telemetry data

Unlike sightings data, telemetry methods record individual-based time-series movement data. Methods range from visual tracking to radio telemetry to geolocation and real-time satellite telemetry. Making population-level inferences from these is often problematic for several reasons, particularly the relatively small and potentially biased sample recorded, and the observation errors inherent in many of these tracking technologies (Aarts et al. 2008). The incorporation of effort data into maps of individual tracks involves binning data into time-unit intervals, with observations in each segment analysed as counts. Alternatively, pseudo-absences (i.e. representatively selected locations where the animals could have been sampled but were not) can be added to the data (Matthiopoulos & Aarts 2010).

Relating sightings or telemetry data to population-level spatial or habitat usage is difficult due to geographical, seasonal or individual biases. For the analysis of habitat usage, covariate data are required in addition to animal (sightings or telemetry) data. By incorporating habitat variables collected simultaneously with animal data, descriptive methods can be used to study the habitat relationships (correlational analysis in terms of occurrence versus each habitat variable, or goodness-of-fit assessment of whether the distribution of sightings differs from the distribution of each environmental variable; Redfern et al. 2006).

There are also several modelling methods to describe the relationship between species occupancy and environmental characteristics. Redfern et al. (2006) reviewed several types of regression models and examples where they have been used. These include environmental envelopes that describe the environmental space in which an organism is expected to occur (Kaschner et al. 2006); ordination techniques, which allow the use of multiple environmental variables; and principal component analysis, which transforms a set of continuous variables into new variables (the principal components) that are linear combinations of the originals (Reilly & Fiedler 1994). Non-linear relationships between the variables can be modelled using canonical correspondence analysis, the graphical output of which is a scatter plot with the axes as the new variables, the points being the different species, and with arrows for the untransformed, original environmental variables (Redfern et al. 2006). Lastly, classification and regression trees use either presence/absence (classification tree) or usage (regression tree) to repeatedly split the data to minimise the number of groups and maximise homogeneity within groups (Panigada et al. 2008).

Regression models may range from linear models of a single habitat variable assumed to vary linearly with the species response variable, to generalised linear models assuming parametric linear relationships between several variables, to generalised additive models which use a non-linear smooth function and assume non-parametric relationships between variables (Redfern et al. 2006).

Spatial modelling (or density surface modelling) incorporates data on the environment to generate a spatial prediction of relative or absolute density based on the preference for habitats defined by combinations of environmental covariates shown to be important. This therefore represents a great improvement over simple measures of occurrence. Despite non-equal coverage probability, when combined with line-transect sampling (post hoc rather than designed), the outcome is a spatially explicit prediction of the distribution and abundance of the focal species. This therefore provides map output critical for conveying the results to resource managers (Fig. 1; Cañadas et al. 2005). However, it is crucial to acknowledge that these products are predictive rather than explanatory. Furthermore, these models can only incorporate covariates sampled throughout the entire study area, and results cannot be extrapolated beyond the study area, unless to test for putative species distributions.

social system and phenology) and the species' susceptibility to specific threats and impacts should be incorporated into wildlife habitat models. In particular, Harwood (2001, p. 632) suggested that 'an ecological unit can be identified as providing critical habitat for a population if changes in the unit's characteristics affect survival, fecundity, or movement rates resulting in a change in the size of the population.' He added that habitats 'can be ranked in importance by carrying out a sensitivity analysis of the effect of small changes in each habitat on the intrinsic rate of increase of the population in question'. This means developing integrated models, with quantitative inputs of animal and threat distributions and, inevitably, with qualitative input influenced by value judgements and expert opinions.

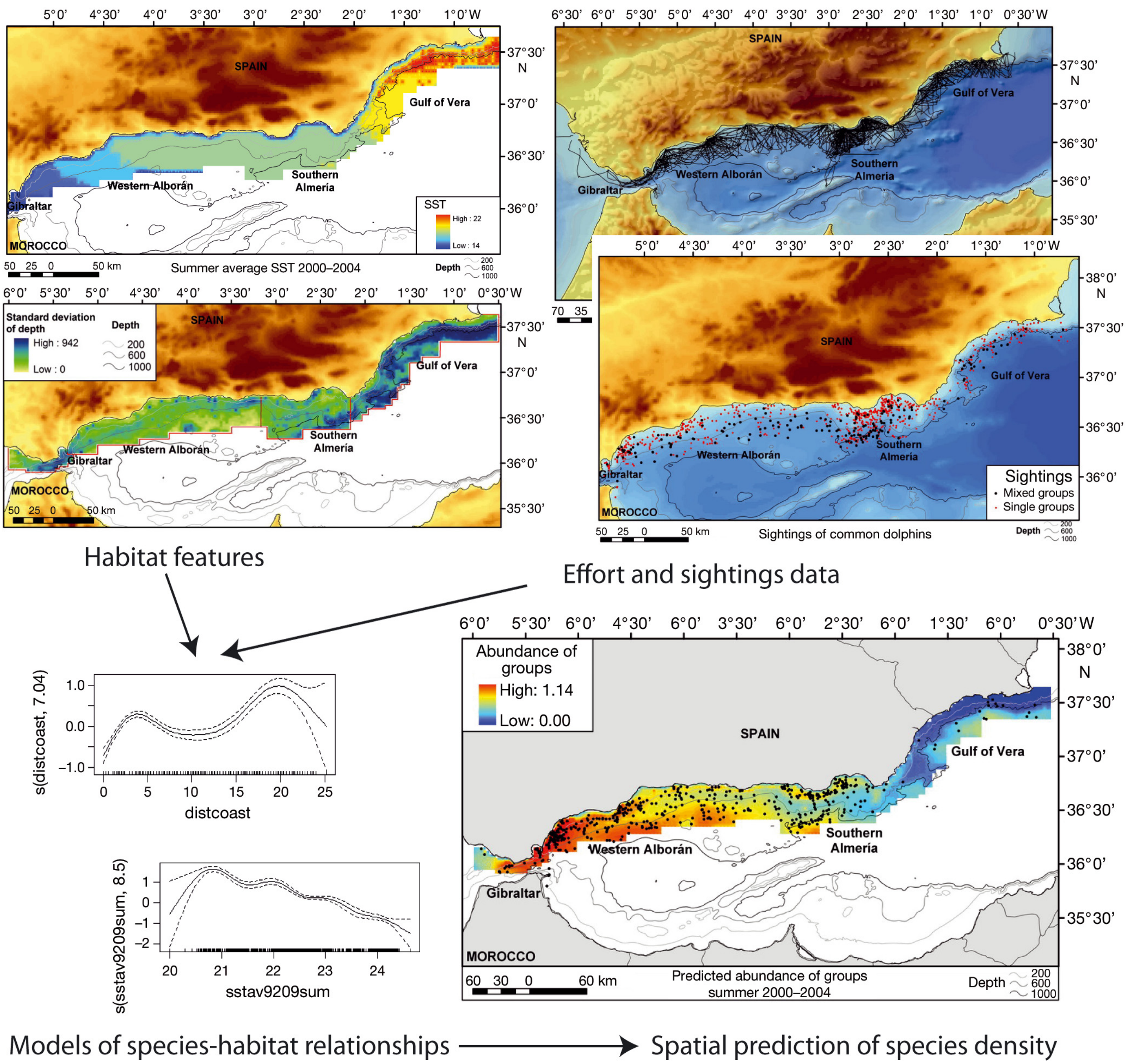

Fig. 1. Effort and sightings data can be combined with environmental data to develop models of species–habitat relationships, which can in turn be used to derive predictions of spatial density (figure compiled from data presented by Cañadas & Hammond 2008)

Importance of life history and behaviour: 3 examples

Spatial maps of animal density rarely take account of differences in life history. However, in many cases the distribution of animals varies (often quite markedly) depending on life-history stage or phase, related to behavioural and social factors. Following are 3 examples.

Behavioural segregation

Often, animal distribution is partitioned according to behaviour. For instance, spinner dolphins *Stenella longirostris* rest in shallow coves close to shore during the day and commute to slope water in the evening, returning to shore the following morning (Karczmarski et al. 2005). Central-place foragers (e.g. seabirds, pinnipeds) foraging from a colony may be observed commuting through 'poor habitat' en route to or from distant 'rich' foraging grounds. To address this bias, distinct habitat models and maps can be created for travelling versus foraging individuals. These behaviours can be ascribed on the basis of direct observations (at-sea surveys) or inferred from tracking and bio-logging (diving intensity, movement and turning rates; e.g. Guinet et al. 2001, Nel et al. 2001).

Sexual segregation

For many species, particularly those with pronounced sexual dimorphism, the distributions of males and females vary. For instance, the movement patterns and distribution of male and female Antarctic fur seals *Arctocephalus gazella* are quite different outside of the breeding season (Boyd et al. 1998). Similarly, the distribution of adult male versus immature male and female sperm whales *Physeter macrocephalus* is highly segregated, with the former found at higher latitudes and the latter at lower latitudes (Whitehead 2003). These segregated distribution patterns can cause unequal susceptibility to human impacts in males and females from the same species.

Age-based segregation

In cetaceans and some pinnipeds (e.g. walruses *Odobenus rosmarus*), the behaviour, size, distribution and movements of groups containing young are often quite different from those without young. For example, in common dolphins *Delphinus delphis* in southern Spain, feeding individuals and groups containing calves are more likely to be found near shore, whereas socialising groups and groups without calves are more likely to be found offshore (Cañadas & Hammond 2008). Similarly, the spatial segregation of mother–calf humpback whale *Megaptera novaeangliae* pairs in breeding grounds, and the disjunct nature of the calving and breeding areas of large cetaceans, plays a critical role when attempting to delineate their important habitats (Craig & Herman 2000, Kenney et al. 2001). Given the likely greater impacts of anthropogenic threats in nearshore habitats, this information appears relevant to the design of protected area networks for these species.

Dealing with multiple species

The inclusion of spatial maps for multiple species can be useful in identifying commonalities between species and therefore in identifying ecologically important areas (Worm et al. 2003, BirdLife International 2004). In particular, when representation is sought in the designation of protected areas, multi-species mapping allows assessment of the complementarity of protected area choices in terms of species composition. The incorporation of information on important prey taxa may further contribute to a mechanistic understanding of the physical and biological factors that shape species distributions and behaviour (e.g. the link between oceanography and high-use foraging areas; Fiedler et al. 1998, Nel et al. 2001).

It is rare that all species are considered equal in conservation planning (Joseph et al. 2009). Variation in species status may need to be taken into account, and some form of priority setting for species may be required. How do we weight the inputs from different species? Simply combining all species will give priority to those that are most abundant, so it may be preferable to develop a weighting index for species input by conservation status.

The accumulation and provision of open-access data from the scientific community is helping to decrease the gaps in knowledge of species ranges, needs and interactions in the light of threats and future management (e.g. OBIS-SEAMAP; Halpin et al. 2009). Such open-access data are therefore likely to vastly improve our ability to design multi-species MPA networks. However, the ready availability of such data may also lead to difficulties in reconciling data collected using different survey techniques (as mentioned above). Furthermore, because different species maps may have distinct underlying uncertainties linked to the output density surfaces, any further processing using spatial conservation prioritisation techniques (maximising biodiversity targets, endangered species protection) may mask or obscure these underlying assumptions and constraints (Harwood & Stokes 2003, Moilanen et al. 2006). Thus, sensitivity analyses are imperative to test the influence of individual datasets and species distributions on any multi-species mapping and site selection exercise. This approach will allow the investigation of the impacts of variability in the species-specific base maps on the resulting protected area derivations, by assessing whether slight changes in the base maps influence the resulting protected area placements (Moilanen et al. 2006).

Consideration of threats

Although species maps provide a means to begin the process of identifying areas of importance, that process also requires an assessment of the spatial and temporal nature of threats to the species of interest

(Halpern et al. 2008). Maps of threats or threat factors can be overlaid on species distributions to identify areas of greatest concern. Interestingly, some studies have suggested that the mapping of costs and threats is of more value to conservation decision-making than the mapping of different taxa (Bode et al. 2008).

Alternatively, from a primarily socioeconomic perspective, threats, such as fisheries, might be incorporated into the MPA network design process with the objective of minimising negative effects of MPA designation on fishermen and other resource users. For example, Klein et al. (2008) argued that incorporating the interests of multiple stakeholders into MPA design, without compromising biodiversity conservation goals, is more likely to lead to effective protection. To this end, the concept of integrated marine zoning may offer a way to integrate MPAs as additional stakeholders in the comprehensive spatial management of marine ecosystems (Crowder & Norse 2008, Douvere 2008).

It is clear that the consideration of threats is important at the design stage for MPA networks, but the issue is often more complex than suggested by most studies to date. Threats to marine predators are varied and will likely vary in their course of action (either direct or indirect) and magnitude (catastrophic events or chronic disturbances; Hooker & Gerber 2004). In addition, some human activities can drive several types of threats (trawling leads to the mechanical destruction of benthic habitat and depletion of prey and in turn results in alteration of foraging strategies), and some threats can be caused by several types of human activity (acoustic pollution is caused by shipping, seismic surveys and military training exercises). Furthermore, some threats may have broad-scale impacts on groups of species with similar habitat (swordfish longlines incidentally kill albatrosses, sea turtles and cetaceans, Lewison et al. 2004, Read et al. 2006, Wallace et al. 2010), and maps of such threats may be applicable to multiple species, obviating the need for laborious, time-consuming habitat modelling of every threat–species combination. This can be especially useful when distribution data do not exist for all of the species of interest. However, in some cases, the nature and seriousness of a given type of threat varies depending on the species. For example, some cetaceans and sea turtles appear to be much more vulnerable to entanglement in certain types of fisheries than in others (Lewison et al. 2004). In these cases, mapping the distributions (and densities) of multiple species, together with threats, might benefit from species-specific modelling to account for the different levels of threat to different parts of the ecosystem.

In addition, the impacts of threats may vary depending on the life-history stage and sex, especially if individuals of different ages and sexes forage in different ways (e.g. dive to different depths, behave differently toward fisheries) or have distinct diets (e.g. Hawkes et al. 2006). Thus, whenever possible, species maps should be broken down according to behavioural and age-structured categories. Such a stage- or sex-specific approach will greatly facilitate the use of demographic studies to link potential impacts with the monitoring and modelling of population trends. An example of this approach has been taken for resident killer whales *Orcinus orca* along the west coast of the US and Canada where, since the whales are more vulnerable to disturbance while feeding than during resting, models of whale habitat use and behaviour were used to identify a candidate MPA for a foraging area (Ashe et al. 2010).

SPATIAL AND TEMPORAL SCALES

A major criticism of MPAs for many pelagic species has been the inability of the associated protective measures to encompass the full range of individuals in a population, such that individuals continue to be exposed to threats when they move outside of the protected area (Game et al. 2009). Yet, species are not equally vulnerable over their entire range. Many threats to pelagic organisms are either site-specific or cumulative and can be reduced through spatial protection (Hooker & Gerber 2004). MPAs have the potential to dramatically reduce the likelihood of mortality, even if this likelihood cannot be reduced to zero. For example, protection of an area in which an animal spends 50% of its time, although this represents only 10% of its range, will reduce its likelihood of mortality substantially. Therefore, both the distribution and the usage of areas are crucial for establishing the spatial and temporal parameters of protection. Notably, even if protection is not complete, small reductions in mortality rates (or, put another way, the avoidance of even very small increases in mortality rates) can have decisive demographic benefits, especially for rare and endangered species (Caswell et al. 1999).

Static versus dynamic ocean features

While protected areas have traditionally been static, particularly in the ocean, there may be value in adopting more dynamic designs (Box 2). Hyrenbach et al. (2000) described 3 types of pelagic MPAs based on (1) static bathymetric features, (2) persistent hydrographic features or (3) ephemeral hydrographic features. While the latter 2 types of features cannot be addressed adequately by a traditional static MPA, they could be

Box 2. Static versus dynamic protection: 2 examples

Most protected areas (both terrestrial and marine) operate in a static fashion both temporally and spatially. By this we mean that protected areas are fixed in space and permanent in time. An example of this is the Gully MPA in eastern Canada. In contrast, protective measures could entail dynamic boundaries in both space and time, with seasonally implemented protection and with flexible continuously changing co-ordinates for protection. An example of this approach is the TurtleWatch program, which although not established as an MPA, fulfils the criteria in terms of spatial conservation of loggerhead turtles *Caretta caretta* from bycatch in longline fisheries (Howell et al. 2008).

The Gully MPA was established largely to protect the small, resident population of northern bottlenose whales *Hyperoodon ampullatus* regularly found in the waters above this submarine canyon (Fig. 2). Analysis of the spatial and temporal distribution of cetaceans in this region suggested that depth was of most value in describing species distributional preferences and that a fixed MPA should be based on bathymetry (Hooker et al. 1999). A simple bioenergetic model for the northern bottlenose whale population further indicated a likely spatial subsidy (influx of material) into the area supporting its high productivity. This was interpreted to mean that the MPA boundaries and thus the associated conservation measures should be extended to the head, mouth and feeder canyons of the Gully (Hooker et al. 2002). The Gully MPA was fully designated in 2004, and the current management plan includes 3 zones of protection (Fig. 2).

The TurtleWatch product is a tool to reduce the number of loggerhead turtles taken in the Hawaii-based longline fishery (Fig. 3). The relationship between turtle distribution and movements and environmental data can be used to predict areas of concern, i.e. those areas most likely to contain higher densities of turtles. Since the fishery is allocated a set number of takes after which it is closed, it is in the best interest of the fishery to attempt to mitigate (actually, to minimise) turtle bycatch. After being notified of the areas most likely to contain turtles, fishermen choose to exclude these areas from fishing activity. This dynamic forecasting can be issued to fishermen weekly, with updated maps of areas to exclude. Such dynamic closure allows smaller but changing areas to be protected, rather than the larger fixed area otherwise required for the same level of protection.

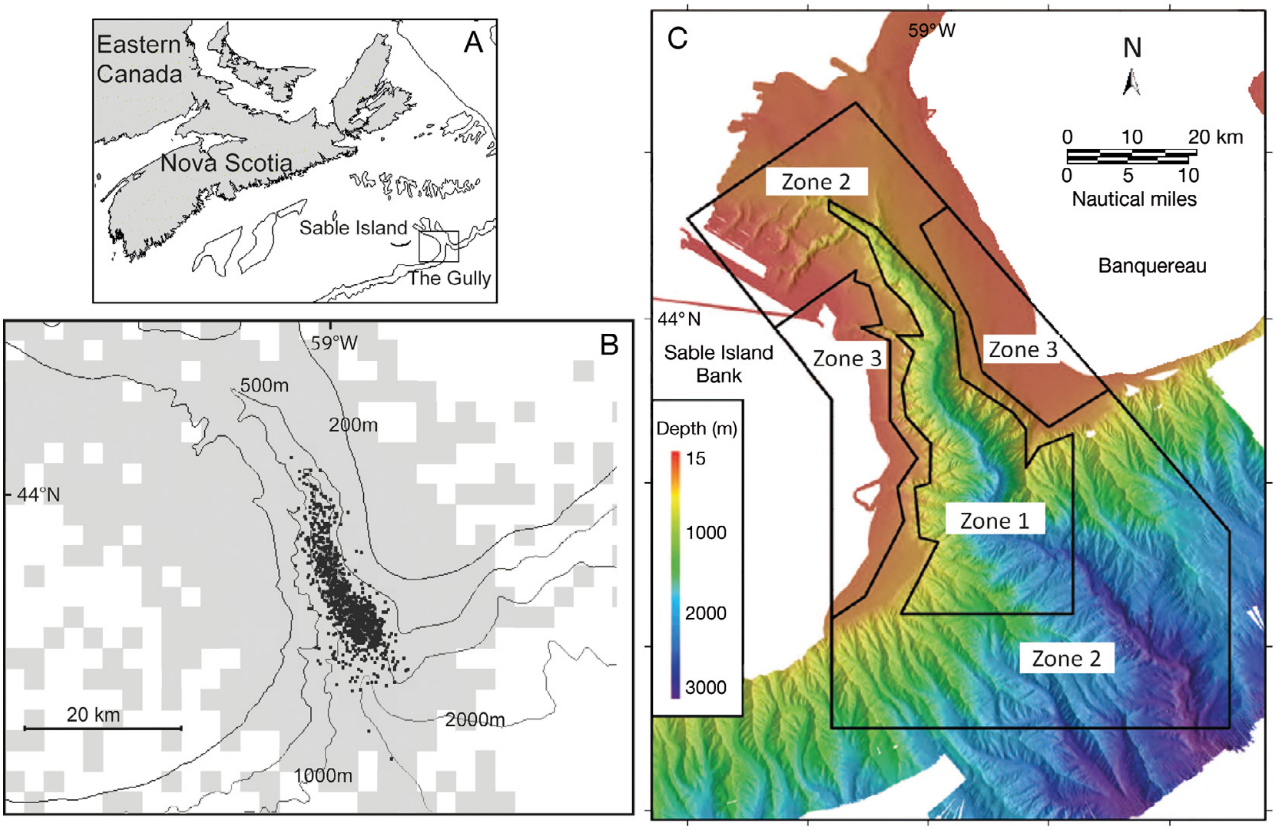

Fig. 2. (A) The Gully submarine canyon off eastern Canada provides an example of static MPA boundaries. (B) Northern bottlenose whale sightings from 1988 to 1998 shown as black dots over the canyon bathymetry (200, 500, 1000 and 2000 m), and 2.5 × 2.5 km pixels showing distribution of search effort (figure redrawn from Hooker et al. 2002). (C) The current Gully MPA designation (from www.mar.dfo-mpo.gc.ca/e0010439, full plan available from www.dfo-mpo.gc.ca/Library/333121.pdf) includes 3 zones: Zone 1 includes the majority of bottlenose whale sightings, Zone 2 allows limited human activities such as fishing and extends to head, mouth and feeder canyons, and Zone 3 allows activities within the range of natural disturbance and extends onto shallow banks on either side of the canyon

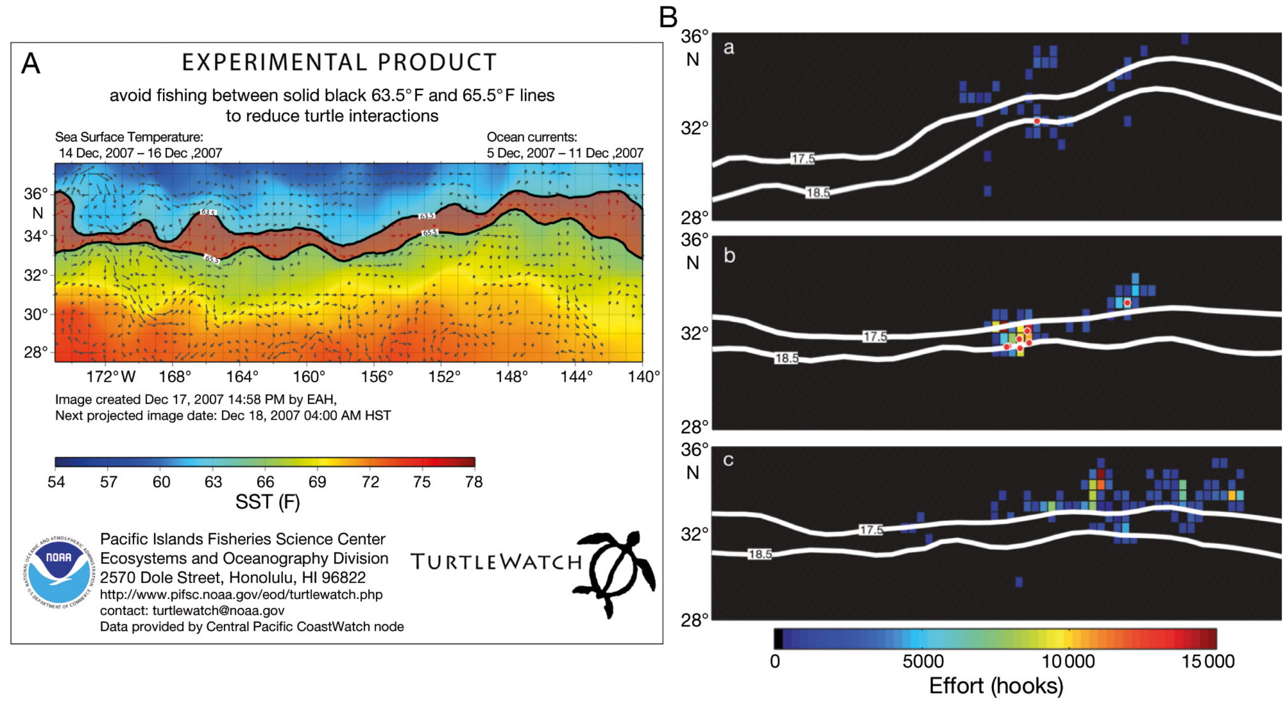

Fig. 3. (A) Example TurtleWatch advisory map (available at www.pifsc.noaa.gov/eod/turtlewatch.php) showing sea surface temperature in pseudocolour, black arrows showing geostrophic currents and black lines showing the 63.5°F (17.5°C) and 65.5°F (~18.5°C) isotherms. (B) The success of this tool can be seen based on spatial position of fisheries sets (pseudocolour blocks) and loggerhead turtle interactions (red circles) for January (a) 2005, (b) 2006, (c) 2007. Fisheries sets within white lines (showing average monthly positions of the 17.5 and 18.5°C isotherms) tend to result in turtle interactions, while those outside this dynamic boundary result in fewer interactions. (From Howell et al. 2008)

addressed by dynamic design that relies on forecasting and updating of boundary coordinates on a fine temporal scale (e.g. daily or weekly). Such dynamic MPAs have received little attention because they have been deemed unfeasible. Yet in situations where the animals are using well-defined, spatially dynamic ocean features, these types of MPAs have much potential. One example comes from research north of Hawaii on loggerhead turtles, which use the Transition Zone Chlorophyll Front (TZCF) as foraging and migration habitat. An indicator of the position of the TZCF is the 18°C sea surface temperature (SST) isotherm. TurtleWatch, produced by the Pacific Islands Fisheries Science Center (NOAA), tracks the link between the turtles and the 18° SST. It uses fine-scale (9 km pixel size) near-real time (8 d composites) SST satellite-derived imagery data to map a narrow band around the 18° SST as the area to be avoided by longline fishermen to reduce their interactions with loggerhead turtles (Howell et al. 2008). Since this region changes at a weekly time scale, these maps provide fishermen with a dynamic perspective on turtle distribution that matches the spatial and temporal scale of the underlying habitat (Fig. 3).

Corridors

Despite their potentially critical importance to long-term population viability, corridors have been largely neglected in the protection of marine vertebrates. Instead, MPAs have focussed mainly on boxes drawn around 'hotspots' of animal occurrence and aggregation, taking account of political, economic and social feasibility (Game et al. 2009). However, movement corridors may be amenable to management either via dynamic protected areas targeting predictable habitat features (e.g. temperature fronts delineate migrating loggerhead turtles in the central Pacific; Box 2, Fig. 3) or through spatially explicit measures guided by real-time surveys and tracking (e.g. right whale *Eubalaena glacialis* sightings and acoustic detections trigger slow-speed zones for shipping in the eastern US; Van Parijs et al. 2009).

A clear and instructive example, albeit from the terrestrial realm, is provided by the jaguar *Panthera onca*, a species that, like some cetaceans, has a vast but highly fragmented range. Initially, conservationists regarded the protection of hotspots — basically large areas harbouring at least 50 of the big cats — along with buffer zones around them as the optimal approach for conserving jaguars. However, genetic evidence of panmixis in the overall population pointed to the importance of 'connecting the dots'. Thus, the currently preferred conservation strategy for jaguars is to protect a large network of interconnected corridors and refuges from the US–Mexico border to the southern tip of South America (Rabinowitz & Zeller 2010, White 2009). Corridors, even though they may contain low densities of animals at any one time, are seen as critical in allowing these large cats to wander and maintain their genetic mixing on a continental scale. In this case, innovative science (both genetic analyses and satellite tracking) provided vital information on which to base protected area planning. Protected area planners must not allow themselves to become boxed-in by a triage mentality that, before careful study and weighing of evidence, concedes the loss of small areas of low density in favour of large areas with high density.

ASSESSING EFFECTIVENESS

Integration of demographic assessment in MPA planning

The need for quantitative goals in the establishment of MPAs and MPA networks is paramount (Roff 2009). It remains extremely difficult to quantify the proportion of a region that requires protection in order to achieve defined (quantitative) goals for conservation. For marine top predators, this has required the consideration of threats together with analyses of population viability. Such an approach has been used in the designation and ongoing evaluation of the MPA network for Hector's dolphins *Cephalorhynchus hectori* in New Zealand. In this instance, the focus has been on evaluating the sizes and shapes of protected areas required to achieve specific limits on dolphin bycatch in order to achieve specified management goals (Slooten et al. 2006a,b). As Roff (2009, p. 249) pointed out, however, defining management goals and evaluating progress toward them is even more problematic for networks of MPAs for which he asked 'How do we know, in any region, whether we have enough MPAs — covering a large enough area — to achieve a sufficient level of protection?'

When giving advice to policy makers, it is therefore helpful to frame recommendations concerning MPA location, size and criteria in terms of consequences for the population(s) of concern, i.e. to incorporate the results of demographic modelling. Ideally, advice should encompass a range of scenarios, from no protection of the population to full protection, and the likely consequences of these and intermediate scenarios. This approach shifts the burden of decision making to managers, who are accountable via legal, administrative and political processes, and leaves scientists to provide their advice in terms of a range of possible scenarios and their likely impacts on the protected species and their habitats, and potentially also the impact on resource users.

In many cases it would seem desirable to enable wild populations to recover to their previous levels (Marsh et al. 2005). However, estimates of historical population size may not always be appropriate targets for recovery, given that there have been changes in the environmental carrying capacity over time (Marsh et al. 2005). Thus, any MPA network must be framed and managed within an ecosystem, and its historical context, and monitoring and assessment should give due regard to past and ongoing ecosystem-level changes in environmental conditions.

The official designation of an MPA is typically a slow process due mainly to the associated bureaucracy. Such designation should be considered as a step in the process towards conservation, not as a conservation end point. An array of conservation tools (legislative, management, capacity building, public awareness, monitoring) must be brought into play within the framework of a management plan for any protected area or protected area network (Pullin & Knight 2003, Pullin et al. 2004).

Such management should be adaptive, requiring ongoing research, monitoring and evaluation set within a regional context (Sutherland et al. 2004). Therefore, monitoring should be an integral and indispensable part of any MPA network management plan (Margules & Pressey 2000). In particular, quantitative synthesis methods such as gap analysis should be regularly used to highlight deficiencies within the current MPA network in terms of areas where significant resources (species, habitat or important ecological features) and threats occur (Margules & Pressey 2000). Such analysis may highlight new areas, the protection of which would enhance long-term population survival of species currently protected, or bring into relief the desirability of including additional species currently inadequately represented. Particularly in this era of relatively rapid climate change (Cheung et al. 2009), the planning of protection and effective networks for marine species requires an adaptive approach (Wilson et al. 2004).

International agreements and jurisdictional issues

Within countries, the legislation involved in the designation or management of MPAs is often separated between government agencies (e.g. fisheries, agriculture, environment, parks, tourism, Coast Guard, natural resources) administering various aspects of fisheries, aquaculture, conservation, shipping, oil and gas and mining. Crowder et al. (2006, p. 617) likened this to 'a scenario in which a number of specialist physicians who are not communicating well, treat a patient with multiple medical problems', and for whom the combined treatment can exacerbate rather than solve problems. Although this approach may simplify management activities within each sector, it often leads to a poor ability to resolve conflicts across sectors. In some cases, such conflict can lead to the stalling of required conservation action for several years (Crowder et al. 2006).

The establishment of MPAs in offshore and international waters is even more problematic, despite scientific backing for the concept, and is often hindered by the need for international agreement (Box 3). Political boundaries are permeable both to marine species of concern and to the human impacts facing them. Transboundary management agreements are therefore crucial to any multinational protected area. A number of developments and scientifically rigorous proposals are being advanced to increase protection of areas beyond national jurisdiction as well as open-ocean and deep-sea areas within national territories (12 nautical miles) and jurisdictions (200 n miles where claimed). Good governance and advances in technologies for monitoring of these areas is likely to be as important as the declarations of protected area status.

For wide-ranging marine species, protection on the high seas is critical. To this end, 3 additional steps would help advance the establishment of networks of high-seas MPAs: (1) evaluate existing pelagic MPAs to ensure that they have clearly articulated goals and measurable objectives (Zacharias et al. 2006, Notarbartolo-di-Sciara et al. 2008); (2) undertake gap analyses to identify unrepresented areas and habitats in the existing MPA networks at a series of nested biogeographic scales (Spalding et al. 2007, Abdulla et al. 2009); and (3) fill in the gaps by selecting areas of 'high ecological value' (e.g. productive oceanic features) and 'high impact' (e.g. intense fisheries effort) as areas of potential importance to migratory marine vertebrates that deserve enhanced study (Worm et al. 2003, Shillinger et al. 2008).

The involvement of stakeholders is crucial to reconcile the conservation of biodiversity with economic development (Lundquist et al. 2005). Provision of relevant information to demonstrate both short- and long-term conservation benefits can mitigate potential conflicts. Involvement in the process from brainstorming to the development of management plans fosters community support, without which there is no guarantee of success for conservation measures (Charles & Wilson 2009).

Global assessments of MPAs

Initiatives to document the existence of MPAs (such as the joint work between IUCN and UNEP-World Conservation Monitoring Centre on the World Data-

Box 3. The political arena and the need for international cooperation: the Alborán Sea

Species distributions frequently do not correspond to political or jurisdictional boundaries, and cooperative management is needed. In order to protect areas which straddle the boundaries of multiple countries, high-level political initiatives by governments, local groups or third-party interventions by non-governmental organisations (NGOs), academic institutions or international conventions are often required.

The Alborán Sea, as the 'gate' to the Mediterranean and as the junction of the Lusitanian, Mauritanian and Mediterranean biogeographic areas, has over the last decades concentrated attention in the framework of international strategies for the conservation of biodiversity (Fig. 4). Spain, Gibraltar, Morocco and Algeria border on this region and would each need to sign up to measures to protect this area.

The extraordinary oceanography makes it a unique laboratory for scientists to tackle the challenge of managing and monitoring the open ocean. This has resulted in important research and conservation efforts from various fields of natural and social sciences. All of these have a common goal: making the socioeconomic development of this strategic region compatible with the conservation of the natural and cultural treasures of this sea.

Yet, the social–economic–political differences between the northern and the southern parts represent obstacles to the comprehensive management of the basin, with the disparities in logistics and capacity leading to differences in data availability, existing protections and the mechanisms for MPA implementation (Notarbartolo-di-Sciara et al. 2008, Abdulla et al. 2009). Thus, identifying synergies and marshalling the scientific and parallel political efforts of Alborán states (Gibraltar, Morocco, Algeria and Spain) in a collaborative spirit is currently perceived as a top priority, both for dealing with the complexities of governance and for ensuring an ecosystem approach to management for what should soon become a major element in the Mediterranean Specially Protected Areas of Mediterranean Importance (SPAMI) network and Europe's Natura 2000 Network.

As a result of the push in this direction from several scientists, the IUCN Mediterranean Cooperation Centre initiated a process focusing on this goal. At the beginning of 2008, through the creation of working groups, it started the first phase of the 'Initiative for the sustainable management of the Alborán Sea', which brings together all of the people and institutions interested in the conservation of the natural and cultural values of this region.

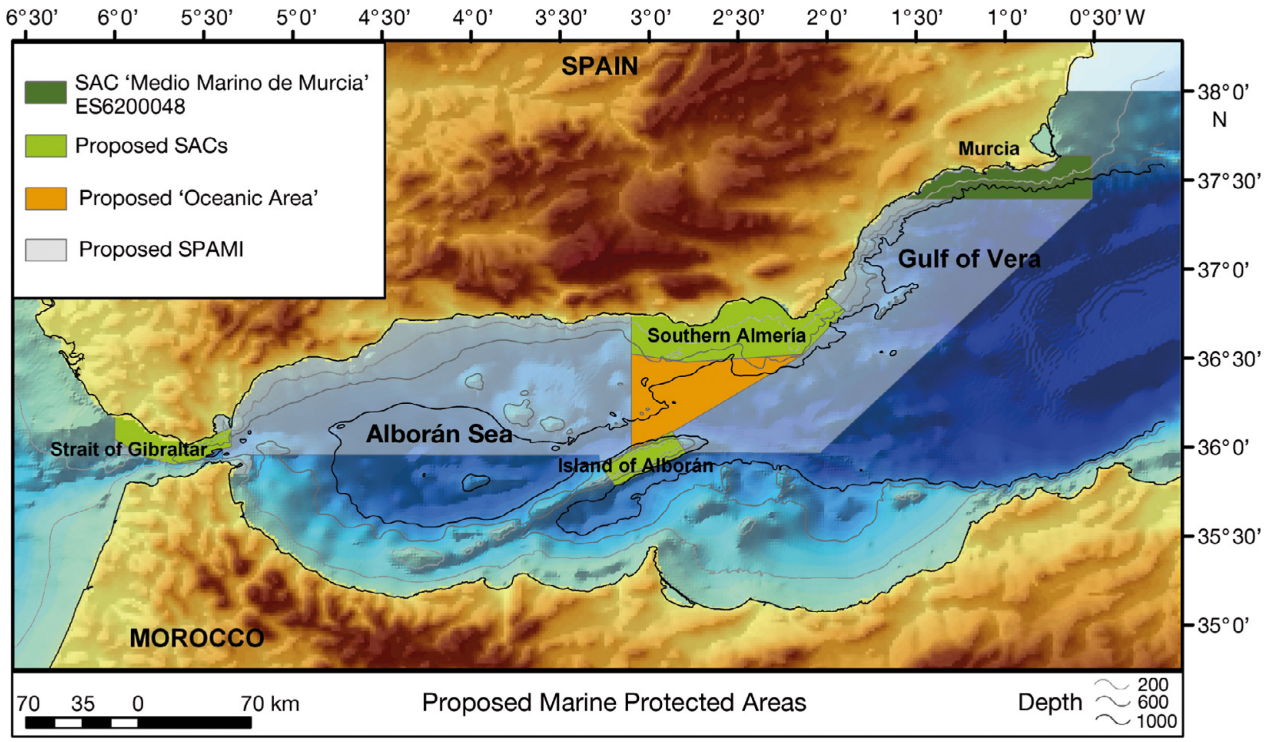

Fig. 4. Proposed marine protected areas suggested by Cañadas et al. (2005) extending into the Alborán Sea. These include designated and proposed EU Special Areas of Conservation (SACs), a proposed Specially Protected Area of Mediterranean Importance (SPAMI) and an Oceanic Area proposed as warranting further protection. (See Cañadas et al. 2005 for more details; illustration drawn for EU Life Project on the conservation of cetaceans and turtles in Murcia and Andalucia, Spain)

base on Protected Areas, www.wdpa.org, and Protect Planet Ocean portal, www.protectplanetocean.org) provide baseline information which can support ecological gap analysis, environmental impact assessment and private sector decision making. Such tools compile and make accessible information about MPAs, in order to improve future planning and protection efforts for marine species and their environments. However, there is a further need to assess the effectiveness of MPAs to verify that they are having the desired effects. For example: Are MPAs protective in name only? What are the underlying conservation goals, and are these being achieved? The development of a classification system to assess the effectiveness of MPAs and MPA networks would help avoid the false sense of security that 'paper parks' provide. Standardisation of the evaluation of management effectiveness is recognised as a priority across many protected areas (Hockings et al. 2009). Rigorous science-based design involving prioritisation algorithms based on quantitative conservation goals will aid this process. Demographic modelling may also help by linking the measures associated with MPAs and MPA networks with the population trends of the species. However, it can be very difficult to determine whether and at what rate populations are recovering, particularly when population sizes are small (Taylor & Gerrodette 1993). It may therefore be more productive to set targets for sustainable levels of human-caused mortality using the potential biological removal method (Wade 1998) rather than attempting to monitor trends or manage against fixed recovery metrics. This will again require clear management plans that set measurable objectives for assessing effectiveness.

CONCLUSION

Ecologically designed MPA networks for wide-ranging marine top predators need to accommodate the life history of these species, the dynamics of their ocean habitats and the nature of the threats they face. To this end, we advocate the following recommendations:

(1) Emphasise the identification of important habitats based on broad-based ecological information (e.g. behavioural, social and movement data), rather than mapping high-density areas derived exclusively from distribution data. Investigate the influence of diverse data types and survey designs on the results and interpretation of the resulting predictive habitat models.

(2) Assess species-specific susceptibility to individual threats, and use commonalities in distribution to

identify shared habitats for the design of multi-species MPA networks.

(3) Adopt a flexible design approach tailored to match the species-specific ecology and the bio-physical ocean environment. This will require implementing dynamic designs in offshore protected habitats and, if relevant and feasible, designs for the protection of temporally explicit life stages.

(4) While encouraging delivery on policy commitments generally, provide design advice to policy makers ranging from no protection to complete protection and their likely demographic consequences.

(5) Integrate demographic assessment with management plans, designed to provide clear and measurable population-level objectives. Devise a classification and ranking system for MPA effectiveness, which will help prioritise management actions and evaluate positive impacts on protected species. Throughout these processes, involve adaptive management as a critical step to deal with dynamic seascapes of changing threats and species distributions, especially in light of anticipated climate change.

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