REPRESENTATION OF MULTISTANZA LIFE HISTORIES
IN ECOSPACE MODELS FOR SPATIAL ORGANIZATION
OF ECOSYSTEM TROPHIC INTERACTION PATTERNS

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ABSTRACT
The Ecospace model for spatial organization of trophic interactions has seen limited use for evaluation of policies such as marine protected areas, partly because of concern about representing key indicator populations only by spatial biomass distributions. The software has been improved to include spatial representation of age structure for such species, by means of the Ecosim “multistanza” population submodel, which assumes similar diet compositions, predation risk, and vulnerability to fishing over blocks or stanzas of fish ages. A computationally efficient version of Ecospace now preserves the multistanza age structure over spatial habitat and ecosystem biomass maps, evaluating body growth and mortality rates as spatial averages weighted by relative biomass use of each model spatial cell. A more computationally intense version divides each multistanza population into spatial packets (an individual-based model approach) for more precise analysis of how movement patterns and movement histories over mosaics of trophic opportunities and risks affect population performance and variability. The two approaches give surprisingly similar predictions of abundance patterns over both time and space, agreeing well in case-study applications to the Gulf of Mexico and California coast with each other and with nonspatial Ecosim predictions.

The Ecopath with Ecosim (EwE) software is widely used for synthesis of information on trophic interactions and for screening of ecosystem-management options that may alter trophic interactions (Christensen and Walters, 2004). The Ecopath component of the software is used to manage basic input data (abundances, diet compositions, productivity) and to provide static mass-balance analyses. The Ecosim component provides dynamic predictions and capabilities similar to those of single-species assessment models for parameter estimation by statistically based fitting to historical time-series data. The realism of Ecosim models has recently been improved dramatically through inclusion of “multistanza” population-dynamics accounting. Multistanza accounting replaces the simple biomass-dynamics relationships of Ecopath and early Ecosim versions with detailed, age- and size-structured population-dynamics relationships for key species within the ecosystem. The different age ranges (stanzas) can be represented as having distinct diet preferences and vulnerabilities to predation and fishing mortality (Walters and Martell, 2004; Walters et al., 2008).

The EwE software package also includes a spatial modeling scheme called Ecospace, which replicates the Ecopath-Ecosim biomass variables over a grid of spatial cells and represents mixing of biomass (diffusion, advection, and seasonal migration) among the cells (Walters et al., 1999; Walters, 2000). Ecospace was originally intended to provide only crude equilibrium predictions of how spatially oriented management policies and spatially explicit distributions of fishing effort might alter trophic-interaction patterns (e.g., through trophic-cascade effects within protected areas). Ecospace can also make dynamic predictions (see Walters and Martell, 2004:...
has been used to explore spatial management options for a wide variety of ecosystems (see, e.g., Pitcher et al., 2002; Gribble, 2003; Martell et al., 2005; Le Quesne et al., 2008), but when the multistanza population dynamics capability was added to Ecosim, only a crude, equilibrium approximation for age structure was included in the Ecospace software. At the time, we assumed that representing full age- and size-structure dynamics on each of the many grid cells (1000 or more) typically used in Ecospace representations would require massive computational and memory capacity and prevent rapid simulations needed in workshop situations. The crude-approximation approach that was implemented allowed very fast solutions but was recognized to limit severely the ability of Ecospace to represent the spatial habitat shifts that typically accompany trophic ontogeny (different stanzas very often use different spatial cells). These ontogenetic shifts can be critical in evaluating impacts of policies, such as marine protected areas, that often only affect certain stanzas in the life cycles of the key species. The inclusion of multistanza dynamics will permit tracking of the changes in abundance and growth of key species over both space and time, while representing other ecosystem functional groups by means of simpler biomass-dynamics equations with spatial mixing processes.

Here, we describe two approaches to integration of multistanza population-dynamics predictions into the Ecospace framework. Full representation and solution of multistanza dynamics will allow for more realistic, and yet still computationally efficient, Ecospace models. The first approach is based on making multistanza age- and size-structured predictions for an overall spatial region, then predicting distribution of stanza biomasses over spatial cells by means of predicted proportional cell use from continuous spatial mixing models. The second, much more detailed, approach is to divide each multistanza age cohort into a large number of subcohorts or “packets,” essentially an individual-based modeling approach (Van Winkle et al., 1993), then to predict movement patterns of these packets over the spatial map. The first approach is computationally efficient and therefore facilitates multiple model runs in policy-screening and gaming situations, whereas the second is intended mainly to check scenarios developed with the first approach for impacts of complex spatial effects such as differential body-growth rates of fish in different cells or in subareas of the spatial grid. These two new multistanza approaches greatly improve the capability of Ecospace to deal with policy questions not only about marine protected areas but also about changes in essential fish habitat available to each stanza for species with complex spatial and trophic ontogenies.

**Alternative Representations of Multistanza Life Histories in Ecospace**

**Review of General Ecospace Model Structure for Biomass Dynamics.**—For functional groups not represented by multistanza population dynamics accounting, Ecospace represents biomass \( B \) dynamics over a set of spatial cells \( k \) with the spatially discretized rate formulation

\[
\frac{dB_{ik}}{dt} = e_i Q_{ik} - Z_{ik} B_{ik} - \left( \sum_k m_{ik} B_{ik} \right) + \sum_k m_{ik} B_{ik}
\]

where \( B_{ik} \) is the biomass of functional group \( i \) in spatial cell \( k \); \( e_i \) is conversion efficiency of food intake by group \( i \) into net production; \( Q_{ik} \) is total food consumption
rate by group $i$ in spatial cell $k$; $Z_{ik}$ is total mortality rate of group $i$ biomass due to predation, fishing, etc.; $m_{ik}$ is instantaneous movement rate of group $i$ biomass from cell $k$ to cell $k'$; and $m_{ik}$ is movement rate of group $i$ biomass from cell $k$' to cell $k$.

All of the terms on the right hand side of Eq. 1, except $e_j$, are treated as dynamically variable over time so as to reflect changes in food availability ($Q_{ij}$), fishing effort and predation risk ($Z_{ij}$), and seasonal changes in movement patterns ($m_{ik}$). Food consumption rates $Q_{ijk}$ are calculated as sums over prey types $j$ (i.e., $Q_{ijk} = \Sigma Q_{ijk}$). Likewise, total mortality rates are calculated as sums over predator types and fishing fleets $f$: $Z_{ik} = M_u + \Sigma_f F_{ijk} + \Sigma Q_{ijk}/B_{ik}$, where $M_u$ is unexplained mortality rate, the fishing rate components $F_{ijk}$ by fleets $f$ are predicted from spatial distributions of fishing effort for each “fleet” $f$ over the grid cells $k$, and the $Q_{ijk}/B_{ik}$ ratios represent predation rate components of $M$ (i.e., $M_{ik} = Q_{ijk}/B_{ik}$) calculated from predator $j$ consumption rates $Q_{ijk}$.

The Ecospace grid cells are arranged as a rectangular grid with rows $r$ and columns $c$, so that each cell $k$ exchanges biomass directly only with those cells $k'$ that are in adjacent rows and columns. If cell $k$ represents row $r$, column $c$, then $k'$ is restricted to cells $(r - 1, c), (r + 1, c), (c - 1, r)$, and $(c + 1, r)$. Exchanges at the map perimeter are set to zero, except for groups that are assumed to be advected across the map, in which case biomasses at the map boundary are set to constant (Ecopath base estimate) values.

A critical feature of Ecospace is that trophic interactions are not treated as occurring randomly over space within each grid cell. The Ecosim “foraging arena” formulation (Walters et al., 1997; Christensen and Walters, 2004) is used for predicting the $Q_{jk}$'s by means of vertically averaged velocity fields provided by physical models. Second, each spatial cell can be assigned a distinct user-defined habitat type, and each group can be designated to use one or more such types. Given these designations, dispersal rates are modified so as largely to prevent movement into cells with “bad” habitat types, and movement rates for animals currently in bad cells are increased in the direction of more suitable cells. This convention is particu-
larly important for simulation of behaviors that move larval and juvenile fishes from offshore spawning areas into coastal nursery areas, which can often involve using behavioral tactics such as vertical migration and movement only on incoming tides in conjunction with oriented swimming. Third, dispersal rates can be modified to represent movements oriented toward seasonally varying preferred spatial positions; movement can be more strongly oriented (m’s reduced more in directions away from preferred positions) to simulate seasonal migration patterns. Under this option, scaling parameters for north-south and east-west orientation can be specified by model users to concentrate biomasses more or less tightly around the preferred locations. Fourth, movement rates (and optionally directions) can be linked to indices of fitness (food consumption rate $Q/B$, mortality rate $Z$) to concentrate animals in more favorable cells (Martell et al., 2005). Fitness-driven dispersal typically causes dispersal rates to be density dependent, leading to large-scale patterns such as range contraction when overall abundance declines.

Typical Ecospace models developed to date have represented 20–60 functional groups (denoted $i$) on spatial grids with 20–50 rows and columns ($k$ cells) and simulated time horizons on the order of 50 yrs, commonly run with monthly time steps. The Eq. 1 system therefore has on the order of 10,000–150,000 $i,k$ elements and must be solved by some very efficient implicit numerical procedure so that new results can be generated quickly for management-policy comparisons and gaming. We have chosen to use a fully implicit, second-order backward differentiation algorithm. Such implicit algorithms have the valuable property of being numerically stable even at very large time steps and even when some of the system variables can change very rapidly (when the system is numerically “stiff”). The “fast” variables therefore do not force the whole solution method to use a very short time step (e.g., minutes to hours for models with high spatial mixing rates and fast variables like small phytoplankton); instead, the implicit integration method “discards” fast variation, essentially treating fast variables as remaining near a moving equilibrium with respect to changes in the slower variables that affect them (e.g., phytoplankton is treated as remaining near equilibrium with respect to changes in zooplankton biomass). That is, the moving equilibria for fast variables are assumed to be good estimates of average variable values over whatever complex, cyclic patterns such variables may exhibit over time if shorter solution time steps were used.

**Review of Ecosim Multistanza Population Dynamics Accounting.**—Selected biomass groups can be designated life-history stanzas within single-species populations. In such cases, the Ecosim differential equation representation for biomass change (Eq. 1) is replaced by a monthly-difference equation system, with full age-structured accounting for population age and size structure at monthly age increments. The basic accounting relationships are

$$N_{a,t+1} = N_{a,t} \exp(-Z_{a,t}/12)$$  \hspace{1cm} (2)

$$W_{a+1,t} = \alpha_{a} q_{a,t} + \rho W_{a,t}$$  \hspace{1cm} (3)

$$B_{a,t} = \sum_{a=a_{1}(t)}^{a=a_{2}(t)} N_{a,t} W_{a,t}$$  \hspace{1cm} (4)
Here, \( N_{a,t} \) is number of age \( a \) (in months) animals in calendar month \( t \), \( W_{a,t} \) is mean body weight of age \( a \) animals in month \( t \), and \( B_s \) is the biomass of stanza \( s \), defined as the mass (numbers \( \times \) weight) of animals aged at \( 1\text{st} \) through \( 2\text{nd} \) months. \( Z_s \) is the total mortality rate of stanza \( s \) animals, defined the same way on the basis of fishing and consumption as for other model biomass groups \( i \) as \( Z_{i,t} = M_i + \Sigma F_{s,i} + \Sigma Q_{s,i} / B_i \). All animals in stanza \( s \) are treated as having the same predation risk and vulnerability to fishing. The aggregated bioenergetics parameters \( a_r \) and \( r \) are calculated to make body growth follow a von Bertalanffy growth curve (with length-weight power 3.0) with user-defined metabolic parameter \( K \). Exact von Bertalanffy growth occurs when predicted per-capita food intake \( q_{a,t} \) is equal to a base food intake rate that is calculated from the consumption per biomass parameter \( (Q/B) \) provided by the user for each stanza. The metabolic parameter \( r \), which equals \( \text{exp}(-3K/12) \), is based on the assumption that metabolism is proportional to body weight (Essington et al., 2001). Actual or realized food intake \( d_{a,t} \) at each time step is calculated from the total predicted food-intake rate for the stanza \( (Q) \) as \( q_{a,t} = Q_w a^{2/3} / P_{a,t} \), where \( P_{a,t} \) is the relative total area searched for food by stanza \( s \) animals and is computed as \( P_{a,t} = \Sigma a_i N_{a,i,t} w^{2/3} \). For foraging-arena food-intake and predation-rate calculations involving stanza \( s \), \( P_{a,t} \) is used instead of \( B_s \) as the predictor of total area or volume searched for food per unit time. The assumption that area searched and food intake vary as the 2/3 power of weight (i.e., as the square of body length) is a basic assumption that also underlies the derivation of the von Bertalanffy growth function.

For notational simplicity, Eqs. 2–4 above are presented without a species index. Typical Ecosim models developed to date have included multistanza accounting for 2–10 species, each divided into 2–5 stanzas that capture basic ontogenetic changes in diet, predation risk, and vulnerability to fishing. The first age for stanza 1 is always set to \( a,(1) = 0 \) (hatching), and \( a,(1) \) is usually set to 3–6 mo of age to represent the larval and early juvenile periods separately. Then \( a,(2) \) is most often set at 12–24 mo (to represent older juveniles), and additional stanza breaks are set at key ages like maturity and first vulnerability to fishing.

Recruitment rates \( N_{0a,t} \) for Eq. 2 (i.e., animals entering the first stanza) are assumed to be simply proportional to total egg production \( E_e = \Sigma N_{a,t} f_{a,t} \), where age-specific fecundity \( f_{a,t} \) is assumed to be zero for fish with body weights less than weight at maturity \( W_{\text{mat}} \) and proportional to weight above \( W_{\text{mat}} \); \( f_{a,t} = W_{a,t} / W_{\text{mat}} \) for larger, older fish. Model users can also define monthly relative egg-production multipliers to represent seasonality in reproduction. Note that this age-0 recruitment formulation for newly entering animals proportional to egg production does not explicitly account for density dependence in early mortality rates (i.e., an explicit stock-recruitment function is not used). Density-dependent effects occur through (1) impacts of animal density on food consumption, growth, and fecundity (a time-lagged effect that can result in violent population cycles) and, more importantly and commonly, (2) density dependence in \( Z_{s,t} \), caused by foraging-time adjustments in the Ecosim foraging-arena model for \( Q_{a,t} \). Foraging-time adjustments typically result in emergent stock-recruitment relationships of Beverton-Holt form (Walters and Korman, 1999; Walters and Martell, 2004).

The Ecosim multistanza model has been fitted to many time series of population abundances that were reconstructed from single-species age-structure data by methods like VPA (Sparre, 1991) and stock-reduction analysis (Walters et al., 2006). Species fitted range from tunas to groupers to small pelagics like menhaden. For large,
relatively long-lived species (piscivores, benthivores), behavior of the multistanza population model is typically indistinguishable from those of other age-structured models commonly used for stock assessment. For small-bodied species subject to high and temporally varying predation-mortality rates (e.g., small tunas, herrings, menhaden), Ecosim can sometimes capture effects such as relative stability of $Z$ as $F$ increases (decreases in $M$ with increasing $F$) that are typically missed by single-species models that assume stable natural mortality rate $M$ (see, e.g., Walters et al., 2008).

**Original Representation of Multiple Stanza in Ecospace.**—When the multistanza option was originally developed for Ecosim, it was not incorporated directly into Ecospace. Instead, each stanza was treated as its own higher-order functional group for Ecospace biomass-dynamics calculations (Eq. 3), without accounting for age structure within the stanza. Rather, the age-structure of each stanza was assumed to be in equilibrium. Body weight was computed grid-wide (not cell-specifically) for each stanza. Feeding rates were assumed proportional to a relative search-area index $P_s$ calculated from a prediction of the numerical abundance of the stanza $N_s$ as $P_s = N_s/P_s$, where $P_s$ is the initial ($t = 0$) per-capita mean of the relative area-searched index $P_{s,t}$, i.e.,

$$P_s = \sum_a N_{a,0} W_{a,0}^{2/3} / \sum_a N_{a,0}.$$

Dynamics of the numbers in each stanza $N_s$ were computed for each cell by a differential equation similar to Eq. 1:

$$\frac{dN_{sk}}{dt} = R_{sk} - Z_{sk} N_{sk} - (\sum_k m_{skk} N_{sk})$$

where $R_{sk}$ is an approximate difference between recruitment (incoming) rates and exit (to next stanza) rates for stanza $s$ in spatial cell $k$. If the age structure within the stanza is assumed to remain near equilibrium, the $R_{sk}$ term in Eq. 5 can be approximated as

$$R_{sk} = E_{sk} (1 - \exp[Z_{sk} (a_z(1))/12]) \quad \text{for } s = 1$$

$$R_{sk} = N_{s-1,k} Z_{s-1,k} / (\exp[Z_{s-1,k} (a_z(s-1) - a_z(s-1))/12] - 1) \quad \text{for } s > 1$$

Eq. 6a represents egg production rate minus survival rate to the age at exit from stanza $s = 1$; egg production is assumed to be approximately proportional to biomass $B_{s,k}$ of the oldest (adult) stanza $s$ in cell $k$. Eq. 6b is derived from the equilibrium of the delay-differential equation for $N_s$ that results from assuming spatial gain and loss rates to be approximately balanced, so that the dominant effects on $N_s$ are gains from individuals progressing from the previous stanza and from losses of individuals as they progress to the next stanza and mortality within the stanza.

The equilibrium assumption needed for derivation of Eq. 6 can lead to inaccurate predictions because it can result in incorrect size distributions if incoming and outgoing numbers are not in balance, and size then affects the predation-rate parameters (areas searched, maximum prey-consumption rates). Eq. 6 is a relatively poor approximation for both egg production and net rates of numbers gained through graduation from younger stanzas and loss to older stanzas, so this early version of
Ecospace tended to predict incorrect absolute values for cell-specific numbers $N_{sk}$ relative to Ecospace-predicted cell-specific biomasses $B_{st}$, but the predicted spatial distributions of abundances were at least qualitatively reasonable. In past applications, Ecospace generally predicted that $N_{sk}$ was relatively high in cells with high egg production, in cells with favorable habitat, and in cells near seasonally varying optimum migration positions for migratory stanzas.

**New Approach 1: Predicting Spatial Distribution of Overall Abundances and Biomasses from Continuous Mixing-Rate Models.**—In an effort to avoid the large computer-memory requirements and massive accounting calculations (for typical models, on the order of $10^3$ more calculations per time step) required for replicating the full age-structure accounting of Eqs. 2–4 for every grid cell of large Ecospace models, we developed a simple approach based on combining the overall population accounting of Eqs. 2–4 with the relatively simple Eq. 6 diffusion model for predicting relative spatial abundances by stanza. This approach depends on two key assumptions: (1) that Eqs. 2–4 can be applied for each multistanza population as a whole (totaled over all Ecospace grid cells), given reasonable estimates of mean food consumption rates $q_{st}$ and mortality rates $Z_{st}$, averaged over the grid cells (a basic assumption that is made anyway in the nonspatial Ecosim representation of any large area) and (2) that the diffusion model, Eqs. 5–6, gives reasonable predictions of the relative distribution of the biomass of each stanza over grid cells whether or not the absolute numbers $N_{sk}$ are predicted correctly, hence preserving effects of complex spatial-overlap patterns among stanzas.

We then perform the Ecospace time solution on monthly time steps using the following four-step procedure. First, we use the results from integration of Eqs. 5–6 to apportion the spatial distribution of total stanza biomass $B_{st}$ (Eq. 4) over spatial cells $k$ to give $B_{sk}$ cell biomasses comparable to those from integration of Eq. 1, using $B_{sk} = B_{st}N_{sk}/\Sigma_{k}N_{sk}$. Second, the spatial $B_{sk}$ biomasses (and relative predator-search areas $P_{sk} = P_{st}N_{sk}/\Sigma_{k}N_{sk}$) are then used in the Ecosim foraging arena and fishing rate calculations for each cell $k$ to predict food-consumption rates $Q_{sk}$ and mortality rates $Z_{sk}$. Third, biomass-weighted average food-consumption rates $	ilde{q}_{st}$ and mortality rates $	ilde{Z}_{st}$ for the whole population are calculated as

$$\tilde{q}_{st} = \sum_{k} B_{sk}q_{sk}/B_{st} \quad \text{and} \quad \tilde{Z}_{st} = \sum_{k} B_{sk}Z_{sk}/B_{st}.$$  

Fourth, the system-scale multistanza accounting is done by means of Eqs. 2–3 with the biomass-weighted averages $(\tilde{q}_{st}, \tilde{Z}_{st})$ to give predicted total population age and size structure and total stanza biomasses $B_{s,t+1}$ at the start of the next month.

This procedure retains some information about predicted changes in spatial abundance patterns due to mixing processes and spatial variation in mortality rates $Z_{sk}$ because $Z_{sk}$ is included in the prediction of relative numbers $N_{sk}$ by cell from Eqs. 5–6, but it discards information about spatial variation in growth rates $q_{sk}$ in favor of using a single system-scale prediction of body growth (Eq. 3 with consumption rate $q_{st}$ represented by $\tilde{q}_{st}$).

Further, it fails to account for the cumulative divergence that can take place in both age and size structure for relatively sedentary species resident in spatial cells that are protected from fishing. That is, for “adult” stanzas containing many age classes, it fails to represent the potential accumulation of older, more fecund animals.
in protected areas, considered by some to be a key benefit of marine protected areas (MPAs; see, e.g., Gaylord et al., 2005). One possible solution to allowing accumulation of large adults in specific areas is to split the oldest stanza group into a number of stanzas, but doing so is an approximate fix rather than a solution.

For resident species, the mixing-model approach also fails to account for regional variation in growth rates associated with spatial cells that have higher basic (primary and lower-trophic-level) productivity or reduced intraspecific competition due to limited recruitment. For these reasons, the mixing-model approach is best suited to analyses of pelagic systems, where relatively high mobility results in averaging of feeding and mortality rates over substantial areas. When used for systems with many resident or sedentary species, the approach is potentially misleading and should be used only to provide computationally “quick-and-dirty” policy screening for options such as size and spacing of MPAs, to be followed by more careful screening according to the more detailed individual-based approach described below.

**New Approach 2: Individual-Based Approach for Predicting Spatial Patterns in Growth, Survival, and Distribution.**—Most regional populations exhibit at least some degree of localized or cell-scale variation in recruitment, body growth, and survival rates, and erosion of this local structure has serious implications for maintenance of both biodiversity and overall productivity. The original and mixing-model approaches described above cannot adequately capture such local structure, which can result from the cumulative effects of the development of a fishery or from MPAs. We therefore decided to develop a much more detailed and realistic approach to the representation of localized trophic-interaction effects based on concepts of individual-based modeling (IBM).

In the IBM approach, we retain the spatial biomass-dynamics accounting for non-multistanza species represented by Eq. 1 and the multistanza population-dynamics accounting of Eqs. 2–4, but rather than solving Eqs. 2–4 once for each stanza using spatially averaged (grid-wide) food-consumption and mortality rates, we divide the age-0 recruits for each multistanza population \( N_{0,t} \) into a large number \( n_p \) of packets (cohorts). Each packet is assumed to represent some number of identical individuals of the population, and all packets from the monthly recruitments start out with the same individual biomass and numbers at recruitment \( N_{0,t} / n_p \). Each packet is then followed independently as it moves among spatial cells on the grid. This approach is similar to that recommended by Rose et al. (1993) and Scheffer et al. (1995). The growth-survival Eqs. 2 and 3 are then solved for each packet, yielding its predicted age and size dynamics \( N_{p,a,t} \) and \( W_{p,a,t} \), and movements of the packet over time are predicted from both random (diffusive) and oriented (migratory) changes in position. At each simulation time step, the ecological conditions (food intake rates, mortality rates) for the spatial cell in which each packet is located are used in Eqs. 2–3. The overall accounting for \( B_{s,k} \) and \( P_{s,k} \) needed for trophic-interaction predictions (impacts from and on biomasses of nonstanza species in each cell \( k \)) then involves simply summing \( B_{p,k,t} \) and \( P_{p,k,t} \) packet biomasses and predation search areas over those packets present in each cell \( k \), before foraging-arena predictions of \( Q_{sk} \) and \( Z_{sk} \) are performed for that cell.
The obvious advantage of the IBM approach is that it retains the cumulative history of each packet’s space-use pattern, in the form of the packet’s numerical (worth) and body-size (weight) states. For sedentary species, local differentiation in growth and accumulation of older animals is represented by how packets in different local areas (cells) fare over time. Further, through use of restricted movement rules, collections of packets can easily be made to form distinctive local populations, presumably key units of local adaptation and biodiversity.

A disadvantage of the approach is that it requires massive computation, both for the survival-growth calculations and for movement of a sufficient number of packets over the simulated grid to permit realistic spatial distributions and variation. This number must be determined by trial and error; the number of packets must be increased until results stop changing. Most of the computational effort (typically about 90%) ends up being in the simulation of movement as changes in the locations $X_{p,a,t}$, $Y_{p,a,t}$.

Monthly survival-bioenergetics updates for each packet are based on food intake and mortality rates predicted for the spatial cell where the packet is located at the start of the month. No attempt is made to integrate $q$ or $Z$ rates over times within the month spent in different cells; doing so would be prohibitively computationally intensive. This omission amounts to assuming either that cell sizes are set large enough that most movements over any month occur within a single cell or that spatial correlation in productivity and predation risk among nearby cells there is reasonably high, so movements over such cells would result in the same predicted food intake and mortality rates obtained from the initial cell. Effects of violating this assumption could be tested if the model were run with varying grid cell sizes.

The initial or spawning position for each packet ($X_{p,0,t}$, $Y_{p,0,t}$) is set to the center of a cell $k$, where the probability of recruiting to cell $k$ is set equal to $E_{k,t}/\Sigma_{k}E_{k,t}$ and $E_{k,t}$ is the predicted total egg production in cell $k$ for month $t$ summed over all packets that are in cell $k$ at the start of the month. This procedure allows spawning to occur well away from locations of larval settlement or juvenile growth because larval dispersal and juvenile migration can be explicitly represented, through either different or similar movement-simulation rules as used for packets of older fish. In particular, the IBM approach “encourages” formation of local stock structure; recruitment tends to occur near centers of egg production. In the context of MPAs, lower mortality rates $Z$ in designated cells can result in the accumulation of older, more fecund fish, and those cells can thus become local areas of high reproduction.

Monthly movements by each packet are simulated as a set of $n_s$ increments to the $X,Y$ values that determine location on the grid. The user specifies an average annual movement distance, which implies an average monthly movement distance. The number of moves $n_s$ each month is then set so that the distance per increment cannot exceed the width of one cell. Each movement is made only in a cardinal direction (N,S,E,W), so that only $X$ or $Y$ (not both) changes for each move. The probability of choosing each of the four directions, $k'$, is set to $m_{skk}/\Sigma_{k'}m_{skk}$, where $m_{skk}$ is the instantaneous movement rate from cell $k$ to $k'$ calculated for the continuous biomass model (see Eq. 1). As noted above, the $m_{skk}$ can be set equal for all $k'$, to represent purely diffusive movement, or biased to represent avoidance of cells with unsuitable habitat, movement toward preferred habitats, or seasonal migration patterns. This method for choosing movement directions allows users to employ the same user interface for entering assumptions about movement distances and orientation for
multistanza populations as for groups represented only by biomasses, and it ensures that the multistanza movement patterns are broadly comparable with predictions from the computationally faster continuous mixing-model version of Ecospace.

**Case Examples**

Realistic representation of ontogenetic shifts in habitat usage and migration and dispersal patterns is critical to proper evaluation of MPAs. In both cases presented here, conservation groups have exerted considerable pressure in favor of relatively large MPAs for protection of biodiversity and for the restoration of depleted fish populations. The assumption is that traditional fisheries-management approaches (e.g., harvest regulation and habitat protection) are inadequate to the task.

In both cases, currently available population-dynamics and ecosystem-response data are clearly recognized to be inadequate to provide unambiguous predictions of response to various policy options, and clearly, therefore, protected-area plans must be implemented as adaptive-management experiments with the expectation that considerable adjustments will be needed as response information becomes available. The Ecospace models being developed are specifically intended to provide only broad “policy-screening” predictions. Such screening helps to eliminate proposals that would clearly be inadequate to meet various management objectives or would create substantial risks though unintended dynamics such as shifting effort into areas that remain open to fishing.

These two case studies should be viewed as works in progress, where the EwE modeling framework is intended to act as a focus for scientific communication, data synthesis, and progressively refined policy testing over a number of years. Further development of useful ecosystem models will require active involvement and participation by quite large teams of scientists with diverse interests and knowledge. The case-study models represent what practitioners of adaptive environmental assessment and management (Holling, 1978; Walters, 1986) would call “straw man” results, intended specifically to cross the initial intellectual hurdle of getting some model working that can be used as a basis for future improvement and to attract scientific and management interest in that improvement.

Here, we do not provide details about the Ecopath and Ecosim parameters (biomasses, $Z$s, $QB$s, diet compositions, prey vulnerability exchange rates, etc.) used in the simulations. Databases containing all parameter values for the two models, along with the EwE software needed to read the databases and run the Ecosim and Ecospace model scenarios described below, are freely available for download at [http://www.ecopath.org](http://www.ecopath.org) (model references Gulf of Mexico, California MLPA).

**Shrimp Fishery Closures in the Gulf of Mexico.**—The Gulf of Mexico has some of the more valuable fisheries of North America, in particular for shrimp, northern red snapper [*Lutjanus campechanus* (Poey, 1860)], and Gulf menhaden (*Brevoortia patronus* Goode, 1878). Controversy has developed over impacts of the shrimp trawl fishery on the red snapper (Gallaway and Cole, 1999). By-catch estimates of age 6- to 24-mo-old juvenile red snapper have exceeded 20 million fish per year (Ortiz et al., 2000), far larger than the number of older fish caught in commercial and recreational fisheries (SEDAR, 2005). Management proposals for the red
WALTERS ET AL.: MULTISTANZA LIFE HISTORIES IN ECOSPACE MODELS

Figure 1. Time trends of harvestable biomass for key indicator stocks in the Gulf of Mexico (GoM) and central California coast (CA), estimated from single-species stock-assessment models (stock reduction analyses) and simulated time trends predicted by Ecosim’s multistanza age-structured approach and by two Ecospace methods for predicting spatial distribution of size-age stanzas. The y-axis indicates relative abundance, scaled to the same mean for each simulation (all simulations started with the same absolute biomass).

snapper have called for by-catch reduction to promote the recovery of red snapper from historical overfishing.

During development of a demonstration Ecosim model for the Gulf of Mexico Fishery Management Council, Walters et al. (2008) obtained very good fits to historical stock-assessment data using a multistanza Ecosim population model for a variety of important commercial fish species in the Gulf (Fig. 1). The demonstration model is quite complex, including 63 Ecopath biomass pools of which 31 represent life-history stanzas for multistanza population modeling of 10 commercially and recreationally important species, so perhaps not surprisingly, we were able to fit historical data for some species quite well despite very limited information on details of ontogenetic changes in diets, mortality rates, and predation risk, but when model scenarios were run that assessed possible responses of the red snapper to reductions in by-catch mortality of its age 6- to 24-mo juveniles in the Gulf shrimp trawl fishery, we found
that model predictions diverged dramatically depending on details of the protocol followed in selecting Ecosim parameters for inclusion in model fitting to the historical assessment data. Some apparently credible parameter combinations (based on fit to the data) resulted in dramatic increases in red snapper recruitment after by-catch reduction, but other combinations led to predictions of practically no recruitment increase, because of increases in competitor and predator species that are also assumed to be subject to shrimp trawl by-catch (Walters et al., 2008).

We found that this divergence of model predictions resulted from differences in modeled dynamics of several “minor” fish species like marine catfishes, for which very few historical data are available to inform the model-fitting procedures. That is, we cannot resolve uncertainty about how such species would respond to by-catch reduction simply by building more models and including more available data in model parameterization; data critical for model testing were simply not collected during development of the shrimp trawl fishery.

Now, therefore, two basic management options are available. One is to proceed with plans for by-catch reduction, in hopes that various single-species model predictions, and the more optimistic Ecosim predictions, will turn out to be correct. The other is to proceed with an experimental adaptive-management approach, in which some areas are first closed to trawling (or where by-catch reduction devices are required) and are monitored for improvement in red snapper juvenile production, before the decision is made whether to proceed to large-scale trawl closures or by-catch-reduction requirements.

The Ecospace models being developed for the Gulf of Mexico offer an opportunity to provide at least broad, qualitative predictions about likely abundance responses of a range of species to implementation of MPAs aimed at testing effects of trawl closures. Accordingly, we are developing a suite of alternative models for the Gulf region, differing in spatial resolution (grid cell size) and model complexity (number of functional groups) so as to determine which model predictions are robust to these modeling details.

The crudest spatial representation uses $0.5^\circ \times 0.5^\circ$ (~50-km × ~50-km) cells and is therefore capable of looking only at very large closed areas; this model gives fits to historical abundance trend data that are comparable to the nonspatial Ecosim model fits (Fig. 1). The crude spatial version predicts that large closed areas (100 km wide onshore-offshore bands spaced evenly along the coast) would result in dramatic increases in abundance of a number of species that are heavily exploited (Fig. 2). Interestingly, the model predicts quite strong trophic-cascade effects within such large protected areas, involving substantial increases in demersal piscivores (groupers, snappers) at the expense of small planktivores (menhaden) and nearshore pelagic piscivores (mackerels). We note though that both of these prey groups exhibit seasonal migration beyond the MPA borders, which may result in a lowering of the cascading effects if incorporated.

Extreme scenarios like the closure pattern in Figure 2 are probably not practical to implement from a political, economic, or monitoring-cost perspective, but they at least provide a benchmark against which to evaluate more modest adaptive-management proposals. For example, using finer spatial grids (e.g., $0.125^\circ \times 0.125^\circ$, 25-km × 25-km cells), we find with reasonable estimates of spatial dispersal rates that small protected areas (e.g., 25 km wide onshore-offshore strips, widely spaced around the Gulf coast) would probably not produce measurable responses except in a few rela-
Figure 2. Spatial distributions of some indicator biomasses for the Gulf of Mexico, as predicted by Ecospace for calendar year 2005 (end of simulations in Fig. 1). Spatial cells are 0.25° × 0.25° (approximately 25 km × 25 km); cells designated as marine protected areas (MPAs) are shown in grey. Modeled ontogenetic habitat shifts are represented as successive biomass distributions of (A) juvenile (0–12 mo old) menhaden *Brevoortia tyrannus* (Latrobe, 1802), (B) adult menhaden (age 12+ mo), (C) juvenile (age 0–5 mo) red snapper (*Lutjanus campechanus*), (D) juvenile (age 6–24 mo) red snapper, and (E) older (24+ mo old) red snapper. Individual-based modeling (IBM) results with MPAs are not shown because these were indistinguishable from results shown in the MPA column.
tively sedentary species (groupers) and probably not in the key experimental target species, red snapper.

When we repeated the simulations with the crude Ecospace model using the IBM approach to multiple stanzas, rather than the mixing-model approach, we were somewhat surprised to see very little difference between model predictions. In particular, the IBM representation typically predicts spatial patterns very similar (Fig. 2) to those obtained with the much simpler, computationally efficient approach of allocating stanza biomasses over grid cells according to simple biomass mixing-rate predictions and spatially averaged mortality and feeding rates.

To increase the possibility of divergence between the mixing-model and IBM versions, we forced the Ecospace model to have a strong spatial pattern of primary production. We scaled phytoplankton production rates for each cell to mean model-derived primary production estimates based on the approach of Platt and Sathyendranath (1988) tuned to Sea-WiFS satellite data. Such data show that a high proportion of the Gulf’s primary production occurs near the mouth of the Mississippi River, obviously a massive nutrient-loading source. A high proportion of the total shrimp and fish harvest of the Gulf also comes from this very productive area; Ecospace correctly predicts this pattern for both the mixing-model approach and the IBM approach to multiple stanzas (Fig. 2).

**Protection of California Coastal Fish Communities.**—From the 1970s through the 1990s, intensive commercial and recreational fisheries along the California coast apparently led to severe depletion of a variety of demersal fish species, especially long-lived rockfishes (Starr et al., 2002, but see also Stephens et al., 2006). In federal waters (outside California’s 3-mile limit of jurisdiction), this depletion has led to severe restrictions on commercial fishing and, in particular, to closure of large areas as rockfish conservation areas (RCAs). In state waters, a key public reaction to the perception of widespread overfishing has been passage of the Marine Life Protection Act (MLPA). The MLPA mandates development of a network of MPAs along the coast with broad objectives including protection of fish habitat, restoration of ecosystem function, and restoration of natural population size and age structures for long-lived species. The MLPA resulted in a complex planning process that included extensive consultation with the scientific community for development of size and spacing guidelines for MPAs. These guidelines presently call for protected areas to be at least 10 km in long-shore extent, to extend offshore to at least the limits of state jurisdiction, and to be no more than 50 km apart so as to ensure “connectivity” through larval dispersal processes.

Single-species, one-dimensional spatial population-dynamics models of MPA plans developed to date under the MLPA indicate that the size and spacing guidelines will provide effective protection only for the most sedentary demersal fish species (Walters et al., 2008) and will have almost no impact on ecosystem “function” as measured by fish biomass or production. This lack of impact arises because over 90% of the production involves species whose annual dispersal or migration rates are far too high for small inshore MPAs to have any impact on their exploitation rates. We hope that Ecospace models will be able to provide improved policy screening (development of size and spacing guidelines needed to provide effective protection of ecosystem function) in two regards: (1) we will be able to examine two-dimensional spatial dynamics (i.e., inshore-offshore mixing effects and federal and state
MPA policies), and (2) we will be able to account for trophic-interaction effects (e.g., trophic-cascade dynamics) that previous Ecospace modeling has indicated may substantially reduce the efficacy of small protected areas (Walters et al., 1999; Walters and Martell, 2004).

We have developed an initial Ecospace model using most of the Ecopath functional groups and parameter estimates developed by Field et al. (2006) for the large-scale dynamics of the Northern California Current region off California, Oregon, and Washington (Cape Mendocino to Cape Flattery). The Field et al. model included 63 functional groups, but no multistanza components. We aggregated some lower-trophic-level biomasses and left out species (e.g., marine mammals) that are not likely to be affected by MLPA plans to produce a model with 35 functional groups. We then selected six representative demersal species or life-history types (lingcod, thornyheads, shortbelly rockfish, nearshore rockfish, widow rockfish, and abalone) to represent with multiple stanzas using the mixing-model approach. Common features of the modeled life histories of all of these species are that the first life-history stanza represents pelagic larvae and early postsettlement juveniles that are dispersed more or less widely along the coast, that the second stanza represents juveniles that migrate into and grow in inshore (shallow) waters, and that the third stanza represents older (> 4-yrs) juveniles and adults that either remain in shallow areas (abalone, inshore rockfish, lingcod) or migrate offshore to reside in deeper reef and canyon areas. The three-stanza representation allows us to examine “connectivity” among protected areas by larval dispersal, impacts of protection from fishing and other disturbances on juveniles inshore, and impacts of federal management policies in offshore waters.

As for the Gulf of Mexico case, and as did Field et al. (2006), we obtained good agreement between simulated trends in decline of major species and estimates of these trends from single-species stock assessments. The multistanza models predict quite long recovery times (20–50 yrs) to productive stock levels (e.g., stock sizes for maximum sustainable yield) for the depleted species even given complete protection from fishing. A comparison of Ecospace predictions for three spatial protection policies (Fig. 3), using 2" × 2" (3.3-km × 3.3-km) grid cells for the MLPA’s North Central Coast planning unit, indicated that only abalone, with its very short larval and older animal dispersal rates, was likely to increase greatly under the protection afforded by MPAs developed under current size and spacing guidelines, unless the federal RCAs are maintained for at least 20 yrs. Ecospace predicted that implementing the federal RCAs alone would lead to more rapid depletion of inshore species (like lingcod and nearshore rockfishes), because of concentration of fishing effort inshore after closure of offshore grounds. Anecdotal reports and hints in catch statistics imply that this shift actually did start to occur when the RCAs were implemented, but the shift was at least partially countered by introduction of other fishing restrictions like trip limits and license reductions (R. Parrish, NMFS retired, Pebble Beach, CA, pers. comm.).

We then repeated the baseline Ecospace simulation that was previously fitted to the time-series data, but we used the IBM version of the multiple stanzas. We did not try to refit the IBM version to the same time-series data used to fit the mixing-model version. The California Current model generated larger differences between the mixing-model and IBM versions than the Gulf of Mexico model. In particular, the IBM formulation predicted more severe declines of the long-lived rockfishes than were estimated from single-species assessments, from nonspatial Ecosim, or from the mixing-model Ecospace version. The divergence is caused by two factors: (1) con-
Figure 3. Spatial distributions of biomasses of indicator species for an area of the central California coast, calculated by Ecospace for the year 2035 as a future reference point. Maps show three alternative MPA configurations. Species distributions shown are for (A) lingcod (*Ophiodon elongatus* Girard, 1854) adults age 36+ mo, (B) cabezon (*Scorpaenichthys marmoratus* Girard, 1854) adults age 48+ mo, (C) widow rockfish [*Sebastes entomelas* (Jordan and Gilbert, 1880)] harvestable juveniles plus adults age 36+ mo, and (D) abalone (*Haliotis* spp.) harvestable juveniles plus adults age 36+ mo. Cabezon and abalone represent species largely restricted to inshore waters within California's state jurisdiction, whereas lingcod and widow rockfish are more widely distributed and subject to impact from recent U.S. federal regulations (RCAs, rockfish conservation areas).
centration of Ecopath base biomasses on a much smaller proportion of the total habitat than in the Gulf of Mexico case, causing more severe intraspecific competition for food (and therefore reduced growth rates and fecundities wherever IBM packets are concentrated through chance movements), and (2) greater concentration of fishing effort on cells where more packets are concentrated by chance at each model time step.

Ecospace includes a procedure for adjusting prey-vulnerability and fishing-mortality rate parameters for concentration of abundance in cells with favorable habitats, but the adjustments are apparently not great enough to prevent reduced mean productivity and higher overall fishing mortality in the IBM version. This problem could, in principle, be remedied by refitting of the model, but with present computing capability, making the many IBM simulation runs that would be necessary for the nonlinear search procedures used in Ecosim model fitting is not practical. One comforting point is that, although the IBM representation overestimates stock depletion, it still predicts the same relative response to spatial closure patterns as does the simpler Ecospace representation, indicating that the simpler representation can be used effectively for rapid policy screening.

Discussion

The two new approaches presented complement each other and should be used in tandem. The faster and less expensive mixing-model version can be used for data fitting and gaming, and periodic comparison of predictions with those of the more computationally intensive IBM version can ensure high confidence in the overall results.

Although Ecospace now has the accounting procedures needed for realistic representation of multistanza life histories, the case examples illustrate a key gap in information that suggests caution in interpreting model predictions. For both case models, the first or early juvenile stanzas are assigned high annual natural mortality rates Z on the order of 1–3, and small changes in these rates can cause large changes in predicted recruitment rates. Presumably most of this juvenile mortality is due to predation, but modeled “ecotrophic efficiency” (proportion of Z caused by modeled predators, calculated from predator abundances, food consumption rates, and diet compositions) is low for most juvenile groups. Early juvenile biomass is typically low, and high mortality rates can be caused if the juveniles make up only a tiny proportion of the diet of abundant predators. Diet data are typically inadequate even to detect, let alone to estimate accurately, such tiny proportions. Low ecotrophic-efficiency values in the models mean that juvenile mortality rates do not vary substantially with changes in abundance of modeled competitors and predators, so the models may greatly underestimate effects of changes in community structure on recruitment rates. A major and unfortunately very common problem is that we have only very incomplete information about causes of mortality for juvenile fishes, and this is an area that should see increased research focus.

Individual-based or packet models for fish dynamics have typically represented dynamics at much finer scales (hours to days, meters to kilometers) than is usual for Ecospace models (see, e.g., Van Winkle et al., 1993; Tyler and Rose, 1994; Ault et al., 1999; Werner et al., 2001). The main emphasis in those models has been on capturing effects of individual variation in foraging and predation circumstances on growth.
and survival patterns. To date, few IBMs (e.g., that of Ault et al., 1999) have included dynamic calculations on fine enough time and space scales (minutes, meters) to capture the predation-risk-management effects (spatially and temporally restricted foraging, bout feeding dynamics) that have been found to be critical for representing recruitment relationships, long-term predator-prey stability, and maintenance of biodiversity in Ecosim models (Walters and Martell, 2004).

Comparison of IBMs for very fine-scale spatial behavior (K.A.R., unpubl. data) with Ecospace reveals a key structural limitation in the Ecospace formulation. In assuming that the Ecosim foraging-arena equations (for exchange of prey biomass between vulnerable and invulnerable behavioral states) apply within each Ecospace cell, we implicitly assume that each model cell is at least large enough to contain all of the “routine” (diurnal, feeding and resting) activities for each individual. We do not allow for the possibility that individuals use one spatial cell or habitat type for resting and hiding and other cells for foraging (and exposure to increased predation risk). For example, suppose we set up an Ecospace model with small enough grid cells to display a mosaic of reef habitat cells and a corresponding mosaic of soft (sandy or mud) bottom areas between these reefs. Any model species that is treated as using only reef habitat is then restricted to spend all its time in the reef-type cells, when in reality many such species make periodic, extensive (and risky) foraging excursions onto open bottom areas. In restricting such species to the reef cells, Ecospace underestimates food resources available to them, as well as exposure to some predators and fishing pressure, and their local impact on abundances of food organisms on adjacent soft bottom areas. We can crudely represent such use of multiple habitat types by creating a new habitat type called something like “soft bottom near reef,” and placing a “halo” of such cells around each reef, but this arbitrary approach assumes that we can predict the sizes of such habitat halos a priori rather than as part of the Ecospace IBM movement dynamics. Further, Ecospace provides no simple way to predict the proportion of time that animals choose to spend in relatively safe (reef) cells as opposed to relatively risky foraging (soft-bottom) cells. For larger Ecospace cells, where daily movements are contained within cells, that time allocation is automatically estimated from Ecopath base feeding rates and maximum feeding rates, and changes in time allocation are calculated automatically (when desired) as relative time spent feeding and at risk to predation.

Although this structural limitation may be seen as a weakness of Ecospace by scientists concerned with understanding how the details of fine-scale behavioral ecology contribute to limitation of trophic interaction rates, it is also a strength in the sense of allowing use of large spatial cells for exploration of policy options like MPAs over large regions (e.g., Figs. 1–2). Representing such large regions with spatial cells and time steps small enough to represent resting-foraging behavioral exchanges explicitly—while still making long-term ecosystem response predictions quickly enough to allow for model fitting and comparison of multiple policy options in planning settings like management gaming workshops—is presently impractical, limited by insufficient data and computational speed. Further, running highly detailed models over very large spatial grids is an invitation to generation of pathologically large, cumulative errors in model predictions. The challenge is to meld the detailed IBMs with the broad-scale Ecospace model to be able to scale small-scale IBM results to more ecologically meaningful regional scales and to increase our confidence in how fine-scale dynamics are approximated in Ecospace.
Another potential weakness in the current Ecospace formulation is that habitat structure (habitat “type” for each spatial cell) is treated as constant over time. Some temporal changes in cell habitat type can be accommodated. If cell habitat is defined by biologically produced habitat features like macrophyte biomass, then the variable can be included as Ecopath/Ecosim variables and linked to trophic interactions through “mediation functions.” Model users can introduce arbitrary changes in the habitat type map as simulations proceed, but the capability has not yet been developed to model how such changes might happen dynamically over time as a result of processes like industrial development and land subsidence (as occurs in the Gulf of Mexico near the Mississippi River mouth). Further, no easy way is available to model dynamics of physical-chemical variables like turbidity, salinity, and dissolved oxygen as defining variables for habitat type or habitat quality. Time series of spatial salinity fields and relative primary production rates can be input to the software as spatial forcing fields and then linked to feeding and mortality rates, but this approach does not allow complete flexibility in how the input variables affect habitat quality.

Much modeling of ocean ecosystems has focused on understanding linkages between physical dynamics (hydrodynamics), chemistry (nutrient cycling), and lower trophic levels (phytoplankton, zooplankton), by means of “nutrient-phytoplankton-zooplankton” models like ERSEM (Baretta et al., 1995) and NEMURO (Werner et al., 2007), and efforts have been made to link these models with Ecosim (Aydin et al., 2005) and with IBMs (Megrey et al., 2007) and, more recently, to real-time coupling of Ecosim to biogeochemical models (B. Fulton, CSIRO, pers. comm.; S. Mackinson, CEFAS, pers. comm.). Such efforts will eventually lead to synthetic models that overcome at least some of the limitations of Ecospace related to habitat structure and productivity, but as for most IBMs, such models are not yet computationally efficient enough to be useful for interactive policy analysis.

Clearly, we need to view Ecospace not as a fixed, completed modeling application but rather as an evolving framework, subject to continuing improvement as the model is challenged with new “what-if” questions and with opportunities for integration with other modeling approaches. We hope the steps we have taken to improve the population-dynamics representations in Ecospace will be just one component in a much larger process of further model development and testing.

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