

AGE STRUCTURE OR FUNCTIONAL RESPONSE? RECONCILING THE ENERGETICS OF SURPLUS PRODUCTION BETWEEN SINGLE-SPECIES MODELS AND ECOSIM

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Whole-ecosystem foodweb models, specifically the dynamic model ECOSIM, contain specific hypotheses for surplus production that differ from traditional single-species management models. Specifically, ECOSIM begins with an assumption that all species are tightly connected and energetic surplus does not arise through fishing, whereas single-species fishing theory implies that fishing leads to surplus by removing larger, older, less-productive fish from populations. Although ECOPATH production ratios and single-species estimated production levels are both derived from the dynamics of von Bertalanffy consumption and growth equations, the dynamics of ECOSIM differ from the implied bioenergetics of fishing as applied to age-structured populations. Specifically, while the ECOSIM "Arena" functional response and the von Bertalanffy equations both lead to the appearance of density-dependence in predator consumption per unit biomass, the difference in starting assumptions between the models leads ECOSIM to "fix production energetics" while age-structured models capture changes in within-population energetics between populations of younger versus older fish. This may cause ECOSIM to greatly overestimate the amount of biomass supportable in "pristine" systems of large, mature fish, especially when projections are based on models of currently exploited ecosystems. However, if the ECOSIM Arena is seen as a proxy for age structure rather than as a function of predator/prey behaviour, the original derivation of von Bertalanffy growth equations, applied as a modification of ECOSIM, may allow the predictions made by biomass dynamics ecosystem models to incorporate critical life-history characteristics of modelled populations.

Key words: bioenergetics, ECOPATH, ECOSIM, modelling, multispecies, surplus production, von Bertalanffy growth

As multiple fish species in large marine ecosystems are harvested increasingly, predator-prey interactions have become a subject of growing concern. Worldwide, the question has been raised on whether there are enough fish to satisfy both the demands of humans and of other top predators such as marine mammals. This concern has affected policies in fisheries management even in cases where human demand is controlled by current "best" fisheries management practice: the questions have led on the one hand to public calls for specific set-asides of marine forage species for top predators (e.g. Greenpeace vs National Marine Fisheries Service 80 F. Supp. 2d 1137 WD. Wash., 2000), and on the other hand to campaigns for predator culling to increase fish available for human harvesting (e.g. "Whales' diets threaten fish stocks, whaler says"; The Japan Times, Sept. 23, 2000; see discussions in Yodzis 2001).

At the heart of this debate is the concept of surplus production. Historically and currently, the concept of "surplus" is central to fisheries management practice. In theory, if a species is held in equilibrium below its natural carrying capacity by a fishery, surplus production is the yield achieved by the fishery (Ricker

1975). This catch is considered surplus to single species' requirements, because it is the production that is "left over" after subtracting the species' requirements for remaining at a given equilibrium. At some level of fishing, the surplus is at a maximum: this surplus then represents the stock's Maximum Sustainable Yield (*MSY*).

Much modern fisheries assessment has moved beyond this equilibrium viewpoint by setting risk-averse goals for fishing that are below *MSY* levels of fishing mortality (e.g. Myers *et al.* 1994), or by including variation in the assessment of mortality or production rates. However, underneath all these techniques still lies the strategic assumption of surplus, a surplus controlled by fishing as a population tends towards its carrying capacity. In contrast, a developing "holistic" ecological viewpoint is that surplus does not exist in a "natural" system (one unperturbed by human activity). Rather, the natural evolution of ecosystems has led to energy flow between species being strongly interconnected, through predator/prey relationships and/or other interactive interrelations between component species. Under this hypothesis, the fishing down of a species to develop positive surplus production invari-

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ably takes energy and structure from other species (such as marine mammals) or critical processes (such as nutrient recycling). The development of “whole foodweb” models, such as ECOPATH with ECOSIM (EwE; Polovina 1985, Walters *et al.* 1997, Christensen and Walters 2004), plays strongly towards this second hypothesis.

In a strict sense, this second hypothesis is true. Energy removed from an ecosystem is, by definition, no longer available to other components in the ecosystem. This leads to strong tradeoffs when simultaneously prosecuting fisheries on prey and predator species, and such tradeoffs have been successfully highlighted and brought to the management arena by models such as ECOSIM (e.g. Kitchell *et al.* 2000). A fundamental message of ECOSIM modelling to date has been the message of biological tradeoff. For example, it may not be possible to maintain the historical fisheries yield of a particular predator while considerably reducing its prey (Christensen and Walters in press).

However, the whole-foodweb approach is not merely a logical extension of single-species *MSY* theory, but is at times a fundamental change in underlying assumptions. For example, as described in this paper, a prevalent concept in single-species and multispecies age-structured models (e.g. Multispecies Virtual Population Analysis [MSVPA], Sparre 1991) is that age-dependent production, as captured in the von Bertalanffy growth equations (Beverton and Holt 1957), explicitly creates surplus as fishing shifts the structure of a fish population from older and larger “less productive” fish towards younger “more efficient” fish (more efficient in terms of energy conversion to biomass). Conversely, a heavily fished population becomes “less efficient” if lesser fishing pressure leads to populations of older, slower-growing fish.

This age-structured interaction is absent from most current ECOSIM models, a specific concern if ECOSIM is used to “reconstruct” pristine ecosystems by removing fishing or by “fishing exploited ecosystems backwards” to determine the pre-fisheries expectations for biomass levels that are “naturally” supportable by the foodweb. EwE energetic efficiencies, fixed during contemporary fishing regimes with a preponderance of younger animals, would unrealistically overestimate the energetic efficiency of unfished populations of large, mature fish, thereby greatly overestimating the biomass supported or supportable in past pristine ecosystems.

In this paper, some of the assumptions underlying production in most current age-structured models, including single-species and MSVPA models, and ECOSIM, are examined. The original derivation of the relation between von Bertalanffy (VB) growth equations

in age-structured population models and the ECOSIM Arena model is revisited, with the purpose of demonstrating the implications of model-specific assumptions of surplus production. Whereas the mathematical results are derived for equilibrium conditions, a practical example is shown by comparing the results of modelling Bering Sea walleye pollock *Theragra chalcogramma* using both single-species and ECOSIM energetics assumptions in conditions far removed from equilibrium. The results suggest the use of caution in interpreting models with untested assumptions, but at the same time offer a method for extending ECOSIM, with minimal increase in data requirements, to cover a more complete range of surplus production hypotheses.

COMPARISON OF ENERGETIC HYPOTHESES

Development of the ECOSIM production model

Surplus production is based on the concept of compensation. If the fishing rate on a population increases and biomass decreases as a result, the production rate of the population (production per unit biomass, P/B) must increase (compensate) for the species to remain stable at the higher fishing pressure. Therefore, to produce surplus, the relationship between P/B and biomass (B) must be inverse. This relationship may be “phenomenological”, an inverse relationship between P/B and B that is implied by a detailed age-structured model, or it may be a direct function between P/B and B , as in ECOSIM.

For multispecies models, production must have a source, generally predation on other species. To reflect this, P/B can be written as the consumption (ingestion) rate of prey by the population (Q/B) times a gross food conversion efficiency, or growth efficiency (GE). Bioenergetically, GE is a conversion from units of prey biomass to units of predator biomass, and includes the differences between prey and predator caloric density, the removal of indigestible portions of food, and finally, the actual respirative costs of production (heat loss). Therefore, the production rate P/B of a species may increase if either the consumption rate Q/B or the growth efficiency GE increase.

In the development of ECOPATH, Polovina (1985) made a critical addition to the work of Allen (1971), which showed that, under assumptions of (a) a population with an equilibrium age structure with (b) exponential mortality and (c) VB growth, the P/B ratio of the population, integrated over all age-classes, was equal to Z , the instantaneous mortality rate (by numbers

of fish) of the population. In cases where Z varies by age, P/B is the biomass-weighted average of Z across ages. Because Z is a value that is required for conducting single-species stock assessments, this relationship provides a ready source of information for baseline calculations of P/B .

ECOPATH is not a dynamic population model, where a dynamic model is defined as any model where the biomass at time t (B_t) of a species is predicted (hypothesized) from B_{t-1} (or in retrospective evaluation, where B_{t-1} is estimated from B_t). As such, the term “equilibrium” cannot be applied to any particular ECOPATH model for a specific ecosystem, and it is not necessary to specify the relationship between P/B and B . For the dynamic model ECOSIM (Walters *et al.* 1997, Christensen and Walters 2004), the differential equation used for each species may be written as:

$$\frac{dB_i}{dt} = GE_i \sum_{prey} Q(B_i, B_{prey}) - F_i B_i - M_{0i} B_i - \sum_{pred} Q(B_{pred}, B_i) .$$

The parameters GE , F (fishing exploitation rate) and M_0 (non-predation mortality and passive respiration loss) are parameters that may be fixed or time-variant in response to external forcing or process error (fishing or climate). $Q(B_i, B_j)$ are the predator/prey equations, as described below. Note that there is nothing inherent in these equations that requires the initial conditions of this model to start in equilibrium. However, the EwE default method of calculating initial ECOSIM parameter values from ECOPATH inputs creates an initial equilibrium condition by default (Christensen *et al.* 2000, Aydin and Friday 2001).

The consumption functions $Q(B)$, relating diet composition and consumption rates from ECOPATH to ECOSIM predator/prey functional responses, are the heart of the ECOSIM formulation. In general, the practical measurement of functional responses and predator/prey interaction strength has plagued theoretical ecology for years (e.g. Power 1992, Abrams 1994). In developing ECOSIM, Walters *et al.* (1997) did not pursue the energetics of age-structure implied by the equations underlying the $P/B = Z$ relationship. Rather, they derived their predator/prey functional responses on the basis of individual prey behaviour under the hypothesis of prey “vulnerability” to predation risk (the Foraging Arena model). Walters *et al.* (1997) hypothesized that predation risk could be a major force shaping dynamic changes in production, and derived the following functional response for dynamic changes in consumption per unit biomass (Q/B) for a predator, based on

the assumption of prey existing in fast equilibrium between “vulnerable” and “invulnerable” states, the so-called “Arena” form of the predator/prey functional response¹:

$$\left[\frac{Q}{B_{pred}} \right]_{pred, prey, t} = \frac{\left(\left[\frac{Q}{B_{pred}} \right]^* X_{predprey}^* \right) DC_{predprey}^* \frac{(B_{prey})_t}{B_{prey}^*}}{(X_{predprey}^* - 1) + \frac{(B_{pred})_t}{B_{pred}^*}}, \quad (1)$$

where $B_{pred,t}$ and $B_{prey,t}$ are the biomasses of the predator and prey respectively at a given time, Q/B^* the consumption per unit predator biomass of the predator at the reference (ECOPATH) starting point, DC^* the diet proportion of the prey in the predator’s diet at that starting point, and B_{pred}^* and B_{prey}^* the biomasses of the predator and prey at the reference point. As before, $P/B = Q/B \times GE$. The reference point need not be an equilibrium state of the model. $X_{predprey}^*$, the “vulnerability multiplier” in ECOSIM, is a measure of the density-dependent compensation of predator consumption, and therefore a measure of a predator’s instantaneous production response to changes in its own density. In this equation, X ranges from 1 to ∞ .

The behaviour of the ECOSIM functions with respect to predator biomass can be examined by assuming as an illustrative example that prey biomass is constant and X is the same for all of a predator’s prey, so all diet compositions may be summed to 1 (all examples here are calculated directly, outside of the EwE software itself). As an example, the estimated ECOPATH P/B and Q/B for 1980s Bering Sea walleye pollock (Aydin *et al.* 2002) are used as starting points for the ECOSIM functions of P/B and Q/B in relation to biomass, using the ECOSIM default $X_{pred=pollock} = 2$ (Fig. 1). At a predator biomass of zero, P/B and Q/B have finite values of $(P/B^*)X/(X-1)$ and (Q/B^*)

¹ This equation is algebraically equivalent to the form given in Walters *et al.* (1997) and is preferred for fitting and comparison purposes, because it uses only a single additional parameter (X) in addition to ecologically meaningful ECOPATH parameters. It differs from the “full” EwE equations of Christensen and Walters (2004) in fixing multiplicative terms for alternative external hypotheses (feeding time, mediation, prey switching, handling time) to 1 as in “default” EwE simulations. These additional terms do not affect the energetic assumptions of the equation. See Plagányi and Butterworth (2004) for derivation details.

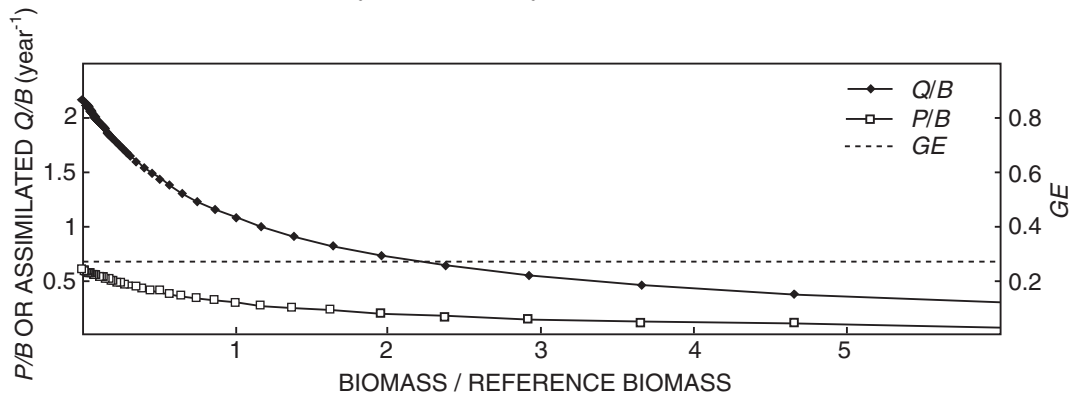


Fig. 1: Q/B , P/B and GE as functions of biomass, as predicted by the ECOSIM functional response (the Arena model). P/B and Q/B levels are calibrated to walleye pollock. For scaling, Q/B is presented as assimilated Q/B ($Q/B \times$ assimilation efficiency A). The equilibrium biomass for a total mortality (Z) of 0.3, i.e. $B(Z = 0.3)$, is used as a reference biomass

$X/(X-1)$ respectively. As biomass increases, both P/B and Q/B approach zero, always differentiated by the constant proportion $GE = 0.28$. This compensatory shape comes from increasing consumption: all a single species' compensatory surplus in ECOSIM comes from the consumption of other species.

Returning to von Bertalanffy (VB)

The VB equations themselves are based on the allometric scaling of feeding. Specifically, for a given animal of age a and body weight W_a :

$$Q_{Assim} = hW_a^{2/3} \quad (2)$$

where Q_{Assim} is the amount of consumed food assimilated, in units of predator biomass. In multispecies models, an additional constant proportion A must be included to scale appropriately the conversion between prey and predator biomass, so $Q_{Tot} = Q_{Assim}/A$, and h is a consumption rate constant. This constant proportional correction is for scaling pre-respiration caloric density conversions and losses of indigestible prey material (pre-metabolic biomass loss) that make up the pre-respiration portion of gross conversion efficiency (GE). Respiration (R) is an allometric function of body weight:

$$R = rW_a \quad (3)$$

where r is a respiration rate constant.

The allometric exponents in Equations (2) and (3),

$2/3$ for consumption and 1 for respiration, make these equations a special case of the general VB function (Essington *et al.* 2001). In this paper, only this special case is explored, because analytical solutions for integrating the general VB equations across age-classes do not exist. However, approximations for the general case may be calculated numerically for given allometric exponents (Essington *et al.* 2001) and are used in the later non-equilibrium example.

Subtracting respiration from consumption gives individual production, or the rate of individual growth over time:

$$P = \frac{dW}{dt} = Q - R = hW_a^{2/3} - rW_a \quad (4)$$

The overall gross food conversion efficiency (GE) in units of predator biomass is defined as $P/Q = (Q_{Assim} - R)/Q$, and between prey and predator biomass as $A(Q_{Assim} - R)/Q_{Assim}$. Solving differential Equation (4) for W_a gives the familiar von Bertalanffy equation for weight-at-age:

$$W_a = W_\infty(1 - e^{-Ka})^3 \quad (5)$$

where $K = r/3$ and $W_\infty = (h/r)^3$. For a population at equilibrium age structure under exponential mortality and constant weight-at-age, time t may be substituted for age a in the above equations, and the consumption, respiration, production or biomass may be calculated by integrating the equation $\int_{t=0}^t N_0 e^{-zt} f(W_{t-t_0}) dt$, where $f(W_t)$ is the right side of Equations (2)–(5), respectively,

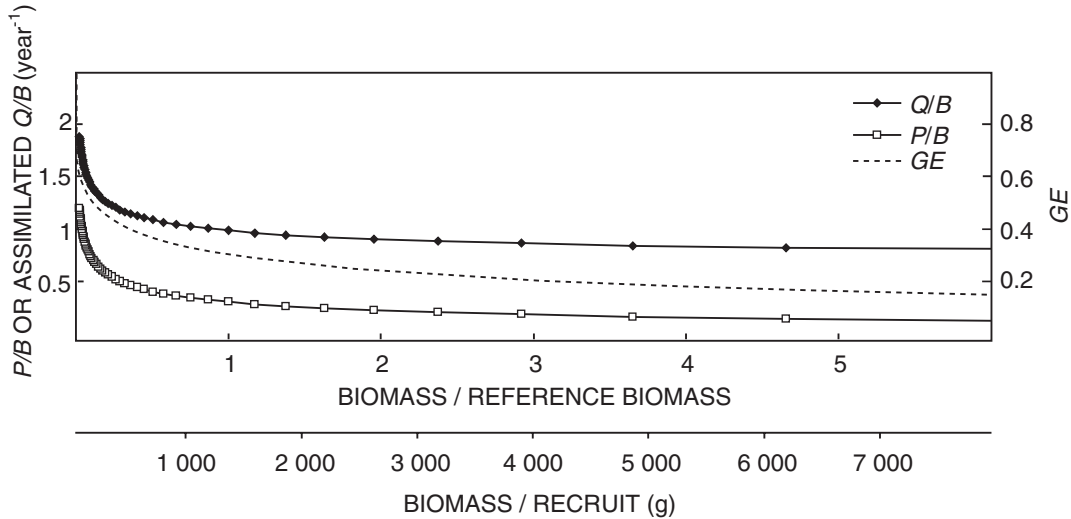


Fig. 2: Q/B , P/B and GE as functions of biomass, as predicted for equilibrium age structured populations by varying Z , using the von Bertalanffy consumption and growth parameters for walleye pollock. P/B and Q/B levels are calibrated to walleye pollock. For scaling, Q/B is presented as assimilated Q/B ($Q/B \times$ assimilation efficiency A). The equilibrium biomass for a total mortality (Z) of 0.3, i.e. B ($Z = 0.3$), is used as a reference biomass

and W_t in Equations (2)–(5) is replaced with the right side of Equation (5) for W_a . Prior to integration, an additional substitution is made. Equation (5) assumes that $W_t = 0$ and $N = N_0$ at the same $t = 0$. More commonly, $t = 0$ at the time at which recruits are first measured ($N = N_0$), but W_t equals 0 at an offset age t_0 . To generalize the above equations, t is therefore replaced with $t - t_0$ in Equation (5), where $t = 0$ at the age for which N_0 is supplied.

Taken as an integration of biomass, consumption, or production of a single recruit over the lifetime (dividing the integration for a fixed N_0), given a fixed mortality rate Z , the contribution of a single recruit over its lifetime is the same as the equilibrium per-unit-time population values for consumption, production, and biomass per recruit as follows:

$$\left[\frac{Q}{N_0} \right]_{pred,z} = 3KW_\infty \left[\frac{1}{Z} - \frac{2e^{(Kt_0)}}{Z+K} + \frac{e^{(2Kt_0)}}{Z+2K} \right] \times \left[\frac{1}{A} \right] \quad (6)$$

$$\left[\frac{P}{N_0} \right]_{pred,z} = 3KW_\infty \left[\frac{e^{(Kt_0)}}{Z+K} - \frac{2e^{(2Kt_0)}}{Z+2K} + \frac{e^{(3Kt_0)}}{Z+3K} \right] + W_{t=0} \quad (7)$$

$$\left[\frac{B}{N_0} \right]_{pred,z} = W_\infty \left[\frac{1}{Z} - \frac{3e^{(Kt_0)}}{Z+K} + \frac{3e^{(2Kt_0)}}{Z+2K} - \frac{e^{(3Kt_0)}}{Z+3K} \right] \quad (8)$$

Equations (7) and (8) are those given by Allen (1971) under the simplifying assumption that $t_0 = 0$, in other words, the age at which N_0 is calculated is the same at which $W_t = 0$. In this special case, $(P/B)_z = Z$ and $(Q/B)_z = (Z + 3K)/A$. The subscript (z) indicates that levels are equilibrium levels for given values of Z . The overall gross food conversion efficiency (including pre-respiration loss) is:

$$(GE)_z = AZ/(Z + 3K) \quad (9)$$

If t_0 is not 0, the P/B and Q/B expressions do not readily simplify, but can be calculated from Equations (6) and (7).

The specific implications for these P/B and Q/B expressions, with regard to ECOSIM, may be seen in Figure 2. As Z increases and biomass decreases towards 0, P/B and Q/B increase infinitely while $GE \rightarrow A$. On the other hand, as Z decreases and biomass increases, P/B approaches 0, while Q/B approaches $3K$, so $GE \rightarrow 0$.

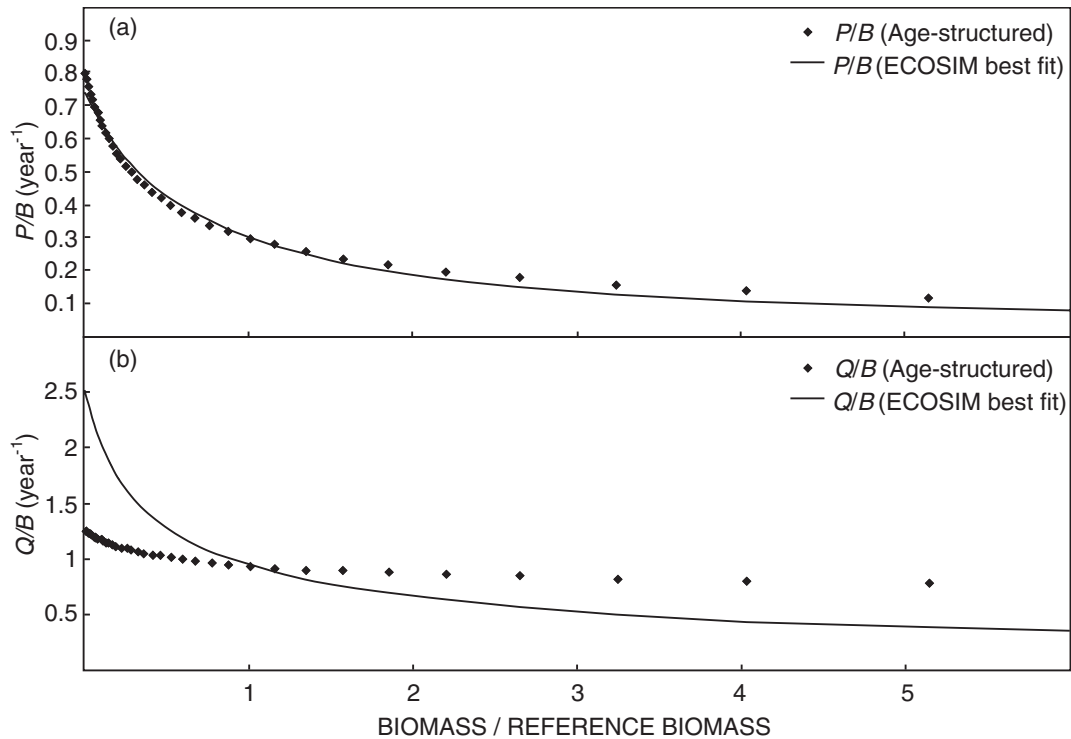


Fig. 3: (a) Equilibrium age-structured P/B vs B , for varying levels of Z , from von Bertalanffy growth parameters and Beverton-Holt recruitment parameters for walleye pollock, and best sum-of-squares fit for ECOSIM functional response. (b) Equilibrium age-structured Q/B vs B , for varying levels of Z , from von Bertalanffy growth parameters and Beverton-Holt recruitment parameters for walleye pollock (points), Q/B implied by ECOSIM functional response for fit in (a)

Therefore, whereas some of the single-species surplus comes from increases in consumption with decreasing biomass, additional surplus arises as growth efficiency increases for younger fish. Another interesting feature of this formulation is that the use of explicit VB growth parameters differentiates species with differing life-history strategies, as indexed by Z and K .

A comparison of Figures 1 and 2 highlights the difference in assumptions between the two models. A total mortality of $Z = 0.3$ represents a single-species estimate of mortality for unexploited biomass of pollock (single-species $M = 0.3$): using $B(Z = 0.3)$ as a reference point and an assumed constant assimilation efficiency of $A = 0.6$, the overall growth efficiency at $Z = 0.3$ is 0.28 under both assumptions. As described above, under ECOSIM assumptions, this value of $GE = 0.28$ remains fixed for all levels of mortality. However, under VB assumptions, if Z is increased to 0.5, GE

of the population is increased to 0.37, whereas if Z is lowered to 0.2, GE is decreased to 0.20. Further, as $B \geq 0$, the ECOSIM P/B and Q/B approach a finite limit, whereas the P/B and Q/B for VB equations approach infinity. Here, if the ECOSIM consumption Equation (1) is used as a proxy for the VB compensatory response over a certain range of biomass, the estimates of consumption made by the two model types may diverge arbitrarily as B is pushed away from its calibration range.

If N_0 is independent of biomass, then the equations in Figure 2 are sufficient. However, as the equations give an infinitely increasing P/B for the population at low stock sizes, the relation between B and N_0 should be included. As an example, a Beverton-Holt stock/recruitment relationship may be used:

$$N_0 = \frac{S}{a + bS} \quad (10)$$

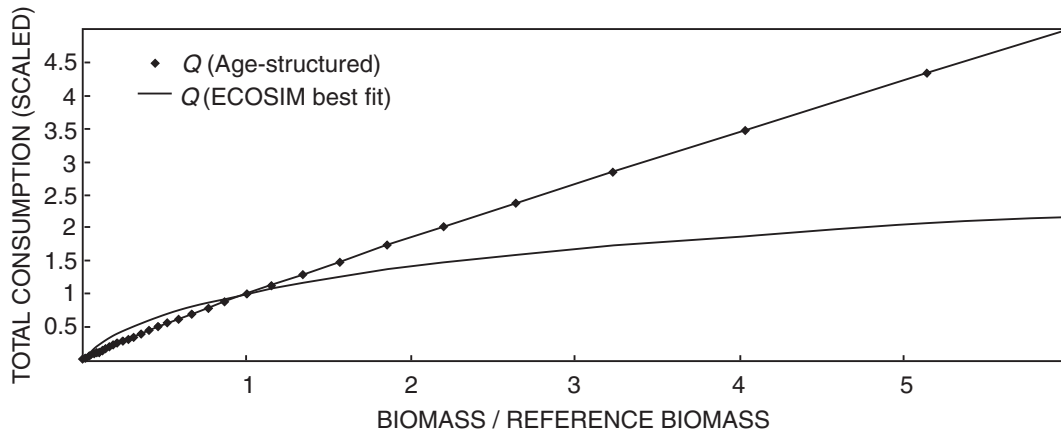


Fig. 4: Total population consumption predicted for von Bertalanffy growth parameters and ECOSIM, from fits shown in Figure 3. Y-axis is scaled so that the consumption equals 1 when biomass equals 1. The equilibrium biomass for a total mortality (Z) of 0.3, i.e. B ($Z=0.3$), is used as a reference biomass

where S is spawning stock biomass, a function of adult biomass, and a and b are Beverton-Holt parameters (Hilborn and Walters 1992). If t_0 is suitably offset from recruitment age, so that recruits may be considered to have sufficient weight to have reproductive value, it may be possible to make the simplifying assumption that the spawning stock biomass S equals the total biomass B of animals with ages $>t_0$. If this formulation is used, substituting Equation (10) for N_0 in Equation (8) and solving for B gives:

$$B_z = \frac{\left[\frac{B}{N_0} \right]_{pred,z} - a}{b} \quad (11)$$

Analogous solutions may be obtained from other stock/recruitment relationships. Finally, substituting Equations (10) and (11) for N_0 in Equations (6) and (7) allows expressions for consumption, production, and growth efficiency to be derived.

For the example discussed here, t is taken to differ from t_0 because the Beverton-Holt parameters are calculated for recruits of age $>t_0$. The term $(B/N_0 - a)$ in Equation (11) shifts the relationships between P/B or Q/B and B shown in Figure 2, so that the functions intercept the $B = 0$ axis at the finite value of $B/N_0 = a$. The shifted relationship between P/B and B implied by Equations (7), (8) and (11) is shown in Figure 3a, and the shifted relationship between Q/B and B (Equations 6, 8 and 11) in Figure 3b. In particular, the VB relationship between P/B and B shown in Figure 3a has the same qualitative limits for $B \geq 0$ and $B \geq \infty$

as does the ECOSIM functional response in Figure 1. Therefore it was possible to fit an ECOSIM vulnerability parameter X to the von Bertalanffy P/B vs B curve (Fig 3a). However, using this fit to compare ECOSIM and VB assumptions of consumption show the divergence of hypotheses even where the P/B vs B relationships match. Figure 3b shows the Q/B - B relationships implied by the P/B vs B curves of Figure 3a: in the case of ECOSIM, consumption is projected with a fixed growth efficiency, whereas with the VB estimates GE to vary with biomass.

This difference in population growth efficiency (GE) assumptions causes divergence between the two models. The implication of this divergence is clearly seen in the relationship between total population consumption and biomass (Fig. 4). As biomass increases through decreased Z , population consumption under VB assumptions increases without limit. Under ECOSIM assumptions, the total consumption reaches a finite limit. However, under VB assumptions, every decrease in Z increases the equilibrium numbers of older, slower-growing fish with lower growth efficiencies, and consumption increases without limit while production approaches a limit.

Testing under non-equilibrium conditions

The above equations both depart from “real world” situations in that they calculate results for unrealistic assumptions of equilibrium. To examine the effects of departures from equilibrium on the equations presented

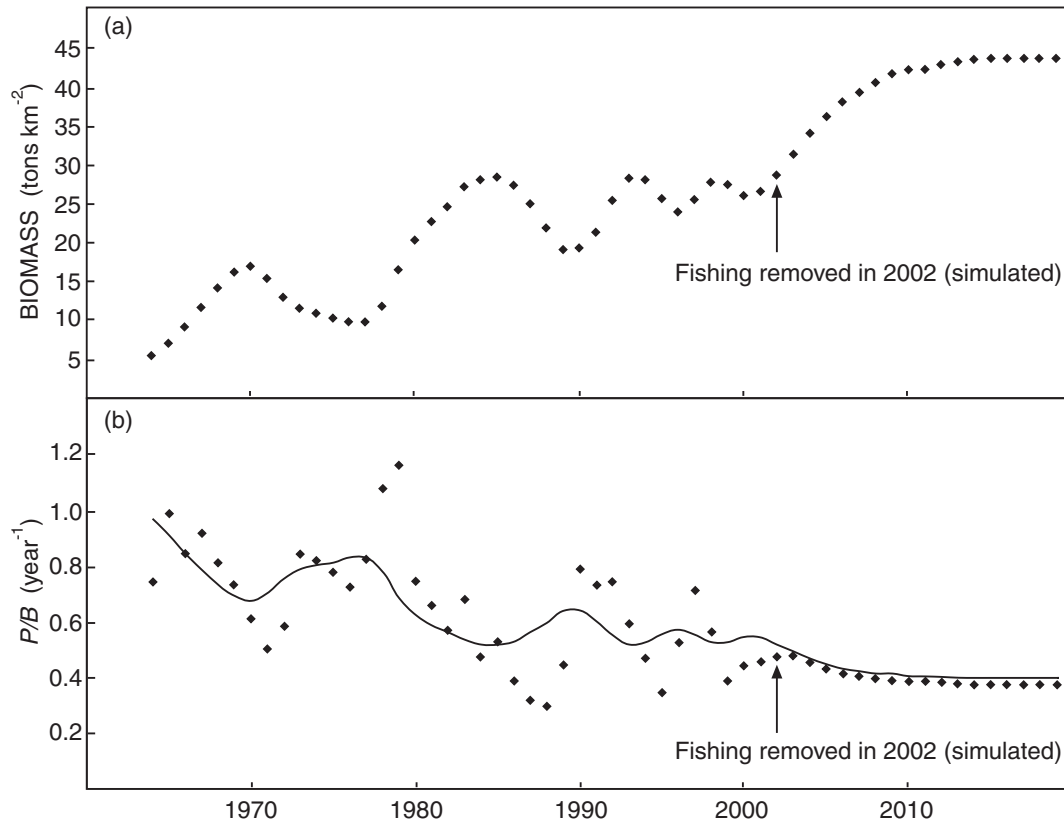


Fig. 5: (a) Stock assessment biomass of walleye pollock, 1964–2002 (from Ianelli *et al.* 2002). The removal of fishing after 2002 is modelled assuming average recruitment and fixed natural mortality at age. (b) P/B implied from the stock assessment model (points), and ECOSIM best fit of P/B to B by tuning P/B and vulnerability X to match stock assessment P/B (line). Projection after 2002 is not fitted

here, time-series of walleye pollock numbers-at-age and weight-at-age estimated in a single-species age-structured model (Ianelli *et al.* 2002) were used to estimate P/B values for walleye pollock over time, for comparison with ECOSIM. The age-structured model included the assumption that both natural and fishing mortality vary with age. The values were used as a potential “true” P/B series for tuning ECOSIM to VB production rates. Note that this is not a “fitting” exercise, but rather a comparison exercise: the stock assessment assumption of constant natural mortality over time is used, which would not be true in ECOSIM or real ecosystems.

Figure 5a shows a simulation in which the biomass of walleye pollock was used from the stock assessment for the years 1964–2002, and a simple age-structured projection of the effects of removing fishing for 20 years was performed, assuming “average” recruitment for

the previous time-series during those years. As a result of removing fishing, biomass increased by approximately 35% before reaching an equilibrium. Natural mortality was assumed constant throughout the simulation. Figure 5(b) shows the resulting P/B s arising from VB assumptions, calculated empirically from year-to-year differences in weights-at-age and numbers-at-age from the stock assessment model. P/B s ranged from 0.4 to 1.2 year⁻¹ across the measured time period (Fig. 5b). A similar calculation, using average weights-at-age instead of varying weights-at-age, did not differ appreciably (results not shown), indicating that variation in numbers-at-age had a much greater effect on population P/B than did variation in weight-at-age over the measured time period.

The ECOSIM production Equation (1) was then fit as a function of stock assessment biomass B over the period 1964–2002, using a sum-of-squares criterion

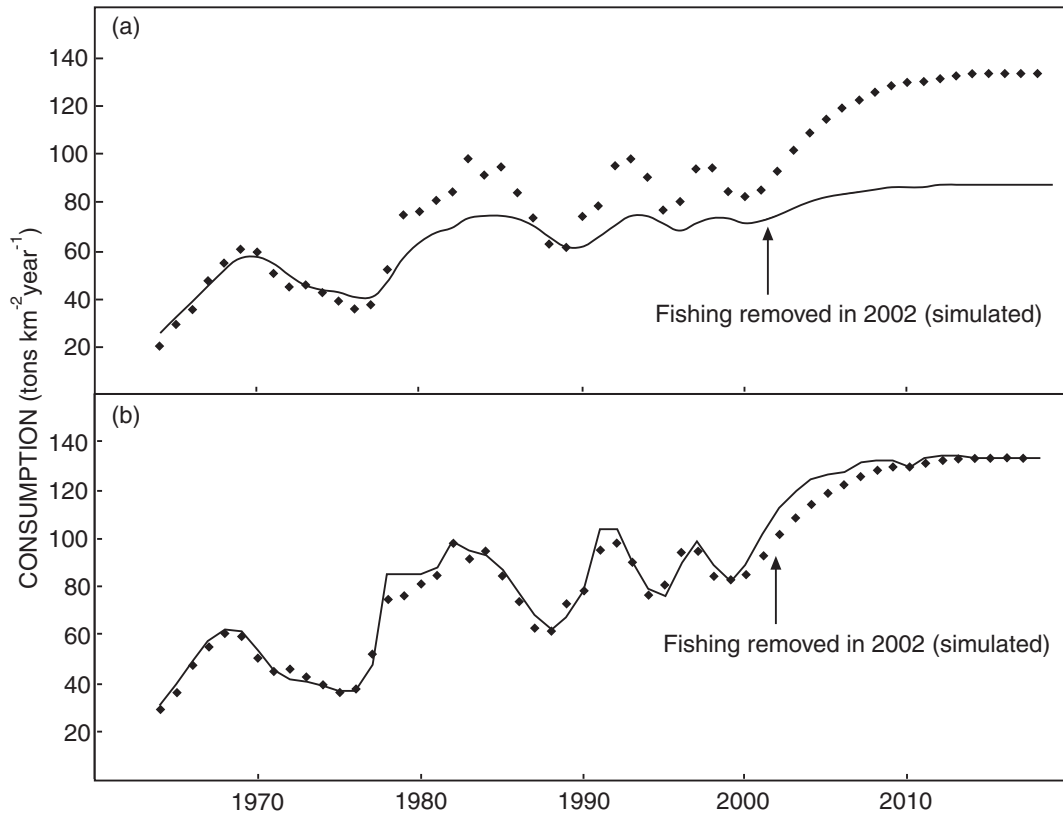


Fig. 6: (a) Consumption resulting in B and P/B in Figure 5, for von Bertalanffy equation assumptions (points) and ECOSIM assumptions (line). (b) Consumption rates as in (a), with ECOSIM consumption corrected by time-varying growth efficiency as described in the text

to fit two parameters, P/B in a reference year (1991) and vulnerability X in the same year. The resulting fit is shown by the line in Figure 5b. During the time period fitted, the ECOSIM prediction for P/B generally follows the age-structured P/B , although it does not fluctuate as widely as the VB estimates. Because the ECOSIM Equation (1) was fitted with the assumption of fixed prey populations, it is possible that the addition of varying prey to the ECOSIM model would improve the match between the two models. For both models, when fishing was removed after 2002, P/B decreased as biomass increased (Fig. 5a, b). Although the final equilibrium biomass is outside the range of biomass over which the ECOSIM equations were calibrated, the VB and ECOSIM models produce nearly identical predictions of $P/B = M$ at equilibrium, where M is the assumed unfished natural mortality averaged over all age-classes ($M \sim 0.3$).

The total implied population consumption for the

two P/B time-series in Figure 5b was then calculated. To compare models under departures from VB assumptions, an empirical age-structured estimate of consumption was made by fitting weight-at-age data for more than 3 000 pollock to the generalized VB growth (Essington *et al.* 2001), in which the exponent of allometric growth ($2/3$ in Equation 2), was fitted as a parameter rather than assumed to be $2/3$. In addition, the parameters h in Equation (2) and respiration rate r in Equation (3) were used to fit measured weight-at-age from the samples. By definition, the VB K was set equal to $r/3$. Because this generalization cannot be integrated to find total population consumption through Equations (6)–(8), consumption was numerically estimated using Equations (2) and (3), and the numbers-at-age and weight-at-age from the stock assessment for the period 1964–2002, and the relationship $Q_{Tot} = Q_{Assim}/A$, where $A = 0.6$. The results for the generalized VB consumption are shown in Figure 6a.

For ECOSIM, the relationship $Q/B = P/B/GE$ was used, where the P/B s were the ECOSIM values in Figure 5b, and an overall growth efficiency GE was estimated to best fit the consumption estimates from the generalized VB model for the period 1964–2002. As shown in Figure 6a, both these methods were used to project predicted consumption Q during the “no fishing” manipulation modelled past 2002. In this case, the predictions from the ECOSIM model diverged from the VB model, because the former assumed a constant GE calculated during periods of fishing, whereas for the latter equations, GE decreased for the same production as the population aged. The estimate of consumption for the unfished population in ECOSIM was about 35% lower than that of the VB estimate.

The current version of ECOSIM includes a “stanza” formulation in which a single species may be split into multiple pools, between which the VB assumptions of differing growth efficiency are assumed (Christensen and Walters 2004). To test the improvement that comes from stanzas, a two-stanza ECOSIM formulation was also tested as in Figure 6a: the inclusion of the second stanza improved the match somewhat, bringing the ECOSIM to within 20% of the VB prediction (not shown).

Finally, a “mixed” ECOSIM/VB model was created by using the ECOSIM P/B from Figure 5b and the assumption $Q/B = P/B/GE$, but allowing GE to vary as in Equation (9). In this case, Z was calculated as ECOSIM would measure it, as the total biomass lost by the population in a given year, divided by the average biomass for that year. Figure 6b shows that, even out of equilibrium, the addition of varying GE as a function of mortality greatly increases the match between ECOSIM and VB assumptions of consumption.

DISCUSSION

At first glance, the functional relationships between consumption and biomass for a population are qualitatively similar under the VB growth assumptions and the vulnerability-derived Arena functional response (Figs 3a, 5b). Both the Arena and VB growth assumptions produce, on a population level, a compensatory response between biomass and production per unit biomass. In this sense, the compensatory shape of either the Arena or the VB model is more appropriate for use than pure Holling Type-II functional responses with no predator density adjustment. This would hold true for any model in which predators and prey are measured in terms of total population biomass integrated over multiple age-classes, regardless

of the underlying assumptions of feeding behaviour. Whereas models such as MSVPA may use Type-II responses to set diet compositions at specific ages, the net effect of integrating fixed at-age rations across a stable population is compensatory, which ensures relative model stability when compared with biomass dynamics models driven by Type-II interactions alone.

Walters *et al.* (1997) derive the vulnerability term of ECOSIM compensation theoretically, from assumptions of the changes in prey risk avoidance in response to predator populations (the Arena hypothesis), and therefore rely on very short time-scale mechanisms to derive and explain the Arena model. In practical use of EwE, most parameter exploration has focused on the density-dependence of predator foraging on prey density, and fitting the “vulnerability” parameter that governs the relative strength of top-down versus bottom-up forcing in the ECOSIM formulation (Walters *et al.* 1997, Shannon *et al.* 2000). More recently, attempts using such models to predict results from marine mammal culls have hinged between selecting the “appropriate” behavioural functional response between the Arena model and the Holling Type-II (prey-limited) and Type III (prey switching, Holling 1959) functional responses (Mackinson *et al.* 2003).

However, returning to the original derivations of the VB equations used in ECOPATH shows that the empirical fits achieved by ECOSIM may be a phenomenological description of age-structure shifts under fishing: the dynamics of age structure offer an alternative explanation with far-reaching implications for model predictions. First and foremost is the question of surplus production. As shown in Table I, in the models discussed here the components of production rate (consumption rate and growth efficiency) increase with fishing rate. However, a key difference between ECOSIM and age-structured models is that, for multi-species age-structured models such as MSVPA, part of this increase (Q/B increase) comes at the expense of other species, whereas part (increase in GE) is essentially “free” because it comes from reduced respiration rates (energy lost as heat). Conversely, all increases in production under ECOSIM are assumed to come from increases in Q/B , at the expense of prey species. If fishing is reduced under VB assumptions, this “free” energy must be bought back as the population ages, resulting in greater consumption of prey or less supportable predator biomass than in ECOSIM.

For a single species, such as Bering Sea walleye pollock, the differences might be minor (35% in Fig. 6a). However, this difference occurs over all species, and is greater for more heavily fished populations where biomass is much lower for the calibration period (usually fished) than for the unfished ecosystem. The overall effect may be magnified considerably, espe-

Table I: Changes in components of a species' production rate (consumption rate times growth efficiency) modelled to occur with an increase in fishing rate for three types of models: single-species age structure, multispecies age structure (MSVPA) and ecosystem biomass dynamics (ECOSIM). "Cost" indicates source of production increase (redirection from other parts of the ecosystem)

Component change in response to increase in fishing	Single-species age structure	Multispecies age structure (MSVPA)	ECOSIM
Q/B	Increases: P/B ($Q/B \times GE$) is fixed for each age and is higher for younger ages. As fishing increases, overall production increases as fishing shifts population to "younger, hungrier, but more energy efficient" animals. Changes in production from increasing weight-at-age may be included	Increases: Q/B is fixed for each age; as fishing increases, overall Q/B increases as fishing shifts population to "younger, hungrier" fish Cost to ecosystem: decrease of prey species (may be offset by shift of younger fish to smaller prey). Free for lowest trophic levels	Increases as per Arena functional response (see text) Cost to ecosystem: decrease of prey species (Stanza model may offset cost by modelling a shift to smaller prey)
GE	Cost to ecosystem: not modelled	Increases: fixed for each age, as fishing increases proportion of younger more "energy efficient" fish. Cost to ecosystem: essentially free (from reduction in heat loss)	Fixed (Stanza model may offer limited inclusion of MSVPA-type increase from heat loss) Cost to ecosystem: not modelled

cially when full models with varying predators and prey are examined. The above examples are for a single species in isolation; the next step is to compare MSVPA and ECOSIM models for which both predator and prey vary.

Walters *et al.* (1997) point out that the ECOSIM functional response creates Beverton-Holt stock/recruitment as an "emergent" property. However, as shown by Equation (11) and Figure 3a, this can be turned around to suggest that a Beverton-Holt relationship gives rise to the ECOSIM compensatory response. In cases where recruitment may have strong nonlinearities, such as differential survival based on local feeding competition, winter survival bottlenecks or climate interactions, starting with independently-estimated Beverton-Holt or other stock recruitment functions might be more appropriate than expecting stock-recruitment to arise out of an explicit accounting of predation. Indeed, attempts to explain Bering Sea recruitment through ECOSIM predation-controlled recruitment alone have been largely unsuccessful (KYA, unpublished data) or have relied on fit "primary production anomalies" to account for the energetic shifts that arise from variations in age structure (e.g. National Research Council 2003)."

In some sense, it is not necessary to select between the two hypotheses for the practical use of these models. The similarity between P/B predictions in the two models is unlikely to allow single-species data to distinguish between hypotheses, and the ability to fit

parameters of one hypothesis to those of another (Fig. 3a) indicates that changes in consumption and growth efficiency might be minor for small simulated perturbations.

For strategic management projections, however, it is critical to note the direction of bias between the two hypotheses. Specifically, if fishing is reduced from reference exploited biomass levels under ECOSIM (because most current ECOPATH models begin with exploited ecosystems), ECOSIM would predict an increase of species biomass with a fixed growth efficiency rather than with a decreasing growth efficiency associated with older animals. This would greatly overestimate the amount of top predator biomass supportable by prey species in "pristine" ecosystems under VB assumptions. Conversely, ECOSIM would underestimate the amount of prey released by top predator removal compared with VB assumptions. In seeking to address the fundamental question of the existence of ecosystem surplus production, the difference between these hypotheses must be acknowledged and explored.

There are three possibilities for such exploration. The first is to build fully age-structured models separate from ECOSIM that include individual vulnerability or other behavioural functions for each age-class – this is the approach taken for MSVPA. The second is to move towards a "stanza-based" split of life-history stages within ECOSIM, as suggested by Christensen and Walters (2004). On a practical level,

explicit splitting of age-classes involves a large increase in data requirements, especially for the specification of juvenile diets, and the initial results of stanza modelling indicate that several life-history stages would be required to reduce the bias noted here significantly. If dynamic simulations starting from ECO-PATH are to remain “whole foodweb” models, it is likely that “single biomass pools” will need to be seen as the unit of measurement for most functional groups.

The final alternative is to use whole-biomass pools and the functional responses of ECOSIM with a few modifications. The first and most important modification is to replace the fixed growth efficiency of ECOSIM with the function where growth efficiency is a function of both mortality and energetics: $GE(Z) = AZ(Z + 3K)$. The initial results in Figure 6b suggest that, even out of equilibrium, this correction may successfully replicate VB assumptions within ECOSIM. As is the case here, there is no direct way to perform this adjustment in the current ECOSIM software without independent implementation of the ECOSIM algorithms. The second modification is to set the initial ECOSIM vulnerabilities (X) by fitting such values to known VB parameters from fisheries data, using Equations (6)–(8) and fitting ECOSIM X to P/B , either by assuming equilibrium for any given mortality rate Z (Fig. 3a) or by non-equilibrium age structured information (Fig. 5a). This does not preclude Arena-model adjustments to vulnerability: such settings may be further modified by the inclusion of hypotheses of prey risk and foraging time.

Regardless of the hypotheses explored, the fact that the original $P/B = Z$ is strongly dependent on age structure of a population within an ecosystem argues against the practice of “borrowing” age-structure-dependent consumption parameters between ecosystems, even for Q/B where changes are relatively minor. If borrowing is necessary because of data paucity, the VB parameters and the equations provided here could be used as a starting point, which would give at least a basis for parameter use based on life history and past mortality.

Viewing “vulnerability” as a function of age-structure rather than predator risk has one final advantage: it allows the compensatory stock dynamics based on life-history strategies, growth and recruitment to be captured by applying VB and Beverton-Holt recruitment parameters, to obtain initial estimates of vulnerability. Given that these life-history parameters have been suggested to have a strong impact on species behaviour under fishing (King and McFarlane 2003), applying these calculations allows explicit avoidance of modelling species as essentially identical biomass pools (the “cod is not a tuna” problem, Longhurst 1998). The inclusion of bioenergetic aspects of life-

history strategies, as implemented by the inclusion of growth and recruitment parameters, may greatly strengthen the modelling of varying life histories within ECOSIM.

CONCLUSIONS

Overall, just as selecting between alternate empirical stock/recruitment relationships has not prevented single-species modellers from applying their results (Hilborn and Walters 1992), the selection between alternate relationships describing predator/prey interactions will rely to a certain extent on the continuing process of data gathering and formal model fitting. All models require a healthy degree of scepticism to allow their “sustainable” use. On a case-by-case basis, ECOSIM models have shown some predictive benefits over single-species models. In cases where species have been clearly fished down or overfished, multispecies models, and specifically EwE, may provide better predictions of future recovery than do single-species models (e.g. Cox *et al.* 2002). Collapsed fish stocks, many of which have not recovered as predicted by single-species models, may be attributable to the presence of “replacement” competitors that a multispecies model might consider. Furthermore, the general prevalence of depensatory stock/recruitment relationships (Hilborn and Lierman 1998) may be explained in part by trophic mechanisms such as compensation/depensation (Walters and Kitchell 2001).

The use of predictions of “whole ecosystem” multispecies models that encompass a majority of predator/prey interactions within ecosystems has been strongly recommended for ecosystem-based fisheries management (NMFS 1998) and may serve as useful exploratory tools for separating plausible from implausible hypotheses and scenarios. Foodweb modelling as a formal statistical process is in its infancy: exploration of multispecies interactions as ecological explanations has been more a matter of hypothesis generation than formal mechanism selection (Hollowed *et al.* 2000). However, even if these models are “consulted” rather than “used” (Schnute and Richards 2001), their assumptions must be evaluated carefully.

Successful fitting of models does not guarantee a mechanistic explanation across multiple scales. The fits that the Arena model achieves should be viewed as an empirical multispecies extension to year-scale, compensation/recruitment dynamics, rather than as a mechanistic description of fine-scale foraging interactions. It is possible that both processes are captured in the model to a certain extent, but the use of fisheries data for fitting strongly suggests that the age-structure

interactions may dominate the model's dynamics, especially in seasonal seas with high variation in recruitment. This must be considered when extending projections beyond the territory of measured correlations; the bias may lead ECOSIM to overestimate "pristine" biomass levels or show bias in some policy optimizations, especially when beginning with models of highly exploited ecosystems.

By specifically acknowledging alternate hypotheses underlying the empirical compensation in the ECOSIM functional response, one is left with an opportunity. By varying assumptions and species interactions between alternative mechanistic formulations, these models may be used to examine the multiple time-scales of natural variability for better addressing the issue of ecosystem sustainability.

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