

Linking recruitment to trophic factors: revisiting the Beverton–Holt recruitment model from a life history and multispecies perspective

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Abstract

The Beverton–Holt recruitment model can be derived from arguments about evolution of life history traits related to foraging and predation risk, along with spatially localized and temporarily competitive relationships in the habitats where juvenile fish forage and face predation risk while foraging. This derivation explicitly represents two key biotic factors, food supply (I) and predator abundance (R), which appear as a risk ratio (R/I) that facilitates modelling of changes in trophic circumstances and analysis of historical data. The same general recruitment relationship is expected whether the juvenile life history is simple or involves a complex sequence of stanzas; in the complex case, the Beverton–Holt parameters represent weighted averages or integrals of risk ratios over the stanzas. The relationship should also apply in settings where there is complex, mesoscale variation in habitat and predation risk, provided that animals sense this variation and move about so as to achieve similar survival at all mesoscale rearing sites. The model predicts that changes in food and predation risk can be amplified violently in settings where juvenile survival rate is low, producing large changes in recruitment rates over time.

Key words: dispersal, environmental regimes, microhabitat, predation, recruitment models

Introduction

There are two great questions in the study of fish recruitment: (1) what causes high variation, and (2) why is recruitment most often nearly independent of egg or larval production over wide ranges of parental abundance? A simplistic approach to these questions has been to assume that recruitment is 'limited' not by egg production but by environmental factors, and that variation is driven by changes in such factors over time. Two main criticisms of this approach have been that the term limitation is dangerously vague, and that correlations between recruitment and environmental indices are notoriously prone to breaking down soon after they are published (Drinkwater and Myers, 1987; Walters and Collie, 1988; Walters and Juanes, 1993). If average recruitment does not change with parental abundance, there must be powerful compensatory changes in larval or juvenile survival rates to result in similar recruitments when egg production is reduced, and we should not be surprised if the processes causing large compensatory changes are also somehow responsible for causing the variability in recruitment. Perhaps more important, now that we are starting to acquire longer time series of recruitment estimates, we are starting to see more examples of strong, persistent changes in survival rates that cannot be adequately explained on the basis of any obvious changes in environmental regimes. For example, both marine survival rates of coho salmon (*Oncorhynchus kisutch*) in southern British Columbia (Coronado and Hilborn, 1997) and recruitment per spawner in some Atlantic salmon (*Salmo salar*) stocks from New Brunswick have shown essentially linear declining trends since the mid to late 1980s (Friedland et al., 1993). In these cases, there have been substantial changes in oceanographic indices like temperature, but not in the form of simple trends that correspond well with the survival trends (Beamish et al., 1997). Abrupt changes in physical regimes are common, but survival patterns often do not show corresponding abrupt shifts or persistent change following shifts. At least in such cases, we might be wiser to seek explanations in biotic factors such as predator abundance and cannibalism, the dynamics of which are likely to involve progressive change, and hence trends in impact (Walters and Juanes, 1993).

Three alternative explanations are possible for the general failure to relate environmental factors clearly to persistent changes in survival rates: (1) other abiotic factors may have caused the persistent changes in

survival rates; (2) biotic factors may have caused the persistent changes; or (3) a combination of abiotic and biotic factors may be responsible for the changes. In this paper, we develop a model that assumes that biotic factors, namely predation and food supply, influenced by environmental factors, are the dominant causes of persistent survival rate changes. This argument is not new; for example Friedland et al. (1993) concluded that a significant proportion of variation in North American Atlantic salmon recruitment is driven by changes in marine winter habitat area affecting both intraspecific competition for space and food resources, and predation of post-smolts.

The Beverton and Holt (1957) recruitment model has provided a useful description of cases in which recruitment is nearly independent of parental stock size over a wide range of egg depositions. It was derived by assuming that juvenile mortality rate varies linearly with juvenile density. We have not taken this assumption very seriously, preferring to view the time integral equation for final recruitment mainly as an empirical model with desirable shape properties (recruitment falling toward zero at zero stock size, but independent of stock size for higher stock sizes) for harvest policy analysis. Hints that there may in fact be good reasons for mortality rates to vary linearly with juvenile densities have arisen from evolutionary arguments about how juvenile fish should respond to food competition and predation risk (Walters and Juanes, 1993). Such arguments have not led specifically to the Beverton–Holt model, nor have they attempted to account explicitly for temporal variation in the main biotic factors that could influence juvenile survival (food availability and predation risk). There is also empirical evidence that we should look specifically at juvenile (as opposed to egg or larval) stages for explanation of density-dependent effects on recruitment (Lockwood, 1980; Myers and Cadigan, 1993).

Here we show that Beverton–Holt models with explicit representation of effects of changes in food supply and predation risk can be derived from simple arguments about how juvenile fishes compete and adjust behaviour to changes in opportunities and risks. Such models predict that very large changes in recruitment and survival rates can, and should, accompany relatively small changes in food availability and predator abundance. If the arguments presented below are correct, even in broad outline, we have very likely been looking and measuring at the wrong scales and in the wrong places for causes of recruitment variation.

Derivation of the Beverton–Holt model from risk-sensitive foraging arguments

The following analysis is based on the representation of mortality factors at three time scales (Figure 1): (1) very fast variation on scales of hours to days in behaviour of juvenile fish faced with predation risk while foraging, with the assumptions that competition for food can be locally intense and that most predation mortality is likely to occur while juveniles are actively foraging or dispersing to seek improved foraging sites; (2) cumulative mortality on time scales of single and multiple life history stanzas within the first year or two of life, with food and predation risk treated as constant (or noisy but with no temporal trend) within each seasonal stanza; and (3) interannual (or among-cohort) variation caused by longer-term dynamic changes in food and predator abundances. This section shows how linear variation in mortality rates with juvenile density could arise within single life history stanzas.

A basic implication of risk-restricted foraging behaviour

Walters and Juanes (1993) pointed out that juvenile fishes generally forage in highly restricted spatial ‘arenas’ in close proximity to refuges from predation, and that competition for food can be intense within such arenas even when total food abundance appears unlimited when measured at larger spatial scales. They pointed out that a remarkable variety of physical and behavioural circumstances lead to the arena foraging structure on small space-time scales, ranging from juveniles hiding in littoral shallows to juveniles hiding behind their neighbours in dense shoals. They noted that food density f_t within such foraging arenas can be dominated on small scales by exchange and foraging processes, with f_t varying rapidly according to a differential equation of the form:

$$df_t/dt = kI_t - mf_t - (a/A)N_t f_t. \quad (1)$$

Here I_t is overall food density in the water surrounding the foraging arenas, delivered to the foraging arenas through processes like prey and water movement at rates kI_t ; mf_t represents loss of prey from foraging arenas owing to the same processes (and others such as insect emergence); and (a/A) is a , the area or volume swept per foraging juvenile N_t per time in the arena (which may or may not involve active movement by the juvenile), divided by A , the arena area or volume.

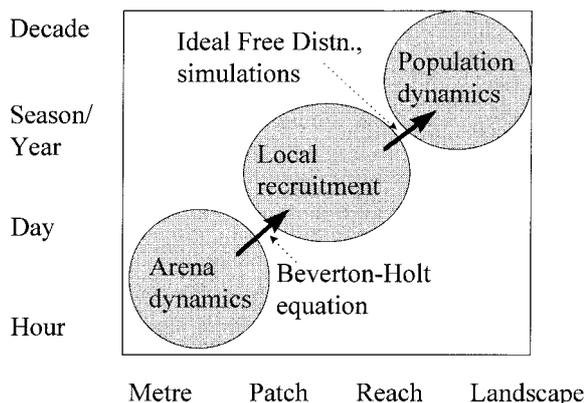


Figure 1. Analysis of recruitment relationships should involve at least three space-time scales: (1) the very fine scales at which juveniles forage and face predation risk; (2) larger scales at which we observe net recruitment rates; and (3) long-term population dynamics scales over which the recruitment relationship has an impact on population change. The extended Beverton–Holt model derived in this paper provides a convenient way to bridge from the first to second of these scales.

High values of the small-scale exchange and feeding parameters k , m , and (a/A) imply that f_t will quickly move to and remain near a moving equilibrium (with I_t and N_t) defined by setting the derivative in Equation 1 to zero:

$$f_t = kI_t / [m + (a/A)N_t]. \quad (2)$$

This proposition, that there should be a strong inverse relationship between available food density f_t and juvenile density N_t even when total food supply I_t appears unlimited, is critical to the arguments that follow. Note that the arena parameters k , m and (a/A) are defined by a very complex interaction of habitat structure, behavioural properties of food organisms, and how juveniles perceive severity of predation risk in choice of arena sizes A . Within any large juvenile rearing area, the ‘arena’ is not a single place but rather a complex spatial set of foraging sites-times.

It is not critical to the arguments that follow whether we can measure (or even define precisely) the parameters of Equation 2 in the field. Perhaps the best way to think about foraging arenas is as what philosophers of science call “theoretical objects” (Kuhn, 1962), which are things that we cannot define completely, or measure directly, but help us to make useful predictions when we pretend they exist (the Bohr atom is an obvious example).

Temporal variation in mortality rate for animals selected to seek minimum growth trajectories

The next step in the derivation is to suppose that juvenile fish adjust the proportion of time p_f that they spend in foraging areas so as to try and achieve per capita food consumption rates c^* , where natural selection has adjusted these feeding rate goals so that the fish will achieve a growth trajectory that is in some sense optimal. Here optimal is used in an evolutionary sense, with respect to the balance of growth versus predation risk, and with respect to potentially harsh constraints such as the need to reach some critical minimum size by the end of a growth stanza in order to be able to overwinter successfully or minimize some size-dependent risk later in life (review, Walters and Juanes, 1993). Again, for the arguments that follow, we need not be precise in predicting what c^* should be; it matters only that animals do in fact make adjustments in foraging time when faced with changes in food availability driven by abiotic factors (I_t , k in Equation 2) and competition (N_t in Equation 2). Further, the arguments will hold if there is considerable individual variation in response, as predicted for example by dynamic programming models that show how individuals with large size or energy storage should be less prone to make risky foraging decisions (have lower p_f) than individuals that have fallen behind an overall best growth trajectory (Mangel and Clark, 1988).

If animals do attempt to achieve consumption rate c^* , whether due simply to hunger or because of long-term natural selection, they need on average to adjust p_f so that

$$c^* = ap_f f_t \quad (3)$$

where again a is the volume or area of arena swept per time foraging and f_t is arena food density. In the presence of competitor abundance N_t , combining Equations 2 and 3 implies the relationship

$$c^* = ap_f k I_t / [m + (a/A)N_t] \quad (4)$$

which implies that p_f should be adjusted so that

$$p_f = [m + (a/A)N_t]c^* / (akI_t). \quad (5)$$

That is, animals seeking to achieve feeding rate c^* should vary the mean proportion of time spent foraging linearly with density of competitors (N_t), and in inverse proportion to overall food abundance as measured by kI_t .

An obvious next step is to suggest that instantaneous mortality rate due to predation is directly proportional to time spent foraging, i.e.

$$dN_t/dt = -Z_t N_t = -R_t p_f N_t \quad (6)$$

where R_t is the instantaneous mortality risk per time spent foraging. Here we assume that when juveniles are not feeding, they minimize predation risk by hiding, remaining stationary or by schooling tightly. Substituting Equation 5 into this model results in a differential equation for cumulative impact on N_t :

$$dN_t/dt = -R_t [m + (a/A)N_t]c^* / (akI_t)N_t. \quad (7)$$

Over time scales short enough to treat c^* , R_t , I_t and the foraging parameters k , m , (a/A) as constant, we can express Equation 7 in terms of aggregated parameters α_1 and α_2 as

$$dN_t/dt = -\alpha_1 N_t - \alpha_2 N_t^2 \quad (8)$$

where:

$$\alpha_1 = [R_t/I_t]c^*m / (ak) \quad (9a)$$

and

$$\alpha_2 = \alpha_1 a / (mA). \quad (9b)$$

That is, instantaneous juvenile mortality rate should vary linearly with N_t , having an intercept or base rate α_1 and a compensatory slope α_2 . Each of these mortality parameters should vary over longer time scales (multiple life history 'stanzas', years) in proportion to the risk ratio R_t/I_t , where again R_t is instantaneous predation risk per time foraging and I_t is overall food abundance. The base mortality rate α_1 should be higher in environments with more predators or less food, where food is delivered to foraging arenas more slowly (k small), and/or where animals seek higher consumption rates c^* owing to factors such as increased metabolism at higher temperatures. Interestingly, the compensation parameters α_2 should vary in the same way, but should be lower in situations where foraging arena size (A) is larger. Beverton and Holt (1957) suggested in deriving the original model that predation effects should be concentrated in the α_1 parameter, whereas the above formulation suggests that both the rate parameters should vary with R_t .

The single-stanza Beverton–Holt Model

Solving differential Equation 8 for N_t over any life history stanza s of duration T_s short enough so that α_1

and α_2 are relatively constant, we immediately obtain the familiar Beverton–Holt input–output relationship

$$N_{T_s} = \beta_1 N_0 / (1 + \beta_2 N_0) \quad (10)$$

where the slope and carrying capacity parameters β_1 and β_2 are defined from the rate parameters by:

$$\beta_1 = \exp(-\alpha_1 T_s) \quad (11a)$$

$$\beta_2 = (\alpha_2/\alpha_1)(1 - \beta_1) = a / (mA)(1 - \beta_1) \quad (11b)$$

in which N_{T_s} is the output number of recruits surviving the stanza and N_0 is the input number of juveniles entering it.

As α_1 and α_2 in Equations 11a and 11b are predicted as a function of factors controlled by small-scale interactions (Equations 9a and 9b), the Beverton–Holt parameters are therefore defined by these same small-scale interactions and vary with changes in the risk/food ratio R_t/I_t (Figure 2). Equation 11a points out a robust feature of the derivation: we obtain basically the same prediction about recruitment by assuming either that p_f is adjusted to achieve c^* in fixed time T_s , or that p_f stays constant so that c^* varies so as to cause a longer time T_s needed to reach some size that defines the end of the stanza (only the product c^*T_s need be constant).

Surprisingly, the Beverton–Holt model can be derived by reversing the basic assumption that animals vary p_f so as to try and achieve ration c^* over a fixed stanza period T , and assuming instead that animals feed for a fixed fraction p_o of the time while allowing growth rate to vary so the total time T needed to reach some critical total size or cumulative consumption C^* also varies. Under this density-dependent growth model, instantaneous mortality rate $Z = R_t p_o$ due to feeding should be constant (cohorts should die off at the same rate given similar predation risk R_t , whether their initial density is high or low), and T should vary from year to year with changes in initial abundance N_0 . The Beverton–Holt model for numbers reaching total consumption C^* over a stanza is then given by (Appendix 1):

$$\begin{aligned} N_T &= N_0 e^{-ZT} \\ &= \exp(-\alpha_1) N_0 / [1 + \alpha_2(1 - \exp(-\alpha_1)) N_0] \end{aligned}$$

where $\alpha_1 = C^* R_t m / I_t k a$ and $\alpha_2 = a / (mA)$. That is, in terms of risk ratio (R/I) and habitat size (A) effects, it does not really matter whether we view animals as varying p so as to achieve constant ration c^* , or having to live with variable total time T needed to reach a

critical total food consumption C^* at which they can undertake some ontogenetic shift or reach a size large enough for size-selective mortality rate to decrease substantially (Figure 3). In the field, situations where p is fixed are probably not uncommon, as a result of prey and predator behaviour factors such as diurnally restricted emergence times of insects.

For high initial juvenile input N_0 , Equation 10 predicts that recruitment N_{T_s} should be essentially independent of N_0 , at a limiting value

$$N_{T_s}^{(\text{limit})} = \beta_1 / \beta_2 = (mA/a) \exp(-\alpha_1 T_s) / [1 - \exp(-\alpha_1 T_s)]. \quad (12)$$

That is, asymptotic recruitment from any stanza should be proportional to habitat size A and exponentially decreasing in the risk ratio R_t/I_t . Equation 12 is used below to evaluate sensitivity of N_{T_s} to changes in R_t/I_t ; this sensitivity should be high in any case where there is large absolute change in α_1 with change in the risk ratio, i.e. when the maximum total survival rate $\exp(-\alpha_1 T_s)$ through the stanza is low. Note also that if maximum (absent competitive effects) total survival $\exp(-\alpha_1 T_s)$ through the stanza is low, Equation 12 is well approximated just by $(mA/a) \exp(-\alpha T_s)$.

Representing complex ontogenetic changes in risks and opportunities

Suppose we think of recruitments that we finally measure as the result of a sequence of life history stanzas, each described by a Beverton–Holt function of the Equation 10 form but with different parameter values owing to changes in foraging opportunities, predation risks, and environmental factors over time and as juveniles grow. It is easily shown (by substituting output from each stanza into the Beverton–Holt equation for the next stanza) that any such sequence of input–output relationships is itself a Beverton–Holt function, i.e. $N_f = \alpha_1^* N_0 / (1 + \beta_2^* N_0)$, where N_f is final recruitment and N_0 is the number of fish entering the first stanza (Beverton and Holt, 1957, pp. 48–49). For an n -stanza life history, the overall recruitment parameters β_1^* and β_2^* are functions of the stanza-scale parameters:

$$\beta_1^* = \beta_1^{(1)} \beta_1^{(2)} \dots \beta_1^{(n)} \quad (12a)$$

$$\beta_2^* = \beta_2^{(1)} + \beta_1^{(1)} \beta_2^{(2)} + \beta_1^{(1)} \beta_1^{(2)} \beta_2^{(3)} + \dots \quad (12b)$$

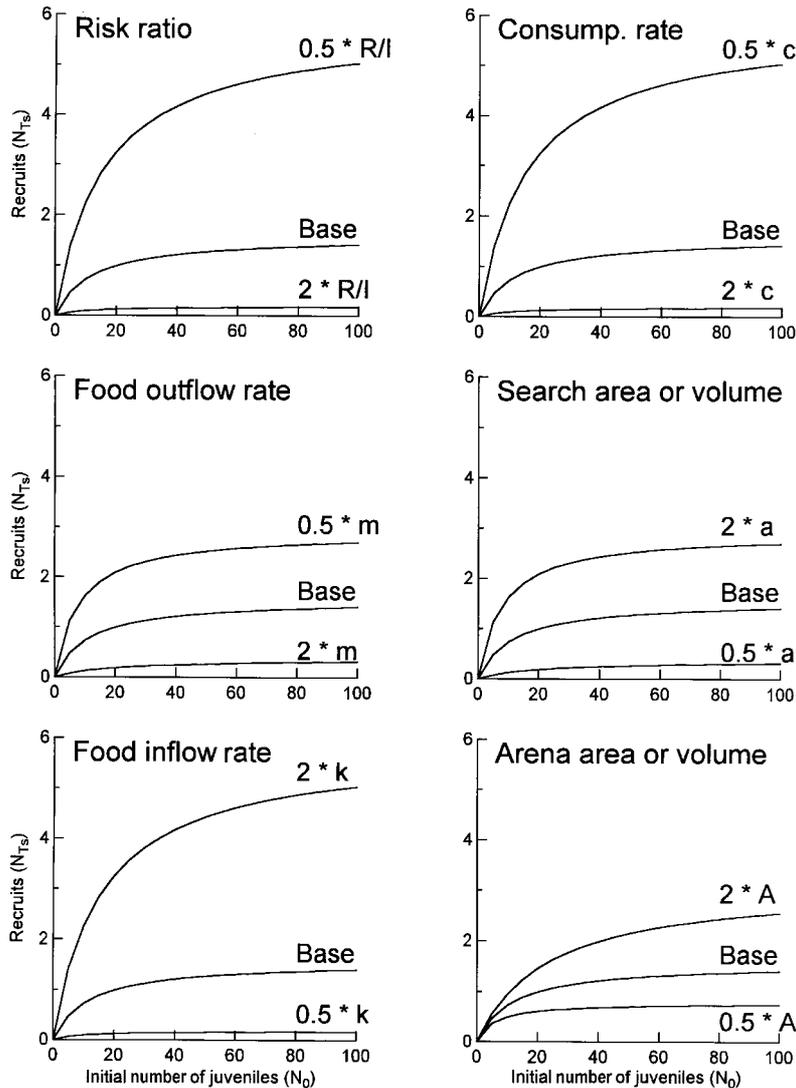


Figure 2. Summary of the effects of foraging arena model parameters on the shape of the Beverton–Holt relationship.

where the superscripts in parentheses denote stanzas. That is, the overall recruitment slope parameter β_1^* is just the product of the slope parameters for the individual stanzas, and β_2^* is a survival-weighted ($\beta_1^{(i)}$ are survival rates) sum of the stanza compensation parameters. This peculiar algebraic feature of the Beverton–Holt equation is very likely a key reason why the relationship keeps appearing in such a rich variety of data sets, where we believe that there are radically different patterns of life history stanzas, feeding ontogenies, and predation risks.

Consider what happens if we progressively divide the early life history into more and more, shorter

stanzas, of progressively shorter durations T_s . Then in the limit as these T_s durations approach 0 (become differentials dt), we can think of the by-stanza foraging and risk parameters $\alpha_1^{(s)}$ $\alpha_2^{(s)}$ (or the β s) as continuously changing functions of size and age, i.e. to think of s as a continuous time variable and the parameters as functions of this variable. The sum of terms in the exponent of β_1^* then becomes just an integral, as does the sum of terms defining β_2^* . These integrals may be difficult to calculate numerically for any particular choice of functional representation for how the parameters vary with s , but that is not the point: the basic Beverton–Holt structure will still be preserved. This

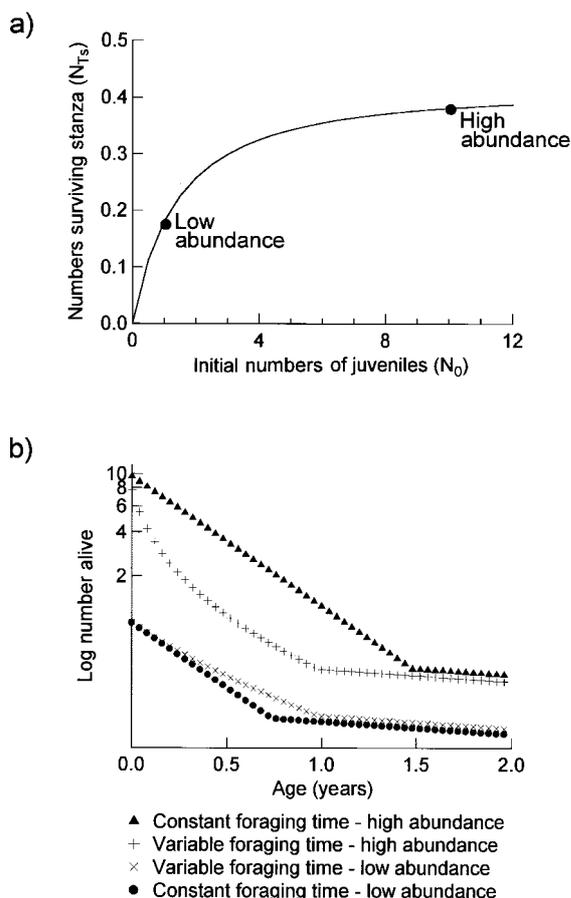


Figure 3. The same Beverton–Holt relationship between abundance entering and leaving a life history stanza is predicted whether animals vary foraging times within the stanza, so as to maintain constant growth rates while accepting variable mortality rate with foraging time, or instead adopt fixed foraging time and hence accept variable total time required to pass through the stanza. Relationships in (b) under these two foraging time assumptions are shown for situations of both low and high abundance as shown in (a).

same mathematical result can be obtained by treating α_1 , α_2 as continuous functions of time in the first place when integrating Equation 8; β^*_1 is $\exp[-\int \alpha_1(t)]$, and α^*_2 is a convolution integral of $\alpha_2(t)$ weighted by $\exp[-\int \alpha_1(t)]$ terms.

There is one obvious condition under which the equations defined above could predict a dome-shaped relationship between final recruitment N_f and initial juvenile numbers N_0 . That is where the risk ratio R_s/I_s (now thinking of this ratio as varying with stanza s rather than time t) is dependent on the number of older animals in the population, so R_s is some function of the same older juvenile and/or adult abundance that causes variation in N_0 . However, the competi-

tion and risk-sensitive foraging arguments leading to the basic Beverton–Holt formulation imply that any such dome-shaped relationships should often be much less pronounced than predicted by the Ricker model, except perhaps in circumstances where juveniles must spend a very high proportion of time foraging and at risk to cannibalism for some reason.

Representing mesoscale variation in habitat structure and risk

The derivation above is based on thinking about habitat structure, food competition, and predation risk at only two spatial scales: a large rearing area, with microscale foraging arenas distributed in some reticulated structure over that area. In many cases this conceptual picture could be misleading. Obvious examples are (1) juvenile fish distributed along a large river that has strong spatial gradients in productivity and predator populations, and (2) juvenile fish dispersing into potentially very large rearing areas from restricted spawning/larval settlement sites, e.g. into estuarine and coastal areas from freshwater spawning areas. For the following analysis, the potential overall rearing area is viewed as a collection of subareas (rearing reaches) each containing arena substructure but differing in terms of predator populations and food supplies (e.g. river reaches, coastal bands progressively further from spawning areas). Should we still expect a relatively simple Beverton–Holt relationship in such cases? If so, should mesoscale spatial patterns in juvenile density be clearly related to variation in risk ratios (R_t/I_t) and relative area of foraging arenas (A)?

Very interesting answers to these questions are obtained if we assume that natural selection has acted on dispersal behaviours (of juveniles, and of adults in settings where adult site selection restricts juvenile movement opportunity) to make these behaviours sensitive to risk ratios in the same ways assumed in the basic derivation above. If dispersal behaviour is sensitive to opportunity and risk, animals should redistribute themselves so that no mesoscale rearing area ends up standing out as much better (or worse) than surrounding areas. That is, better areas should accumulate animals, and poorer areas should lose animals, until dispersing individuals see no particular advantage to any area they encounter or test (MacCall, 1990). If we do see high differential survival/growth rates among areas, such differences

should be persistent only if juveniles do not have enough time to seek out the better areas or if the dispersal search process has extreme cost (energetics or mortality risk). The following subsections examine three situations where we can make specific predictions about overall recruitment and spatial distribution patterns by using the idea that dispersal tends to equalize fitness (i.e. survival) over space.

Juveniles move freely among mesoscale rearing areas with negligible dispersal cost

Suppose there are a set of habitat units $h = 1 \dots H$ that juveniles can freely test, with each such unit having predation/food/arena size parameters R_h, I_h, A_h that do not change rapidly over the stanza(s) of highest juvenile mortality. *Habitat units* are spatially distinct areas to which juveniles can disperse. However, these units do not have to be morphologically different (e.g. littoral vs. pelagic zones in a lake). If juveniles seek a particular target food consumption rate c^* (as above) and seek to minimize mortality risk to achieve this rate, they should move around so that instantaneous mortality rates $Z_h = \alpha_{1h} + \alpha_{2h} N_h$ are the same for all h , i.e. $Z_h = Z$. That is, each rearing unit should satisfy the relationship $Z = \alpha_{1h} + \alpha_{2h} N_h$, implying juveniles distributed as $N_h = (Z - \alpha_{1h})/\alpha_{2h}$. This prediction can be reexpressed using the definitions of α (Equation 9) as:

$$N_h = [ZkA_hI_h / (c^*R_h)] - (mA_h/a). \quad (13)$$

If the habitat units h have (or are defined so as to have) similar A_h , this prediction reduces to the linear relationship:

$$N_h = \{[(ZkA/c^*)I_h] / R_h\} - (mA/a) \quad (14)$$

(N_h should be zero in habitat units where this equation predicts negative numbers.)

That is, we should see linear variation in juvenile densities over habitats h of similar arena size (A), with variation in the food/predation ratio I_h/R_h . The slope of this relationship should decrease over time as total mortality rate Z decreases with decreasing juvenile density, assuming that densities are not maintained by schooling or other antipredator behaviours. Further, spatial evening in mortality risk (Z) implies that total juvenile numbers summed over habitats h should decline according to a weighted Beverton–Holt relationship $dN/dt = -\sum_h \alpha_{1h} N_h - \sum_h \alpha_{2h} N_h^2 = -\bar{\alpha}_1 N - \bar{\alpha}_2 N^2$, where the $\bar{\alpha}$ are weighted averages

of habitat-specific values (each α_{1h} in $\bar{\alpha}_1$ weighted by N_h/N , each α_{2h} in $\bar{\alpha}_2$ weighted by N_h^2/N^2).

Adults select mesoscale areas, then juveniles are restricted to the area of birth

In this case, suppose juveniles are restricted to the habitat h where they are born, delivered, or tended by adults, and that adult densities N_{Ah} are adjusted through adult habitat site selection processes or local adult population dynamics so that no habitat ends up standing out as a better site for producing young. From an adult perspective, the quality of each h is measured by net per-capita recruitment performance $S_h = N_{T_s}/N_A$ where N_{T_s} is the net recruitment predicted from Equation 10 so as to include Beverton–Holt effects of competition among the juveniles (and predation risk). Equalization of performance among sites (or local population growth to an equilibrium where recruitment balances adult mortality, assuming similar adult mortality in all habitats) implies similar values of N_{T_s}/N_A for all habitats, which can be expressed in terms of Equation 10 as:

$$S_h = S = \beta_{1h}F / (1 + \beta_{2h}FN_{Ah}) \quad (15)$$

where adult fecundity is F (so $N_0 = FN_A$) and the β_{1h}, β_{2h} are given by Equation 11 with local predation and food parameters R_h, I_h used in the α calculation for each h . Solving Equation 15 for adult distribution N_{Ah} results in the prediction that N_{Ah} should vary linearly with the β_{1h}, β_{2h} parameters, as $N_{Ah} = [\beta_{1h}(F/S) - 1]/(\beta_{2h}F)$. This prediction can be expressed in terms of a function that varies exponentially with risk ratio R_h/I_h , as:

$$N_{Ah} = (mA/aS)\exp(-\alpha_{1h}T_s) / [1 - \exp(-\alpha_{1h}T_s) - mA/(aF)] \quad (16)$$

(with no adults predicted to use habitats where this equation evaluates to less than 0).

The adult relationship (Equation 16) is not as tidy as the linear juvenile pattern of Equation 14, but makes the same qualitative prediction that there should be a strong positive relationship between N_{Ah} and the inverse risk ratio I_t/R_t (because α_{1h} is proportional R_t/I_t). It again predicts an overall Beverton–Holt relationship for the summed relationships over habitats (total recruits vs. $\sum_h N_{Ah}$) but with complicated weightings for the local recruitment contributions.

Juveniles disperse into a large habitat from restricted spawning/settlement site

Suppose we now think of the mesoscale habitat index h as a continuous variable representing distance from a spawning or larval settlement site, and treat juvenile densities N_{ht} as a continuous function of h and time t during the recruitment process. Assume that micro-scale arena structure and behavioural responses result also in continuous variation in mortality rate Z_{ht} with h and t , where as above we would expect $Z_h = \alpha_1 h + \alpha_2 N_{ht}$. But now suppose that juveniles residing at point h can expect to suffer mortality risk $D_h dh$ for dispersing a distance dh across the habitat field. In this setting, it only makes evolutionary sense for an animal to move to position $h + dh$ if Z_{h+dh} is less than $D_h dh$, i.e. if the mortality cost of moving is less than the expected gain through reduced mortality risk at a new residence location. Animals should be indifferent to moving at break-even situations where $Z_h - Z_{h+dh} = D_h dh$ because there will be no survival advantage to moving when the costs of moving are considered. If α_1 and α_2 do not change rapidly with h , this break-even condition can be expressed as $D_h = -\alpha_2 \partial N_h / \partial h$, implying that animals should disperse along the habitat variable h unless α_2 (proportional to the local risk ratio R_h/I_h) is small and/or there is a strong spatial gradient in juvenile density ($\partial N_h / \partial h$ large negative).

So if juveniles can somehow detect spatial density gradients $\partial N_h / \partial h$ via local movement forays or evolution of genetic expectations based on local risk conditions Z_h , the gradient break-even condition results in three main qualitative predictions. (1) Dispersal should be most rapid (or common) near the start of the process, when juveniles are most concentrated and the gradient $\partial N_h / \partial h$ is strongest. (2) Dispersal rates should be much lower later on, when density gradients (and odds of finding a better site) are much weaker (lower). (3) If risk $D_h dh$ per move is high, the juvenile distribution should show a relatively sharp boundary, with this boundary perhaps moving between years with changes in initial juvenile abundance N_0 . As in the previous cases, the general Beverton–Holt response pattern should occur, but with parameter values that are complex spatial averages of local risk ratios and dispersal risk.

Unfortunately, there is at least one very serious weakness and lack of generality in this whole line of argument: many kinds of animals *define* foraging arenas through shoaling behaviours, i.e. treat shoals of

conspecifics as their main hiding places (see Figure 1 in Walters and Juanes, 1993). To such species, gradients in N_h can mean opportunities for reduced rather than increased predation risk albeit with trade-offs in terms of increased intraspecific competition. It is easy to visualize how the competing effects of N_h might be expressed in patterns like rapid initial dispersal of juveniles from natal areas followed by consolidation into shoals that then move over large areas, in a sense then carrying their Beverton–Holt foraging arena structure with them. But it may be difficult or impossible to prove that such complex ontogenies should result in the overall form of a Beverton–Holt stock–recruitment relationship.

Sensitivity of recruitment rates to risk/food ratios: amplification of biotic variation

An intuitive argument about longer-term (interannual) recruitment variation might be that risk-sensitive changes in foraging behaviour should dampen the impacts on recruitment of changes in predator abundance. The analysis above indicates that this intuition is wrong. The β_1 parameter ($= \exp(-\alpha_1 T_s)$, where α_1 is proportional to the risk ratio R_t/I_t), or more generally β_1^* for multiple stanzas, can be quite sensitive to the risk ratio R_t/I_t . The proportional effect of β_1 on recruitment should not be cancelled via the β_2 parameter because the dependence of this parameter on the risk ratio is likely to be weak: β_2 is proportional to $1 - \exp(-\alpha_1 T_s)$, which is close to 1.0 if the maximum survival rate $\exp(-\alpha_1 T_s)$ is low. A further intuitive argument for multistanza cases might be that compensatory effects at a later stanza might ameliorate or dampen high variation due to biotic factors in early stanzas. This intuition is again likely to be wrong, for the same reasons; note that $\beta_1^* = \exp(-\sum \alpha_1^{(s)} T_s)$, which is sensitive to changes in $\alpha_1^{(s)}$ at all stages for which $\alpha_1^{(s)}$ or T_s are large.

Consider situations where egg or larval input N_0 is large enough for recruitment to be near the recruitment $N_{T_s}^{(\text{limit})}$ predicted by Equation 12, i.e. for recruitment to not increase with respect to changes in N_0 . Assume further that the maximum survival rate $S_0 = \exp(-\alpha_1 T_s)$ is relatively low, implying the instantaneous mortality rate $Z_s = \alpha_1 T_s = -\ln(S_0)$ is high; this is the typical situation for juvenile fish. For low S_0 , Equation 12 behaves as $N_{T_s}^{(\text{limit})} \approx (mA/a)\exp(-\alpha_1 T_s)$. We can easily reparametrize the mortality rate Z_s so as

to evaluate how it should vary with the risk ratio R_t/I_t , by expressing this approximation as:

$$N_{T_s}^{(\text{limit})} \approx (mA/a)\exp(-G_0H_t) \quad (17)$$

where the gain parameter G_0 is defined as:

$$G_0 = mc^*T_sR_0 / (akI_0) \quad (18)$$

and H_t is the relative risk ratio for year (or cohort) t :

$$H_t = (R_t / R_0) / (I_t / I_0) \quad (19)$$

measured relative to some base risk ratio R_0/I_0 that has historically led to survival rate S_0 . Note that $G_0 = -\ln(S_0)$ because $H_0 = 1.0$. Now suppose we look at relative recruitment rates for years (or cohorts) t , $N_{T_s}^{(t)}$, as ratios to the $N_{T_s}^{(\text{limit})}$ implied by S_0 . Using Equations 17 to 19, such relative recruitment rates can be expressed simply as:

$$N_{T_s}^{(t)} / N_{T_s}^{(\text{limit})} = \exp[-G_0(H_t - 1)] = S_0^{(1-H_t)}. \quad (20)$$

That is, recruitments ought to vary from year to year relative to some base or average by amounts that are greater if base mortality rate $G_0 = Z_0$ is high and/or if the relative risk ratio H_t is much different from 1.0.

Figure 4 shows just how big the effects of changes in the relative risk ratio H_t could be, for alternative base survival rates S_0 . If base survival rate were really low, say 0.001, it would take only $\pm 10\%$ change in H_t to cause $\pm 50\%$ changes in recruitment. At base survival rate 0.1, it should take $\pm 30\%$ changes in H_t to cause $\pm 50\%$ recruitment variation. That such large effects could arise from relatively small changes in trophic circumstances reminds us of the key point made by Beyer (1989) and Ursin (1982), that the really remarkable thing is not how much recruitment varies, but rather why it varies so little. To avoid predicting really massive changes in recruitment with changes in risk ratios H_t in the Beverton–Holt model derived above, we have to suppose either that the critical stanza(s) where H_t applies are very short (so Z_s for these stanza(s) is quite low), or that there are additional compensatory responses (such as changes in foraging arena sizes A with H_t) not recongized in the basic model above.

Simplified parametrization for multispecies assessments

The Beverton–Holt formulation above provides a tempting starting point for multispecies modelling. It

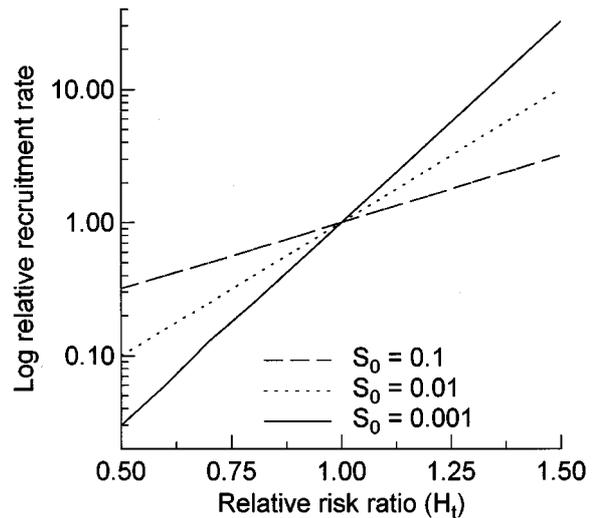


Figure 4. Effect of changes in the relative risk ratio H_t (predator abundance/food abundance) on relative recruitment rate (rate in year t divided by mean rate), for alternative values of maximum total survival rate S_0 through a limiting juvenile life stage.

reflects the widespread observation that recruitments tend to be independent of parental abundance unless that abundance is very low, it contains explicit terms that link recruitment variation to food, predator abundance, and habitat scale, and it is based in reasonable assumptions about behavioural ecology at fine space-time scales. And it seeks explanation for population changes at those early life history stages that we suspect to be most sensitive to interactions and environmental changes. But as presented, it is grossly overparametrized for most practical applications. This section shows one fairly simple way to reparametrize it so as to maintain the multispecies linkages even when it is difficult or impossible to measure relevant variables in commensurate units, to provide a framework that is open to improvement as more refined information becomes available about trophic interactions and impacts of habitat change, and to allow incorporation of basic hypotheses and results from comparative studies about likely recruitment responses to extreme circumstances (e.g. very low spawning stock size). These are ambitious goals for any model; the following results are intended to be a starting point rather than a definitive assertion about how to best parametrize the model.

Assume we seek to make predictions of relative abundances N_{it} over years t for a set of $i = 1 \dots n$ species or functional groups, with each species represented by Beverton–Holt recruitment at age 1. Assume

we want to express age 1 recruitments N_{it} (i for species, 1 for age 1, t for time) as:

$$N_{it} = \beta_{1it} F_i N_{it} / [1 + \beta'_{2it} (1 - \beta_{1it}) F_i N_{it}] \quad (21)$$

where F_i represent the mean age 1 + fecundity for species i , $\beta'_{2it} = a/(mA)$ represents only effects of changes in habitat size (Equation 11), and the recruitment parameters β vary over time in relation to predation risk ratios and changes in habitat factors like A . Ordinarily we would approach this problem by first estimating all the N s on some commensurate scale (often involving some very questionable assessment assumptions), then use methods like Ecopath (Christensen and Pauly, 1992; Polovina, 1984) and multispecies virtual population analysis (MSVPA; Sparre, 1991) to provide initial estimates of feeding rates and mortality trophic flows from which we would attempt to calculate juvenile mortality rates and risk ratio components. Here it will be assumed that such standardization is either impossible or highly questionable, and that the N_{it} are measured in a variety of disparate units, not necessarily even numerical abundances (e.g. N representing aquatic insects might be in g m^{-2} biomass unit, N for some small fish might be expressed in beach seine catch rate unit, and trout might be measured in numbers backcalculated using VPA). Those who enjoy accounting models might wish to replace N_{it} with a full age-structured model, using sum of age-specific fecundities \times numbers at age in the recruitment function; this elaboration does not change the basic approach at all.

Next suppose we define a set of baseline abundance levels N_{i0} that we believe on the basis of past data (or propose as a working assessment hypothesis) would be naturally sustainable, i.e. display $N_{it+1} \approx N_{it} = N_{i0}$ on average in the absence of habitat changes. This is exactly the same as assuming the existence of a natural unfished biomass or abundance B_0 in single-species assessment. If species i has average annual survival rate s_i for age 1 + animals, we know that the multispecies recruitment functions evaluated at $N_{it} = N_{i0}$ should satisfy $(1 - s_i)N_{i0} = \beta_{1i0} F_i N_{i0} / [1 + \beta'_{2i0} (1 - \beta_{1i0}) F_i N_{i0}]$, i.e. predicted recruitment should just balance natural mortality of older animals. We can use this constraint to calculate the habitat-population scale parameter β'_{2i0} given by any estimate of the survival rate parameter β_{1i0} , as:

$$\beta'_{2i0} = [\beta_{1i0} F_i / (1 - s_i) - 1] / [F_i N_{i0} (1 - \beta_{1i0})]. \quad (22)$$

That is, given N_{i0} and the sustainability assumption, we do not have to treat at least the basic habitat size parameters β'_{2i0} as uncertain, and we can concentrate attention on representation of the survival parameters β'_{1i0} . Changes in habitat sizes A can be represented by relative variation in β'_{2i0} from the base value given by Equation 22.

Next, note that there are ordinarily (and, it is to be hoped from a management perspective) no good data upon which to directly estimate β_{1i0} ; $\beta_{1i0} F_i$ is the slope of the recruitment curve for very low spawning stock, and that slope is certainly something that we do not want to see very often if at all. But from stock–recruitment summaries like Myers and Barrowman (1996), we can obtain likely values measured as ratios to the natural survival rate $N_{i10}/(F_i N_{i0}) = (1 - s_i)/F_i$. Typically for fish, we expect β_{1i0} to be on order 5–10 \times this natural rate (5 \times to 10 \times improvement in juvenile survival at very low stock sizes; Myers and Cadigan, 1993). Letting the assumed ratio be K_i (e.g. $K = 5$), we then know that β_{1i0} should be calculated so as to satisfy the constraint $\beta_{1i0} = K_i (1 - s_i)/F_i$. This approach amounts to reparametrizing β_{1i0} so that we can easily make it consistent with general experience (K) and the relatively stable population characteristics s_i and F_i .

From the original derivation, β_{1i0} can be expressed as $\beta_{1i0} = \exp(-\lambda_{i0} R_{i0}/I_{i0})$, where $\lambda_{i0} = T_s c^* m/(ak)$ is a complex constant (for which it would be very unusual to have direct field estimates) and R_{i0} , I_{i0} are predation risk and food abundance indices for species i evaluated at the baseline situation N_{i0} . But if we use the constraint $\beta_{1i0} = K_i (1 - s_i)/F_i$, then we know that λ has to satisfy:

$$\lambda_{i0} = -\ln[K_i (1 - s_i)/F_i] I_{i0} / R_{i0} \quad (23)$$

so we can calculate it immediately once we choose a reasonable method for calculating and scaling the risk ratio factors I_{i0} and R_{i0} . For simulations of changes in habitat factors that influence the components of λ (T_s , c^* , m , a , and k), we can vary λ_{it} relative to λ_{i0} (e.g. make it larger in warm years to reflect increases in c^* , lower in years of high water turbidity to reflect reductions in food search rate a).

Units of measurement for food availability I_{i0} and predation risk R_{i0} are absorbed in the calculation of λ_{i0} using Equation 23, so we need be concerned about calculating these ratios in a way that correctly represents the *relative* impact of changes in the N_{it} on these ratios. We cannot simply calculate R and I as sums

over the N_{it} that represent predators and food, without accounting somehow for differences in measurement units and relative impacts (predatory N_{it}) and availability as food (food N_{it} components). Here is one approach for scaling the R and I calculations. First, for each significant consumption linkage of a prey species i to a predator j , attempt to estimate the following two relative interaction factors:

$$P_{ij}^{(f)} = \text{proportion of the diet of type } j \text{ animals represented by type } i \text{ prey, at baseline abundances } N_{i0}, \text{ and}$$

$$P_{ij}^{(p)} = \text{proportion of the total mortality of type } i \text{ juveniles that is due to predator type } j, \text{ for baseline abundance conditions.}$$

Note that these proportions need not sum to 1.0; having them sum to lesser values means assuming that some other (but constant) food and predatory impacts occur besides those represented by changes in modelled N_{it} and N_{jt} . For each i and j , next calculate the base proportions of food $P_{0j}^{(f)}$ and predation impact $P_{i0}^{(p)}$ not represented by the above proportions (1.0 – sums of the modelled proportions). Then in time simulations and other analyses of interactions, calculate the risk and food indices R_{it} and I_{it} as:

$$I_{jt} = P_{0j}^{(f)} + \sum_i P_{ij}^{(f)} N_{it} / N_{i0} \quad (24a)$$

$$R_{it} = P_{i0}^{(p)} + \sum_j P_{ij}^{(p)} N_{jt} / N_{j0}. \quad (24b)$$

This scaling method has the property that I and R evaluate to 1.0 when food and predator abundances are all at N_{i0} . Increases and decreases in N_{it} relative to N_{i0} result in ratio changes relative to the proportions $P^{(f)}$ and $P^{(p)}$ initially estimated, no matter what units of measurement are used for the N . Note that the I_{jt} calculation requires a potentially questionable assumption that all prey types i have similar exchange rates k , m into and out of foraging arenas; without this assumption, the I_{jt} calculation would have to account for potentially complex changes in apparent prey densities with changes in densities of competing predators (N_{jt}), due solely to differences in susceptibility of prey types to local depletion within arenas. Further, localized interspecific competitive effects of different species foraging in the same arenas are not represented in the I_{jt} calculation. For example, if the availability of a prey item (N_{it}) increases over time,

food availability (I_{jt}) may not increase proportionally according to Equation 24a at higher levels of interspecific competition.

In summary, this parametrization method requires users to specify baseline relative abundances N_{i0} , survival and fecundity estimates s_i , F_i , compensatory response factors or abilities K_i , and the diet/predation impact proportions $P_{ij}^{(f)}$, $P_{ij}^{(p)}$, along with any parameters needed to describe temporal variation in habitat capacity/quality as reflected in the derived parameters β'_{2it} and λ_{it} . In the authors' experience, these requirements can quite often be met, with the possible exception of the relative predation impact factors $P_{ij}^{(p)}$ which depend on somehow apportioning mortality among the predators that cause it. Time simulations proceed by first calculating these derived parameters, then calculating the risk ratio factors in Equation 24 and applying them in Equation 21 with β_{1it} given by $\exp(-\lambda_{it}R_{it}/I_{it})$. In terms of familiar stock assessment estimation methods, the N_{i0} can be treated as key leading parameters for fitting multispecies time series, just as we often treat B_0 as a leading parameter in single species estimation. Ambitious analysts might even try to estimate the K_i , and the truly heroic among us might even include the $P^{(f)}$ and $P^{(p)}$ in time series fitting procedures (until they see how badly confounded the effects of these parameters generally are in times series settings).

Particular care needs to be taken in defining effective fecundities F_i for Equation 21. These should be measured net of any density-independent egg and larval mortality rates that might apply before animals become large enough to display the sort of behavioural responses assumed in the foraging arena relationships. Otherwise, the estimated exponential factors λ_{it} could be far too large and hence lead to unrealistically high sensitivity of predicted recruitments to the risk ratios R_{it}/I_{it} .

Discussion

The derivation above rests on two key, testable propositions: (1) that spatially restricted foraging creates competitive conditions that can drive juvenile fish to alter foraging time (or dispersal) with increasing density of competitors, and (2) that mortality is due mainly to predation associated with foraging (and dispersal). Similar arguments could be applied in relation to other potentially limiting resources such as spatial hiding places, with the

central theme being that evolution of responses to predation risk should involve behavioural changes that create localized resource competition. This leads to a worrisome point about how testable the extended Beverton–Holt theory described above really is. Suppose we go out and measure habitat use patterns and measure (or experimentally impose) changes in risk ratios R_t/I_t for some key life history stanzas, and suppose we get a negative result (no recruitment response to the measured changes in R_t/I_t). We can salvage the theory just by arguing that we have failed to identify the right risk index R_t or resource index I_t , or that compensation is actually occurring in another stanza. It may be impossible in practice, if not in principle, to weed out all such alternatives.

Obviously the model offers a nice excuse for why we have been so unsuccessful at finding clear, persistent correlations between recruitment and environmental factors. Direct effects of such factors can be overridden by small, difficult-to-monitor changes in biotic variables. For example, Spencer and Collie (1997) found that application of a surplus production model incorporating a nonlinear predation rate (Steele and Henderson, 1984) to Georges Bank haddock provided the best fit to a long-term historical data set showing prolonged periods of high and low stock productivity. Further, the main impact of environmental factors could very well be indirect, through effects on parameters like c^* , a , A , m , k and R_t/I_t , and it is easy to see how some of these effects could work in opposite directions (e.g. increase in temperature may increase c^* but also prey exchange rate k , leading to the same value of G_0 in Equation 18). At the very least, the derivation above implies that we need to be much more careful about how we articulate hypotheses concerning effects of environmental factors, with emphasis on describing precisely how any factor should influence interactions at the small space-time scales where these actually occur.

Fisheries scientists have long recognized that growth and mortality rates are highly correlated (Pauly, 1980), but we most often explain this correlation by arguments about linkage between physiological activity and ageing. At least for juvenile fish, experience with aquaculture suggests that this argument is fundamentally wrong: it is generally possible to obtain quite good survival rates just by providing adequate food while protecting juveniles from predation, and growing little animals faster in such protected settings does not generally lead to big increases in natural mortality rate. Such experience supports our

basic assumption that eating and dying are positively linked in nature not for physiological reasons, but because small animals cannot eat without exposing themselves to being eaten. In other words, it is not solely the bioenergetics of growth that should interest fisheries scientists, but rather the implications for mortality of the time spent feeding to achieve this growth.

So the generalized Beverton–Holt model comes very close to being a real theory of recruitment, representing observations and links to other ecological theory across a wide range of time-space scales. It even has an actual theoretical entity, the foraging arena, and is clearly well insulated from direct experimental test and invalidation. It appears able to explain a wide variety of observations, ranging from the nearly ubiquitous observation of recruitment being nearly flat when plotted against egg or larval abundance to the occurrence of high variation without obvious environmental correlates or explanation.

Whether or not the model provides a useful general theory for description of variation in natural populations, it could be of considerable practical value as a relatively simple way to model alternative hypotheses about impact of major habitat alterations in freshwater and coastal marine environments. For instance, we are currently developing models for population dynamics of endangered fish species in the Grand Canyon region of the Colorado River (Walters and Korman, unpublished data). Warm-water species such as humpback club (*Gila cypha*) Cyprinidae have apparently been severely affected by a whole series of changes associated with the Glen Canyon Dam: clear, cold water released from the dam has created not only unfavourable thermal conditions for warm-water species, but also a massive trophic gradient through the Canyon with much higher primary and benthic insect production in the upper reaches (Stevens et al., 1997) and much increased abundances of exotic predatory fishes such as trout. In this setting, the model provides a framework for representing possible effects of various mitigative measures (like warm water flow augmentation), on both recruitment parameters related directly to physical habitat factors (e.g. effects of temperature or turbidity on spawning, size of rearing areas A , predator search rates a) and on trophic relationships (R/I ratios over space and time). In this case, we need to develop recruitment submodels for a variety of species about which there is variable quality of life history and population data, so the Beverton–Holt relationship is computationally convenient as well as

helpful in directing attention to key parameters that may influence juvenile mortality rates.

The cross-scale arguments presented in this paper should serve as warning to the growing number of population ecologists who are trying to develop very detailed, spatially explicit and individual-based models for recruitment prediction and analysis of impacts of habitat alteration (Van Winkle et al., 1993, 1997). To date, such models do not simulate processes at the very fine space-time scales where mortality rates are actually determined by behavioural interactions. Trophic arenas and their competitive impacts are most likely to be defined by habitat structures and behavioural processes at scales of a few metres and minutes to hours. While it is possible in principle to map structure and function at such scales, fully explicit simulations of the cumulative impact of everything happening at these scales probably will never be practical from data acquisition or computational perspectives. Further, it is not clear that there would be any real point to such explicit modelling exercises. There may be great value in developing spatially explicit models to help understand the consequences of some mesoscale processes such as juvenile dispersal on spatial scales of hundreds of metres to kilometres. But when we develop such models, we need to be much more careful about how we represent processes at scales too fine to represent explicitly; in short, it is just not good enough to assume microscale homogeneity in food availability and simple relationships such as feeding rates limited by handling time or satiation.

Our derivation casts grave doubt on the conclusion of Walters and Parma (1996) that fixed exploitation rate strategies may be a good way to cope with long-term regime shifts in recruitment. That conclusion was based on the proposition that the β_1 parameter (proportional to recruitment curve slope near origin) may often be relatively stable, while the recruitment carrying capacity β_1/β_2 parameter may be more sensitive to environmental changes (i.e. stable reproductive performance at very low stock sizes but long-term variation in competitive outcomes at higher stock sizes). Stable β_1 implies stable optimum exploitation rate (optimum rate calculations generally do not depend on β_2). Our assumption of stable β_1 may have been only wishful thinking; if changes in β_1 are in fact driven substantially by long-term changes in predation and competitive regimes as measured by R/I ratios, mediated by changes in habitat variables as well, fishing mortality rate goals should be adjusted to such changes. That is a very difficult assessment

problem: we generally cannot measure β_1 directly, and how can we decide when we see a change in recruitment whether β_1 has changed, or instead the carrying capacity β_1/β_2 ? Perhaps it is time to start looking very hard for field methods to monitor long-term changes in juvenile mortality rates (β_1) directly, and for regulatory options that are robust to unpredictable changes in β_1 .

In some ways the most important result in this paper is buried in Appendix 1, where we hint at just what a wide range of different behavioural ecologies can give rise to the Beverton–Holt relationship. In view of this generality, it is hard not to shout in outrage when we see flat-topped recruitment relationships interpreted mindlessly and wrongly as indicative of recruitment limitation by environmental factors. Such interpretations fail not only to recognize what the word ‘limitation’ means in the first place; worse, they direct research attention away from the fascinating world of ecological interactions where recruitment limitation actually occurs.

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Appendix 1. Why a Beverton–Holt relationship may occur even if foraging time is fixed and time spent in a juvenile stanza varies with density of competitors

At the heart of the derivation above is the presumption that food consumption rate c is proportional to available food density f_t , which in turn depends on local competitive conditions such that $c = apkI_t / (m + (a/A)N_t)$. Suppose we assume that p is fixed at some daily time proportion p_0 ; we then replace mortality Equation 7 with the simpler exponential model

$$dN/dt = -R_t p_0 N_t \quad (\text{A1})$$

which implies that density declines over time within a stanza as

$$N_t = N_0 e^{-Zt} \quad (\text{A2})$$

where $Z = R_t p_0$.

But now assume that graduation from a juvenile stanza occurs at time T when juveniles have achieved total food consumption C^* , where C^* accumulates according to

$$\begin{aligned} C^* &= \int_{t=0}^{t=T} c dt \\ &= I_t k a p_0 \int_{t=0}^{t=T} dt / [m + (a/A) N_0 e^{-Zt}]. \end{aligned} \quad (\text{A3})$$

This is just the integral of the arena-scale time model for variation in food consumption rate c with changes in competitor density N_t , where N_t is predicted from Equation A2. Integrating Equation A3 to obtain an analytical expression for C^* results in:

$$C^* = (I_t k a / R_t m) \{ \ln[m + (a/A) N_0 e^{-ZT}] + ZT - \ln[m + (a/A) N_0] \}. \quad (\text{A4})$$

Then solving this relationship between C^* and T , for the total time T required to achieve C^* , we obtain:

$$T = (1/Z) \ln \{ \exp[C^* R_t m / I_t k a + \ln(m + (a/A) N_0)] - (a/A) N_0 \} / m. \quad (\text{A5})$$

Substituting this prediction of T into Equation A2 and rearranging the terms into familiar Beverton–Holt equation format results finally in:

$$\begin{aligned} N_T &= \exp(-C^* R_t m / I_t k a) N_0 / \\ &\quad \{ 1 + (a/mA) [1 - \\ &\quad \exp(-C^* R_t m / I_t k a)] N_0 \}. \end{aligned} \quad (\text{A6})$$

It should be noted that this equation should not be applied (as a single stanza predictor of survival) for contexts where T can be large enough for the risk ratio R_t/I_t to change substantially over t , owing either to juvenile growth (declining R_t due to larger body size) or to changes in predator and food abundances. However, the fact that it may need to be calculated for a number of short stanzas does not invalidate the basic prediction that overall recruitment relationship should be Beverton–Holt in form except when older juveniles and parents are a large component of R_t .

References

- Beamish, R.J., Mahnken, C. and Neville, C.M. (1997) Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. *ICES J. Mar. Sci.* **54**, 1200–1215.
- Beverton, R.J.H. and Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations* (Fisheries Investigations, Ser. 2, Vol. 19). UK Ministry of Agriculture and Fisheries, London.
- Beyer, J.E. (1989) Recruitment stability and survival – simple size-specific theory with examples from the early life dynamics of marine fish. *Dana* **7**, 45–147.
- Christensen, V. and Pauly, D. (1992) ECOPATH II – a software for balancing steady-state models and calculating network characteristics. *Ecol. Modelling* **61**, 169–185.
- Coronado, C. and Hilborn, R. (1997) Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. *Can. J. Fish. Aquat. Sci.* **55**, 2067–2077.
- Drinkwater, K.F. and Myers, R.A. (1987) Testing predications of marine fish and shellfish landings from environmental variables. *Can. J. Fish. Aquat. Sci.* **44**, 1568–1573.
- Friendland, K.D., Reddin, D.G. and Kocik, J.F. (1993) Marine survival of North American and European Atlantic salmon: effects of growth and recruitment. *ICES J. Mar. Sci.* **50**, 481–492.
- Kuhn, T.S. (1962) *The Structure of Scientific Revolutions*. University of Chicago Press, Chicago.
- Lockwood, S.J. (1980) Density-dependent mortality in 0-group plaice (*Pleuronectes platessa* L.) populations. *J. Cons. Int. Explor. Mer* **39** 148–153.
- MacCall, A.D. (1990) *Dynamic Geography of Marine Fish Populations*. Washington Sea Grant Program, University of Washington Press, Seattle, 153 pp.
- Mangel, M. and Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, NJ, 308 pp.
- Myers, R.A. and Barrowman, N.J. (1996) Is fish recruitment related to spanwmer abundance? *Fishery Bull.* **94**, 707–724.
- Myers, R.A. and Cadigan, N.G. (1993) Density-dependent juvenile mortality in marine demersal fish. *Can. J. Fish. Aquat. Sci.* **50**, 1576–1590.
- Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mar.* **39**, 175–192.
- Polovina, J.J. (1984) Model of a coral reef ecosystem I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* **3**, 1–11.
- Sparre, P. (1991) Introduction to multispecies virtual population analysis. *ICES Mar. Sci. Symp.* **193**, 12–21.
- Spencer, P.D. and Collie, J.S. (1997) Effect of nonlinear predation rates on rebuilding the Georges Bank haddock (*Melanogrammus aeglefinus*) stock. *Can. J. Fish. Aquat. Sci.* **54**, 2920–2929.
- Steele, J.H. and Henderson, E.W. (1984) Modeling long-term fluctuations in fish stocks. *Science* **224**, 985–987.
- Stevens, L.E., Shannon, J.P. and Blinn, D.W. (1997) Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary, and geomorphological influences. *Regulated Rivers: Res. Manage.* **13**, 129–149.
- Ursin, E. (1982) Stability and variability in the marine ecosystem. *Dana* **2**, 51–68.
- Van Winkle, W., Rose, K.A., Winemiller, K.O., DeAngelis, D.L., Christensen, S.W., Otto, R.G. and Shuter, B.J. (1993) Linking life history theory and individual-based modeling to compare responses of different fish species to environmental change. *Trans. Am. Fish. Soc.* **122**, 459–466.

- Van Winkle, W., Coutant, C.C., Jager, H.I., Mattice, J.S., Orth, D.J., Otto, R.G., Railsback, S.F. and Sale, M.J. (197) Uncertainty and instream flow standards; perspectives based on hydropower research and assessment. *Fisheries* **22**(7), 21–22.
- Walters, C.J. and Collie, J.S. (1988). Is research on environmental factors useful to fisheries management? *Can. J. Fish. Aquat. Sci* **45**, 1848–1854.
- Walter, C.J. and Juanes, F. (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can. J. Fish. Aquat. Sci.* **50**, 2058–2070.
- Walters, C.J. and Parma, A.M. (1996) Fixed exploitation rate strategies for coping with effects of climate change. *Can. J. Fish. Aquat. Sci.* **53**, 148–158.