Part I
Biology, Population Dynamics and Recruitment
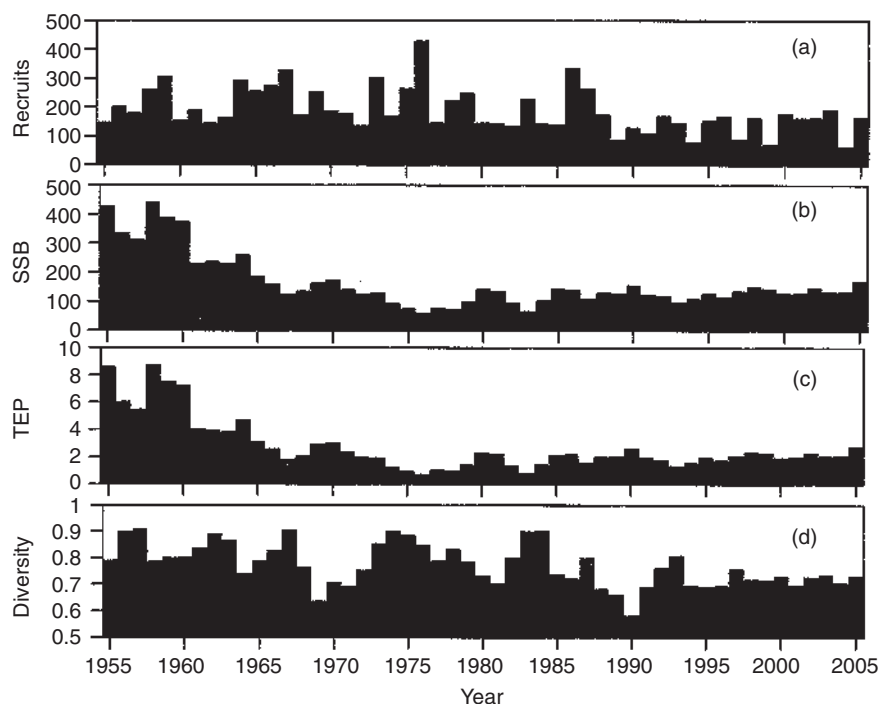
Chapter 1
Recruitment in Marine Fish Populations

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1.1   Introduction

The production of viable eggs by a population provides the raw material for recruitment (the number of young ultimately surviving to a specified age or life stage). Recruitment processes in the sea reflect the interplay of external forcing mechanisms such as physical drivers in the environment that affect demographic rates, and stabilizing mechanisms exhibited by the population. Many marine populations fluctuate widely in space and time (Fogarty *et al.* 1991). These dramatic changes are attributable to fluctuations in biotic and abiotic factors affecting growth and/or mortality rates during the early life history (Fogarty 1993a). Potentially countering these sources of variability are internal regulatory mechanisms that can compensate for population changes. Considerable attention has been devoted to the development of recruitment models embodying different types of compensatory processes operating during the pre-recruit phase of the life history (see Rothschild 1986, Hilborn & Walters 1992, Quinn & Deriso 1999 and Walters & Martell 2004 for reviews). In contrast, the issue of compensatory changes in factors such as fecundity, adult growth, and maturation affecting reproductive output has received less attention in modeling recruitment dynamics (but see Ware 1980, Jones 1989, Rothschild & Fogarty 1989, 1998). We argue that a complete model of population regulation of marine fishes must allow for the possibility of compensatory processes operating during both the early life history and the adult stages and that a refined understanding of reproductive processes as described in the contributions to this book is essential in the quest to understand recruitment of marine fishes.

This chapter attempts to set the stage for several themes found throughout this volume—factors controlling the effective reproductive output of the population, the fate of fertilized eggs and larvae, and the implications for assessment and management of exploited marine species. In subsequent chapters, these issues are explored in greater individual detail. An understanding of recruitment processes is essential if we are to predict the probable response of a population to exploitation and to proposed management actions. These predictions require an analytical framework. Here, we trace the theoretical developments relating recruitment to the adult population to provide such a framework. Our interest centers on exploring the consequences of different recruitment mechanisms, demonstrating how these processes can be modeled, and illustrating their importance for stability and resilience of the population. In a variable environment, sustainable exploitation is possible only if the population exhibits

Figure 1.1   Time series of estimates of (a) recruitment (millions of 3-year-old fish), (b) spawning stock biomass (thousand Mt), (c) total egg production (billions) and (d) age diversity of spawners (Shannon–Weiner index) for Icelandic cod (G. Marteinsdottir, personal communication).

some form of compensation in response to variation in population size at some stage in the life history. The general issue of the role of compensation in population dynamics is therefore of both theoretical and practical importance. Correctly accounting for the effective reproductive output of the population, including consideration of factors such as maternal effects on egg and larval viability, age composition of the adult population, female condition, and how these are affected by population density or abundance, is critical in understanding the form of the relationship between recruitment and egg production and how the population will respond to exploitation.

An illustration of the magnitude of change in these population components is provided by trajectories of recruitment and adult biomass over the last five decades for Icelandic cod, an economically and ecologically important fish population (Figure 1.1(a),(b)). Attempts have now been made to refine estimates of reproductive output by reconstructing the total egg production by the female population (Figure 1.1(c)) and to understand how factors such as the age diversity of the spawning stock (Figure 1.1(d)) affect recruitment success. Although estimates of each of these quantities are currently available for relatively few populations, the importance of obtaining these and other metrics of reproductive output is now increasingly recognized (e.g. Marteinsdottir & Thorarinsson 1998, Trippel 1999, Marshall *et al.* 1998, 2003) and serves as a recurrent theme throughout this book. We will return to the relationship between recruitment and spawning stock biomass or total egg production for Icelandic cod in Section 1.2.3

to further explore these issues and in Section 1.8.1 we will ask whether consideration of the age diversity of the adult population improves the predictability of recruitment for this population.

In the following, we describe several models incorporating factors affecting survivorship from the egg stage to recruitment. These include competition for limiting resources, cannibalism, and the interaction of compensatory growth and size-dependent mortality. Our initial treatment will focus on deterministic processes for a single pre-recruit stage. We then broaden our development to encompass consideration of compensatory processes operating during the post-recruit phase of the life history, the stability properties of these models, multistage life-history patterns, the implications of maternal effects, and the effects of environmental and demographic stochasticity. Throughout, the implications of these factors for management of exploited populations are of primary interest.

1.2   Recruitment theory

Consider the life cycle diagram depicted in Figure 1.2. For the population to persist, a sufficient number of progeny must, on average, survive to replace the parental stock. For the purposes of illustration, we show several stanzas including egg, larval, juvenile and adult stages. The eggs produced by the different adult stages can in principle exhibit different viabilities and have different probabilities of successful transition to the larval stage. For the purposes of this simple illustration we do not trace the effect of the size or age of the adult females beyond the egg stage but we can readily extend this treatment to later stages as well. The transitions between stages represent the probability of surviving and growing into the next stage during a specified time interval. Note that the population becomes vulnerable to exploitation following the first juvenile stage in this example. In the following, we use the size or age at first harvest as the demarcation point for recruitment. The life cycle is completed with the production of eggs by the adult component of the population. The fishery reduces the probability of survival in the late juvenile and the adult stages with important consequences for the overall reproductive output of the population. The number and quality of eggs produced by different segments (age or size classes) of the adult female population vary in relation to spawning history, condition, and other factors–a central theme of many contributions found in this book (see Chapters 2, 4 and 8) with potentially important management implications (see Chapters 9, 10 and 11).
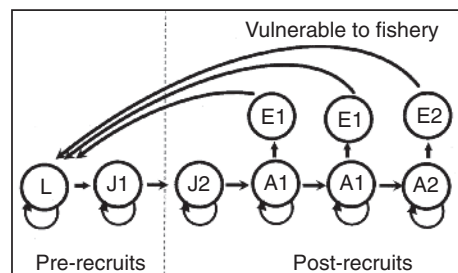
Figure 1.2   Life cycle life diagram including egg, larval, juvenile and adult stages. Eggs produced by adults of different ages can have different viabilities.
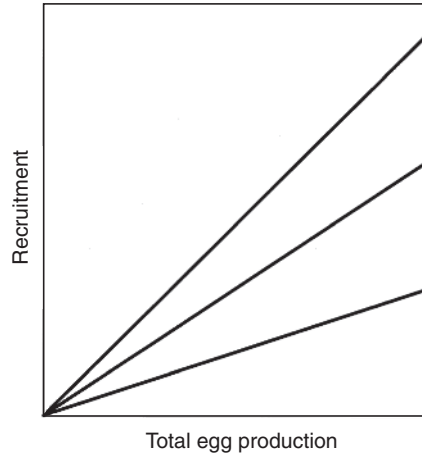
Figure 1.3 Density-independent model relating recruitment and egg production for three levels of the density-independent mortality rate.

To model this process, we begin with the simple observation that for a closed population, the number of individuals in a cohort can only decline over time. Here a cohort is defined as the number of individuals hatched in a specified period (spawning season, year, etc.). In the very simplest case where no compensation occurs, the number of recruits (R) is given by the product of the proportion surviving (S) from the egg to the recruit stage and the initial number in the cohort (the number of viable eggs—designated E):

$$R = S\,E \tag{1}$$

This gives a simple linear relationship between egg production and recruitment with slope equal to the survival fraction (Figure 1.3). For a closed population, the relationship goes through the origin. Being able to correctly identify the members of the population and their spatial domain is of course a critical prerequisite for defining this relationship (see Chapter 6). For metapopulation structures with interchange among populations, the relationship may not pass through the origin (e.g. for a sink population receiving a subsidy from a source population; see also Section 1.2.2).

In subsequent sections we will expand the density-independent case to include compensatory processes resulting in non-linear relationships between the number of viable eggs produced and recruitment, random variation in vital rates, and other factors. For now, we will focus on the underpinnings of the simple density-independent model. We will consider this to be our null recruitment model. Note that a straight line with zero slope is not an appropriate null model in this context—it implies that recruits can be produced when the egg production has been reduced to zero. Adopting such a null model would entail high risk to the population (see Fogarty *et al.* 1992, 1996).

The null model can be derived from first principles by describing the rate of change of a cohort:

$$\frac{dN}{dt} = -\mu N \tag{2}$$

where N is the number in the cohort and μ is the instantaneous rate of mortality during the pre-recruit phase. This model of course captures the idea that the number in the cohort can only decline over time (in this case, at a constant rate). Separating variables we have:

$$\int_{N=E}^{R} \frac{dN}{N} = -\mu \int_{t=0}^{tr} dt \tag{3}$$

where E is again the initial number in the cohort (the number of viable eggs produced), and R is the number surviving to the age of recruitment (t_r). The solution to this simple model is given by:

$$R = E\,e^{-\mu t} \tag{4}$$

where for simplicity we have set $t = t_r - t_o$ and where $e^{-\mu t}$ is the survival fraction (S; cf., Equation 1).

1.2.1   Compensatory and overcompensatory models

The null recruitment model implies that there are no constraints on the number of recruits produced for a given level of egg production, leading to unrealistic predictions of unrestrained population growth (Chapter 7). We can readily extend the density-independent recruitment model to incorporate various types of compensatory processes affecting growth and survival during the pre-recruit phase. Because the density-independent model cannot account for limitations in recruitment that emerge as a result of competition for limited resources (food, space, etc.) or factors such as cannibalism known to be important in many marine populations, we need to expand our consideration of underlying recruitment mechanisms. For a lucid verbal description of the underpinnings of the classical stock–recruitment models embodying these mechanisms, see Chapter 7. These considerations lead to non-linear models with important implications for the stability of the population. The principal focus of this book is in incorporating increased biological realism in our measures of reproductive output of the population. We are no less interested in incorporating biological realism in the development of recruitment models. We view recruitment models not simply as heuristic guides to the shape of the egg production–recruitment relationship but as the elaboration of testable biological hypotheses concerning different compensatory mechanisms.

1.2.1.1   Intracohort competition

In situations where members of the cohort compete for critical resources (food, space etc.) density-dependent mortality may be critically important. The simple null model can be extended to account for a linear increase in mortality with increasing cohort density by making the substitution $\mu = (\mu_o + \mu_1 N)$. Our model for the rate of decay of the cohort can then be expressed:

$$\frac{dN}{dt} = -(\mu_o + \mu_1 N)N \tag{5}$$
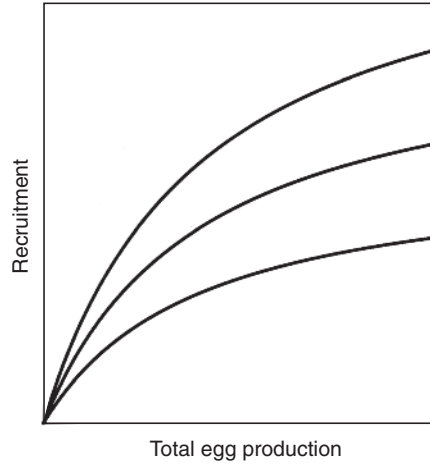
Figure 1.4 Beverton–Holt-type model relating recruitment and egg production for three levels of the parameter α.

where μ_o is the instantaneous rate of density-independent mortality and μ_1 is the coefficient of density-dependent mortality (Beverton & Holt 1957). Note that this model simply indicates that the per capita rate of change of cohort size (*dN/Ndt*) declines linearly with increasing N.

The solution is given by:

$$R = \left[\frac{1}{E} e^{\mu_o t} + \frac{\mu_1}{\mu_o}(e^{\mu_o t} - 1) \right]^{-1} \tag{6}$$

which can be simplified to:

$$R = \left[\frac{\alpha}{E} + \beta \right]^{-1} \tag{7}$$

where $\alpha = \exp(\mu_o t)$ and $\beta = ((\mu_1/\mu_o t)(\exp(\mu_o t) - 1))$. For this model, recruitment initially increases rapidly with increasing egg production and then approaches an asymptote (Figure 1.4). We note further that intracohort cannibalism could also result in a model of this general form.

In this chapter, we will refer to this asymptotic form as a compensatory recruitment model and will distinguish it from 'overcompensatory' models in which recruitment actually declines at higher levels of egg production (see next section) although some authors define these terms differently. Rothschild & Fogarty (1998) describe generalized models in which the per capita rate of change as a function of cohort size is not limited to the linear case as in the model above.

1.2.1.2   *Cannibalism by adults*

Cannibalism has been shown to be an important population regulatory mechanism in many marine fish populations (Dominey & Blumer 1984). In some cases, the adults are the principal

predators of earlier life stages. To represent intraspecific predation by adults on pre-recruits, we can let $\mu = (\mu_o + \mu_2 P)$ and the model for the decay of the cohort now can be specified:

$$\frac{dN}{dt} = -(\mu_o + \mu_2 P)N \tag{8}$$

where μ_2 is the coefficient of 'stock-dependent' mortality (Harris 1975), and P is a measure of the cannibalistic component of the adult population. Here, the per capita rate of change declines linearly with the adult population size. Note that some segments of the adult population may contribute more to cannibalism and the index of the adult population used can and should reflect this fact where available. The solution is:

$$R = E\, e^{-(\mu_o + \mu_2 P)t} \tag{9}$$

and in this form, we require information on both total egg production (E) and the relevant index of adult population size. For some applications we are ultimately interested in a bivariate model relating recruitment to total egg production. This requires a substitution of the index of population size by one for total egg production in the model. Later in this chapter, the potentially complex relationship between egg production and population size is explored in the context of these models. For the moment we will consider only the simplest case where egg production is related to the measure of adult population size by a constant of proportionality (ϖ) to illustrate the translation to a bivariate form. Letting $\kappa = \exp(-\mu_o t)$ and $\delta = \mu_2 t / \omega$ the model can be written:

$$R = \kappa E\, e^{-\delta E} \tag{10}$$

This overcompensatory model produces a characteristically domed-shape relationship between recruitment and egg production (Figure 1.5). We note that the model implicitly assumes random encounters between the progeny and the adult predators. If the early life stages are aggregated and the encounter probabilities are non-random, the degree of curvature of the relationship decreases (i.e. becomes less convex; see Ricker 1954).
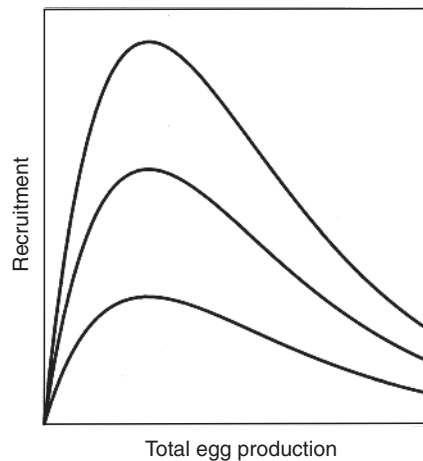
Figure 1.5   Ricker-type model relating recruitment and egg production for three levels of the slope at the origin parameter.

Ricker (1954) also noted that in instances where there is a delayed response by a predator to the initial number in the cohort, an overcompensatory response may be generated. In this case, our specification of the model for the rate of change of the cohort would directly include a term for the number of eggs produced, generating a model identical in form to Equation 10 but with a different interpretation of the parameter in the exponent.

1.2.1.3   Size-dependent processes

Compensatory recruitment models based on size-specific mortality rates have also been developed to reflect the interaction of compensatory growth and mortality rates. If smaller individuals are more vulnerable to predation, then density-dependent factors that affect the time required to grow through a 'window of vulnerability' to predation will have a direct effect on recruitment (see Chapter 3 for an overview). In particular, size can have critical effects on vulnerability when the ratio of predator to prey size is relatively low (Miller *et al.* 1988). Accordingly, density-related effects on growth can have potentially important implications for survival rates even if mortality itself is independent of density.

Beverton & Holt (1957) first illustrated this concept in a derivation of a two-stage pre-recruit life-history model. The pre-recruits were subjected to differing levels of mortality during the two stages. Beverton & Holt considered the case where the time required to grow from the first to the second stage was inversely proportional to the food supply and directly proportional to the initial number in the cohort and showed that such a formulation resulted in an overcompensatory stock–recruitment relationship.

It is possible to directly model growth processes and their interaction with mortality during the pre-recruit stage. Consider a model for individual growth in weight:

$$\frac{dW}{dt} = G(W) \tag{11}$$

where $G(W)$ is a compensatory function for individual growth. If the mortality rate is size-dependent then we have:

$$\frac{dN}{dt} = -\mu(W)N \tag{12}$$

and the rate of change of cohort size with respect to weight (size) is therefore:

$$\frac{dN}{dW} = -\frac{\mu(W)}{G(W)}N \tag{13}$$

The solution to this model is:

$$N(W_1) = N(W_o)\,e^{-\int \frac{\mu(W)}{G(W)}dW} \tag{14}$$

where $N(W_1)$ is the number in the population surviving to weight (size) W_1 which we will take to be the size at recruitment. This model has been discussed by Werner & Gilliam (1984). Without further specification of the functions $\mu(W)$ and $G(W)$, it is not possible to determine the functional form of this size-based recruitment function. However, if the growth rate is taken to be dependent on the cohort size and the mortality rate to be density-independent, then the recruitment function will generally be compensatory. If instead the growth rate is taken to be dependent on the *initial* number in the cohort, then the recruitment function will be overcompensatory (Ricker-type) (see Rothschild & Fogarty 1998).

Shepherd & Cushing (1980) assume that $G = G^*/(1 + N/K)$ where G^* is the maximum growth rate, N is cohort size, and K is a constant related to the abundance of food. It is further assumed that the mortality rate μ is independent of density. When $N = K$, the growth rate is exactly one half of the maximum rate. Separating variables, we can then write the model as:

$$\frac{dW}{W} = -\frac{G^*}{\mu} \frac{dN}{\left[\left(1 + \dfrac{N}{K}\right) N\right]} \tag{15}$$

and the solution is:

$$\log_e \left(\frac{W_1}{W_o}\right) = -\frac{G^*}{\mu} \log_e \left[\frac{(K + \mathrm{E}) N_1}{(K + N_1)\mathrm{E}}\right] \tag{16}$$

where again, the initial number in the cohort (E) emerges as the lower limit to integration on the right hand side of Equation 16. Exponentiating and letting $A = \exp\{-(\mu/G^*)ln(W_1/W_0)\}$, the model becomes (after further rearranging terms):

$$R = N(W_1) = \frac{A\mathrm{E}}{1 + (1 - A)\mathrm{E}/K} \tag{17}$$

which describes an asymptotic relationship between total egg production and recruitment (here, the number surviving to some specified weight class ($R = N(W_1)$); see Figure 1.6).

These examples should suffice to show that many different mechanisms can underlie recruitment dynamics and that in some cases, very different mechanisms can give rise to similarly shaped recruitment curves. Therefore, it will not generally be possible to understand the important regulatory mechanisms operating in the population based on information on spawning egg production and the resulting recruitment alone. However, an understanding of the underlying biological mechanisms can guide the choice of appropriate recruitment models, an issue of considerable importance in the face of the characteristically high levels of recruitment variability exhibited by many marine populations which tends to obscure the underlying relationship (see Section 1.8).
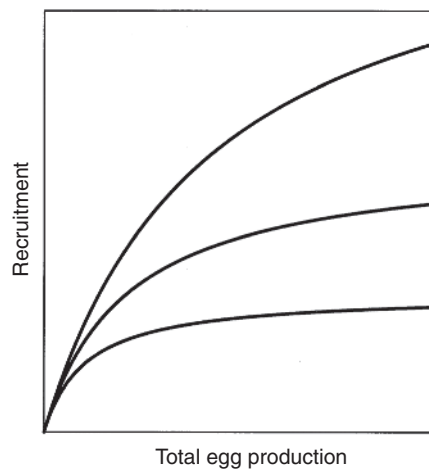
Figure 1.6   Cushing–Shepherd-type model relating recruitment and egg production for three levels of the density-dependent parameter K.

### *1.2.2   Depensatory processes and the Allee Effect*

The preceding sections focus on compensatory and overcompensatory mechanisms. For closed populations, these processes generally lead to stable non-zero equilibrium points (see Section 1.4), although for the case of overcompensatory models, quite complex dynamics can emerge (Ricker 1954), including chaos. Depensatory mechanisms of various types are also potentially of interest and can lead to multiple equilibria. Depensatory recruitment dynamics occur when the per capita rate of change of recruitment increases over some range of population or cohort size rather than declining monotonically as in compensatory and overcompensatory models. For such a system, we observe an inflection in the relationship between egg production and recruitment and this characteristic can lead to multiple equilibrium points for the population (see Section 1.4). For the case of 'critical depensation', a lower unstable equilibrium point exists and if the effective egg production by the population is driven below some threshold level, a sudden population collapse is predicted.

Depensation can occur under a number of mechanisms including when fertilization success is low at low population densities or there is a reduced probability of finding a mate. More broadly, when fitness or population growth is enhanced in the presence of conspecifics over some range of population size we have a so-called Allee Effect. For a description of the array of behavioral and ecological mechanisms that can lead to this effect, see Stephens *et al.* (1999). Among the mechanisms of direct interest in this chapter are effects related to fluctuations in the sex ratio at low population sizes (Stephens *et al.* 1999) which affect fertilization success.

The Beverton–Holt model can be generalized to allow for depensation as follows:

$$R = \left[\frac{\alpha}{E^{\gamma}} + \beta \right]^{-1} \tag{18}$$

where γ is a 'shape' parameter and all other terms are defined as before (when $\gamma > 1$ depensatory dynamics occur; see Figure 1.7(a)). Similarly for a generalized Ricker model, we
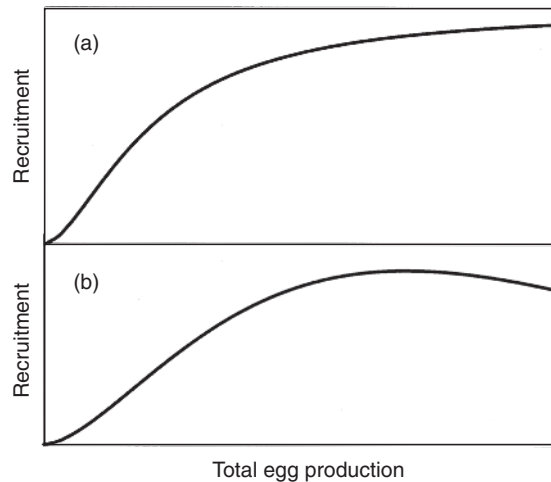
Figure 1.7   Models allowing for depensatory effects based on generalizations of (a) Beverton–Holt-type and (b) Ricker-type models relating recruitment and egg production.

can write:

$$R = \kappa E^{\gamma}\, e^{-\delta E} \tag{19}$$

where for economy of notation γ again represents the shape parameter (Figure 1.7(b)). Attempts to discern widespread evidence for depensatory dynamics in exploited fish populations have so far provided relatively few direct examples (Myers *et al.* 1995) but a lack of information at very low population levels may be responsible, in part, for this result. Marshall *et al.* (2006) did find that the relationship between recruitment and spawning stock biomass for Northeast Arctic cod was depensatory when the analysis focused on more recent years (since 1980) although estimates based on female spawning biomass and total egg production did not indicate depensatory dynamics.

Frank & Brickman (2000) considered a Ricker-type model incorporating a specific form of Allee Effect in which no recruitment at all occurs below a threshold population level. Frank & Brickman further considered a system comprising a number of spatially defined substocks, each of which is subject to the Allee Effect. Reframing this model in our notation and expressing in terms of egg production levels, we have:

$$R_i = \kappa_i (E - E_o)\, e^{-\delta(E - E_o)} \tag{20}$$

where E_o is the threshold level of egg production below which no recruitment occurs and the subscript i indicates an individual substock. Frank & Brickman show that if Allee Effects are important and managers either ignore or are unaware of the substock structure, the Allee Effect may be masked and lead to risk-prone decisions concerning appropriate harvest levels. This example reinforces the importance of both understanding the true population structure (see Chapter 6) and the nature of population regulatory mechanisms.

1.2.3   *Egg production or spawning stock biomass: does it matter?*

We have framed our analysis of recruitment dynamics in terms of total viable egg production by the population and factors affecting growth and survival during the pre-recruit period. Because estimates of total egg production were not widely available at the time, the earliest recruitment models were recast in terms of spawning stock biomass. Ricker (1954) and Beverton & Holt (1957) assumed a simple proportional relationship between egg production and adult biomass and used the latter as a proxy for the former (Chapter 11). Rothschild & Fogarty (1989) noted that the assumption of proportionality may be questionable and Marshall (Chapter 11) shows that other implicit assumptions such as a constant sex ratio and mean fecundity are not generally valid. As noted by Marshall (Chapter 11), the use of spawning biomass as a proxy for total egg production remains common today and will likely remain so until refined estimates of reproductive output are more widely available.

Estimates of recruitment and adult population size are available for many species using well established stock assessment methods (see Chapter 7) and these provide an important foundation for our analysis of recruitment dynamics. Although fecundity estimates are now routinely made for relatively few populations, rapid measurement techniques have been developed that promise to transform the availability of this type of information (Chapter 11). With the diversity of reproductive patterns in marine fishes, and the range of reproductive strategies and tactics represented, obtaining a proper accounting of fecundity and reproductive output is

no trivial matter (Chapters 2 and 8) but important progress is now being made. Given reliable estimates of fecundity in concert with age-specific estimates of sex ratios and abundance, it is possible to derive estimates of total egg production. Alternatively, for some populations, egg abundance can be measured directly at sea and corrected to provide estimates of viable egg production (Chapter 5). Given the documented changes in sex ratios, female condition, and other factors over time (Trippel 1999, Marshall *et al.* 1998, 1999, 2000, 2003, 2006), there is ample justification for broader application of estimates of total egg production in recruitment studies (see Chapter 11).

Relationships between recruitment and adult biomass and between recruitment and total egg production for Icelandic cod are illustrated in Figure 1.8. The high levels of recruitment variability common to many marine fishes is clearly evident in both representations. Cod are cannibalistic and we accordingly fit Ricker-type models to these data. For this population, a recruitment model based on egg production explains somewhat more of the variability in recruitment than does one based on spawning stock biomass (the coefficient of determination was 0.44 for the recruitment–spawning stock biomass relationship and 0.50 for the recruitment–total egg production relationship). We show in Section 1.8.1 that further improvements in the fit of the model are obtained by also considering the age diversity of spawners.

In addition, the modeled relationship between recruitment and egg production reveals subtle differences that are important in understanding how a population will respond to exploitation when compared with a model based on spawning stock biomass. In particular, the slope of the recruitment curve at the origin is steeper for the recruitment–egg production relationship (Figure 1.9). Relatively small differences in the slope of the recruitment curve at the origin can have important implications for inferences concerning the resilience of a population to high levels of exploitation. Later in this chapter, we will explore how these considerations shape our view of the resilience of a population to harvesting and the ways in which a refined understanding of the reproductive output of a population can help in setting appropriate management objectives.

1.3   Completing the life cycle

The previous sections dealt strictly with processes during the pre-recruit phase, operating on the initial number of viable eggs produced by the population. To complete our consideration of the life cycle dynamics of a cohort, we next examine models of the reproductive output of the adult population. Many of the topics covered in this book of course deal with this issue in detail.

### 1.3.1   *Viable egg production*

The number of individuals of a cohort alive at each successive age following recruitment is simply the product of the survival rates over the age classes considered and the number of recruits (taken as the starting point for this phase of the life history):

$$N_{a+1} = R \prod_{a=a_r}^{a_{\max}} \exp^{-(M_a + p_a F)} \tag{21}$$
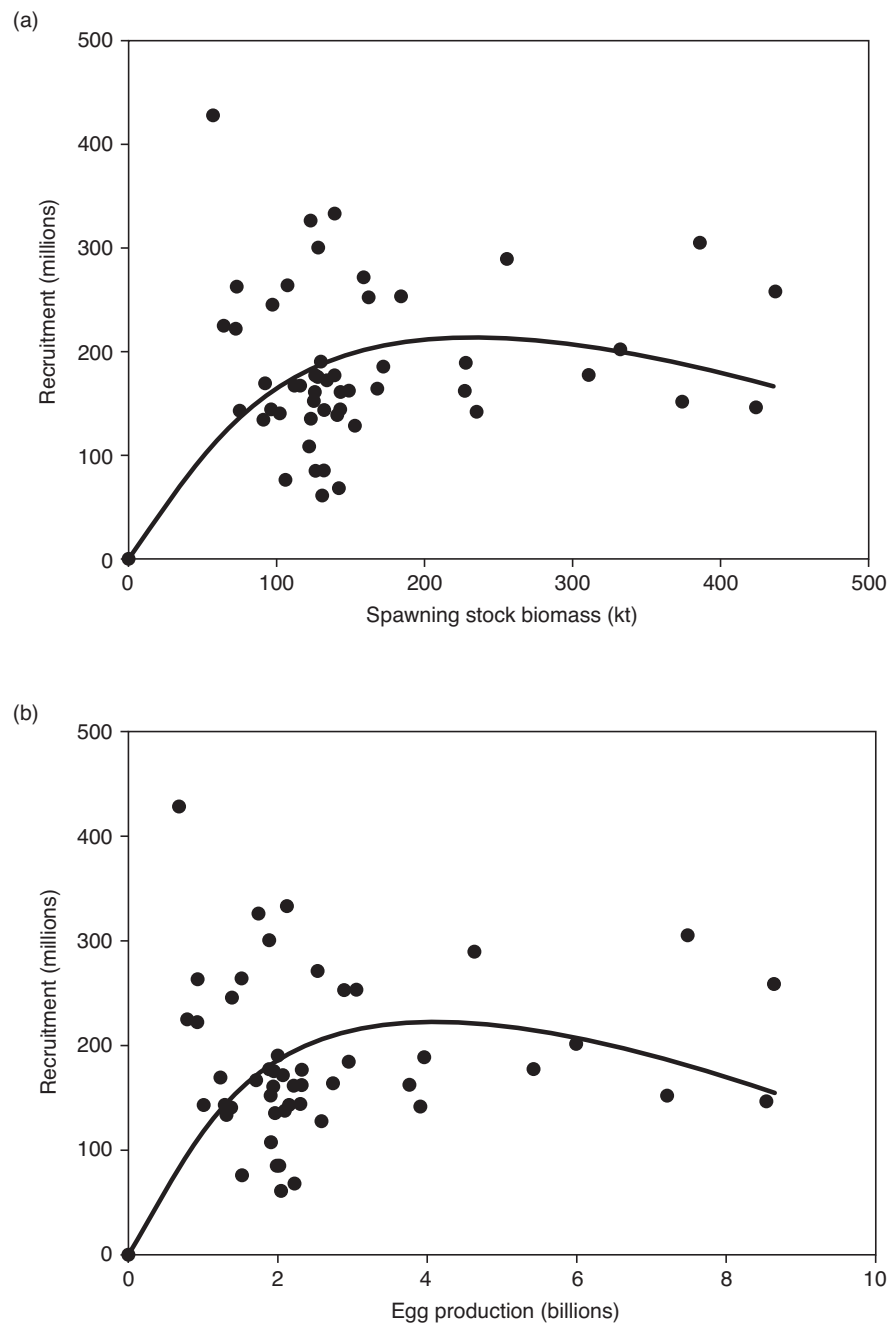
Figure 1.8   Relationship between recruitment and spawning stock biomass (a) and recruitment and total egg production (b) for Icelandic cod (G. Marteinsdottir, personal communication).
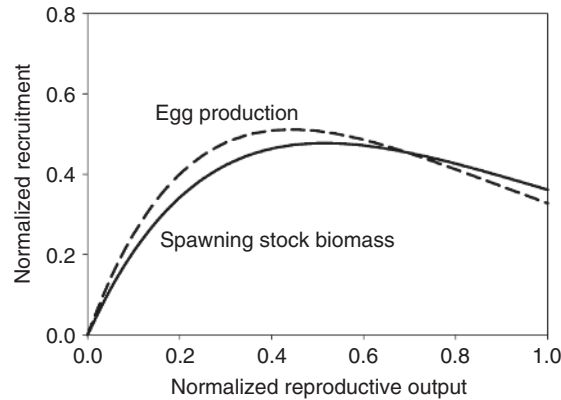
Figure 1.9 Fitted Ricker models for normalized recruitment and reproductive output using total egg production (solid line) and spawning stock biomass (dotted line) for Icelandic cod (G. Marteinsdottir, personal communication).

where M_a is the natural mortality rate at age a, p_a is the proportion vulnerable to the fishery at age a, F is the instantaneous rate of natural mortality, $a = a_r$ is the age at recruitment, and $a_{\max}$ is the maximum age. The expected number of viable eggs produced by a cohort over its lifespan can be expressed:

$$E = \sum_{a=a_r}^{a_{\max}} v_a \, m_a \, f_a \, s_a \, N_a \tag{22}$$

where v_a is the relative viability of eggs produced by females at age a (expressed as a proportion), m_a is the proportion of mature females, s_a is the sex ratio, f_a is the fecundity, and N_a is the number in the population at age a (see also Rothschild & Fogarty 1998; Chapter 11). If we normalize these results for the initial number of recruits, we define the egg production-per-recruit—a quantity of interest in a number of analyses presented later in this chapter. Chapter 7 describes the conceptual foundation for this approach in terms of spawning biomass as currently applied to most fish stocks (see also Chapter 9). In principle, each of these parameters can be expressed as functions of some measure of population size to reflect compensatory processes operating during the post-recruit phase (see below). We have explicitly allowed for differences in the viability of eggs produced by females of different ages or size classes. Larger females may produce larger eggs with higher energetic reserves (see Chapters 2 and 11). Developmental success may be higher for progeny of these individuals (Chapters 2 and 8). In principle, it may also be possible to make the age-specific viability term time-dependent and account for interannual variation in condition of female spawners. For example, information on total lipid energy in liver tissue has successfully been used as a proxy for egg production (Marshall *et al.* 1999, 2000; Chapter 9) and this might be used to develop an index of egg viability.

   With increasing levels of fishing mortality, the expected lifetime reproductive potential of the cohort decreases exponentially (Figure 1.10). Note that if eggs produced by older females have a higher hatching success, the decline is sharper than for the case of no age-specific differences in egg viability. This holds important implications for understanding the stability and resilience of populations to harvesting pressure (see Section 1.7).
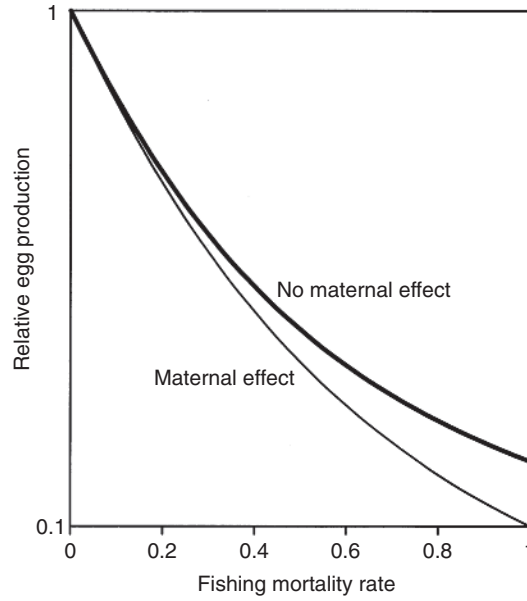
Figure 1.10 Normalized egg production per recruit (proportion of maximum) as a function of fishing mortality assuming no maternal age effects (thick line) and a maternal age effect on egg viability (thin line). Normalized egg production on a logarithmic (base 10) scale.

It is also possible to modify this expression to reflect not only the age of spawners but their reproductive history (Murawski *et al.* 2001, Scott *et al.* 2006). If hatching success is a function of the previous number of reproductive events experienced by a female, we have:

$$E = \sum_{a=a_r}^{a_{\max}} \sum_{j}^{n} m_a \, f_a \, s_a \, p_{a,j} \, h_j \, N_a \tag{23}$$

where $p_{a,j}$ is the proportion of females of age a spawning for the jth time, h_j is the hatching success for a female experiencing her jth spawning event, and all other terms are defined as before.

1.3.2   Production of viable larvae

Some empirical studies have indicated that egg hatching success *per se* may not depend on the age of the spawners but that larval viability does increase with egg size and energetic reserves which are functions of the age and, possibly, the reproductive history of the female. If we incorporate larval survival rates, the output then would be the number of larvae surviving to some specified age or size (see Murawski *et al.* 2001, O'Farrell & Botsford 2006, Spencer *et al.* 2007). We then have:

$$L = \sum_{a=a_r}^{a_{\max}} m_a \, f_a \, s_a \, \ell_a \, N_a \tag{24}$$

where L is the number of larvae surviving to a specified point in time (e.g. settlement), ℓ_a is the proportion of larvae from females of age a surviving to this point, and all other terms

are defined as before. Murawski *et al.* (2001) provide an expression for the case where the reproductive history of the female is also considered.

1.3.3   Sex ratios

As noted by Marshall (Chapter 11), it has often been assumed that the sex ratio remains constant over time in analyses that attempt to substitute spawning biomass as a proxy for total egg production. Larkin (1977) had earlier called attention to the potential pitfalls of making this assumption (see Chapter 11). For species exhibiting sexual dimorphism in growth, the vulnerability to size-selective fishing gear differs by sex. Changing levels of fishing mortality in turn result in systematic changes in the sex ratio. Sex-specific differences in natural mortality and longevity may also contribute to this effect. Given an equal sex ratio at hatching, the expected proportion of females in a cohort as a function of age, fishing mortality, and natural mortality can be expressed:

$$s_a = \left[\frac{e^{-(M_{a,f}+p_{a,f}F)}}{e^{-(M_{a,m}+p_{a,m}F)}} + 1 \right]^{-1} \tag{25}$$

where the subscripts *m* and *f* indicate males and females. For species in which the females grow more rapidly and reach larger sizes (e.g. many flatfish species) the ratio of females to males will decline with increasing age as the fishing mortality rate increases. An illustration is provided in Figure 1.11 and Plate 1 for a hypothetical long-lived population. Conversely, if males grow more quickly, the ratio of females to males will increase (see also Chapter 11). At low population levels in particular, distortions in the sex ratio of this type can lead to adverse effects on fertilization success. This can exacerbate chance variations in sex ratios at low population sizes and lead to Allee Effects by affecting the probability of finding a mate or other mechanisms.
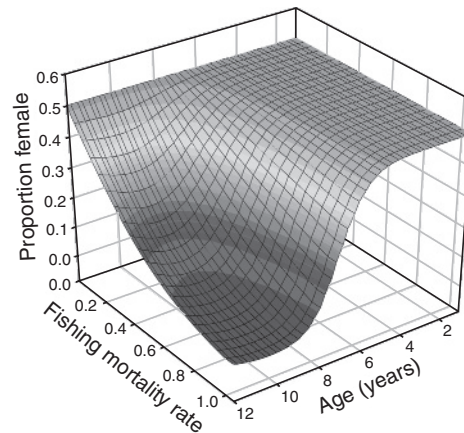
Figure 1.11   Proportion of females in a population as a function of age and fishing mortality when females exhibit faster growth and males and females experience identical natural mortality rates. The sex ratio at birth is assumed to be 1:1. For a color version of this figure, please see Plate 1 in the color plate section.

1.3.4 *Effects on genetic structure*

We have thus far focused on ecological processes and dynamics. It must be appreciated that exploitation also may potentially affect the genetic structure of populations with important consequences for sustainability and reversibility of the effects of fishing (see Chapter 4 for a detailed overview). Life-history theory predicts that increased adult mortality will select for earlier maturation (Gadgil & Bossert 1970) and that increased juvenile mortality will select for later maturation (Reznick *et al.* 1990). Direct evidence that size selective removals from a population can contribute to rapid evolutionary change has been examined in small-bodied fishes amenable to experimental manipulation and/or field observation (Reznick *et al.* 1997, Conover & Munch 2002). Reznick *et al.* (1997) demonstrated that size selective predation in natural populations of guppies resulted in significant evolution of life-history traits of age and size at maturity (Reznick *et al.* 1990, Reznick *et al.* 1997). Experiments in size selective harvesting over four generations of Atlantic silverside resulted in the evolution in egg size, larval growth, and other life-history traits (Conover & Munch 2002).

Attempts to determine potential evolutionary effects of fishing on natural populations of marine fishes have focused on estimating reaction norms (see Chapter 4). A reaction norm is derived by measuring the phenotypic expression of one genotype when exposed to different environmental conditions. Although reaction norms are generally determined experimentally, the need to understand the possible genetic impact of fishing on natural populations has led to an emphasis on the development of probabilistic reaction norms in wild populations. These studies have focused in particular on maturation and have attempted to disentangle environmental effects on phenotypic characteristics from genetic effects attributable to harvesting (see Marshall & Browman 2007 and contributions within). Evidence for changes in maturation attributable to selective fishing effects have now been reported for a number of marine fishes based on probabilistic maturation reaction norms (Dieckmann & Heino 2007) and work continues on further attempts to separate environmental from fishing effects (Marshall & McAdam 2007).

1.3.5 *Compensation during the post-recruitment phase*

If no compensatory processes operate during the post-recruit phase of the life history affecting fecundity, maturation schedules, etc., then the relationship between viable egg production and recruitment is linear and the slope of the relationship is a function of the age-specific fishing and natural mortality rates. We next turn to the case where compensatory response in fecundity and maturation schedules is important.

1.3.5.1 *Compensatory fecundity*

Fecundity is potentially affected by changes in abundance (see Ware 1980, Rothschild & Fogarty 1989, 1998, Cushing 1995). Although direct estimates of fecundity as a function of population size are comparatively rare, there is substantial information on changes in body size of fish as a function of abundance. The fecundity of marine fishes is generally a linear function of body weight and we can infer changes in mean fecundity with changes in body size if we can evaluate trade-offs between allocation of energy for growth and reproductive output.

Ware (1980) and Rothschild & Fogarty (1989) considered the case where the total population fecundity is a non-linear function of the spawning biomass (S):

$$E = dS\,e^{-gS} \tag{26}$$

where d and g are model parameters which incorporate terms for sex ratio and mean fecundity. This model arises when the mean fecundity per unit biomass decays exponentially with increasing population biomass. Ware (1980) combined this result for stock-dependent fecundity with a density-dependent mortality structure to derive his energetically-based stock–recruitment model. Rothschild & Fogarty (1989) showed that this relationship combined with a density-independent mortality function results in a Ricker-type stock-recruitment function.

A simpler power function may be appropriate in some instances to describe the relationship between total egg production and spawning biomass:

$$E = kS^h \tag{27}$$

where k and h are model parameters which again incorporate terms for sex ratio and mean fecundity. For the case when mean fecundity declines geometrically with increasing stock biomass, we obtain a compensatory relationship between total egg production and stock size (in this case, $h < 1.0$). However, Marshall *et al.* (1998) found that for Northeast Arctic cod during the period 1985–1996, total egg production *increased* with spawning biomass ($h = 1.286$; Figure 1.12), implying a depensatory relationship over the range of available observations (see also Section 1.2.2).

1.3.5.2   *Maturation schedules*

Shifts in the age or size at maturation with changes in abundance have been documented for a number of exploited fish populations (see reviews in Rothschild 1986, Cushing 1995). If the maturation schedule is affected by population size (reflecting density-dependent effects on
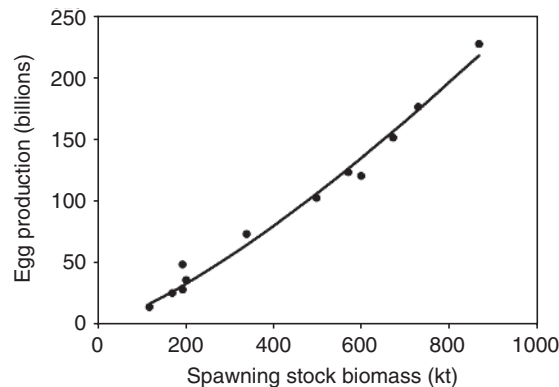
Figure 1.12   Relationship between spawning stock biomass and total egg production for Northeast Arctic cod for the period 1985–1996 (after Marshall *et al.* 1998; T. Marshall, personal communication).
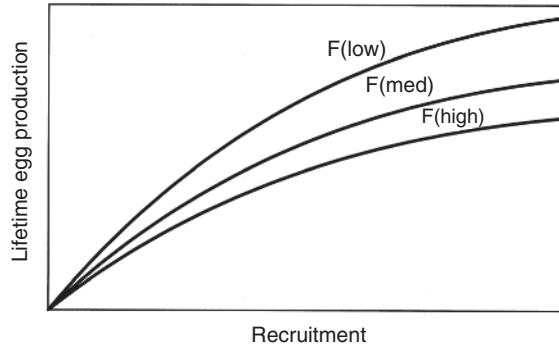
Figure 1.13 Lifetime egg production as a function of recruitment for a model incorporating density-dependent maturation at three levels of fishing mortality.

energy available for growth and maturation), the proportion of mature females for the ith age or size class can be described by the logistic function:

$$m_i = \frac{1}{1 + e^{a - bi + cN'}} \tag{28}$$

where a, b, and c are coefficients, i represents age or size, and N' is a measure of population size (e.g. total abundance, adult abundance, abundance of the ith size or age class etc).

Density-dependent maturation results in a non-linear relationship between the number of recruits and the lifetime egg production of the cohort. We show the expected form of the relationship between egg production and recruitment in Figure 1.13 for the case where maturation follows the logistic maturation model with explicit consideration of abundance effects (Rothschild & Fogarty 1998). Harvesting affects the lifetime reproductive output by affecting the number of reproductive opportunities; accordingly, we provide results in Figure 1.13 for several levels of fishing mortality.

1.4 Stability properties

We next examine the stability and resilience of the population to sustained perturbations such as exploitation. Previous sections illustrated relationships between egg production and recruitment and between recruitment (Section 1.2) and lifetime expected egg production (Section 1.3) We can combine these representations of the two major stanzas of the life history to examine stability points. First, we return to the relationship between egg production and recruitment and use an overcompensatory relationship to represent this life-history stanza (Figure 1.14(a)). Next, if compensatory mechanisms are not important in the post-recruit phase of the life history, we can represent the relationship between recruitment and lifetime egg production as a family of straight lines for different levels of fishing mortality (Figure 1.14(b)). Essentially, for any level of fishing mortality we have a single value of egg production per recruit (refer to Figure 1.10) which specifies the slope of these lines. Next can we overlay these relationships (Figures 1.14(a) and (b)) on the same graph (this will involve exchanging the axes for the recruitment–lifetime egg production relationship so that the relationships can be superimposed; Figure 1.14(c)). The points where the relationships for egg production–recruitment and
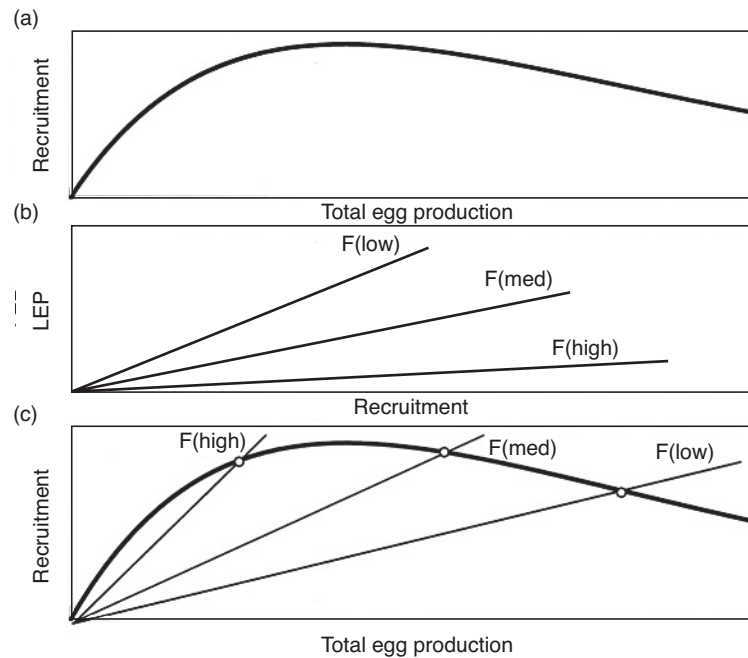
Figure 1.14   The relationship between (a) recruitment and total egg production, (b) lifetime egg production and recruitment for three levels of fishing mortality (low, medium, and high) assuming no compensation in post-recruitment processes, and (c) superposition of panels (a) and (b) to illustrate intersection points representing stable equilibria.

recruitment–lifetime egg production now intersect represent equilibrium points. Note that as the fishing mortality rate continues to increase, we eventually reach a level where there is no intersection point and a stock collapse is predicted. It follows that the steeper the recruitment curve at the origin, the more resilient the population will be to exploitation. With this type of information, we can estimate the levels of fishing mortality rate that would result in high risk of population collapse and employ a precautionary approach to ensure that these levels are not approached.

These basic principles hold when we also observe compensatory processes during the post-recruit phase. Now we have non-linear relationships between recruitment and lifetime egg production but as long as we have an intersection point between the curves, an equilibrium point exists (see Rothschild & Fogarty 1998 for a graphical illustration).

As noted earlier, for the case of critical depensation, we have the possibility of multiple equilibria. This is illustrated in Figure 1.15 for the case where the post-recruit dynamics are density-independent and for one level of fishing mortality. Note that in this case, the upper intersection point at higher egg production gives a stable equilibrium point while the lower one represents an unstable equilibrium. If the total egg production is driven below the lower level, a sudden population collapse is predicted.

1.5   Multistage models

Earlier in this chapter, we collapsed the life history into two principal stanzas: pre- and post-recruitment. We can represent the life history with finer resolution within each of these stanzas. We have seen that it is important to account for relationships between the adult female
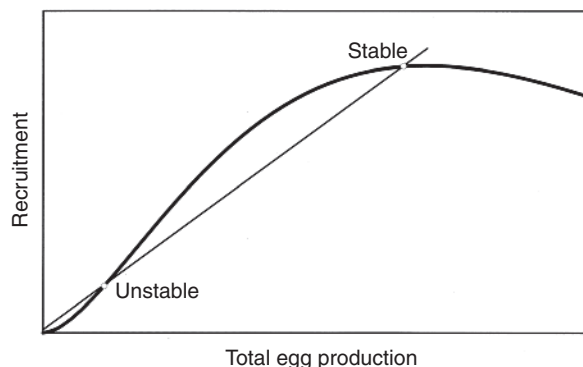
Figure 1.15   Stable and unstable equilibrium points for a depensatory model at one level of fishing mortality assuming no compensation in post-recruitment processes.

population and viable egg production, between the egg and larval stages, from larvae to recruits, and from recruits to adults. An illustration of such a system is provided in Figure 1.16 (see also Rothschild & Fogarty 1998). This graphical representation (or Paulik diagram; Paulik 1973, Rothschild 1986) allows a ready visualization of the implications of linear and non-linear transitions between life stages for the stability properties of the population. In this example, the relationship between the adult female population and egg production is taken to be overcompensatory (Quadrant I), the transition between eggs and the larval settlement stage is linear (no density-dependence; Quadrant II), and the relationship between larvae and recruits (Quadrant III) is compensatory. In this example, the relationship between recruitment and the adult stage is linear. This relationship of course varies with the exploitation rate and we have pictured results for two levels of fishing mortality with the dashed line in Quadrant IV representing
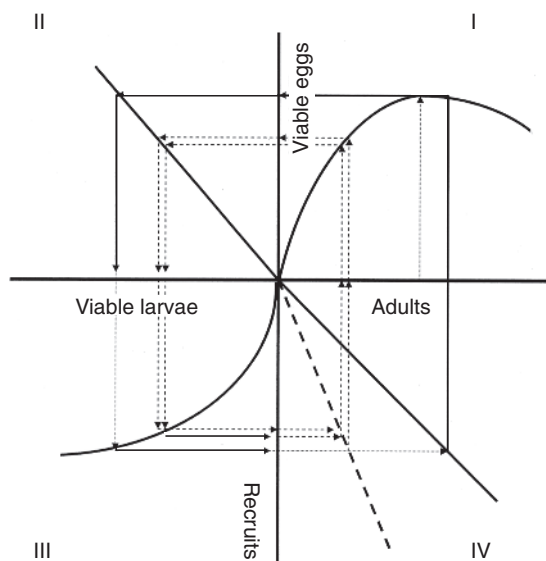
Figure 1.16   Paulik diagram for a four-stage life-history pattern with non-linear dynamics in two quadrants. Two levels of fishing mortality are represented in Quadrant IV. Arrows trace the trajectories of the population over several generations under the lower and higher fishing mortality rates.

higher exploitation. For the lower exploitation rate we trace the transitions between life stages for two generations from an arbitrary starting point (see thin lines). Note that the compensatory processes result in a stabilization after three generations from the starting conditions in this example. When we increase the fishing mortality rate in the exploitation module (Quadrant IV; see dashed line), we find that tracing the trajectories between successive life stages results ultimately in convergence to a lower adult population level but one that still results in a stable population.

In principle, any of these quadrants or modules can involve compensatory, overcompensatory processes, or depensatory processes. Some interesting mechanisms affecting the relationship between larval settlement and recruitment (Quadrant III) have been explored by Walters & Juanes (1993) and Walters & Martell (2004). Walters & Juanes (1993) evaluate the trade-offs between individual growth and predation risk associated with foraging behavior of juvenile fish. The system comprises spatial refuges and nearby foraging areas. The survivorship during the juvenile phase (S_j) can then be expressed:

$$S_j = e^{-(M_0 + M_1 T_f)} \tag{29}$$

where M_o is the instantaneous mortality rate due to all sources other than predation, M_1 is the instantaneous predation risk per unit time, and T_f is the time spent foraging. Walters & Juanes (1993) define fitness as the product of the survival rates in the juvenile and adult stages and the mean fecundity and show that for a simple but robust relationship between fecundity and foraging time, the optimum time spent foraging (R_{opt}) is:

$$R_{opt} = R_o + 1/M_1 \tag{30}$$

where R_o is the minimum foraging time required to survive and reproduce after leaving the juvenile refuge area. If the optimum time spent foraging is directly proportional to the larval settlement (L_s), then the recruitment relationship will be overcompensatory:

$$R = L_s\, e^{-(M_o + M_1' L_s)} \tag{31}$$

where M_1' is the product of the predation risk coefficient and the constant of proportionality between R_{opt} and L_s (Walters & Juanes 1993). If, instead, the foraging time of the cohort changes continuously with abundance of the cohort, a compensatory (asymptotic) recruitment curve results.

Walters & Martell (2004) consider a different scenario in which juveniles compete for a limited number of shelter sites. In this model, the juvenile population is partitioned into two groups, one of which is in a dispersal state and another comprising individuals who have located shelter. The rate of change for the dispersal component is:

$$\frac{dN_d}{dt} = -M_d N_d - r N_d (m - N_s) \tag{32}$$

where M_d is the mortality rate for dispersers, r is the search rate for dispersing individuals, m is the number of shelter sites and N_s is the number of individuals in shelters. The model for individuals having found shelter is:

$$\frac{dN_s}{dt} = -M_s N_s + r N_d (m - N_s) \tag{33}$$

Although this system of equations does not appear to have an analytical solution, Walters & Martell show that the numerical solution indicates an asymptotic recruitment model. Interestingly the solution reveals a more abrupt transition to the asymptotic state than the Beverton–Holt model and is more similar to the results obtained with the so-called hockey-stick representation of Barrowman & Myers (2000) in which recruitment increases linearly from the origin until a threshold level of reproductive output is reached and recruitment remains constant thereafter (see Marshall *et al.* 2006 for an application to Northeast Arctic cod).

1.6   Yield and sustainable harvesting

In general, information from a stock–recruitment model can be combined with information from a yield- and spawning-per-recruit analysis to estimate total equilibrium yield (see Chapter 7 for an overview and verbal description). Here we illustrate this process when egg production is the metric used to represent reproductive output. In the following, we will consider just the case where the post-recruitment processes do not exhibit any form of compensation. To begin, note that we can solve the recruitment model in terms of total egg production. For example, returning to our earlier specification for the Ricker model we can write:

$$\log_e \left[\frac{R}{E} \right] = \log_e \kappa - \delta E \tag{34}$$

Solving for total egg production we have:

$$E = \frac{1}{\delta} \log_e \left[\kappa \left[\frac{E}{R} \right] \right] \tag{35}$$

Notice that the expression inside the brackets includes (E/R), or egg production per recruit. Given estimates of the parameters of the Ricker model and an egg production-per-recruit analysis, we can substitute estimates of E/R for different levels of fishing mortality $(E/R)_F$ to determine the total egg production for each of these fishing mortality rates. This general approach can of course be followed using other recruitment models. Once the total spawning biomass corresponding to a particular level of fishing mortality is determined, the corresponding recruitment can be obtained by the simple identity:

$$R_F = \frac{E_F}{(E/R)_F} \tag{36}$$

and in essence, we have simply provided the analytical framework for the graphical analysis presented in Figure 1.14.

We can now obtain the predicted equilibrium yield for each level of fishing mortality by combining the yield per recruit at each level of fishing mortality with this predicted recruitment level to obtain an estimate of the total yield at each level of fishing mortality:

$$Y_F = (Y/R)_F \, R_F \tag{37}$$

An illustration of this approach is provided in the next section to evaluate the implications of factors such as maternal effects on viable egg production.

1.7   Implications of maternal effects

When differences in age-specific egg viability are important, our *perceptions* of the relationship between egg production and recruitment (the pre-recruit phase) and the relationship between recruitment and lifetime egg production (the post-recruit phase) are altered. In particular, for observed levels of recruitment, if the viable egg production is lower than the nominal total egg production because of fishing effects on the age-structure of the population, the slope of the recruitment curve at the origin may be steeper than if we ignore or are unaware of this effect. This can occur because the observed levels of recruitment are actually derived from lower levels of effective reproductive output relative to our perception if we use egg production uncorrected for maternal effects. This seemingly paradoxical result also of course holds when spawning biomass is used as the index of reproduction when maternal effects on viable egg production are in fact important (as shown for Icelandic cod in Figure 1.9).

Countering this effect is the fact that the lifetime reproductive output of viable eggs by a cohort will be lower than perceived if maternal effects are important and we don't take them into account (see Figure 1.10). If we ignore or are unaware of maternal effects, the consequences of fishing on the population will then depend on the interplay of these two factors—the potential underestimation of the slope of the recruitment curve at the origin and the overestimation of the lifetime reproductive output of viable eggs.

Recall the development in Figure 1.14 showing equilibrium points and the limiting level of fishing mortality beyond which the risk of stock collapse is high. Suppose now we have a 'perceived' relationship between egg production and recruitment in which maternal effects are not recognized (see Figure 1.17(a), thin line) and an 'actual' relationship with a steeper slope at the origin (Figure 1.17(a), bold line) with a proper accounting of realized egg production levels. Next consider the case where we calculate the lifetime egg production per recruit for a particular level of fishing mortality but are unaware of important maternal effects (Figure 1.17(b), thin line; labeled F(s)) and contrast this with two cases of maternal effects on viable egg production at the same level of fishing mortality as for line F(s), one of which reflects a stronger maternal effect (labeled F(m2) in Figure 1.17(b)). Note that 'stronger' here refers to the case where there is a larger differential in egg or larval viabilities with age. We now overlay panels (a) and (b) as before. For the case where we do not account for maternal effects either in the egg production–recruitment relationship or in the calculation of lifetime egg production, we do have an intersection point and we would predict that this level of fishing mortality would be sustainable under our (mis)perceived view of the dynamics of this population. Now consider the case where we correctly portray maternal effects both in the egg production–recruitment relationship and in the calculation of lifetime viable egg production. Under the more moderate maternal effect on lifetime egg production (labeled F(m1)), we still predict a stable equilibrium point. In effect, for this hypothetical case the steeper slope of the recruitment curve at the origin for the 'actual' case is sufficient to offset the lower level of lifetime egg production at this level of fishing mortality when maternal effects are in fact important. However, with the second case representing a stronger maternal effect on lifetime viable egg production, we no longer have an intersection point with the egg production–recruitment curve and we predict a stock collapse at this level of fishing mortality. In this case, our prediction of a sustainable fishery when we did not properly account for maternal effects would place the population at risk.
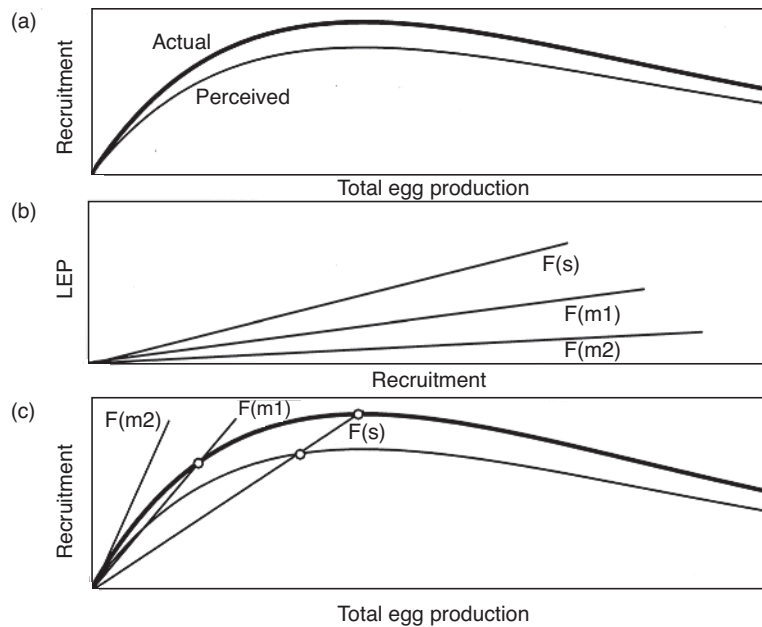
Figure 1.17 (a) Recruitment curves for the case of maternal age effects ('actual'; thick line) and when maternal effects are important but are unrecognized ('perceived'; thin line). (b) Estimated lifetime egg production as a function of recruitment at the same level fishing mortality assuming the 'standard' model of no maternal effect (F(s)), a 'moderate' maternal effect (F(m1)) and a 'strong' maternal effect (F(m2)). (c) Superposition of these relationships to determine equilibrium points.

Using the approach described in Section 1.6, we can construct yield curves corresponding to the hypothetical cases described above. The 'normalized' yield predicted for the case of no maternal effects is depicted in Figure 1.18 (thick line). We contrast the normalized yield as a function of fishing mortality for the case where maternal effects on viable egg production
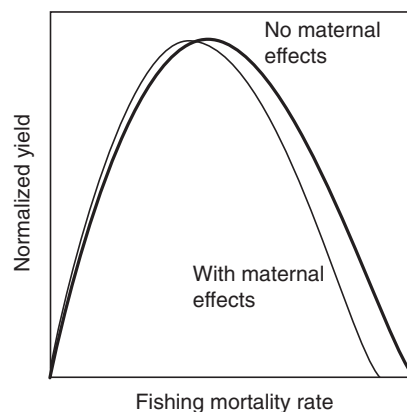
Figure 1.18 Normalized yield as a function of fishing mortality for the case of no maternal age effects (thick line) and maternal age effects (thin line) on viable egg production.

are important (Figure 1.18, thin line). In this instance, the population is less resilient at high levels of fishing mortality when maternal effects on lifetime viable egg production is more than sufficiently strong to offset the steeper slope of the recruitment curve at the origin.

Scott *et al.* (1999) demonstrated that if age and maternal effects were not properly accounted for, substantial overestimates of predicted recruitment would be made when fishing mortalities were high. In analyses relating larval production to recruitment, Murawski *et al.* (2001) reported that Atlantic cod on Georges Bank was in fact more vulnerable to fishing than perceived if maternal effects were unrecognized. Spencer *et al.* (2007) also predicted an increased vulnerability to high fishing mortality rates for Pacific Ocean perch off Alaska when maternal effects were properly taken into account. O'Farrell & Botsford (2006) found that if maternal effects were only important for a restricted range of younger age groups of rockfish species on the west coast of the United States, little effect on the perceived resilience of the population to harvesting would be evident. However, if maternal effects were important for a broader range of ages in the adult population, the discrepancy between the perceived and actual resilience of the population would be greater, possibly resulting in higher risk to the population.

1.8   Recruitment variability

The models described above do not consider exogenous environmental effects (either biotic or abiotic) on recruitment nor do they explicitly account for factors such as the age diversity of spawners that may serve to dampen the effects of fluctuations in the environment. Yet, as noted earlier, recruitment is extremely variable, largely as a result of the effects of exogenous forcing factors. In the context of the major theme areas of this book, we are interested in questions such as whether a proper accounting of the relationship between reproductive output and recruitment improves the predictability in recruitment (see Chapter 11) and how recruitment variability is related to egg production (see below). Houde (Chapter 3) describes the many sources of variability in growth and mortality during the early life stages and their implications for recruitment variability. In the following, we explore two general approaches to this problem. In the first, additional factors are explicitly represented in the recruitment model in an attempt to partition the variance in recruitment into definable sources. In the second, recruitment is treated as a stochastic process as a result of random variation in mortality rates during the pre-recruit stage (environmental stochasticity) or, for small populations, chance variation in the number of deaths in a given time interval (demographic stochasticity).

1.8.1   Multidimensional recruitment models

The models described earlier treat recruitment solely as a function of egg production; other aspects of the biotic and abiotic environment are not explicitly considered. However, it is appreciated that recruitment processes are highly dimensional (Rothschild 1986, Fogarty *et al.* 1991). To the extent that specific environmental factors affecting recruitment can be identified and quantified, these should be incorporated into recruitment–stock formulations (see Chapters 3, 9 and 10). This approach has received considerable attention as an extension to traditional recruitment models (see Hilborn & Walters 1992 for an overview and caveats).

Consider a simple extension of the Ricker model to account for an additional physical or biological environmental variable:

$$R = \kappa \mathrm{E}\, e^{-\delta \mathrm{E} + \upsilon X} \tag{38}$$

where υ is the coefficient for the environmental factor X and all other terms are defined as before. We now have a three-dimensional surface rather than a bivariate egg production–recruitment plane. The effect of projecting multidimensional data into an artificially reduced two-dimensional system as in the classical egg production recruitment models will then show a potentially highly variable representation as a result of this compression. Pope (Chapter 7) shows that incorporating temperature into the stock–recruitment relationship for Northeast Arctic cod substantially improves the fit of the model. For examples of recruitment models including biotic (multispecies) interactions, see O'Brien (Chapter 10). Cochrane (Chapter 9) reviews additional applications involving physical variables. Note that this approach can accommodate multiple environmental variables.

We can also think of this multidimensional system as a family of recruitment curves for given levels of the biotic and abiotic variables. Consider the egg production–recruitment relationship under two environmental regimes representing low and high productivity states (Figure 1.19). We can see immediately that although a relatively low fishing mortality rate may be sustainable under either the low or high productivity regime (there are equilibrium points under both environmental states when the exploitation rate is low), the combination of low productivity and high fishing mortality can result in a stock collapse at an exploitation rate that is sustainable when productivity is high (Figure 1.19). We therefore need to be concerned about the interaction between environmental change and fishing pressure and not ascribe changes to either fishing or the environment alone (Fogarty *et al.* 1991).

It is also possible to consider additional types of explanatory variables in these recruitment models. In keeping with the focus of this book on identifying critical factors affecting spawning success, we considered the effect of including an index of the age diversity of spawners in
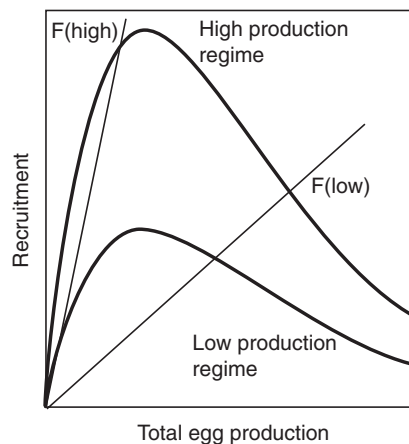
Figure 1.19 Relationship between recruitment and egg production under two environmental regimes and two levels of fishing mortality demonstrating the interaction between harvesting and changes in productivity states on stability of the population.

an extended Ricker model for Icelandic cod. Marteinsdottir & Thorarinsson (1998) had previously demonstrated an improvement in the fit of a recruitment model when age-diversity of spawners was incorporated in the model for this population. Age diversity was measured using the well-known Shannon–Weiner diversity index (Figure 1.1(d)). It has been hypothesized that higher levels of age-diversity in the spawning stock increases the spawning window in time and may serve as an important bet-hedging strategy for reproduction in a variable environment (Chapter 11) by spreading reproductive effort over a range of environmental conditions throughout the spawning season.

In our updated analysis using a linearization of Equation (38), we found a significant improvement in the fit of the model. The adjusted coefficient of determination increased from 0.50 to 0.68 when the age diversity of spawners was included. Other analyses including consideration of the age-diversity of spawners have provided mixed results. For example, O'Brien *et al.* (2003) found that including an index of age diversity along with measures of bottom temperature and the spatial distribution of spawned eggs improved the fit of a model of egg survival rates for Georges Bank cod. Morgan *et al.* (2007), however, found no consistent improvement in model fit when adding consideration of the age composition of the spawning stock for three Canadian cod populations and one American plaice population.

1.8.2   *Environmental stochasticity*

We have thus far provided an overview of key issues in pre-recruit processes in a deterministic setting to focus attention on fundamental demographic principles. However, as described above, the high dimensionality of the marine environment virtually assures that the full complexities of pre-recruit processes cannot be represented in simple models. Variation in physical forcing mechanisms and predator and prey fields translates into variation in survival and/or growth rates during the pre-recruit phase (Houde 1987, 1989, Chapter 3). Clearly, when these mechanisms have been identified, they should be incorporated into recruitment models (see Section 1.8.1 and discussions in Chapter 9 and Chapter 10. In this section, we describe an alternative approach for the case where key physical and biological environmental variables have not been identified (or the case where substantial random variation remains after key variables have been incorporated into recruitment models). We will illustrate the development of stochastic recruitment models for the density-independent case to explore the expected form of recruitment variability when the pre-recruit mortality rate is not constant but instead is a random variable (see Fogarty 1993a for an overview of stochastic models for other functional forms). We will also consider questions such as whether the magnitude of egg production affects the expected level of variability in recruitment.

First, consider the case where the density-independent mortality term is assumed to be a normally distributed random variable. The assumption of normally distributed mortality rates can be justified under the Central Limit Theorem (see Fogarty 1993b). If the mortality coefficient varies randomly during the pre-recruit phase, then the overall mortality can be viewed as the accumulated sum of random variables. For the case of independent mortality rates and for a relatively large number of such intervals, the overall mortality rate will be normally distributed. However, the Central Limit Theorem holds under much more general conditions for non-independent stationary processes (see Fogarty 1993b for a review). In the following, we will illustrate some results using the null (density-independent) model although
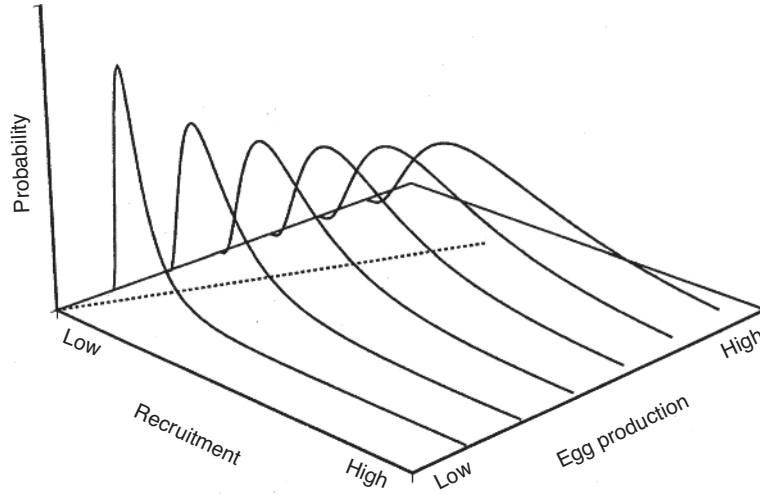
Figure 1.20 Representation of the conditional probability distributions of recruitment for the density-independent models (after Fogarty *et al.* 1991).

extension to the various compensatory recruitment models considered earlier can be readily made (Fogarty 1993a).

Under these assumptions, the conditional probability density function of recruitment for the density-independent model is lognormal:

$$p(R|E) = \frac{R^{-1}}{\sqrt{2\pi}\,\sigma_\mu\,t} \exp \frac{[-(\log(R/E) + \bar{\mu}t\,)^2]}{2\,\sigma_\mu^2\,t^2} \tag{39}$$

where μ is the mean density-independent mortality rate and σ_μ^2 is its variance. The shape of the distribution for several levels of initial cohort size is illustrated in Figure 1.20. The mean is:

$$\overline{R} = E\,e^{(-\bar{\mu}+\sigma_\mu^2/2)t} \tag{40}$$

and its variance is:

$$V(R) = E^2\,e^{(-2\bar{\mu}+\sigma_\mu^2)t^2}[e^{\sigma_\mu^2 t^2} - 1] \tag{41}$$

The mean recruitment level is higher for the stochastic model than for the corresponding deterministic case by the factor $\exp[(\sigma_\mu^2/2)t^2]$. The modal recruitment is, however, lower for the stochastic case than the deterministic recruitment level. Notice that the expression for the variance of recruitment conditioned on egg production is a function of the square of the total egg production. We would therefore expect that populations with higher levels of egg production would exhibit higher absolute variability in recruitment (although the coefficient of variation of recruitment is independent of the initial number of eggs; see below).

Several general consequences emerge from the properties of the lognormal recruitment distributions. First, we expect low to moderate recruitment levels most of the time with occasional strong year classes (represented by the strong right hand tails of the distributions). Second,

relatively small variation in mortality rates translates into large variation in recruitment. To see this, note that the coefficient of variation (CV) for the model described above can be expressed:

$$CV(R) = (e^{\sigma_\mu^2 t^2} - 1)^{1/2} \tag{42}$$

The CV therefore depends on the variance of the density-independent mortality rate but not on the number of eggs in this model. The instantaneous rate of density-independent mortality is typically on the order of $\mu = 10.0$. Even a relatively low level of variability in the mortality rate translates into a high level of recruitment variability. For example, when $\mu = 10.0$, a CV as low as 10% in mortality would result in over a 100% CV in recruitment. It is clear that small changes in mortality can result in large changes in recruitment. Indeed, given the potential range of variation, it is surprising that fish populations are not more variable than actually observed (Gulland 1982; Chapter 3). This observation suggests that mechanisms exist to dampen variability (see also Chapter 3). Fogarty (1993a) noted that density-dependent mechanisms can serve to reduce variability in this context. This analysis also suggests that to the extent that species characterized by higher mean fecundity exhibit higher coefficients of variation in recruitment, it is because they are susceptible to higher variation in mortality rates. These general results also suggest that even with a more detailed accounting of effective reproductive output, we should still expect high levels of variability in recruitment for many marine species because of events following the production of viable eggs by the population. It is therefore perhaps not surprising that equivocal results have been obtained for the proportion of variation explained by recruitment models in comparisons using spawning stock biomass as the indicator of reproductive output with ones using total egg production (see Chapter 11).

Attempts to relate recruitment variability to fecundity have provided conflicting results (Rothschild & DiNardo 1987, Mertz & Myers 1996, Rickman *et al.* 2000). Rothschild & DiNardo (1987) found such a relationship for anadromous fish but not for marine fish. Mertz & Myers (1996) were also unable to detect an empirical relationship between fecundity and recruitment variability. In contrast, Rickman *et al.* (2000) demonstrated a relationship between fecundity and recruitment variability for marine fish after accounting for phylogenetic relationships in an analysis of 52 fish stocks.

1.8.3 Demographic stochasticity

The model for environmental stochasticity described above is appropriate for the case where mortality rates vary during the course of the pre-recruit period. We can also consider a model for the number of individuals in a cohort based on time-invariant survival probabilities where the cohort size can assume only discrete values (see Fogarty 1993b). Models of this type are particularly appropriate for species with relatively low population sizes and substantial energetic investment in the progeny by the parents such that variability in mortality is relatively low. For example, application to certain threatened elasmobranch populations might be appropriate in this context. In the following, it is assumed that the probabilities for each individual are independent and constant through time. The probability of an individual dying in an interval of time Δt is $\mu \Delta t + o(\Delta t)$ where $o(\Delta t)$ is a quantity of smaller order than Δt. The probability of obtaining exactly N individuals at time $t + \Delta t$ is given by:

$$P_N(t + \Delta t) = P_{N+1}(t)\mu(N + 1)\Delta t + P_N(t)(1 - \mu N \Delta t) \tag{43}$$

where the first term on the right hand side is the probability of exactly one death in a small interval of time Δt and the second term is the probability of no deaths in the interval. The interval is defined to be sufficiently small that the probability of two or more events is negligible. These probabilities are taken to be independent and therefore additive. The model can be expressed:

$$\frac{P_N(t + \Delta t) - P_N(t)}{\Delta t} = \mu(N + 1) P_{N+1}(t) - \mu(N) P_N(t) \tag{44}$$

and taking the limit as $\Delta t \to 0$ and solving yields the probability density function (PDF) for recruitment. The PDF is now binomial:

$$P(R|\mathrm{E}) = \binom{E}{R} (e^{-\mu t})^R (1 - e^{-\mu t})^{\mathrm{E}-R} \tag{45}$$

with mean:

$$\overline{R} = \mathrm{E}\, e^{-\mu t} \tag{46}$$

and variance

$$V(R) = E\, e^{-\mu t}[1 - e^{-\mu t}] \tag{47}$$

The coefficient of variation is given by:

$$CV(R) = \left[\frac{1 - e^{-\mu t}}{E\, e^{-\mu t}}\right]^{1/2} \tag{48}$$

Although the exact shape of the probability distribution is dependent on the level of mortality, in general it is much more symmetrical than for the case of the environmental stochasticity (it also of course is a discrete rather than continuous distribution). Note that in contrast to the model of environmental stochasticity, the mean is identical to the deterministic level and the coefficient of variation does depend on E; in this case, the CV *decreases* with increasing E and the results converge to the deterministic case.

Shelton (1992) constructed a simulation model in which the fate of individual eggs and patches of eggs was traced. For the latter, individuals in a patch all shared the same fate. Shelton further considered the important case where individuals or patches could exhibit different survival probabilities. Fogarty (1993b) showed that Shelton's simulations could be cast as a pure death stochastic process of the form described above. In Shelton's simulations the mean recruitment can be written:

$$\overline{R} = n\mathrm{E}^* S \tag{49}$$

where n is the number of patches and E^* is the number of eggs in the group and S is the survival fraction ($S = e^{-\mu t}$); the total egg production is of course $\mathrm{E} = n\mathrm{E}^*$. The variance is now:

$$V(R) = n\mathrm{E}^{*2} S(1 - S) \tag{50}$$

and the coefficient of variation is:

$$CV(R) = \left[\frac{\{nS(1 - S)\}^{1/2}}{nS}\right] \tag{51}$$

Notice that the CV does not depend on the number of eggs in a patch in this case.

The significance of this formulation is that it is now possible to consider the fate of groups of eggs that could, for example, represent reproductive events for individual females (each comprising a patch) or eggs derived from more than one female in a given location forming a patch. In his simulations, Shelton contrasted results for individual eggs (E = 1) with patches of eggs (E > 1). Shelton equated the former with bet-hedging strategies in which the risk is spread by placing a large number of eggs in space and time with effectively independent survival probabilities.

Shelton's extension to the case of different survival probabilities for individual eggs or groups of eggs further allows consideration of factors such as maternal effects or the effects of spatial heterogeneity in survival rates. The mean recruitment is now:

$$(\overline{R}) = \mathrm{E}^* \sum_{i=1}^{n} S_i \tag{52}$$

where the subscript i indexes the individual or group. The variance is given by:

$$V(R) = \mathrm{E}^{*2} \sum_{i=1}^{n} S_i(1 - S_i) \tag{53}$$

Interestingly, the variance is actually lower relative to the case of identical survival rates. The coefficient of variation for this case is:

$$CV(R) = \left[\frac{\left\{ \sum_{i=1}^{n} S_i(1 - S_i) \right\}^{1/2}}{\sum_{i=1}^{n} S_i} \right] \tag{54}$$

and we see that the CV depends only on the survival rates for individuals or patches.

It is therefore possible to incorporate some of the considerations related to maternal effects and other factors in these simple models to understand what we might expect for patterns of variability in recruitment. The models can be extended to consider more complicated cases where the survival within a patch is not a completely dependent all or nothing response structure (Fogarty 1993b). It is also possible to include environmental stochasticity in these models (Fogarty 1993b).

The simple consideration of patch dynamics in the above representation is a stepping stone to increased realism in modeling. O'Brien (Chapter 10) provides an illustration of a much more detailed spatially explicit model for cod around the British Isles where careful attention is paid to physical processes, ecological interactions and demographic structure. Scott *et al.* (2006) develop a model with full representation of size and age structure, female condition and seasonal dynamics to estimate reproductive output.

1.9 Summary

The renewed emphasis on recruitment processes as a function of total egg production of the population rather than spawning stock biomass represents a return to the origins of recruitment theory. The contributions to this book explore the current state of knowledge and the importance

of returning to these roots. Information is now accruing that will allow broader utilization of information on the relationship between total egg production and recruitment in fishery management although a concerted effort is needed to collect the necessary information for many more populations. Although time series of fecundity estimates required to estimate total egg production remain relatively rare, the development of rapid estimation methods promises to revolutionize the acquisition of this vital information. In general, it is currently possible to examine the relationship between total egg production and recruitment only for restricted time periods for selected species. To reconstruct longer time series, it has sometimes been possible to use predictive relationships derived from the shorter series and/or proxies and expand these to the full time series (see Marshall *et al.* 1998, 2006; Chapter 11). Even where information on fecundity is not available, it will be valuable to account for changes in sex ratios over time to develop estimates of female spawning biomass in place of total spawning stock biomass as a stepping stone to a fuller utilization of information on actual reproductive output (see Marshall, Chapter 11).

An understanding of how a fish population will respond to harvesting requires not only an accurate accounting of its effective reproductive output but an understanding of the relative importance of compensatory mechanisms operating at different points in the life cycle. Under some circumstances, the choice of different measures of reproductive output (total spawning biomass, female spawning biomass, total egg production) results in different views of the types of regulatory mechanisms that are operative. Marshall *et al.* (2006) show that this choice results in models for Northeast Arctic Cod that indicate depensatory dynamics when spawning stock biomass is used while overcompensatory models are indicated when female spawning stock biomass or total egg production is employed.

Even relatively low levels of variability in growth and mortality can translate into high levels of recruitment variability. This variability in recruitment should be viewed as an integral part of the life-history strategies of many marine species. Occasional strong year classes (represented by the tails of the distributions depicted in Figure 1.20) can be important in maintaining the population. This so-called 'storage' effect (Chesson 1984) may permit population persistence in a variable environment. It must be appreciated that harvesting can interfere with this mechanism by truncating the age distribution of females and reducing the number of lifetime reproductive opportunities (Fogarty 1993a, Longhurst 2002, Beamish *et al.* 2006). Coupled with information showing the importance of maternal effects and that the age-diversity of spawners is a critical attribute of many populations, the implications of overharvesting can be more severe than previously appreciated.

Evidence from a relatively small but growing number of species currently suggests that maternal effects are important in determining egg and larval viability and that the age, condition, and/or reproductive history of an individual female may be critically important. The consequences of these maternal effects can depend greatly on their relative importance for our perception of the relationship between recruitment and the adult population (particularly the slope of the recruitment curve at the origin), and their implications for the effective lifetime reproductive output of an individual female. The interplay of these two factors determines whether the resilience of the population to exploitation will be misestimated if maternal effects are ignored or unappreciated.

These considerations can in turn inform the choice of tactical management tools (for an overview of management tools and their application in a conventional fishery management

setting, see Chapter 9). Although management strategies such as reductions in fishing effort and fishing mortality result in increased probability of survival to older and larger sizes, other methods can be tailored specifically to enhance the population of older individuals. For example, the use of marine protected areas has been shown to be effective in rebuilding the age and size structure of fish populations within reserves for species characterized by low to moderate mobility. The potential buildup of larger, older individuals within the reserve can then serve as a source for replenishment of adjacent areas through export of eggs and larvae. If larger, older females produce eggs and/or larvae with higher survival probabilities, the utility of the protected area is enhanced and this should be accounted for in evaluations of the efficacy of the reserve as a fishery management tool. The elimination of size-selective harvesting in at least parts of the population area may also help reduce adverse selective pressure on the genetic composition of exploited species (Law 2007).

For harvesting methods that result in capture of fish that can be released alive (e.g. hook and line, certain traps), it is possible to consider the use of maximum size limits in which the taking of larger individuals is prohibited or 'slot' limits in which both minimum and maximum size limits are employed. Of course, in the face of high exploitation rates, the number of individuals that reach the upper size limit can be sharply reduced and slot or maximum size limits must be used in conjunction with controls on overall fishing mortality to be effective.

These considerations all point to the utility of developing a refined understanding of reproductive dynamics in order to enhance the resilience of harvested populations to exploitation through the management choices we make. By quantifying the effect of factors such as maternal effects on egg and larval survival, we can develop more realistic models of the dynamics of exploited populations and devise more effective fishery management strategies. The following chapters provide important insights into the current state of knowledge and directions for future research in reproductive dynamics that will substantially advance this critically important goal.

References

Barrowman, N.J. & Myers, R.A. (2000) Still more spawner-recruitment curves: the hockey stick and its generalizations. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 665–76.

Beamish, R.J., McFarlane, G.A. & Benson, A. (2006) Longevity overfishing. *Progress in Oceanography*, **68**, 289–302.

Beverton, R.J. & Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations*. Fisheries Investigations Series II, **19**. Ministry of Agriculture, Fisheries and Food. London. 533pp

Chesson, P.L. (1984) The storage effect in stochastic population models. *Lecture Notes in Biomathematics*, **54**, 76–89.

Conover, D.O. & Munch, S.B. (2002) Sustaining fisheries yields over evolutionary time scales. *Science*, **297**, 94–6.

Cushing, D.H. (1995) *Population Production and Regulation in the Sea*. Cambridge University Press, Cambridge.

Dieckmann, U & Heino, M. (2007) Review: probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecology Progress Series*, **335**, 253–69.

Dominey, W.J. & Blumer, L.S. (1984) Cannibalism of early life stages in fishes. In: G. Hausfater & S.B. Hardy (Eds) *Infanticide: Comparative and Evolutionary Perspectives*. Aldine, New York.

Fogarty, M.J. (1993a) Recruitment in randomly varying environments. *ICES Journal of Marine Science*, **50**, 247–50.

Fogarty, M.J. (1993b) Recruitment distributions revisited. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2723–8.

Fogarty, M.J., Mayo, R.K., O'Brien, L. & Rosenberg, A.A. (1996) Assessing uncertainty and risk in exploited marine populations. *Reliability Engineering and System Safety*, **54**, 183– 95.

Fogarty, M.J., Rosenberg, A.R. & Sissenwine, M.P. (1992) Fisheries risk assessment—sources of uncertainty; a case study of Georges Bank haddock. *Environmental Science and Technology*, **26**, 440–7.

Fogarty, M.J., Sissenwine, M.P. & Cohen, E.B. (1991) Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecology and Evolution*, **6**, 241–6.

Frank, K.T. & Brickman, D. (2000) Allee effects and compensatory population dynamics within a stock complex. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 513–17.

Gadgil, M. & Bossert, W.H. (1970) Life historical consequences of natural selection. *American Naturalist*, **104**, 1–24.

Gulland, J.A. (1982) Why do fish numbers vary? *Journal of Theoretical Biology*, **97**, 69–75.

Harris, J.G.K. (1975) The effect of density-dependent mortality on the shape of the stock recruitment curve. *Journal du Conseil International pour l'Exploration de la Mer*, **36**,144–9.

Hilborn, R. & Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment*. Chapman & Hall, New York.

Houde, E.D. (1987) Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, **2**, 17–29.

Houde, E.D. (1989) Subtleties and episodes in the early life of fishes. *Journal of Fish Biology*, **35** (Supplement A), 29–38.

Jones, R. (1989) Towards a general theory of population regulation in marine teleosts. *Journal du Conseil International pour l'Exploration de la Mer*, **45**, 176–89.

Larkin, P.A. (1977) An epitaph for the concept of maximum sustainable yield. *Transactions of the American Fisheries Society*, **106**, 1–11.

Law, R. (2007) Fisheries-induced evolution: present status and future directions. *Marine Ecology Progress Series*, **335**, 271–7.

Longhurst, A. (2002) Murphy's law revisited: longevity as a factor in recruitment to fish populations. *Fisheries Research*, **56**, 125–31.

Marshall, C.T. & Browman, H.I. (2007) Introduction. *Marine Ecology Progress Series*, **335**, 249– 51.

Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P. & Ulltang, Ø. (1998) Is spawner biomass a sensitive measure of the reproduction and recruitment potential of Northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1766–83.

Marshall, C.T. & McAdam, B.J. (2007) Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference. *Marine Ecology Progress Series*, **335**, 301–10.

Marshall, C.T., Needle, C.L., Thorsen, A., Kjesbu, O.S. & Yaragina, N.A. (2006) Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: implications for stock-recruit theory and management. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 980–94.

Marshall, C.T., O'Brien, L., Tomkiewicz, J., Marteinsdóttir, G., Morgan, M.J., Saborido-Rey, F., Köster, F.W., Blanchard, J.L., Secor, D.H., Kraus, F., Wright, P., Mukhina, N.V. & Björnsson, H. (2003) Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. *Journal of Northwest Atlantic Fisheries Science*, **33**, 161–90.

Marshall, C.T., Yaragina, N.A., Ådlandsvik, B. & Dolgov, A.V. (2000) Reconstructing the stock/recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2433–42.

Marshall, C.T., Yaragina, N.A., Lambert, Y. & Kjesbu, O.S. (1999) Total lipid energy as a proxy for total egg production by fish stocks. *Nature*, **402**, 288–90.

Marteinsdottir, G. & Thorarinsson, K. (1998) Improving the stock–recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1372–7.

Mertz, G. & Myers, R.A. (1996) Influence of fecundity on recruitment variability of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1618–25.

Miller, T.J., Crowder, L.B., Rice, J.A. & Marschall, E.A. (1988) Larval size and recruitment in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 1657–70.

Morgan, M.J., Shelton, P.A. & Brattey, J. (2007) Age composition of the spawning stock does not always influence recruitment. *Journal of Northwest Atlantic Fisheries Science*, **38**, 1–12.

Murawski, S.A., Rago, P.J. & Trippel, E.A. (2001) Impacts of demographic variation in spawning characteristics on reference points for fishery management. *ICES Journal of Marine Science*, **58**, 1002–14.

Myers, R.A., Barrowman, N.J., Hutchings, J.A. & Rosenberg, A.A. (1995) Population dynamics of exploited fish stocks at low population levels. *Science*, **269**, 1106–8.

O'Brien, L., Rago, P.J., Berrien, P. & Lough, R.G. (2003) Incorporating early-life history parameters in the estimation of the stock-recruit relationship of Georges Bank Atlantic cod (*Gadus morhua). Journal of Northwest Atlantic Fisheries Science*, **33**, 91–205.

O'Farrell, M.R. & Botsford, L.W. (2006) The fisheries management implications of maternal- age-dependent larval survival. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 2249–58.

Paulik, G.J. (1973) Studies of the possible form of the stock-recruitment curve. *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer*, **164**, 302–15.

Quinn, T.J. II & Deriso, R.B. (1999) *Quantitative Fish Dynamics*. Oxford University Press, New York.

Reznick, D.A., Bryga, H. & Endler, J.A. (1990) Experimentally induced life-history evolution in a natural population. *Nature*, **346**, 357–9.

Reznick, D.N., Shaw, F.H., Rodd, F.H. & Shaw, R.G. (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science*, **275**, 1934–7.

Ricker, W.J. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**, 559–623.

Rickman, S.J., Dulvy, N.K., Jennings, S. & Reynolds, J.D. (2000) Recruitment variation related to fecundity in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 116–24.

Rothschild, B.J. (1986) *Dynamics of Marine Fish Populations*. Harvard University Press, Cambridge.

Rothschild, B.J. & DiNardo, G.T. (1987) Comparison of recruitment variability and life history data among marine and anadromous fishes. *American Fisheries Society Symposium*, **1**, 531–46.

Rothschild, B.J. & Fogarty, M.J. (1989) Spawning stock biomass as a source of error in recruitment-stock relationships. *Journal du Conseil International pour l'Exploration de la Mer*, **45**, 131–5.

Rothschild, B.J. & Fogarty, M.J. (1998) Recruitment and the population dynamics process. In: A. Robinson & K. Brink (Eds) *The Sea.* Vol. 10. pp. 293–325. John Wiley, New York.

Scott, B.E., Marteinsdottir, B., Begg, G.A., Wright, P.J. & Kjesbu, O.S. (2006) Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modeling*, **191**, 383–415.

Scott, B., Marteinsdottir, G. & Wright, P. (1999) The potential effects of maternal factors on spawning stock–recruitment relationships under varying fisheries pressure. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1882–90.

Shelton, P.A. (1992) The shape of recruitment distributions. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1734–61.

Shepherd, J.G. & Cushing, D.H. (1980) A mechanism for density-dependent survival of larval fish as the basis for a stock-recruitment relationship. *Journal du Conseil International pour l'Exploration de la Mer*, **39**, 160–7.

Spencer, P., Hanselman, D. & Dorn, M. (2007) The effect of maternal age at spawning on estimation of F(msy) for Alaska Pacific Ocean Perch. Biology, Assessment, and Management of North Pacific Rockfishes. Alaska Sea Grant College Program AK-SG- 07-01.

Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–90.

Trippel, E. (1999) Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. *Journal of Northwest Atlantic Fisheries Science*, **25**, 61–81.

Walters, C.J. & Juanes F. (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking bu juvenile fishes. *Canadian Journal of Fisheries and Aquatic Science*, **50**, 2058–70.

Walters, C.J. & Martell, S.D. (2004) *Fisheries Ecology and Management*. Princeton University Press, Princeton.

Ware, D.M. (1980) Bioenergetics of stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1012–24.

Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Reviews in Ecology and Systematics*, **15**, 393–425.