Adding realism to foraging arena predictions of trophic flow rates in Ecosim ecosystem models: Shared foraging arenas and bout feeding

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ABSTRACT

We update the Ecopath with Ecosim software for aquatic ecosystem modeling to allow users to represent intensification of inter-specific competition through shared use of space–time restricted foraging arenas, as well as predation occurring in periodic short feeding bouts rather than continuously over time. Our study indicates that assuming shared use of foraging arenas can have pathological impact on the ability of ecosystem models to predict maintenance of biological diversity in complex food webs, in cases where multiple predators have similar diet compositions but in fact avoid direct competition through fine-scale separation of feeding locations or times. We further find that the assumption of bout feeding leads to essentially the same predictions about how predation rates ought to vary with predator abundances as does the more unrealistic assumption of continuous feeding.

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1. Introduction

Since its incorporation in the Ecopath software in 1997 (Walters et al., 1997), the Ecosim dynamic model for trophic interactions in aquatic ecosystems has been widely used as a tool for exploring possible implications of such interactions for fisheries management policy (Pauly et al., 2000; Christensen and Walters, 2005; Walters et al., 2005). In response to user requests for more realistic representation of various aspects of ecosystem dynamics, the ‘Ecopath with Ecosim’ or ‘EwE’ software package has grown from a simple scheme for examining biomass dynamics (Christensen and Pauly, 1992) into a very flexible (but quite formidable) package (Plaganyi, 2007), with capabilities ranging from detailed ‘multi-stanza’ age-structured population modeling (Walters and Martell, 2004) to the Ecospace representation of spatial dynamics (Walters et al., 1999), providing tools for policy optimizations (Christensen and Walters, 2004b). This flexibility has created opportunities for scientists to examine the sensitivity of policy predictions to a wide range of assumptions (e.g., to compare simple versus complex models), though many users have not taken advantage of this capability and have used the software uncritically as a ‘black box’ (Plaganyi and Butterworth, 2004).

The functional heart of Ecosim is its ‘foraging arena’ representation of trophic interaction rates, derived from arguments about how trophic interactions generally take place in space–time restricted foraging arenas so that interaction rates may be severely limited relative to predictions from sim-
ple mass-action models that assume predators to distribute their searching at random with respect to prey distributions (Walters and Janues, 1993). Restriction of interactions is represented by pretending that prey of any predator exchange between vulnerable and invulnerable behavioral or positional states, so that the density of vulnerable prey may be severely impacted by predators even when overall prey abundance is high. The foraging arena representation has major implications for dynamic properties ranging from the form of single-species recruitment relationships to overall ecosystem stability and biodiversity (see review in Walters and Martell, 2004). Indeed, until we started using the foraging arena representation, we were generally unable to build realistically complex (many species or functional groups) ecosystem models that did not exhibit such pathologies as predator-prey instability and self-simplification (predator-prey instability at the more productive end of productivity gradients; Persson et al., 2001).

Despite its success at explaining many aspects of ecosystem dynamics, there have been two nagging problems with the Ecosim foraging arena representation. First, we have assumed that every predator-prey interaction takes place in a unique arena, where vulnerable prey density is affected only by intraspecific competition among the predators. That is, we have ignored the possibility of multiple predators feeding on a given prey type in a single space-time arena so as to intensify rather than reduce inter-specific competition (see, e.g., Sokol-Hessner and Schmitz, 2002). Second, we have treated foraging as occurring continuously over time so as to result in equilibrium vulnerable prey densities that remain near equilibrium with respect to slower changes in overall prey and predator abundances. This assumption is obviously unrealistic to anyone who has watched how aquatic organisms feed; most trophic interactions involve ‘bout feeding’, i.e., most animals obtain the bulk of their food intake in short feeding bouts (Collier and Johnson, 2004), most commonly at dawn and/or dusk (Rickel and Genin, 2005).

This paper documents how we have attempted to remedy those concerns. The EwE software now allows representation of shared foraging arenas by multiple predators, and we allow users to specify use of foraging arenas either as continuous or in periodic feeding bouts. The following sections describe the mathematical derivations used in these representations, and note in particular the rather surprising result that bout versus continuous feeding representations result in essentially the same system-scale dynamics despite apparently very different functional assumptions and equations. We also note the un-surprising finding that assumptions of wide-spread overlap in shared foraging arenas indeed leads to system self-simplification and model inability to maintain biodiversity.

2. Representing use of the same foraging arena by multiple predators

The basic Ecosim formulation for predation interactions assumes that each non-zero consumption of a prey type $i$ by a predator type $j$ takes place in a foraging arena unique to that interaction (Walters et al., 1997, 2000; Christensen and Walters, 2004a). The rationale for this assumption is that each arena is defined by the combined behaviors of both the prey and the predator, and possibly also by selection of particular prey sub-types (e.g., sizes), such that multiple predators can feed on the same prey type in different ways (at different depths, times of day, spatial microhabitats) without competing directly for prey within the typically very confined space represented by each arena.

The general foraging arena assumption that predation typically is concentrated within restricted arenas, and hence at restricted rates, has profound implications for model predictions about ecosystem stability, and the further assumption that each predator-prey interaction takes place within a unique arena has equally profound implication for the maintenance of ecosystem structure and diversity (Walters and Martell, 2004). It essentially represents the possibility of a distinct ‘feeding niche’ for each of the predators that takes type $i$ prey, hence allowing for the possibility that multiple predators can coexist while feeding on only that prey type. A prototype example of this possibility is with rockfishes (Sebastes spp.) along the Pacific coast, where a diverse collection of species all feed on euphausids, but avoid direct competition for these euphausids by feeding at different depths and times of day. An obvious evolutionary argument in favor of assuming such fine structure in feeding interactions is that if several predators were to feed within the same micro-scale foraging arena, the intense inter-specific competition caused by such behavior would result in very strong natural selection favoring differentiation of behaviors to avoid it, e.g., by feeding at different depths or times.

While there are evolutionary arguments in favor of assuming a distinct foraging arena for every interaction, Aydin and Gaichas (2007) emphasize that there are some situations where multiple predator types are likely to feed on exactly the same prey and at the same place and time. An example could be where the predator types represent different life history stanzas (age-size classes) of the same predator species with very similar feeding modes.

We here represent this possibility in a new formulation in Ecosim by allowing model users to enter the base proportions of each predator type’s diet that occurs in each of the possible foraging arenas defined by all non-zero predator-prey consumption linkages. Vulnerable prey density in each arena is then represented as varying over time in response to abundances of all predator types that feed in the arena.

In Ecosim we now define a list $a=1, \ldots, N_a$ of possible foraging arenas, where $N_a$ is the number of non-zero consumption interactions in the Ecopath diet matrix representing consumption of each prey type $i$ by predator type $j$. Each of these potential arenas has a defining prey type $i(a)$ and defining predator type $j(a)$.

Note that when only predator type $j(a)$ feeds in arena $a$, vulnerable prey density $V_a$ is predicted by the basic foraging arena equation:

$$V_a = \frac{v_a B_{i(a)}}{v_a + v_j + \alpha_a P_{j(a)}}$$

(1)

Here, $v_a$ and $v_j$ are vulnerability exchange rates of prey to and from arena $a$, $B_{i(a)}$ is prey biomass, $P_{j(a)}$ is predator abundance...
(biomass or sum of numbers times search rates per predator for multi-stanza predators), and $\alpha_k$ is the predator rate of effective search (volume swept per time divided by foraging arena volume). The predation flow rate (biomass of prey $i$) consumed per unit of time by predator $j(i)$ is then predicted as $Q_{i,j}(0) = \alpha_k V_k P_j$. The $V_k$ and $\alpha_k$ are parameterized by having model builders define $V_k$ from maximum possible mortality rates expressed as multiples $K_a$ of Ecopath base instantaneous predation rates $M_{i,j}^{(0)} = Q_{i,j}^{(0)}/B_i^{(0)}$, simply by setting $V_k = K_a M_{i,j}^{(0)}$ where the superscript $(0)$ designates $Q$'s and $B$'s estimated as base (initial) values of abundances and flows in the Ecopath baseline model. The back-exchange parameter $\nu^i$ is set equal to $\nu$ since it cannot be estimated separately from the $\alpha_k$ parameter.

The shared-arena extension of Eq. (1) is straightforward:

$$V_a = \frac{v_a B_{a(0)}}{\nu_a + \sum_k \alpha_{a,k} P_k} \quad (2)$$

Here the predator impact on $V_a$ is represented by a sum over all possible predators $k$ of arena-specific search rates $\alpha_{a,k}$ times predator abundances $P_k$. In the software-implementation of this, we do not actually sum over all $k$ but instead construct a list of all non-zero $\alpha_{a,k}$ flow combinations, and sum the $\alpha_{a,k} P_k$ denominator terms only over the elements of that list.

To parameterize Eq. (2) in a relatively simple way while assuring that it predicts predation rates equal to Ecopath base rates when the system is at its Ecopath base state, we require that model users specify base proportions $p_{a,k}$ of each predator $k$'s diet that is taken in arena $a$. These proportions are constrained to sum to Ecopath base consumption rates $Q_{a,k}^{(0)}$ over all $a$ for which $i(a) = i$. That is, we take the by-arena base flows $Q_{a,k}^{(0)}$ to be $p_{a,k} Q_{a}^{(0)}$. These base flows then imply a base instantaneous mortality rate $M_a^{(0)}$ to be $\sum_k \alpha_{a,k} P_k$, summed over predators feeding in $a$, for prey $i(a)$:

$$M_a^{(0)} = \sum_k \frac{\alpha_{a,k} Q_{a,k}^{(0)}}{B_{a(0)}} \quad (3)$$

Using this input or baseline estimate of $M$ for each arena and an assumed $K_a$ for that arena, we simply set $v_a = K_a M_a^{(0)}$ (and $\nu_a = v_a$).

Next, note that to be consistent with Ecopath baseline inputs, we must require that Ecosim predict $Q_{a,k}^{(0)}$ when all biomasses (and $p$'s) are at their Ecopath base values. The Ecosim prediction of rate $Q_{a,k}$ (flow rate of prey into predator $k$ from feeding in arena $a$) at any time is $Q_{a,k} = \alpha_{a,k} V_a P_k$, implying we must constrain the $\alpha_{a,k}$ so that $Q_{a,k}^{(0)} = \alpha_{a,k} V_a^{(0)}$, i.e., we must set $\alpha_{a,k} = Q_{a,k}^{(0)}/(V_a^{(0)} P_k)$. This means that to estimate the $\alpha_{a,k}$ we must first estimate the base vulnerable abundances $V_a^{(0)}$. This estimation turns out to be remarkably simple, when we note that the Ecopath base value of $V_a$ must equal $\sum_k Q_{a,k}^{(0)}/V_a^{(0)}$ (simply sum $Q_{a,k}$ over $k$, which must equal $V_a = \sum_k \alpha_{a,k} P_k$, and solve for $\sum_k \alpha_{a,k} P_k$). Substituting $\sum_k Q_{a,k}^{(0)}/V_a^{(0)}$ for $\sum_k \alpha_{a,k} P_k$ in Eq. (2), then solving for $V_a^{(0)}$, we calculate the base vulnerable abundances to be simply,

$$V_a^{(0)} = v_a \cdot B_{a(0)} - \sum_k Q_{a,k}^{(0)} \quad \frac{v_a + \nu_a}{}\quad (4)$$

The $\alpha_{a,k}$ are then calculated from these base vulnerable biomasses. Time-varying values of $Q_{a,k}$ are computed efficiently in Ecosim by setting up a list $h = 1, \ldots, N_h$ of all non-zero by-arena flows ($N_h > N_a$), where for each list element we store its associated prey type $i(h)$, predator type $k(h)$, and arena $a(h)$.

To calculate $Q_{a,k}$, we sweep down this list repetitively. On the first sweep, we accumulate the denominator sums $\sum_k \alpha_{a,k} P_k$ for Eq. (2). We then sweep down the arena list and calculate $V_a$ for every $a$ using Eq. (2). Then we sweep again down the $h$ list, calculating $Q_{a,k} = \alpha_{a,k} V_a P_k$ and accumulating predictions of total predation rates on the prey $i(a)$ and food consumption rates by predators $k(a)$.

As an added bit of model realism, when model users have specified non-zero prey handling times for predator $k$ (type II functional response; Holling, 1959), the $Q_{a,k}$ calculation is modified to be $Q_{a,k} = \alpha_{a,k} V_a P_k$, where $H_k$ is the denominator of the multispecies disc equation for predator $k$ feeding. This handling time correction is also applied in the bout-feeding formulation described in the next section.

To allow Ecosim users to edit the $p_{a,k}$ diet proportions array, we display a matrix for each prey type $i$ of the non-zero $i-k$ consumption proportions, as shown schematically in Table 1. In this table, $m$ is the number of non-zero flows from prey $i$ to predators $k$ where each such flow defines a potential foraging arena. Note that each column of the table must sum to 1.0, i.e., all of the consumption by predator $k$ of prey type $i$ must be accounted for by feeding in one of the $m$ identifiable arenas for prey type $i$. The Ecosim default proportions for this table imply that each predator takes all of its consumption of prey type $i$ in a unique arena, i.e., the table is an identity matrix (with values of 1 on the shaded diagonal in Table 1).

The opposite extreme of this default assumption would be that all consumption of prey type $i$ by its predators occur in only one arena or behavioral state for prey $i$, as shown in Table 2. This case implies maximum possible impact of

<table>
<thead>
<tr>
<th>Table 1 - Matrix showing linkages in the arena structure for a given prey with multiple predators ($k_1$ to $k_m$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arena</td>
</tr>
<tr>
<td>Arena 1</td>
</tr>
<tr>
<td>Arena 2</td>
</tr>
<tr>
<td>…</td>
</tr>
<tr>
<td>Arena $a$</td>
</tr>
</tbody>
</table>

Each entry indicates the proportion ($p_{a,k}$) of the activity for the given predator–prey interaction occurring in the corresponding arena $a$. In the default arena structure each predator is assumed to occupy a separate foraging arena indicated by the shaded cells on the diagonal. In such a case the diagonal will have a value of 1, and the other cells a value of 0. Each column must sum to 1.
predators $k$ on availability of prey $i$ to one another, and will cause competitive exclusion of at least some predator types in Ecosim unless the predators are well-differentiated in terms of overall diet composition, i.e., where each predator ‘specializes’ on a different prey type $i$, which dominates the diet composition, as for instance shown by Schmidt (2004). Studies rather tend to indicate resource partitioning between competing predator species, leading to non-additive predation rates (see, e.g., Griffen and Byers, 2006). Separation where diet compositions indicate predator overlap may also be caused by temporal exclusion of prey based on availability to the predator (Scheuere et al., 2005).

In the special case where a set of predators feeds on only one prey type in a single arena (Table 2), and where there are no complications such as multistanza population dynamics where abundance of one or more predator types may be limited by recruitment rates from younger stanzas, the above formulation implies that there is not even a unique equilibrium point for predator abundances. Rather, all predator abundance combinations that predict $V = V^\infty$ in Eq. (2) are neutral stable points provided predator mortalities remain at Ecosim base values, such that any temporary pulse of differential mortality that causes one or more predators to decline will then be followed by persistence of the new predator abundance combination if mortality rates return to the base values. Any predator that suffers a persistent differential increase in mortality rate is predicted to decline toward extinction.

### Table 2 - Example of an extreme arena structure where all predators ($k_i$) share a common foraging arena ($a_k$), i.e., compete fully for the same given prey

<table>
<thead>
<tr>
<th>Arena</th>
<th>Predator</th>
<th>Predator $k_1$</th>
<th>Predator $k_2$</th>
<th>...</th>
<th>Predator $k_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arena $a_1$</td>
<td>1.0</td>
<td>1.0</td>
<td>...</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td>Arena $a_2$</td>
<td>0.0</td>
<td>0.0</td>
<td>...</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td></td>
</tr>
<tr>
<td>Arena $a_m$</td>
<td>0.0</td>
<td>0.0</td>
<td>...</td>
<td>0.0</td>
<td></td>
</tr>
</tbody>
</table>

This will likely be an unstable situation with strong predator competition effects.

In this section we show that overall trophic flow rates $Q_{ak}$ (for predators $k$ feeding in arena $a$) over longer time scales can still be closely approximated by a continuous rate equation of the mass-action form $Q_{ak} = \alpha_{ak} V^*_a(t)$ where the bout search rates $\alpha^*$ and mean vulnerable prey densities $V^*$ per feeding bout are comparable to (but differ numerically from) the $\alpha, V$ predictions for continuous feeding.

Consider a single feeding bout in arena $a$ of duration $d$ ($d \ll 1$ day), during which an initial prey density $V_a(0)$ is depleted by predators $k(a)$. Assume that $d$ is short enough that prey renewal and loss during the bout (e.g., due to prey spatial movement and other mortality sources) can be safely ignored. Assume that $V_a(0)$ is a proportion $f_a$ of total prey biomass $B_i(a)$ and that renewal mechanisms between bouts make $V_a(0) = f_a B_i(a)$. Note that when used over multiple bouts, this prediction of $V_a(0)$ for each bout requires that arena prey abundance be independent of predation effects in previous bouts except through effects on $B_i(a)$, i.e., that there are no carryover effects from previous bouts (extreme opposite of continuous feeding assumption). Then if predators $k$ search randomly within the arena, vulnerable prey density $V_a(t)$ will change during the bout according to the simple rate equation:

$$\frac{dV_a(t)}{dt} = -V_a(t) \sum_k \alpha_{ak} P_k$$

(5)

where the $\alpha_{ak}$ are predator rates of effective search with the same interpretation as for continuous feeding.

Integrating Eq. (5) over the bout duration $d$ leads to the familiar exponential exploitation equation $V_a(d) = V_a(0) \exp \left(-d \sum_k \alpha_{ak} P_k\right)$ and to predicted total prey consumption per bout $Q_{ak}^{\text{bout}}$ by each predator $k$:

$$Q_{ak}^{\text{bout}} = \frac{\alpha_{ak} P_k}{\sum_k \alpha_{ak} P_k} f_a B_i(a) \left[1 - \exp \left(-d \sum_k \alpha_{ak} P_k\right)\right]$$

(6)

Note that the first term of Eq. (6) simply apportions total prey consumption $V_a(0) - V_a(d)$ over the bout among competing predators. Note further that mean prey density $V_a$ during the bout is given by the integral of $V$ over the bout divided by bout duration $d$, and that this mean is just:

$$V_a = f_a B_i(a) \frac{1 - \exp \left(-d \sum_k \alpha_{ak} P_k\right)}{d \sum_k \alpha_{ak} P_k}$$

(7)

Expressed in terms of this mean arena prey density, consumptions per bout (Eq. (6)) can be expressed more simply as

$$Q_{ak}^{\text{bout}} = \alpha_{ak} P_k V_a$$

(8)

We could use this formula directly in a complex simulation model that steps forward in time by the interval $\Delta t$ between feeding bouts, adding in other components of prey and predator abundance change over each such short interval. Fortunately, such a tedious calculation is generally unnecessary.

3. Representing overall predation rates when predator feeding occurs in short bouts

Most natural predators do not feed continuously over time as assumed in derivation of the vulnerable abundance $V_a$ in Eq. (1). Rather, they obtain most of their food intake in short, intensive feeding ‘bouts’, typically at dawn and dusk when light levels are changing rapidly (Helfman, 1993; Rickel and Genin, 2005). Particularly when predators such as juvenile fish have severely restricted habitat use as a tactic for managing predation risk (hiding, schooling), only a small fraction of the system-scale prey biomass is available to them in the foraging arenas that they use during each feeding bout. As an example, juvenile Atlantic salmon have been shown to restrict the time they spend feeding rather than maximizing their growth when food is abundant (Orpwood et al., 2006).
Consider the component of overall prey biomass change caused by each feeding bout, where there are \( n_b = 1/\Delta t \) bouts per year. That (typically small) change in \( B_{(i)} \) per bout is given by the sum of Eq. (6) terms over predators \( k \), i.e.

\[
\Delta B_{(i)} = f_i B_{(i)} \left[ 1 - \exp \left( -d \sum_k a_{ak} P_k \right) \right]
\]  

(9)

Dividing this by the bout duration \( \Delta t \) gives a discrete-time component of the prey rate of change:

\[
\frac{\Delta B_{(i)}}{\Delta t} = \frac{1}{\Delta t} f_i B_{(i)} \left[ 1 - \exp \left( -d \sum_k a_{ak} P_k \right) \right] = n_b f_i B_{(i)} \left[ 1 - \exp \left( -d \sum_k a_{ak} P_k \right) \right]
\]  

(10)

Since the time \( \Delta t \) between bouts is typically very short (\( n_b \) is typically of the order of several 100 bouts per year), we can approximate Eq. (10) very accurately by treating it as a continuous rate component \( d B_{(i)} / dt \). This approximation leads immediately to a continuous rate equation for \( Q_{ak} \) comparable to the continuous feeding case where \( Q_{ak} = a_{ak} P_k V_a \), namely

\[
Q_{ak} = a^*_{ak} P_k v^*_a B_{(i)} \frac{1 - \exp \left( -\sum_k a^*_{ak} P_k \right)}{\sum_k a^*_{ak} P_k} = a^*_{ak} P_k V^*_a
\]  

(11)

where \( a^*_{ak} \) are the duration-weighted search rates \( a^*_a = a_{ak} \Delta t \), \( v^*_a = n_b f_i \) represents a total prey ‘fraction’ that would become vulnerable over a 1-year time scale, and \( V^*_a \) comparable to Eq. (2) is given by

\[
V^*_a = v^*_a B_{(i)} \frac{1 - \exp \left( -\sum_k a^*_{ak} P_k \right)}{\sum_k a^*_{ak} P_k}
\]  

(12)

This model for vulnerable prey density obviously exhibits the same ‘ratio dependence’ of available prey density on predator abundance as does Eq. (2), but with the ratio effect \( 1/(v + v^* + \sum_k a_{ak} P_k) \) replaced by a negative exponential effect. At high predator abundances it also implies an upper bound \( v^*_a B_{(i)} \) on total removal rate \( Q_a \) and hence on total instantaneous predation mortality rate \( Q_{ak} B_{(i)} \).

We can parameterize the continuous approximation to bout feeding from Ecopath inputs and assumed maximum predation rates in the same way as described in the previous section for continuous arena feeding. That is, we set \( v^*_a = K_a M_{(i)}^{V_a} \), where \( K_a \) as above is a user-defined ratio of maximum to Ecopath baseline predation rate. We calculate base mean prey density per bout \( V^*_a(0) \) by substituting Ecopath base prey and predator abundances \( B_{(i)}(0) \) and \( P_k(0) \) into Eq. (12) along with \( \sum_k a^*_{ak} P_k(0) = Q_a(0)/V_a(0) \) (where \( Q_a(0) \) is the base total consumption rate summed over predators \( k \)), and solving for \( V^*_a \), to give

\[
V^*_a(0) = -\frac{Q_a(0)}{\ln(1 - 1/K_a)}
\]  

(13)

Fig. 1 – Comparison of instantaneous mortality rates expressed relative to Ecopath baseline predation mortality rates for the original model formulation (‘Continuous’) and compared to bout feeding with \( v^*_a = v_a \) in case (A), and with \( v^*_a < v_a \) set to give same limiting maximum \( Q/P \) in case (B). Then we simply calculate the \( a^*_{ak} \) as

\[
a^*_{ak} = \frac{Q_{ak}(0)}{P_k(0) V^*_a(0)}
\]  

(14)

where as above the arena-specific base consumption rate is calculated using assumed arena feeding proportions \( P_k \) as \( Q_{ak}(0) = P_k Q_{(i)ak}(0) \) and \( Q_{(i)ak}(0) \) is the Ecopath base total consumption rate of prey \( i(0) \) by predator \( k \).

It is instructive to compare the predictions of instantaneous predation mortality rate \( M = Q_{ak}/B_{(i)} \) from Eq. (10) to those of the continuous model defined by Eq. (2) and \( Q_a = \sum_k a_{ak} P_k V_a \), for varying predator abundances \( P_k \) while holding prey biomasses \( B_{(i)} \) constant (Fig. 1). If we set \( v^*_a = v_a \), i.e., use the same \( K_a \) to calculate \( v^*_a \) as we would for \( v_a \) in the continuous case (case A in Fig. 1), the exponential term in the bout feeding model generally predicts steeper variation in \( M \) than the continuous model, i.e., it predicts that \( M \) will drop off more rapidly if \( P \) decreases from \( P(0) \) than does the continuous model. This leads to weaker ‘compensation’ measured in terms of increase in potential \( Q/P \) as \( P \) declines. But if we set \( v^*_a \) smaller than \( v_a \), so as to predict the same limiting maximum \( Q/P \) at very low predator densities (case B in Fig. 1), the two arena models give predicted patterns of variation in \( M \) that are the opposite, i.e., bout feeding predicts saturation of \( M \) at lower \( P \) than the continuous case. This means that in Ecosim cases where \( K_a \) has been estimated by fitting the continuous arena model to time series data (the only option up to now), and where feeding in reality has been of the bout type, the fitted \( K_a \) estimates have probably been somewhat too large, i.e. \( K_a \) is in reality closer to 1.0 and predators are already causing (in the Ecopath base situation) closer to their maximum possible predation rates from bout feeding.
Table 3 – Models that have been fit to historical data using the continuous feeding arena equations of Ecosim, and here used to evaluate impact of bout feeding on goodness-of-fit (see Fig. 2)

<table>
<thead>
<tr>
<th>Model name</th>
<th>Number of functional groups</th>
<th>Number of reference data points</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gulf of Mexico</td>
<td>63</td>
<td>556</td>
<td>Walters et al. (unpublished data)</td>
</tr>
<tr>
<td>Tampa Bay</td>
<td>52</td>
<td>262</td>
<td>Walters et al. (unpublished data)</td>
</tr>
<tr>
<td>Central North Pacific</td>
<td>31</td>
<td>181</td>
<td>Cox et al. (2002)</td>
</tr>
<tr>
<td>Baltic Sea</td>
<td>17</td>
<td>471</td>
<td>Harvey et al. (2003)</td>
</tr>
<tr>
<td>Benguela Current</td>
<td>32</td>
<td>787</td>
<td>Shannon et al. (2004)</td>
</tr>
<tr>
<td>Georgia Strait</td>
<td>27</td>
<td>652</td>
<td>Martell et al. (2002)</td>
</tr>
<tr>
<td>Gulf of Thailand</td>
<td>40</td>
<td>409</td>
<td>FAO/FISHCODE (2001)</td>
</tr>
<tr>
<td>North Sea</td>
<td>32</td>
<td>383</td>
<td>Christensen et al. (2002)</td>
</tr>
<tr>
<td>West Coast Vancouver Island</td>
<td>15</td>
<td>1649</td>
<td>Martell (2002)</td>
</tr>
</tbody>
</table>

For Ecosim models that include multi-stanza population dynamics, a critically important capability is to represent adjustments in foraging time, particularly for juvenile stanzas. Such adjustments allow juvenile fish to translate increases in potential feeding rate $Q/P$ into reduced foraging time and predation risk when competitor abundance $P$ decreases (see, e.g., Orpwood et al., 2006), leading to compensatory changes in juvenile mortality rates and emergent stock-recruitment relationships of the Beverton–Holt form (Walters and Korman, 1999). Foraging time adjustments are modeled in Ecosim by

Fig. 2 – Changes in sum of squares goodness-of-fit criterion (SS) for an assortment of models that have been fit to historical data using the continuous feeding arena equations of Ecosim, when bout feeding is assumed instead for all trophic linkages initially without re-estimation of vulnerability exchange parameters $K_a$. (A) represents SS from original model. (B) SS from original model but with bout feeding. (C) SS for bout feeding, after fitting by varying 20 most important $K_a$. (D) SS for continuous feeding after fitting.
including a dynamic variable $T_i$ for each biomass type, with $T_i$ at time zero set to 1.0. Then $T_i$ is varied over time so as to try and maintain Ecopath base feeding rate per predator ($Q/P$), by multiplying all search rates of type $i$ for its prey by $T_i$, and all vulnerability exchange rates of type $i$ into arenas where predators take it by $T_i$. In the bout foraging representation, this means simply that (1) search parameters $a^*$ for type $i$ as a predator are adjusted by varying bout durations $d$ in proportion to $T_i$ (i.e., setting $a^*(t) = a^*(0)/T_i$, with $T_i$ defined as the relative bout duration $d(t)/d(0)$ and (2) the vulnerable fractions $f_i$ that define $v^*$ of $i$ to its predators are also treated as being proportional to $d$ by setting $v^*(t) = v^*(0)/T_i$.

As a simple test of whether bout feeding is likely to make much difference to the ability of Ecosim models to fit historical time series data, we examined changes in a simple fitting criterion (sum of squared deviations, SS, from historical data, summed over all time series used in model fitting) for a collection of models that had been fitted to data using the continuous arena equations, when all trophic linkages were simply reset to assume bout feeding without correction or refitting of the $K_a$ parameters (Table 3, Fig. 2; an Ecopath Access database with all of these models and fitting data is available on request from the authors). Ability of several of these models to fit historical data are reviewed in Walters and Martell (2004, Fig. 12), and these were mostly the same models used in single-species versus multispecies MSY comparisons by Walters et al. (2005).

Surprisingly, there was little change in the fitting criterion for many of the models, and one (Central North Pacific) even gave a better fit immediately. For those models where there was a substantial increase in SS, we were easily able to remedy the poor fits by re-estimating $K_a$ under the global bout arena assumption. When we refitted the models under both feeding assumptions (by nonlinear estimation search over the 20 $K_a$ values with largest contributions to the sum of squares), we were easily able to find fits at least as good under the bout feeding assumption for most cases, and qualitatively as good for all cases.

4. Discussion

The equations introduced here obviously give considerable flexibility to represent trophic interactions in the Ecosim model more realistically than previously possible (Walters et al., 2000). It is particularly comforting to see that the much more realistic assumption of bout rather than continuous feeding leads to very similar predictions of how prey mortality rates should vary with predator abundances as have been assumed in previous Ecosim models based on the unrealistic but mathematically convenient assumption of continuous feeding with rapid equilibration of vulnerable prey densities.

We recommend extreme care in using either the continuous or bout feeding equations to represent feeding by multiple predators in a relatively small number of arenas. As noted above, the intense inter-specific competition implied by such concentration of feeding has very likely driven natural selection for differentiation in feeding behavior (use of different fine-scale arenas) as well as in diet composition. See for instance Berec et al. (2006) for an experiment illustrating this. If such differentiation is excluded from the model parameterization, the Ecosim user risks building a model that will not retain observed biodiversity over time.

A few authors have referred to the basic Ecosim equation for predicting total flow rates $Q = a_vBP/(v + a^*P)$ as though it were a functional response equation comparable to assuming mass-action encounters and type II predation, e.g., $Q = aBP/(1 + hB)$; see, e.g., Koen-Alonso and Yodzis (2005). Such comparisons reflect a misunderstanding about a basic proposition of foraging arena theory, namely that predators very generally encounter their prey in space–time restricted circumstances (foraging arenas), such that it is almost never appropriate to predict $Q$ from the ecosystem-scale mean prey density $B$ when trying to account for effects such as handling time and switching (changes in $v$). We would argue that it is sometimes appropriate to account for handling time effects, but only if these are predicted using arena-scale vulnerable prey densities $V$, i.e., $Q = aVP/(1 + hV)$, where $V$ is adjusted away from the system-scale average $B$ using assumptions about localization of foraging (effects of vulnerability exchanges $v$’s and/or available prey fractions per bout $f$’s in the arena equations). We explicitly allow switching in Ecosim, but again caution that it should be used in conjunction with predictions of vulnerable, rather than overall, prey densities.

It would be ignorant to assert that the equations presented in this paper are the only or best way to represent differentiation of vulnerable prey biomasses $V$ from system-scale average prey biomasses $B$ in prediction of trophic interaction rates. They do not for example account explicitly for some very gross system-scale effects that occur in highly disturbed systems, such as changes in overall prey and predator distributions and overlap patterns (e.g., due to range contractions), and changes in spatial arena structure due to obvious habitat changes like growth and destruction of biogenic spatial refuges (e.g., Rodriguez et al., 2005). Some such changes can be accounted for in Ecosim through trophic ‘mediation functions’ that link $v$’s and $a$’s to abundances of species besides those engaged directly as predators and prey (e.g., one can make $a$’s and $v$’s for juvenile fish that hide in macrophyte beds dependent on macrophyte biomass). But there is still a long way to go in development of fully-defensible predictions of $V$ for systems that are massively disturbed.

One option for dealing with the prediction of $V$ would be to construct very detailed spatial models (with habitat and its use modeled at scales of a few m$^2$) running on very short (bout) time scales (time steps of 1h or less). But we strongly suspect that such models would be plagued by lack of detailed spatial data, lack of understanding of how organisms move and concentrate their activities at such fine scales, and risk of cumulative divergence of predictions from reality simply due to explosions over simulated time and space of small errors in behavioral movement predictions.

A key advantage of the relatively simple foraging arena equations for $Q$ prediction is that we can easily force them to agree with baseline ‘observations’ or estimates of system-scale abundances ($B$’s, $P$’s), feeding rates, and diet compositions $(Q_{ij})$ as summarized in static (point-in-time) mass-balance assessments like Ecopath. But this is also a dis-
advantage, in the sense that the rate parameter estimates then become dependent on the often shoddy, incomplete, and badly biased estimates entered as Ecopath inputs. It is clear that Ecosim-type dynamic predictions are sensitive to those baseline inputs, and that this represents an especially severe issue for interactions involving small fish as prey (where the small fish typically represent only trivial and often overlooked proportions of their predators’ diets).

Even absent difficulties with Ecopath inputs, i.e., empirical knowledge of baseline ecosystem biomass flow rates and states, the most troublesome parameters for Ecosim users to specify have been the ‘vulnerability multipliers’ \( K_a \) representing ratios of maximum to Ecopath base predation mortality rates. One source of trouble is obviously that Ecopath inputs provide no information about the \( K_a \), and such information can only come from either fine-scale analysis of spatial arena structures or from data collected at different times and/or places about how Q’s have varied with predator and prey abundances. Indeed, this is why we have emphasized the importance of fitting Ecosim models to time series data by varying the \( K_a \) parameters (see, e.g., Walters and Martell, 2004; Christensen and Walters, 2005). Another source of trouble is that the \( K_a \) are not purely ‘behavioural’ or ecological parameters; rather, they depend as well on how large the Ecopath initial predator abundances \( P_0 \) are compared to what the ecosystem might naturally support (Christensen et al., 2005). So for example a model that includes Atlantic cod stocks off Newfoundland, and uses the current low stock size as the Ecopath base, must have very high \( K_a \) values (1000+) for interactions between cod and its prey, else the model will not make enough prey available to the simulated cod stock for it to recover to anywhere near its historical abundance when simulated fishing is removed.

We will soon be able to provide guidance about reasonable ecological \( K_a \) values (corrected for effects of historical depletion on biomass) from meta-analysis of \( K_a \) estimates for many fitted models. One pattern that is becoming broadly evident from cases like those in Table 3 is that fitted \( K_a \) values tend to be small (\(<2.0\)) for most trophic linkages in temperate and tropical systems, and for feeding by juvenile stanzas in all systems. In contrast, fitted \( K_a \) values tend to be much larger for most interactions (except juvenile stanzas of demersal fish species) in high-latitude ecosystems like the Bering Sea. The low \( K_a \) values are easily explained for juvenile fish and reef-associated older fish, as a consequence of severe spatial restriction in habitat use leading to low proportions of prey populations being available the fish at any time (e.g., Gonzalez and Tessier, 1997). High \( K_a \) values in high-latitude systems likely reflect the wider spatial movement characteristic of northern fish, and tactics such as diel vertical migration that bring high proportions of widely distributed predators and prey into daily contact with one another (i.e., high \( F_0 \)s for bout feeding during periods of diurnal contact; see, e.g., Hrabik et al., 2006).

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