

Recruitment Limitation as a Consequence of Natural Selection for Use of Restricted Feeding Habitats and Predation Risk Taking by Juvenile Fishes

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Juvenile fishes generally have spatial refuges from predation, and forage in limited but risky areas near refuges. Models of food density dynamics within such limited foraging areas predict that food availability and consumption per time spent feeding should depend strongly on juvenile density. Selection should act on the time that juveniles spend foraging, so as to strike a balance between growth and predation risk; we predict that optimum balance will occur at foraging times proportional to the minimum needed to reach viable sizes for later survival and reproduction plus an additional time inversely proportional to the predation risk per time. Combining the food availability and optimal foraging time predictions leads to stock–recruitment patterns similar to classic Beverton–Holt and Ricker forms, depending on how food organisms respond over time. Very strong density-dependent mortality can occur even without noticeable changes in juvenile growth rates or average food densities over large spatial scales, but intraspecific competitive effects should always be evident through density-dependent changes in foraging time.

Les poissons juvéniles disposent généralement de refuges qui les abritent de la prédation, et s'alimentent dans un périmètre limité mais risqué près des refuges. Des modèles de la dynamique de la densité de nourriture dans ces zones limitées prévoient que la disponibilité de nourriture et la consommation en fonction de la durée passée à s'alimenter doivent dépendre fortement de la densité des juvéniles. La sélection doit agir sur le temps passé par les juvéniles à se nourrir, de façon à établir un équilibre entre la croissance et le risque de prédation; nous prédisons que l'équilibre optimal se produira pour des durées de périodes d'alimentation proportionnelles au minimum nécessaire pour atteindre des tailles viables permettant la survie puis la reproduction, plus une période additionnelle inversement proportionnelle au risque de prédation en fonction du temps. En combinant les prédictions sur la disponibilité de nourriture et la durée optimale de la période d'alimentation, on obtient des schémas de recrutement des stocks similaires aux formes classiques des modèles de Beverton–Holt et Ricker, qui dépendent de la façon dont les organismes proies réagissent en fonction du temps. On peut observer une mortalité très forte dépendante de la densité sans même qu'il se produise de changement notable dans les taux de croissance des juvéniles ou les densités moyennes de nourriture sur de grandes échelles spatiales, mais les effets de la compétition intraspécifique doivent toujours se manifester par des changements de la durée de la période d'alimentation qui dépendent de la densité.

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Food competition and predation have long been suspected to limit recruitment rates in fishes, but field evidence to support or refute these suspicions has proven very difficult to find (Leggett 1986; Houde 1987, 1989b). Often, total recruitment appears to vary strongly and to be, on average, independent of adult spawning stock or egg deposition. However, even in such cases there must be strong density-dependent changes in average larval or juvenile survival rate to prevent recruitment from showing some increasing trend with increasing egg deposition. Average recruitment levels resulting from such density-dependent changes are seldom correlated in any obvious way with food production or predator abundance (see reviews in Rothschild 1986; Anderson 1988; Daan et al. 1990; Heath 1992).

We develop a series of models to show that the lack of simple correlation between food, predators, and recruitment could result from natural selection for restriction of foraging time in habitats

with high predation risk. We show first that food densities and consumption per time foraging in restricted foraging habitats can depend strongly on juvenile densities even when juveniles are not sufficiently abundant to affect large-scale food densities or production. We then show that natural selection should favor increasing foraging time and hence predation mortality as juvenile density increases, so that mortality rates can be density dependent even without food competition effects being exhibited through changes in growth rate. We examine the form of stock–recruitment relationships resulting from such interactions and show that forms like the Beverton–Holt and Ricker can result from differences in the way juveniles respond to changes in food density. We conclude that investigation of how density affects the way juvenile fishes distribute themselves on very small space and time scales is critical to understanding stock–recruitment relationships and trophic interactions.

It is certainly possible for recruitment limitation to arise from lack of suitable spawning habitat or mechanisms that cause density-dependent and/or density-independent mortality of eggs

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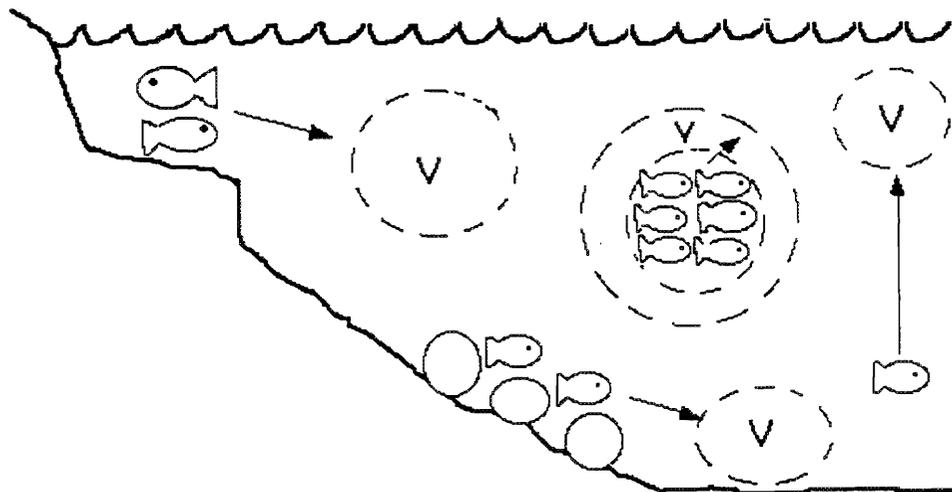


FIG. 1. Juvenile fishes use a remarkable variety of spatial refuges from predation and may be restricted to limited foraging volumes V near these refuges. Author's son William Walters, age 9, was able to identify several and produce this illustration, even with his limited fish experience.

and larvae. We restrict attention here to the later period in juvenile life during which individuals (1) have at least some limited control of their movements, allowing habitat choice, and (2) are small enough to face potentially high predation risk and are not yet capable of reproduction. Various workers have suggested that an understanding of the ecology and dynamics of juvenile stages should be an integral part of assessing and managing fish populations (Rothschild 1986; Houde 1987; de Lafontaine et al. 1992), particularly because it appears that the early juvenile phase can be critical in determining future year-class strength (Nielsen 1980; Sissenwine 1984; Peterman et al. 1988; Hallowed and Bailey 1989; Wooster and Bailey 1989; Szedlmayer et al. 1990; Bailey and Spring 1992; Bradford 1992). The important point is that even if density-dependent losses have acted in a major way on earlier stages, the mechanisms discussed below could still act to further reduce recruitment or to "override" the earlier limits, and hence to substantially dampen variability caused by environmental factors (as suggested by Gulland's (1965) idea of coarse and fine control of year-class strength variation). This effect has been shown for North Sea plaice stocks (see Beverton and Iles 1992), where although year-class strength is roughly determined ("fast coarse" control) during the pelagic larval phase (Rauck and Zijlstra 1978; Zijlstra and Witte 1985), a further readjustment ("fine" control) occurs early in the postsettlement phase (van der Veer 1986; van der Veer et al. 1990; Pihl 1990) when juveniles experience strong density-dependent mortality (Lockwood 1980; van der Veer 1986; van der Veer and Bergman 1987; Pihl 1990; Rijnsdorp and van Leeuwen 1992).

Prediction of Food Availability in Restricted Foraging Areas

Juvenile fishes generally spend most of the daylight hours in restricted spatial refuges where they are not highly vulnerable to visual predators (Helfman 1993). These refuges usually offer few or no feeding opportunities, and usually juveniles only move out from them to feed during short periods near dawn and dusk (e.g., diel vertical migration in juvenile sockeye salmon (*Oncorhynchus nerka*), Clark and Levy 1988) or at night (e.g., nocturnal inshore movement and feeding by juvenile cod,

Atlantic cod (*Gadus morhua*), Robb 1981; Pihl 1982; Clark and Green 1990; Keats 1990). The remarkable diversity of refuges used by juvenile fish (Fig. 1) hints at how strong the selection pressures must be to favor such behavior: some gather in very shallow water (Gibson 1993), others in the darkness of deep water (Neilson and Perry 1990; Greenberg and Stiles 1993; L'Abée-Lund et al. 1993), and still others find hiding places in rocky substrates or reef structures (Keats et al. 1987; Lough et al. 1989; Ebeling and Hixon 1991; Helfman 1993), and many species gather into tight shoals or schools where each individual spends most of its time with many neighbours between itself and the hungry mouths (Pitcher and Parrish 1993). For example, grunts spend the day schooling inactively on coral reefs, and after dusk migrate to nearby seagrass beds to feed (Ogden and Ehrlich 1977). The timing of these feeding migrations is strongly influenced by the activity of lizardfish, the primary piscivore in this system (Helfman 1986). The rapidity with which small fish vacate dangerous habitats when predators are experimentally added to a system (Werner et al. 1983; Schlosser 1987; He and Kitchell 1990; He and Wright 1992) and the increased survival of prey fish that is observed when refuge availability increases or predator density decreases (reviewed in Hixon 1991) suggest that selection must favor not only strong avoidance behavior in general, but also flexibility to vary its use.

But the use of such refuges implies very tight limits on the volume (or area) of potential feeding habitat available to juvenile fishes during those periods when they do move out (or as schools break up to feed in the twilight hours). Moving further or spending more time moving both imply increasing predation risk. To simplify the following discussion, we will treat the accessible feeding habitat volume (V) as fixed and consider only the effects of variation in the time spent in this volume; similar predictions are obtained for some more complex models where accessible habitat volume is admitted to vary with time spent feeding and juvenile size (swimming speed), but the impacts of varying juvenile density on food density (and hence growth per time feeding) are more difficult to calculate and visualize for such models. Below, we will sometimes refer to the refuge habitat and nearby foraging volume V together, calling this combination the juvenile "nursery habitat."

We now develop two extreme models for the effect of juvenile

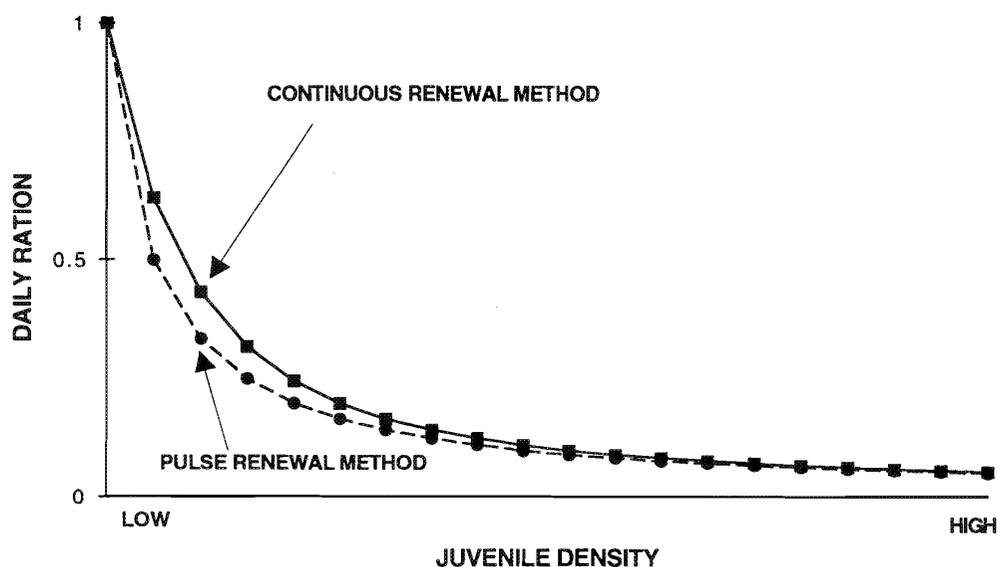


FIG. 2. Predicted effect of juvenile density on daily ration within restricted foraging volumes near predation refuges. Pulse and continuous renewal models represent alternative temporal patterns of delivery of food organisms to the foraging area.

density and time spent in the feeding volume V on the biomass density B of food organisms and resultant daily rations. For both, we assume that (1) food densities are generally low enough that handling time and satiation effects on daily rations can be ignored and (2) prey are widely enough distributed within V that juveniles cannot simply sit in one place and feed to satiation (the prey may be randomly distributed or clumped within V but we assume that juveniles are unable to hold in place and feed very efficiently for a long time on any clump they find). Under these two assumptions, daily rations F per fish should be proportional to the effective volume v swept per juvenile per time spent feeding (dependent on swimming speed, reaction distance to prey, and capture success), proportion of time spent feeding R , and prey biomass density B . If prey density does not vary over the feeding period, the per capita daily ration would then be just $F = vRB$.

Consider first a "pulse renewal" model, where food biomass is assumed to be renewed to a level B_0 each day during the time when juveniles are not feeding, through processes such as dispersal or migration of food organisms into the feeding volume V , water mixing processes, and food life history events like pupation. Processes such as these may well make B_0 totally independent of the number N of juvenile fish, at least if V is small compared with the volume (or area) over which longer term food production processes (growth, reproduction) occur. To simplify the algebra, let us assume further that R is small enough each day that we can ignore prey loss processes other than juvenile fish feeding during the feeding period(s). Then the biomass dynamics of B during the feeding period will be given by

$$(1) \quad dB/dt = -(v/V)NB$$

where v/V represents the instantaneous rate of food organism mortality per juvenile fish N . Note that the total mortality rate $(v/V)N$ can be large due either to (1) high v per fish (unlikely for small fish), (2) small V , or (3) high juvenile density N . The solution to eq. (1) is the familiar exponential decay equation, and

the predicted total food consumption over the period R by juveniles is just $VB_0(1 - \exp[-(v/V)NR])$, i.e., the volume times the change in food biomass density per volume. The daily ration per juvenile will be this total consumption divided by N :

$$(2) \quad F = VB_0(1 - \exp[-(v/V)NR])/N.$$

This model predicts exponential or hyperbolic decrease in daily ration F with increasing N (or N/V) as shown in Fig. 2, with F being most sensitive to N when N is low. The basic mechanism in this case is exploitation competition during the feeding period R .

As an extreme alternative, consider the "continuous renewal" model where food enters the volume V continuously at a rate E and is lost at an instantaneous rate m in addition to the loss rate due to fish feeding:

$$(3) \quad dB/dt = E - mB - (v/V)NB.$$

E may involve biological processes such as insect pupation and emergence as well as physical mixing processes carrying food organisms into V from some larger production environment. If E and m are fairly large (as could occur for example due to physical mixing processes in a small volume where juveniles feed on plankton), then this model predicts that B will quickly reach equilibrium at a concentration B_e , where

$$(4) \quad B_e = E/[m + (v/V)N]$$

and daily ration per fish is predicted to be $F = vRB_e$. Again, this model predicts a hyperbolic pattern of decrease in daily ration with increasing N/V (Fig. 2), with the largest effects occurring at the lowest juvenile densities.

Above, we treat R as fixed and predict food density B and consumption F as functions of fish density N ; thus, we have ignored satiation effects. An alternative approach would be to assume that juveniles can generally feed to satiation (until they

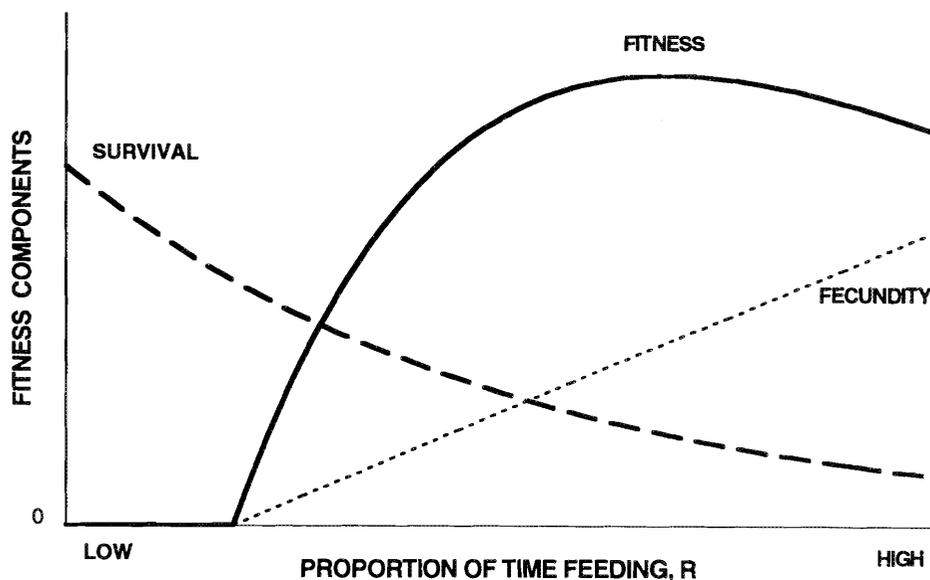


FIG. 3. Fitness as a function of proportion of time spent feeding. Survival decreases with increasing time due to predation risk, while long-term survival–fecundity increases only when some minimum or threshold feeding time is exceeded. Note that threshold time may be strongly density dependent.

achieve some target F) and to predict the foraging time R needed to achieve this satiation. In this approach, we would still conclude that N affects B and hence the time R needed to achieve satiation. The basic effect is the same in either case: as N increases relative to the available foraging volume V , juveniles must either accept lower F or increase R to maintain the same F .

The key point of these models is that it is flatly misleading to assert that competition for food should have little effect when juvenile abundance is low. Daily rations should in fact be most sensitive to abundance changes when abundances are low and will depend entirely on (1) how large the volume V is where the juveniles compete and (2) renewal rates of food into this volume. Moreover, the models above predict that competitive effects can be large even when juvenile feeding has no long-term effect on prey abundance through prey population dynamics mechanisms (i.e., overexploitation of some prey species) and replacement of preferred prey types with species/morphs that are less vulnerable to predation. It is of course possible for νN to be so small relative to V that competition effects are insignificant.

The above models link daily ration F to juvenile density N and proportion of time spent feeding R . In the next section, we discuss the relationship between R and lifetime fitness, which presumably depends on the size that juveniles reach before leaving refuge areas and/or how long they take to reach some minimum viable size for emergence. Before proceeding to the fitness discussion, we thus need to point out the functional linkage between F , R , and size predicted by basic bioenergetics models (Beyer 1989; Adams and Breck 1990). One simple representation of this linkage is the density-dependent growth model of Walters and Post (1993). That model combines eq. (4) with the assumptions that (1) search volume ν varies as roughly the square of body length L and (2) metabolism of small fish is approximately proportional to body weight (Giguere et al. 1988; Houde 1989a). These assumptions result in the growth model

$$(5) \quad dL/dt = k_1 R / (1 + k_2 L^2 N) - k_3 L$$

where the constants k_1 and k_2 combine the food turnover parameters of eq. (4) with the length–weight parameters and bioenergetics parameters for assimilation efficiency and specific dynamic action, while k_3 represents effects of routine metabolism (for details of the derivation, see Walters and Post 1993). Numerical integration of equations like (5) over time, under various assumptions about how N changes during the juvenile stage, leads to the prediction that the foraging time R required to reach a given threshold size L_0 should be roughly proportional to the initial density N_0 when the juveniles begin to use the refuge habitat. This rough prediction breaks down if L_0 is close to the maximum size that the juveniles can reach even when N_0 is low; in such cases, the R required to reach L_0 within some reasonable time horizon may increase exponentially with N_0 . However, such exponential increase would simply exaggerate the effects predicted below from simpler proportional increase.

Prediction of Optimal Foraging Time

Here we show that natural selection for behaviors that optimize the risk taking time R should very generally result in density-dependent juvenile mortality. The key conditions for this prediction to hold are shown to be (1) existence of a minimum or threshold foraging time R_0 below which the juvenile can never successfully leave the nursery habitat and (2) heritable variation in behavioral traits that result in variation in R with changes in food density. There is a substantial literature on how predation risk should influence optimal foraging behavior and growth (i.e., reviews by Helfman 1986; Sih 1987; Gilliam and Fraser 1988; Godin 1990; Lima and Dill 1990; Werner 1992; Milinski 1993); our presentation here is really just a review and restatement of those findings, with linkage to the predictions of the previous section.

The expected lifetime fitness W of a juvenile fish beginning at the time it enters the juvenile nursery habitat can be expressed as

$$(6) \quad W = S_j S_m \bar{f} = S_j f$$

where S_j is survival rate through the juvenile stage, S_m is survival to maturity after leaving the juvenile nursery, and f is adult fecundity (or sum over mature ages of survivorships from maturity to age times fecundities at age for iteroparous species). f merely combines survival and fecundity effects after leaving the nursery: $f = S_m f$. Both S_j and f presumably vary with R . Let us assume that predation loss simply involves random encounters with predators during feeding times (no complex predator behavioral responses such as type III switching or satiation at high juvenile densities); then we expect S_j to vary as

$$(7) \quad S_j = \exp \{-M_0 - M_1 R\}$$

where M_0 is a base natural mortality rate that would occur even in the absence of predators, and M_1 is the instantaneous predation risk per time spent foraging. In this case, it is easily shown by differentiating eq. (6) with respect to R that W is maximized at that R value R_{opt} where

$$(8) \quad (df/dR)f = M_1,$$

i.e., fitness is maximized at the feeding time "investment" where the relative gain in long-term survival-fecundity $(df/dR)f$ is just balanced by the predation risk per time feeding.

Suppose next that long-term survival-fecundity f is an increasing function of feeding time R (increased feeding time generally leads to larger body sizes (Wootton 1990), and fecundity and survival are positively related to body size in fishes (Bagenal 1978; Peterson and Wroblewski 1984), for R above some minimum threshold R_0 necessary to successfully emerge from the refuge, survive, and/or reproduce at all (see Fig. 3). The exact form of f is not critical to our arguments, so for convenience, let us assume that f is linear:

$$(9) \quad f = k_f \cdot (R - R_0) \text{ for } R > R_0 \text{ and } f = 0 \text{ for } R < R_0$$

where k_f is the slope of the f versus R relationship for $R > R_0$. For this functional form, application of eq. 8 leads to a very simple prediction for the optimum feeding time:

$$(10) \quad R_{opt} = R_0 + 1/M_1,$$

i.e., fitness is maximized by spending a proportion of time spent feeding equal to the bare minimum needed to survive/reproduce after leaving the juvenile nursery, plus additional time inversely proportional to the predation risk M_1 per time spent feeding. Remarkably, the optimum time is completely independent of the absolute slope k_f of the long-term survival-fecundity relationship, i.e., it does not matter how rapidly survival-fecundity improves for feeding times greater than R_0 . We have checked the eq. (10) prediction for a variety of more complex f functions (polynomial, logistic, etc.), and it appears to be very robust. An interesting special case is $R_0 = 0$ (any nonzero feeding time leading to proportional increase in long-term fitness); for this case, $R_{opt} = 1/M_1$, i.e., the optimum feeding time would depend only on predation risk and would be entirely independent of density (since R_0 is related to juvenile density as shown in the previous section) except insofar as M_1 might vary with density through effects such as attracting predators to the feeding volume or long-term increase in the number of cannibalistic adults.

Note that eq. (10) can predict $R_{opt} > 1$ for low values of predation risk M_1 and/or high values of R_0 . In this case the optimization

is predicting that juveniles should either feed all the time or extend the total time spent in the nursery habitat, as in models for the timing of ontogenetic habitat shifts (Werner and Gilliam 1984; Werner and Hall 1988). We do see such extensions, at least when R_0 is large; for example, anadromous salmonids rearing in very unproductive lakes/streams tend to spend more years in freshwater, and the proportion smolting at younger ages sometimes appears to be lower when densities are high (see reviews in Groot and Margolis 1991). Growth rates, rather than just threshold smolting size, can also determine smolting age so that faster growing parr smolt younger and smaller than slow-growing parr (Okland et al. 1993). However, if only M_1 is very low, it is questionable whether a refuge-use strategy would be optimal in the first place; we suspect that very few (if any) juvenile fish enjoy this circumstance under natural conditions. However, refuge-use tends to be minimized when predation risk is low. For example, shoaling tendency decreases with increasing size in goatfish (Uiblein 1991), in many species, shoals become more compact and cohesive when predators are detected or in daylight (Luo 1993; Pitcher and Parrish 1993), shelter affects goby distributions only in the presence of predators (Utne et al. 1993), and diel migrations of various juvenile fish are less intense in turbid lakes than in clear lakes (likely related to the visual searching ability of the dominant piscivores) (Levy 1990; Gliwicz and Jachner 1992).

We can now state the key result of our analysis: if the minimum feeding time R_0 needed for successful emergence from the juvenile nursery is density dependent (and it should be strongly so based on the arguments of the previous section), then selection for optimization of feeding time according to eq. (10) should lead to density-dependent juvenile mortality. That is, juvenile survival $S_j = \exp \{-M_0 - M_1 R_{opt}\}$ should be a decreasing function of juvenile density because R_0 should increase with increasing density. Young-of-the-year steelhead (*Oncorhynchus mykiss*) show density-dependent dispersal, growth, and survival. Over-winter survival is contingent upon fish reaching a threshold weight, and the proportion of fish attaining the threshold size is inversely related to age-0 density (Close and Anderson 1992). Although the authors did not examine the mechanisms causing density-dependent threshold sizes, the arguments presented above would suggest that the main cause may be density-dependent changes in R_0 .

The density-dependent survival effect may or may not be accompanied by noticeable changes in growth rate or juvenile size at the time of emergence from the nursery. If the predation risk M_1 during juvenile feeding is high, then the optimum feeding time will be near R_0 and juveniles should always emerge at or near the minimum viable size after electing not to take the additional risks needed to improve growth rate. Note that this conclusion is not affected by arguments about how increased growth rates and size may lead in the long term to reduced predation risk; if the feeding time required to achieve increased size is density dependent, then the overall effect on juvenile survival will still occur even though increased size contributes to higher f values later in life.

In the derivation of eq. (7)–(10) we have treated predators as a proximate or incidental source of mortality, with an overall impact on juvenile survival dependent on how feeding conditions affect time exposed to predation risk. This assumption is certainly parsimonious, and is probably the most realistic for most juvenile fishes, who face a wide suite of potential predators and are rarely numerous enough to cause strong predator

handling time or satiation effects (predator stomach contents data rarely suggest satiation for long periods of time on any one type of juvenile fish; see reviews in Dill 1983; Wootton 1990; Yamaoka 1991). But there are two complications worth mentioning. First, some predators may “switch on” or aggregate in juvenile feeding areas when juvenile densities are high (Mittelbach and Chesson 1987); this would simply exaggerate the density-dependent effects predicted earlier. Second, in some situations, especially with schooling juveniles, short daily feeding periods may combine with efficient predator searching and relatively long handling times per prey to produce predation rates that are depensatory at high juvenile densities. That is, predators may each take a nearly constant number of juveniles per feeding period, so that the instantaneous predation risk M_1 varies as

$$(11) \quad M_1 = mRP/N$$

where m is the daily number of juveniles eaten per predator, P is predator abundance, and N is juvenile abundance. This inverse dependence of risk on N could result in selection for longer feeding times R and ultimately lead to essentially density-independent net predation effects (R proportional to N due to food competition would make M_1 in eq. (11) independent of N). However, it is hard to imagine such happy situations for the predators lasting very long, due both to eventual decreases in N and to responses of predator abundance given an essentially unlimited food supply.

Another possible objection to the survival model (eq. (7)) leading to the fitness-maximizing prediction of eq. (10) is that incidental predation risk may increase more violently with R than is assumed in the proportional model M_1R . This would be expected for example in situations where juveniles feed mainly near dawn and dusk, so that feeding a bit longer in the morning or starting earlier in the evening means moving around when light levels are higher and visual predators can search larger water volumes (effects of light level on reaction distances, see Confer et al. 1978; Zaret 1980; Henderson and Northcote 1985). If such effects lead to harsh selection against increasing R , then at high densities, juveniles may have little choice but to grow more slowly and take longer to reach sizes where they can move out of the nursery habitat. The basic selection model for this case is the same as presented above, but with R replaced by a variable representing total time spent in the nursery. This model predicts strong changes in both growth and survival with density, as in the recruitment models proposed by Ware (1975, 1980), Shepherd and Cushing (1980, 1990), and Beyer (1989) and in the individual-based models of DeAngelis et al. (1991, 1993). Thus, previous recruitment models based on density-dependent growth and time exposed to size-selective predation may be viewed as a special or limiting case of the theory presented here, for situations where M_1 is very large.

Foraging Time Decisions and Stock–Recruitment Relationships

While the analyses presented above indicate that we should very generally expect to see some pattern of density-dependent mortality in juvenile fish, they unfortunately do not lead directly to simple predictions about the functional form of the stock–recruitment (or more precisely, the larval settlement–recruitment) relationship. Such predictions require examination of at least two additional relationships involving space–time

scales that we have so far ignored: (1) how juveniles adjust their risk-taking behavior over the rearing period, as densities decrease and body size increases and (2) how density-related changes in larval dispersion pattern, and juvenile dispersal behaviors, are related to the mesoscale spatial structure of nursery habitats (where we assume that the feeding volume V most often consists of a set of localized subvolumes V_i that vary in food availability and predation risk). In the following discussion, we will refer to “recruitment” as the number N_r of juveniles that successfully emerge from the juvenile nursery; if N_0 fry or larvae enter the nursery, then $N_r = N_0S_j$. Obviously, we could extend the prediction using S_m of eq. (6) to predict recruitment of mature fish, although we would need to be careful about whether density-dependent variations in optimal body size at emergence might lead to further density dependence in S_m (e.g., density-dependent decreases in smolt size of sockeye salmon are probably associated with decreases in subsequent marine survival; see review in Burgner 1991).

There are at least three alternative possibilities for how juveniles might adjust their foraging times in relation to density-related changes in food availability: (1) no individual adjustment — changes in foraging times result from density-dependent selection for animals with different foraging time phenotypes; (2) early adjustment — foraging time for each individual is determined by the competitive conditions that it encounters early in life; (3) continuous adjustment — juveniles make rapid adjustments in foraging times as densities change during the development of each cohort. The following subsections discuss the widely differing predictions arising from each of these possibilities, and further subsections discuss the implications of mesoscale structure in nursery habitats and the use of stock–recruitment equations as empirical descriptions for the net effects of behavioral responses.

No Individual Adjustment of Foraging Time

Suppose each individual i in a population has a fixed foraging time phenotype R_i , and does not adjust foraging behavior to changing competitive conditions. Suppose further that there is heritable variation in R_i among individuals. These are the classical conditions for density-dependent selection. At high population densities, selection should favor “ K -type” animals with high R values (R_0 high if density high); at low densities, selection should favor “ r -type” animals with low R values (less foraging time needed, so avoid predators instead). In this case, it is meaningless to talk about a single stock–recruitment relationship because the relationship should change over time as selection alters the mix of low- R and high- R type individuals in the population, and hence the juvenile mortality rates due to predation. Such response delays have some very frightening implications for what we might see in the field under varying exploitation regimes.

Consider a population that has stabilized at a high level, such that competition among juveniles is intense and selection has favored relatively high R values. Now suppose that exploitation rate increases such that egg production and recruitment of juveniles to the nursery habitats decreased greatly. These juveniles will initially be mostly high- R types and will show substantial improvements in growth rate; meanwhile, juvenile survival rates will remain relatively low (due to high R and associated predation), and recruitment rates may decline. But selection will now favor individuals who spend less time foraging, so over time the average R value will decrease and growth

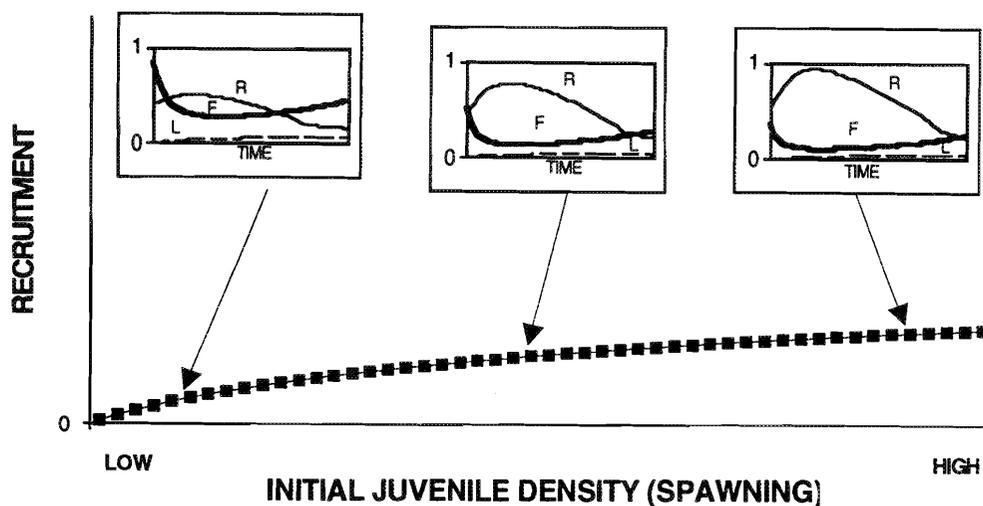


FIG. 4. Simulated stock–recruitment relationship for a population where juveniles vary foraging time during development by following a myopic decision rule. Inset graphs show sample time trajectories over the juvenile rearing period of body length (L), food density (F), and proportion of time spent feeding (R).

rates will fall back toward the pattern seen before the population decline; during this period, juvenile survival rates will improve, tending to stabilize total recruitment. Precisely this sort of density-dependent improvement but later decline in growth rates has been seen in major Atlantic cod stocks but has been attributed either to ecosystem changes or to selection against fast-growing fish by the fisheries (Hanson and Chouinard 1992); recruitment rates also appear to have declined and then stabilized as we predict. Although juvenile Atlantic cod are known to be sensitive to predation risk (Nordeide and Svasand 1990; Gotceitas and Brown 1993), the flexibility and heritability of predation risk behavior remain largely unexplored (but see Johnson and Abrahams 1991 for an example of inherited predation risk behavior).

The density-dependent selection scenario becomes even more frightening when we ask what should happen when fishing is stopped to allow stock recovery, as has recently occurred with the Northern cod stock off Canada's east coast. If the stock has been kept down long enough for growth rates to decline, signalling predominance of low- R type juveniles, then increases in spawning associated with the fishery closure will at first cause increases in the density of competing juveniles, causing growth rate declines and possibly other signals of recruitment limitation (delays in leaving nursery habitats, reduced survival S_r to recruitment). Selection will now begin to favor high- R juveniles, but there may be considerable delay before these individuals become abundant enough to result in high total recruitment rates. In short, the linkage of the selection process with population increase may cause the increase to be drastically delayed compared with what we would predict from simple stock–recruitment relationships based on recruitment data obtained during the population decline.

One might object at this point that the whole argument about low- R and high- R individuals is silly because surely natural selection should favor at least some degree of behavioral plasticity (alteration of R by individuals, with changing competitive conditions) of the types discussed below. But is behavioral plasticity always favored, especially in long-lived species like the Atlantic cod that have probably been very abundant for a long time? Under such circumstances, it is entirely

possible that selection has indeed favored specialized genotypes rather than flexible phenotypes (Real 1980; Van Tienderen 1991). For example, even diet generalists such as bluegill (*Lepomis macrochirus*) have evolved relatively inflexible habitat-specific foraging behaviors (Ehlinger and Wilson 1988; Ehlinger 1990).

Early Adjustment of Foraging Time

If juveniles are slow to adjust their risk-taking behaviors with changes in the density of conspecific competitors, then they may persistently act as though R_{opt} in eq. (10) is high if N_0 was high at the time when they began to use the nursery. If R_{opt} is roughly proportional to N_0 , the overall recruitment relationship will then be a dome-shaped or Ricker form:

$$(12) \quad N_r = N_0 \exp\{-M_0 - M_1 R_{opt}\} = N_0 \exp\{-M_0 - M_1' N_0\}$$

where M_1' is M_1 times the proportionality constant between R_{opt} and N_0 . The exponential effect could of course be exaggerated by increases in M_1 , if increases in N_0 are associated with increases in number of cannibalistic older fish.

Continuous Adjustment in Foraging Times

At the opposite extreme, juveniles might adjust their daily times at risk rapidly as available food density varies with body size and N (eg., if it varies inversely with $L^2 N$ as in eq. (5)). If mortality rate then ends up being roughly proportional to N remaining at each time during the juvenile stage, the overall recruitment relationship will be precisely the asymptotic form known as the Beverton and Holt relationship (Shepherd and Cushing 1980). However, the mechanism need not be so simplistic; an asymptotic relationship can arise from rapid behavioral adjustments even if prey availability and foraging time vary in a complex way over time due to changes in both juvenile lengths and abundance. Figure 4 shows an example of this situation. To construct the example, we simulated food density and growth changes over a hypothetical rearing period using eq. (3) and (5) while assuming instantaneous predation mortality rate each day proportional to R treated as a daily proportion of time spent feeding. R was varied over time by

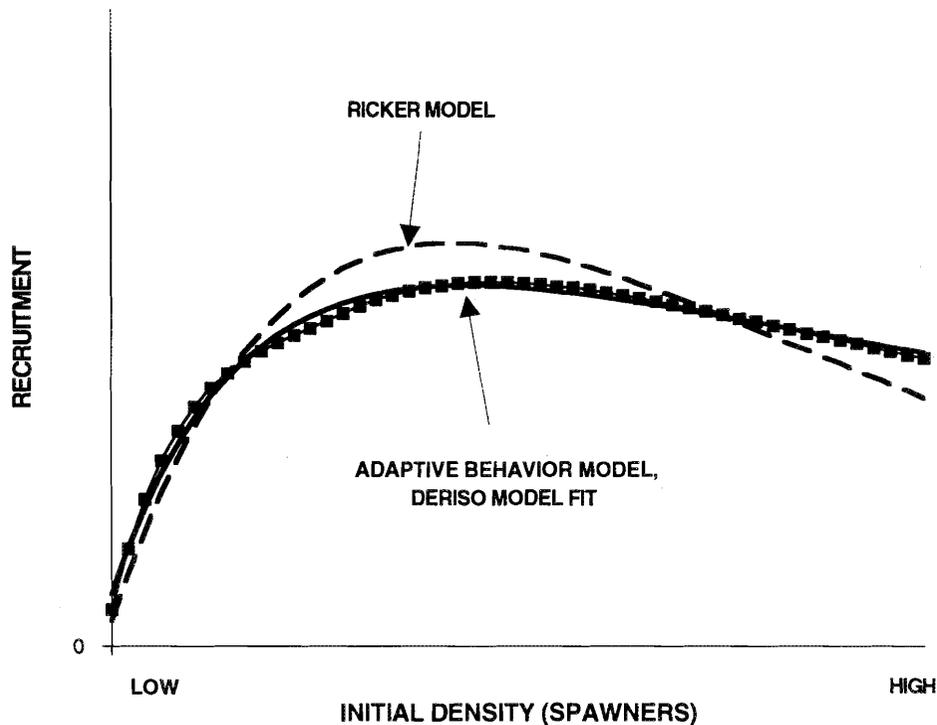


FIG. 5. Simulated stock–recruitment relationship for a population where juveniles vary foraging time during development in relation to both changing food density and predation risk, where predation risk is assumed due to cannibalism and is proportional to initial juvenile density. Fitted equations are the Ricker model and the recruitment model of Deriso (1980).

assuming that the fish follow a “myopic decision rule,” choosing an R each day that would optimize fitness if food densities remained the same after that day (over the rest of the rearing period). Note in Figure 4 that such a behavioral decision rule would result in the juveniles spending too much time feeding early in the juvenile period (when L^2N is still high), but then stopping entirely later when they “discover” that food supply has recovered due to reduced N .

A fascinating question is whether natural selection could result in the evolution of decision rules that avoid the overcompensation in R shown in Figure 4, to somehow make the juveniles act as though they were able to predict future changes in competitive conditions during the rearing period. Such optimal decision rules can be computed using dynamic programming (Mangel and Clark 1988) and compared with observed trajectories in feeding times.

Suppose that cannibalism is the main cause of M_1 and that individuals can adjust rapidly to both changing food densities and predation risks. In this situation, we would expect N_0 and M_1 to be positively related (in the simplest case, proportional to adult density), and the myopic decision rule used to produce the results in Fig. 4 leads instead to a dome-shaped recruitment relationship similar to the Ricker curve (Fig. 5). However, we simulated this situation for a variety of growth–mortality parameter combinations, and all produced a characteristic pattern of deviations from the classic Ricker form: higher recruitment rates at very low stock sizes than predicted by the Ricker model, along with a flatter dome and less pronounced decrease at high stock sizes. These differences are perhaps trivial from a management point of view, and are certainly not helpful in terms of recruitment forecasting considering other sources of recruitment variation,

but nevertheless represent a “signature” that might be useful in empirical studies aimed at determining whether adaptive changes in juvenile behavior may be influencing recruitment patterns.

Mesoscale Structure in Nursery Habitats

If the overall juvenile rearing environment consists of a series of sites with feeding volumes N_i varying in size or quality (maximum prey density), recruitment prediction is complicated by questions of whether juveniles can somehow find and occupy better areas first and whether selection will favor behavioral decision rules for dispersal (MacCall 1990). Assuming that dispersal between sites involves the same kind of predation risks as feeding, we can obviously construct selection models that imply density-dependent dispersal mortality (i.e., do not move unless your current site is crowded enough to prevent successful growth through adjustment of R , or balance risks associated with variation in R against the odds/risks of finding a better site). Depending on habitat structure and the riskiness of dispersal, such models might predict very complex recruitment relationships. One possibility is apparent multiple equilibria or “plateaus” in recruitment if dispersal is very risky; in this case increases in density up to some threshold point may result in increased foraging time and hence a flattening of the recruitment function, but accidents that push density beyond the threshold may lead to dispersal that in turn results in a higher plateau due to colonization of more habitat sites. Another possibility is an “ideal free” situation where all individuals achieve the same R through dispersal (Fretwell and Lucas 1970; Fretwell 1972).

Empirical Equations for Stock–Recruitment

Various behavioral response lags could produce recruitment relationships intermediate between the Ricker and Beverton–Holt extremes. Such a spectrum of outcomes is predicted by the recruitment model of Deriso (1980), which Schnute (1985) showed is conveniently parameterized as

$$(13) \quad N_r = aN_0 (1 - bcN_0)^{1/c}$$

where a , b , and c are parameters to be determined empirically (Fig. 5). Deriso (1978) derived this function from a two-variable model for the joint time dynamics of juvenile numbers and biomass of prey, where the prey are assumed to have density-independent population growth rate and are eaten at a constant rate per juvenile fish, while instantaneous mortality rate of juvenile fish is assumed proportional to the ratio of fish to prey densities. Although his submodel for prey dynamics is quite different from the ones we suggest above, that submodel could be interpreted as representing how juveniles perceive or measure changes in prey density (i.e., with behavioral response lags). Further, his ratio-dependent mortality term can be interpreted as one simple way to predict the outcome of time-dependent risk-taking behaviors associated with both feeding and dispersal. Thus, we predict that Deriso's formula will turn out to be a good way to empirically represent the varied recruitment patterns that might result from selection on R (Fig. 5). Another expression that may do a good job at empirically representing delay effects is the one proposed by Gomez Muñoz (1986).

Discussion

Although there is nothing really new in the arguments presented above, our analysis has brought together disparate models to yield new insights into how individual behavioral mechanisms might lead to whole-population dynamics. Biologists have long speculated that intense food competition may arise from restriction of feeding in small areas, whatever may cause the restriction (e.g., see Mittelbach and Chesson 1987; Persson and Greenberg 1990; Persson 1991). Previous models analyzing the trade-off between predation risk and energy gain have focused on the adaptive control of foraging effort as it relates to the forager's life history (Abrams 1991), various individual responses in activity level related to the presence of predators (reviewed in Werner 1992), trade-offs mediated through habitat choice (Werner and Gilliam 1984; Gilliam and Fraser 1987; Brown 1988; Abrahams and Dill 1989; Ludwig and Rowe 1990), the effects of uncertainty in predation risk on optimal patch use (Sih 1992), and the prediction of population bottlenecks when predation risk exceeds species-specific maximum potential reproductive rates (r_{\max}) (Williamson 1993). Density dependence has usually been incorporated into such models using notions of the ideal free distribution (Rosenzweig 1991) or to predict the joint effects of changing resources and predators on habitat choice of competing species (Gilliam and Fraser 1988).

What is new in our analysis is that we combine models of food density dynamics in limited foraging areas and predict that food availability and daily rations should be strongly density dependent leading to density-dependent mortality. Many workers have found that growth and survival are density dependent, particularly for small postsettlement sizes of demersal and reef fish (Lockwood 1980; Ware 1980; Zijlstra et al. 1982; Cook and

Armstrong 1986; van der Veer 1986; Peterman and Bradford 1987; Doherty and Williams 1988; Sundby et al. 1989; Daan et al. 1990). However, the mechanism(s) leading to density dependence are rarely identified (Anderson 1988; Shepherd and Cushing 1990) and the potential importance of these processes for population regulation is rarely specified (Daan et al. 1990; Shepherd and Cushing 1990; Rijnsdorp and van Leeuwen 1992).

It is also not news that natural selection should favor some balancing act in relation to the growth and survival implied by correlation of predation risk and feeding (Abrams 1991; Werner 1992), although the relatively simple balance implied by eq. (10) is perhaps a bit surprising. However, the very existence of a selection balance has at least two profound implications for prediction of the role of ecological factors in recruitment limitation. First, according to the selection argument, it is meaningless to pose simplistic, single-factor hypothesis like "recruitment is limited by food" or "recruitment is limited by predation" or "recruitment is limited by cannibalism"; the single factor to start with is the selection process itself (i.e., the balancing act). Second, we should distrust trophic predictions of the form "increased predation risk should lead to reduced density and less effect of intraspecific competition." As noted earlier, selection arguments lead to exactly the opposite prediction: increased predation risk should lead to shorter foraging times and smaller foraging volumes V , hence increasing competition and exaggerating density-dependent effects of growth rate.

Moreover, the models we present have serious implications for fisheries enhancement programs aimed at improving early survival. For example, recruitment limitation resulting from predation risk avoidance may explain the apparent failure of hatchery programs to increase abundance of coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) off the Pacific coast of North America (Walters and Riddell 1986; Emlen et al. 1990) (Fig. 6). During the 1970's, there were various efforts to assess the "carrying capacity" of the North Pacific Ocean for hatchery salmon, based on total food supply and production estimates over large areas (Walters et al. 1978); our general conclusion was that severalfold increases in production should be possible. Instead, what we have seen under increasing hatchery releases is declining marine survival, and little or no increase in large-scale production (small-scale increases from some stocks and hatchery facilities have been mostly balanced by losses in other, usually wild, stocks). While various long-term environmental trends could explain declining trends in marine survival, these survival patterns are certainly consistent with the hypothesis that juvenile coho and chinook are using only a very restricted portion (something like one fifth) of the food production system potentially available to them. Similar conclusions to ours were reached by Salvanes et al. (1992) who developed a model that suggested that juvenile cod enhancement may not always lead to increased production. Increased juvenile stocking may instead result in food and refuge limitation leading to density-dependent growth and survival.

We do not imply from these examples that all enhancement efforts are a waste of time. Predation-related habitat restriction can also explain the dramatic increase in recruitment often seen in marine fish when artificial reefs are provided: these reefs create both "cover" for juvenile fish and feeding volumes V where predators may be attracted by the presence of juveniles.

The arguments presented above also contain the seeds of a possible explanation for the apparent compensatory recruitment patterns (Clark 1974; Murphy 1980) and the delays in stock

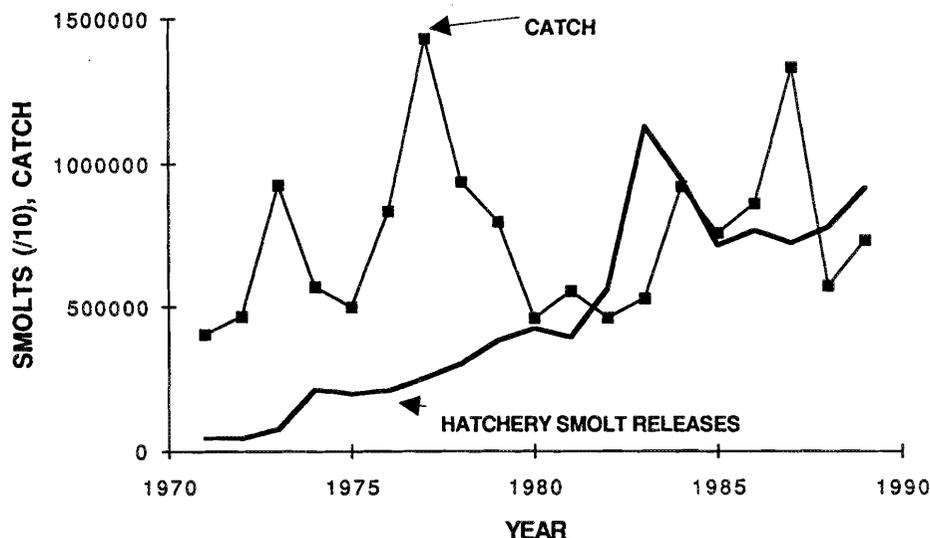


FIG. 6. Increases in coho salmon smolt releases from hatcheries around the Strait of Georgia, B.C., have not been accompanied by consistent increases in sport and commercial catch. Hatchery fish now make up nearly 50% of the catch, so the wild stock contribution has declined substantially. (Source: Department of Fisheries and Oceans catch statistics, Cross et al. 1991.)

recovery that have concerned managers of schooling clupeoid fishes (Wyatt and Larrañeta 1988). If a schooling stock is very low, increases in abundance and shoal/school size may initially result in density-dependent mortality due to individuals spending more time foraging at the school boundaries (“fuzzing” the school boundary), breaking away from schools earlier in the evening, and/or rejoining schools later each morning. This density-dependent effect would tend to stabilize stock size at a low level. But increases in movement and feeding time may also lead to increased probability of localized “range extensions” through formation of new schools and associated colonization of larger areas, with each such relatively rare event leading to a temporary reduction in school size (and mortality rate) and a new, higher apparent “limit” on total recruitment. The apparent limit should increase more rapidly over time as more schools/shoals contribute to the dispersal and colonization process. Under this scenario, oceanographic variations such as changes in current regimes near spawning areas could act as important “triggers” for stock expansion, by altering probabilities of successful dispersal, without being correlated in any obvious way with short-term changes in recruitment rates. Also, any attempt to directly relate recruitment to stock size will show strong and apparently unpredictable patterns of “nonstationarity” (Walters 1987).

A further broad implication of spatial restriction in foraging and associated density-dependent effects is ratio dependence in overall predator-prey relationships between fish and their food organisms, except in cases where foraging volume V is a large proportion of total volume over which food production dynamics take place. (see Ecology Special Feature articles beginning with Berryman 1992, and especially Ginsburg and Akcakaya 1992). Ratio dependence can explain the lack of field evidence in fish-food systems for patterns predicted by classical predator-prey models. In particular, there is little field evidence of predator-prey cycles with periods predicted by classical models, or of the “paradox of enrichment” (destabilization under enrichment or along natural gradients in prey productivity; see McAllister et al. 1972). Fish food organisms are presumably subject to the same

selection forces as juvenile fish, trading off behavioral and developmental traits that would maximize their productivity against traits that make them less vulnerable to the fish.

Thus, when we finally see a coevolved food chain, where selection at each link has been influenced by the risks represented by links higher up the chain, we should not expect to see any simple production relationships between successive trophic levels. In other words, selection may well drive ecological efficiencies to far lower values than would be predicted by simple energy flow/loss models. Hence, we should not expect studies of basic aquatic production processes to help much in predicting recruitment to particular fish species.

While evolutionary arguments lead us to be pessimistic about predicting recruitment limits from simple trophic studies, they do not imply that field studies on recruitment mechanisms are a waste of time in general. Based on the models above, we would recommend careful attention in recruitment studies to (1) spatial habitat use by juveniles (assessment of V and variation in prey density within it), (2) a shift in emphasis from study of density-dependent growth and size dependence in mortality to study of how density affects individual time budgets and exposure to predation risk, and (3) study of behavioral and physiological mechanisms for adjusting foraging time and behavior to varying food density and predation risk. In terms of theoretical and modelling research, we recommend the inclusion of time budget optimization calculations in all multispecies modelling efforts.

One useful research approach may be to do careful habitat mapping and juvenile distribution/time budget studies leading to comparative analysis of variation in V among species and locations. This would also lead to estimates of vN/V , a key determinant of impact on local food concentrations within feeding areas.

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