Appendix A. Detailed description of model application and derivations.

Here we provide background and technical information about the food web models that were used and assumptions that we needed to make to apply them to our generalized equilibrium trade-off model. We also describe the derivation of the trade-off model, and show the expected trade-off in a multi-species model under simplified assumptions about trophic transfer in food webs.

Adjustments to Ecopath Models

The Ecopath modeling framework permits model developers to represent a single species as multiple biomass pools with different trophic positions within the food web. For instance, a large fish predator might be represented as both a juvenile and an adult stage, with separate rates (productivity, mortality, consumption) and feeding habitats for each stage. When species are split in this way, the generalized trade-off model because they cannot account for a flow of energy across biomass pools to represent a stage transition from juvenile to adults. We therefore aggregated models so that a single biomass compartment represented a single population or stock. We used standard aggregation approaches (Gaichas et al. 2009) that conserve the total biomass and biomass flux in and out of compartments.

We had to make additional assumptions when previously published models did not depict steady state conditions. In these models, most biomass pools are assumed to be at steady state while some biomass levels for some groups were assumed to be changing through time (a non-zero rate of biomass accumulation was specified). We note a logical inconsistency in making these assumptions, as it is exceedingly unlikely that in a multi-species food web all populations but a few would be at steady state. This logical inconsistency made it impossible to analytically solve for steady state conditions without achieving non-zero population levels. For that reason, we

made the simplifying assumption that the models represent a steady state system by adjusting population productivity parameters as needed to create a balanced, steady-state condition. We implemented this assumption by adjusting the non-predation mortality rate or total production rate of each species so that each biomass compartment was at steady state. In no cases did this require changes to total mortality rates and / or productivity rates that exceeded 20%.

Derivation of Generalized Trade-off Model

We start with a generalized model of population dynamics for any given species:

$$\frac{dx_i}{dt} = x_i r_i(\mathbf{x}) - y_i \qquad \text{(A.1)}$$

Where x_i is some measure of abundance (density, numbers, biomass) of species i, the vector $\mathbf{x}$ indicates the collection of abundances $(x_i, \ldots x_s)$ for all s species in the system, and y_i is the removal of species i due to fishing, The function $r_i(\mathbf{x})$ gives the per capita growth rate of species i as a function of all other species abundances, and our derivation is independent of the form of this function.

It follows then that at equilibrium densities, $\bar{\mathbf{x}}$, yield equals:

$$y_i = \bar{x}_i r_i(\bar{\mathbf{x}}) \qquad \text{(A.2)}$$

Next, we assume that fisheries yield near equilibrium is proportional to current abundance. Specifically,

$$y_i = \bar{x}_i F_i \qquad \text{(A.3)}$$

where F_i is the fishing mortality rate on species i. Combining (A2) and (A3), at equilibrium we have

$$F_i = r_i(\bar{\mathbf{x}})$$

(A.4)

The remainder of the derivation is greatly simplified by the introduction of some matrix notation. Let $d(\mathbf{x})$ be the diagonal matrix obtained by placing the elements of vector $\mathbf{x}$ on the diagonal, i.e. $d(\mathbf{x})_{i,i}=x_i$ and $d(\mathbf{x})_{i,j}=0$. We can then write the system of s equations in A2-A4 as

$$\mathbf{y} = d(\bar{\mathbf{x}})\mathbf{r}(\bar{\mathbf{x}})$$

(A.5)

$$\mathbf{y} = d(\mathbf{F})\bar{\mathbf{x}}$$

(A.6)

$$\mathbf{F} = \mathbf{r}(\bar{\mathbf{x}})$$

(A.7)

Our object of interest is the vector of changes in $\mathbf{y}$ for a change in y_j which we obtain by differentiating A5-A7 with respect to F_j and then rearranging to obtain derivatives with respect to y_j. Note that for any two vectors, $\mathbf{a}$ and $\mathbf{b}$, the product $d(\mathbf{a})\mathbf{b}$ corresponds to elementwise multiplication of the two vectors, i.e. the Schur or Hadamard product. Because of this, $d(\mathbf{a})\mathbf{b} = d(\mathbf{b})\mathbf{a}$ which we use in obtaining Eq A8 and A9:

$$\frac{\delta y}{\delta F_j} = [d(\mathbf{r}(\bar{\mathbf{x}})) + d(\bar{\mathbf{x}})J_r(\bar{\mathbf{x}})]\frac{\delta \bar{\mathbf{x}}}{\delta F_j}$$

(A.8)

$$\frac{\delta \mathbf{F}}{\delta F_j} = J_r(\bar{\mathbf{x}})\frac{\delta \bar{\mathbf{x}}}{\delta F_j}$$

(A.9)

Here, $\mathbf{J}_r(\bar{\mathbf{x}})$ is the Jacobian matrix of partial derivatives of the per capita growth rates, i.e. $\mathbf{J}_r(\bar{\mathbf{x}})_{i,j}=\delta r_i(\bar{\mathbf{x}})/\delta x_j$. To find the change in yield of species i for a given change in yield of species

j, we assume that changes in yield are initially driven by changes in F_j and that the fishing mortality rates for the other species don't respond directly, i.e. $\delta F_i/\delta F_j = 0$ for $\neq j$, or in vector form $\partial \mathbf{F}/\partial F_j = 1_j$, where 1_j is a column vector whose j$^{\text{th}}$ element is 1 and all others are 0. Assuming that $\mathbf{J}_r(\bar{\mathbf{x}})$ is invertible, we can combine Eqs A8 and A9 to get

$$\frac{\delta y}{\delta F_j} = [d(\mathbf{r}(\bar{\mathbf{x}})) + d(\bar{\mathbf{x}})\mathbf{J}_r(\bar{\mathbf{x}})][\mathbf{J}_r(\bar{\mathbf{x}})]^{-1}\,\mathbf{1}_j$$

(A.10)

Eq. A10 gives us the change in yield for a change in the j$^{\text{th}}$ fishing mortality rate. We can obtain the change in yield for changes in all F by stacking these side-by-side for $j=1...s$, to obtain

$$\frac{\delta y}{\delta \mathbf{F}} = [d(\mathbf{r}(\bar{\mathbf{x}})) + d(\bar{\mathbf{x}})\mathbf{J}_r(\bar{\mathbf{x}})]\,[\mathbf{J}_r(\bar{\mathbf{x}})]^{-1}$$

(A.11)

where the indicator vector has disappeared because the collection of indicator vectors is just the identity matrix. To make the trade-off between yields of different species explicit, we need derivatives with respect to y_j. To get these from Eqs A10-A11 we use the fact that $\delta y_i/\delta y_j = (\delta y_i/\delta F_j)/(\delta y_j/\delta F_j)$ and note that the denominator is just the jth diagonal element of A11. Using $D(\mathbf{A})$ to represent a matrix with the same diagonal as matrix $\mathbf{A}$ but with off diagonal elements set to 0, we can divide each element of A11 by the appropriate partial derivative by multiplying (A11) by the inverse of the $D(\mathbf{A})$. The resulting matrix $\mathbf{T}(\bar{\mathbf{x}})$ summarizes the trade-offs in yield near equilibrium $\bar{\mathbf{x}}$. Specifically,

$$\mathbf{T}(\bar{\mathbf{x}}) = \frac{\delta y}{\delta y} = \{d(\mathbf{r}(\bar{\mathbf{x}}))[\mathbf{J}_r(\bar{\mathbf{x}})]^{-1} + d(\bar{\mathbf{x}})\}D(\{d(\mathbf{r}(\bar{\mathbf{x}}))[\mathbf{J}_r(\bar{\mathbf{x}})]^{-1} + d(\bar{\mathbf{x}})\})^{-1}$$

(A.12)

Note that we have multiplied through the $[\mathbf{J}_r(\bar{\mathbf{x}})]^{-1}$ term in (A12) to simplify the notation. The jth column of $\mathbf{T}(\bar{\mathbf{x}})$ represents the vector of changes in yield from all species that would result from a change in yield of species j, assuming a constant level of fishing mortality on all other species.

We can also reveal the changes in biomass levels associated with a change in yields (i.e., of $\partial\bar{\mathbf{x}}/\partial\mathbf{y}$) for each species using an analogous approach. Namely, we begin by taking the derivative of equation A7 with respect to F to find that

$$\frac{\delta\bar{\mathbf{x}}}{\delta\mathbf{F}} = \mathbf{J}_r(\bar{\mathbf{x}})^{-1}$$

(A13)

Finally, to derive the matrix of $\partial\bar{\mathbf{x}}/\partial\mathbf{y}$, we use the fact that $\partial\bar{x}_i/\partial y_j=(\partial\bar{x}_i/\partial F_j)/\{\partial y_j/\partial F_j)$, which can be obtained by combining (A13) and the diagonal elements of (A11):

$$\frac{\delta\bar{\mathbf{x}}}{\delta y} = \mathbf{J}_r(\bar{\mathbf{x}})^{-1} D(\{d(\mathbf{r}(\bar{\mathbf{x}}))[\mathbf{J}_r(\bar{\mathbf{x}})]^{-1} + d(\bar{\mathbf{x}})\})^{-1}$$

(A.14)

Derivation of yield trade-off in two species donor-control system

Here we show that the yield trade-off between two species donor-control system should be a linear function of the predator mortality fraction, the predator conversion efficiency and the fishing rate on predators. Consider two species whose biomass is represented by x_1 and x_2, where x_2 feeds upon x_1 in addition to other species $x_3.....x_n$. Each species' production is governed by its conversion efficiency and consumption of its prey which is dictated by donor controlled linkages, minus predation and fishing.

$$\frac{dx_2(t)}{dt} = \sum_{i=1}^{n} GCE_{i,2}\alpha_{i,2}x_i(t) - x_2(t)\sum_{j=1}^{n}\alpha_{2,j} - F_2x_2(t)$$

$$\frac{dx_1(t)}{dt} = \sum_{i=1}^{n} GCE_{i,1}\alpha_{i,1}x_i(t) - x_1(t)\sum_{j=1}^{n}\alpha_{1,j} - y_1 \tag{A.15}$$

where $\alpha_{i,j}$ is the proportion of biomass in prey i flowing to predator j, $GCE_{i,j}$ is the conversion efficiency of predator j consuming prey i, y_1 is yield of prey and F_2 is fishing mortality rate on predator. Note that the sum of the terms $\alpha_{i,j}$ is the total non-fishing mortality, which we denote M_i, and the sum of product $a_{ij}x_i$ equals total consumption rate of predator j, C_j. For simplicity here, we assume that conversion efficiency is primarily driven by metabolism, so that we can assume that it is constant over all prey types for each species (GCE_1, GCE$_2$ for prey and predator, respectively). Under this assumption, the steady state biomass levels are:

$$\bar{x_1} = \frac{GCE_1C_1 - y_1}{M_1}$$

$$\bar{x_2} = \frac{(1 - p_{1,2})GCE_2C_2}{F_2 + M_2} + \frac{GCE_2\alpha_{1,2}}{F_2 + M_2}\left[\frac{GCE_1C_1 - y_1}{M_1}\right] \tag{A.16}$$

where $p_{1,2}$ is the diet fraction of prey 1 to predator 2. Because predator yield equals $F_2\bar{x_2}$, we differentiate this product with respect to y_1 to derive the yield trade-off:

$$\frac{\delta y_2}{\delta y_1} = -\frac{GCE_2\alpha_{1,2}F_2}{M_1(F_2 + M_2)} \tag{A.17}$$

This can be simplified by recognizing that $\alpha_{1,2}/M_1$ is the proportion of total non-fishing mortality of the prey that is due to predation to this focal predator (the predator mortality fraction). We define this as M'$_{12}$. Also, $F_2/(F_2+M_2)$ is proportion of all predator mortality that is due to fishing, defined as F$_2$'. Substituting these terms, the yield trade-off equals:

$$\frac{\delta y_2}{\delta y_1} = -GCE_2 M'_{12} F'_2$$

(A.18).

Thus, in a donor control system where there is no indirect energy pathway from predators to prey, the yield trade-off is always negative and has a magnitude equal to the product of predator conversion efficiency, predation fraction, and relative fishing intensity on predators.

LITERATURE CITED

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