

Empirical and Theoretical Approaches to Size-Based Interactions and Recruitment Variability in Fishes

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ABSTRACT. Traditional age-based population models have been widely used both in ecology and fisheries management. But age-based models have been difficult to apply to fishes and other organisms where survivorship and fecundity depend more strongly on size than age. In fishes, recruitment variation is often high and has important population implications. The mechanisms controlling survival and recruitment of fishes appear to operate at the level of the individual, so modeling this process may best be done using individual-based models. Individual-based models have been widely used in fish behavioral and physiological ecology, but the population implications of variation among individuals have not been carefully examined.

Our studies of recruitment mechanisms of Lake Michigan bloater (*Coregonus hoyi*) have shown the importance of body size and growth rate variation to recruitment. Based on a literature review, body size and growth variation in larval fishes seems to be of widespread importance. An individual-based model for predation on larval bloaters suggests that variation among individuals in growth rate can influence cohort survival and size structure. Size-dependent mechanisms controlling recruitment in fishes may be successfully integrated using individual-based models.

Introduction

Population Modeling

Population modeling in ecology has traditionally based classes or categories on age. This probably derives from the dependence of early population modelers on human demographic models (Hutchinson 1978). But humans are not necessarily representative of other animal populations; they are long lived, show little variation in offspring number and are extremely age-specific in rates of fecundity and survival. Most animals, including many

vertebrates, are relatively short-lived, show high variation in the number of offspring produced, and vital rates may be more directly linked to body size than age *per se* (Kirkpatrick 1984, Sauer and Slade 1987, Sebens 1987).

Frequently, these models combine many individuals into the same group that is modeled with a single state variable, such as population size or the number of individuals in age class three. In some cases this approach may be appropriate, but in many cases, the biology dictates a lower level of aggregation in the model. For example, differences among individuals within a class due to either genetics or environment may force the consideration of finer classes and ultimately an individual-based approach (Huston et al. 1988). In addition, most models exclude localized effects and assume all interactions among individuals are homogeneously distributed. For sessile organisms, in particular, this may be an inappropriate assumption. This also leads to a finer scale of resolution in the model (Huston et al. 1988). In the final analysis, the appropriate scale of aggregation in a model of population dynamics must depend upon the questions being asked and the systems under examination.

Modeling fish population dynamics is a practical enterprise that derives from an interest in managing commercial stocks of fishes. In particular, one seeks to model fish populations to understand how to enhance the yield of the fishery while sustaining the population's capacity to produce that yield. Models of fish population dynamics also enhance our ecological insights regarding how these populations function. Because fishes have highly plastic growth rates, traditional age-based models might have seemed inappropriate, *a priori*, but their application has a long and venerable history in fisheries (Gulland 1977).

The link between fisheries and population modeling in basic ecology is an old one, but ecological and fisheries theories have tended to develop separately (Kerr 1982, Werner 1982). Our goal here is to summarize the major approaches taken in modeling fish populations, and in this context to review our work over the last 10 years.

Demographic techniques initially used in fisheries management as well as for other organisms were "borrowed" from human demography (Hutchinson 1978). Early population models in general ecology treated all individuals as identical (as in the classic exponential and Pearl-Verhulst logistic models of population growth). Early fishery yield modeling did the same (as in the surplus-yield model, Schaefer 1954). Later models from both general ecology and fisheries considered age classes explicitly (in fisheries, the dynamic pool model, Beverton and Holt 1957). The data necessary for such models could be organized in a life table that outlined the age-specific survivorship and age-specific fecundity typical of those populations. Age could be formally accommodated using the population projection matrix approach (Leslie 1945).

While this approach often proved acceptable for mammals and birds, where key parameters of fecundity and survivorship are fairly predictable (but see Sauer and Slade 1987), age-based models have been difficult to apply to fishes, insects, other invertebrates, and many plants where survivorship and fecundity at age are much less predictable (Sebens 1987). These organisms generally produce large numbers of offspring which experience high mortality during their early life history, and highly variable survival.

To resolve this problem, the population projection approach can be extended to include stages rather than ages as the unit of aggregation in the models (for a review see Caswell 1989). These models are particularly appropriate when different ontogenetic stages of organisms with complex life histories have substantially different population parameters, or spend variable periods of time within a stage (Hartshorn 1975, Werner and Caswell 1977, Caswell 1986, Crouse et al. 1987, Werner 1988). The mathematics and analyses of matrix population models are now well developed.

Fishes also have highly plastic growth and may span a wide range of sizes at a single age. In fishes, age is relatively easy to estimate although this can be difficult in the tropics (Pauly 1980). However, survivorship and fecundity depend more directly on size than on age *per se* due to variability in growth rates (Beyer 1989). Because a wide variety of processes can affect growth rates and size structures of fish populations (e.g., food, temperature, population density, predators, exploitation), age specific survival and fecundity can change dramatically from one period to the next. This requires re-parameterizing the age-based model for the "new" conditions. An alternative, only recently being explored, is to develop parallel size-based population models (e.g., VanSickle 1977, DeAngelis et al. 1979, 1984, Kirkpatrick 1984, Ebenman and Persson 1988, Beyer 1989).

Recruitment Variation

One of the key characteristics of fish populations, which challenges our ability to understand or manage populations effectively, is variation in survival and recruitment. Most fisheries biologists consider that this variation occurs due to processes in the early life history (e.g., egg-larva-juvenile stages). By recruitment, fisheries biologists refer to the addition of fish to the harvestable population. One may also think of recruitment to the population (e.g., year class strength is determined during the first year of life).

Variable recruitment is a big problem from two perspectives. From an ecological view, variable recruitment is important because the population dynamics and community structure we see in adults are often determined by events very early in the life history. Populations with variable survival in their early life history are common, and their variable recruitment has been studied from ecological and life history perspectives (Strong 1984, Sale 1990). In fisheries, understanding the mechanisms underlying variable recruitment

is one of the major research problems (Steele et al. 1980, Rothschild and Rooth 1982, Fritz et al. 1990). From a management perspective, variable recruitment is a serious issue, because uncertainty in the amount of fish available for harvest makes management uncertain, and errors can have significant political and economic implications (Beddington et al. 1984, Steele 1984, Walters 1984). For this reason, many fisheries managers would prefer to believe in classic fishery models where simple deterministic functions relate adult stock size to number of recruits. Put quite simply, this approach has failed. It is possible that the traditional approaches to recruitment variability and fish population modeling will not lead us to either greater understanding of the recruitment process or to improved ability to predict recruitment (Larkin 1977, Beyer 1989).

In the last 10–15 years, the emphasis in recruitment studies has shifted from predicting recruitment based on regression or stock/recruit relationships toward understanding the mechanisms underlying recruitment variability. Nevertheless, most recruitment studies still have two problems. First, many researchers still focus on estimating mortality in the early life history stages. However, estimating mortality with the precision required is extremely difficult (Smith 1981). Second, most programs still look at recruitment as a population or cohort-level phenomenon. The mechanisms governing survival and recruitment (and ultimately evolution) operate at the level of the individual. When individuals differ substantially, the results we see at the population level may derive from a small minority of atypical individuals. For example, survivors (recruits) from a cohort of spawned larvae are probably not average fish (Sharp 1987). When this is the case, interpretations based on modeling the average individual are likely to be misleading.

Individual-Based Models in Fish Ecology

Ecologists have long been interested in modeling the behavior and physiology of animals. These frequently are individual-based models rather than population-based models, in the sense that what is being modeled is individual behavior or physiology rather than population level effects of these behaviors. Models of foraging behavior of individuals have been widely studied for 25 years (c.f. Pyke 1984, Real and Caraco 1986, Stephens and Krebs 1986). Foraging in fish has been extensively modeled (Werner and Hall 1974, Mittelbach 1981, Werner, Mittelbach, et al. 1983, Crowder 1985), although all of these attempts have dealt with how an *average* individual may be expected to choose prey (or patches of food) given a particular encounter rate with prey of differing utility. In general, these models can successfully predict food size choice and habitat switching based on the relative value of prey resources (Mittelbach 1981, Werner, Mittelbach, et al. 1983).

Habitat choice can also be modified by predation risk (Werner, Gilliam, et al. 1983, Gilliam and Fraser 1987, Abrahams and Dill 1989). More elaborate models of habitat choice involve tradeoffs of predation risk and growth in various habitats (Gilliam 1982, Werner and Gilliam 1984, Gilliam and Fraser 1987). These models are also based on an "average" individual. Some data are beginning to suggest, however, that individuals may differ substantially in their foraging behaviors, and thus not all individuals conform to the theoretical predictions (Marschall et al. 1989).

Another well-regarded set of individual-based models of fishes are the bioenergetic-growth models of Kitchell and colleagues (Kitchell et al. 1977, Stewart et al. 1981, Rice and Cochran 1984, Kitchell 1983, Stewart and Binkowski 1986, Hewett and Johnson 1987). In these models, the energy budget of an *average* individual is simulated. By knowing something about the physiology of fishes as a function of their body size and temperature, one can estimate either cumulative consumption from growth *or* growth from consumption. These models have been thoroughly tested and validated (Rice and Cochran 1984), but they are based on an average individual. In order to extrapolate to the population level, one must multiply the consumption by individuals in each size (age) class by the number of individuals in that class. This approach has been successfully used to assess the effects of free ranging predators on their prey resources in Lake Michigan (Stewart et al. 1981, Kitchell and Crowder 1986). While this approach adequately predicts cohort level consumption or average growth of individuals in a cohort, it does not necessarily predict growth or consumption of any specific individual. Further, it does not deal with causes or consequences of variation in growth rate among individuals.

Individual-based models in fish ecology have been pursued when the process of interest occurs on an individual level or when aggregation at a higher level (age/size groups) was not considered representative of the process. Foraging models clearly fall into the former category, whereas recruitment models probably fall into the latter category. In recruitment to a fish population, small differences among individuals may have big effects on their probability of being represented among the survivors of a cohort. Modeling recruitment by modeling the average fish is problematical because the average fish dies in less than a week (Sharp 1987).

Recruitment Mechanisms in Bloater (*Coregonus Hoyi*)

For the past decade, we have been studying recruitment mechanisms of fishes. Through work with the bloater, our thinking has focused on the importance of body size, size-dependent interactions and the characteristics of individuals in determining survival.

Bloaters are Coregonine fishes, one of a suite of seven ciscoes that co-

existed in Lake Michigan until serious abiotic and biotic modifications of that system from the 1900s to 1960s led to local extinctions of all species other than bloater (Smith 1970, Wells and McLain 1973). Bloaters spawn primarily during January through March, depositing their eggs on the bottom at 70–100 m depth. Their eggs are relatively large, about 2 mm in diameter; larvae hatch in late spring or early summer at about 9.5–10 mm body length (Wells 1966). After hatching, the larvae spend 5–10 days in the hypolimnion and then migrate to the surface where they feed on zooplankton during their first summer (Rice, Crowder, and Holey 1987). Late in the summer, the juveniles migrate to the hypolimnion and feed on benthic prey for the remainder of their life (Crowder and Crawford 1984).

Bloaters experienced dramatic reductions in recruitment success beginning in the mid 1960s (Brown 1970), and were placed on the threatened species list in Michigan by the mid 1970s. This decline seems to have been due to both direct and indirect effects of alewife, (*Alosa pseudoharengus*), an exotic fish which invaded Lake Michigan, establishing large populations by the mid 1960s (Crowder 1980, Crowder et al. 1987, Luecke et al. 1990, Miller et al. 1990). In studying bloater recruitment, we wanted to consider the range of possible mechanisms and use an approach which would allow us to reduce the list from all possible recruitment mechanisms to those which are most likely. From a thorough review of the literature on marine fish larvae, we outlined the commonly hypothesized mechanisms thought to control recruitment. Starvation in some critical life stage (e.g., first feeding) was popular (Hjort 1914, Lasker 1975, 1978), as was physical environmental variation (e.g., failed transport or retention in an appropriate habitat, Smith 1981, Sinclair 1989). Predation was also popular, particularly as an alternative to starvation (Crowder 1980, Hunter 1981).

We adopted a "strong inference" approach to screen among the alternative hypotheses and eliminate one or more (Platt 1964). We sought to turn the problem around—instead of studying sources of mortality to explain why 99+% of the fish die, we wanted to test the null hypothesis that survivors (i.e., recruits) are drawn at random from the cohort of spawned offspring. If recruits are just average fish, there is no point to look for particular explanatory hypotheses based on individual differences. Rather than looking at the relative success of cohorts across years (as in stock/recruit relations), we focused on which individuals within a cohort survived. We also let their unique characteristics tell us what was important, thus narrowing the scope of hypotheses we needed to explore.

Fortunately, larval fishes carry a detailed record of their birthdate and growth rates in their otoliths. From daily rings in these small inner ear bones, we could estimate birthdate, growth rates and often detect periods of low growth or other "stress" (Rice et al. 1985). By examining the otoliths of larvae caught at successively later points in their early life history, distri-

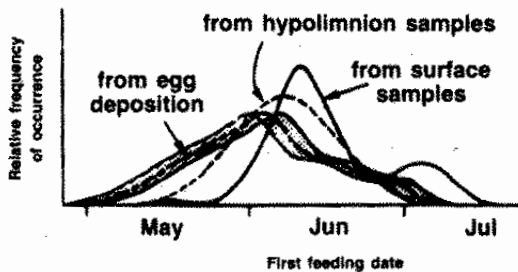


Figure 11.1 Comparison of combined distributions of first-feeding dates observed for larval bloaters in 1983 surface and hypolimnion samples with expected distributions of first-feeding dates from egg deposition and incubation temperatures. Because absolute abundances at each stage are unknown, all curves are scaled to the same area. Mismatches between curves identify periods of differential relative mortality within the season. From Rice, Crowder, and Holey 1987.

butions increasingly differed (Fig. 11.1); we found that survivors to one month of age were drawn disproportionately from those which were spawned and hatched later (Rice, Crowder, and Holey 1987). Furthermore, daily growth rates of larvae caught in the field and of larvae from laboratory studies (Rice, Crowder, and Binkowski 1987) confirmed that starvation was unimportant as a direct source of mortality for bloater. We found that growth rate was important—early larvae grew half as fast as later larvae and were under-represented among the survivors. Stress marks also correlated with those fish that failed to survive and did not correlate with specific dates or environmental events.

These results suggested that recruitment success was related to size or growth dependent mortality. Subsequent experiments in the laboratory identified alewife as one of the most important predators and showed that their predation on bloaters was strongly size-dependent (Luecke et al. 1990). In other experiments we showed that reductions in zooplankton size due to intense planktivory (e.g., by alewife) can indirectly reduce bloater growth rates, particularly in the early juvenile stage, potentially reducing recruitment (Crowder et al. 1987, Miller et al. 1990). Thus, bloater recruitment success seems to depend on the size and growth dynamics of larvae and juveniles. Direct predation is strongly size-dependent, and reduced food or temperatures can prolong exposure to predators, leading to reduced survival. Clearly, the physical milieu and the biotic mechanisms *interact* to influence ultimate recruitment. Furthermore, it is particular individuals that are successful, and their condition (size, growth rate, etc.) is decidedly not average.

Our approach allowed us to narrow the range of possibilities and focus

our efforts on the key hypotheses. It also confirmed our notion that the survivors tend to be atypical rather than average individuals. This implies that our understanding of recruitment might be enhanced most rapidly by focusing on the unique characteristics of individual survivors rather than on estimating mortality at the population level (Rice, Crowder, and Holey 1987). The approach of comparing the characteristics of individual survivors to those of earlier samples has been applied successfully to other fishes (Methot 1983, Crecco and Savoy 1985), but will be difficult to apply to organisms other than fishes (e.g. marine invertebrates) unless one can identify structures that contain a record of characteristics important to an individual's recruitment.

Larval Size and Recruitment Success

Bloaters did not fit some of our expectations based on the marine fish larvae literature. They were robust and highly resistant to starvation relative to typical marine fish larvae (time to 50% mortality for starved larvae was 25 days vs. less than 7 for typical marine larvae!). Body size scaling is well known from the ecological and physiological literature (Thompson 1917, Haldane 1927, McMahon and Bonner 1983, Peters 1983, Calder 1984), but had never been thoroughly examined for larval fish. Further, body size and growth dynamics in the presence of size-selective predators can have complex population level implications (Ebenman and Persson 1988).

Fishes grow through 4–5 orders of magnitude of length in their life history, and often 2–3 orders of magnitude of this growth occurs in the first year of life (Werner and Gilliam 1984). Furthermore, sizes of larval fishes at hatching span at least one order of magnitude; even within a species, size at hatching may vary by more than 50% (Blaxter and Hempel 1963). Variation in body size among species may account for some of the substantial ecological differences observed across larval fishes (Miller et al. 1988).

In our recent paper (Miller et al. 1988), we reviewed various aspects of the larval ecology of 72 species of marine, freshwater and anadromous fishes with respect to hatching size and larval growth. The review included fish which hatch between 1.6 mm and 17 mm in length. Physiological response times were standardized to 15 C using a Q_{10} of 2.3 (Checkley 1984). Times to yolk absorption, 50% mortality for starving larvae and point of no return (irreversible starvation) all increased linearly with hatching size. The "window of opportunity" to feed (time to point of no return minus time to first possible feeding) also increased with larval size (Fig. 11.2). Even small increases in body size at hatching confer large benefits in terms of flexibility at first feeding. For every 0.1 mm increase in length at hatching, larvae gain about 6 hours in which to find food; each 1 mm increases the "window of opportunity" 2.5 days (Fig. 11.2).

In addition, vulnerability to predators was found to be size-specific. Probability of capture per encounter declines with increasing larval prey size,

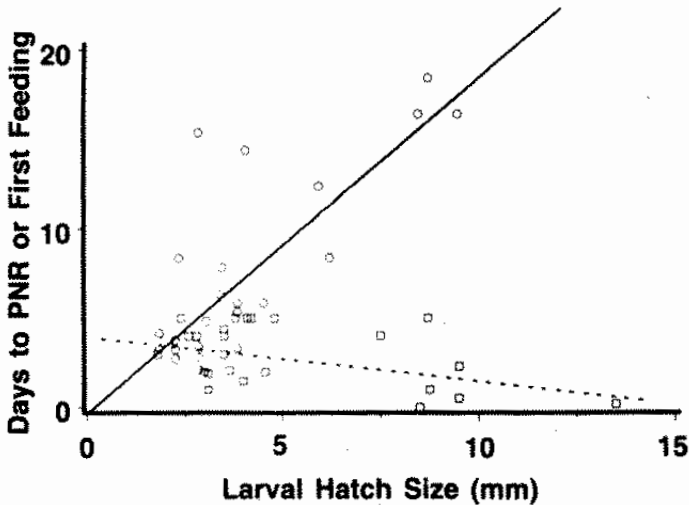


Figure 11.2 Time to point of no return (solid line) or to first possible feeding (dotted line) as a function of total larval length at hatching. The regression equation for the difference between these lines for the six paired data points on the same species is $y = 2.46(\text{length}) - 4.81$, $r^2 = 0.89$. From Miller et al. 1988.

and the slopes of these functions are steepest for small predators and shallowest for large predators. In fact, it was possible to fit an equation to predict capture success per encounter as a function of predator-prey size ratio (Fig. 11.3). This equation seemed to describe probability of capture reasonably well whether the predators were fishes, jellies or euphausiids! Probability of capture increases from zero at a predator-prey size ratio of about 2.5, to 1.0 at a predator-prey ratio of 15. A consideration of body size does much to explain differences among species in ecological performance.

Individual-Based Modeling of Larval Fish Recruitment

We came by our interest in individual-based modeling from an appreciation of the biology of the recruitment process in fishes. It is *individuals* that survive to recruit; the unique characteristics of individuals, and not population averages, determine which individuals survive. Individual-based models are not only interesting, but are perhaps the only logical way to model these processes.

Not only are many of the individual processes that determine recruitment size dependent, but they also interact. Slow growth leads to prolonged exposure to a size-dependent predator. To examine the population level im-

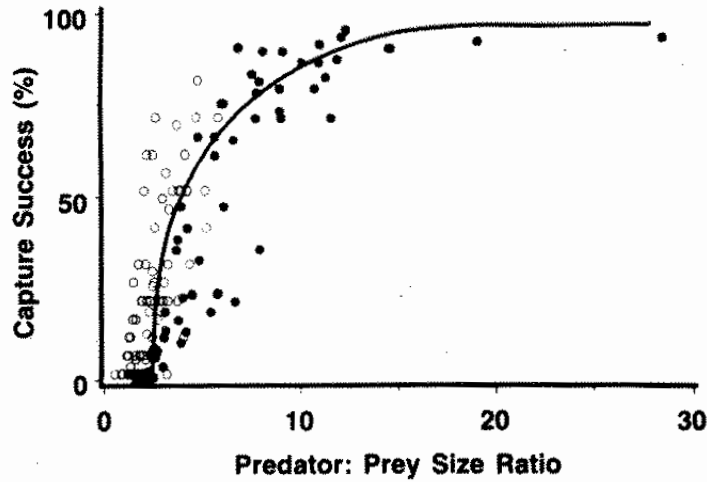


Figure 11.3 Capture success (CS) as a function of predator-prey length ratio. Points are original data from various invertebrate (open circles) and fish (closed circles) predators. The equation for the fitted line is $CS = 100 - ((\text{ratio} + 3.37)/44.76)^{-2.28}$. From Miller et al. 1988.

lications of these processes, we formulated a conceptual model summarizing these interactions (Fig. 11.4). All steps in the model are size-dependent, interact, and occur at the level of the individual, but the results of these interacting factors are not always intuitively obvious. We are collecting data both on Great Lakes fishes and on fishes from southeastern US estuaries to enhance this model, but the basic form of the model has already been developed independently by Don DeAngelis, Kenny Rose and others at Oak Ridge National Laboratories. We have been working closely with them to test, enhance and exercise it.

This individual-based model structure provides an ideal framework for evaluating the recruitment implications of individual variability and size-dependent interactions. For example, the strong size-dependence of predation on larval and juvenile fishes (Miller et al. 1988) suggests that variation in growth rate among individuals, which is often observed, could have a substantial impact on the number and characteristics of fish surviving exposure to predation. We have explored this hypothesis using the predation component of the model, parameterized for size-dependent predation by yearling alewife on bloater larvae and juveniles (Luecke et al. 1990). Simulations tracked the growth and survival of each individual in a cohort of bloater larvae as they were exposed to alewife predation over the first 60 d of life.

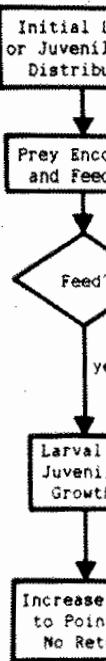


Figure 11.4



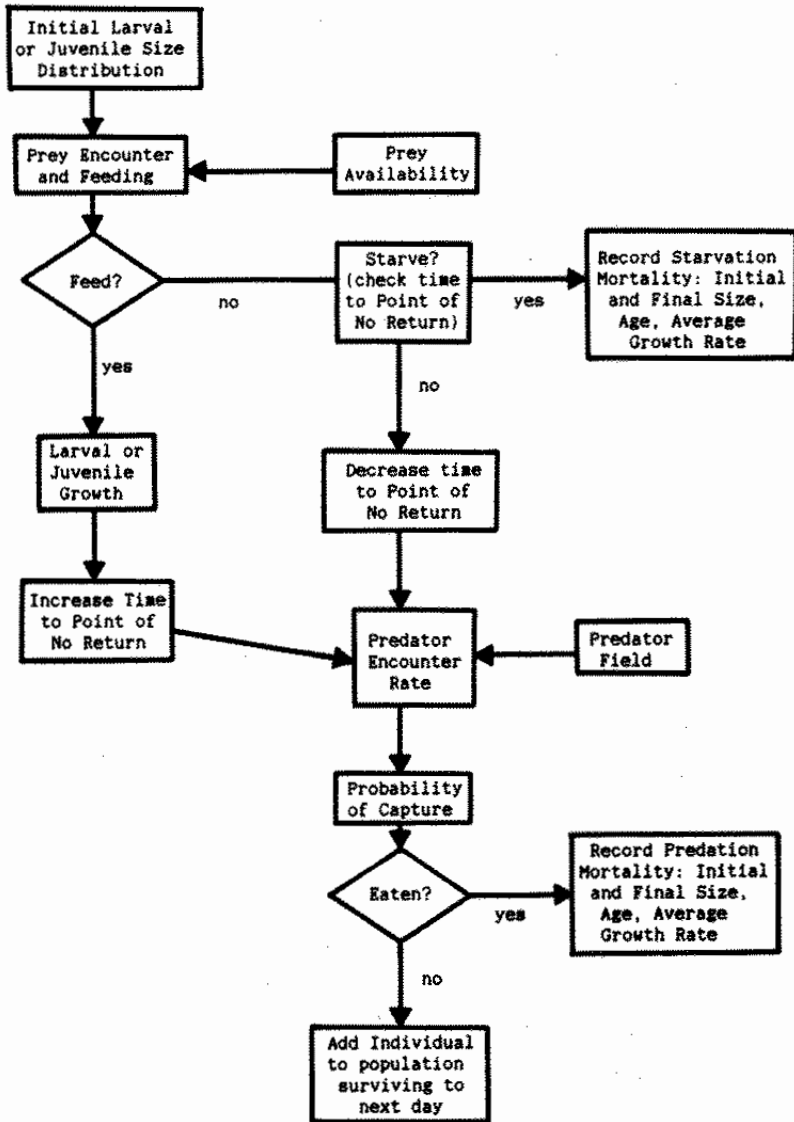


Figure 11.4 Structure of the conceptual model for larval and juvenile fish recruitment. Each step has a size-dependent component.

When cohorts of larvae with the same initial mean growth rate, but different levels of variance in growth rate among individuals, were exposed to size-dependent predation, there were substantial effects on the number and characteristics of survivors. Our results suggest that survival could be 3–4× higher for cohorts with high variance in growth rate among individuals than for low variance cohorts, with all other conditions held constant. Also, selection for fast growing (and therefore larger) individuals increased with increasing variance in growth rate; at high variance almost all survivors were drawn from the upper 25% of the initial growth rate distribution. (Rice et al. ms.) Clearly, survivors are not average individuals!

In nature, prey are often exposed to growing predators or to different sized predators as they grow (Wilbur 1988), small changes in hatching size, growth rate, or predator size can all have major effects on survival. As a result, the recruitment process can be highly dynamic, and the results may not be intuitively obvious. We see individual-based models as a powerful and flexible approach for evaluating the outcome of these interactions.

Discussion and Conclusions

Size-dependent interactions provide a unifying framework for understanding mechanisms governing survival and recruitment in fishes. We suspect that this may also be true for the many other organisms with high fecundity and variable survival (Strong 1984). Our understanding of the interacting size-dependent factors controlling recruitment has already been enhanced through individual-based models. Unfortunately, one can apply individual-based models only to populations from which individual-based data can be obtained.

In recruitment, key processes occur at the level of the individual. While we have stressed body size as an individual characteristic, we acknowledge that a variety of other factors can also contribute to differential survival. Maternal contributions of yolk, lipids, proteins and growth hormones, may influence individual embryo quality and subsequent larval growth (and survival) without changing egg size *per se*. Furthermore, these higher quality or larger eggs may derive from females which are themselves decidedly non-average; for example, larger and older females may contribute eggs which have a differential chance for survival (Bagenal 1973, Moodie et al. 1989, Zastrow et al. 1989).

Not all individual-based models examine the consequences of variability among individuals. For example, most individual-based models in behavioral ecology treat an average individual and do not address directly the population level implications of such behaviors (Zomnicki 1988). Optimal foraging models deal with individual behaviors and choices, but they do so for an average individual. The same is true of individual-based bioenergetics

then ask, at a given scale of aggregation, is the average individual representative? If behavior, physiology or other vital rate functions vary importantly among individuals, then the model would benefit from an individual-based approach. When individuals can be aggregated into larger categories, the modeling is simplified and can employ better-known techniques.

Individual-based models are attractive tools for ecologists, but like all tools they must be handled carefully to produce the desired results. We suggest that apprentice modelers (i.e., most biologists) find an expert under which to learn the trade. Biologists also have much to bring to this process, particularly in identifying the key questions and observations, and in establishing the appropriate level of aggregation for modeling the biological process of interest. For some modelers, "the real world is but a special case," but it is this world biologists hope to understand and manage.

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