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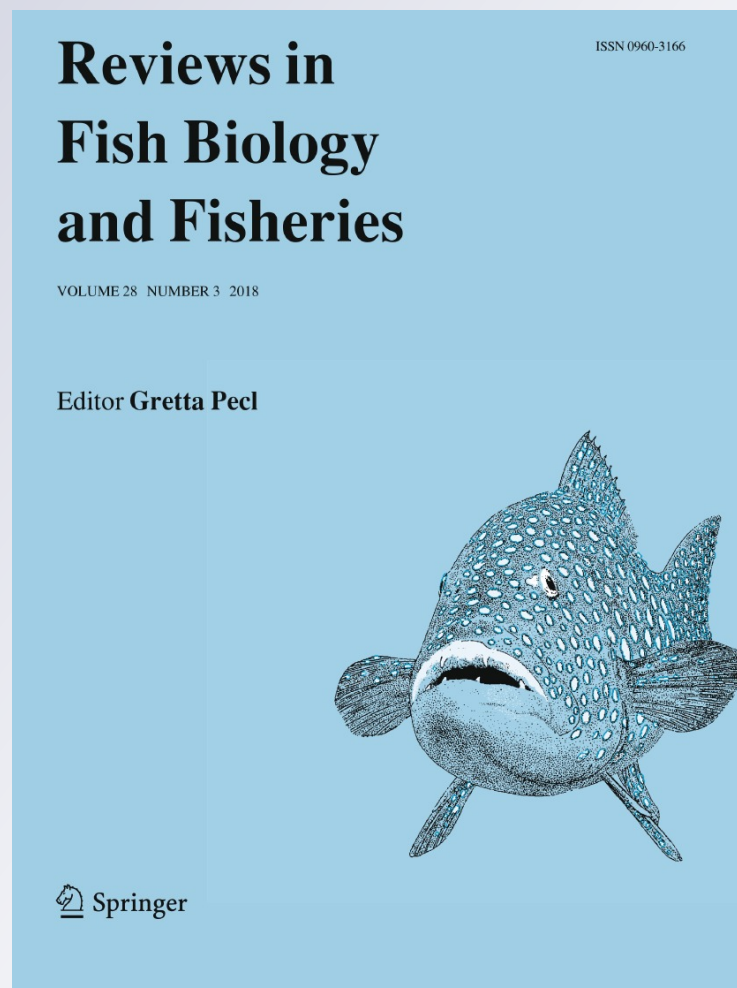
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RESEARCH PAPER

Revisiting Beverton–Holt recruitment in the presence of variation in food availability

Brett van Poorten · Josh Korman · Carl Walters

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Abstract Understanding density-dependent changes in juvenile survival and growth rates is of great importance because these rates determine recovery rates for imperiled populations and/or sustainable harvest rates. Unfortunately, the mechanisms leading to density dependent survival and growth are among the least understood process in biology and fisheries. Previous work has shown that small fish may vary foraging times to achieve a target growth rate, resulting in the well-known Beverton–Holt recruitment function with variation in food availability affected the initial slope of the recruitment curve. We amend their derivation to show that incorporating fish growth under a variety of evolutionary strategies for balancing foraging time and predation risk still leads to recruitment approximately as expected under the Beverton–Holt recruitment model but that changing food availability affects both the initial slope and maximum recruitment level. We demonstrate that

when food availability is known to vary over time, these models often result in a more parsimonious alternative than the standard Beverton–Holt function. Further, Beverton–Holt recruitment is expected when foraging times are adjusted to balance fitness gains from growth against mortality risk. Finally, linking recruitment success to food availability warns that species with high scope for density dependent survival (high compensation ratio or steepness) may be extremely sensitive to changes in available food densities. This work emphasizes the sensitivity of stock-recruitment parameters to food availability and strongly suggests a need to carefully monitor lower trophic levels to better understand and predict dramatic changes in juvenile recruitment and carrying capacity.

Keywords Density-dependent · Growth · Juvenile survival · Predation · Prey density · Recruitment · Risk

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Introduction

During early life when fishes may be subject to density-dependent mortality leading to stock recruitment relationships like the Beverton–Holt, mortality rates are likely to be high due to predation and to be dependent on growth rates and/or time spent foraging, both of which could be sensitive to food availability in

restricted juvenile foraging areas (Anholt and Werner 1998). In an early attempt to model this dependence, Walters and Korman (1999); see also (Walters and Martell 2004) argued that small fish might vary foraging times so as to maintain a growth rate target, leading to linear density dependence in foraging times and predation mortality rates which would in turn lead to the Beverton–Holt recruitment relationship. Unfortunately there was a basic logical error in their derivation, because their model ignored effects of growth during the period of exposure to high predation risk on foraging patterns and predation risk.

In this paper we derive alternative predictions about how food availability and resultant foraging times ought to vary with juvenile fish density, particularly in cases where juveniles forage in short daily bouts near dawn and dusk as well as for the continuous feeding case examined by Walters and Korman (1999). We show that more complex foraging behaviors and changes in foraging efficiency with juvenile size still lead to recruitment relationships of basically the Beverton–Holt form, whether or not juvenile fish adjust their foraging times to maintain stable growth rates. Consistent with Walters and Korman, as well as a number of field observations (e.g. Biro et al. 2003; Stallings 2008), these models link foraging time to the risk ratio between food availability and predation risk. We use these models that incorporate food availability based on foraging times to fit to a variety of data and show that when food density is variable across years, these models provide a more parsimonious alternative than the standard two-parameter Beverton–Holt model. We further demonstrate that the Beverton–Holt form is predicted when foraging times are adjusted to maximize an evolutionary fitness criterion that balances gain in fitness from growth with increasing mortality risk as foraging time increases. Finally, we show that stock-recruitment parameters should be highly sensitive to food availability and/or productivity.

Predicting effects of density and food supply on foraging time and mortality rate

The original Beverton–Holt recruitment model was derived by assuming that juvenile fish numbers N die off according to the rate equation $\frac{dN}{dt} = -MN$ for some

pre-recruit period of duration T years, with M (instantaneous mortality rate) varying linearly with N during the period, i.e. $M = M_1 + M_2N$. Integrating this rate equation to predict recruit numbers $N(T)$ at time T from initial numbers $N(0)$ results in the stock-recruitment equation

$$N(T) = N(0) \frac{e^{-M_1 T}}{1 + \frac{M_2}{M_1}(1 - e^{-M_1 T})N(0)} = \frac{\beta_1 N(0)}{1 + \beta_2 N(0)} \quad (1)$$

where $\beta_1 = e^{-M_1 T}$ is the maximum survival rate at low $N(0)$ and $\beta_2 = \frac{M_2}{M_1}(1 - e^{-M_1 T})$ is a density-dependence parameter. Beverton and Holt identified various mechanisms like predator attraction that could cause M to vary linearly with N . Walters and Korman (1999) predicted linear variation in M by assuming that selection has driven fish to maintain a base or target growth rate through a linear increase in foraging time and hence increasing exposure to predation risk as N increases, due to localized competition for food among juveniles in spatially restricted foraging areas/times. However, the Walters-Korman equation for predicting competition effect on food availability was incorrect, in a way that causes incorrect predictions of how the β_1 and β_2 parameters of Eq. (1) should vary with food abundance. The details of this error will be explained below.

In this section we first examine the basic pattern of food intake and foraging times that juvenile fish need to follow if their growth is described by the von Bertalanffy growth equation. Then we derive alternative predictions for how foraging time needs to vary in order to maintain the same basic growth pattern when food availability is increased, or reduced due to competition, for juvenile fish that feed continuously versus in short daily feeding bouts. These predictions show that foraging times, hence predation risk, do indeed need to increase at higher juvenile densities, but are only linearly related to juvenile densities if foraging times are short (< 20% of each day). Finally we show that the Beverton–Holt recruitment relationship resulting from approximate linear relationship between foraging time and juvenile density, for the short foraging time case, has β parameters that depend strongly and nonlinearly on food biomass and availability.

Target feeding rates

Suppose that juvenile fish encounter mean food densities V (mass/volume) while foraging, and forage for a proportion p of each day where p may be limited by either juvenile behavioral choices (such as defending territories or shelter sites; Tupper and Juanes 2017) or by behaviors of their prey (such as diel migration of prey organisms or emergence behavior of benthic insect prey). Suppose further that as juveniles grow in length L , the volume S that they search per time foraging varies as $S = \alpha L^2$, where α is a scalar e.g. if both reactive distances to prey and swimming speed vary linearly with juvenile length (but see van Poorten and Walters (2015) for possible exceptions to this prediction). Then their feeding rate Q (mass intake per day) will vary as

$$Q = \alpha L^2 V p. \tag{2}$$

Now suppose juveniles maintain a length–weight relationship near $W = \alpha L^3$, and that weight growth rate varies according to the basic bioenergetics model

$$\frac{dW}{dt} = eQ - mW, \tag{3}$$

where e is the product of assimilation efficiency and efficiency of converting assimilated food into potential growth (i.e. 1-proportion of food intake used for specific dynamic action and food acquisition efficiency), and m is routine metabolic rate. For fixed V and p , the juveniles will then exhibit von Bertalanffy length growth (see e.g. Walters and Post 1993; Essington et al. 2001), with “growth” parameter $K = \frac{m}{3}$ and maximum length L_∞ given by

$$L_\infty = \frac{expV}{ma}. \tag{4}$$

We can use these relationships in two ways: (1) to predict how length growth, in particular L_∞ , will vary with changes in food density V if fish maintain (or are constrained to) fixed foraging time proportion p , or (2) to predict how fish must vary their foraging time proportion p in order to maintain some “target” growth pattern with parameters K, L_∞ . It is worth noting here that fish can adjust other aspects of their physiology or behaviour to adjust growth rate, such as variation in metabolism (Tupper and Juanes 2017). For case (2), Eq. (4) implies that to maintain constant

L_∞ , juveniles must vary p with changes in food density V , as

$$p = \frac{L_\infty ma}{e\alpha V}. \tag{5}$$

Equivalently, we can express p needed to satisfy Eq. (5) in terms of food intake rate target Q_{tar} , where Q_{tar} is given over time (as L increases) by van Poorten and Walters (2016)

$$Q_{tar} = 3aKL^2L_\infty/e, \tag{6}$$

with foraging time p varying with food density V (based on Eq. (2)) as

$$p = \frac{Q_{tar}}{\alpha L^2 V}. \tag{7}$$

Note that Eqs. (5) and (7) imply constant p over time to maintain given von Bertalanffy growth parameters, if food density V is constant over time.

The von Bertalanffy model predicts approximately linear growth over the early juvenile period, with growth rate approaching $\frac{dL}{dt} = KL_\infty$. Combining this prediction with Eq. (4) implies that early length growth rate should be proportional to foraging time p and vulnerable prey density V , so that the time required to reach some critical juvenile size, e.g. a size above which predation risk declines substantially, should be inversely proportional to both p and V . For fixed p , this inverse dependence implies that total mortality rate over the time required to reach the critical size should be positively related to juvenile abundance N , i.e. should be density-dependent, if vulnerable prey density V varies inversely with N .

Effect of juvenile density on available prey density and foraging time

The effective prey density V that juvenile fish encounter while foraging in spatially and temporally restricted locations is likely to be a small fraction of the overall prey biomass B that we would observe in representative sampling of larger areas in ecosystem studies. Foraging arena theory models (Ahrens et al. 2012) have represented this differentiation by treating B as largely invulnerable to the juveniles, with V arising from spatial mixing processes (prey movement, dispersal, advection) such that V can be much

more sensitive to juvenile abundance N than would be predicted from the overall effect of N on B . Two models have been used to represent this sensitivity: (1) continuous foraging models, where the mixing processes and juvenile consumption are viewed as occurring continuously over time, and (2) bout foraging models, where juvenile consumption occurs in short diurnal feeding bouts that deplete prey that have moved into foraging arenas during non-feeding periods (Walters and Christensen 2007). Here we show that these models lead to similar predictions about how V should vary with N , and how foraging time should vary if juveniles attempt to maintain stable von Bertalanffy growth rates.

The continuous foraging model is derived by assuming that V varies according to the mixing rate and predation removal equation

$$\frac{dV}{dt} = vB - v'V - \alpha^*pVN \tag{8}$$

where v and v' are instantaneous exchange rates into and out of foraging areas, and α^* is the time-varying search rate constant $\alpha^* = \frac{\alpha L^2}{365 \cdot A}$ where A is the total foraging arena volume over which juveniles are distributed while feeding (the factor 365 scales from annual α rate for growth calculations to more convenient daily rates for choosing reasonable values of v , v'). Note that both body length L and utilized volume A are expected to increase so as to cause α^* to increase as juveniles grow. Walters and Korman (1999) incorrectly omitted foraging time proportion p from this model. Assuming that V moves rapidly to equilibrium compared to temporal changes in B and N , so as to vary around this time dependent equilibrium, solving Eq. (8) for V when $\frac{dV}{dt} = 0$ implies the average V will vary as

$$V = \frac{vB}{v' + \alpha^*pN} = \frac{V_0}{1 + \alpha^*pN/v'} \tag{9}$$

where $V_0 = (\frac{v}{v'})B$ is the predicted mean vulnerable prey density when juvenile abundance is zero. If juvenile fish vary their foraging time p so as to maintain the same growth pattern as N varies, substitution of the Eq. (9) prediction for V into Eq. (5) then implies that p needs to vary as

$$p = \frac{p_0}{1 - \gamma N} \tag{10}$$

where p_0 and γ are the combined parameters

$$p_0 = \frac{L_\infty m a}{e \alpha V_0} \quad \text{and} \quad \gamma = \frac{p_0 \alpha^*}{v'} \tag{11}$$

Note here that p_0 is interpreted as the minimum foraging time proportion needed to achieve target L_∞ in the absence of competition ($N = 0$). Note that Eq. (10) predicts impossibly high values of p as γN approaches 1.0, i.e. that there is no way to achieve the target growth rate for sufficiently high N . Note further that for γN less than about 0.2, Eq. (10) predicts approximately linear variation in p , i.e.

$$p \approx p_0(1 + \gamma N) \tag{12}$$

This was the form of dependence of p on N assumed by Walters and Korman, but their derivation ignored the effect of overall prey biomass B on V_0 and hence on γ (see Eqs. 9 and 11).

For the bout foraging case, we assume that mixing processes while fish are not foraging leads to an initial prey density $V_0 = vB$ at the start of each foraging bout, and that vulnerable prey density declines over the bout according to the simple exponential depletion rate $\frac{dV}{dt} = -\alpha^*NV$. Integrating this model over $t = 0$ to p leads immediately to a prediction of mean V over each bout:

$$V = V_0 \frac{(1 - e^{-\alpha^*Np})}{\alpha^*Np} \tag{13}$$

Performing the same substitution of V into Eq. (5) as for the derivation of Eq. (10), we again obtain a solution for p needed to achieve target growth rate:

$$p = \frac{-\ln(1 - p_0 \alpha^* N)}{\alpha^* N} \tag{14}$$

where p_0 is again the base foraging time needed as N approaches 0. This model again predicts a juvenile density for which p would have to be impossibly high (as $p_0 \alpha^* N$ approaches 1.0), and for $p_0 \alpha^* N$ less than about 0.2 can be approximated by the linear relationship

$$p \approx p_0(1 + \gamma N) \tag{15}$$

where $\gamma = p_0 \alpha^*$, i.e. similar to the continuous V renewal case but without the V loss rate parameter v' .

So both models for the effect of vulnerable prey density predict approximately linear increase in foraging time proportion p needed to achieve a target von Bertalanffy growth pattern, with higher densities N leading to sharp, nonlinear increase in required foraging times for high values of α^*N . Both cases predict a base required foraging time p_o that varies inversely with base food density V_o , which in turn is proportional to overall food biomass B , and increases in foraging time with N that are inversely proportional to the volume over which juveniles forage (since $\alpha^* = \alpha L^2/A$, where again A is the volume of the foraging arena). Both models depend strongly on the assumption that A is small enough compared to the overall area over which prey are produced to insure that overall prey biomass is not strongly affected (depleted) at higher juvenile abundances N . (In our experience with development of mass balance models that include juvenile life history stanzas (particularly Ecopath/Ecosim, which incorporates foraging arena theory), we have generally found that juvenile consumption of prey are almost always estimated to be small compared to overall prey biomasses, at least for juvenile fish preying on planktonic food organisms.)

Emergent Beverton–Holt recruitment relationship

If at least some component of juvenile mortality rate is due to predation risk while foraging, i.e. is proportional to relative foraging time p , and if juveniles do adjust p so as to try to achieve relatively stable growth rates, then we expect their natural mortality rate M to vary with density N , i.e. we expect M to vary as

$$M = M_o + Rp = M_o + Rp_o(1 + \gamma N) = (M_o + Rp_o) + (Rp_o\gamma)N \tag{16}$$

where R is predation risk per time foraging and M_o is a base non-predation mortality rate, if p varies (is varied by individual fish) according to Eq. (12) or (15). That is, we expect the basic relationship $M = M_1 + M_2N$ used to derive the Beverton–Holt stock recruitment model Eq. (1), with

$$M_1 = M_o + Rp_o \quad \text{and} \tag{17a}$$

$$M_2 = \frac{Rp_o^2\alpha^*}{v'} \quad \text{or} \quad M_2 = Rp_o^2\alpha^*. \tag{17b}$$

Note again from Eq. (11) that p_o is predicted to vary inversely with overall food abundance, i.e. $p_o = \frac{k}{B}$ where k depends on vulnerability exchange and growth parameters. This means we can explicitly predict the form of dependence of M_1 and M_2 on food abundance, as

$$M_1 = M_o + \frac{k'}{B} \quad \text{and} \quad M_2 = \frac{k''}{B^2} \tag{18}$$

where k' and k'' are aggregate parameters. We then predict that maximum density dependent survival (slope at the origin) of the stock-recruitment relationship (Eq. (1)) over any period T^* short enough for α^* and R not to change greatly should be given by

$$\beta_1 = e^{-M_1T^*} = e^{-(M_o + \frac{k'}{B})T^*}, \tag{19}$$

i.e. slope at the origin should vary inversely with prey abundance with highest possible survival set by non-predation mortality rate M_o at high prey abundances. The density dependence parameter $\beta_2 = \frac{M_2}{M_1}(1 - \beta_1)$ should also vary inversely with B since $\frac{M_2}{M_1} = \frac{k''}{M_o B^2 + k' B}$ which approaches $\frac{k''}{k' B}$ if most mortality is due to predation risk. Asymptotic maximum recruitment $(\frac{\beta_1}{\beta_2})$ should therefore be approximately proportional to the product of two factors, one increasing with B as $e^{-M_o - \frac{k'}{B}}$ and the other proportional to B . In short, increasing food availability should strongly affect both the slope and the asymptote of the Beverton–Holt relationship. The formulation error for V in Walters and Korman (1999) caused them to predict only the food effect on the first product factor affecting R_{max} , i.e. to greatly underestimate the possible effect of food abundance on maximum recruitment.

As noted in Walters and Korman (1999), Beverton and Holt (1957) showed that the overall recruitment relationship over a collection of successive time periods T^* , with different β parameters (risks, fish sizes, food densities) in each period, is still predicted to be of Beverton–Holt form if mortality rate is predicted to vary linearly with N within each time period. The overall (to recruitment age T) β_1 parameter is easy to calculate, but the overall β_2 is a complex function of the by-period β_s .

Numerical integration of $\frac{dN}{dt} = -M_1N - M_2N^2$ is required to determine the exact Beverton–Holt relationship predicted by the models above (and by

Eq. (26) below), since predation risk per time, R , is likely to depend on L , and since V (and hence both the M 's) is predicted to vary over time with γ which is proportional to L^2 . Example numerical solutions are shown in Fig. 1.

For empirical estimation of food effects for cases where food abundances B along with egg or early juvenile abundances E and recruitments $N(1)$ have been measured, we suggest avoiding the complex parameterization described above, by fitting a three parameter (c_1 – c_3) approximation of the full model:

$$N(T) = e^{-c_1 - \frac{c_2}{B}} \frac{N(0)}{1 + c_3 N(0)/B}, \quad (20)$$

where

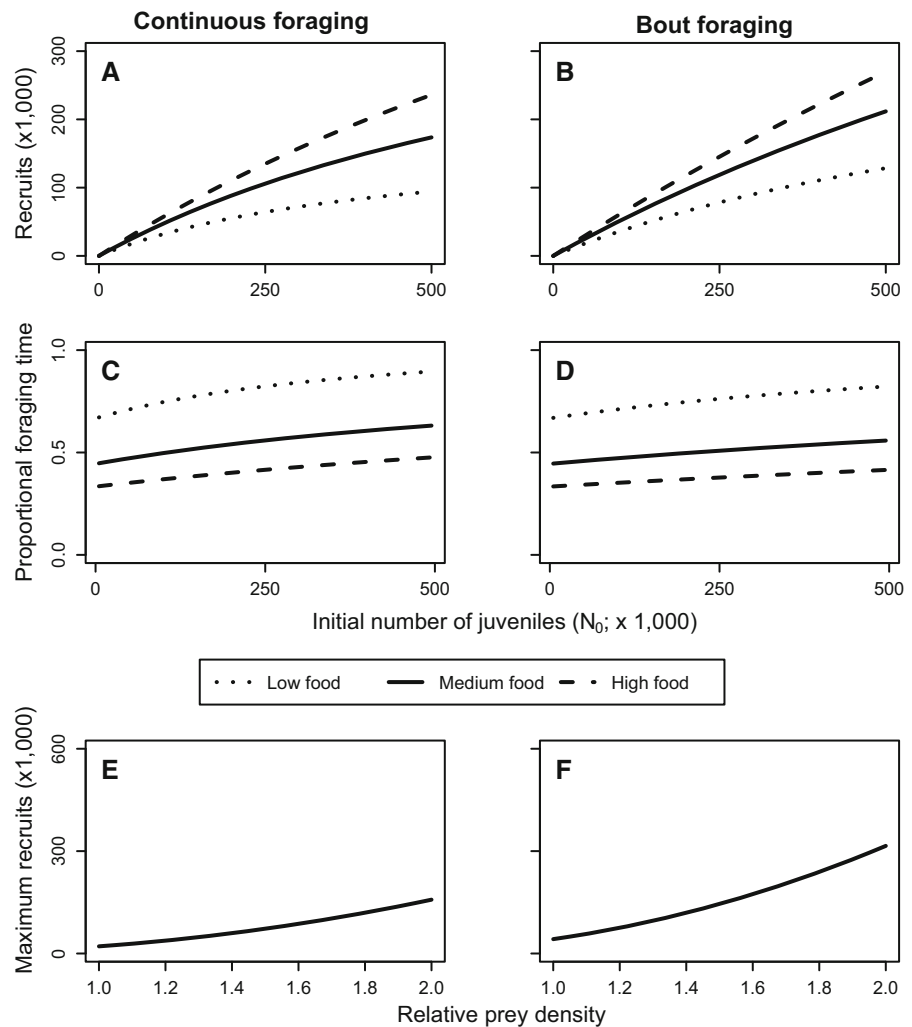
$$c_1 = M_0,$$

$$c_2 = k'$$

$$c_3 = \frac{k''}{k' + M_0 B} \left(1 - e^{-(M_0 + \frac{k''}{B})T^*} \right).$$

Note in this model that all three c parameters depend on how recruitment, spawning abundance, and food biomass are scaled, and cannot be directly interpreted in terms of the growth and foraging parameters above. Note also that there can be strong density-dependence in $N(0)$ even before juveniles compete, via effects of density on adult body size, fecundity, maturation, and egg quality (reviewed in Rose et al. 2001).

Fig. 1 Numerical solutions for the continuous foraging and bout foraging recruitment models. **a–d** show recruitment after 50 days (**a, b**) and relative foraging time (**c, d**) assuming low, medium and high food density under the continuous and bout foraging assumptions. **e, f** show maximum recruitment across a range of food densities under the two foraging assumptions



Alternative formulation based on fixed foraging time, linear growth, and size-dependent mortality rate

In this section we show that a recruitment relationship of Beverton–Holt form is still expected if (1) juvenile fish forage for the same proportion p_o of each day, due to constraints such as timing of food availability (e.g. vertical migration of food organisms) and high predation risk at some times of day; (2) length growth is linear as predicted by the model of Lester et al. (2004) and inversely related to density via effects as above of juvenile density on vulnerable prey density V ; and (3) mortality rate is inversely proportional to body length as suggested by Lorenzen (1996, 2000; see also Cushing 1975; Sogard 1997). That is, density-dependent growth combined with size-dependent mortality can generate a Beverton–Holt pattern, even without any assumptions about how juvenile fish might adjust their foraging behavior. Many studies suggest that this model may apply more often than the stable growth-variable p model. Lorenzen and Enberg (2002) demonstrated density-dependence in growth, at least for older fish in 9 of 16 populations that they compared. Post et al. (1999) found strong density dependence in growth of multiple older age-classes, but not first-year growth, in stocked ponds with predators present. Lobon-Cervia (2007) demonstrated density dependent growth in brown trout, and others (e.g. Ward et al. 2007; Vincenzi et al. 2012) argue this to be common for stream-dwelling salmonids. Lester et al. (2014) suggest similar responses in other species like walleye (*Stizostedion vitreum*). Vandenbos et al. (2006) found density dependent growth in fathead minnow (*Pimephales promelas*).

We note first that the linear growth model for juvenile fish proposed by Lester et al. (2004) can be derived from the bioenergetics model

$$\frac{dW}{dt} = e\alpha L^2 V p_o - mW^{2/3}, \tag{21}$$

i.e. the same food intake-conversion efficiency model as the von Bertalanffy, but routine metabolic rate varying as the $2/3$ power of body weight. Assuming $W = aL^3$, Eq. (21) results in the length growth rate

$$\frac{dL}{dt} = \frac{e\alpha V p_o}{3a} - \frac{m}{3a^{1/3}}. \tag{22}$$

For both of the foraging arena models (continuous and bout feeding), V is expected to vary inversely with juvenile N , approximately as predicted by Eq. (9), i.e. $V = \frac{V_o}{1+\gamma N}$ with γ representing L^2 -dependent changes in search rate, and also foraging arena area. Substituting this approximation for V into Eq. (22) results in the density-dependent growth model

$$\frac{dL}{dt} = g = \frac{q_o}{1 + \gamma N}, \tag{23}$$

where maximum consumption rate q_o at low N is equal to the prediction from Eq. (22) with $V = V_o$. For any period t over which $\frac{dL}{dt} = g$, length varies as $L = L_o + gt$, or simply $L = gt$ if we assume $L_o = 0$ at the start of the period.

The Lorenzen mortality model (Lorenzen 1996, 2000) implies that $M = \frac{M_{ref}}{L}$, where M_{ref} is mortality rate at reference length $L = 1$. Assuming this rate relationship and $L_o = 0$, juvenile abundance is predicted to decline as

$$\frac{dN}{dt} = -MN = -\left(\frac{M_{ref}}{L}\right)N = -\frac{M_{ref}}{gt}N. \tag{24}$$

Then assuming that g varies with N as predicted by Eq. (23), predicted $\frac{dN}{dt}$ varies with N as

$$\begin{aligned} \frac{dN}{dt} &= -M_{ref} \left(\frac{(1 + \gamma N)}{q_o t}\right)N \\ &= -M_{ref} \left(\frac{1}{q_o t}\right)N - \left(\frac{M_{ref}}{q_o t}\right)\gamma N^2. \end{aligned} \tag{25}$$

That is, $\frac{dN}{dt}$ is predicted to vary linearly with N as assumed in the Beverton–Holt derivation, with base rate parameter $M_1 = M_{ref} \left(\frac{1}{q_o t}\right)$ and density-dependence parameter $M_2 = \frac{M_{ref}\gamma}{q_o t}$. Note in this model that q_o depends on overall abundance B of food organisms, since q_o is proportional to V_o , which in turn should be proportional to B . Therefore, in the face of food variation across years, a more accurate depiction of Eq. (25) would be

$$\frac{dN}{dt} = -\frac{M_{ref}}{B(q_o^* t)}N - \frac{M_{ref}\gamma}{B(q_o^* t)}N^2 = -\left(\frac{k'}{B}\right)N - \frac{k''}{B}N^2, \tag{26}$$

where q_o^* is the maximum consumption rate per-food unit (B) at low N ; k' and k'' are aggregate parameters.

Equations (25) and (26) predict somewhat “weaker” effects of food competition and food abundance on recruitment than models with foraging time adjustment, for two reasons. First, γ is proportional to L^2 , so slower growth at higher densities should lead to lower values of k'' (smaller fish search smaller volumes hence have lower per-capita impact on vulnerable prey density V). Second, the ratio component of the Beverton–Holt β_2 parameter is predicted to be independent of food density:

$$\beta_2 = \frac{k''}{k'}. \quad (27)$$

This implies a linear rather than accelerating relationship between maximum (asymptotic) recruitment and food abundance B (Fig. 2c). Note some obvious limitations of this model in Fig. 2. First is that low competitor and/or high prey densities can lead to unrealistically high first-year growth (Fig. 2b). This obviously occurs because juveniles cannot reduce their foraging time (p) in the case of abundant resources per individual, a situation relatively rare in most natural systems. Second, high competitor and/or low prey densities will lead to the situation where growth is impossible and lead to all fish dying prior to the age-at-recruitment (Fig. 2a). This leads to a truncated Beverton–Holt function where the “asymptote” is actually the spawner density at which no survival occurs (i.e. the recruitment function will not show saturating recruitment because negative growth occurs at high densities). This suggests that while density-dependent growth and survival may co-occur in the pre-recruit stage in some species, it may only occur in certain conditions and these populations must begin adjusting foraging time to persist in conditions of high spawners and/or low prey densities.

Can variation in available food affect recruitment in real populations?

We fit the three models listed above, namely: (1) full model with variable foraging time and target growth rate (Eq. 18); reduced target growth rate model (Eq. 20); and constant foraging time model (Eq. 26), to various published datasets to evaluate whether these models might explain recruitment variation more parsimoniously than the standard Beverton–Holt model. Each data set was transformed by dividing by

spawners and taking the natural log of both recruits per spawner and spawners. Models were then fit to data assuming transformed data were normally distributed (Hilborn and Walters 1992). All estimated parameters were estimated with uniform priors, except precision, which was estimated with a gamma prior with shape and rate parameters each set to 0.001. Each model was fit to each transformed data set in JAGS (Just Another Gibbs Sampler; Plummer 2003), implemented in R (R Core Development Team 2016). Models were run for 100,000 iterations after a burn-in of 150,000 iterations and posteriors were thinned to 1000 posterior samples. Convergence was evaluated using the Gelman–Rubin diagnostic (Gelman et al. 2004) and by visual examination of posterior samples.

The first dataset was of freshwater kokanee salmon (*Oncorhynchus nerka*) in Kootenay Lake Reservoir, British Columbia (Kurota et al. 2016). This kokanee population is intensively monitored, as it is the major prey item of highly valued large-bodied Gerrard rainbow trout (*O. mykiss*), as well as providing a directed fishery. Kokanee densities have been monitored continuously from 1992 to 2015 using a combination of hydroacoustic assessments and trawling, which provides estimates of age-1 recruits and age-3 spawners. Wild recruitment of Kootenay Lake kokanee is enhanced through use of a spawning channel as well as nutrient restoration in the reservoir. The nutrient restoration program promotes growth of zooplankton, and particularly cladocerans, which are the primary diet of kokanee. Zooplankton densities are monitored at up to eight stations multiple times annually as part of the nutrient restoration program. Zooplankton densities in the reservoir increased dramatically following the initiation of the nutrient restoration program in 1992 and subsequent variation in N:P ratios and amounts to maximize benefit to kokanee and trout.

The kokanee recruitment time-series from Kootenay Lake were found to be best explained by the reduced model assuming a target growth rate based on the Bayesian Information Criterion (Table 1; Schwarz 1978). However, the Beverton–Holt model produced a higher Bayesian R^2 (ratio of predicted to predicted plus error variance: Gelman et al. 2017). This population has experienced relatively high variation in spawner densities, yet recruitment has been relatively stable because of the stabilizing effect of food (Fig. 3 left panels). These external pressures on juvenile

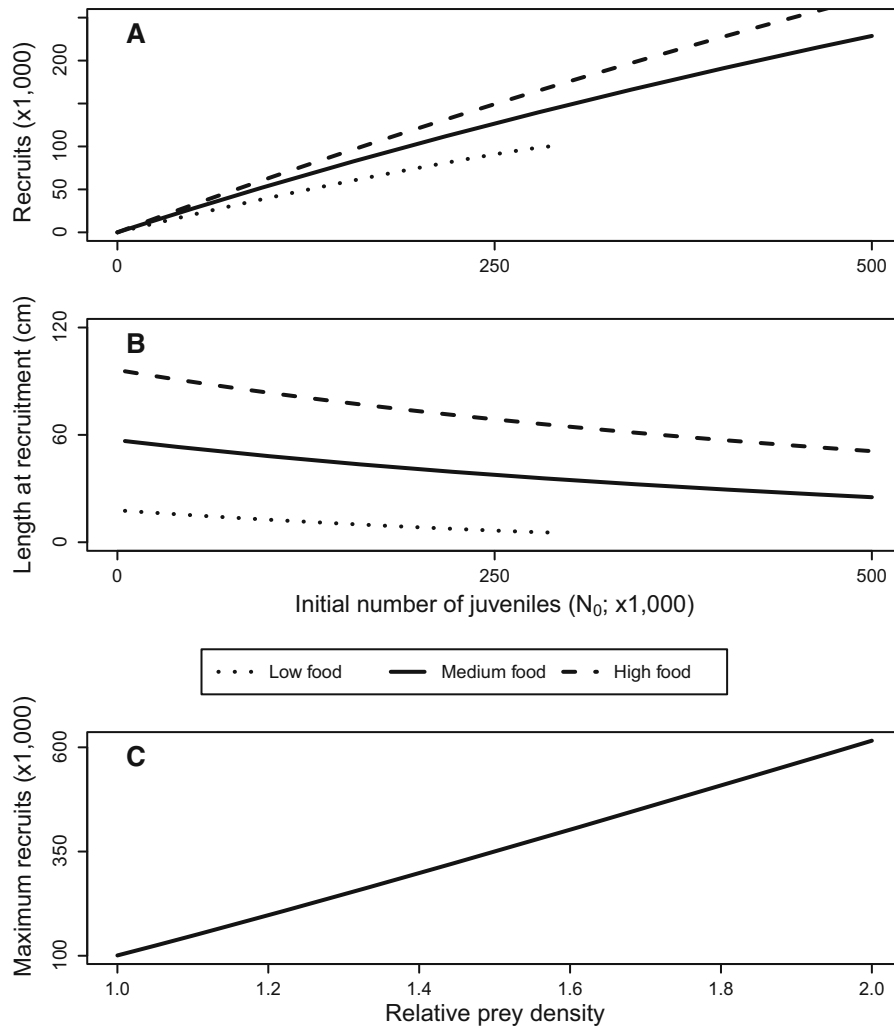


Fig. 2 Numerical solution for the fixed foraging time model. **a** shows recruitment after 50 days, truncated at initial juvenile competitor densities that result in negative growth and **b** shows

length at recruitment under this model. **c** shows how maximum recruitment varies across a range of food densities

recruitment, especially linked to food availability, appear to influence juvenile recruitment, resulting in a better fit for the food-dependent Beverton–Holt model than the standard model.

The second dataset was of kokanee salmon in Wahleach Reservoir, British Columbia. This kokanee population is intensively monitored as a basis for a nutrient restoration program and a targeted fishery (Perrin et al. 2006). Kokanee spawners have been monitored using redd surveys in each of the spawning streams sporadically since 1969, and continuously since 2003; age-1 densities have been monitored from 2009 to 2015 using hydroacoustic assessment and

trawling. Zooplankton densities, of which the majority of each sample is cladocerans, have been monitored each year since 1993 (except 2002). We use the continuous dataset from 2009 to 2015 in this analysis.

Recruitment patterns for kokanee in Wahleach Reservoir were best explained by the standard Beverton–Holt recruitment function (Table 1), which assumes no correlation between variation in food availability and juvenile survival. This should not be surprising because there is very little variation in food availability over the time series evaluated, with only one high food year and a correspondingly high recruitment that same year (Fig. 3 centre left panels).

Table 1 Relative model performance of the full target growth rate model, the reduced target growth rate model, the constant foraging time model and the standard Beverton–Holt recruitment function

Dataset	Years of data	Model	Bayesian R^2	BIC	Δ BIC
Kootenay Lake kokanee	1992–2015	Full target growth	0.55	11.9	2.2
		Reduced target growth	0.59	9.8	0.0
		Constant foraging time	0.59	84.8	75.0
		Beverton–Holt	0.65	37.8	28.1
Wahleach Reservoir kokanee	2009–2015	Full target growth	0.43	18.7	15.1
		Reduced target growth	0.53	15.8	12.2
		Constant foraging time	0.56	14.9	11.3
		Beverton–Holt	0.80	3.6	0.0
Escanaba Lake muskellunge	1987–2006	Full target growth	0.26	79.4	0.2
		Reduced target growth	0.37	81.5	2.4
		Constant foraging time	0.56	89.1	9.9
		Beverton–Holt	0.12	79.2	0.0
Delta smelt	1995–2006	Full target growth	0.09	29.8	2.9
		Reduced target growth	0.04	30.7	3.9
		Constant foraging time	0.13	26.8	0.0
		Beverton–Holt	0.27	35.3	8.4

Model performance is evaluated using the Deviance Information Criterion, which balances the effective number of parameters (pD) and model deviance

Bold values indicate the best approximating model for each dataset as determined using calculated BIC values

The nutrient restoration program began long before recruitment was monitored. Despite similarities with kokanee in Kootenay Lake, food is not a strong driver in recruitment variability in this system.

The third dataset was of muskellunge (*Esox musquinongy*) in Escanaba Lake, Wisconsin (data from (Eslinger et al. 2010)). This population is the focus of an intensively monitored recreational fishery (Kempinger and Carline 1977). Age-0 muskellunge were captured by shoreline electrofishing annually from 1987 to 2006 to create a recruitment index; adults were estimated annually using mark recapture of fish during spring spawning (Eslinger et al. 2010). Bluntnose minnow (*Pimephales notatus*) and age-0 densities white suckers (primary food for age-0 muskellunge in Escanaba Lake; Eslinger et al. 2010) were estimated annually at four randomly located shoreline stations using multiple perpendicular sweeps of a seine net. These data were collected as an exploratory analysis of various biological and environmental impacts on recruitment (Eslinger et al. 2010).

Recruitment variability in Escanaba Lake muskellunge was found to be equally explained by the full

model assuming juvenile fish forage to achieve a target size by the age-at-recruitment as well as the standard Beverton–Holt model (Table 1; Fig. 3 centre right panels). Eslinger et al. (2010) fit a series of Ricker-type models with recruitment variation correlated with a variety of environmental and biotic factors. They found that mean age of spawners and availability of bluntnose minnow were the two variables that explained the most variability in their dataset. Indeed, bluntnose minnow varied between 10 and more than 20,000 fish/km shoreline over the course of their study. This large variation in food combined with the importance of bluntnose minnow as a food source for juvenile muskellunge, helps explain some of the variation in recruitment, but not all, which explains why both the food-dependent and standard Beverton–Holt model was selected. It is interesting to note that the two selected models had the lowest Bayesian R^2 .

The final dataset was of delta smelt (*Hypomesus transpacificus*), endemic to the San Francisco estuary, USA. Delta smelt almost exclusively live for one year and one spawning season (Maunder and Deriso 2011) and are well-monitored given multiple threats to the population and their listing as threatened under the US

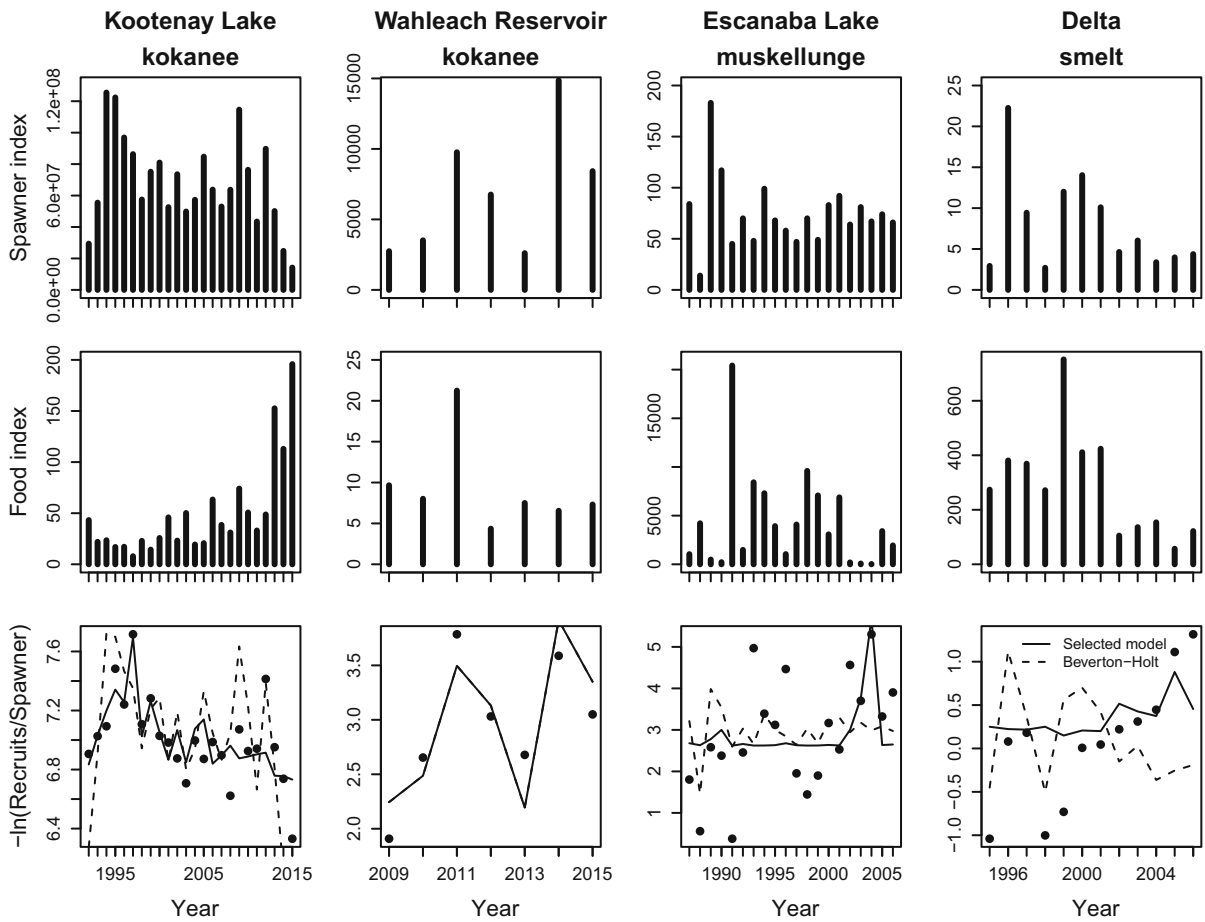


Fig. 3 Spawner index, food index and mortality rate from eggs to recruitment [measured as $-\ln(\text{Recruits}/\text{Spawner})$] for the four fitted datasets. Points on bottom panels are observations, solid

lines are the BIC-selected models and dashed lines are the standard Beverton–Holt model

and California Endangered Species Acts in 1993 (Maunder and Deriso 2011). Multiple life-stages are monitored; we chose to focus on the larvae-juvenile stage. Larvae survival is believed to be influenced when there is a shortfall in available food; this is measured as the minimum *eurytemora* and *pseudodiaptomus* density from April to June.

Recruitment variability in delta smelt was best explained by the full model assuming juvenile fish forage to achieve a target size and by the model assuming fish forage for a fixed time (Table 1; Fig. 3 right panels). In their study, Maunder and Deriso (2011) found survival between life stages to be influenced by many environmental and biological factors, but *eurytemora* and *pseudodiaptomus* densities were consistently included in the first stage of their step-wise analysis, suggesting prey densities as

important drivers in population regulation. However, our inability to distinguish between the two different foraging mechanisms is unexpected and points to a need for more information about foraging tactics for the species.

Foraging time predictions for fitness models that include the possibility of reduction in growth rates at higher densities

We have shown above that approximately linear variation in mortality rate with juvenile density is expected in the two extreme cases when juvenile fish either adjust foraging time proportion p to maintain stable growth or maintain constant foraging time proportion in the face of size dependent mortality rate.

In this section we show that linear variation in mortality rate is also expected when juveniles exhibit changes in p and growth rate consistent with foraging time adjustments that would maximize simple evolutionary fitness measures representing the trade-off between benefits of larger size and survival costs of spending more time foraging (the classic risk-reward trade-off examined in a many studies e.g. Werner and Gilliam 1984; McNamara and Houston 1987; Abrams 1994a, 1994b; Tupper and Boutilier 1995; Biro et al. 2003; Creel and Christianson 2008; Fiksen and Jorgensen 2011; Jorgensen et al. 2016).

Consider a cohort of juvenile fish that begins some short time period Δ of its life at initial length L_0 and density N , and grow at the linear rate predicted by the Lester et al. (2004) growth model (eq. 22). Assume that the fitness f of these fish is proportional to the weight W they achieve by the end of the period, times their probability of surviving the period. Both W and survival rate depend on p :

$$f = We^{-\Delta(M_0+Rp)} = a[L_0 + \Delta(g_1p - g_2)]^3 e^{-\Delta(M_0+Rp)} \tag{28}$$

where $g_1 = \frac{e2V}{3a}$ and $g_2 = \frac{m}{3a^{1/3}}$. Differentiating f with respect to p and solving for the p that maximizes f , we immediately obtain the prediction that $L_{t+\Delta}$ at the end of the period should vary as

$$L_{t+\Delta} = \frac{3g_1}{R}, \tag{29}$$

i.e. growth should vary positively with g_1 (which depends on food density V) and negatively with predation risk (the classic gain/risk ratio prediction about how food and risk should affect growth). The p that maximizes f should vary as

$$p_{\max f} = \frac{3}{R} + \frac{(g_2\Delta - L_0)}{g_1}. \tag{30}$$

That is, foraging time should vary inversely with predation risk R per time, positively with metabolic loss rate g_2 , and negatively with initial size L_0 . Finally, noting that g_1 is proportional to food density V and assuming that V varies inversely with N as in the previous models, we obtain

$$p_{\max f} = \frac{3}{R} + \frac{(g_2\Delta - L_0)(1 + \gamma N)}{g_{1_0}} \tag{31}$$

where g_{1_0} is the value of g_1 at $V = V_0$ (i.e. when density $N = 0$). Note that this model predicts positive, linear change in foraging time (and hence in instantaneous predation mortality rate Rp) for small fish, i.e. for fish with small initial length L_0 . For larger fish (larger L_0) subject to lower predation risk R per time foraging, Eq. (31) predicts increased foraging times (due to higher values of the $\frac{3}{R}$ term) and either no response or negative response to increasing density N .

If we assume fitness to be proportional to weight growth rate $\frac{dW}{dt}$ rather than W in Eq. 28, while noting that $\frac{dW}{dt} = (\frac{dW}{dL})(\frac{dL}{dt})$ and ignoring changes in $\frac{dW}{dL}$ over the short time Δ , we obtain basically the same prediction of $p_{\max f}$ as Eq. (31). But the term $\frac{3}{R}$ is replaced by just $\frac{1}{R}$, and L_0 disappears from the second term. $p_{\max f}$ is still predicted to vary linearly with N and to be lower at all N when overall food abundance as measured by V_0 is higher, and the length growth over the interval is predicted to be $\frac{g_1\Delta}{R}$.

The simple fitness functions above do not account for the notion that fitness may be best measured by the product of size at recruitment and overall probability of surviving to reach that size, and that maximizing fitness is likely to involve changes in foraging time p as the juvenile fish grow (i.e. it is a dynamic programming problem sensu Mangel and Clark (1988) to determine the sequence $p(t)$ that maximizes overall fitness as measured by ultimate size and survival rate). We can approximate the time dependent $p(t)$ optimal foraging time solution by directly predicting effects of choices $p(j)$ for a sequence $j = 1 \dots n$ short time steps (e.g. months) over the recruitment period using nonlinear optimization. For each step, we need to predict (1) mean food density $V(j)$ for the period as a function of number of fish $N(j)$ entering the period, fish length $L(j)$ at the start of the period, and $p(j)$ using for example Eq. (14); (2) growth for the period using $V(j)$, $L(j)$, and a bioenergetics model like Eq. (4) for von Bertalanffy growth; and (3) survival rate over the period as a function of $p(j)$ and $L(j)$, using a size and foraging time dependent mortality rate model like the Lorenzen equation (Eq. 25). We can then find the $p(j)$ sequence that maximizes the net fitness measure

$$f = [aL(n+1)^3 - W_0] \frac{N(n+1)}{N(1)}, \tag{32}$$

for average sized fish without resorting to use of the dynamic programming recursion equation, simply by having a function optimizer seek the $p(j)$ “open loop” sequence that maximizes f . Here, $\frac{N(n+1)}{N(1)}$ is overall survival rate, and the parameter W_0 represents a minimum body weight needed to successfully complete later life history processes (overwinter survival, mate selection and egg production, ontogenetic migration to other habitats). An example calculation like this is shown for a salmon or trout-like species in Fig. 4. At lower initial densities $N(1)$, the $p(j)$ sequence that maximizes Eq. (32) shows increasing foraging time as juveniles grow and hence have decreased predation risk, with possibly some decrease in $p(j)$ for larger fish if these fish reach digestive rate limits on consumption. At higher densities, the optimum $p(j)$ for the first few time steps (for smaller fish) increase dramatically with increasing $N(1)$, implying strong density dependence in mortality rate particularly for the first few months of the recruitment process. The emergent overall stock recruitment relationship (between $N(n + 1)$ and $N(1)$) is obviously Beverton–Holt in form (Fig. 5), and is highly sensitive to food availability as measured by V_0 (food density at

low N) parameter of Eq. (14). Interestingly, there is predicted to be less variation in body length at recruitment than from the simpler fitness models, and body length is predicted to increase almost linearly (as in the Lester model); both of these effects are associated with compensatory increases in foraging time as the juveniles grow.

As in the simpler behavior models, the key to predicting increase in foraging time (and predation mortality rate) with N in the fitness models is the assumption that food density varies inversely with N , approximately as $\frac{V_0}{1+\gamma N}$. This assumption in turn depends as noted above on the assumption that spatially and/or temporally restricted foraging results in localized depletion of food density (Walters and Juanes 1993).

Predicted relationship between recruitment compensation and vulnerable food density

Observed stock recruitment relationships can be characterized in terms of the unfished recruitment rate and the recruitment compensation ratio (CR) defined as the ratio of survival to recruitment at low densities to the survival to recruitment at the unfished stock size (Walters and Martell 2004). It turns out that the Beverton–Holt derivations predict a simple relationship between the observed compensation ratio and the likely depression in vulnerable food density for juveniles (V) at the unfished stock size compared to V_0 , the food density at very low stock size.

The total mortality rate M of juveniles from egg to recruitment can be calculated from the survival rate (recruits/eggs) as $M = -\ln(\text{survival rate})$. The compensation ratio can then be expressed as change in this M , as

$$\ln(CR) = M_0 - M_{\min} \tag{33}$$

where M_0 is the egg-recruitment total M for the unfished stock and M_{\min} is the minimum M at low stock size. Using Eq. (16) above for variation in M with initial juvenile number, and assuming relatively stable V and p over the pre-recruit period, average relative food density $\frac{V}{V_0}$ is predicted to vary with measured CR approximately as

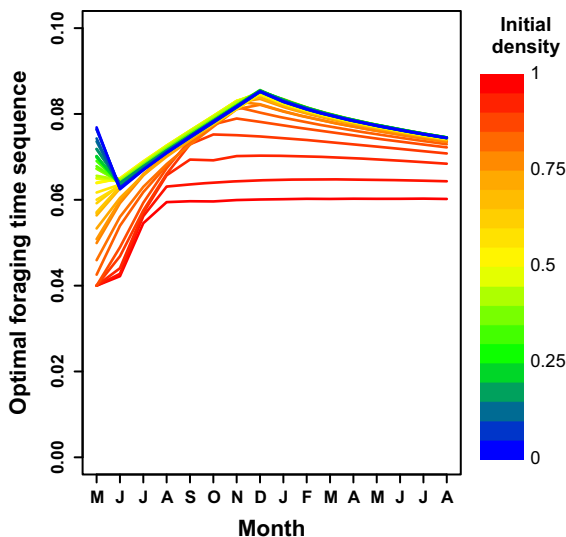
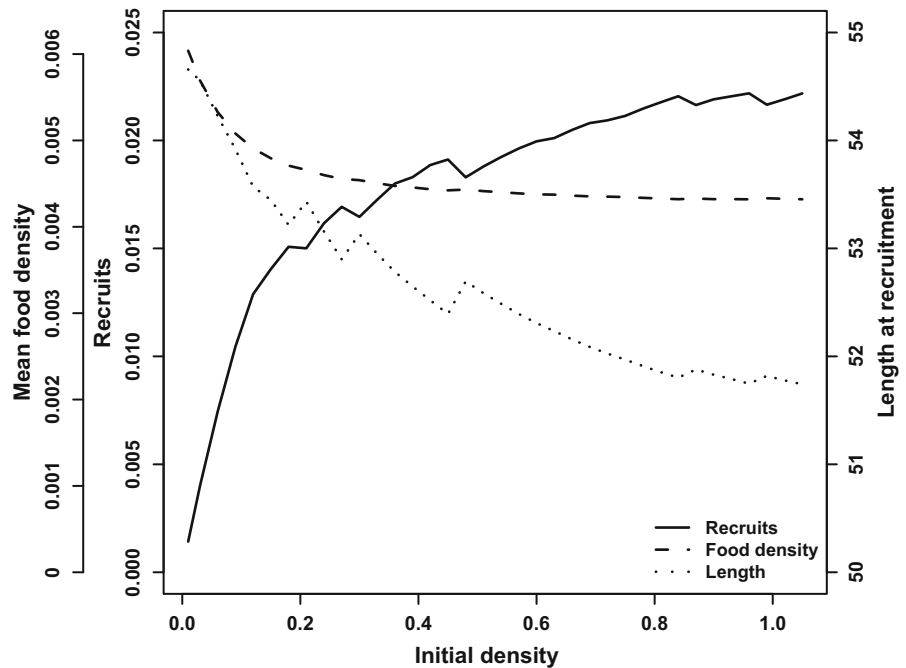


Fig. 4 Optimal foraging time over a theoretical recruitment period from May through August the following year under different initial densities. Each sequence is found by optimizing the sequence of monthly foraging times that maximizes fitness given initial density and food abundance. Fitness is described as the product of size at recruitment and overall survival probability to age-at-recruitment

Fig. 5 Recruitment numbers, mean available food density and length at recruitment calculated based on each foraging time sequence in Fig. 4



$$\frac{V}{V_0} \approx \frac{Rp_0}{\ln(CR) + Rp_0} = \frac{M_{\min}}{\ln(CR) + M_{\min}}. \quad (34)$$

Validity of this approximation was tested by comparing its prediction to alternative assumed CR values (initial juvenile N values) for the full fitness maximization model above (Eq. 32), and the approximation works well despite the complex variation in foraging times and prey densities V over the juvenile life predicted by that model.

For highly fecund species like cod, M_{\min} is expected to be in the range 10–15. For such species, estimated CR are typically in the range 10–20 [steepness h averaging near 0.8, see e.g. Goodwin et al. (2006)] implying $\ln(CR) \approx 2.3$ to 3.0. This means that for such species, predicted impact on available food density $\frac{V}{V_0}$ of high, unfished juvenile abundances need only be about 20–30% ($\frac{V}{V_0} = 0.7$ to 0.8). Put more vividly, relatively small changes in food density (that we would likely be unable to measure with typical plankton or benthic biomass sampling methods) can result in large enough changes in cumulative foraging time and predation risk to imply quite steep (high CR) stock-recruitment relationships.

Discussion

Empirical evidence about variation in recruitment with food availability has come mainly from spatial comparisons of recruitment rates in areas of varying food density and from various statistical analyses of time series data that have included food abundance in various ways in functional and statistical recruitment models. Early spatial comparisons (e.g. Hixon and Carr 1997) failed to find strong food effects. In contrast, evidence for strong, perhaps nonlinear increases in recruitment with food supply has been found in some recruitment modeling exercises. Okamoto et al. (2012, 2016) estimate strong, nearly proportional effects of food density on black surf perch (*Embiotoca jacksoni*). Stige et al. (2011) estimate strong, nearly linear relationship for cod (*Gadus morhua*). Maunder and Deriso (2011) found food effects on delta smelt (*Hypomesus transpacificus*). Le Pape and Bonhommeau (2015) found highly variable conclusions about food effects in the many (67) flatfish studies that they reviewed, and warned that we only see the survivors in growth studies.

A serious difficulty in empirical studies is to determine just what constitutes “food”. Small fish feeding on zooplankton typically select only particular sizes and species from the zooplankton community,

determined by juvenile size and prey characteristics such as vertical migration (van Poorten and Walters 2015). Small fish feeding on benthic organisms most often take these organisms when the organisms are drifting (in streams) or dispersing (moving over the bottom). This means that “*B*” is poorly defined in many cases. Further, we know of no long term studies where vulnerable food biomass *V* has been measured in the highly localized foraging areas and times where juveniles forage, while the juveniles are actually foraging.

An interesting variation on the basic models described above can arise in situations where both predation risk per time foraging [*R* in Eq. (16), (17)] and food are variable over time, in particular when a substantial component of *R* is due to cannibalism by adult or older juvenile fish. In this case, the exponent in prediction of β_1 has a negative term proportional to the ratio of adult abundance to food abundance, and β_2 also has a component proportional to this ratio. The basic effect of this “ratio dependence” can be to shift the stock recruitment relationship from being Beverton–Holt in form at higher food biomass, to having Ricker model form (dome-shaped) at lower food abundances. Olsen et al. (2010) and Stige et al. (2015) show a pattern like this for arctic cod recruitment changes, as do Okamoto et al. (2012, 2016) for black surfperch.

Another variation on the models can be used to predict inter-cohort effects of competition between juvenile fish of different ages, as have been observed for age-classes that share the same foraging arenas (e.g. Nordwall et al. 2001; Samhoury et al. 2009; Marjomaki et al. 2014; Ricard et al. 2016). If abundance of older cohorts affects food density and/or cause predation risk directly (component of *R*), those abundances can be used in prediction of both the β_1 and β_2 parameters. Such patterns could help better explain cyclic recruitment in some populations (Borgstem et al. 1993).

Yet another variation on the basic Beverton–Holt relationship can occur in situations where the biomass of food available to older fish is correlated with food biomass for juveniles, e.g. though variation in overall ecosystem productivity or food available to the prey of larger fish. In this case, there can be strong density dependence in growth and fecundity of larger fish, sufficient in some cases (e.g. Lorenzen and Enberg 2002; Lorenzen 2008; Lorenzen et al. 2016) to result

in population regulation even if there is no density dependence in juvenile survival rates. Walters et al. (2016) note that an overall recruitment relationship of Beverton–Holt form still results if adult fecundity (or proportion of fish spawning) is a type II (disc equation) function of food biomass, and if survival of initial juvenile numbers (fecundity \times adult abundance) then follows a Beverton–Holt relationship. The parameters of the combined adult foraging/juvenile foraging Beverton–Holt model are expected to be strongly related to overall food biomass.

Long term changes in stock-recruitment parameters can be estimated by examining changes in a_1, a_2 of the log recruits per spawner Ricker approximation $\ln\left(\frac{R}{S}\right) = a_1 - a_2 S$. Britten et al. (2016) suggest that changes in the carrying capacity or density dependence parameter a_2 are more common than changes in a_1 . But the models above predict changes in both parameters with changes in food abundance *B*. This is because we model effects of juvenile density *N* on food density *V* with the basic form $V = \frac{vB}{1+\gamma N}$, so that V_0 , base food density when $N = 0$, is assumed proportional to total food biomass *B*. But it is not obvious that food density V_0 should in fact increase with *B*; it is quite possible that food organisms show density dependent dispersal or range expansion, such that V_0 remains constant but the volume *A* over which juveniles can forage successfully increases instead at higher *B*. The γ parameter is assumed to be inversely proportional to foraging volume *A*, so increases in that volume with *B* could lead to changes in the stock-recruitment a_2 parameter (approximately proportional to γ) only, rather than in both a_1 and a_2 .

As indicated by the basic derivations and by the variations discussed above, a remarkable variety of biological circumstances are predicted to lead to recruitment relationships of Beverton–Holt form, all with high sensitivity to changes in food supplies and predation risks. But we should not be comforted by this observation of robustness, since in most cases it means that we should expect both high variability around the long-term mean relationship and in often severe non-stationarity in the relationship, because neither food supplies nor predation risk are likely to show simple random variation from year to year.

However, we cannot argue that the models presented in this paper apply to all species or stocks. There are at least three mechanisms that could cause

the predictions to fail. First, in some cases vulnerability exchange rates (mixing) of food in and out of foraging arenas may be very high, such that the predicted effect of juvenile density on food density V is trivial or non-existent and juveniles just see the average overall food abundance B (or a well-mixed but complex size-dependent food field as argued by Rossberg et al. 2013). Second, other factors such as a requirement to defend resting/shelter sites for reef fishes or variation in metabolic rates, may drive density-dependent energetic costs and predation risks so as to mask any food density effects (Tupper and Juanes 2017). Third, in some cases cannibalism risk (R) may be so high as to prevent juvenile densities from ever being high enough to drive down local food densities.

How should we use the findings of this study? In fitting four recruitment models to four different datasets, we found each model was chosen for a different dataset. However, this apparent contradiction

suggests a path forward (Fig. 6). First and foremost should be an examination of motives and objectives: if explaining how variation in food affects recruitment predictions is not important for the questions of interest, the models presented here are unnecessary. Obviously if there is no data on variation in food density over time, it is necessary to use a standard recruitment function such as the Beverton–Holt or Ricker model (Hilborn and Walters 1992). Likewise, if there are data on food density collected but they do not vary greatly, it is unlikely that variation in food drives variation in juvenile survival and ultimately, recruitment, as evidenced from the Wahleach Reservoir example presented here. In situations where knowledge of feeding biology suggests limited foraging per day, as suggested by complex spatial–temporal behaviour of prey organisms or predators, it makes sense to use the constant foraging time model (Eq. 26). Finally, if there is high variation in food, but no constraints on foraging time, the full (Eq. 18) or

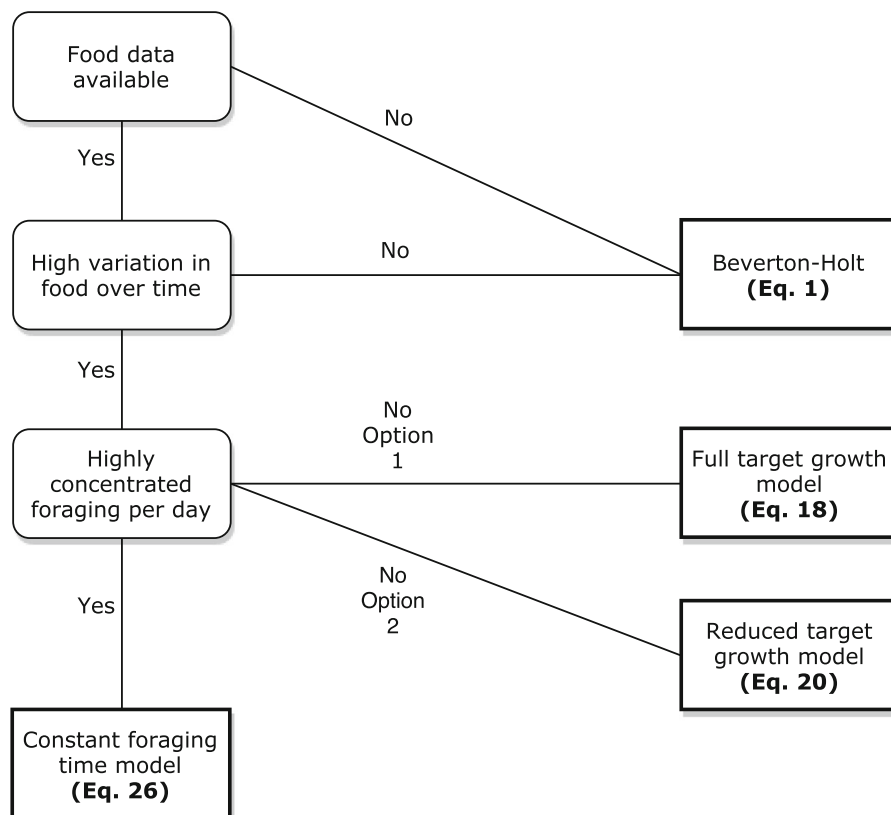


Fig. 6 Flow diagram suggesting how to analyse data in cases where variation in food density is perceived to influence recruitment variation

reduced growth (Eq. 20) models should be used to determine if these models provide useful predictions of recruitment. We have presented a variety of models that account for a variety of behaviours. It is our hope that these models will encourage researchers to think carefully about their objectives and the ecology of the species being studied. Through this understanding, the models presented here should provide a useful mechanism to incorporate available data on prey variation, thereby improving predictions of recruitment.

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