Appendix A-G (online)

Appendix A. Derivation of predation mortality

Predators with a size between m and $m + dm$ have a food intake rate of $s(m_p, m)f(m)hm^n\theta N(m)dm$ for m_p sized prey. The total density of food available from all prey sizes to the predators in $[m\,;m + dm]$ is $\phi(m)$ (5), meaning that the mortality experienced by a m_p sized individual is:

$$\mu_{p,i}(m_p) = \sum_j \int \frac{s(m_p, m)f_j(m)hm^n\theta_{j,i}N_j(m)}{\phi_j(m)}\, dm. \tag{A.1}$$

The maximum food intake may be expressed as a function of $f(m)$, $v(m)$, and $\phi(m)$ via (6), such that the predation mortality can be written as:

$$\mu_{p,i}(m_p) = \sum_j \int s(m_p, m)(1 - f_j(m))v(m)\theta_{j,i}N_j(m)\, dm. \tag{A.2}$$

By using the EQT assumptions of constant feeding level and a power law community spectrum (cf. section 3) the mortality reduces to $\mu_p(m_p) = \overline{\theta}(1 - \overline{f}) \int s(m_p, m)v(m)\kappa_c m^{-\lambda}\, dm$, which can be solved analytically:

$$\mu_p(m_p) = \alpha_p m_p^{n-1}, \tag{A.3}$$

where $\alpha_p = \overline{\theta}(1 - \overline{f})\sqrt{2\pi}\kappa_c\gamma\sigma\beta^{1+q-\lambda} \exp\left[\frac{1}{2}\sigma^2(1 + q - \lambda)^2\right]$.

Appendix B. Available food and the physiological level of predation a

Using the EQT assumption of a power law community spectrum allows calculation of the available food density $\phi(m) = \overline{\theta} \int s(m_p, m)\kappa_c m_p^{-\lambda}m_p\, dm_p$:

$$\phi(m) = \alpha_\phi\overline{\theta}\kappa_c m^{2-\lambda}, \tag{B.1}$$

where $\alpha_\phi = \sqrt{2\pi}\sigma\beta^{\lambda-2} \exp\left[\frac{1}{2}\sigma^2(2 - \lambda)^2\right]$.

Using the EQT assumption of constant feeding level yielding $\lambda = 2 + q - n$ allows us to write $\overline{\theta}\kappa_c = \overline{f}h/(\alpha_\phi\gamma(1 - \overline{f}))$ by rearranging the expression of the feeding level (6). Using this and the definition of $\hbar$ allows writing $\alpha_p = c(\hbar + k)\beta^{2n-q-1}/\alpha$ where $c = \exp\left[\frac{1}{2}\sigma^2\left((1 + q - \lambda)^2 - (2 - \lambda)^2\right)\right] = 1.03 \approx 1$. Ultimately using the definition of f_c allows writing the physiological level of predation $a = \alpha_p/\hbar$ as:

$$a = c\frac{\overline{f}}{\overline{f} - f_c}\beta^{2n-q-1}/\alpha. \tag{B.2}$$

Appendix C. Calculating efficiency ε of offspring production

The efficiency of turning energy into offspring is denoted ε. It includes losses due to behavioural aspects, pre-hatching mortality, and that the energy contents in gonadic tissue is higher than in somatic tissue. It is a quantity that is difficult to measure, but for $n = p$ its value can be derived.

The energy (in units of mass) routed into reproduction (for $n = p$) is $\psi(m, m_*)\hbar m^n$ where $\hbar = \alpha\overline{f}h - k$. The energy of the produced offspring is then, $E_o(m) = \varepsilon\psi(m, m_*)\hbar m^n$:

$$E_o(m) = \varepsilon\hbar\eta_*^{1-n}m_*^{n-1}m. \tag{C.1}$$

From Gunderson (1997) we have the yearly mass-specific allocation to reproduction:

$$\varrho(m_*) = \varrho_0\eta_*^{1-n}m_*^{n-1}, \tag{C.2}$$

where $\varrho_0 = 1.2\,\mathrm{g}^{1-n}$/year is obtained using least sum of squares in fitting the curve to the data for oviparous fish in Gunderson (1997). Equalling (C.2) and E_o/m allow us to determine the efficiency of offspring production ε:

$$\varepsilon = \frac{\varrho_0}{\hbar} \approx 0.12. \tag{C.3}$$

Appendix D. Setting the search rate prefactor γ from initial feeding level f_0

Food for the smallest individuals in the spectra will be supplied by the background spectrum. If we assume that the resource spectrum is at carrying capacity κ then an equilibrium initial feeding level f_0 for the small individuals can be calculated using (6).

Alternatively we may specify an initial feeding level f_0 and derive one other parameter. By solving the feeding level for γ by using the analytical solution for the density of food $\phi(m)$ (B.1) we find γ as a function of f_0:

$$\gamma = \frac{f_0 h}{(1-f_0)\alpha_\phi \theta_{i,R}\kappa} \approx \frac{f_0 h \beta^{2-\lambda}}{(1-f_0)\sqrt{2\pi}\sigma\theta_{i,R}\kappa}. \tag{D.1}$$

Appendix E. Parameter estimation

Individual growth: From Kitchell and Stewart (1977) we obtain an estimate of specific dynamic action on 15 % of food consumption, and conservative estimates of egestion and excretion on 15 % and 10 % respectively. This results in an assimilation efficiency of $\alpha = 0.6$.

The maximum intake scales with a 0.6–0.8 exponent, with $n = 0.75$ being an approximate average value (Jobling, 1994). Andersen and Riis-Vestergaard (2004) provides a length-based relationship for the maximum intake rate based on a whiting study adopted for saithe. Using $m = 0.01 l^3$ (m in g and l in cm) (Peters, 1983), and an energy content of $5.8\,\text{kJ/g}$ (fish) or $4.2\,\text{kJ/g}$ (invertebrates) (Boudreau and Dickie, 1992) yields a prefactor h for the maximal food intake on $83\,\text{g}^{1-n}/\text{year}$ or $114\,\text{g}^{1-n}/\text{year}$ (at 10°C). These intake values overestimate the intake of large individuals since Andersen and Riis-Vestergaard (2004) use an intake exponent of 0.67 instead of $n = 0.75$. Due to this a value of $h = 85\,\text{g}^{1-n}/\text{year}$ is selected, which also provides reasonable fits to 'cod-like' growth curves ($m_* = 5$ kg).

The standard metabolism scaling exponent p for fish is slightly higher than for other taxa, around 0.8 from intra- and interspecies measurements (Winberg, 1956; Killen et al., 2007). For simplicity we assume $p = n$. The first term (acquired energy) in the growth model (8) is $\alpha f(m) h m^n$ where the feeding level $f(m)$ is a decreasing function of body size (see *Results*). This has the effect that even when $n = p$ is assumed the acquired energy term still effectively scale with a smaller exponent than the maintenance term km^p in accordance with the experimental data on food intake and standard metabolism. Furthermore it is noted that this clearly makes the individuals in each functional species non-neutral. The bioenergetic consequences of $n \neq p$ has been explored in detail by Andersen et al. (2008).

The prefactor for standard metabolism can from Peters (1983) be determined to $6.5\,\text{g}^{1-n}/\text{year}$ if the diet is composed of only invertebrates and $4.7\,\text{g}^{1-n}/\text{year}$ if all the energy is from fish. Both values were corrected to 10°C using $Q_{10} = 1.83$ (Clarke and Johnston, 1999). It is assumed that energy costs due to activity can be described with an activity multiplier on the standard metabolic rate. Estimations of activity costs are difficult to obtain, but activity multipliers are often reported in the range 1 to 3; e.g. 1.25 for North Sea cod (Hansson et al., 1996), 1.7 for dace (Trudel and Boisclair, 1996), and 1.44-3.27 for saithe (Andersen and Riis-Vestergaard, 2004) (however see also Rowan and Rasmussen (1996); He and Stewart (1997)). A reasonable value of the prefactor for the standard metabolism and activity costs is assumed to be $k = 10\,\text{g}^{1-n}/\text{year}$ corresponding to an activity multiplier in the range 1.5 to 2.1.

Food encounter: The preferred predator-prey mass ratio is set to $\beta = 100$ (Jennings et al., 2002) and the width of the selection function to $\sigma = 1$, which catches the general picture for at least cod and dab (Ursin, 1973). It should be noted that small organisms such as copepods have a larger σ of 3–4.5 (Ursin, 1974), but for simplicity and since focus is on species with rather large m_* the width σ will be held constant.

The exponent for swimming speed is $q = 0.8$ (Andersen and Beyer, 2006). The prefactor γ for the volumetric search rate is difficult to assess from the literature. An alternative approach is to determine it as a function of of initial feeding level f_0 via (D.1). Experience with the model shows that feeding level is a decreasing function of body size. This means that it is sensible to use an initial feeding level f_0 that is larger than the expected average feeding level $\overline{f}$. In this study a default value of $f_0 = 0.6$ is used. This along with default parameters yields $\gamma = 0.8 \cdot 10^4\,\text{m}^3\text{g}^{-q}/\text{year}$ (Table 1). An alternative estimate of γ is possible by multiplying the prefactors for swimming speed (Ware, 1978) and swept reactive field area (reactive radius assumed equal to body length): $\gamma = 20.3 \cdot \pi \cdot 0.01^{-2/3}\text{cm}^3\text{g}^{-q}/\text{s} \approx 4.3 \cdot 10^4\,\text{m}^3\text{g}^{-q}/\text{year}$, which indeed justifies the use of $f_0 = 0.6$.

Mortality: Realistic energy reserve sizes may be $\xi \in [5\%; 20\%]$, and in the present study $\xi = 0.1$ is used. A widely used background mortality for 'cod-like' $m_* = 5$ kg fishes is $\mu_b = 0.1\,\text{year}^{-1}$, which yields $\mu_0 = 0.84\,\text{g}^{1-n}/\text{year}$.

Reproduction: The efficiency of offspring production was not found in the literature. However, an analytical expression may be obtained (for $n = p$) by combining the calculation of yearly mass-specific allocation to reproduction from the bioenergetic model (Appendix C) with empirical measurements (Gunderson, 1997), which yields $\varepsilon = \varrho_0/\hbar \approx 0.1$. The fraction of asymptotic size to mature at is $\eta_* = 0.25$ (Andersen et al., 2008). Offspring mass is $m_0 = 0.5$ mg which corresponds to an egg diameter of 1 mm (Wootton, 1979; Chambers, 1997).

Resource spectrum: The carrying capacity of the resource spectrum should equal the magnitude of the community spectrum: $\kappa m^{-\lambda}$, with an exponent $\lambda = 2 - n + q = 2.05$ (Andersen and Beyer, 2006). The magnitude of the resource spectrum is set to $\kappa = 5 \cdot 10^{-3}$ g$^{\lambda-1}$/m^3, which is comparable with findings from empirical studies (Rodriguez and Mullin, 1986). The constant for resource regeneration rate is $r_0 = 4$ g^{1-p}/year at $10°$C (Savage et al., 2004). The cut-off of the resource spectrum is set to include mesoplankton, $m_{cut} = 0.5$ g.

Appendix F. Expected Lifetime Reproductive Success

The expected lifetime reproductive success can be split into two components: 1) the probability of surviving to become adult, and 2) lifetime reproduction per adult.

Appendix F.1. Survival probability

If we set $\frac{\partial N}{\partial t} = 0$ in (1) we may obtain the steady-state solution as:

$$N(m) = \frac{K(m_*)}{g(m, m_*)} \exp\left(-\int \frac{\mu(m)}{g(m, m_*)} dm \right), \tag{F.1}$$

where $K(m_*)$ is the constant from the integration along m. We notice that the probability of surviving from size m_0 to size m is $p_{m_0 \to m} = \exp\left(-\int_{m_0}^{m} \frac{\mu(m')}{g(m', m_*)} dm' \right)$, which along with $p_{m_0 \to m_0} = 1$ allow us to write the survival probability as:

$$p_{m_0 \to m} = \frac{N(m)g(m, m_*)}{N(m_0)g(m_0, m_*)}. \tag{F.2}$$

Appendix F.2. Lifetime adult reproduction

The amount of energy an adult belonging to a m_* population will spend on reproduction throughout its life is:

$$R_{life}(m_*) = \int_{t_*}^{\infty} p_{t_* \to t} \psi(m, m_*) E(m) dt,$$

where t_* is maturation age, and $\psi(m, m_*)E_i(m)$ the rate at which energy is allocated to reproduction. Noting that $g(m, m_*) = \frac{dm}{dt}$ allows us to write this as:

$$R_{life}(m_*) = \int_{m_*}^{M} p_{m_* \to m} \frac{\psi(m, m_*) E(m)}{g(m, m_*)} dm. \tag{F.3}$$

Appendix G. Details of Numerical Methods

The model is in the form of a series of coupled partial-integro-differential equations (1), one for each species with the size preference function (4) being the integral kernel. The equations are of the first order in mass (i.e. hyperbolic) in which case shocks could be formed in the solutions. However the integral kernel smooths out any discontinuities and the equations can be solved effectively and accurately using a standard semi-implicit upwind finite-difference scheme for solving PDEs (Press et al., 1992). The McKendrick-von Foerster PDE (1) is discretised by calculating $g(m, m_*)$ and $\mu(m)$ explicitly and making the time update implicit, to yield:

$$\frac{N_w^{i+1} - N_w^i}{\Delta t} + \frac{g_w^i N_w^{i+1} - g_{w-1}^i N_{w-1}^{i+1}}{\Delta m_w} = -\mu_w^i N_w^{i+1}, \tag{G.1}$$

where i denotes the time step, and w the grid index on the mass axis ($i, w \in \aleph^+$). First order approximations have been used for both the time and mass derivatives. The discretisation in mass is known as the upwind approximation since the derivative is calculated from w and $w - 1$, which is possible since the growth

function is non-negative. It is further noted that the ∂m approximation is semi-implicit since densities at time step $i+1$ are used. Equation (G.1) may be written as:

$$N_{w-1}^{i+1}\underbrace{\left(-\frac{\Delta t}{\Delta w_w}g_{w-1}^i\right)}_{A_w}+N_w^{i+1}\underbrace{\left(1+\frac{\Delta t}{\Delta w_w}g_w^i+\Delta t\mu_w^i\right)}_{B_w}=\underbrace{N_w^i}_{C_w}, \qquad (G.2)$$

which allows us to write an explicit solution for the density spectrum at the $i+1$ time step:

$$N_w^{i+1}=\frac{C_w-A_wN_{w-1}^{i+1}}{B_w}, \qquad (G.3)$$

which can be solved iteratively since N_1^{i+1} is given by the boundary condition. The flux in the boundary $g(m_0,m_*)N(m_0,t)$ is equal to the reproduction flux of new recruits R (11) such that $g_0^iN_0^{i+1}=R$, which yields: $A_1=0$, and $C_1=N_1^i+\frac{\Delta t}{\Delta m_1}R$.

This semi-implicit upwind scheme is very stable but diffusive. The third order QUICK (Quadratic Upwind Interpolation for Convective Kinematics) scheme along with the techniques by Zijlema (1996), which prevents overshooting problems introduced by the QUICK method, were used to check that numerical diffusion poses no problem for $\Delta t = 0.02$ years, and a m_w mass grid with 200 logarithmically evenly distributed points. To ensure stability the Courant condition (i.e. Press et al. (1992)):

$$\frac{|g_w^i|\Delta t}{\Delta m_w}\leq 1, \qquad (G.4)$$

is prudent to fulfill. The essence of the criterion is that Δt should be small enough not to allow individuals to skip any mass cells m_w during their growth trajectory.

The grid m_w spans the offspring size m_0 to 85 kg to include maturation sizes up to the order of 20 kg. The grid for the background spectrum ends at m_{cut}, and the lower limit should be low enough to ensure food items for the smallest individuals in the functional species, i.e. 3 decades lower than m_0. Identical Δm_w is used for the background and species spectra to ease computations in the overlap $[m_0; m_{cut}]$.

To save computational time the ODEs for the background spectrum (15) are solved analytically. The solution at time $t_0 + \Delta t$ for the semi-chemostatic equation is:

$$N_R(m,t_0+\Delta t)=K(m)-\Big(K(m)-N_R(m,t_0)\Big)e^{-[r_0m^{p-1}+\mu_p(m)]\Delta t}, \qquad (G.5)$$

where $K(m)=\frac{r_0m^{p-1}\kappa m^{-\lambda}}{r_0m^{p-1}+\mu_p(m)}$ is the effective carrying capacity at resource size m.

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