

6 Recruitment: Understanding Density-dependence in Fish Populations

RANSOM A. MYERS

6.1 INTRODUCTION

The process of recruitment is the conversion of eggs, through a series of density-dependent and density-independent processes, to the fish that reproduce in the next generation. Many simple questions concerning recruitment are quantitative questions that require estimates of quantities that are very difficult to determine. For example, the question 'When is the magnitude of recruitment determined?' requires a quantitative estimate of the density-dependent and density-independent components of mortality. This question has usually been addressed by correlating estimates of abundance at early ages with later ages, as reviewed by Cushing (1996). Although such studies are useful, they are very seldom carried out with estimates of measurement error variability that are crucial for the estimation of the truly important parameters. At the very least, a measure of the estimation error variance of all estimates should be used.

No standard definition of recruitment is accepted by all fish ecologists. While all agree that recruitment is the number of fish at some certain age or stage, the choice of the age and stage varies. Coral reef fish ecologists often define recruitment as the settlement of pelagic larvae or juveniles from the plankton (Hixon and Webster 2002; Jones et al., Chapter 16, this volume), marine fisheries biologists usually refer to recruitment as the first age where fishing occurs, while salmon biologists usually refer to recruitment as the return of adults

to spawn. Here, I discuss population regulation and variability from the egg stage to first reproduction.

There are two principal sources of information on recruitment. First, there are time-series of data, containing spawner abundance and subsequent recruits. These come primarily from commercially exploited fish stocks (see Fig. 6.1). Fisheries biologists, with their access to long-term research surveys and extensive catch data, have concentrated on evidence from larger geographical scales that may contain data from more than one population. Many crucial questions can be addressed with such information but it can seldom be used to study mechanisms. Second, there are experimental and observational data on a much smaller scale. The best of this kind are from coral reef systems, where local populations are studied. Coral reef ecologists typically work on relatively common species, where zygote limitation (i.e. limitation by the number of eggs) is usually viewed as an unimportant source of variability in recruitment (Hixon and Webster 2002).

I proceed as follows: I first discuss the maximum reproductive rate, the carrying capacity and the life stages in which density-dependent and stochastic density-independent mortality occurs. This ends with a discussion of future directions for research. I then discuss generalizations that appear to be valid across many studies or populations, and on processes that have been shown to be of wide applicability from various published synthetic analyses. I only briefly review the large literature

on the influence of short- or long-term variation in the environment on recruitment, as it is well covered in a number of recent books, e.g. Cushing (1996).

Throughout this chapter, I use the empirical recruitment data that I have compiled and which is freely available from my website (<http://fish.dal.ca/welcome.html>).

6.2 THE LINK BETWEEN SPAWNER ABUNDANCE AND SUBSEQUENT RECRUITMENT

The spawner–recruit relationship is the basis for estimation of the key parameters needed to understand and manage fisheries, e.g. carrying capacity, maximum reproductive rate and the variability in recruitment. The wide scatter and the relatively ‘flat’ relationship often seen between spawners and subsequent recruitment misled the naive into dismissing such data without understanding what can be learned from it. Many fisheries biologists believed that the maximum reproductive rate is so high that recruitment would not decline at low spawner abundance. This belief was due to several factors. First, it had been observed for many fish populations that a reduction in spawner abundance was not accompanied by a corresponding reduction in the production of juvenile fish (Gilbert 1997). Furthermore, since many individual fish can produce a million eggs or more, this has been taken as proof that there can be no shortage of juvenile fish (McIntosh 1899). It was only through a very large meta-analysis of over 300 spawner–recruitment datasets that it has been widely accepted that the production of juvenile fish does in fact decline when spawner abundance is greatly reduced (Myers and Barrowman 1996; Myers 1997).

The maximum reproductive rate for the population, or equivalently the maximum slope of the spawner–recruit curve, which is realized as the origin is approached where stock size is zero, determines the limits to sustainable fishing and other sources of anthropogenic mortality that a population can sustain. The quantity, sometimes known

as the compensatory reserve, is the most fundamental of all population parameters. Population biologists and national and international management agencies have come to a consensus that the maximum reproductive rate is the appropriate measure of the potential for a population to ‘compensate’ for fishing, and is used to construct management targets and limits (Sissenwine and Shepherd 1987; Clark 1991; Mace and Sissenwine 1993; Mace 1994; Myers and Mertz 1998). In this section, I examine examples of how this parameter is estimated. When spawners and recruits are expressed as absolute estimates of abundance, the maximum reproductive rate can be estimated directly from the fitted spawner–recruit relationship. This section explains the most common types of stock–recruitment models and provides examples of stock–recruitment data from a variety of fish populations.

The relationship between recruitment (R) and spawner abundance (S), perhaps expressed as numbers or biomass, both of which are proxies for egg production, would take the form

$$R = \alpha S f(S), \quad (6.1)$$

where α is the slope at the origin, and $f(S)$ is usually a monotonically decreasing function. As such $f(S)$ is the relationship between survival and spawner abundance.

The parameter α in equation 6.1 defines the scope a population has to compensate for any form of increased mortality. For this parameter to be calculated in equation 6.1, it is necessary that the units of spawners and recruitment be the same. For species that die after reproduction (e.g. Pacific salmon, *Oncorhynchus* spp.) this is simple: one can count the number of female recruits for each female spawner. For species that do not die after reproduction, this is more complex. The process is explained below.

The estimation of α requires an extrapolation because we seldom have abundance estimates at extremely low population sizes. For this estimation we require a functional form of the density-dependent mortality, $f(S)$, above:

$$\text{Ricker} \quad E(R) = \alpha S e^{-\beta S} \quad (6.2)$$

$$\text{Beverton-Holt} \quad E(R) = \frac{\alpha S}{1 + (S/K)} \quad (6.3)$$

$$\text{Shepherd} \quad E(R) = \frac{\alpha S}{1 + (S/K)^\gamma} \quad (6.4)$$

where $E(R)$ is the expected recruitment and $-\beta$ is the density-dependent mortality. The parameter K has the same dimensions as the spawners, S , and may be interpreted as the 'threshold biomass' for the model. For values of biomass S greater than the threshold K , density-dependent effects dominate. The Ricker model shows overcompensation, i.e. at high spawner abundances recruitment declines. The parameter γ in the Shepherd model may be called the 'degree of compensation' of the model, since it controls the degree to which the (density-independent) numerator is compensated for by the (density-dependent) denominator (Shepherd 1982).

The Ricker and Beverton-Holt formulations are standards in fisheries science, but require some explanation for general ecologists. First, the units of R and S may be in biomass as opposed to numbers. The reason for this convention is that egg production in many species is more closely related to the biomass of spawners than to the number of spawners. The slope, α , determines the highest fishing mortality that can be sustained in a deterministic equilibrium. Note that in these models, all density-dependent mortality occurs during the egg, larval or juvenile stage. That is, density-dependent mortality occurs before the fish mature. This approximation is consistent with most analysis of data for marine fish (Myers and Cadigan 1993a).

The estimation of the slope at the origin requires an extrapolation to zero spawner abundance, and thus is an approximation. It is clearly necessary to have at least two individuals for successful reproduction, and in general almost always more for a population to be self-sustaining. Any management system will attempt to keep the population size above the point where such depensation occurs. Myers et al. (1995a) and Liermann and Hilborn (1997) examined a large number of commercially exploited fish stocks for depensa-

tory density-dependent mortality. There was no evidence for depensation in most spawner-recruitment time-series because compensatory mortality appeared to occur throughout the observed range of spawner abundances (Myers et al. 1995a). The clearest evidence for depensation occurred when population size was reduced to very low levels, e.g. below 100 spawners. Some species groups, such as the Clupeidae, contained some datasets that were consistent with depensation at a moderate abundance of around 20% of unfished spawner abundance, but it is unclear if this was due to long-term environmental change or to depensation (Myers et al. 1995a; Liermann and Hilborn 1997). We thus conclude that the assumption that survival, $f(S)$, is a monotonically decreasing function for the observed range of spawner abundances appears to be an adequate approximation for most commercial species except at very low spawner abundances. However, if populations are reduced to very low abundance, recovery may be very slow. For example, the spring-spawning herring (*Clupea harengus*) population in Iceland has not recovered since the 1960s, and the cod (*Gadus morhua*) populations in eastern Canada have increased at a slower rate than predicted by the data before the collapse.

I now examine several examples of spawner-recruit data in which absolute abundances are estimated. These examples are from a wide variety of habitats, include heavily exploited and non-exploited populations, and use a great variety of techniques in their assessment of the populations. We begin our examples with a sockeye salmon (*Oncorhynchus nerka*) population because its life history is simple to understand: almost all females mature at 4 years, spawn once, and die. We next consider brook trout (*Salvelinus fontinalis*), a slightly more complex example that was experimentally manipulated to investigate density-dependent mortality. The last two examples examine more complex life histories.

6.2.1 Sockeye salmon

For the population of sockeye salmon in the Adams River, British Columbia, females almost

always live for 4 years. Spawning females are counted in the river; this is the number of spawners on the x-axis (Fig. 6.1). The number of females produced from this group of spawning females is simply the number that return to spawn 4 years later in the river, plus the number which were harvested on their way to the spawning site. Plotting the number of returning females against the number of females that produced them yields a classic spawner–recruit plot.

Both the spawners and recruits are in the same

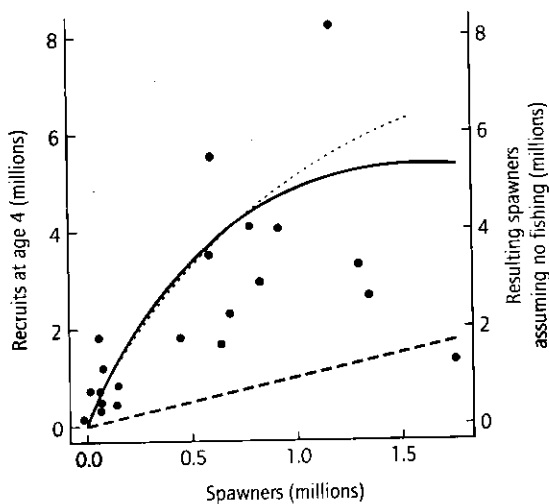


Fig. 6.1 Spawner–recruitment data for Adams River sockeye salmon (*Oncorhynchus nerka*), British Columbia, Canada. On the x-axis is the number of spawning females in the river for any one year. Each point represents the production of spawners produced for each batch of spawners in a given year. These 'recruits' are adults that return to spawn 4 years later. The solid and dotted lines are the maximum likelihood fit for the Ricker and Beverton–Holt models respectively. The straight dashed line is the replacement line. That is, if a point is above this line, the population should increase if no fishing occurs. If 1000 spawning females produced 5000 recruits 4 years later, the population would have increased by five times during the 4-year generation if no fishing had occurred. The solid curved line is the maximum likelihood estimate of the mean for Ricker spawner–recruitment functions under the assumption that the probability distribution for any SSB is given by a lognormal distribution. The curved dotted line is the equivalent line for the Beverton–Holt model.

units, in this case millions of females. If we plot the one-to-one line, or the replacement line, then it is a simple matter to see how much the population would increase if there was no fishing on the population. It can be seen that in most years the number of replacement females produced per female was approximately five or six. The average replacement rate at low abundance, where density-dependent mortality is not important, is given by the slope at the origin of the spawner–recruit curve; this quantity is usually termed, by ecologists, the maximum reproductive rate. Based on the fitted spawner–recruitment curves, at low abundance a female can produce approximately nine replacements. This allows the population to persist at very high fishing mortalities; typically around 80% of the returning fish from the population are harvested. However, this quantity also defines the limits of exploitation: the population will decline if much more than 80% of the population is harvested on average, and a lower harvest rate would be a much better management strategy.

For Pacific salmon, it is relatively easy to calculate the maximum reproductive rate because the fish are usually relatively easy to count, and because complications caused by multiple spawning and complex age structure are avoided.

6.2.2 Experimentally manipulated brook trout populations

Most good population dynamics data come from heavily exploited populations. We now examine seven populations that have experienced very little fishing pressure but which have been experimentally depleted to determine the nature of density-dependent mortality (DeGisi 1994). An experimental approach has clear advantages in that the experimenter can manipulate the populations at will.

The seven brook trout populations are from small lakes in the Sierra Nevada Mountains in California. Population sizes were estimated using maximum likelihood depletion methods from experimental gill-net surveys. These gave estimates of the number of mature fish present in the population at the time of spawning and an estimate of the number of fish produced from each

group of spawners that survived to age 1. In this example, the unit of spawner abundance is the number of mature fish present at the time of spawning, and the recruits are the resulting number of fish that survive to age 1.

In interpreting these data, one problem immediately becomes apparent: the units of spawners and recruits are not the same, and thus it is not possible to use these units to estimate the slope at the origin as in the sockeye salmon example. To overcome this problem, the standard procedure is to convert the units of recruits into the same units as spawners. That is, we estimate the number of spawners that would be produced from a given number of recruits, if no fishing has occurred. We use the same natural mortality as estimated by the analysis of these data (DeGisi 1994) and ask how many spawners would be produced from the observed level of recruitment. In this case, the age at maturity is 2 and the natural mortality was assumed to be close to 20% a year, although a slightly different value was estimated by DeGisi. We simplify slightly. Thus 80% of fish that reach age 1 would survive to spawn if 20% died each year. Once a fish reaches maturity, we need to estimate how many times it would spawn on average in the absence of anthropogenic mortality. For this calculation, we sum the probability that a fish will be alive in each year after it reaches the age of reproduction. This probability is 0.8 for the first year after spawning, $0.8 \times 0.8 = 0.64$ for the second year, and so on. This is known as a geometric series, and its sum is 5 in our case. That is, a fish that survived to 1 year of age would spawn an average of four times. This is calculated from the probability of surviving to spawn once, 0.8, multiplied by the average number of times the fish would spawn, five. To plot the spawners and recruits in the same units, we multiply the number of recruits from each age-class by the average number of times they would spawn over their lifetime. This is the scale on the right-hand axis of Fig. 6.2.

In each of the seven populations, the unexploited population persists around an equilibrium population size. For example, the Hell Diver 3 population appears to produce an equilibrium when the number of spawners is between 150 and 200 (Fig. 6.2). Above this level, the production of

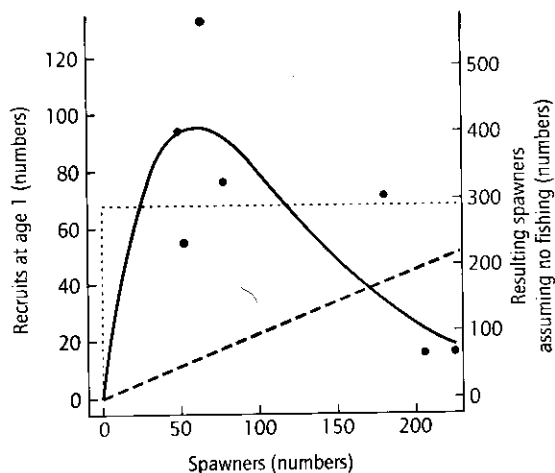


Fig. 6.2 Spawner–recruitment data for brook trout [*Salvelinus fontinalis*] in the Hell Diver 3 lake in the Sierra Nevada. On the x-axis is the number of spawning adults for any one year. Each point represents the production of 1-year-old recruits for each level of observed recruitment on two different scales: on the left-hand side is the estimated number of trout that survive to age 1, and on the right-hand side is the resulting number of spawners that would be produced if no fishing occurred on the cohort over the lifetime of the cohort. The scale on the right-hand side is the scale on the left-hand side multiplied by the average number of times a 1 year old would be expected to spawn if no fishing occurred [see text for explanation]. The straight dashed line is the replacement line. The intersection of the Ricker spawner–recruitment curve (solid line) with the replacement line represents the approximate equilibrium for the population. The dotted line is the Beverton curve.

recruits decreases below the equilibrium level, while below this population size the production of recruits increases.

When the population was increased to high levels, average recruitment decreased in each of the seven experimental lakes. This form of density-dependent mortality, called overcompensation, has rarely been so clearly demonstrated. The maximum reproductive rate for these populations is estimated to be around 19 replacement spawners per spawner from the Ricker model, a value that is similar in all the seven experimental populations (Myers et al. 1999).

It is useful to examine Fig. 6.2 in detail to under-

stand the nature of the extrapolation to the origin. There are three data points where approximately 50 spawners were observed, and we calculate a production of replacement spawners of around 400 for this case, which results in a slope of around 8. The extrapolation to the origin increases a pattern that is typical for a curve with overcompensation. If there are observations at low spawner abundances, such as in Fig. 6.1, this is much less of a problem. Also note that the Beverton–Holt model does a very poor job of fitting these data, and results in an effectively infinite slope at the origin.

6.2.3 Iceland cod

The next example is the cod population from Iceland, based on data collected between 1928 and 1995 (Fig. 6.3). The history of this population has been reconstructed from detailed catch-at-age records over this time period and represents one of the best-documented fish populations in the world (Schopka 1994). This population has recently shown only a small decline in recruitment even though spawning biomass has been reduced to less than one-tenth of what it was 50 years ago.

More importantly, from the relatively low population level of 200 000 tonnes of mature fish, the stock can produce about 200 million 3-year-old recruits. Again, we can convert the production of these 200 million recruits to the same units as the spawners. To do this, we ask how much spawning biomass would be produced for each recruit, and then calculate the spawning stock biomass per recruit with no fishing, $SPR_{F=0}$, where the subscript F indicates dependence on fishing mortality, which is zero for this definition (Mace 1994). This is calculated as

$$SPR_{F=0} = \sum_{a=a_{\text{rec}}}^{\infty} w_a l_a p_a, \quad (6.5)$$

where l_a is the natural survival from the age of recruitment to age a , p_a is the proportion of fish mature at age a , w_a is the weight at age a , and a_{rec} is the age of recruitment, which is 3 years old for Iceland cod. For explicitness, we must state that a_{rec} represents the first age at which abun-

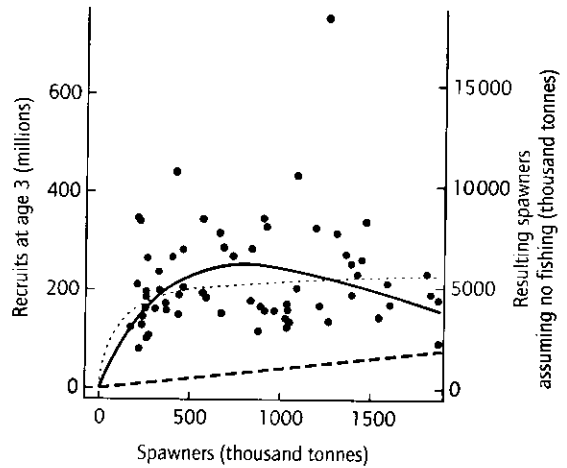


Fig. 6.3 Spawner–recruitment data for cod from Iceland. On the x-axis is the biomass of spawning adults for any one year. Each point represents the production of recruits for each level of observed spawner biomass on two different scales: on the left-hand side is the recruits in millions of 3-year-old cod, and on the right-hand side is the resulting spawning biomass if no fishing occurred on the cohort. To convert the scale on the left-hand axis to the one on the right-hand axis, multiply the number of 3-year-old fish by the average spawning lifetime biomass produced by one 3-year-old if no fishing occurred (see text for explanation). The straight dashed line is the replacement line. The intersection of the spawner–recruitment curves with the replacement line represents the approximate equilibrium for the population if no fishing occurred.

dance can be estimated, and it is also generally the first age at which it is feasible to harvest. This calculation results in the estimate that one 3-year-old cod is expected to produce around 24 kg of spawning biomass, if no fishing occurs. That is, the 200 million recruits would be expected to produce around 4.8 million tonnes of spawning biomass over their lifetime. The maximum reproductive rate can be calculated from the Ricker curve in Fig. 6.3: at low population sizes, a spawner should produce more than 20 replacements over its lifetime. This population has sustained a relatively high rate of exploitation, which has typically seen over 50% of the fish removed in any one year. Note that the slope at the origin for the Ricker model is much

less than that estimated for the Beverton–Holt model (the dotted line).

The cod population in Iceland and the brook trout population from lakes in the Sierra Nevada Mountains differ in almost every possible way; however, their maximum reproductive rate is approximately the same in both cases.

6.2.4 Striped bass on the east coast of North America

Recently, a detailed assessment of striped bass (*Morone saxatilis*) on the east coast of North America has been completed (National Marine Fisheries Service 1998). The NMFS assessment can be used to estimate spawner recruitment for the years 1982–95. The biomass of spawners increased by a factor greater than five during this period, primarily due to reduced fishing mortality. The reduction in fishing mortality allowed many more fish to reach maturity, which also produced a subsequent increase in recruitment (Fig. 6.4).

The maximum reproductive rate is given by the slope at the origin of the spawner–recruitment plot. In this case, both the Beverton–Holt and Ricker models give similar estimates of the slope at the origin of the curve. The recruitment was

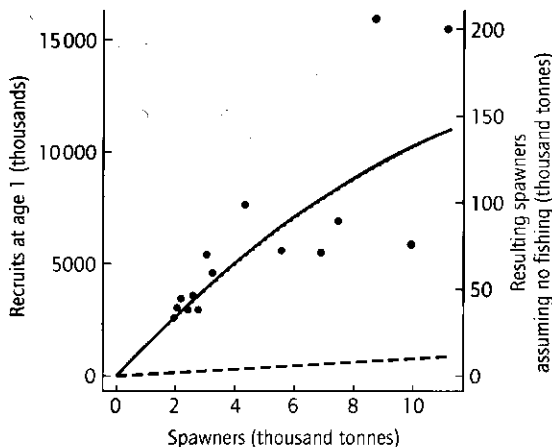


Fig. 6.4 Spawner–recruitment data for striped bass on the east coast of North America. The explanation of the scales is the same as for Fig. 6.3.

converted to spawning biomass in the same way as for cod described in the last section. These data show that, at low levels, the replacement level is almost 20 spawners per spawner in the absence of anthropogenic mortality, similar to that for the Iceland cod.

The high levels of compensatory reserve estimated from the spawner–recruit data are also seen from research surveys of the Hudson River population of striped bass. Pace et al. (1993) showed that the young-of-the-year (YOY) index of striped bass in the Hudson River was unrelated to the number of larvae. This implies either density-dependent mortality between the early larval stage and the establishment of the YOY index, or inadequate sampling of the YOY when their abundances are high (see Persson, Chapter 15, this volume). Since the analysis of Pace et al. (1993), spawning stock has continued to increase in the Hudson River. Resulting YOY indices have also remained relatively constant despite this increase in stock size (National Marine Fisheries Service 1998).

6.3 GENERALITIES THROUGH META-ANALYSIS

The previous examples of spawner–recruitment relationships come from a wide variety of fish species with very different life histories and patterns of exploitation. For example, the cod population in Iceland and the brook trout population from lakes differ in almost every possible way; however, their maximum reproductive rates are very similar. Despite the wide variety in the species examined, one central biological point remains: the maximum reproductive rate was substantial (i.e. >1) for all the populations examined. However, the maximum reproductive rate is not so high that overfishing, particularly of pre-reproductive fish, will not cause stock collapse. Since time-series for individual populations are often short and noisy, we can use meta-analysis to estimate, for example, the rate of fishing that would lead to stock collapse.

Meta-analysis refers to the process of combin-

ing and assessing the findings from several separate research studies that bear upon a common scientific problem (Hedges and Olkin 1985; Cooper and Hedges 1994). The use of statistical methods of meta-analysis for research synthesis is now the standard accepted method for making crucial decisions in medical treatment, drug evaluations, and issues in public health and social policy. Recently, it has become a standard approach for evaluating the critical population parameters needed to understand fisheries dynamics (Mace and Sissenwine 1993; Myers and Barrowman 1996; Liermann and Hilborn 1997; Punt and Hilborn 1997; Myers and Mertz 1998; Myers et al. 1999). For its use in examining the effects of fishing on marine ecosystems, see Kaiser and Jennings, Chapter 16, Volume 2.

Until recently the formal implementation of meta-analytic methods was hampered by a lack of appropriate statistical methods and of compiled datasets. These two problems have been largely overcome. The compilations by Mace and coworkers (e.g. Mace and Sissenwine 1993) and by Myers and coworkers (e.g. Myers et al. 1995b) provide examples of the databases required for a thorough meta-analysis of compensatory reserve. Mace's data have been incorporated into the ongoing compilation by Myers. Recent advances in statistical software allow for the implementation of complex linear and non-linear mixed effects (variance components) models. These models have been used to great effect in meta-analysis (Myers et al. 1999).

Meta-analysis of compensatory reserve has received a great deal of attention because of its usefulness in estimating limits to fishing mortality, maximum sustainable yield and the shape of the spawner-recruit relationship. The broadest examination of compensatory reserve is an analysis of 246 fish populations by Myers et al. (1999). These analyses demonstrate that compensatory reserve appears to be relatively constant within a species and within groups of related species. The analyses employed variance components models that assume that the log of the standardized slope at the origin of the spawner-recruit curve is a normal random variable (Searle et al. 1992). This analysis suggested a new and unsuspected finding: the maximum annual reproductive rate, which is

the maximum reproductive rate divided by the average number of spawnings in an exploited population, for any of the species examined is usually between one and seven. This number may be less for some species and more for others, but the relative constancy of the annual reproductive rate is an unanticipated and very important finding.

The common belief that there is no relationship between spawner biomass and recruitment is founded on the notion that the maximum reproductive rate for fish is essentially infinite. This belief is based on the observations that fecundity of fish is often large and that no strong reduction of recruitment is observed at low spawner abundances over the range of the observations. The problem lies in that little information can be gleaned from individual datasets, particularly as data at low spawner abundance is sparse. Instead, we need to examine a variety of datasets simultaneously in order to make proper inferences about spawner-recruitment relationships (Myers and Barrowman 1996; Myers 1997).

6.4 CARRYING CAPACITY

A cursory examination of the spawner-recruit data for an Icelandic cod stock suggests that the carrying capacity is around 200 million 3-year-old recruits (Fig. 6.3). It would be extremely useful to have a theory to explain differences in carrying capacity, yet none exists. This is perhaps the greatest outstanding, and overlooked, problem in recruitment. One exception are students of salmon biology, who have studied this issue with some care (e.g. Bradford et al. 1997). Only recently have we begun to study marine species in the same way (Iles and Sinclair 1982; Rijnsdorp et al. 1992; Myers et al. 2001).

No serious ecologist believes that carrying capacity is constant for any population, as it is certain to change with the environment and the abundance of predators, parasites and competitors. It is crucial that fisheries ecologists begin developing a predictive understanding of the variability in carrying capacity as it is central to many ecological and management issues. It is clear that a meta-

analytic perspective will be required, so as to estimate the variability in carrying capacity both within and between populations. The first step to such an analysis is to standardize carrying capacity on a per unit area basis, so that it can be compared across populations. Then it will be possible to employ non-linear mixed effect models to carry out a meta-analysis of the carrying capacity for all regions simultaneously, and to analyse cofactors, such as primary productivity and species interactions, that could cause the carrying capacity to vary (Myers et al. 2001). I believe that such an analysis will greatly improve our understanding of the factors that limit carrying capacity, and thus recruitment.

6.5 VARIABILITY IN RECRUITMENT

Thus far, I have concentrated on the mean relationship between spawner abundance and subsequent recruitment; however, variability in recruitment is often the most notable feature of such data. I now look at recruitment variability using the spawner–recruitment database that I have assembled. I examine two estimates of the variability: the coefficient of variation (CV) of recruitment and the standard deviations of log residuals from a Ricker spawner–recruitment function (Fig. 6.5). Maximum likelihood was used to estimate the parameters of the spawner–recruitment function under the assumption that the variability in recruitment for any spawner abundance was lognormally distributed (see Myers et al. 1995b for details). Similar estimates of the variability were obtained if alternative spawner–recruitment functions were used. Unfortunately, it is very difficult to obtain unbiased estimates of recruitment variability. For example, ageing errors will reduce estimated variability in recruitment for catch-at-age analyses (Bradford 1991), while research surveys may overestimate the variability because estimation error may be an important source of variability. Thus, these results should serve only as a rough guide (see my website for more information).

There are very large differences among families in recruitment variability; however, most of the data shows recruitment variability with a CV of around 50% (Fig. 6.5). Surprisingly there exists no theory to explain this important observation. For example, why is the typical value not around 10% or 100%? We cannot pretend to have a quantitative theory of recruitment until we have explanations of this and similar observations.

There are other generalities that emerge about recruitment variability. The spectrum of the time-series of animal abundance typically contains significant low-frequency variation. Anyone familiar with recruitment time-series will realize that this effect is almost always present; however, a few time-series, e.g. recruitment for Icelandic cod, do not show this effect. This may be because this species lies within the centre of its range (Myers 1991). Several empirical patterns have been proposed to help explain the patterns in recruitment variability; these are summarized in Table 6.1.

6.6 AT WHAT LIFE-HISTORY STAGE DOES DENSITY-DEPENDENT MORTALITY OCCUR?

In the spawner–recruit examples, we do not know at what stage density-dependent mortality and stochastic density-independent mortality occurs. This question was first addressed in terms of the critical period hypothesis that states ‘the numerical value of a year class is apparently stated at a very early age, and continues in approximately the same relation to that of other year classes throughout the life of the individuals’ (Hjort 1914). This is certainly true to some extent but with the following limitations: (i) some stochastic mortality after and (ii) density-dependent mortality changes the relative abundance, but good year-classes remain good. For some populations we can examine how interannual variability changes with age, and use models to examine when density-dependent and density-independent mortality occurs. Two contrasting situations can be seen in the data for

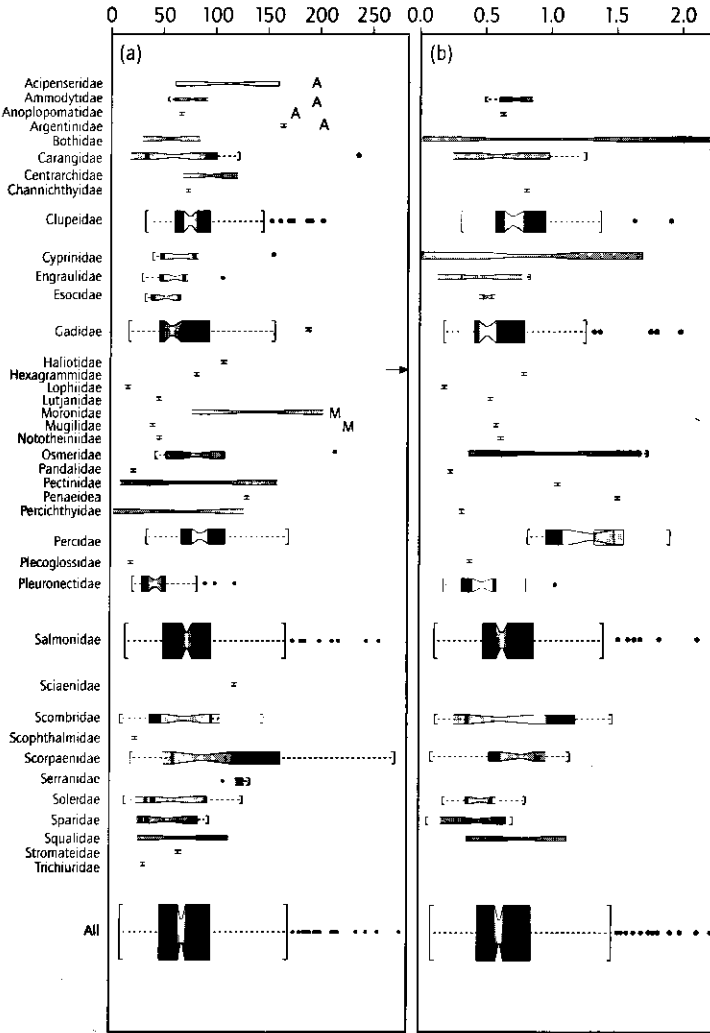


Fig. 6.5 Boxplots by family of (a) the coefficient of variation in recruitment ignoring the effect of spawner abundance and (b) the maximum likelihood estimate of the standard deviation of the natural log of the residuals from fits of the Ricker model σ assuming lognormal variability in recruitment (which is an estimate of the standard deviation of the density-independent mortality). Note that not all recruitment series have spawner estimates, so that (a) has more data than (b). The boxplots show the limits of the middle half of the data (the white line inside the box represents the median). The amount of data is shown as the width of the boxes, which are proportional to the square root of the number of data points. The notches are the approximate 95% confidence intervals of the median. If the notches on two boxes do not overlap, this indicates a difference in a location at a rough 5% significance level. The upper quartile and lower quartile provide the outline of the box. Whiskers are drawn to the nearest value not beyond 1.5* (interquartile range) from the quartiles; points beyond are drawn individually as outliers. Outliers are plotted as points, except for one that falls outside the range of the plot, which has been replaced by an arrow.

brown trout (*Salmo trutta*) from Black Brows Beck (Elliott 1994) and cod from the North Sea (Fig. 6.6). Very strong density-dependent mortality occurs in the first 6 months after eggs are deposited for brown trout, while mortality that varies among years, and is largely independent of density, occurs until maturity at age 3. For brown trout, recruitment variability increases with age (Fig. 6.7).

The pattern is quite different for cod in the North Sea where the variability in recruitment decreases with age. The decrease in recruitment

variability at age in cod is caused by strong density-dependent mortality during the demersal juvenile stage, and is seen in the 17 populations of demersal fish studied by Myers and Cadigan (1993a,b). Several observations from the cod data should be noted: (i) year-classes that are large soon after settlement remain relatively large for all subsequent surveys, (ii) the variability decreases with age and (iii) larger spawner abundances are slightly positively correlated with higher recruitment. The first two observations are clear from virtually all

Table 6.1 Patterns in recruitment variability.

Pattern	Species	Reference
CV(R) ~50%	Most species	This chapter
Var(R) ↑ with length of time-series	Most species	Myers et al. (1995a)
Var(R) ↑ at edge of species range	Cod, haddock, herring	Myers (1991)
Var(R) ↑ for greater fecundity (slight effect)	57 species	Mertz and Myers (1996), Rickman et al. (2000)
Var(R/S) ↑ at low spawner abundance	10 families	Myers (2001)
Var(R) ↑ with smaller duration of spawning	Cod	Mertz and Myers (1994)
Var(R) ↑ on offshore banks	Cod, haddock, American plaice	Myers and Pepin (1994)
Var(R) ↓ at older ages	Marine demersal fish	Myers and Cadigan (1993a)
Var(R) ↑ at older ages	Anadromous salmonids	Bradford (1995)
Var(R) is greater for anadromous than marine		Rothschild and DiNardo (1987)
Spatial scale of R ~500 km	11 marine species	Myers et al. (1997a)
Spatial scale of R ≤50 km	7 freshwater species	Myers et al. (1997a), Bradford (1999)

Var(R), variance of recruitment; CV(R), coefficient of variation in recruitment; Var(R/S), variance of survival for egg production to subsequent recruitment.

population dynamics data of demersal fish with a planktonic life stage (I return to this in a later section). The last observation is certainly weak for these data, but is a persistent feature of the vast bulk of spawner–recruit data (Myers and Barrowman 1996). Note that both of these very reliable datasets show similar levels of variation at age 3, with a CV of about 0.5, which we have previously seen to be commonly observed for fish (Fig. 6.5).

While the result for demersal fish appears to hold for many populations, the result for trout may not be true for salmonids in general, although there is sometimes increased variance in demersal fish due to density-dependent mortality in the juvenile stage (Myers and Cadigan, 1993b; Fromentin et al. 2001). For example, Bradford (1995) found that the variance in survival increased with age for many Pacific salmon species, and about half the variability in natural survival occurred after migration to the sea. It would be of great interest to apply the methods that I developed with Cadigan, which include estimation error, to examine the general question of the creation of variability in survival by density-independent mortality and the reduction in the variance by density-dependent mortality for salmonid data.

A complementary approach to this problem is

to use otolith analysis to examine variation in survival within and among cohorts (Rice et al. 1987). If a cohort is sampled multiple times, it is possible to use otolith microstructure to measure patterns of daily growth, and hence greatly increase our understanding of recruitment processes. However, the amount of sampling required to test statistical models with such data can be overwhelming; careful modelling should precede such a project.

6.7 ESTIMATING DENSITY-DEPENDENT MORTALITY FROM LONG-TERM SURVEYS

Studies of recruitment have been hampered by the unwillingness of many biologists to use methods that account for the estimation error inherent in estimating the abundance of fish populations. With newer methods, it is possible to make better use of the many long-term research surveys of fish abundance. These surveys can be used to estimate the extent of density-dependent mortality and, if performed over multiple life-history stages, can be used to infer at which life-history stage compensation is occurring. Such an analysis is best carried out using an extension of key-factor analysis that includes estimation error. The original version of key-factor analysis assumed that measurements

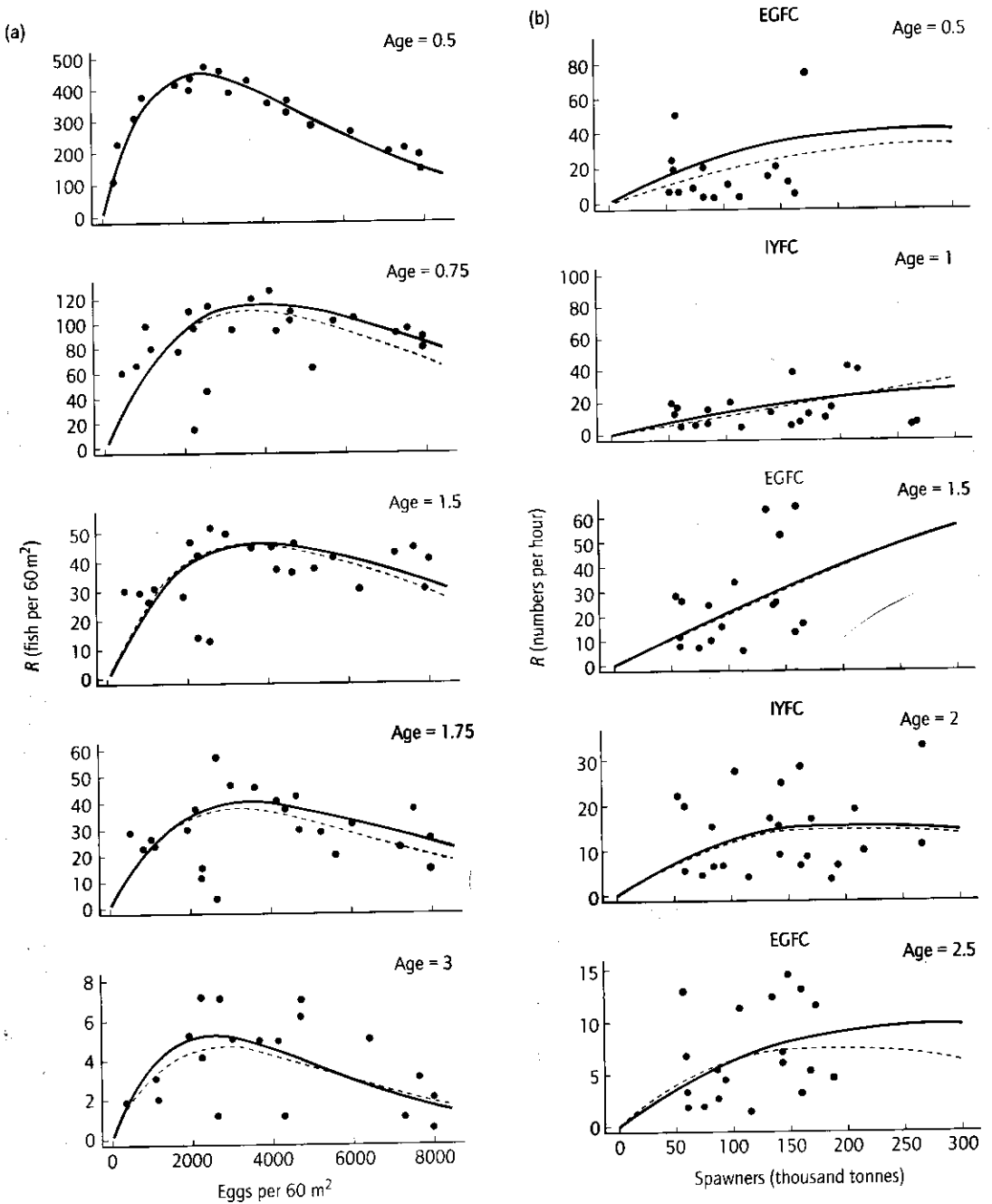


Fig. 6.6 Recruitment versus spawner abundance at five ages for (a) brown trout and (b) cod. Note that recruitment is estimated from two different surveys for North Sea cod: EGFS is the English Groundfish Survey and IYFS is the International Young Groundfish Survey, which covers a longer time period.

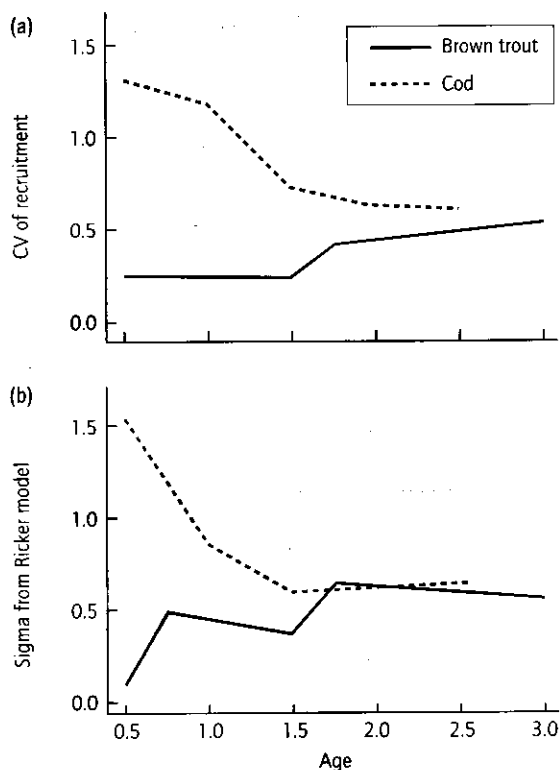


Fig. 6.7 Changes in (a) the coefficient of variation (CV) in recruitment and (b) the standard deviation of the log residuals of the recruitment from a Ricker model at five ages for brown trout and cod.

were made without error; this is not an adequate approximation for fish population data.

Myers and Cadigan (1993a,b) considered a population in which each generation is surveyed at several stages or ages. Let the number of individuals entering stage a be N_a . Consider the dynamics between two stages, a and $a + 1$, where the natural mortality is divided into three components: (i) the average mortality between the two stages that is independent of density, τ_a ; (ii) the density-dependent component, δ_a , which is assumed to be proportional to the logarithm of the initial density; and (iii) the variable component unrelated to abundance, ϵ_a . The dynamics between two stages is described by:

$$N_{a+1} = N_a \exp(-\tau_a - \delta_a \log N_a + \epsilon_a). \quad (6.6)$$

Note that the above formulation assumes that density-dependent mortality occurs before the stochastic component of density-independent mortality; this should be kept in mind when interpreting the results.

Myers and Cadigan showed that if estimates of the observation error variance are available from the sampling variability, or if multiple surveys of the same cohort occurred, it was possible to estimate the density-dependent mortality and the variance of the density-independent mortality. Furthermore, it is possible to estimate the delayed density-dependent mortality as well. They tested the hypothesis that population variability is created and regulated at the juvenile stage for 17 populations of groundfish. Density-dependent mortality was estimated using an extension of classical key-factor analysis (Varley and Gradwell 1960) that explicitly included estimation error. Myers and Cadigan concluded that the juvenile stage was crucial for density-dependent population regulation in these species, but that the source of interannual variability in year-class strength occurs during the larval stage or the very early juvenile stage. These quantitative estimates confirm previous analyses that show the strong influence of density on mortality in the juvenile demersal stage after settlement to the bottom (Rauck and Zijlstra 1978; Lockwood 1980; Van Der Veer et al. 1990).

One major disadvantage of Myers and Cadigan's method was that it was restricted to the assumption that density-dependent mortality is proportional to the logarithm of the initial density. This assumption was needed to obtain linearity of the model equations. However, it should be possible to consider much more general forms of density-dependent mortality using more modern methods, such as non-linear state space models estimated using the hierarchical Bayes methods (Gilks et al. 1994).

Much less is known about density-dependent mortality from research surveys of pelagic fish, probably because of the much greater difficulty of estimating abundance of pelagic fish compared

to demersal species. We know of no analysis for pelagic species similar to the work of Myers and Cadigan that have included the role of estimation error in the statistical models.

Long-term surveys of lakes have also generally shown strong density-dependent mortality during the preadult life stages. For example, long-term surveys using research traps for European perch in Windermere, UK (Mills and Hurley 1990), trawls for yellow perch in Oncida Lake, New York (Nielsen 1980) and mark-recapture studies of walleye in Escanaba Lake, Wisconsin (Serns 1982) have demonstrated the importance of density-dependent mortality during preadult life stages.

Density-dependent mortality has been observed in many long-term research surveys of stream fish. This was observed in those cases where cohorts were observed multiple times, for example brown trout (Elliot 1994), brook trout (McFadden et al. 1967), Atlantic salmon (Chadwick 1985) and several Pacific salmon species of the genus *Oncorhynchus* (Ricker 1954; Myers et al. 1997b). Strong density-dependent mortality and/or growth is expected in species that have territorial behaviour, which is typical of stream-dwelling species (Elliott 1994).

Extensive surveys of anadromous fish have been helpful for establishing the timing of density-dependent mortality. For example, the monitoring of the number of anadromous alewife (*Alosa pseudoharengus*) spawners into, and the number of seaward migrants out of, Damariscotta Lake, Maine showed that a five-fold change in egg production resulted in almost no change in recruits; strong compensation was occurring in the egg or larval stages (Walton 1987). These results are consistent with other studies of *Alosa* species (Loda and Crecco 1987), and contrast with those of the demersal fish described above for which strong density-dependent mortality existed later in the post-larval stage.

In summary, long-term research surveys have provided valuable insights into the nature of population dynamics and compensation from fishery independent sources. If estimation error is explicitly included in the analysis of the results from such surveys, they allow quantitative estimates of

the importance of density-dependent and density-independent mortality at various life stages. Fisheries ecologists have made very inefficient use of the excellent survey data available to them; the analysis is difficult and requires the use of subtle statistical methods. We should make better use of such data.

6.7.1 Density-dependent mortality within and between cohorts

Spawner-recruit data relies on a regression approach. Another source of evidence, the within-cohort data, is usually ignored. Although traditional methods of analysis of data within cohorts, such as key-factor analysis, are useless for fisheries work because of the assumption that abundance is measured without error, it is possible to extend this type of analysis using modern statistical methods (Myers and Cadigan 1993a,b). The basic idea of these methods is not to treat each cohort abundance as an unrelated number but to assume that the initial recruitment comes from a statistical distribution, usually lognormal, and to treat all variation in subsequent ages as also coming from a statistical distribution. This allows a much deeper understanding of the process.

Previous work has been limited by rather strict distributional assumptions, for example that recruitment is lognormal. The methods appear to be reasonably robust to this assumption; perhaps the more important assumption is the nature of the functional form of the density-dependent mortality. Recent state-space and non-linear time-series methods should allow this to be studied in the near future.

6.8 PELAGIC EGG, LARVAL AND JUVENILE STAGES

The population biology of the pelagic stages remains the most difficult of all problems related to understanding recruitment. The primary source of variability in recruitment is the enormous interannual variability in density-independent mortality during the pelagic egg and larval stages

of marine fish; however, it has been difficult to identify the source of this variability (Leggett and DeBlois 1994). Before discussing these issues in depth, I detail the most influential theory concerning interannual variability in larval survival.

6.8.1 Match/mismatch hypothesis

The match/mismatch hypothesis of Cushing (1969, 1990) has provided considerable insight about year-class success and its variability in marine fish populations. The central idea is that the closeness of the temporal match between the abundance peaks of larvae and their planktonic prey controls larval mortality. This may be a result either of the vulnerability of first-feeding larvae to starvation or to the fact that poorly fed larvae grow slowly and are more susceptible to predation. Since larval mortality is thought to be very high, the larval stage may be the principal determinant of year-class strength. This picture seems very plausible and it enjoys some empirical support (see Cushing 1990 for a review).

Figure 6.8, adapted from Cushing (1982), illustrates the match/mismatch hypothesis. The im-

portance of the match depends on (i) the length of time between peaks of the two distributions (t_0) and (ii) the width of the distributions, where δ and σ are measures of the width of the zooplankton and larval distributions respectively. For example, if the larval distribution has a width of 2 months, a mismatch of peaks equal to 2 weeks may be inconsequential. Cushing's idea can be put in a simple mathematical model (Mertz and Myers 1994), which results in powerful testable predictions. Namely, we can calculate how year-to-year changes in the food consumed by the entire cohort, F , are related to those changes in the delay between the peak of first-feeding larvae and the peak in their food supply, t_0 . Since F is a maximum for $t_0 = 0$, we expect that the average value of t_0 is zero. The difference in food consumption, and hence survival from the assumption of the hypothesis, can now be simply calculated approximately as

$$-\frac{t_0^2}{\delta^2 + \sigma^2} \tag{6.7}$$

(see Mertz and Myers 1994 for details). That is, a difference in survival is now hypothesized to de-

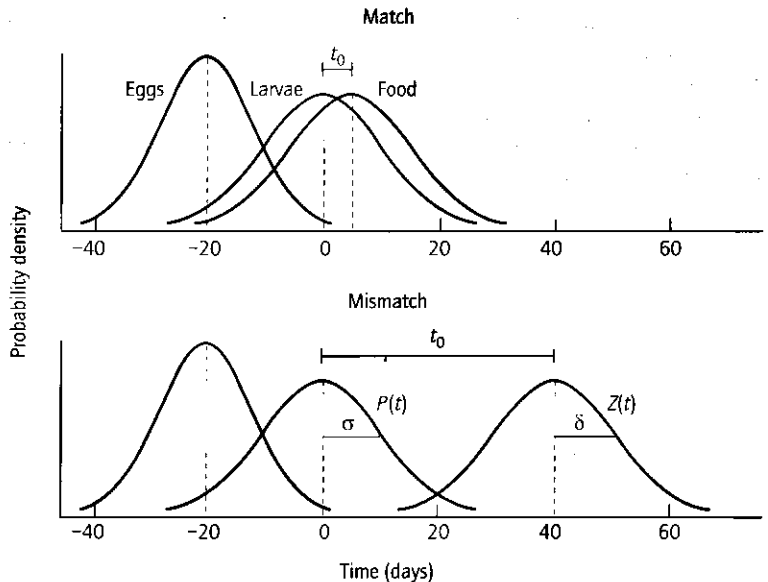


Fig. 6.8 Illustration of a match and a mismatch of larval fish to their planktonic prey (time units are arbitrary). Production of larvae $P(t)$ follows egg release and in a match situation (top panel) the larval production peak closely coincides with the peak of palatable zooplankton (curve designated $Z(t)$). The match condition is characterized by $t_0 \sim 0$. The representative widths of the larval production and zooplankton peaks are σ and δ respectively.

cline by the square of the difference in timings of the peaks, t_0 divided by the sum of the variances of the seasonal distribution of first-feeding larvae and zooplankton abundance. This formulation allows a priori quantitative testing of the match/mismatch hypothesis using data that is presently available from regions with regular plankton surveys.

There are other predictions from the above model that have been tested. Cushing (1990) noted that the effect of variable and unpredictable timing of the plankton peak will be mitigated if a fish stock spreads its spawning effort over a broad temporal window. This corollary of the match/mismatch hypothesis also suggests that there might exist a relationship between the width of the spawning window, measured by the standard deviation of the estimated egg production versus time curve, for a given stock and its recruitment variability. Mertz and Myers (1994) were able to confirm this hypothesis for cod stocks in the North Atlantic.

6.8.2 Density-dependent mortality in the pelagic stage

Density-dependent mortality has been often hypothesized as a key factor in population regulation in the pelagic larval stage; however, it has rarely, if ever, been convincingly demonstrated for any marine species (Cushing 1996). For example, attempts to demonstrate food limitation, which is the mechanism most often proposed for mortality, have generally yielded ambiguous results at best (Heath 1992; Leggett and DeBlois 1994; Lochmann et al. 1997). On the other hand, density-dependent mortality in the pelagic stage in freshwater species, or pelagic freshwater stages of anadromous species, has been clearly demonstrated in a number of cases (Walton 1987).

There are several reasons for the difference between our understanding of freshwater and marine systems (see Jones et al., Chapter 16, this volume). First, recruitment variability in fresh water may depend predominantly on biotic influences, particularly the predation by adults of one species on juveniles of another. Walleye (*Stizostedion vit-*

reum) predation has been shown to have a significant impact on year-class strength of yellow perch (*Perca flavescens*) in Oneida Lake (Mills et al. 1987). In contrast, these effects have not been convincingly demonstrated in marine systems (Leggett and DeBlois 1994). Verity and Smetacek (1996) have conjectured that predation is a less dominant influence in marine systems because fish densities appear to be 10–1000 times smaller than in freshwater systems (Horn 1972); however, Horn's estimate may not be relevant because he did not estimate densities that should actually occur in the ocean. The orders of magnitude difference in the density of larvae clearly suggests that density-dependent mortality may be more important during pelagic larval and juvenile stages in fresh water.

Second, there are fewer sampling difficulties in lakes than in the ocean, although some difficulties are similar, for example larvae avoid the sampling device and the avoidance behaviour changes with age or size. Many marine populations spawn over a wide geographical and temporal window, which may change among years (Hutchings and Myers 1994a), making sampling difficult. For example, the very well studied cod population off Lofoten (Pedersen 1984) actually also spawns outside the fjord. The strong advection that occurs for marine populations makes estimation very difficult (Helbig and Pepin 1998). The advected larvae may die, if they are advected into regions where they cannot survive (Myers and Drinkwater 1988), or they may survive and return to the spawning region at an older age (Polacheck et al. 1992).

Error in estimating abundance poses fundamental limitations to the kinds of questions that can be addressed. For demersal fish, it is possible to estimate the density-dependent and density-independent component of mortality between egg and demersal stage, or within the demersal stage. However, reliable estimates of the sources of variability within the egg and larval stage are almost impossible except for a very few species using enormous sampling effort, as illustrated by the California Cooperative Oceanic Fisheries Investigation.

Finally, an experimental approach is much

easier to undertake in freshwater systems than in the ocean. For example, out-planting artificially reared larvae or juveniles has been widely used in freshwater systems to study density-dependent growth and mortality. Whitefish (*Coregonidae*) has been experimentally stocked at controlled densities in lakes in Finland (Salojarvi 1991), gizzard shad has been experimentally stocked in reservoirs in Kentucky (Buynak et al. 1992), walleye in ponds in the midwestern USA (Fox and Flowers 1990) and steelhead (*Oncorhynchus mykiss*) fry into tributaries of Lake Superior (Close and Anderson 1992). Each of these studies demonstrated strong density-dependence in growth and/or mortality.

Research in this area has concentrated on the sources of stochastic density-independent mortality caused by lack of food, predation or advection. The first two are potentially density dependent, but we have little evidence for marine species that they are density-dependent in the pelagic stage. The most likely mechanism in the observed cases is food limitation. This has been clearly demonstrated for pelagic juvenile sockeye salmon, where large year-classes substantially reduce the zooplankton abundance (Hume et al. 1996). Food limitation during the freshwater phase of anadromous species that fluctuate greatly in abundance, such as the sockeye salmon, will be the most easy to demonstrate.

Although density-dependent mortality is probably important for many species in the pelagic stage, it cannot be quantified until a systematic approach is taken to estimation and meta-analysis.

6.8.3 Stochastic density-independent mortality in the pelagic stage

The most expensive research efforts in recruitment have been to understand the creation of variability in recruitment at pelagic stages of marine fish. Although progress has been made, the overall results are meagre; this ambitious research programme has not resulted in a fully predictive theory.

This research is usually justified because of the

importance of predicting recruitment. Approaches to this task may involve finding environmental correlates of recruitment or the field sampling of pre-recruit life-history stages. Predictions of recruitment have been sought through the correlates of recruitment with environmental factors. Wind speed has been proposed as a determinant of recruitment in that storm-driven mixing can disperse larvae and their prey, reducing food availability (Lasker 1975, 1981; Peterman and Bradford 1987). Larval food supply may also be influenced by the lag between appearance of larvae and the peak of abundance of their prey (Cushing 1990). The intensity of turbulence may control the frequency of contact between larvae and their prey (Rothschild and Osborn 1988). Larvae may be exported to inhospitable waters by the action of wind-driven currents or the incursion of Gulf Stream rings (Myers and Drinkwater 1989). For thorough discussions of environmental influences on recruitment see Fogarty (1993), Wooster and Bailey (1989) and Cushing (1996).

The complexity of the mechanisms that have been proposed can be seen by examining one factor. Consider the effect of the wind, described by the vector w , on the survival of pelagic eggs and larvae in the Northern Hemisphere. The cross-shelf wind stress component, τ_x , will have little effect except on the neuston. The long-shelf wind stress component, τ_y , and the turbulence generated by the wind, which is proportional to $|w|^3$ and which will generally be non-linear, may have a plethora of important effects on survival (Cury and Roy 1989; MacKenzie et al. 1994; Dower et al. 1997). These factors may be critical for only short periods of the pelagic stage. For example, Ekman transport caused by the long-shelf wind stress component may decrease survival by transporting larvae offshore (Bailey 1981) or increase survival by increasing larval food supply (Bakun 1996). Recent theoretical models have shown that small-scale turbulence enhances encounter rates between larval fish and their prey (Rothschild and Osborn 1988), while earlier work suggested it would decrease survival by dispersing food (Peterman and Bradford 1987). Empirical laboratory and field observations have helped to clarify the issues

(MacKenzie and Kiorboe 1995); understanding the physics of the upper ocean allows the relative magnitude of the effects to be estimated, but the final link to resulting recruitment has not been established. Similarly, food limitation via Cushing's match/mismatch hypothesis has been investigated and some empirical links from field data demonstrated, again its overall importance is uncertain. It is difficult to produce quantitative estimates from any of these models but it is often possible to use data-driven physical oceanographic models of historic data to quantitatively estimate the effects (Myers and Drinkwater 1988).

One approach to understanding the sources of interannual variability in density-independent mortality is primarily empirical, by correlations with many environmental correlates. Much of this work has been marred by the extreme unwillingness to look at the statistical difficulties of the analyses (reviewed by Myers 1998) and the desire to blame all fisheries problems on the environment. For example, 5 years after there were claims that recruitment of 'northern' cod could be partially predicted from the presence of cold water that led to a greater probability of good survival of cod larvae, the collapse of the stock was being blamed primarily on cold water, a claim that did not stand up to scrutiny (Hutchings and Myers 1994b). The claim that poor recruitment of Northern cod was caused by warm water, and then by cold water, was based on the use of statistical methods that were at best unreliable. The resulting comedy of errors, which resulted in the loss of around 50000 jobs, should cause any fisheries scientist to carry out such analyses with more care.

There are theoretical reasons to doubt that recruitment can be predicted with sufficient accuracy from environmental data to be useful for management (Bradford 1992; Mertz and Myers 1995). The basis of the simulations by Bradford (1992) and the analytical models of Mertz and Myers (1995) is the distribution of mortality across life-history stages that is typically observed (Bradford 1992; Bradford and Cabana 1997) and the strength of density-dependent mortality in the juvenile demersal stages (Myers and Cadigan 1993b). When these factors are combined, the ability to

predict recruitment from environmental factors is very limited, even if the principal mechanism determining interannual survival during the egg and larval stage is well understood, which is seldom the case. The utility of spending large amounts of public research funding to establish predictions of recruitment based on environmental indices should thus be questioned (Walters and Collie 1988). Nevertheless there are broadly two main patterns that emerge from the empirical analysis of such data from a meta-analysis of over 50 studies where previously published environment-recruitment correlations had been retested with new data (Myers 1998). The two conclusions were, first, that correlations for populations at the limit of a species' geographical range have often remained statistically significant when re-examined and, second, that a dome-shaped relationship appears to exist between the recruitment success of small pelagic fish in eastern boundary current upwelling systems (Bakun 1996) and the upwelling intensity (optimal environmental window, OEW) (Cury and Roy 1989). Unfortunately, these environment-recruitment correlations do not appear to be very useful in practice. I recently examined the 47 environment-recruitment correlations reviewed by Shepherd et al. (1984) and found that only one was being used in the estimation of recruitment in routine assessments (Myers 1998).

6.8.4 Demersal stages

Density-dependent mortality probably occurs chiefly in the juvenile demersal stages for coral-reef fish, shelf demersal species and tidepools (Pfister 1996). We know much more about the mechanisms for density-dependent mortality in demersal stages of coral-reef fish than any other group. The mechanisms have largely been unravelled by field experiments that examine how food limitation interacts with predation. Predation mortality can be mediated through territorial behaviour or the 'growth mortality hypothesis' that proposes that greater competition for food increases the time required to grow to a size where they are less vulnerable to predation (Ricker and Forrester 1948). Forrester (1995a) experimentally demonstrated the second mechanism by artifi-

cially supplementing food for damselfish (*Dascyllus aruanus*). The link between predation and structural complexity was examined by Beukers and Jones (1998).

Hixon and Carr (1997) translocated 32 live coral-reef heads to a large sand flat so that they could manipulate orthogonally the density of prey and the presence of predators. They demonstrated that density-dependent mortality of juvenile coral-reef fish was dependent upon the presence of two suites of predators: transient piscivores attacking from above and resident piscivores attacking from below. If either predator was absent, mortality was entirely density-independent. Similarly, Steele (1997) has shown strong density-dependent mortality using manipulative experiments on temperate juvenile gobies; again, the density-dependent mortality was primarily due to predation. Forrester (1995b) also showed that juvenile and adult mortality of gobies was strongly density-dependent in a series of manipulative experiments. The experimental results that demonstrate that structural shelter for prey refuges is often limiting (Hixon 1991) strongly supports the importance of protecting the sea bottom from destructive fishing practices (Watling and Norse 1998).

The great success of manipulative field experiments for coral-reef fish should be emulated by researchers who study other systems. There have been some notable successes in other regions. DeGisi's (1994) whole-lake experiments on brook trout, discussed above, is one of the most ambitious. Another experimental approach is to supplement natural populations with artificially reared competitors. Such large-scale experiments have been undertaken on a marine species, cod, in Norway. These have revealed strong density-dependent mortality in the juvenile stage and shown that artificial enhancement of the species in the wild is generally not possible (Nordeide et al. 1994). Density-dependent mortality in this case appears to be caused by competition for limited food supply.

There are remarkably few experimental manipulations of abundance for stream populations. In one of the few such studies, LeCren (1965) used enclosures to demonstrate extremely strong density-

dependent mortality during the egg to fry stage in brown trout. I find this study particularly interesting because the pattern of density-dependent mortality was not observed in Elliott's study of interannual variability.

The most direct method of assessing compensation is by experimental manipulations of abundance in a carefully controlled manner. The advantage of this approach is obvious: powerful statistical methods of experimental design can be used to construct experiments that can resolve questions that are difficult to answer from observational data alone.

6.9 FUTURE RESEARCH

6.9.1 *The need for quantitative theories*

At present, our understanding of recruitment is limited to conceptual theories and empirical models, meaning spawner-recruitment functions. Although we can estimate biologically meaningful parameters such as carrying capacity and make quantitative predictions, we lack mechanistic models of basic biological and physical processes. Although we have physical models of some mechanisms (Rothschild and Osborn 1988), they are seldom capable of making predictions about recruitment. Thus, few recruitment studies are taken beyond the interpretive stage and can only claim that observations are consistent with a model or a concept. Ultimately, in order for 'recruitment science' to make progress, we need mechanistic models that make quantitative predictions about the functional form and mean of different processes. Such modelling is difficult, and unappreciated.

My late friend, Gordon Mertz, was a master of models that yielded testable quantitative predictions. For example, Mertz developed a model of Cushing's match/mismatch hypothesis which predicted that recruitment variability should increase as spawning duration decreases, a prediction supported by an analysis of Atlantic cod data (Mertz and Myers 1994). Similarly, he was able to transform very vague concepts of the relationship between fecundity and recruitment variability

into a quantitative predictive theory (Mertz and Myers 1996). I believe that it is this type of model that will yield a greater understanding of recruitment, not vague 'conceptual', non-parametric or black-box models.

It is useful for recruitment biologists to examine the role of the fit of a functional model to data. For example, Max Planck developed a quantitative model for black-body radiation that gave the world the beginnings of quantum theory 100 years ago (Pais 1982). If Max Planck, and the physicists of the day, had been satisfied with a non-mechanistic, non-parametric fit to the data or if the experimentalist at the University of Berlin had been satisfied with anything less than the most exacting measurements, we would not now have quantum mechanics. Thus, functional models are not the goal of science; rather they serve as intermediary steps between ever more refined mechanistic models. If progress is to be made towards understanding recruitment, **we must take models and data more seriously.**

6.9.2 *The individual and recruitment*

Modellers of fish populations traditionally assumed that all individuals of a given age are identical. However, we know that this is not the case since competition often takes place between individuals; this is the basis of recent work on individual-based models (Cowan et al. 1996; Letcher et al. 1996; Huse et al., Chapter 11, Volume 2).

Individual-based models that predict that the skewness and the coefficient of variation of weight distributions increase with population density assume density-dependent growth and unequal competition among individuals of a given age (Kimme 1986). Unequal competition assumes unequal resource partitioning, which can result from a combination of territorial control of resources, plastic growth, selective mortality and emigration. Since an animal's size is highly correlated to its competitive ability, relevant models predict a positive feedback cycle, whereby better competitors grow larger and become even better com-

petitors (Latto 1992). Therefore, the weight distributions of such populations are expected to be positively skewed. Perhaps the reason why such predictions have not been considered to apply well to animal populations is the lack of effort to test these models under field conditions. Sampling throughout the range of a population under a large variety of densities is beyond the resources of most field biologists. However, such data are readily available for many fish populations from research surveys. For example, it is a simple matter to plot the length frequencies for Atlantic cod for a year of high abundance and low abundance (Fig. 6.9). For the year-class with high abundance, 1981, the mean size is reduced and the CV and skewness are greater compared with a year-class of relatively low abundance. This relationship holds over all years of the surveys. Atlantic cod shows clear territorial behaviour for the first year of life after the larval stage (Tupper and Boutilier 1995) and often shows strong density-dependent mortality (Myers and Cadigan 1993a) and growth. That is, cod may be more like coral-reef fish, at least during the demersal stage, than most people believe. Such analysis of data from surveys may be very useful in understanding recruitment.

6.9.3 *Empirical analysis of multispecies interactions on recruitment*

Perhaps the most exciting work in the near future will be the combination of the study of spawner-recruitment relationships with multispecies interactions. I predict that the synthesis of these two approaches will yield wonderful new discoveries. The massive analysis of many aquatic communities by Pauly, Christensen and many coworkers (Christensen and Pauly 1998; Pauly and Christensen, Chapter 10, Volume 2) and the recent extensions to dynamic models (Walters et al. 1997), allied to the approaches outlined here, could yield remarkable results.

It is crucial that the interspecific interaction coefficient be comparable over studies. This can be done by the same standardization as used in the delayed density-dependent analysis above or by a

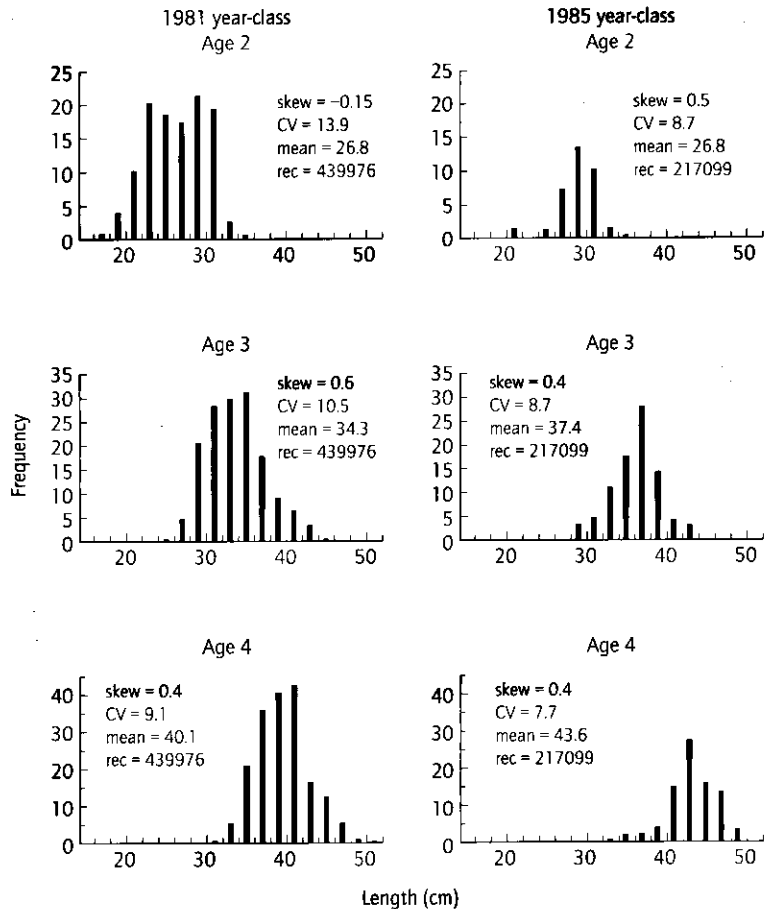


Fig. 6.9 Length frequencies of 2–4-year-old cod at low (1985) and high (1981) population levels for NAFO Subdivision 2J.

modification of the generalized key factor. All singles-species spawner–recruitment models are extreme approximations because they ignore species interactions. The complexity of multi-species interaction requires a meta-analytic approach. An excellent informal meta-analysis was carried out by Daan (1980) in a comparative study of species replacement.

6.9.4 Better use of data and the need for meta-analysis

When studies are being reviewed, effects are often examined to determine how frequently they are statistically significant. This can be a very mis-

leading approach, even though it is intuitively appealing. For example, if the reviewer simply examines how often an outcome is statistically significant, then there will be a strong bias towards the conclusion that the process or treatment has no effect (Hedges and Olkin 1985). Furthermore, this bias is not reduced as the number of studies increases. If a large number of studies or populations are examined, the proportion of studies that yield statistically significant results is approximately the average power of the test used (Hedges and Olkin 1985). That is, reviewers of research studies may assume that they are examining the importance of an ecological process, but may only be examining the power of the tests used to ex-

mine it. Research synthesis without considering the statistical problems can lead to serious mistakes. I believe it is a mistake to expect 'definitive studies'.

Work should focus on obtaining quantitative estimates of the components of density-independent mortality that can be attributed to different causes, such as starvation, predation and advection, and quantitative estimates of density-dependent mortality at different stages. Results should be presented in such a way that they can be compared among populations and species. The components of the interannual variability in mortality can be compared among populations and species (Myers 1995). Similarly, if mortality is proportional to log density, then the coefficient of density dependence can be compared across populations (Myers and Cadigan 1993a). Virtually no systematic attempts have been made to carry out these studies.

6.10 CONCLUSIONS

Attempts to understand recruitment have dominated much of fisheries research in the last century. We have made good progress on some issues. The actual practice of managing fisheries is being changed into a quantified science, i.e. something closer to engineering instead of an art, because we discovered quantitative generalities and have developed the tools to apply them, e.g. Bayesian methods. For example, we now have estimates of the maximum reproductive rate, which allows the limits and exploitation to be well understood. Furthermore, we have a much greater theoretical and empirical understanding of the nature of recruitment variability (Table 6.1).

Further progress will require improved experiments, observations and analytical methods. Although experiments have elucidated many aspects of post-settlement recruitment processes for coral reef fish, experimental manipulations need to be extended to other systems. Recruitment studies have been limited to a few species that are either commercially important or easily studied. The most important outstanding questions concerning

recruitment revolve around multispecies interactions; meta-analytic methods to infer these interactions from the present data are sorely needed.

ACKNOWLEDGEMENTS

I thank J. Gibson, B. MacKenzie and C. Reiss for suggestions.

REFERENCES

- Bailey, K.M. (1981) Larval transport and recruitment of Pacific hake, *Merluccius productus*. *Marine Ecology Progress Series* **6**, 1–9.
- Bakun, A. (1996) *Patterns in the Ocean: Ocean processes and Marine Population Dynamics*. La Jolla, CA: California Sea Grant College System, National Oceanic and Atmospheric Administration.
- Beukers, J.S. and Jones, G.P. (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* **114**, 50–9.
- Bradford, M.J. (1991) Effects of aging errors on recruitment time series estimated from sequential population analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 555–8.
- Bradford, M.J. (1992) Precision of recruitment estimates from early life stages of marine fishes. *Fisheries Bulletin* **90**, 439–53.
- Bradford, M.J. (1995) Comparative review of Pacific salmon survival rates. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1327–38.
- Bradford, M.J. (1999) Temporal and spatial trends in the abundance of coho salmon smolts from western North America. *Transactions of the American Fisheries Society* **128**, 840–6.
- Bradford, M.J. and Cabana, G. (1997) Interannual variability in survival rates and the causes of recruitment variation. In: R.C. Chambers and E.A. Trippel (eds) *Early Life History and Recruitment in Fish Populations*. London: Chapman & Hall, pp. 469–93.
- Bradford, M.J., Taylor, G.C. and Allan, J.A. (1997) Empirical review of coho salmon smolt abundance and the prediction of smolt production. *Transactions of the American Fisheries Society* **126**, 49–64.
- Buynak, G.L., Hale, R.S. and Mitchell, B. (1992) Differential growth of young-of-year gizzard shad in several Kentucky reservoirs. *North American Journal of Fisheries Management* **12**, 656–62.
- Chadwick, M. (1985) The influence of spawning stock on production and yield of Atlantic salmon, *Salmo*

- salas L., in *Canadian rivers. Aquaculture and Fisheries Management* **1**, 111–19.
- Christensen, V. and Pauly, D. (1998) Changes in models of aquatic ecosystems approaching carrying capacity. *Ecological Applications* **8** (Suppl. 1), S104–9.
- Clark, W.G. (1991) Groundfish exploitation rates based on life history parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 734–50.
- Close, T.L. and Anderson, C.S. (1992) Dispersal, density dependent growth, and survival of stocked steelhead fry in Lake Superior tributaries. *North American Journal of Fisheries Management* **12**, 728–35.
- Cooper, H. and Hedges, L.V. (1994) *The Handbook of Research Synthesis*. New York: Russell Sage Foundation.
- Cowan, J.R., Houde, E.D. and Rose, K.A. (1996) Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment. *ICES Journal of Marine Science* **53**, 23–38.
- Cury, P. and Roy, C. (1989) Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 670–80.
- Cushing, D.H. (1969) The regularity of the spawning season of some fishes. *Journal du Conseil International pour l'Exploration de la Mer* **33**, 81–97.
- Cushing, D.H. (1982) *Climate and Fisheries*. London: Academic Press.
- Cushing, D.H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* **26**, 249–93.
- Cushing, D.H. (1996) *Towards a Science of Recruitment in Fish Populations*. Oldendorf-Luhe, Germany: Ecology Institute.
- Daan, N. (1980) A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. *Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **177**, 405–21.
- DeGisi, J.S. (1994) *Year class strength and catchability of mountain lake brook trout*. Master's thesis, University of British Columbia, Vancouver, British Columbia.
- Dower, J.F., Miller, T.J. and Leggett, W.C. (1997) The role of microscale turbulence in the feeding ecology of larval fish. *Advances in Marine Biology* **31**, 169–220.
- Elliott, J.M. (1994) *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.
- Fogarty, M.J. (1993) Recruitment in randomly varying environments. *ICES Journal of Marine Science* **50**, 247–60.
- Forrester, G.E. (1995a) Factors influencing the juvenile demography of a coral reef fish. *Ecology* **71**, 1666–81.
- Forrester, G.E. (1995b) Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. *Oecologia* **103**, 275–82.
- Fox, M.G. and Flowers, D.D. (1990) Effect of fish density on growth, survival, and food consumption by juvenile walleyes in a rearing pond. *Transactions of the American Fisheries Society* **119**, 112–21.
- Fromentin, J.M., Myers, R.A., Bjornstad, O.N., Stenseth, N.C., Gjoseter, J. and Christie, H. (2001) Effects of density-dependent and stochastic processes on the regulation of cod populations. *Ecology* **2**, 567–79.
- Gilbert, D.J. (1997) Towards a new recruitment paradigm for fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 969–77.
- Gilks, W.R., Thomas, A. and Spiegelhalter, D.J. (1994) A language and program for complex Bayesian modelling. *The Statistician* **43**, 169–78.
- Heath, M.R. (1992) Field investigations of the early life stages of marine fish. *Advances in Marine Biology* **28**, 1–133.
- Hedges, L.V. and Olkin, I. (1985) *Statistical Methods for Meta-analysis*. San Diego, CA: Academic Press.
- Helbig, J.A. and Pepin, P. (1998) Partitioning the influence of physical processes on the estimation of ichthyoplankton mortality rates. I. Theory. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2189–205.
- Hixon, M.A. (1991) Predation as a process structuring coral reef fish communities. In: P.F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*. New York: Academic Press, pp. 475–508.
- Hixon, M.A. and Carr, M.H. (1997) Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**, 946–8.
- Hixon, M.A. and Webster, M.S. (2002) Density dependence in reef fishes: coral-reef populations as model systems. In: P.F. Sale (ed.) *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. San Diego, CA: Academic Press, pp. 303–25.
- Hjort, J. (1914) Fluctuations in the great fisheries of Northern Europe. *Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **20**, 1–228.
- Horn, M.H. (1972) The amount of space available for marine and freshwater fishes. *Fisheries Bulletin* **70**, 1295–8.
- Hume, J.M.B., Shortreed, K.S. and Morton, K.F. (1996) Juvenile sockeye rearing capacity of three lakes in the Fraser River system. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 719–33.
- Hutchings, J.A. and Myers, R.A. (1994a) Timing of cod reproduction: interannual variability and the influence of temperature. *Marine Ecology Progress Series* **108**, 21–31.
- Hutchings, J.A. and Myers, R.A. (1994b) What can be

- learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2126–46.
- Iles, T.D. and Sinclair, M. (1982) Atlantic herring: stock discreteness and abundance. *Science* **215**, 627–33.
- Kimme, M. (1986) Does competition for food imply skewness? *Mathematical Biosciences* **80**, 160–71.
- Lasker, R. (1975) Field criteria for the survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fisheries Bulletin* **73**, 453–62.
- Lasker, R. (1981) Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. *Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **164**, 375–88.
- Latto, J. (1992) The differentiation of animal body weights. *Functional Ecology* **6**, 386–96.
- LeCren, E.D. (1965) Some factors regulating the size of populations of freshwater fish. *Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* **12**, 88–105.
- Leggett, W.G. and DeBlois, E. (1994) Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research* **32**, 119–34.
- Letcher, B.H., Rice, J.A., Crowder, L.B. and Rose, K.A. (1996) Variability in survival of larval fish: disentangling components with a generalized individual-based model. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 787–801.
- Liermann, M. and Hilborn, R. (1997) Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1976–85.
- Lochmann, S.E., Taggart, C.T., Griffin, D.A., Thompson, K.R. and Maillet, G.L. (1997) Abundance and condition of larval cod (*Gadus morhua*) at a convergent front on western bank, Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1461–79.
- Lockwood, S.J. (1980) Density-dependent mortality in O-group plaice (*Pleuronectes platessa* L.) populations. *Journal du Conseil International pour l'Exploration de la Mer* **39**, 148–53.
- Lorda, E. and Crecco, V.A. (1987) Stock–recruitment relationship and compensatory mortality of American shad in the Connecticut River. In: M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson and J.E. Cooper (eds) *Common Strategies of Anadromous and Catadromous Fishes: Proceedings of an International Symposium held in Boston, Massachusetts*. Bethesda, MD: American Fisheries Society, Vol. 1, pp. 469–82.
- Mace, P.M. (1994) Relationships between common biological reference points used as threshold and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 110–22.
- Mace, P.M. and Sissenwine, M.P. (1993) How much spawning per recruit is enough? In: S.J. Smith, J.J. Hunt and D. Rivard (eds) *Risk Evaluation and Biological Reference Points for Fisheries Management*. Ottawa: National Research Council, pp. 101–18.
- MacKenzie, B.R. and Kiorboe, T. (1995) Encounter rates and swimming behavior of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. *Limnology and Oceanography* **40**, 1278–89.
- MacKenzie, B.R., Miller, T.J., Cyr, S. and Leggett, W.C. (1994) Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnology and Oceanography* **39**, 1790–9.
- McFadden, J.T., Alexander, G.R. and Shetter, D.S. (1967) Numerical changes and population regulation in brook trout. *Journal of the Fisheries Research Board of Canada* **24**, 1425–59.
- McIntosh, W.C. (1899) *The Resources of the Sea*. London: C.J. Clay and Sons and Cambridge University Press.
- Mertz, G. and Myers, R.A. (1994) Match/mismatch predictions of spawning duration versus recruitment variability. *Fisheries Oceanography* **3**, 236–44.
- Mertz, G. and Myers, R.A. (1995) Estimating the predictability of recruitment. *Fisheries Bulletin* **93**, 657–65.
- Mertz, G. and Myers, R.A. (1996) Influence of fecundity on recruitment variability of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 1618–25.
- Mills, C.A. and Hurley, M.A. (1990) Long-term studies on the Windermere populations of perch (*Perca fluviatilis*), pike (*Esox lucius*) and Arctic charr (*Salvelinus alpinus*). *Freshwater Biology* **23**, 119–36.
- Mills, E.L., Forney, J.L. and Wagner, K.J. (1987) Fish predation and its cascading effect on the Oneida Lake food chain. In: W.C. Kerfoot and A. Sih (eds) *Predation: Direct and Indirect Impacts on Aquatic Communities*. London: University Press of New England, pp. 113–18.
- Myers, R.A. (1991) Recruitment variability and range of three fish species. *Northwest Atlantic Fisheries Organization Scientific Council Studies* **16**, 21–4.
- Myers, R.A. (1995) Recruitment of marine fish: the relative roles of density-dependent and density-independent mortality in the egg, larval, and juvenile stages. *Marine Ecology Progress Series* **128**, 308–9.
- Myers, R.A. (1997) Comment and reanalysis: paradigms

- for recruitment studies. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 978–81.
- Myers, R.A. (1998) When do environment–recruit correlations work? *Reviews in Fish Biology and Fisheries* **8**, 285–305.
- Myers, R.A. (2001) Stock and recruitment: generalizations about maximum reproductive rate, density dependence and variability using meta-analytic approaches. *ICES Journal of Marine Science* **58**, 937–51.
- Myers, R.A. and Barrowman, N.J. (1996) Is fish recruitment related to spawner abundance? *Fisheries Bulletin* **94**, 707–24.
- Myers, R.A. and Cadigan, N.G. (1993a) Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1576–90.
- Myers, R.A. and Cadigan, N.G. (1993b) Is juvenile natural mortality in marine demersal fish variable? *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1591–8.
- Myers, R.A. and Drinkwater, K. (1988) Ekman transport and larval fish survival in the Northwest Atlantic. *Biological Oceanography* **6**, 45–64.
- Myers, R.A. and Drinkwater, K.F. (1989) The influence of Gulf Stream warm core rings on recruitment of fish in the Northwest Atlantic. *Journal of Marine Research* **47**, 635–56.
- Myers, R.A. and Mertz, G. (1998) The limits of exploitation: a precautionary approach. *Ecological Applications* **8** (Suppl. 1), S165–9.
- Myers, R.A. and Pepin, P. (1994) Recruitment variability and oceanographic stability. *Fisheries Oceanography* **3**, 246–55.
- Myers, R.A., Bridson, J. and Barrowman, N.J. (1995a) Summary of worldwide stock and recruitment data. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2024**, 327.
- Myers, R.A., Barrowman, N.J., Hutchings, J.A. and Rosenberg, A.A. (1995b) Population dynamics of exploited fish stocks at low population levels. *Science* **269**, 1106–8.
- Myers, R.A., Mertz, G. and Bridson, J.M. (1997a) Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1400–7.
- Myers, R.A., Bradford, M.J., Bridson, J.M. and Mertz, G. (1997b) Estimating delayed density-dependent mortality in sockeye salmon (*Oncorhynchus nerka*): a meta-analytic approach. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2449–63.
- Myers, R.A., Bowen, K.G. and Barrowman, N.J. (1999) The maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2404–19.
- Myers, R.A., MacKenzie, B.R., Bowen, K.G. and Barrowman, N.J. (2001) What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1464–76.
- National Marine Fisheries Service (1998) 26th Northeast Regional Stock Assessment Workshop. NEFSC Ref. Document 98/03. Woods Hole, MA: NMFS.
- Nielsen, L.A. (1980) Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 11–19.
- Nordeide, J.T., Fossa, J.H., Salvanes, A.G.V. and Smedstad, O.M. (1994) Testing if year-class strength of coastal cod, *Gadus morhua* L., can be determined at the juvenile stage. *Aquaculture and Fisheries Management* **25**, 101–16.
- Pace, M.L., Baines, S.B., Cyr, H. and Downing, J.A. (1993) Relationships among early life stages of *Morone americana* and *Morone saxatilis* from long-term monitoring of the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1976–85.
- Pais, A. (1982) *Subtle is the Lord: the Science and the Life of Albert Einstein*. Oxford: Oxford University Press.
- Pedersen, T. (1984) Variation of peak spanning of Arcto-Norwegian cod (*Gadus morhua* L.) during the time period 1929–1982 based on indices estimated from fishery statistics. In: E. Dahl, D.S. Danielssen, D.S. Moksness and E. Solemdal (eds) *The Propagation of Cod Gadus morhua* L. Arendal, Norway: Flødevigen rapportser, pp. 301–16.
- Peterman, R.M. and Bradford, M.J. (1987) Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science* **235**, 354–6.
- Pfister, C.A. (1996) Consequences of recruitment variation in an assemblage of tidepool fishes. *Ecology* **77**, 1928–41.
- Polacheck, T., Mountain, D., McMillan, D., Smith, W. and Berrien, P. (1992) Recruitment of the 1987 year class of Georges Bank haddock (*Melanogrammus aeglefinus*): the influence of unusual larval transport. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 484–96.
- Punt, A. and Hilborn, R. (1997) Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries* **7**, 35–65.
- Rauck, G. and Zijlstra, J.J. (1978) On the nursery aspects of the Wadden Sea for some commercial fish species and possible long-term changes. *Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **172**, 266–75.
- Rice, J.A., Crowder, L.B. and Holey, M.E. (1987) Explo-

- ration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. *Transactions of the American Fisheries Society* **116**, 703–18.
- Ricker, W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11**, 559–623.
- Ricker, W.E. and Forrester, R.E. (1948) Computation of fish production. *Bulletin of the Bingham Oceanographic Collection, Yale University* **11**, 173–211.
- Rickman, S., Dulvy, N., Jennings, S. and Reynolds, J. (2000) Recruitment variation related to fecundity in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 116–24.
- Rijnsdorp, A.D., Beek, F.A.V., Flatman, S. et al. (1992) Recruitment of sole stocks, *Solea solea* (L.), in the Northwest Atlantic. *Netherlands Journal of Sea Research* **29**, 173–92.
- Rothschild, B.J. and DiNardo, G.T. (1987) Comparison of recruitment variability and life history data among marine and anadromous fishes. *Journal du Conseil International pour l'Exploration de la Mer* **1**, 531–46.
- Rothschild, B.J. and Osborn, T.R. (1988) Small-scale turbulence and plankton contact rates. *Journal of Plankton Research* **10**, 465–74.
- Salojärvi, K. (1991) Compensation in a whitefish (*Coregonus lavaretus*) population maintained by stocking in Lake Kallioinen, Northern Finland. *Finnish Fisheries Research* **12**, 65–76.
- Schopka, S.A. (1994) Fluctuations in the cod stock off Iceland during the twentieth century in relation to changes in the fisheries and environment. *ICES Marine Science Symposia* **198**, 175–93.
- Searle, S.R., Casella, G. and McCulloch, C.E. (1992) *Variance Components*. New York: John Wiley & Sons.
- Serns, S.D. (1982) Influence of various factors on density and growth of age-0 walleyes in Escanaba Lake, Wisconsin, 1958–1980. *Transactions of the American Fisheries Society* **111**, 299–306.
- Shepherd, J.G. (1982) A versatile new stock–recruitment relationship for fisheries, and the construction of sustainable yield curves. *Journal du Conseil International pour l'Exploration de la Mer* **40**, 67–76.
- Shepherd, J.G., Pope, J.G. and Cousens, R.D. (1984) Variations in fish stocks and hypotheses concerning their links with climate. *Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **185**, 255–67.
- Sissenwine, M.P. and Shepherd, J.G. (1987) An alternative perspective on recruitment overfishing and biological reference points. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 913–18.
- Steele, M.A. (1997) Population regulation by post-settlement mortality in two temperate reef fishes. *Oecologia* **112**, 64–74.
- Tupper, M. and Boutilier, R.G. (1995) Effects of conspecific density on settlement, growth and post-settlement survival of a temperate reef fish. *Journal of Experimental Marine Biology and Ecology* **191**, 209–22.
- Van Der Veer, H.W., Pihl, L. and Bergman, M.J.N. (1990) Recruitment mechanisms in North Sea plaice (*Pleuronectes platessa*). *Marine Ecology Progress Series* **64**, 1–12.
- Varley, G.C. and Gradwell, G.R. (1960) Key factors in population studies. *Animal Ecology* **29**, 299–401.
- Verity, P.G. and Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series* **130**, 277–93.
- Walters, C., Christensen, V. and Pauly, D. (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* **7**, 39–172.
- Walters, C.J. and Collie, J.S. (1988) Is research on environmental factors useful to fisheries management? *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 1848–54.
- Walton, C.J. (1987) Parent–progeny relationship for established population of anadromous alewives in a Maine lake. *American Fisheries Society Symposium* **1**, 451–4.
- Watling, L. and Norse, E.A. (1998) Effects of mobile fishing gear on marine benthos: disturbance of the seabed by mobile fishing gear. A comparison to forest clearcutting. *Conservation Biology* **12**, 1180–97.
- Wooster, W.W. and Bailey, K.M. (1989) Recruitment of marine fishes revisited. In: K.J. Beamish and C.A. McFarlane (eds) *Effects of Ocean Variability on Recruitment and an Evaluation of Parameters Used in Stock Assessment Models*. Ottawa, Canada: Department of Fisheries and Oceans, pp. 153–9.