

## **APPENDIX 1: Model Details**

While the ECOPATH modeling method allows for flexibility and “manual adjustments” to model balancing, these methods were not used for developing the eastern Bering Sea, Gulf of Alaska, and Aleutian Islands food web models, as substantial data was available. For most species, estimates of biomass, ration, diet composition, catch, and production rates were available or could be calculated directly from existing data as described in sections 4-6, below. Therefore, the only calculated quantity for each species (“solved” by ECOPATH linear equations) was  $M_0$ , or residual natural mortality (the difference between total mortality and predation + fishing mortality), using the equation in section 2, below. Furthermore, during fitting to time series, the ECOPATH estimate of  $M_0$  was treated as a starting rather than ending point for maximum likelihood estimation.

For species for which biomass estimates were unreliable due to low catchability of the surveys (primarily forage, benthos, and lower trophic levels), biomass was estimated by fixing  $M_0$  to be 20% of production, and calculating the biomass required to sustain consumption (section 1, below). The only situations in which manual “tuning” was necessary were for a few isolated cases of prey identification issues in diets (primarily for gelatinous species of zooplankton) and to account for the mismatch between survey and fishery areas in the Aleutian Islands. This latter issue was a particular difficulty as the shelf survey extended only to 500m depth, however a substantial portion of area, ecosystem processes, and fisheries occur at greater depths, and this mismatch had a great impact due to the extremely narrow shelf around the islands. Therefore, high production shown in the Aleutians is a reflection of oceanic and deep processes “concentrating” on the narrow continental shelf.

All cases in which biomass was estimated through fixing  $M_0$  or where manual tuning was performed were considered to be “lower” data quality and are indicated as such on results graphs, except in cases where likelihood estimation was applied to these initial calculations.

It is important to note that the critical parameter for all of these processes is mortality; mortality not only affects production rates, but affects the relative contribution of different age classes to ration and diet compositions. Here, we do not fit or calculate total mortality but rather use single-species assessment estimates or literature values; therefore uncertainty in the single-species estimates of  $M$  are propagated into the ECOPATH food web model. Since our estimation process explicitly fits mortality components, cases where the data is sufficient to provide estimates of predation mortality and  $M_0$  may be improvements over single-species assumptions.

A full documentation of this process and all data used as inputs to these models is available in Aydin et al. (in review).

### **1. Estimates of biomass and catchability from minimum consumption estimates.**

Forage species are not sampled well by current gear in the Bering Sea and Gulf of Alaska. However, relative biomass (CPUE) from surveys is reported with annual CVs less than interannual variation, implying that CPUE may be useful as an index. To sum these indices, converting to a standard assumption on catchability is necessary. In order to do this, calculating the minimum biomass required to support measured groundfish consumption is one possibility, as follows:

The biomass ( $B$ ), ration (Ration), and diet composition (DC, % wet weight) are calculated for groundfish predators within a reference (base) year. Equations for DC and ration calculations are described in Appendix sections 4 and 5, respectively. For the Bering Sea, the base year is 1991, while for the Gulf of Alaska the default years are 1990 and 1993 combined. Minimum required biomass of prey is then calculated as the sum of consumption by its predators as a fraction of its mortality as follows:

$$\hat{B}_{cons,f}^{1991} = \frac{\sum_{pred} (B_{pred}^{1991} \cdot Ration_{pred}^{1991} \cdot DC_{pred,f}^{1991})}{0.8 \cdot Z_f^{1991}} \quad (1.1)$$

Here,  $Z$  is the mortality (equilibrium production rate) of the forage species, generally taken from single-species estimates from literature review (Appendix section 6). 0.8 is a “default minimal” assumption that 20% of the forage fish production is “unexplained” (attributed to  $M_0$ ). When fit to time trends, this assumption of  $M_0$  is a fit parameter; however for summing relative forage biomass it is a default assumption to this method.

After biomass for the reference year is calculated, the catchability  $q$  of the survey for the forage species is calculated as:

$$\hat{q}_{cons,f}^{survey} = \frac{CPUE_{survey,f}^{1991}}{\hat{B}_{cons,f}^{1991}} \quad (1.2)$$

Then, for years other than the reference year, survey CPUE may be converted to biomass using the conversion:

$$\hat{B}_{cons,f}^{year} = \frac{CPUE_{survey,f}^{year}}{\hat{q}_{cons,f}^{survey}} \quad (1.3)$$

A future improvement will be to specifically estimate  $q$  over multiple years of diet and mortality data to evaluate the stability of this calculation of  $q$ .

## 2. Estimates of unaccounted mortality ( $M_0$ ).

Residual (“unexplained” or “unaccounted”) natural mortality ( $M_0$ ) for a population is calculated from species biomass  $B_f$ , predator biomass ( $B_{pred}$ ), ration (Ration), and diet composition (DC, % wet weight) of the prey in the predators’ diets in a reference (base) year. Equations for DC and ration calculations are described in Appendix sections 4 and 5, respectively. For the Bering Sea, the base year is 1991, while for the Gulf of Alaska the default years are 1990 and 1993 combined.  $M_0$  is then calculated using the following formula:

$$M_{0f} = Z_f^{1991} - \frac{\sum_{pred} (B_{pred}^{1991} \cdot Ration_{pred}^{1991} \cdot DC_{pred,f}^{1991})}{B_f^{1991}} \quad (2.1)$$

Here,  $Z$  is the mortality (equilibrium production rate) of the forage species, generally taken from single-species estimates from literature review (Appendix section 6). It is possible for  $M_0$  to be negative, indicating that consumption is greater than a declining population. In this case, the rate of decline during the reference year is estimated from time series data and added to prey biomass and the value is recalculated.

If one or more predator biomass levels are unknown,  $M_0$  must be estimated simultaneously with predator biomass as described in Equation 1.1. In this case, the vector of unknowns  $M_0$  or  $B$  (one for each species) is solved simultaneously: this solution is the “ECOPATH balance” solution for the food web.

### 3. Maximum likelihood estimation for a biomass dynamics model

The food web model estimated from rates as described in sections 1 and 2 is turned into a biomass dynamics model as follows:

$$\frac{dB_i}{dt} = \sum_{prey} GE \cdot c(B_i, B_{prey}) - M_0 B - FB - \sum_{pred} c(B_{pred}, B_i) + \varepsilon \quad (3.1)$$

GE and  $M_0$  are fit parameters for growth efficiency and unaccounted mortality, F is year-specific fishing rate,  $\varepsilon$  is process error and  $c()$  is the following consumption equation:

$$c(B_{pred}, B_{prey}) = Q_{link}^* \left( \frac{X_{link} \cdot Y_{pred}}{X_{link} - 1 + Y_{pred}} \right) \left( \frac{D_{link} \cdot Y_{prey}^{\theta_{link}}}{D_{link} - 1 + Y_{prey}^{\theta_{link}}} \right) \quad (3.2)$$

where  $Y_i = B_i^t / B_i^*$ .  $B^*$  and  $Q^*$  are biomass and consumption rates in a base year; this base year does not need to be an equilibrium state of the model.  $X_{link}$  is a predator/prey pair specific value greater than 1 which determines predator density dependence on foraging (the numerical response) while  $D_{link}$  is a predator/prey specific value greater than 1 which determines the satiation of handling time/predation mortality for that link.  $\theta_{link}$  is a shape parameters which determines if predation is constant with prey density ( $\theta_{link}=0$ ), saturating (Type II functional response;  $\theta_{link}=1$ ) or prey switching (Type III functional response;  $\theta_{link}=2$ ).  $\theta_{link}$  can take on intermediate values. Since these parameters are link-specific, the dimensionality is reduced by assuming predator and prey specific foraging behavior for each species that is additive for each predator/prey pair, so that:

$$\begin{aligned} X_{link} &= 1 + \exp(x_{prey} + x_{pred}), \\ D_{link} &= 1 + \exp(d_{prey} + d_{pred}), \text{ and} \\ \theta_{link} &= (\theta_{prey} + \theta_{pred}). \end{aligned}$$

Overall, this gives 8 parameters per species to fit: GE,  $M_0$ ,  $x_{prey}$ ,  $x_{pred}$ ,  $d_{prey}$ ,  $d_{pred}$ ,  $\theta_{prey}$ , and  $\theta_{pred}$ .

To run simulations, equation 3.1 is integrated using Adams-Basforth integration with monthly timesteps (finer timesteps did not appreciably affect results). To obtain parameter point estimates, three weighted error functions are used assuming lognormal error (log sum-of-squares minimization criteria):

1. For 1965-2005, stock assessment biomass for species with age-structured assessments and catches are assumed to be “perfectly known” and the annual process error (change in biomass) required to follow these biomass trends is calculated and applied. Functional response parameters are fit to minimize this process error: a future extension of this method may be to apply a nonlinear Kalman filter to allow for error specification within each time trend.
2. For species with no age-structured stock assessments the difference between the dynamic model-predicted 1990-93 average biomass and the initial food web model biomass (e.g. coming from trawl survey data or consumption estimates) was considered as observation error.
3. Finally, there is a persistence criteria: any parameter set which causes one or more species to go extinct (be reduced to below 1/1000 of its initial biomass) following 50 years of equilibrium fishing pressure is rejected; as all species in the model have persisted over the modeled time period this criterion simply establishes a thermodynamic (trophically bounded) parameter set.

In addition, two broad groups of species, whales and commercial crabs, were subjected to substantial depletion through fishing during the modeled time period. For these species, historical catch time series

were applied, and the criteria that the 1990-3 biomass of these species be near their food web biomass levels resulted in estimating ecosystem parameters that could support substantially higher “pre-modern exploitation” levels of biomass.

Two methodological concerns are raised by the fitting method. The first is the matter of degrees of freedom; a total of 8 parameters per species for each of the 119 species in the model results in 952 parameters while the biomass time trends currently used give a total of 672 “data” points for fitting. However, the constraints applied by the persistence criterion (#3, above) greatly influence the parameter covariance, e.g. the predation of upper trophic levels combined is not permitted to greatly exceed lower trophic level production. If parameters are chosen randomly and independently from uniform distributions, over 90% of parameter sets are rejected, indicating that the degrees of freedom for the model are lower than 952 independent parameters. Still, many of the resulting maximum likelihood estimates are not strongly discriminating of whether prey switching may be taking place; the future addition of direct fitting to historical diet data will improve these results.

Second, using single-species stock assessment model outputs as “known” biomass trends requires the multi-species model to try to match the single-species blanket assumption of constant natural mortality, which has the potential for introducing the single-species metaphor of fixed species interaction into a more dynamic simulation. This is partially mitigated by the fact that the adult biomass time trends come from assessments of large groundfish predators, for which predation mortality is generally low. For several of these groundfish species, the ecosystem model tracks separate juvenile and adult components; in these cases, juvenile biomass levels from the stock assessment are not used. The one place this remains an issue is for walleye pollock, which initial results indicate show an increase in adult natural mortality in recent years. One possibility for removing this circularity is to iterate between the ecosystem and single-species models; using the  $M$  reconstructed from the ecosystem model to derive a new single-species estimate for biomass, then using that new biomass in the ecosystem model, iterating until an agreement between the models is reached; this work is planned for the near future.

#### **4. Diet composition calculations**

Notation:

DC = diet composition

W = weight in stomach

n = prey

p = predator

s = predator size class

h = survey haul

r = survey stratum

B = biomass estimate

v = survey

a = assessment

R = ration estimate

The diet composition for a species is calculated from stomach sampling beginning at the level of the individual survey haul (1), combining across hauls within a survey stratum (2), weighting stratum diet compositions by stratum biomass (3), and finally combining across predator size classes by weighting according to size-specific ration estimates and biomass from stock assessment estimated age structure (4). Ration calculations are described in detail below.

Diet composition (DC) of prey  $n$  in predator  $p$  of size  $s$  in haul  $h$  is the total weight of prey  $n$  in all of the stomachs of predator  $p$  of size  $s$  in the haul divided by the sum over all prey in all of the stomachs for that predator size class in that haul:

$$DC_{n,p,s,h} = W_{n,p,s,h} / \sum_n W_{n,p,s,h} \quad (4.1)$$

Diet composition of prey  $n$  in predator  $p$  of size  $s$  in survey stratum  $r$  is the average of the diet compositions across hauls within that stratum:

$$DC_{n,p,s,r} = \sum_h DC_{n,p,s,h} / h \quad (4.2)$$

Diet composition of prey  $n$  in predator  $p$  of size  $s$  for the entire area  $t$  is the sum over all strata of the diet composition in stratum  $r$  weighted by the survey biomass proportion of predator  $p$  of size  $s$  in stratum  $r$ :

$$DC_{n,p,s,t} = \sum_r DC_{n,p,s,r} * B_{p,s,r}^v / \sum_r B_{p,s,r}^v \quad (4.3)$$

Diet composition of prey  $n$  in predator  $p$  for the entire area  $t$  is the sum over all predator sizes of the diet composition for predator  $p$  of size  $s$  as weighted by the relative stock assessment biomass of predator size  $s$  times the ration of predator  $p$  of size  $s$ :

$$DC_{n,p,t} = \sum_s DC_{n,p,s,t} * B_{p,s}^a * R_{p,s} / \sum_s B_{p,s}^a * R_{p,s} \quad (4.4)$$

## 5. Ration Calculations

Size specific ration (consumption rate) for each predator was determined by the method of fitting the generalized Von Bertalanffy growth equations (Essington et al. 2001) to weight-at-age data collected aboard NMFS bottom trawl surveys.

The generalized Von Bertalanffy growth equation assumes that both consumption and respiration scale allometrically with body weight, and change in body weight over time ( $dW/dT$ ) is calculated as follows (Paloheimo and Dickie 1965):

$$\frac{dW_t}{dt} = H \cdot W_t^d - k \cdot W_t^n \quad (5.1)$$

Here,  $W_t$  is body mass,  $t$  is the age of the fish (in years), and  $H$ ,  $d$ ,  $k$ , and  $n$  are allometric parameters. The term  $H \cdot W_t^d$  is an allometric term for “useable” consumption over a year, in other words, the consumption (in wet weight) by the predator after indigestible portions of the prey have been removed and assuming constant caloric density between predator and prey. Total consumption ( $Q$ ) is calculated as  $(1/A) \cdot H \cdot W_t^d$ , where  $A$  is for a fractional conversion between prey and predator wet weights that accounts for indigestible portions of the prey and differences in caloric density. The term  $k \cdot W_t^n$  is an allometric term for the amount of biomass lost yearly as respiration.

Based on an analysis performed across a range of fish species, Essington et al. (2001) suggested that it is reasonable to assume that the respiration exponent  $n$  is equal to 1 (respiration linearly proportional to body weight). In this case, the differential equation above can be integrated to give the following solution for weight-at-age:

$$W_t = W_\infty \cdot \left(1 - e^{-k(1-d)(t-t_0)}\right)^{\frac{1}{1-d}} \quad (5.2)$$

Where  $W_\infty$  (asymptotic body mass) is equal to  $(H/k)^{\frac{1}{1-d}}$ , and  $t_0$  is the weight of the organism at time=0. If the consumption exponent  $d$  is set equal to 2/3, this equation simplifies into the “specialized” von Bertalanffy length-at-age equation most used in fisheries management, with the “traditional” von Bertalanffy  $K$  parameter being equal to the  $k$  parameter from the above equations divided by 3.

From measurements of body weight and age, equation 2 can be used to fit four parameters ( $W_\infty$ ,  $d$ ,  $k$ , and  $t_0$ ) and the relationship between  $W_\infty$  and the  $H$ ,  $k$ , and  $d$  parameters can then be used to determine the consumption rate  $H \cdot W_t^d$  for any given age class of fish. For these calculations, weight-at-age data available and specific to the modeled regions were fit by minimizing the difference between log(observed) and log(predicted) body weights as calculated by minimizing negative log likelihood: observation error was assumed to be in weight but not aging. A process-error model was also examined but did not give significantly different results.

Initial fitting of 4-parameter models showed, in many cases, poor convergence to unique minima and shallow sum-of-squares surfaces: the fits suffered especially from lack of data at the younger age classes that would allow fitting to body weights near  $t=0$  or during juvenile, rapidly growing life stages. To counter this, the following multiple models were tested for goodness-of-fit:

1. All four parameters estimated by minimization;

2.  $d$  fixed at 2/3 (specialized von Bertalanffy assumption)
3.  $d$  fixed at 0.8 (median value based on metaanalysis by Essington et al. 2001).
4.  $t_0$  fixed at 0.
5.  $d$  fixed at 2/3 with  $t_0$  fixed at 0, and  $d$  fixed at 0.8 with  $t_0$  fixed at 0.

The multiple models were evaluated using Aikeike's Information Criterion, AIC. In general, the different methods resulted in a twofold range of consumption rate estimates; consistently, model #3,  $d$  fixed at 0.8 while the other three parameters were free, gave the most consistently good results using the AIC. In some cases model #1 was marginally better, but in some cases, model #1 failed to converge. The poorest fits were almost always obtained by assuming that  $d$  was fixed at 2/3.

To obtain absolute consumption ( $Q$ ) for a given age class, the additional parameter  $A$  is required to account for indigestible and otherwise unassimilated portions of prey. We noted that the range of indigestible percentage for a wide range of North Pacific zooplankton and fish summarized in Davis (2003) was between 5-30%, with major zooplankton (copepods and euphausiids), as well as many forage fish, having a narrower range of indigestible percentages, generally between 10-20%. Further, bioenergetics models, for example for walleye pollock (Buckley and Livingston 1994), indicate that nitrogenous waste (excretion) and egestion resulted in an additional 20-30% loss of consumed biomass. As specific bioenergetics models were not available for most species, we made a uniform assumption of a total non-respirative loss of 40% (from a range of 25-60%) for all fish species, with a corresponding  $A$  value of 0.6.

Finally, consumption for a given age class was scaled to population-level consumption using the available numbers-at-age data from stock assessments, or using mortality rates from stock assessments and the assumption of an equilibrium age structure in cases where numbers-at-age reconstructions were not available.

## 6. Production rates

Production per unit biomass ( $P/B$ ) and consumption per unit biomass ( $Q/B = R$ , ration above) for a given population depend heavily on the age structure, and thus mortality rate of that population. For a population with an equilibrium age structure, assuming exponential mortality and Von Bertalanffy growth,  $P/B$  is in fact equal to total mortality  $Z$  (Allen 1971) and  $Q/B$  is equal to  $(Z+3K)/A$ , where  $K$  is Von Bertalanffy's  $K$ , and  $A$  is a scaling factor for indigestible proportions of prey (Aydin 2004). If a population is not in equilibrium,  $P/B$  may differ substantially from  $Z$  although it will still be a function of mortality.

For the Bering Sea, Aleutian Islands, and Gulf of Alaska ECOPATH models,  $P/B$  and  $Q/B$  values depend on available mortality rates, which were taken from estimates or literature values used in single-species models of the region. It is noted that the single-species model assumptions of constant natural mortality are violated by definition in multispecies modeling; therefore, these estimates should be seen as "priors" to be input into the ECOPATH balancing procedures or other parameter-fitting (e.g. Bayesian) techniques.

Several methods were used to calculate  $P/B$ , depending on the level of data available. Proceeding from most data to least data, the following methods were used:

1. If a population is not in equilibrium, total production  $P$  for a given age class over the course of a year can be approximated as  $(N_{at} \cdot \Delta W_{at})$ , where  $N_{at}$  is the number of fish of a given age class in a given year, exponentially averaged to account for mortality throughout the year, and  $\Delta W_{at}$  is the change in body weight of that age class over that year. For a particular stock, if weight-at-age data existed for multiple years, and stock-assessment reconstructed numbers-at-age were also available,

production was calculated by summing this equation over all assessed age classes. Walleye pollock P/B for both the EBS and GOA were calculated using this method: examining the components of this sum over the years showed that numbers-at-age variation was responsible for considerably more variability in overall P/B than was weight-at-age variation.

2. If stock assessment numbers-at-age were available, but a time series of weight-at-age was not available and some weight-at-age data was available, the equation in (1), above, was used, however, the change in body weight over time was estimated using fits to the generalized Von Bertalanffy equations described in the consumption section, above.
3. If no stock assessment of numbers-at-age was available, the population was assumed to be in equilibrium, so that P/B was taken to equal Z. In cases for many nontarget species, estimates of Z were not available so estimates of M were taken from conspecifics with little assumed fishing mortality for this particular calculation.