

Ecospace: Prediction of Mesoscale Spatial Patterns in Trophic Relationships of Exploited Ecosystems, with Emphasis on the Impacts of Marine Protected Areas

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ABSTRACT

Growing disillusion with the predictive capability of single species fisheries assessment methods and the realization that the management approaches they imply will always fail to protect bycatch species has led to growing interest in the potential of marine protected areas (MPAs) as a tool for protecting such species and allowing for rebuilding populations of target species and damaged habitat. Ecospace is a spatially explicit model for policy evaluation that allows for considering the impact of MPAs in an ecosystem (that is, trophic) context, and that relies on the Ecopath mass-balance approach for most of its parameterization. Additional inputs are movement rates used to compute exchanges between grid cells, estimates of the importance of trophic interactions (top-down vs bottom up control), and habitat preferences for each of the functional groups included in the model. An application example, including the effect of an MPA, and validation against trawl survey data is presented in the form of a color map illustrating Ecospace predictions of biomass patterns on the shelf of Brunei Darussalam, South-

east Asia. A key general prediction of Ecospace is spatial “cascade” effects, wherein prey densities are low where predators are abundant, for example, in protected areas or areas where fishing costs are high. Ecospace also shows that the potential benefits of local protection can be easily negated by high movement rates, and especially by concentration of fishing effort at the edge of the MPAs, where cascade effects generate prey gradients that attract predators out of the protected areas. Despite various limitations (for example, no explicit consideration of seasonal changes or directed migration), the outward simplicity of Ecospace and the information-rich graphs it generates, coupled with the increasingly global availability of the required Ecopath files, will likely ensure a wide use for this approach, both for generating hypotheses about ecosystem function and evaluating policy choices.

Key words: fisheries management; trophic models; cascades; policy evaluation; spatial dynamics; dispersal; habitat preference.

INTRODUCTION

There is ample evidence that fisheries management should not be based solely on single species, dy-

namic pool assessment methods, and models. Even in settings where these approaches seem appropriate, that is, when we see apparently stationary stock–recruitment relationships, public concern about ecosystem integrity now drives us to take at least some account of the fact that fishing always does much more than catch the target fish. In

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contexts where assessment methods and traditional regulatory methods have failed, there is strong demand for policies that are more conservative and somehow will prevent past mistakes from being repeated. One key suggestion that has been offered in response to such demands is spatial management: given present harvesting methods, the only guarantee against overfishing and ecosystem impacts is to subject only parts of the aquatic environment to fishing. At a perhaps radical extreme, a few fishery policy analysts are beginning to change from viewing MPAs as exceptional little places where “seed stocks” and biodiversity can be protected to thinking that perhaps it should be fishing areas that are the exceptional little places (Walters 1998). Traditional stock assessment tools are incapable of even allowing us to ask intelligent questions about spatial management options, let alone about the indirect ecological impacts of policy alternatives. In short, we are being driven toward spatially explicit, multispecies assessment models whether or not we believe that such models are really necessary or practical to develop.

There is little hope of ever developing “complete” ecosystem models for fisheries prediction and doubt about whether such models could be produced even in principle (Rosen 1978). Too many processes are involved, at various time-space scales, from seconds and centimeters (foraging behaviors and predation) to decades and whole oceanic basins (circulation regimes and population dynamics of long-lived species). Existing models have focused mainly on trophic interactions at relatively large spatial scales (areas occupied by key unit stocks) and time scales from months to years. At these scales, the best known approaches are multispecies virtual population analysis (MSVPA; Sparre 1991) aimed at representing how size-age-related trophic ontogenies influence mortality and recruitment rates, and the Ecopath/Ecosim approach, which uses mass-balance and delay-difference models to emphasize whole ecosystem trophic interaction, while allowing, for key species, some representation of the effects of trophic ontogeny (Walters and others 1997). In that approach, Ecopath provides a parameter estimation methodology that is in essence a simplified, equilibrium version of MSVPA, whereas Ecosim provides time-dynamic simulations of changing trophic structure, with emphasis on how small scale (hour-day, km) details of foraging/risk-taking behaviors may limit and structure larger-scale effects. Both MSVPA (see Christensen 1996) and Ecopath/Ecosim (see contributions in Pauly 1998) have behaviors that are relatively well known, and

applications exist outside of the geographic areas for which they were initially developed.

On the other hand, there have been very few attempts to account explicitly for spatial aspects of trophic relationships. This is at least partly due to the staggering computational and information requirements that are implied by conventional brute-force implementations and ad hoc solutions to their parameterization (see, for example, Laevastu and Larkins 1981).

Here we show that the Ecopath/Ecosim trophic modeling approach can be made spatially explicit, yet continue to require only a minimum of input data. We have found a numerically efficient way to solve multiple-pool (or species) biomass dynamics and delay difference equations for a grid of small spatial cells, with the cells linked through dispersal/migration processes. In just a few minutes of PC time, the routine (of Ecopath with Ecosim, version 4.0), which we call “Ecospace,” can generate decadal time scale predictions of spatial biomass patterns for several hundred grid cells, for 15–25 biomass/species pools ranging from phytoplankton to marine mammals. Ecospace does not represent the full variety of physical transport and migratory processes that may be critical in the spatial organization of ecosystems, but it certainly can provide at least some insights about the likely efficacy of alternative MPA policies in relation to questions related to trophic linkages, for example, about “drainage” of large predators from such areas due to impacts on their prey within, and their dispersal out of an MPA, while accounting for the distribution of fishing effort on predators and prey.

We see Ecospace not as a tool for making detailed quantitative predictions, but rather as a “policy screening” method for finding policy alternatives that are worthy of more detailed analysis and experimental field testing. Furthermore, it appears to be a powerful, fun teaching tool for exploring issues of trophic and spatial relationships: the program interface is set up so that users can sketch topographic features (shorelines, islands, areas of high primary productivity, and habitat types and preferences) and policy options (location, size, and shape of MPAs) on the PC screen with a mouse, then watch spatial biomass patterns develop over time as color-coded density maps. Furthermore, we see it as a living, evolving tool; through classroom experience and feedback from users via a website (www.ecopath.org), the model and user interfaces are updated regularly to improve interactive capabilities and provide more options for analysis and policy testing.

ECOSIM/ECOSPACE REPRESENTATION OF TROPHIC INTERACTIONS AND POPULATION DYNAMICS

Ecosim is a modeling tool for representing the spatially aggregated dynamics of whole ecosystems by a combination of relatively simple differential equations for biomass dynamics of some ecosystem components or "pools," along with delay-difference age-size-structured equations for some key populations that have complex trophic ontogenies and selective harvesting of older animals (Walters and others 1997). The differential equations for aggregate biomass (B) of pools (i) are of the form

$$dB_i/dt = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)B_i \quad (1)$$

where g_i = net growth efficiency; I_i = biomass immigration rate; M_i = nonpredation mortality rate; F_i = fishing mortality rate; e_i = emigration rate; while C_{ij} is the consumption rate of type i biomass by type j organisms, that is, the "flow" from pool i to pool j per unit time. For primary producers, the consumption term $g_i \sum C$ is replaced by a biomass-dependent production rate.

A critical concept in Ecosim is that consumption rates or flows may be limited by "risk management" behaviors of prey and predators at very small space-time scales, such that interactions (prey consumption events) may take place mainly in restricted "foraging arenas" where prey make themselves available to predation through their own requirements for resource acquisition (Walters and Juanes 1993). Depending on how fast organisms move in and out of such arenas, flows may range from strongly "donor controlled" (or "bottom-up" controlled or "ratio dependent") to depend solely on total abundance of the prey and predators ("top-down" controlled). To represent arena-scale effects, Ecosim uses a consumption relationship derived by assuming exchange rates into and out of arenas are rapid compared with biomass changes, which results in the rate relationship:

$$C_{ij} = v_{ij} a_{ij} B_i B_j / (v_{ij} + v'_{ij} + a_{ij} B_j), \quad (2)$$

where a_{ij} is rate of effective search for prey type i by predator j ; v_{ij} , v'_{ij} are prey behavioral exchange rate parameters with default setting $v_{ij} = v'_{ij}$.

For derivation of this relationship, see Walters and others (1997); the derivation is based on a variable speed-splitting argument, where the vulnerable biomass V_{ij} of type i prey to type j predators is

assumed to remain near equilibrium with invulnerable biomass $B_i - V_{ij}$, that is, the derivative $dV_{ij}/dt = v_{ij}(B_i / V_{ij}) - v'_{ij} - a_{ij} V_{ij} B_j$ is assumed to remain near zero. Low values of v_{ij} and high a_{ij} imply "ratio-dependent" interaction, whereas high values imply simple "mass-action" interaction; hence Ecosim/Ecospace can represent the range of alternative predictions represented by ratio-dependent versus mass-action models for predation interactions (Abrams 1994; Abrams and Walters 1996).

For selected species with complex trophic ontogeny, Ecosim uses a "split pool" representation of biomass and numbers dynamics. Herein, the juveniles can have feeding ecology and predation losses different from those of the adults, and the simulation accounting keeps track of numbers in juvenile and adult categories as well as body sizes by using delay-difference equations (Deriso 1980; Schnute 1987). Consumption rates by these pools are assumed proportional to numbers rather than biomass [that is, B_j in Eq. (2) is replaced by numbers of predators]. The details of these rather messy accounting equations need not concern us here [see Walters and others (1997) for a first version and Walters and others (forthcoming)]. It suffices here to point out that growth and mortality accounting in the delay-difference framework is structured so that species represented by split pools display overall biomass dynamics and ecosystem linkages/dependences similar to pools represented by Eq. (1), but with the added complexity that adult biomass dynamics can depend strongly on recruitment changes caused by changes in trophic circumstances faced by juveniles. In the delay-difference framework, stock-recruitment "relationships" involving density-dependent juvenile survival rate become an emergent property of treating juvenile production rate as proportional to adult biomass, but juvenile mortality rate as dependent on time spent feeding, time spent in the juvenile stage (and hence time vulnerable to high predation rates), and possibly cannibalism (Walters and others forthcoming).

It is not practical to estimate the many parameters of Eqs. (1-2) by traditional assessment approaches like fitting the model to time-series data. Indeed, such parameterization problems may have prevented follow-up even of the simplified approach proposed by Larkin and Gazey (1982) for simulation of exploited ecosystems. Instead, we use the biomass-flow reconstruction methods of Ecopath (Polovina 1984; Christensen and Pauly 1992) to provide estimates of initial biomasses B_i , g_i , flows C_{ij} , P:B ratios for primary producers, and M_i . We use particularly the C_{ij} estimates (labelled Q_{ij} in Ecopath) along with top-down versus bottom-up assumptions (that is,

hypotheses, reexpressed on a scale from 0 for bottom-up, to 1 for top-down control) to calculate the critical feeding rate parameters a_{ij} , v_{ij} . Some additional growth information needs to be supplied for split pools (age at transition to adult pool, body weight at transition, and von Bertalanffy body growth model parameter K).

The Ecopath estimation procedures are based on assuming mass-balance in trophic flows (biomass equilibrium or known rates of biomass change), and the idea that if some biomasses and/or flows are known, then others can be calculated under the mass-balance assumption. In most applications, Ecopath model developers essentially use a simplified bioenergetics approach: they use basic growth and mortality rate data to estimate P:B ratios and hence consumption rates for some pools, and diet composition information to translate these overall rates into rates of removal from specific prey pools [see contributions in Christensen and Pauly (1993); Pauly and Christensen (1996)]. When total biomass estimates are provided for some pools, Ecopath then calculates biomass estimates (and/or P:B ratios) for the remaining pools necessary to balance the losses that have been provided as input data. One way to think about Ecopath is as a simplification of multispecies MSVPA, with the relatively complex size-age-structured backcalculation of abundances in that methodology replaced by a more flexible method of solving for unknown mass-balance (flow) components. MSVPA works backward from consumption rates estimated from growth (bioenergetics model) and catches to “rebuild” abundances needed to account for these estimated removals; this accounting has been applied mainly within the fish community. Ecopath also seeks to account for such losses other than those due to fishing, and as well, for the fate of production by the lower trophic levels, ignored in MSVPA.

ECOSPACE REPRESENTATION OF SPATIAL STRUCTURE, MIXING PROCESSES, AND HABITAT PREFERENCES

Grid Representation of Biomass Patterns

The intent in Ecospace is to represent biomass dynamics over two-dimensional space as well as time, that is, to represent the biomasses in Eqs. (1) and (2) as varying with spatial coordinates x, y (or u, v) as well as time t . In principle such representations involve very complex sets of partial differential equations. There are two possible ways to discretize dynamic relationships for practical simulation of space-time patterns: the “Lagrangian” approach is to divide biomasses into large numbers of parcels

assumed homogeneous, and to move these about in space. In contrast, the “Eulerian” approach treats movement as “flows” of organisms among fixed spatial reference points or cells, without retaining information about the history (origin and past features) of the organisms present at any point at any moment. The Lagrangian approach can be more accurate and computationally efficient, especially in settings where the variety of things being moved is limited. It is particularly attractive in situations where the spatial movement processes involve mainly well-ordered advective and migratory patterns, and where organisms in any patch are likely to be exposed to similar trophic conditions (feeding opportunities and mortality risks) as they move. But it is not practical to use for whole-ecosystem representations. In Ecospace, we have chosen to take an Eulerian approach and to confront the nasty numerical problems that this approach creates for differential equation solutions. Ordinary solution methods would require very short time-step integration of changes, in situations where movement rates between cells can be high compared with biomasses and other components of biomass change. We have found a way around this “stiffness” problem (see below).

Ecospace users can define rectangular grids of spatial cells, and we solve, for each grid cell, a differential equation system as in Eqs. (1) and (2), along with simplified delay-difference accounting for split pools. For trophic interaction, fishing, and movement calculations, biomass densities are treated as homogeneous (that is, rapidly mixing) within each cell. Cells can be “painted” (with a PC mouse) as land or water, and movement is allowed only across the faces of adjacent cells (no movements across land or between diagonal positions on the grid). Users also can assign each cell (again a painting procedure) to a given habitat type and draw areas of enhanced primary production (that is, of a multiplier of the P:B value of the primary producers) to account for localized productivity variations due to factors such as freshwater nutrient loading and upwelling.

Also, (single or multiple) areas closed to some fishing gears or fleets (restricted areas) or to all fishing (MPAs) can be mapped. Resulting changes in distribution of fishing effort are predicted.

For each cell, the immigration rate I_i of Eq. (1) is assumed to consist of up to four emigration flows from the surrounding cells that share faces with the cell. The emigration flows [up to four components of e_i in Eq. (1)] are in turn represented as instantaneous movement rates m_i times biomass density B_i in the cell (Figure 1). For cells along the boundary of

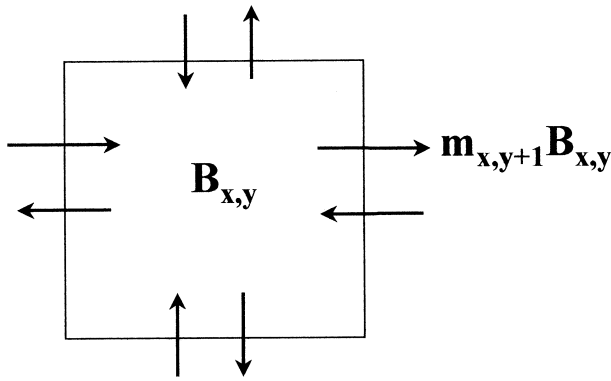


Figure 1. Representing the linkages of a grid cell in Ecospace. Note symmetry of movements into and from adjacent cells, modified only in areas where different habitat types border on each other (see text). Here x, y represents map cell row and column.

the grid (first and last row and column of the grid), emigration rates to the “outside world” are assumed to be balanced by immigration rates from that world, that is, similar biomass conditions are assumed to be present in the nonmodeled grid cell(s) just across the boundary cell face(s) of each cell that has face(s) on the edge of the grid.

Biomass trajectories obtained by integrating the Ecosim/Ecospace differential equations can be viewed in two ways: (a) as the outcome of deterministic interactions; or (b) as an approximation to the trajectories of mean values of stochastic processes that may be locally (in space and time) very unpredictable due to a variety of microscale, “accidental” sources of variation. The second view is obviously more appropriate for ecological settings, where we can easily identify all sorts of behavioral and physical processes that will make spatial response fields far more grainy than can be represented by any continuous model. In this view, the issue is not whether the equations correctly represent all microscale interactions (an impossible task), but rather whether they adequately describe the mean statistical pattern that we would see if we could repeat the solution of some much finer scale model many times. As in all modeling, we ultimately can resolve this issue only through empirical experience. It serves no useful purpose to just point out that the model is “incomplete” in some particular regards (for example, does not account for size-structure effects on foraging and predation risk), since this criticism applies to all models.

Prediction of Mixing Rates among Spatial Cells

The instantaneous emigration/dispersal/mixing rates m_i across cell boundaries are assumed to vary with

(a) pool type i (representing in general how organisms of this type move or are transported by physical processes); (b) habitat type in the source cell side of the boundary (users can define a “preferred” habitat type for each i and relatively higher emigration rate for cells that are not of this type); and (c) response of organisms in the source cell to predation risk and feeding conditions in the cell, as indexed by the “risk ratio” $\Sigma C_{ij}/\Sigma C_{ji}$ (users can specify linear sensitivity of m_i to this index of predation risk/food availability).

Base estimates of the instantaneous emigration rates m_i are calculated from simple input information on average movement (dispersal/advection/diffusion) speeds V_i (mean distance moved per time for organisms of type i). At any instant in time, consider the organisms that are in a spatial band of length L (length of a cell side) and width $dx = V_i dt$ adjacent to a cell side. If the average organism in this band makes a move of length dx over the short time dt , in a completely random direction, it is a simple exercise in calculus to show that a proportion $1/\Pi$ of these organisms will finish the move across the cell boundary (special thanks to calculus student Daniel Walters for this result, which is easy to verify numerically). If animals are distributed randomly over the cell at the start of the interval dt , a proportion Ldx/L^2 will be at risk to emigration across each cell boundary. This implies that the instantaneous rate m_i for randomly moving organisms is given simply by $m_i = V_i/(\Pi L)$, that is, the emigration rate across each cell face should be proportional to movement speed and inversely proportional to cell size as measured by L . Thus, scaling the m_i to reflect higher movement rates for animals that find themselves in cells with unfavorable habitat or high risk ratio only amounts to assuming that such animals either move faster or spend more time moving.

There are two main weaknesses in this dispersal formulation. First, real distributions of movement distances for higher organisms, from which we might estimate V_i , are likely to contain at least two components: (a) many short distance moves representing movement within home ranges; and (b) relatively fewer long distance moves representing migration and dispersal of animals seeking new places to live. The trouble with estimating V as a simple average of these components is that at least type (a) moves are not likely to be random in direction (more likely to move back toward home range center if far from it). In the Eulerian approach, we “lose sight” of movement histories and hence of such oriented moves, treating animals that have crossed cell boundaries as all dispersers who have given up home ranges. We see no simple way

to account for partial exposure of organisms that have home ranges near MPA boundaries to exploitation. In simulations aimed at evaluating efficacy of MPAs, the Eulerian approach is conservative in the sense that it treats all movements that happen to result in leaving any MPA as creating potentially irreversible exposure to harvest risk outside the MPA.

Second, the basic formulation does not account for abilities of mobile organisms to orient movements toward favorable habitats when they find themselves outside such habitats, for example, by using gradients in chemical signatures produced in particular habitat types or simply changes in depth toward preferred shallow or deep habitats. A simple way to think about such oriented movement is to imagine that animals near a boundary (in the Ldx band from which they might move to an adjacent cell) may have a reduced probability of moving toward (or away from) the boundary if the adjacent cell is further from (or nearer to) a cell with favorable habitat. We represent such probabilities in Ecospace by calculating a "habitat gradient function" for each mapped habitat type and pool (i). To start with, every cell is assigned a function value of 1.0 for each pool. This function value becomes 0.0 if pool (i) has been assigned the habitat type in question; subsequently, each cell is assigned a moving average of the function values for surrounding cells if it is not of the type. Such functions increase toward 1.0 with distance from cells of the habitat type and become flat near 1.0 for collections of cells far from any cells of the habitat type (no gradient toward the type). If the difference in this function between any two cells is D , we take the probability of movement toward the cell with a lower function value to be a hyperbolic function $m_i = m_i^{(base)}k / (k + D)$ where $m_i^{(base)}$ is the movement rate in the absence of any gradient and k is a scaling factor representing how strong the gradient (as measured by D) needs to be to result in highly oriented movement. Model users can "turn off" this gradient orientation hypothesis simply by setting k large.

Other Implications of Habitat Preferences

Habitat preferences are likely to be reflected not only in movement rates, but also in feeding efficiencies [represented in Ecospace by the a_{ij} parameters of Eq. (2)] and exposure to predation risk [represented by the v_{ij} parameters of Eq. (2)]. Ecospace users can represent alternative hypotheses about such trophic effects by setting feeding rate and vulnerability "multipliers" for each pool, which are used to scale a_{ij} and v_{ij} during simulations. The multipliers are applied only in the differential equa-

tion for the animals in pool (i) and in those cells that are not preferred habitat for pool (i).

Ecospace users need to be careful about mapping habitat preferences and making complicated assumptions about how such preferences are reflected in rate parameters. Particularly, they must avoid setting up a spatial arrangement of localized interaction patterns that is not consistent with the spatially aggregated Ecopath estimates of overall biomasses, consumption flows, or observed fisheries catches. The Ecosim differential equation parameters for each cell are estimated initially by assuming that cells will be similar *on average* to the overall Ecopath trophic pattern. Thus, if the Ecospace user "ties" some pools to a particular habitat type (for example, by setting high dispersal/mortality rates and low feeding rates for these pools in cells outside that type) then specifies that only a few cells are of the habitat type, Ecospace may be unable to assign as much biomass for the pools in question as was assumed or estimated for the region as a whole in the Ecopath mass balance. Thus, model development should be an iterative process, alternating between Ecopath and Ecospace until the results from the two methods are mutually consistent. Indeed, this iteration also should include Ecosim, to verify that the Ecopath representation of flows and biomass does not lead to models that are dynamically unstable [see contributions in Pauly (1998) for suggestions on this]. The Ecopath with Ecosim (version 4.0) software, whose availability is detailed below, was designed to facilitate the iterative approach suggested here.

Representation of Spatial Dynamics of Fishing Mortality

Ecopath helps develop an overall estimate of fishing mortality rate F_i for each pool, and the overall F_i can be disaggregated by fleet (that is, gear type) in cases where catches are taken by a variety of fleets and/or fishing methods. It is obviously unwise to treat the F_i as spatially homogeneous, especially in (a) evaluation of MPA policies where dispersal of animals across the MPA boundaries may attract higher fishing efforts; and (b) analysis of how spatially varying fishing cost or difficulty may have created "natural" (but potentially unstable to technological/economic change) protected areas for parts of some stocks.

For each gear type included in the initial Ecopath analysis, Ecospace represents spatial distribution of fishing mortality by that gear type by using a relatively simple "gravity model," wherein the proportion of total effort (F) allocated to each cell is assumed to be proportional to the sum over groups

of biomass \times catchability \times price of the target groups, that is, to the relative profitability of fishing in that cell (Caddy 1975; Hilborn and Walters 1987; Pauly and others 1997). If the Ecospace base map contains N active (nonland) grid cells, we first assume that each fleet (gear type) k can exert a total mortality rate NF_k over the whole grid. At each simulation time step, this rate is distributed among cells c ($c = 1 \dots N$) in proportion to gravity weights G_{kc} that are functions of cell profitabilities for the gear type:

$$G_{kc} = O_{kc}U_{kc} \left(\sum_i p_{ki}q_{ki}B_{ic} \right) / C_{kc} \quad (3)$$

where G_{kc} is the weighted “attractiveness” of cell c to fleet k ; O_{kc} is 1 if cell c is open to fleet k , and 0 if cell c is not (allowing to differentiate areas restricted to one or several fleets from MPA, closed to all fleets); U_{kc} is 1.0 if the model user has specified that gear k can fish in the habitat type assigned to cell c , and 0 otherwise; p_{ki} is a relative price received for pool (i) organisms by fleet k fishers; q_{ki} is the catchability of pool (i) animal by fleet k ($= F_{ki}$ from Ecopath); B_{ic} is current biomass of pool (i) in cell c ; and C_{kc} is the relative cost of fishing in cell c by gear k (as mapped by Ecospace user).

Eq. (3) thus implies that cell c will be proportionally more attractive to type k fishing if it is open to it, has the kind of habitat where gear k can fish effectively, has more organisms for which gear k gets good price, and is less costly to access. By using the weights G_{kc} , the total mortality rate NF_k is then distributed among cells c by

$$F_{kc} = NF_k G_{kc} / \sum_c G_{kc} \quad (4)$$

Each biomass pool in cell c is then subject to total fishing mortality rate $F_{ic} = \sum_k F_{kc}q_{ki}$. This multigear-multispecies accounting system is somewhat complex, but we make it as transparent as possible to Ecospace users by asking them to specify only the fishing policy (O_{kc}), fleet-habitat associations U_{kc} , prices p_{ki} , and cost fields C_{kc} that can be “sketched” with a PC mouse along with other spatial pattern information. An obvious choice for the cost fields C_{kc} are sets of values centered around coastal cells representing ports, thus treating the fleet-specific distance between port and fishing ground as the major factor that it is (see, for example, Cruz-Trinidad and others 1997).

NUMERICAL SOLUTION METHOD FOR SPATIAL DYNAMICS AND EQUILIBRIUM

The differential equations of the Ecosim/Ecospace routines have a special structure than can be ex-

ploited to develop relatively efficient computational algorithms. To make the following ideas clear, unnecessary subscripts have been dropped from the equations; references to biomass B should be understood to refer to $B_{r,c,i}$, where r is map grid row, c is map column, and i is an Ecopath biomass pool. At any simulated moment t , the rate equation for each biomass can be expressed as

$$dB/dt = (I + gC) - (Z + E)B, \quad (5)$$

where I = total immigration rate from surrounding cells, C = food consumption rate, Z = total instantaneous mortality rate, and E = total instantaneous emigration rate. If these rate components were constant over time, B would behave as a linear dynamical system and would move exponentially toward the equilibrium

$$B_e = (I + gC)/(Z + E), \quad (6)$$

along the time trajectory

$$B_{t+\Delta t} = B_e + (B_t - B_e)e^{-(Z+E)\Delta t} \quad (7)$$

Note that this solution can be written as

$$B_{t+\Delta t} = W_t B_t + (1 - W_t)B_e, \quad (8)$$

where W_t is the exponential weight $W_t = e^{-(Z+E)\Delta t}$. That is, if input and instantaneous output rates were constant, the time solutions would behave as weighted averages of past time values and equilibrium values with weights dependent on “turnover rates” $Z + E$. We discovered by accident while developing Ecosim that we could use equations like Eq. (8) to greatly speed up solution of the model for “stiff” situations involving a mixture of fast (for example, phytoplankton) and slow changing (for example, most fish and marine mammals) variables. By splitting variables into “fast” (low W_t , high turnover rate, that is, low $P:B$, or Z values) and “slow” categories, and calculating only moving equilibria for the fast variables by using Eq. (8) while integrating slow variable changes with a Runge-Kutta method, we speeded up the Ecosim integration procedures by orders of magnitude without changing the time patterns of the solutions in any noticeable way. That is, we found that the fast variables generally “track” moving equilibria where the equilibria move in response to changes in slow variables. Indeed, it could be argued that all models for macroscopic systems in nature involve some explicit or implicit use of variable speed splitting; for example, the “functional responses” we often use to describe feeding rates in situations where handling

times may be limiting are derived as equilibria of fast dynamics in variables such as hunger.

Another way to think about Eq. (8) is as a “relaxation method” for finding the equilibrium B_e of equations like Eq. (5) by starting at some initial B_o , then repeatedly applying Eq. (8) with some “relaxation parameter” and updating the I, C, Z, and E “parameters” at each step to reflect effects of changes in other variables (for example, biomass in surrounding cells, nonlinear functional relationships between B and the C, Z consumption-mortality rates). For such an iteration to work, it is important that the B_e does not change too rapidly between iterations, and that B_e be easy to compute. In spatial settings, where at least the I term (= $\sum mB$ flows from surrounding cells) can vary rapidly with changes in the B values of surrounding cells, Eq. (8) cannot be applied as a stable iteration method unless W is very large (Δt very small). But for fixed C, Z, a linear equation system results from repeating Eq. (5) over grid cells with the Bs linked through $I = \sum mB$ terms. We can solve this linear equation system very efficiently for spatial patterns of B_e given fixed C, by using column-ordered successive overrelaxation (SOR) methods (Press and others 1992; column ordering here means we solve the linear B_e equation system for each column of the diagonal equation method, then iterate across grid columns by using SOR). That is, we can treat the highly nonlinear consumption function C [sum of Eq. (2) terms over prey types within each spatial cell] and associated mortality rates Z as constant over short time periods, and solve for the often much faster changes in B that result from movement/dispersal. In the original implementation of Ecospace, we did not even try to find time solutions, and instead just set the Ws to 0.5 and used the SOR method to rapidly find equilibrium biomass patterns.

Thus, the solution algorithm now implemented in Ecospace has two parts. First, we precompute W_i weights for each biomass pool i by using movement parameters m_i and initial mortality rates Z_i from Ecopath input (or $Z_i - F_i$ to better reflect speeds of response to imposition of MPAs). Then for each simulation time step, we compute the B_e equilibrium biomass solutions for all pools and grid cells, while holding all consumption inflows C constant at the values predicted from biomasses at the start of the time step, by using SOR. Then we apply the relaxation weighting Eq. (8) to obtain updated biomass estimates to start the next time step. We have found that this method closely approximates full Ecosim Runge-Kutta integration in nonspatial cases, and gives virtually identical Ecospace time

trajectories for reasonably small steps ($\Delta t < 0.2$ yr). Furthermore, by setting Δt very large (2 yr or more), we can find the Ecospace spatial biomass equilibrium very quickly (10–20 iterations) though the biomasses calculated at each such long step are no longer close to those predicted from accumulating changes over shorter time steps.

This solution algorithm was improved further by using an implicit algorithm suggested to the authors by R.B. Deriso (IATTC, San Diego, personal communication). Project a first solution by using Eq. (8), with B_e calculated from base rates I_o , C_o , Z_o , M_o . Then recalculate I_n , C_n , Z_n , M_n rate components for the new state resulting from this solution. Finally, repeat the Eq. (8) time step, with B_e calculated from the average rates $(I_o + I_n)/2$, $(C_o + C_n)/2$, etc.

Two cautionary comments are needed at this point. First, a key reason for being able to obtain Ecospace solutions so quickly using the algorithm described here is that we have ignored the strong seasonal variation that often occurs in ecosystem “forcing” (physical mixing regimes and phytoplankton production), and in dispersal–migration behaviors of vertebrate populations (the physical forcing functions made available in Ecosim are not used in Ecospace). The algorithm relies on ordering of turnover times in food webs (high Z at bottom, lower Z at higher trophic levels) and on the linear mixing terms I,M being large and relatively stable over time. Seasonal variation of “forcing inputs” at lower trophic levels could be dealt with by shortening the integration time step. But it is not clear that this tactic would work for situations where spatial densities of top predators (for example, piscivorous fish and marine mammals) change rapidly over time due to mass migration patterns. We are examining various options for including such migration patterns in future Ecospace versions.

Second, we cannot pretend that the solution method is exact even for very short time steps. In particular, it may not preserve some of the implicit time lag structure that leads to persistent oscillatory behavior in some Ecosim applications. For example, Ecosim models developed by C. Boggs and X. He (National Marine Fisheries Service, Honolulu, personal communication) predict cycles of abundance in mahi-mahi (*Coryphaena hippurus*) in the Central Pacific, apparently in general agreement with fisheries catch statistics. These cycles do not occur in Ecospace simulations from the same Ecopath model. On the other hand, cyclical behavior of predator and prey biomasses, sometimes dampened, sometimes not, does occur when certain Ecopath models are run in Ecospace, even when these models do not include the split pools which generate oscillations in

Biomass distribution of demersal fish

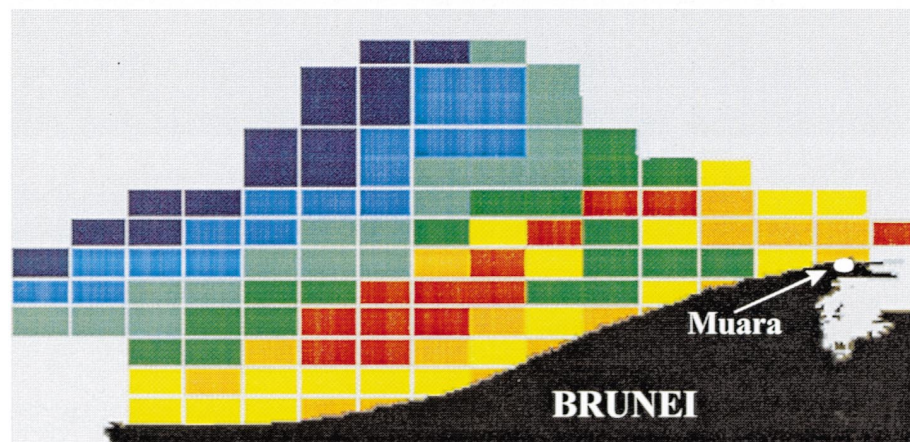


Figure 2. Observed distribution of total demersal biomass off Brunei Darussalam, Southeast Asia, as established from a trawl survey conducted in 1989–90 (Silvestre and Matdanan 1992) and plotted using the B:RUN software (Pauly and others 1997), with red indicating high ($\approx 300 \text{ kg}\cdot\text{h}^{-1}$), and blue low biomass ($\approx 30 \text{ kg}\cdot\text{h}^{-1}$). Note biomass “strips” parallel to the coast, reflective of a productivity rapidly declining with distance from the coast (that is, with depth). Also note high biomass on central coast (that is, in protected areas around rigs and pipelines), and slightly reduced biomass north of Muara, the sole fishing harbor (at tip of northeastern peninsula). Color scale linear in biomass, shading from red (high) to blue (low).

Ecosim runs. Thus, the time behaviors predicted by Ecospace usually provide only general indications of how fast, and in what general directions, biomass responses might occur after changes such as introduction of MPAs. In most situations, we should not expect more than such indications from general biomass dynamics models anyway. We do not see the value of worrying too much about precision in numerical solution methods when the model being solved is very imprecise to begin with.

EXAMPLE APPLICATIONS OF ECOSPACE

Ecospace is being used as an exploratory tool for analysis of trophic and spatial relationships in a variety of cases, involving a broad range of policy issues besides MPAs. For example, in Prince William Sound, Alaska, we hope that Ecospace will help us show how direct effects of the *Exxon Valdez* oil spill may have propagated over large space-time scales via changes in trophic interactions (Okey 1998; Okey and Pauly 1998). Graduate research projects at the University of British Columbia are developing Ecospace models aimed mainly at understanding ecosystem effects of interactions among fishing fleets: L. Hernandez is modeling the Gulf of Mexico to help understand how national/local fisheries management policies may affect abundances available to other nations, S. Martell is modeling fish communities off the coast of British Columbia and is showing that access to MPAs by fleets with special access rights (for example, artisanal, aboriginal, or recre-

ational) can virtually eliminate protective effects even if such fleets are quite small.

When various habitat association and differential movement patterns among trophic groups, top-down versus bottom-up trophic linkage assumptions, and spatial harvest policies are all represented simultaneously, the space-time predictions of Ecospace can be visually very complex and apparently quite realistic. We shall present here only one example, which, however, has the advantage of also representing an opportunity for validation of the biomass distributions predicted by Ecospace. This example is the shelf of Brunei Darussalam. In this case, a well-documented trawl survey was conducted in 1989–90 (Silvestre and Matdanan 1992); a simple Ecopath model has been constructed (Silvestre and others 1993), and there is an effective MPA (an out-of-limit area delimited by oil rigs, and the pipe lines connecting them with the mainland) that reduces the area accessible to commercial trawling.

Figure 2 shows the observed distribution of trawlable biomass along the coast of Brunei Darussalam, as represented by B:RUN, a geographic information system developed to advise coastal area and fisheries managers in Brunei (Pauly and others 1997). This biomass distribution with depth is typical of Southeast Asia (Pauly and Chua 1988), that is, low to intermediate values ($0\text{--}200 \text{ kg}\cdot\text{h}^{-1}$) in shallow waters ($0\text{--}20 \text{ m}$), high values ($300\text{--}400 \text{ kg}\cdot\text{h}^{-1}$) at depth of 20 to 50 m , and very low values ($0\text{--}50 \text{ kg}\cdot$

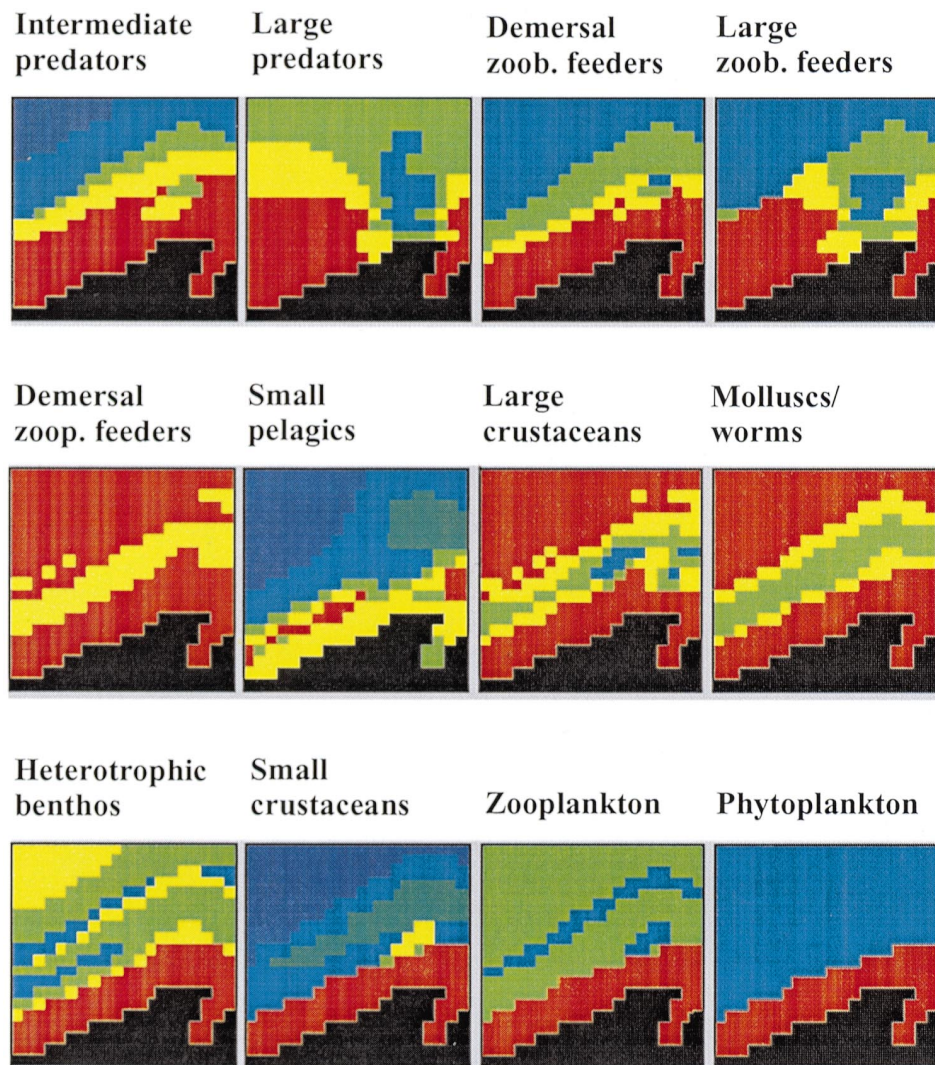


Figure 3. Biomass distribution predicted by Ecospace for the coast of Brunei Darussalam, Southeast Asia, with red indicating high and blue indicating low deviations from the Ecopath baseline for each functional group. Note that the observed distribution pattern in Figure 2 is broadly consistent with predicted biomass functional group with the highest demersal biomass in the underlying Ecopath model ("small zoobenthos feeders"). As expected, the "large zoobenthos feeders," consisting mainly of slow-growing rays, most strongly reflects the impact of commercial trawling around the port of Muara (at tip of north-eastern peninsula). "Small pelagics" refers to small pelagic fishes only. Color scale linear in biomass, shading from red (high) to blue (low).

h^{-1}) in deeper waters (Silvestre and others 1993). This distribution suggests a straightforward definition of three "habitat" types, defined by the bathymetric map presented as Figure 1 of Silvestre and others (1993). We also added a coastal band of increased primary production (3x baseline, three cell rows closest to coast), based on Longhurst and Pauly (1987). Furthermore, an MPA was added, covering the out-of-limit areas around and between oil rings and pipelines (Gayaniilo and others 1998). The scope of the fishery was limited further by high fishing costs (mainly due to fuel costs) away from Muara, the only fishing port of the small trawler fleet (Cruz-Trinidad and others 1997). Dispersal distances for "passive" planktonic organisms were assumed to be on the order of 300 km/y, and for fish, groups were assumed proportional to body size, ranging from 5 to 500 km/y; test runs showed that assuming higher dispersal distances/rates would not change the qualitative patterns, though these

patterns would of course be "smeared" more widely across the map.

Figure 3 shows the distribution of the functional groups included in the Ecopath model of Silvestre and others (1993), as predicted by Ecospace. As might be seen, the different groups display highly patterned distributions, mainly in response to the habitat "bands" along the coast, and to trophic cascade effects. The effect of the trawl fishery near Muara is visible, however, in the distribution of "large zoobenthos feeders" (for example, rays), that are well known to decline upon even light fishing, both in temperate (Brander 1981; Casey and Myers 1998) and tropical areas (Pauly and others 1989; Christensen 1998). The most abundant functional groups in the model, the "small zoobenthos feeders," consisting of fish of the families Leiognathidae, Mullidae, Nemipteridae, Priacanthidae, etc., have, moreover, a predicted distribution largely similar to that of the overall biomass observed during the

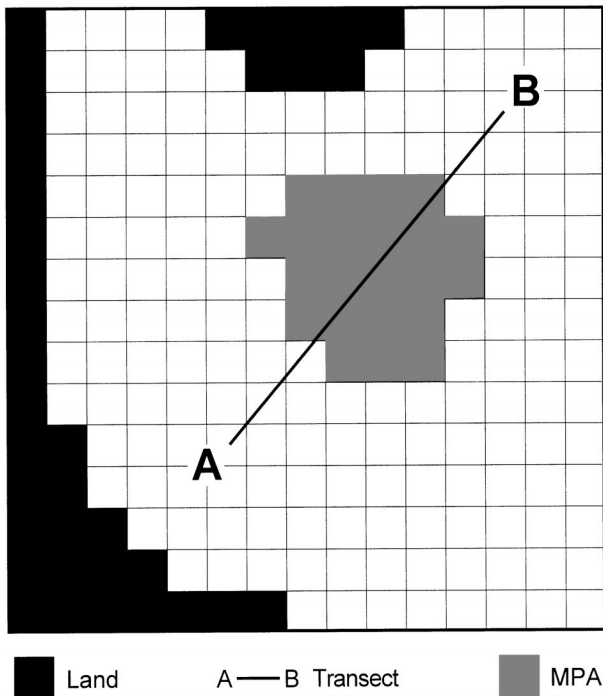


Figure 4. Arrangement of a hypothetical coastline and MPAs sketched with the Ecospace user interface. Simulated spatial biomass and effort variation along the transect line A–B are shown in Figure 5.

trawl survey of 1989–90 (Figure 2). The “fit” between this predicted distribution and the observed one could be improved by various manipulations of the Ecospace settings, but we abstain from this here, the point having been made that Ecospace can predict distribution similar to observed fish distribution, while simultaneously accounting for spatially variable rates of primary production, predation, and fishing.

We now review a few general predictions that have been obtained from Ecospace simulation tests with a variety of Ecopath models, mainly about long-term (steady-state) impacts of MPAs and about spatial organization of trophic interactions. The following predictions are based on results from a hypothetical coastal area “sketched” using the Ecospace interface, with grid cell length $L = 5$ km (Figure 4). To avoid complicating the predictions of MPA effects more than necessary for this demonstration, we assumed only one habitat type, and the same, low movement rates ($V_i = 20 \cdot \text{y}^{-1}$) for all animal pools (the present version of the software proposes default values that are proportional to the trophic level of the pools, as predators are usually more mobile than their prey). Qualitative predictions are similar for higher movement rates especially at lower trophic levels (for example, turbulent

mixing alone would likely result in $V_{\text{phytoplankton}}$ being on the order of $300 \cdot \text{y}^{-1}$), though higher movement rates lead to flattening of the MPA effects over space.

Alternative Predictions about the Efficacy of Marine Protected Areas

Figure 5 represents stylized (exaggerated) Ecospace predictions of steady state biomass densities and fishing effort along a transect line that the user draws across the base map (Figure 4), to illustrate how Ecospace assumptions (that is, settings) affect such predictions. Figure 5A (“Ecopath inputs”) makes explicit the assumption about biomass distribution inherent in a model that has no spatial resolution. Figure 5B shows how Ecospace predictions along the transect look when movement among cells is assumed not to occur (that is, $V_i = 0$). In this case, the basic predictions involve a trophic cascade: the top predators that are impacted strongly by fishing outside the MPA pile up within it and this depresses abundances of the small fishes and invertebrates upon which they feed.

When $V_i = 20 \text{ km} \cdot \text{y}^{-1}$ for all i , the trophic cascade effects are much reduced, and a spatial pattern develops in which top predator abundance is reduced well into the MPA, while a spatially damped enhancement effect occurs outside the MPA (Figure 5C). Abundances are reduced near the MPA boundary compared with the no-movement scenario because of spatial imbalance in movement rates: movement of animals toward and across the MPA boundary from the protected area is not balanced by movement of animals toward the MPA, because there are fewer animals available to move from outside areas.

Figure 5D shows how fishing effort piles up at the boundary of the MPA, in response to local increases in fish availability near that boundary. In this case, densities just outside the MPA boundary cannot increase as much as they would without fishing, creating an even stronger imbalance of immigration and emigration rates for cells near the boundary and hence causing depressed densities even further into the MPA. This is a worrisome scenario indeed, especially for those who believe that having many small MPAs might be a way to protect “seed stock” in settings where fishing effort is difficult or impossible to control.

An even more pessimistic scenario emerges if we include movement and fishing effort response and, in addition, assume that there is strong “risk ratio” response in movement rates. That is, predators move more when they are in areas of low prey density, which causes increased dispersal rates of

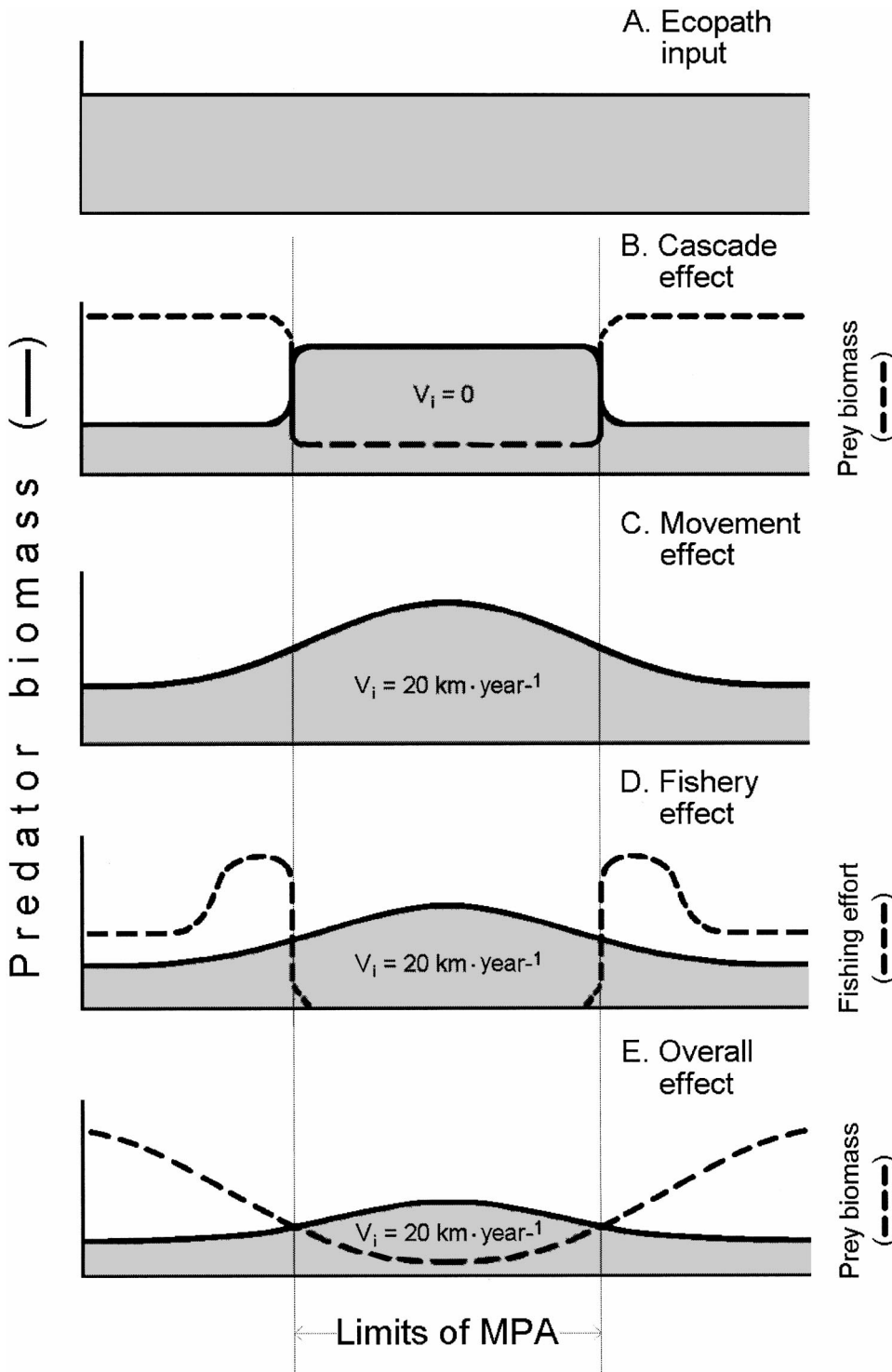


Figure 5. Schematic representation (not to scale) of alternative predictions from Ecospace about biomass variation along the transect line A–B in Figure 4, measured long enough after formation of the MPA in Figure 4 for simulated spatial biomasses to reach equilibrium. B to E show effect of adding progressively more realistic components to the simulations. A no spatial resolution (Ecopath baseline); B no spatial mixing; C spatial mixing at density-independent rates and uniform distribution of fishing effort outside the MPA; D spatial mixing at density-independent rates and concentration of fishing effort at boundaries of MPA; E same as D, but also including density-dependent dispersal rate proportional to the ratio of predation loss rate to food intake in each cell.

top predators away from the center of the MPA. Also, prey move more when there are relatively more predators, which further reduces prey availability near the center of the MPA and hence helps prevent larger populations of predatory fish from developing there. Note that this prediction does not imply that natural, unfished ecosystems should

have low abundances of top predators. It is only when higher movement rates are into areas of higher mortality (by fishing) that we would predict such movement changes to impact on long-term abundance; indeed, higher movement rates of prey in a natural setting could contribute to enhanced abundance of top predators, if prey are differentially

vulnerable to predation while moving. The combined result of these different factors is to reduce the expected positive effect of MPAs on predator populations (Figure 5E).

We suggest that these considerations may help interpret the results of some field studies wherein small MPAs were shown to lead to increases in some species and not in others. On the other hand, field observations of positive effects of even small MPAs on some predator populations (for example, Roberts and Hawkins 1997) suggest that either (a) a key element is missing in our model, or (b) the observed biomass increases are transients, that is, will not be maintained as the system they described reaches equilibrium.

Spatial Expression of Trophic Cascade Effects

Unless the trophic vulnerability parameters v_{ij} of Eq. (2) are set very low to represent bottom-up control of biomass flows, Ecospace generally predicts that gradients in top predator abundance created either by MPAs or habitat preferences should create corresponding inverse gradients in abundance of whatever prey biomass types these predators eat. The effect may or may not propagate still further down the food web in terms of positive spatial correlations between predators and the biomass types fed upon by their prey, depending on complexity of the modeled food web structure and whether or not the lower biomass types have high spatial mixing rates. For example, Ecospace predicts depression in zooplankton abundances near coral reefs where planktivores concentrate, unless the spatial mixing rates of zooplankton are very high compared with predation rates due to advective/diffusive processes. It would appear worthwhile to test such prediction in the field, as we know of no strong field evidence that such “spatial trophic cascade” effects actually exist. If confirmed, these spatial cascade effects would considerably enrich our conceptual toolkit.

Meso-scale (across Ecospace cells) spatial “separation” of some production and consumption processes leads to a form of larger-scale “donor control” in Ecospace interactions than represented in Eq. (2), and hence to both spatial gradients and reduced likelihood of predator–prey oscillations and competitive exclusions. For example, one early Ecopath model for the Gulf of Mexico (Browder 1993) combined all sharks into a “superpredator” represented by a single biomass pool, feeding on a wide range of other pools. In this case, Ecosim predicts that reduction in fishing mortality on this superpredator would result in massive ecosystem changes including elimination of pelagic competitors like

tuna (that is, the sharks build up by feeding on everything, and outcompete the tuna for pelagic food resources). An obvious way to eliminate this problem is to split the shark pool into trophic pools with more specialized feeding relationships (for example, benthic vs pelagic). Ecospace allows us to deal with the problem in even more realistic ways, for example, by further dividing the sharks into pools with complex habitat associations (for example, inshore benthic vs offshore benthic, reef vs sandy bottom). That is, Ecospace can allow us to see far more of the spatial niche structure that probably contributes to natural diversity than is evident from trophic specialization alone.

DISCUSSION

It takes only a few minutes of “play” with Ecospace to raise some very interesting and disturbing questions. Are MPAs really going to work as well as we have hoped, or have we ignored the effects of movements, as in Figure 5B? If trophic interactions do include important “top-down” impacts of predators on prey, should we be able to measure the resulting trophic cascades along spatial gradients created by both natural and managed changes in fishing patterns on top predators? To what extent are natural predator–prey interactions mediated and stabilized through meso-scale separation of the places where prey are produced from the places where predators are concentrated (for example, separation of pelagic plankton production from reef areas where planktivores often concentrate, presumably to use hiding places from predatory fish)?

It is clear from examples like Figure 5 that evaluation of MPA policy options should include careful consideration of dispersal and effort response effects, whether or not these effects can be precisely quantified for models like Ecospace through methods such as tagging and monitoring of spatial effort patterns. Moreover, a clear policy implication is that MPAs may need to be quite large to avoid boundary and behavioral effects that reduce their effectiveness, meaning that in general fewer, larger MPAs should be favored over more, smaller ones in situations where there is a clear mandate to protect a given, limited total area. Thus, a policy that covers all locally unique habitat types and representative organisms through a system of small MPAs may well be ineffective.

There has been some debate about whether marine ecosystems should display the kind of strong trophic cascade relationships that have been demonstrated for freshwater systems (Carpenter and Kitchell 1993). If they exist, such relationships

obviously would have important policy consequences for marine ecosystem management. Arguments against their existence have been based mainly on the idea that marine trophic relationships may be more complex and “web-like” than those of lakes (J.F. Kitchell, University of Wisconsin, personal communication). It is also possible that marine systems have a more complex spatial foraging arena structure and hence more opportunities for evolution of bottom-up control of arena foraging relationships. Ecospace can contribute to a resolution of this question by providing clear, testable alternative predictions about what spatial gradients we should be able to measure under alternative hypotheses about arena structure (that is, v_{ij} parameter values) and spatial mixing rates.

Figure 5 shows how explicit consideration of trophic interactions and spatial movement, in addition to the effect of fishing, may profoundly alter assessments of the impact of spatial management policies such as MPAs. But it also raises an issue about how to obtain the data needed for successful prediction. The predictions require us to specify a very large number of parameters, representing processes across space-time scales ranging from minutes/hours (arena foraging and predation risk) to hundreds of kilometers and decades (dispersal, cumulative biomass change). We can reasonably hope to estimate many of these parameters from field data by using “reconstruction” methods, such as Ecopath and MSVPA, tagging experiments, observations of foraging behavior, etc. But at least some parameters represent processes, such as spatial redistribution of fishing effort and risk/food dependent dispersal that are in some sense novel, that is, not likely to be clearly represented or evident in historical data. We can suggest approximate values for some of these parameters, on the basis of evolutionary or economic “first principles” (for example, the proposition that animals should act to optimize the risk/foraging ratio, or that fishers should distribute their spatial activity in a most profitable way), but it would be foolish to expect such principles to provide accurate quantitative predictions about specific, local situations.

So if we ultimately admit that we cannot make reliable quantitative predictions about the efficacy of particular spatial policy options for which there is inadequate historical experience or precedent, what should we advise policy makers about such options? Unfortunately, it appears that a very strong divergence of opinion is developing in the aquatic science community about how to answer this question. Many of us would immediately recommend adaptive management: implement the policy as an experi-

ment, carefully monitor the spatial structure of changes, and expect to revise the policy substantially in future. But there is a growing number of scientists who appear to believe that improvements in modeling technology and massive field research efforts guided by such modeling can provide policy makers with the correct answers more “safely” and quickly than through large experimental policy tests (Van Winkle and others 1993, 1997). Whether or not such claims are valid, they are certainly attractive to many policy makers: why invest in a risky, contentious, and potentially embarrassing policy experiment when there is a good excuse to delay decisive action while investing in more research?

Thus, we are concerned that the Ecopath/Ecosim/Ecospace modeling approach and software package presented here will be used to justify bigger research programs (“give us more money and we will give you the parameters you need”) rather than for synthesis of existing data, leading to well-designed policy experiments. Unfortunately, this is already happening; at least two substantial proposals for field trophic studies have referenced the Ecopath with Ecosim software as a synthesis tool, without clear specification of the domain of policy options for which predictions are needed.

In contrast, we consider that the most powerful uses of the package will be in settings where it is made very clear beforehand (a) what policy choices are to be compared (what variables/scales/resolution in time and space really need to be considered); (b) why these choices cannot be compared using existing models (concerns about specific changes in trophic relationships, effects of dispersal, etc.); and (c) how the results will be used for policy screening (weeding out alternatives that are predictably hopeless due to inadequate scale, etc.) and design of effective experimental monitoring programs. These are not novel suggestions. For decades, experienced systems analysts have warned about the impossibility of modeling everything and have warned about the importance of beginning analysis with precise and relatively modest objectives (see, for example, Simon 1982). We believe that the key objectives today should be to design better management experiments to evaluate policies, such as MPAs, and monitoring programs to test for existence of spatial cascade effects.

It should soon be possible to improve the Ecospace representation in at least three ways. First, we are developing a link between it and a very efficient hydrodynamic model for computing steady state three-dimensional advection fields. This will allow more realistic representation of how circulation and upwelling patterns influence spatial patterns in

pelagic production components. Second, we are working on ways to overcome computer memory and time problems with spatial delay-difference representations of life histories for species with complex trophic ontogeny and habitat use, to allow better modeling of space-time population dynamics of key indicator species. Third, we are developing hopefully simple ways to enter information on migratory patterns of highly migratory species, and to simulate aspects of the seasonal spatial dynamics associated with such migrations. Note that these improvements are being made not to make the model "complete," but rather to improve basic understanding of how spatial processes influence predictions about trophic relationships and efficacy of spatial management policies.

We invite interested readers to visit the Ecopath home page, (www.ecopath.org), where further examples of Ecospace outputs (maps) can be seen and from which the software can be freely downloaded, along with files allowing these examples to be replicated.

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