Modeling the trophic effects of marine protected area zoning policies: A case study

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Abstract

Marine protected areas (MPAs) are increasingly being recognized as an alternative management tool for conserving marine resources and ecosystems. By integrating organism dispersal rates, ecosystem interactions and fishing effort dynamics, ECOSPACE, a spatially explicit ecosystem-based modeling tool, allowed us to compare the ecological consequences of alternative MPA zoning policies within the proposed Gwaii Haanas National Marine Conservation Area, located off the west coast of British Columbia, Canada. The desired effects of MPAs include higher fishery yields, the conservation of biodiversity, and/or the preservation of intact ecosystems. However, ECOSPACE predicts that when MPAs are small, species interactions and movements may make these objectives difficult to achieve. ECOSPACE suggests that the effects of MPAs are reduced at their boundaries where fishing effort is predicted to concentrate. Furthermore, top predators may become more abundant within MPAs, which could lead to a depression of their prey species and a subsequent increase of species at even lower trophic levels. Trophic cascade patterns and density gradients across boundaries are nontrivial departures from our simple expectations of how MPAs protect areas and will force us to reconsider what constitutes effective conservation. Our ECOSPACE model indicates that the establishment of multi-use buffer zones may help alleviate these realistic but worrisome ecological predictions. When coupled with an overall reduction in harvest pressure, ECOSPACE suggests that a MPA with a large core 'no-take' zone and large buffer will result in the greatest increase in organism biomass. The use of marine zoning may be an effective management tactic to reduce social conflict and conserve marine ecosystems.

Introduction

Humans are imposing unprecedented pressure on marine systems worldwide. As a result, marine resources and the ecosystems in which they are embedded have become severely threatened (National Research Council, 1995; Botsford et al., 1997; Pauly et al., 1998). Accompanying this global crisis is the growing support for a radical departure from conventional fisheries management. The establishment of marine protected areas (MPAs) has become a strongly advocated approach to marine conservation strategies (Dugan & Davis, 1993; Roberts, 1997a; Allison et al., 1998; Guénette et al., 1998; Hastings & Botsford, 1999; Wallace, 1999). However, MPA design issues – How big? What dimensions? Intensity of zoning restrictions? – and the ecological ramifications of such issues remain unclear. This paper illustrates the application of ECOSPACE (Walters, 1998; Walters et al., 1999), an interactive, easy-to-use, spatially explicit,

ecosystem-based 'gaming' tool that generates predictions of how taxon specific biomass will change under different marine management scenarios. We used ECOSPACE to evaluate the ecological consequences of alternative MPA zoning policies within the proposed Gwaii Haanas National Marine Conservation Area (NMCA).

Marine protected areas

Marine protected areas, also referred to as harvest refugia or marine reserves, have been proposed to meet a variety of specific objectives that can be divided into two broad categories, fisheries management and the conservation of biodiversity (see Sobel, 1996; Allison et al., 1998). The ecological impacts of marine reserves in tropical ecosystems have been studied extensively (see Alcala, 1988; Alcala & Russ, 1990; Bennett & Attwood, 1991; Polunin & Roberts, 1993; Attwood & Bennett, 1994; Zeller & Russ, 1998), however, until recently, very few empirical studies in temperate marine ecosystems have been conducted (Palsson & Pacunski, 1995; Estes & Carr, 1999; Babcock et al., 1999). This paucity of research exists in part because there are few 'no-take' marine reserves located in temperate waters in which to test their ecological impact. Ecosystem modeling can provide useful insight into minimum protected area requirements and the scale at which to begin experimenting with marine zoning policies within larger marine conservation areas.

Socio-political issues of the proposed Gwaii Haanas NMCA

Located at the southern tip of the Queen Charlotte Islands, British Columbia, Canada, the proposed Gwaii Haanas NMCA extends up to 17 km off shore and encompasses 3180 km^2 of coastal water (Figure 1). Although a federal-provincial agreement was signed in 1988 (Mercier & Mondor, 1995) and the Gwaii Haanas Agreement was signed in 1993 (Canada, 1993), the NMCA has not yet been legally established under the National Marine Conservation Areas Act. Commercial, sport and native fisheries currently occur in the area and represent the greatest resource management challenge for Gwaii Haanas (Harper, 1995). Under the Gwaii Haanas Agreement, Parks Canada and the Council of the Haida Nation, a committee representing local native tribes, will jointly manage resource use within the NMCA (Canada, 1993). The goal of the Gwaii Haanas NMCA is to 'maintain the

structure and function of marine ecosystems' while 'preserving and respecting Haida culture' (Harper, 1995; Parks Canada, 1994). This includes a native's constitutional right to fish (Canadian Charter of Rights and Freedoms, Part I of the Constitution Act, 1982; Delgamuukw v. British Columbia, 1997; Persky, 1998). Multi-use marine zoning may be a viable compromise to these seemingly incompatible goals.

Multi-use marine zoning, a marine planning tool that can separate potentially conflicting human activities, maintain sustainable fisheries and protect marine biodiversity (Bohnsack, 1996), is currently an essential component of the NMCA management plan for Gwaii Haanas (Parks Canada, 1994). Within the Gwaii Haanas NMCA, Parks Canada and the Council for the Haida Nation will designate zones with varying restrictions allowances in terms of recreational use, scientific research, and which fleets will be allowed to fish what and where.

The establishment of 'no-take' zones within the NMCA will undoubtedly be a contentious issue in Gwaii Haanas. The immediate threat to native culture plus the short-term job losses experienced by both native and non-native fishers will be the main premise for conflict and will present a major social hurdle in the zoning process. The following study identifies some of the ecological and social consequences that temperate MPA design planning processes should consider.

Past ECOSPACE MPA design predictions

The Brunei Darussalam ECOSPACE model of Walters et al. (1999) revealed two significant MPA design predictions; the occurrence of edge effect-induced biomass gradients and trophic cascade patterns. Their model suggests that as fish densities increase within a MPA, fishing effort will concentrate on its periphery and force a relative decline in immigration and emigration rates, thereby depressing predator densities within the reserve. The end result is a spatial density gradient across MPA boundaries. This prediction indicates that the effects of fishing on MPA boundaries may have far-reaching consequences within the reserve itself. Furthermore, ECOSPACE predicts that these edge effect-induced density gradients are likely to be accompanied by spatially organized trophic cascade patterns where top predators within the reserve depress the local abundance of their prey possibly resulting in a biomass increase at even lower trophic levels. Therefore, density gradients are further reduced as predators disperse outside MPA boundaries in re-
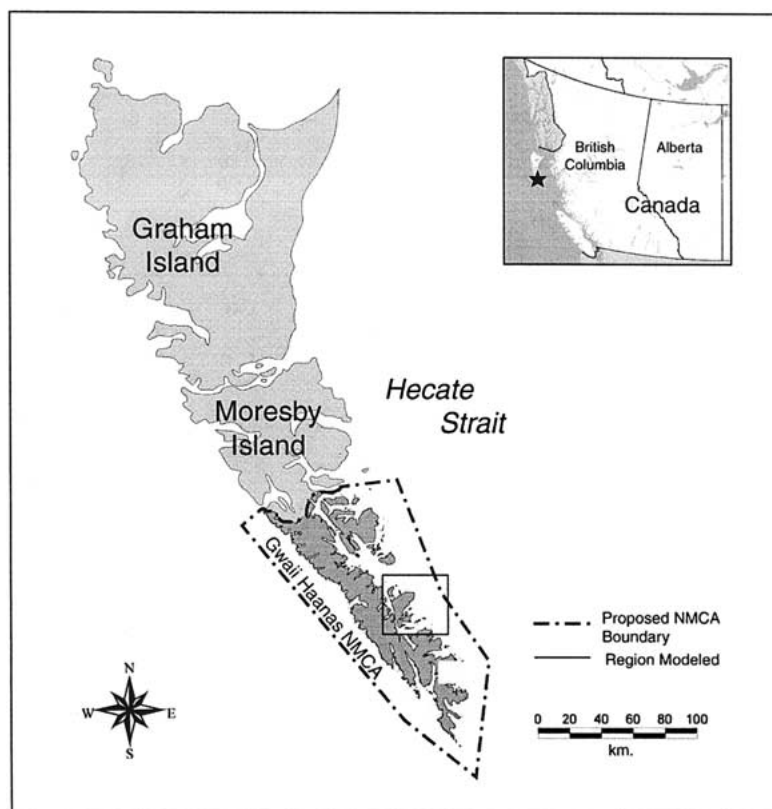
Figure 1. The proposed Gwaii Haanas NMCA is located at the southern tip of the Queen Charlotte Islands in British Columbia, Canada. The specific region modeled, including Burnaby Narrows and a region of Hecate Strait, is approximately 40 km × 40 km.

sponse to declining prey abundance/food availability within the reserve. Indirect trophic interactions and changes in community structure prompted by fishery removals have been documented in coastal marine ecosystems (Castilla & Durán, 1985; Babcock et al., 1999). Walters et al. (1999) concluded that MPAs needed to be large to minimize boundary and behavioral effects that may reduce their effectiveness. Based on this previous work, we chose to screen large-scale marine zoning policies within the Gwaii Haanas NMCA. The predictions described above imply that effective MPA design must also include buffer zones in which fishing effort is limited. Therefore, we tested how multi-use buffer zone placement, size, and intensity of harvest restriction would alter the biomass of various trophic groups within a relatively large (277 km^2) MPA.

Methods

Modeling tools

ECOSPACE is a spatially explicit, ecosystem-modeling tool that illustrates biomass dynamics in two-dimensional space over a grid of spatial cells. It uses the ECOPATH mass-balance approach (Polovina, 1984; Christensen & Pauly, 1992) for parameterization and ECOSIM (Walters et al., 1999) to express biomass flux rates among ecosystem components (or pools). The spatial representation of trophic interactions and population dynamics are based on two main sets of ECOSIM equations. A mix of differential and difference biomass equations describe the biomass dynamics of the ecosystem components such that the change in biomass of ecosystem component i = (consumption) − (predation) + (immigration) − (emigration) − (fisheries catches) (Appendix 1). Consumption equations describe consumption estimates that are limited by a foraging/predation risk tradeoff (for derivation and complete description see Walters

et al., 1997, 1999; Walters, 1998). Here, predator-prey interactions are moderated by the vulnerability of prey to predation (Appendix 1). Trophic flow can be assigned as 'top-down' or 'bottom-up' depending on the risk management behavior of prey and their ability to limit their exposure to predation.

ECOSPACE inputs include dispersal rates and habitat preferences for each ecosystem component which are used to calculate biomass exchanges between grid cells. A spatial map is created to define land, water and the spatial intensity of fishing effort. Essentially, a MPA is created in ECOSPACE by spatially reducing the fishing effort to zero. ECOSPACE users can add detailed spatial information to their base map such as (1) relative primary productivity to account for regions of nutrient upwelling, (2) specific habitat types, and (3) spatial patterns of fishing cost such that fishing effort will be reduced in high-cost cells. The instantaneous dispersal rates across each cell boundary vary with ecosystem component, habitat type, and the response of organisms to predation risk and food availability. The spatial distribution of fishing mortality among grid cells is predicted using a 'gravity model' where fishing effort is proportional to the biomass of the target species and the profitability of fishing it (Hilborn & Walters, 1987). Varying fishing effort spatially in ECOSPACE allowed us to simulate alternative marine zoning policies. Preliminary versions of ECOSPACE can be downloaded as part of the 'ECOPATH with ECOSIM' software system from http://www.ecopath.org.

Our Gwaii Haanas ECOPATH model was constructed with 22 ecosystem components (Figure 2). Ecologically related species were grouped into functional groups, whereas some single species groups were created for commercially important species. ECOPATH inputs (biomass, diet composition, consumption per biomass and production per biomass ratios) were based on Harper (1995), the Hecate Strait Model (Beattie, 1999) and the Prince William Sound Model (Okey & Pauly, 1998). Each simulation was run for ten years and was compared to a baseline simulation of no protection. The change in biomass of each ecosystem component was the 'currency' used to compare the ecological impacts of alternative zoning policies. The changes in biomass are representative of the entire 40 km × 40 km region modeled, not simply the changes that occurred within the boundaries of the modeled MPA itself.

Assumptions of ECOPATH, ECOSIM and ECOSPACE

Although ECOSPACE software is becoming increasingly sophisticated, the preliminary version we used did not represent several factors that may be critical to the spatial organization of ecosystems, such as physical transport and migratory processes. This prevented us from including salmon as an ecosystem component in our model and as a consequence, was an obvious limitation. While detailed information on the link between species and physical processes is not required to evaluate general MPA design policies (Walters et al., 1999), the representation of circulation patterns at a coarse scale would clearly improve the predictive nature of ECOSPACE. Because many marine species have open populations where the recruitment of larvae in one location is dependent on the production of larvae at another, the inclusion of physical processes would allow for a more realistic representation of how local current regimes govern patterns of larval dispersal and recruitment. To date, ECOSPACE does not have the ability to take this into account. Our ECOSPACE model is based on the biomass and production estimates, and diet matrix of our ECOPATH model. These numbers represent 'best guesses'. ECOPATH itself ignores the strong probability that biomass, production and a consumer's diet change dramatically on a seasonal basis (Ruesink, 1998). Current research has been directed at overcoming this shortcoming. Despite these limitations, our Gwaii Haanas model allowed us to test innovative hypotheses and reveal possible outcomes based on available knowledge.

Study area

The region we modeled within the Gwaii Haanas NMCA is approximately 40 km by 40 km (Figures 1 and 3). It encompasses the western edge of Hecate Strait, Burnaby Narrows and several other productive bays and inlets. The area surrounding Burnaby Narrows was chosen to test possible MPA zoning policies because some restrictions have recently been imposed due to harvest and trampling threats to the intertidal community (Harper, 1995).
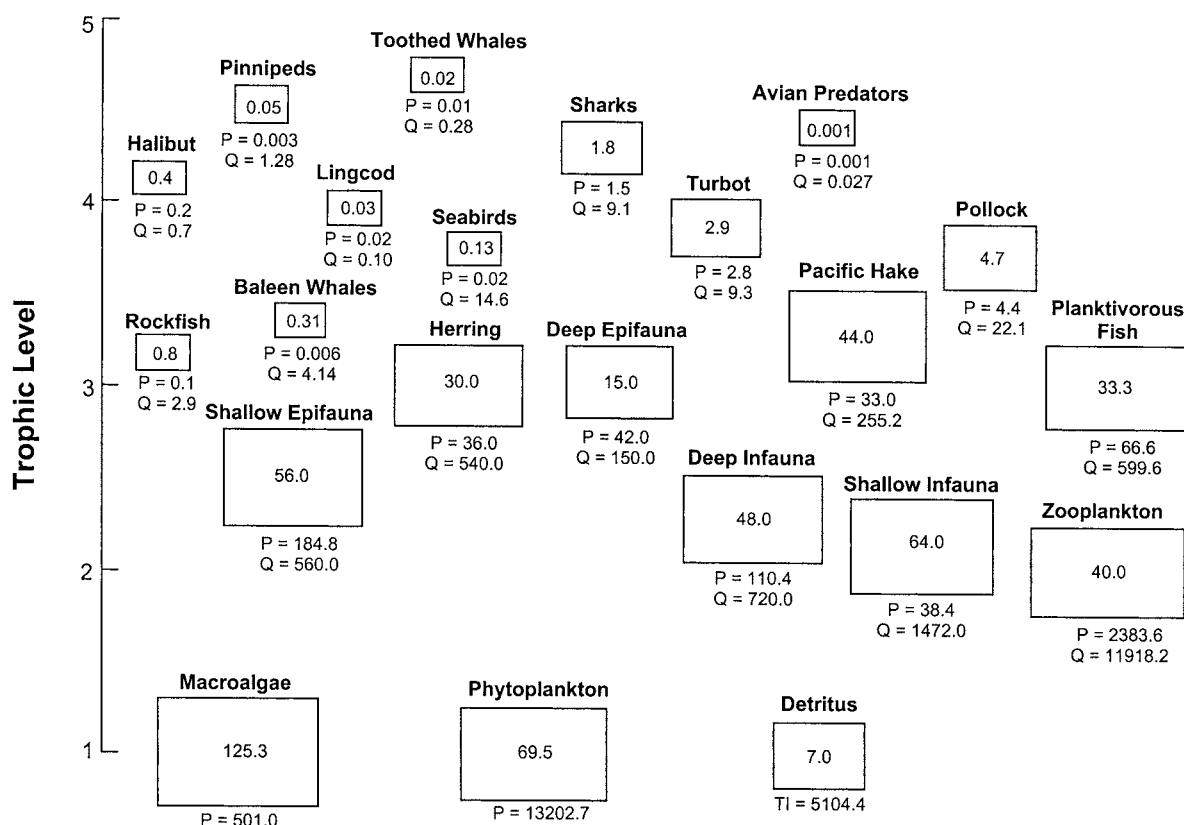
Figure 2. Ecosystem components of the balanced Gwaii Haanas ECOPATH trophic model displayed on a trophic level scale. Biomass estimates located inside each box are expressed in t km^{-2}. The size of each box represents the relative biomass of each ecosystem component on a logarithmic scale. Production (P), consumption (Q), and total input (TI) are expressed in t km^{-2} year^{-1}.

Policy simulations, their predicted ecological consequences and socioeconomic implications

MPA edge effects and trophic cascades

Each of the simulations described below confirmed the edge-induced density gradients and trophic cascade pattern described by Walters et al. (1999) (Figure 3). These ECOSPACE predictions have several important implications. Due to top-down effects, we may not always observe an initial increase in biodiversity within a reserve if an increase in top predators does indeed result in the local depletion of particular prey species. However, an increase in predation on a competitive dominant may, over time, cause a local increase in species diversity by freeing up local resources such as space (Castilla & Durán, 1985) or by reducing the grazing pressure of a herbivore. Recent empirical evidence has in fact documented ecosystem level effects within temperate marine reserves attributable to the build-up of large predators within protected areas (Cole & Keuskamp, 1998; Babcock et al., 1999). Species diversity within a reserve may fluctuate over time due to indirect effects. Consequently, using species diversity as a metric for evaluating the ecological effectiveness of a MPA should be done with caution, at least initially.

MPAs should not be judged as ineffective if high-density hotspots are not observed within their boundaries. Density gradients within marine reserves are predictable when one simply considers the home range size of mobile species, the frequency and direction of home range relocations, and consequently an individual's possible exposure to a fishery (Kramer & Chapman, 1999). As a result, cumulative spatial effects should be considered in the assessment of a MPA's ability to act as a source of propagules to surrounding areas (Roberts, 1997b; Allison et al., 1998).
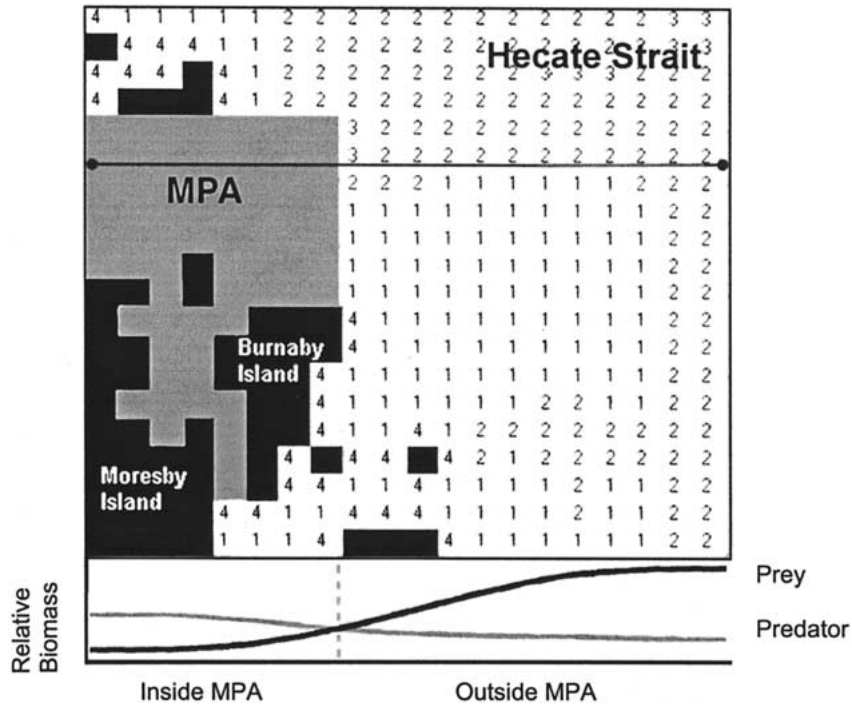
Figure 3. The ECOSPACE base map of the region modeled. ■ = land, □ = water, ▩ = MPA; 1, 2, 3 and 4 represent water depth categories where 4 = 0–30 m, 3 = 31–50 m, 2 = 51–70 m, 1 = 70⁺ m. The stylized representation of the spatial variation in relative predator and prey biomass along a transect line through the 272-km² imaginary MPA created in ECOSPACE illustrates the edge-induced biomass gradients and indirect effects we observed to varying degrees in the policy simulations discussed below.
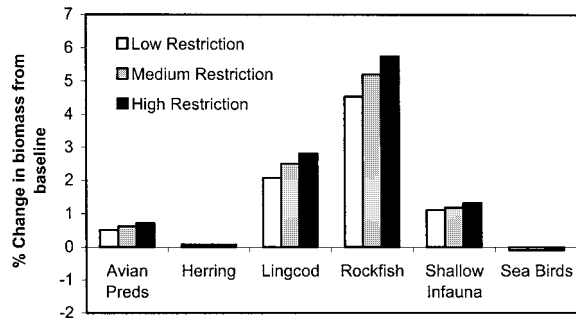

Figure 4. The percent change in biomass from a baseline simulation of no protection when harvest restriction within the 160-km² multi-use buffer zone is varied. Commercial and native finfish and shellfish harvest was varied from low, medium, to high in the buffer zone and each simulation was compared after ten years. Note that the change in biomass of each ecosystem component represents the overall biomass change in the 40 km × 40 km region modeled, rather then the changes that occurred within the imaginary marine protected area itself. Changes in biomass are presented in this manner for all of the zoning policies discussed in this paper.

Multi-use buffer zone size, placement and harvest restriction intensity

To compare the ecological effects of varying restriction intensity within a multi-use buffer zone, three simulations were run on a 272 km² MPA. The area of the multi-use buffer zone and core 'no-take' zone was held constant at 112 km² and 160 km², respectively. The restriction of both commercial and native finfish and shellfish harvest was varied from low, medium, to high in the buffer zone. Figure 4 illustrates that as harvest restriction within the buffer zone was increased, the biomass of lingcod, rockfish and shallow infauna increased. Herring biomass remained unchanged whereas seabird biomass decreased perhaps due to an increase in avian predation by eagles or due to the increase in piscivorous fish competing for a similar prey base. No change in biomass was found for the widely dispersing organisms in our model such as baleen whales, toothed whales, pinnipeds, pollock, halibut, hake, or the planktivorous fish. Although the magnitude of biomass change between policies was relatively small (between 0.25–.75%) these values represent the overall change in biomass of the ecosystem components in the 40 km × 40 km area modeled. Furthermore, the magnitude of each policy effect would likely become more pronounced if simulations were
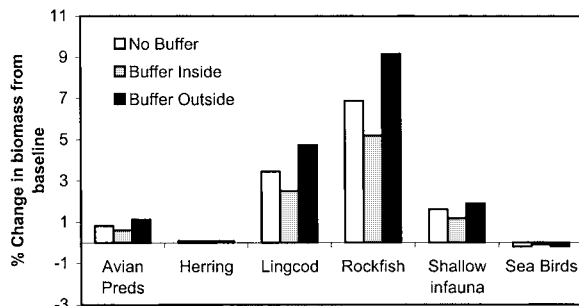
Figure 5. The percent change in ecosystem component biomass after 10 years, from a baseline simulation of no protection, resulting from alternative multi-use buffer zone placement policies. The three policies compared were (1) a 272-km^2 MPA with no buffer, (2) a 4-km wide buffer zone placed inside the MPA, and (3) a 4-km wide buffer placed outside the MPA.

Figure 6. The percent change in biomass from a baseline simulation of no protection as a result of different buffer zone size policies run for 10 years; (1) no buffer zone, (2) a 4-km wide buffer, (3) an 8-km wide buffer of medium harvest restriction intensity, and (4) an 4-km wide buffer of high harvest restriction intensity plus a 4-km wide buffer of low harvest restriction intensity.

run for greater than ten years. This should be kept in mind when interpreting the results of all of the policies presented herein.

Our model suggests that buffer zones are beneficial for organisms with low movement rates because they dissipate the intensity of fishing pressure around the periphery of a MPA and therefore reduce edge effects. However, buffer zones seem to have little effect on widely dispersing species. Clearly, MPAs will have the greatest impact on low dispersing and sessile organisms. These policy simulations also warn us about the use of indicator species to determine MPA effectiveness. If seabirds were one of only a few ecological indicators used in Gwaii Haanas, managers might incorrectly conclude that this MPA is having a small or negative ecological impact. We recommend that the population dynamics and size structure of multiple indicator species should be recorded over time to document the ecosystem level effects of spatial protection.

The ecological impact of protection differed among buffer zone placement policies (Figure 5). A 272 km^2 MPA with no buffer zone and thus a 272 km^2 'no-take' zone, will afford greater protection than a 272 km^2 MPA composed of a 160 km^2 'no-take' zone and a 112 km^2 buffer zone. In essence, when zoned within a 272 km^2 MPA the 4-km wide buffer zone reduces spatial protection. Though seemingly obvious, this simulation was intended to illustrate that buffer zone policy can effectively reduce the size of a MPA's core 'no-take' zone and therefore reduce the protection afforded to low-dispersing organisms. Buffer zones have been proven to be effective at reducing user conflict (Bohnsack, 1996). However, in this case, the
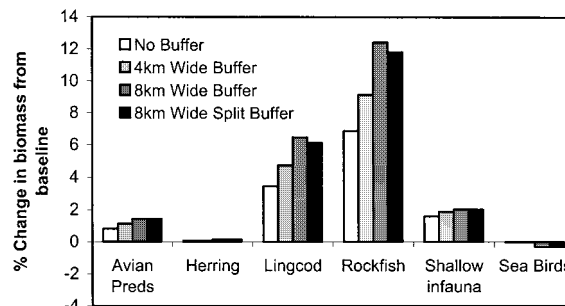
ecological cost of reducing the 'no-take' area to establish a buffer zone outweighs the ecological benefits of a reduction in edge effect due to the buffer. As expected, the greatest protection was achieved by the largest MPA, a 272 km^2 core 'no-take' zone encompassed by a 112 km^2 buffer zone. Note that under all three policies, there was no change in herring biomass and a decrease in seabird biomass.

Buffer zone size and gradient of restriction intensity were shown to affect the overall biomass of several trophic groups (Figure 6). A 4-km wide buffer caused an increase in lingcod, rockfish, shallow infauna, and avian predator biomass when compared to the no buffer zone policy, yet resulted in lower biomass increases than the 8-km wide buffer zone policy. Furthermore, an 8-km wide buffer of medium restriction intensity afforded more protection than a buffer of the same width with a restriction intensity gradient (4-km wide buffer at high restriction intensity plus a 4-km wide buffer at low restriction intensity). Herring biomass slightly increased under each policy whereas seabird biomass declined under the 8-km wide buffer policies.

Aboriginal harvest in MPAs

Aboriginal harvest was simulated in the entire 272 km^2 MPA and then restricted to a 4-km wide, 136 km^2 buffer zone (Figure 7). The change in biomass from a baseline simulation of no spatial protection indicates that a native fishery in the MPA reduced the MPA's ecological benefits by causing a relative drop in lingcod, rockfish, shallow infauna and avian predator biomass. However, restricting the na-
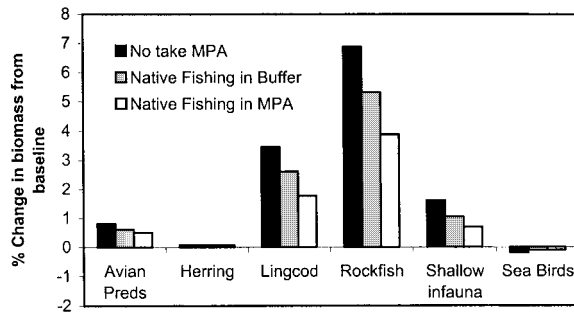
Figure 7. The percent change in biomass of various ecosystem components from a baseline simulation of no protection as a result of 3 different policy simulations run for 10 years; (1) no human exploitation in the MPA, (2) native fishing restricted to a buffer zone, and (3) native fishing in the MPA.

Figure 8. The Single Large or Several Small (SLOSS) debate. The percent change in ecosystem component biomass from a baseline simulation of no protection as a consequence of splitting one large MPA into three small MPAs. Again, simulations were compared once they had run for 10 years.

tive fleet to the multi-use buffer zone helped mitigate the decrease of low dispersers.

Due to the unique nature of the Gwaii Haanas management board, extensive collaboration between Parks Canada and the Council of the Haida Nation over zoning regulations will be necessary. Prohibiting native fishing in a 'no-take' zone is an infringement on a First Nation's constitutional right to fish (Canadian Charter of Rights and Freedoms, Part I of the Constitution Act, 1982; Delgamuukw v. British Columbia, 1997). However, the ecological consequences of a native harvest within a 'no-take' zone will greatly reduce its benefits for both natives and non-natives. A self-imposed restriction by natives, which involves limiting fishing effort to a multi-use buffer zone, may represent a compromise to this contentious issue.

Single large MPA versus several small MPAs; the SLOSS debate

Figure 8 compares the biomass differences resulting from several small MPAs and a single large MPA. Three smaller MPAs, in which the total surface area protected was equivalent to the single large MPA, resulted in a smaller biomass buildup of the low dispersers. This was primarily due to an increase in edge effect. The single large MPA had 24 km of perimeter exposed to fishing effort whereas the several small MPAs had a total of 82 km exposed. However, even the large 272-km^2 MPA conferred little protection to organisms with high movement rates. In fact, a biomass increase in the wide dispersers was only seen when the MPA was coupled with an overall reduction in fishing pressure outside its boundaries (Figure 9).

Relative to small reserves, large MPAs minimize edge effects, include more species and more popula-
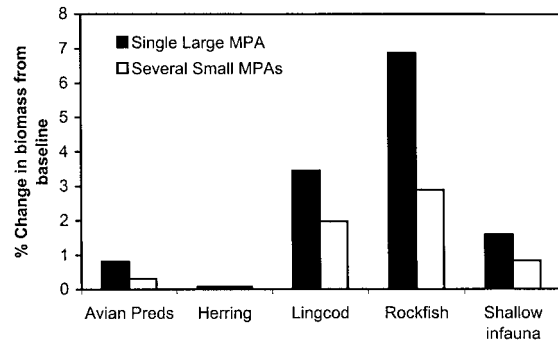
tions, and can encompass species with larger dispersal patterns. Smaller, well-distributed MPAs may include a greater diversity of habitat types and more populations of rare species. However, until a scale of comparison is set and precise conservation objectives are defined, the Single Large versus Several Small (SLOSS) debate remains futile. There is no such thing as an optimum reserve design because each design problem is unique. A MPA's design will depend on its defined goal, whether it be established to conserve a viable source population (Carr & Reed, 1993; Roberts, 1997b), marine biodiversity, or a specified target species. However, if the goal of a MPA is to serve as a harvest refugium for organisms with high movement rates, the bigger the MPA the better.

Spatial restriction coupled with harvest restrictions outside MPA boundaries

Our final simulation compared the effects of combining a 'no-take' MPA and a reduction in the overall fishing pressure outside the MPA with an overall reduction in fishing pressure and no MPA (Figure 9). For the low dispersing organisms, the combined policy caused the greatest increase in biomass. Furthermore, this large-scale spatial reduction of fishing pressure outside the MPA was the only policy of all those simulated that resulted in an increase in biomass of the widely dispersing organisms such as pinnipeds, baleen and toothed whales, hake, pollock and planktivorous fish. Interestingly, the establishment of a 272 km^2 'no-take' MPA, in combination with the overall reduction of fishing effort, actually accounts for very little increase in the biomass of non-migratory organisms and virtually no change in the biomass for organisms with
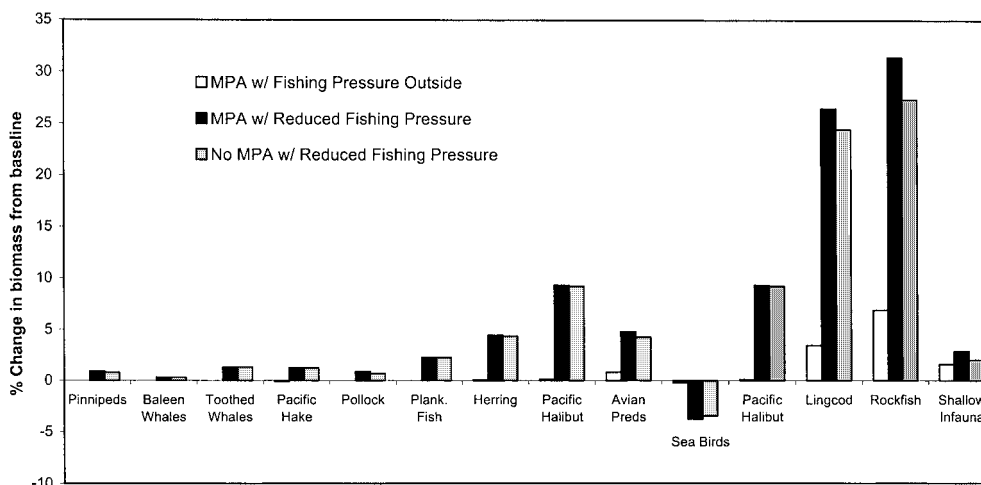
Figure 9. A comparison between the change in ecosystem component biomass from a baseline simmulation of no protection when (1) spatial protection is the only policy simulated, (2) a MPA is coupled with a reduction in fishing pressure (i.e., fisheries quotas) outside its boundaries, and (3) no MPA is modeled yet there is an overall reduction in fishing pressure equivalent to a reduction in fisheries quotas.

high movement rates. However, it is critical to note that although an overall reduction in fishing effort does allow for a significant increase in biomass for both non-migratory and widely dispersing organisms, our model does not account for increases in fishing efficiency over time. Therefore, the predicted increases in biomass as a result of an overall reduction in fishing effort (i.e. fisheries quotas) and no MPA are most likely overestimated. Spatial protection allows us to hedge our bets against the reality that fishers will continue to develop better ways of exploiting marine resources.

Although MPAs are an essential component of marine conservation strategies, they are not isolated from external pressures and therefore provide insufficient protection when unaccompanied by regulations outside their boundaries (Allison et al., 1998). Displacing fishing pressure from one area will result in its concentration in another area. Our model indicates that the concentration of fishing effort on the periphery of a MPA will hinder low-dispersing top predator biomass from increasing within the reserve boundaries. Furthermore, spatially explicit harvest restrictions confer little protection to widely dispersing organisms. The consequent policy implication is obvious; MPAs must be coupled with conservation measures outside their boundaries, otherwise, their effectiveness will be severely compromised.

Conclusions and recommendations

MPAs are becoming an obvious management tactic for conservation to account for the ecological complexity of marine systems (Roberts, 1997a). The establishment of multi-zoned MPAs should be guided by an adaptive, ecosystem-based management approach where management policies are deliberately used as experiments (Walters, 1986). This would entail setting up several MPAs of various designs, monitoring biotic changes over time and quantifying the relative ecological impact of each policy. A framework for management must be sufficiently responsive and flexible to allow for change as better scientific information is gathered and as socioeconomic conditions shift. It is important to recognize that although scientific knowledge about marine and coastal ecosystems is far from complete, this lack of information should not halt conservation strategies. At the very least, MPAs could provide valuable baseline information that would allow for the comparison of harvested and unharvested populations, upon which fishing regimes can be based.

When judging the ecological effectiveness of MPAs, two critical issues should be kept in mind. First, systems are dynamic, therefore, population densities will fluctuate over time. Monitoring programs established to judge ecological effectiveness will have to take this into account. Second, trophic cascades will likely occur. Therefore, the ecological interactions that play out within a reserve may deal us some unexpected results, such as an initial decrease in biodiversity or a

severe decline in a certain prey species. These predictions do not imply reserve ineffectiveness, instead they force us to rethink our marine conservation goals and question how we judge MPA design effectiveness.

Marine conservation policies should be based on ecological factors and consider social and economic needs. Unfortunately, in reality, short-term social and economic costs often act as barriers to MPA establishment and limit MPA design. Therefore, it is important to demonstrate that the long-term gains of preserving ecosystem integrity outweigh short-term job losses and ensuing economic costs. How do we measure these costs and benefits in order to compare policies? What currency should be used? If compensation is demanded, who will ultimately bear the costs? ECOSPACE simulations alone cannot answer these questions, however, they allow the ecological outcomes of each MPA design policy to be compared and thus can form a basis for a management plan. The question remains; how exactly can we assess the ecological effectiveness of a MPA ?

Although ECOSPACE cannot provide detailed quantitative predictions, it does allow managers to generate hypotheses about ecosystem function, screen policy alternatives, identify likely responses, and eliminate ineffective policy options (Walters, 2000). Because ECOSPACE can help identify the range of MPA policy alternatives worthy of experimental field-testing, it is a useful tool to help limit the pathology inherent in current marine resource management and help design an adaptive management approach to MPA design.

Acknowledgements

Appendix 1

Biomass dynamics:

$$\mathrm{d}B_i/\mathrm{d}_t = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F + e_i)B_i,$$

where g_i = net growth efficiency; I_i = biomass immigration rate; M_i = non-predation mortality; F_i = fishing mortality rate; e_i = emigration rate; C_{ij} = the consumption rate on component i by component j; $\mathrm{d}B_i$ = change in biomass of component i.

Consumption dynamics:

$$C_{ij} = v_{ij}a_{ij}B_iB_j/(v_{ij} + v'_{ij} + a_{ij}B_j),$$

where a_{ij} = rate of effective search for prey type i by predator j; v_{ij}, v'_{ij} = prey behavioral exchange rates; C_{ij} = consumption rate on component i by component j; B_i = biomass of component i.

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