Chapter 5

Population Analysis

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5.1 Introduction

To manage wild fish populations conservatively we must have information on the rate at which a stock of reproductively mature animals can renew itself. The underlying stock–recruitment relationship can take a variety of forms, depending on the life history of a species as well as the nature of the environment(s) in which it occurs. Identifying the form of this relationship has not been easy but two key elements necessary to achieve this goal are a measure of the reproductive potential of the population and the number of young that will reach maturity. Fishing can then be targeted to exploit the excess production. Although this may appear relatively simple, the task is in fact rather difficult. To obtain an accurate measure of the abundance of reproducing adults requires surveys that provide quantitative estimates of catch per unit of sampling effort. Often, reproductive potential is taken as the biomass of adults beyond a threshold age or size, without taking into account variations in fecundity. Recruits can sometimes be sampled just before they enter a commercial fishery because they are approaching a size that can be effectively captured by standard fishing gears. However, if managers could obtain an accurate estimate of the true reproductive output of a stock, or some earlier insight about the upcoming fluctuations in recruitment, exploitation strategies might be altered to take advantage of coming booms or to prevent collapse because of persistent low egg production or poor recruitment.

Since the end of the 19th century, scientists realized that the abundance of planktonic early life stages could be used to measure the reproductive output of a fish population. In a classic treatise of 1914, Johan Hjort proposed that the abundance of young surviving through a critical stage in early life could serve as an indicator of the strength of coming year classes. Even if one cannot estimate the number of spawning fish because they can avoid nets or, for whatever reason, cannot be scientifically surveyed, it may be simpler to sample their planktonic offspring. If there is a predictable or measurable relationship for the number of eggs or larvae produced by the average adult, then the information from plankton surveys can be used to approximate the number of adults reproducing, or at least obtain a relative index of their numbers. A good part of this chapter will be dedicated to the concepts surrounding this approach. In addition, the development and use of pre-recruit indices will also be discussed. Identifying a critical stage at which year-class strength is established has proven to be difficult, whether in general terms or within a species or stock, because of the many factors that affect variations in growth and mortality

(see Chapters 2 and 3). Despite this, surveys of young fishes are becoming increasingly important in forecasting recruitment, particularly in heavily exploited populations, and they are providing increasing insight about how individuals are not all equally likely to survive.

5.2 Measuring stock size from egg or larval abundance

5.2.1 The basic concept

For fishery scientists engaged in estimating the size of fish populations, one of the most difficult tasks involves obtaining a measure of abundance whereby all the necessary parameters used in their assessment can be measured and none have to be assumed. The data may come from a commercial fishery, where a measure of effort can be derived, or from research surveys, where a consistent approach to sampling can be used to derive an index of the density of fish in a population. Standard fishery science texts discuss the inherent problems in using commercial catch information, the least of which is our lack of understanding of how fishers alter their tactics. In the case of many populations, such as free-swimming fishes (for example, herring, anchovy, sardines, mackerel, tuna) or in cases where bottom trawls are ineffective at capturing adults, quantitative samples of the density of adult fish derived from scientific surveys are difficult to obtain. It is under such circumstances that techniques based on measures of egg or larval abundance were devised to provide an assessment of population abundance or biomass.

In their simplest form, surveys of planktonic fish eggs and larvae can be used to derive an *index* of stock abundance. I use the plural when dealing with the number of surveys because in most instances, it is essential that an index of ichthyoplankton abundance provides a representative sample throughout the spawning period, which for many species extends over several weeks or months. One may try to schedule sampling during the peak reproductive period but any changes in the timing of spawning, whether caused by the environment or the fish, may lead to inaccurate measures of stock abundance. In addition to using several surveys to describe the spawning cycle, the spatial extent of the sampling should go beyond the spawning range of a population because in many species the range of a population expands and contracts as their numbers increase or decrease, as described for Japanese sardine (*Sardinops melanostictus*) in Section 11.3. If an unknown portion of the spawners is outside the survey area, the index is likely to be biased and thus will not provide a reliable measure of the state of the population. Finally, the index must be derived from the abundance of a specific stage or the abundance of a specific size range of larvae because mortality during early life is generally high, which necessitates the comparison of year classes using animals at similar states of development. The concept is simple:

(1) sample the plankton in a consistent manner during the reproductive period of the species of interest;
(2) ensure that you obtain samples over the entire spawning range;
(3) design the survey so that you can weight the contribution of each station to the index; and
(4) focus on a stage of development that you can effectively and consistently sample.

A high index would be indicative of a large spawning stock and a low index should indicate the converse, or at least that something is happening in the population that you should pay attention to. It is important to remember, however, that an index is not an absolute measure of spawner abundance but it does serve as a starting point to deal with the concept of stock estimation from egg or larval surveys.

The relationship between the spawning biomass of a fish stock and the production of offspring of age t is easily derived. Simply stated, the production of offspring (P_0) must be equal to the female biomass that produced them multiplied by the number of eggs produced per unit weight of female (E)

$$P_0 = (B \cdot R) \cdot E \tag{5.1}$$

Female biomass is represented as the biomass of the entire stock, B, both males and females, and R, the portion of the entire stock that is producing offspring (that is, reproductively mature females). Note here that spawning is measured over a specified period of time, normally, the entire spawning season. The number of offspring of age t produced by the population (P_t) is related to offspring production by taking into account losses that occur between spawning and time t

$$P_t = P_0 \cdot e^{-Z \cdot t} \tag{5.2}$$

where P_0 is the number of offspring produced by the population (Equation 5.1), and Z is the daily mortality rate (Chapter 3). By summing P_t over all surveys, the cumulated value provides an index of spawner abundance.

In deriving a simple index of abundance based on catches of a specific stage of development (that is, individuals at some age t), one assumes that development (or growth), mortality, and egg production per female remain relatively constant. Only wishful thinking would make this true. All these elements are known to vary among cohorts and year classes and there is ample evidence that regional differences can be substantial even within a stock's range. Consider the example of 10% variations around an average mortality rate (Figure 5.1). If it were possible to measure offspring production as the eggs were extruded by the females (that is, $t = 0$), variations in mortality rates will not have sufficient time to cause changes in the relationship between offspring abundance and spawning-stock biomass. As one bases the index on later stages of development, however, the potential error caused by unknown changes in losses from the population will increase exponentially as the age of the index stage increases (Figure 5.1).

A key aspect of Equations (5.1) and (5.2) is that they point to the need for basic biological knowledge about the state of a fish population. If we can measure all the parameters in those equations, then we can derive an estimate of absolute abundance for which we need not make any substantive assumptions. An appealing aspect of moving from an index to a measure of abundance is that fishery scientists are required to make more extensive observations on both the adults and their offspring as well as the relationship between the two stages. There are substantial difficulties and potential sources of error that need to be considered in order to use abundance of eggs and larvae to estimate stock size, but with careful design and planning, the major problems can be overcome.

Various methods have been devised to derive spawning-stock biomass from surveys of early life stages: Annual Egg Production Method (AEPM); Daily Egg Production

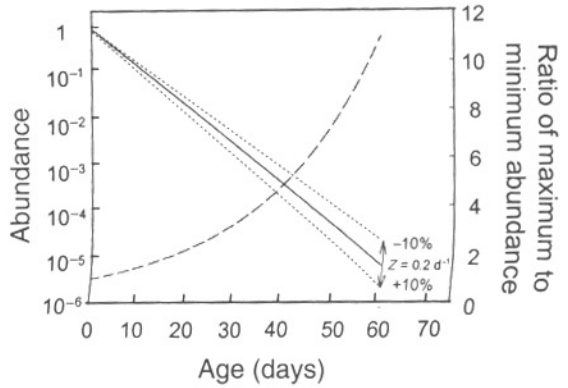

Figure 5.1 Abundance in relation to age for a population subject to a daily mortality rate (Z) of 0.2 (solid line) and the change in numbers caused by variations of $\pm 10\%$ (dotted lines). The dashed line shows the ratio of abundance indices of minimum (-10%) to maximum ($+10\%$) mortality rates.

Method (DEPM); Larval Abundance Index (LAI); Larval Production Method (LPM); and Daily Fecundity Reduction Method (DFRM). A few other methods exist and they will be discussed briefly, but these five represent the most frequently applied approaches. Some of the major developments in the concepts surrounding these various methods are the result of work by scientists from the Coastal Fisheries Resources Division of the Southwest Fisheries Center (California) and scientists from diverse member nations of the International Council for the Exploration of the Seas.

5.2.2 *Egg production methods*

If we start with Equation (5.1) and assume that $t = 0$ in Equation (5.2) and measurements of production and fecundity are derived for the entire spawning season, we effectively have the basis to estimate AEPM (Figure 5.2). In species where it is possible to obtain an accurate measure of the number of eggs produced during a spawning season by sampling

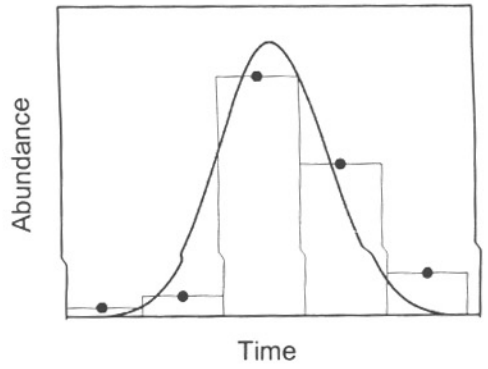

Figure 5.2 The solid line shows the hypothetical offspring production curve for a stock of fish in relation to time, while the circles show the estimated abundance from population surveys, each leg of which is represented by the open bars. Integrating the area under each block and summing among survey legs would provide the estimated offspring production from the population.

female gonads prior to the onset of spawning, the AEPM can be applied because fecundity is considered determinate, whether the eggs are released in small batches or during a single event. Spawning biomass can then be estimated as

$$B = \frac{P_0}{E \cdot R} \tag{5.3}$$

where R is the ratio of reproductive biomass of mature females to total biomass of the population (that is, both males and females, sometimes referred to as the sex ratio). By its name, the AEPM requires that the production of eggs be measured throughout the entire spawning season.

In cases where there is insufficient differentiation of the oocytes in the gonads to assign them to a class that will be spawned during the reproductive season, fecundity is termed indeterminate, and one must turn to the DEPM to estimate spawning biomass from egg production. To achieve this, Equation (5.1) must be modified so that

$$R' = R \cdot f \tag{5.4}$$

where R' is the proportion of females producing biomass, which is composed of the sex ratio, R, and f is the fraction of females spawning during the time interval over which egg abundance is measured (that is, during the surveys). The relationship in Equation (5.4) can be estimated if

(1) females possess a characteristic that indicates when spawning will or has taken place;
(2) the length of time such a characteristic remains detectable can estimated; and
(3) the spawning rate (or frequency) remains constant during the sampling interval over which f is estimated (that is, the number of times a female spawns during the survey period).

Equation (5.3) can then be rewritten as

$$B = \frac{P_0}{E' \cdot R \cdot f} \tag{5.5}$$

where E' is the number of eggs spawned per kilogram of female per batch during the period over which f is estimated, rather than the production over the entire spawning season (fecundity). If a female can spawn more than once over the period of estimation, then the value of f can exceed 1. The beauty of the DEPM is that one is no longer required to sample the plankton throughout the entire spawning season since there is only the need to determine the number of eggs spawned per batch. As a result, the method can be applied to both determinate and indeterminate spawners as long as the three conditions listed above can be satisfied. A complete description of all elements and methodologies for applying this approach to population analysis was provided by Lasker (1985).

5.2.3 *Larval abundance indices and production methods*

For species that produce demersal eggs, it is rarely possible to sample this stage of the life cycle because the habitats over which spawning occurs are poorly known or cannot be sampled easily or effectively. Stocks of herring (for example, in the North Sea) and

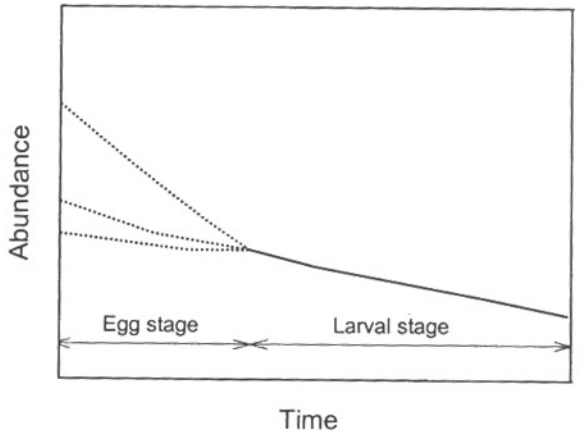

Figure 5.3 Change in abundance observed during the larval period (solid line) in a species for which the egg stage cannot be sampled. The dotted lines show possible paths that could be taken to estimate absolute egg production under scenarios where the environment in which the eggs occur is half, equally, and twice as risky as that of the larvae.

capelin (along the coasts of Newfoundland, Iceland, and Norway) spawn over broad areas of the inter- and sub-tidal zones that are difficult to access or delineate. Many freshwater species build nests or redds, and several guard their young (for example, bass; Figure 1.3i) or brood their young in places inaccessible to easy census (mouth-brooding catfishes and centrarchids). There are viviparous species such as redfish (*Sebastes* spp., Figure 1.1) that produce no eggs but extrude well developed larvae into the plankton. Alternatively, the development time of some eggs may be so short that accurate estimates of their production are not possible. In such cases, the LAI or LPM may be the only suitable approach. These methods, however, can also be applied to species that have planktonic eggs and larvae.

The fundamental principles of the egg and larval production methods are basically the same. In both instances, the objective is to derive a measure of offspring production that closely reflects fluctuations in spawning-stock biomass. In the case of LAI and LPM, however, there is a period separating spawning and hatching during which there can be substantial variations in survival (Figure 5.3). Differences in the nature of the environment may result in differences in mortality rates. Relatively little is known about the magnitude of losses that take place during the incubation of demersal eggs (for example, due to disturbance, predation, or oxygen depletion). For example, between 10% and 90% of the eggs laid on Atlantic herring spawning beds may be lost before emergence of the larvae, and similar values have been reported for egg-to-fry survival in different species of Pacific salmon. Similar values also apply to the survival of pelagic eggs. As a result, any correlation between an index of annual larval abundance and spawning biomass is likely to become weaker with increasing age of the larvae simply due to interannual variations in survival prior to sampling. The objective of sampling programs for LAIs and LPMs should then be to obtain as accurate an estimate of the abundance of hatching larvae as possible. As a result, the application of such methods tends to concentrate on the abundance or production of larvae shortly after hatching. One is still obliged, however, to assume or extrapolate egg mortality from other sources.

A simple LAI (I_t) can be calculated by summing the density ($D_{\Delta L,i}$) of larvae of a selected length interval (ΔL) at each sampling station (i) and weighting the contribution of each station by the area (a_i) it represents

$$I_t = \sum_{i=1}^{X} D_{\Delta L,i} \cdot a_i \tag{5.6}$$

where X is the total number of stations sampled during a survey period t. The limits of the length interval selected for inclusion in the index should reflect the larvae that are produced during the period represented by each survey. As with the AEPM, multiple surveys are required to ensure that the complete larval hatching cycle is adequately described by the sampling. For example, the International Larval Herring Surveys conducted around the British Isles selected larvae between 6.5 and 10 mm in length for inclusion into the index. Earlier field investigations had shown that growth rates ranged from 0.2 to 0.3 mm day^{-1}. Hence the LAI included larvae up to 18 days old. Since each survey was based on a 14-day period, the index would have reflected the production of larvae over the sampling period with little overlap with prior or subsequent surveys. This approach assumes there are no variations in the mortality or growth rate of larvae between regions surveyed, dates of surveys, or different year classes. A more realistic approach is to estimate the production of hatchlings using a method analogous to that used in the egg production methods.

LPMs aim to estimate the number of larvae hatching on successive days throughout the reproductive season. The objective is to back-calculate the abundance of larvae at the hatching length for each length interval that makes up the length–frequency distribution. There are three underlying assumptions to this approach:

(1) growth in length over time can be accurately described using a known formulation (for example, linear or exponential);
(2) mortality and emigration rates are constant over time and independent of length (Equation 5.2); and
(3) there is no immigration into the survey area.

The advantage of this approach over the LAI is that it no longer requires multiple surveys to ensure that the total production cycle is described. As long as sampling is conducted at a time when larval production is complete and when all length classes can be sampled, then it is possible to back-calculate the production cycle. If multiple surveys are available, or required, then independent estimates of larval production can be averaged to increase precision. Michael Heath (1993) provided a simple example of how larvae sampled on different dates can be used to estimate daily production (Figure 5.4). The back-calculated day of production is dependent on knowing the growth rate. The magnitude of the production depends on estimating the mortality rate.

5.2.4 *Egg deposition*

In species that produce demersal eggs, an assessment based on egg deposition may provide an estimate of spawning-stock abundance that is less subject to error than by using approaches based on measures of larval abundance (LAI or LPM). Some of the life-history

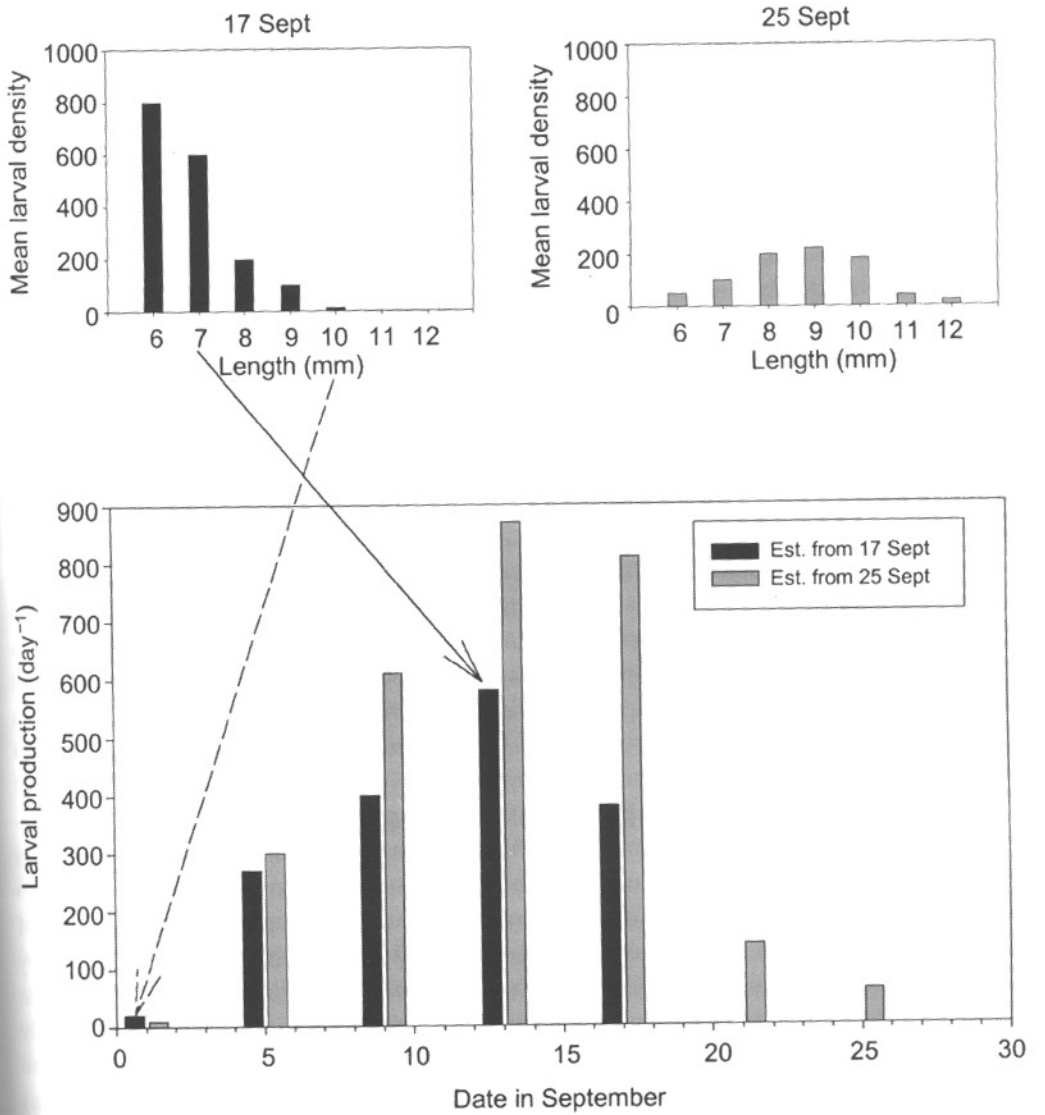

Figure 5.4 Illustration of the back-calculation of larval production based on sampling from the 17th (black bars) and 25th (grey bars) of September. The growth rate (AGR) of larvae is assumed to be 0.25 mm day^{-1}, and the length-specific mortality (Z/AGR) is 0.35 mm^{-1}. Note that as the length of the larvae decreases, the date of production moves to a later time. The earlier sampling period (17th) does not permit the complete description of the production cycle because hatching was not completed. Because larvae are measured to the nearest millimeter, the temporal resolution of the back-calculation is limited to 4-day intervals. Based on Heath (1993).

characteristics of species with demersal eggs limit the use of egg deposition as an absolute measure of spawning-stock biomass. In many species, from both marine and freshwater environments, the production of demersal eggs is often associated with some degree of nesting or parental care (see Chapter 1). When a clutch of eggs represents the investment of a single pair, any removal sampling represents a highly destructive method of estimating the

size of the reproductive stock. Visual surveys of the number of nests or spawning redds can serve as a measure of the number of successful spawners in an area. Such surveys are most effective when spawning and nesting are restricted to easily identifiable habitats, such as the riffle zones used by salmon or the shallows used by largemouth bass. As spawning becomes more geographically widespread, the effectiveness of visual surveys is likely to be reduced. Nest surveys also require reasonably good knowledge of spawning or mating behavior in order to have an index of the number of females represented by each nest. As with any other attempt to estimate stock size based on reproductive output, it is essential to have an estimate of size- or age-dependent maturity of females, their fecundity, as well as the sex ratio.

For species that reproduce in large groups, such as herring and capelin (*Mallotus villosus*), sampling that involves the removal of some eggs to obtain a measure of abundance may not be critical to any one individual or the population. Once a spawning bed is identified, standard approaches can be used to measure the density of eggs (for example, quadrats taken along a line transect), and with knowledge of the average female fecundity, the frequency distribution of mature individuals (as a function of age or body size), and the sex ratio, one can obtain an estimate of spawning biomass in much the same manner as in the AEPM. A critical element of this approach is to have an accurate knowledge of the distribution of spawning beds. In the case of some capelin and Pacific herring (*Clupea pallasi*) stocks, spawning can be restricted to inter-tidal or nearshore areas. But in some stocks, such as many of the Atlantic herring populations, spawning occurs over areas of the continental shelf that cannot be accurately identified or surveyed. Under such circumstances, methods based on sampling the abundance of the larval stages may be a more reliable approach to obtain an estimate of spawning-stock abundance.

The separation in time of larval production from egg production may be subject to mortality by unknown environmental sources, but in the case of demersal eggs, there may be an important density-dependent element that comes into play. If spawning is restricted to specific habitats, increasing egg production beyond a certain level may reduce the level of oxygen available to some eggs, thus reducing survival. Competition for spawning redds by salmon or nest sites in other species may result in eggs being disturbed by late spawners, which in turn may be another source of density-dependent mortality during this very early stage of the life cycle. The result of density-dependent mortality of demersal eggs may be an apparent uncoupling between true egg production (that is, spawning-stock abundance) and a subsequent estimate of larval abundance or production. If other methods are being used to estimate stock abundance (for example, hydro-acoustic integration), one might be tempted to discard some information, such as the data from one assessment method, because of inconsistencies between surveys when, in fact, it is pointing to a significant process affecting that stock. Consequently, care should be taken in interpreting differences in measures of abundance between life-history stages.

5.2.5 Estimating development and mortality rates

To this point, I have intentionally restricted any reference to offspring production as though it were a single stage in order to develop the concepts of spawning-stock estimation using methods that rely on sampling of eggs and larvae. However, we never sample eggs or larvae at a single stage of development. Since production is protracted over time and we cannot capture the

moment of extrusion or hatching at multiple sites, surveys are not instantaneous and only provide a limited snapshot of conditions during the period over which they are conducted. Most methods of estimating stock size from egg or larval surveys rely on developing a catch curve – an age- or length-structured description of the number of individuals caught by the samplers (but see the discussion of catch curves in Chapter 2). From the moment eggs are fertilized and offspring are released into the environment, they begin to undergo developmental changes and their numbers begin to decrease because of mortality. The sequence of developmental changes and increasing length can be used to determine the age of the eggs or larvae. The production of eggs or hatchlings on successive days throughout the spawning season is estimated by back-calculating the abundance of the youngest age category from the age– or length–frequency distribution averaged over the survey area. The rate of change in numbers of offspring (N) over time is often described using a simple exponential decay equation

$$N_t = N_0 \cdot e^{-Z \cdot t} \tag{5.7}$$

where t is time (in days) and Z is the daily mortality rate (day^{-1}) (this is equivalent to Equations 3.3 and 5.2). Other functional relationships have been used to describe the change in numbers over time, particularly when mortality is not constant with age or size. The formulation used in Equation (5.7), however, is the one most typically applied in population analyses based on early life stages. A number of regression procedures can be used to estimate N_0 and Z based on observations of N_t and t, depending on the design of the survey. Equation (5.7) can be used to back-calculate the production of eggs or larvae from several sampling dates using different age classes of eggs or larvae in each case. In order to apply this principle, we must be able to determine the age of early life stages.

The determination of age for eggs differs from that used for larvae. Developing embryos undergo a series of predictable and identifiable developmental changes (Figure 1.4). Following fertilization, the development of different externally identifiable features during cleavage, gastrulation, and subsequent embryonic development can be used to classify eggs into different stages with the aim of determining the age at the transition from one stage to another or the midpoint of the stage. There are numerous staging schemes used to describe the development of fish eggs. Differences in the level of detail among schemes are based on the developmental characters that can be accurately scored in repeated observations of an egg. As the number of stages increases, it may be possible to classify eggs into narrower age categories, but this may be less reliable if the effectiveness of the scoring is decreased by subtle differences in development. Laboratory observations of the sequence of changes can then be used to derive the age of the egg from fertilization. Because development is independent of external energy sources, development rates in fish eggs, like that of most ectotherms, is determined primarily by environmental temperature. By using a series of controlled temperature baths that span the environmental conditions typical of a species range, it is then possible to derive temperature-dependent relationships that describe the time to the onset of any given stage. Typically, development times of fish eggs follow a negative exponential relationship with temperature whereby the development rate accelerates with increasing temperature (Figure 5.5). Once laboratory data on temperature-dependent development times are obtained, measurements of the temperature in which the eggs are captured can be used to estimate their age. The temperature-dependent response, however, may also place limits on our ability to assign ages to developmental stages in some species. For many warm

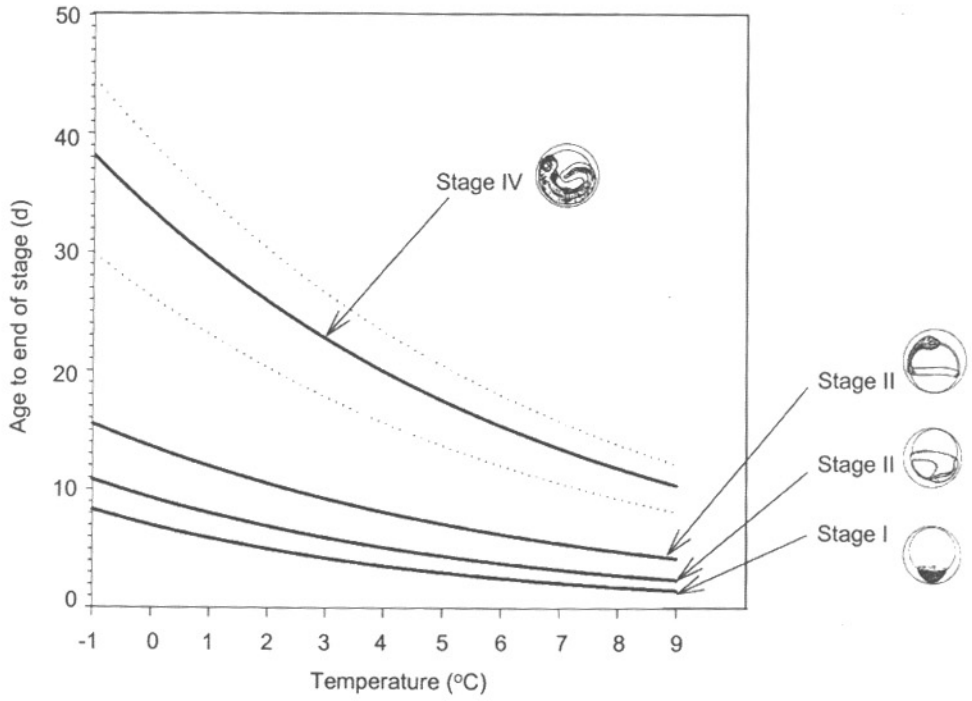

Figure 5.5 Time until the end of four stages (solid lines) used to describe the development of Atlantic cod (*Gadus morhua*) eggs from a study by Pepin *et al.* (1997). The dotted lines show the lower 10th and upper 90th percentiles of the distribution of development times until the end of stage IV. These serve to illustrate that not all individuals pass through a transition point at the same age. Similar distributions could be applied to earlier developmental stages, although the breadth of the distribution would be wider based on the results of that particular study.

water or tropical taxa, incubation times may be so short (<1 day) that sampling programs may not be able to resolve time-dependent changes in development, unless spawning occurs continuously through the day. It is reasonable to assume that the conditions in which each egg is captured reflects the environment in which development has taken place. This is more appropriate than using an overall average for the whole spawning range or period because of spatial and temporal variations in temperature that are likely to occur.

In contrast to ageing eggs, the approach used to age larvae is relatively simple. Once the larvae hatch and absorb their yolk, they begin to feed and allocate most of their surplus energy (that is not used in metabolic processes) to growth and ontogeny. Larvae sampled as part of population surveys are generally classified into 1-mm length intervals, although shorter intervals are used for particularly small species (for example, anchovy; Figure 1.3l). The age of larvae within each interval is generally estimated using a simple age–length relationship. The nature of this relationship is of little importance but the choice must be an accurate reflection of the population's pattern of change in length over time. As seen in Chapter 2, there are many approaches available to estimate the average growth in length of larvae.

It is clear that if we can age larvae using the daily growth increments found in the otoliths, it is possible to obtain an accurate description of the population's average rate of growth in length. Length–frequency analysis for species with relatively short spawning

periods can be used as an alternative to the analysis of otolith microstructure but this approach may be more prone to error (see Chapter 2). As in the assessment of adult fish populations, the development of an age–length key would probably provide the most accurate approach for deriving the age–frequency distribution. The level of sampling required to construct an accurate age–length key, however, is often beyond the scope of most surveys of early life stages. Whereas the sampling of adult fishes can be done effectively onboard ship, plankton samples typically require considerable effort before the larvae can be sorted and measured. A similar contrast in the time required to age adult and larval fishes also applies.

It is also possible to describe the change in numbers with increasing development using a length-structured, rather than age-structured, approach. Prior to the common use of otolith microstructure, length–frequency distributions were most often used in population analysis. Equation (5.7) can then be converted to a length-based form

$$N_{L_t} = N_{L_0} \cdot e^{-\left([Z/AGR][L_t - L_0]\right)} \tag{5.8}$$

where L_0 is the average length at hatching, L_t is the length at time t, Z is the daily instantaneous mortality rate (day^{-1}), and AGR is the absolute growth rate ($mm\,day^{-1}$; Equation 2.3). The basic assumption in this transformation is no longer that growth can be described using any functional relationship, but instead length increases linearly with age. The length-specific mortality (Z/AGR) then becomes a critical parameter that must remain constant over the length range used in the analysis. The term on the right-hand side, however, can be modified if there are deviations from linear growth and constant mortality rates are not a reasonable assumption (for example, Lo 1985). In fact, there is a considerable body of evidence that indicates that increases in length over time are not necessarily linear and that mortality rates are size-dependent (see Chapters 2 and 3). If the functional forms of the growth and mortality rates in relation to increasing body length cancel each other out so that the length-specific mortality is constant, Equation (5.8) may be valid. However, if they do not and the length range sampled differs among year classes, then it is quite likely that the back-calculation to the youngest and smallest stage will lead to erroneous projections.

A critical assumption of all methods used in the estimation of egg and larval mortality rates is that of equilibrium conditions. In deriving the age– or length–frequency distribution from which mortality rates are calculated, it is essential that egg or larval production be approximately constant over the duration of the survey (or at least that the averages for the largest and smallest size classes be equal) or that it be a reflection of the accumulated production over the entire spawning season. Furthermore, growth and mortality rates must be relatively constant over space and time. If either of these conditions cannot be satisfied, back-calculation of the abundance to the youngest stage will not provide an accurate measure of production because determination of the rate of change in abundance with age will reflect the effects of variations in both production and mortality.

The derivation of mortality rates requires that the spatial and temporal pattern of spawning be considered. If there is more than one major spawning area or there are differences in the schedule of production among parts of the population's range, then the survey information should be stratified to reflect those patterns. Not only is it likely that there are differences in the growth, mortality, and production rates over time and space, but variations in the abundance of the different spawning components are likely to reflect significant changes

in the dynamics of a stock. It is common for a stock's range to contract as the biomass decreases, and increase as biomass increases. Although this would be reflected in the distributional data obtained from egg and larval surveys, differences in the realized production among regions may have consequences on the level of exploitation a population may sustain.

5.2.6 *Relating egg or larval production to spawning-stock abundance*

Production methods designed to estimate the number of eggs spawned or the number of larvae hatching are all based on the premise that the rate of change in numbers over time (or length) can be described using a simple functional relationship, such as an exponential decrease in abundance. Mortality rates are estimated for each cohort and the intercept of this relationship – the initial number of eggs or larvae – is then related to spawning-stock abundance or biomass. There are two elements that can contribute to uncertainty in predicting the intercept: increasing age of the youngest stage that can be sampled and environmentally driven variations in the mortality schedule.

As discussed previously, the correlation between spawning-stock abundance and offspring abundance is likely to be stronger if the population is sampled soon after the offspring are produced because there will be fewer uncertainties about variations in the unknown losses among cohorts or year classes. This does not apply, however, to instances where development rate changes because of variations in the environmental temperature. If we were to obtain identical abundance estimates from two populations, one of which took twice as long to undergo development, the precision of our estimate of production (that is, $t = 0$) based on simple linear regression analysis would remain the same (Figure 5.6). For these two populations, the confidence intervals at the origin are dependent on the precision of the relationship between abundance and age, which should not be mistaken for uncertainty in events that are not observed by our sampling.

Beyond the simple statistical consideration, there is also a biological uncertainty associated with the state of a population of eggs or larvae. Does the stage-dependent pattern of loss remain the same as environmental conditions change? Production methods assume that vital rates are constant with age or size, or that they change following a consistent schedule from cohort to cohort. As we have seen in earlier chapters, this assumption may not be reasonable. For instance, differences in the type or abundance of predators from year to year may alter the pattern of vulnerability of eggs and larvae, or there may be simple physiological constraints that alter the pattern of mortality. Developmental abnormalities are known to increase in frequency at the extremes of a species range. For example, in a controlled laboratory study of the embryonic development of Atlantic cod (*Gadus morhua*), my colleagues and I found that the pattern of losses over time varied in relation to environmental temperature (Figure 5.7). Greater overall losses occurred early during development as temperature decreased, and the schedule of losses showed substantial variation among treatments. It is easy to see that assuming a constant mortality rate throughout early development could lead to inaccurate extrapolations of the number of eggs fertilized. Physiological abnormalities that result in temperature-dependent variations in mortality in the laboratory may not play an important role in natural populations if other processes, such as predation, are of greater magnitude, but the issue is worth considering when dealing with data from natural populations.

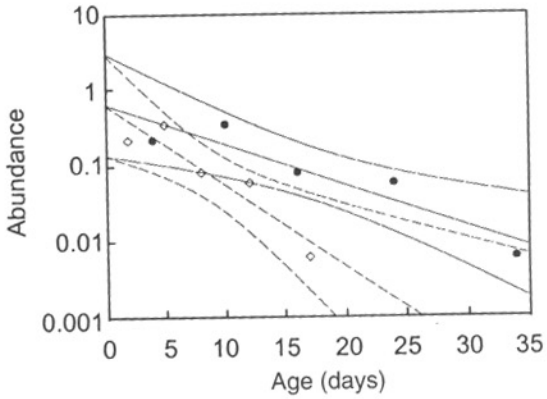

Figure 5.6 Time-dependent catch curve and confidence intervals about the regression of two hypothetical populations of fish eggs. The population represented by the open diamonds and the dashed lines has a development rate that is twice as fast as the one represented by the solid circles and lines. In this example, the catches from both populations for each "stage" are identical.

It might appear that these points raise serious concerns about the applicability of egg or larval production methods simply because some of the processes are not fully understood. My purpose in mentioning them, however, is simply to raise the reader's awareness that such factors might come into play. Departures from constant development or mortality rates with changing environmental conditions may result in changes in the slope of the production curve or in the pattern of residuals, suggesting a change in the functional form of the relationship. My point is to be observant when applying any methodology or fitting a model, and to be aware that some assumptions may not always hold, even if they are valid most of the time.

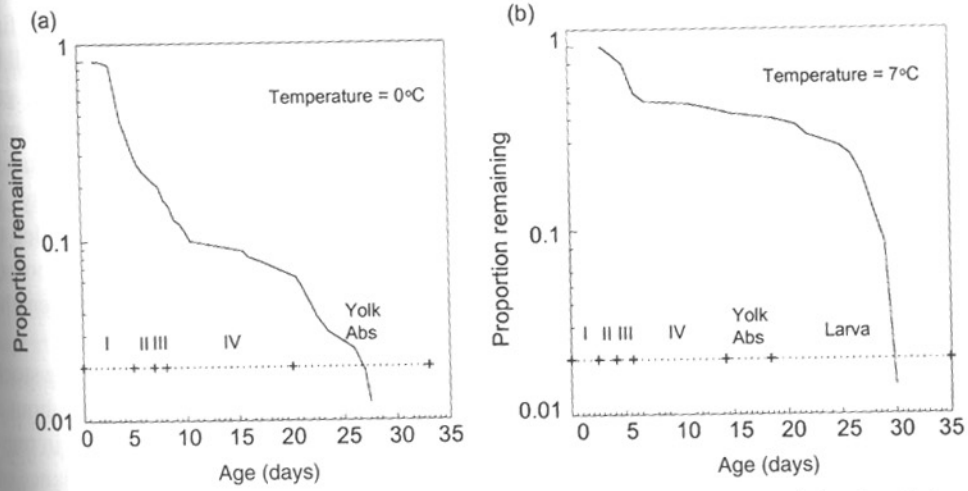

Figure 5.7 Proportion of individual Atlantic cod eggs and yolk-sac larvae surviving in relation to time, through the various developmental stages (dotted line at the bottom of each panel), for two laboratory temperature regimes. Note that losses during the egg stage occur principally during developmental stages I–III. The high losses that occur during the larval stage at 7°C are caused by food deprivation. Based on data from Pepin *et al.* (1997).

5.2.7 Measuring spawner characteristics – knowledge and bottlenecks

Knowing the potential reproductive output of the average female is critical if one intends to relate egg or larval abundance to spawning-stock biomass in terms of absolute numbers. Unfortunately, this is probably one of the weakest elements when we try to link early life stages to the production rate of a stock.

There is no doubt that fishes come from fish eggs, at least in the immediate sense, and their numbers are determined to a large degree by fecundity, the number of eggs produced by a female. As mentioned earlier, egg production can be broadly classified into two categories, determinate and indeterminate, based on our ability to assess the number of eggs likely to be produced during a reproductive season from the standing stock of advanced oocytes in the ovary prior to the onset of the reproductive season (Figure 5.8). The determination of oocyte maturity is done by making histological sections from the gonads of mature female fish and categorizing the oocytes into maturity stages. Fecundity is then determined by counting yolked or hydrated oocytes from a subsample of the gonad using gravimetric or volumetric methods. The gravimetric method is based on counts of mature oocytes from a weighed subsample of the total gonad. The volumetric method is based on egg-size frequencies from an aqueous solution of all oocytes in the ovary.

For determinate spawners, there is often a clear separation in the categories of oocytes present in the ovary, providing a demarcation between small, unyolked oocytes and those undergoing relatively synchronous maturation. In a number of temperate and boreal species, from both freshwater and marine environments, maturation of all the oocytes to be spawned in a season is highly synchronous and their release takes place over a relatively short time period, at least for an individual female (Figure 5.8a). In such instances, estimating fecundity, and any relationship it has to a characteristic of the female (for example, length, weight, condition), can be relatively straightforward. In determinate spawners such as cod, haddock, mackerel, and some flatfishes, the release of eggs occurs in a series of batches of variable size. The distribution of oocyte categories prior to the onset of first spawning may cover a broad spectrum and the classification of eggs into those that will be spawned and those that will not may be less obvious (Figure 5.8b). As long as the gap between categories is not between hydrated oocytes and other yolked oocytes, which may imply that eggs have already been released, the separation in oocyte categories can be taken as evidence that the standing stock is a measure of maximum potential fecundity. In many instances, this is not known with any certainty and the extensive research needed to demonstrate determinacy in annual fecundity is absent. If the discontinuity among oocyte categories is less obvious and they appear to follow a continuous distribution, then the species should be considered an indeterminate spawner (Figure 5.8c).

In indeterminate spawners, annual fecundity cannot be determined by the standing stock of yolked oocytes because fishes continuously mature new spawning batches throughout a protracted reproductive season. This type of life-history strategy is found primarily in temperate and tropical species. The only effective way to quantitatively link the abundance of early life stages with that of the adult spawning stock is to determine the batch fecundity and the spawning frequency. Batch fecundity is based on the number of hydrated oocytes, distinguishable by their relatively large size and greater translucence (water content), observed in weighed subsamples of the ovary. The determination of spawning frequency

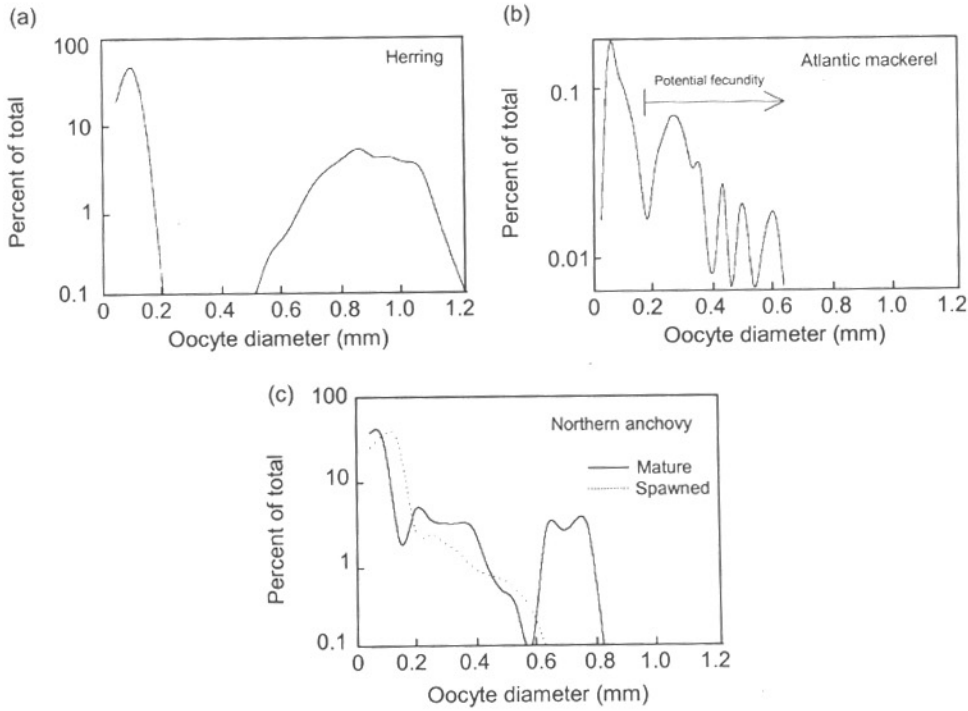

Figure 5.8 Relative size frequency distribution of the oocytes in ovaries of Atlantic herring (Blaxter & Hunter 1982), Atlantic mackerel (Priede & Watson 1993) and northern anchovy (Hunter & Leong 1981). There is a clear hiatus in the distribution of oocyte diameters in herring but there are several peaks in the oocyte size frequency in mackerel which may lead to ambiguity in the determination of annual fecundity. The rightmost peak found in mature northern anchovy (——), reflects the diameter of hydrated eggs, which are no longer present in females after spawning (·····).

relies on knowledge of the cycle of oocyte maturation and vitellogenesis, being able to identify the proportion of a sample of the adult population that shows evidence of being at a particular stage of the oocyte maturation cycle, and knowing the duration of that stage. Laboratory observations of the spawning cycle coupled with the collection of histological samples are necessary to correlate the periodicity in egg production with changes that take place in the developing ovaries. The latter are then used to describe the development of oocytes and post-ovulatory follicles into identifiable categories.

For indeterminate spawners, the coupling of laboratory and field observations is essential in order to derive an accurate understanding of the short term cycle of egg production. Field observations alone would only be adequate under exceptional situations where most of the population followed a synchronous periodic pattern in oocyte maturation. The DEPM was developed specifically for application to indeterminate spawners. Knowing the characteristics of spawners during the course of a population survey is critical for an accurate estimate of spawning biomass. Although a single survey of eggs and larvae can be used to derive an estimate of the abundance of adult fish, as long as most of the population is in the survey area, it is absolutely essential to sample the adults in order to take into account any seasonal or interannual variations in the potential production of eggs.

Of equal importance to any method relating egg or larval abundance to spawning biomass is the need to know that those eggs that we identify as mature (that is, that will be spawned) are actually released and fertilized. Reproduction places significant energetic demands on adult fishes. Not only does gonad development require substantial amounts of energy, but spawning often involves extensive migrations, the cessation of feeding, and aggressive competition for mates. The accumulated physiological stress may place individuals in a dilemma: continue reproduction at the risk of dying, or resorb energy from the gonad with the hope of surviving to another spawning season. The degeneration of oocytes is known as atresia, and histological sections can be used to identify the stages of egg resorption. The occurrence of atretic eggs can serve to determine the end of the spawning season. In determinate spawners, the frequency of atretic eggs must also be known in order to correct the original estimate of annual fecundity for those eggs that will not be spawned. The occurrence of atretic eggs may become particularly important when adults are in poor condition before the onset of, or as a result of events during, the spawning season.

It should be obvious that most egg or larval production methods rely on good knowledge of the relative composition (for example, size or age structure) of females in the population and the state of their gonads. Males seem to be of limited consequence to the reproductive potential of the population. After all, sperm is cheap, plentiful, and generally thought to be readily available. Most population analyses generally assume fertilization of 100% of spawned eggs. In most circumstances, however, this is guesswork at best. Fertilization rates have been shown to vary substantially among individual males and the quality of a female's egg may also play a considerable role in the success of reproduction. As with other elements of production methods, fertilization rate should be assessed from samples taken in conjunction with egg and larval collections. Any deviation from a fertilization rate of 100% will result in an underestimate of spawning biomass. This is an aspect of population analysis, however, that remains an element of research and has yet to be routinely applied to approaches based on egg or larval production.

It is essential to measure the character (for example, fecundity, egg quality) of spawning fish frequently, not only when trying to relate egg or larval abundance to adult biomass, but also to obtain some indication of the population's health and reproductive potential. One of the most complete examples available at this time deals with Atlantic cod in Icelandic and Norwegian waters. Individual egg production increases with increasing size of female but unless the relationship is isometric with weight, changes in the adult population's size or age structure will alter the average production of eggs per kilogram of spawning fish. Thus any loss of larger adults, say through fishing, will alter the reproductive potential per unit of spawning biomass. In the case of Atlantic cod in the Barents Sea, there is clear evidence that an individual's potential annual egg production is affected by its condition at the onset of the spawning season. In a subsequent analysis, Marshall *et al.* (1999) showed that variation in condition was closely linked to variations in the abundance of capelin, the dominant prey of adult cod. Changes in fecundity will lead to corresponding but opposite changes in the relationship between egg or larval production and the estimated spawning-stock abundance. For example, if fecundity decreases but the number of adults remains unchanged, fewer eggs and larvae will result. If fecundity is not monitored carefully, the decrease in egg and larval abundance would suggest a decrease in adult population abundance when, in fact, none has taken place, even though the reproductive output has decreased.

The effect of spawner characteristics may go beyond this. The eggs produced by first time spawners may be less likely to survive: their eggs are smaller and have lower energy reserves for the developing embryo and larva than the eggs of repeat spawners. Although the production methods outlined above should capture the changes in mortality rates of developing eggs and larvae, the implication of the findings for Atlantic cod is that as one moves toward a population structure made up of smaller and younger spawning fish, the reproductive potential is likely to decrease more rapidly than the spawning biomass. It is also possible that smaller adults may be more susceptible to variations in their environment, thus increasing the potential variation in reproductive output and subsequent recruitment.

5.3 Recruitment indices

If the number of animals that will enter the fishery or the spawning population could be measured just before the onset of the fishery or reproduction, then one would likely obtain an accurate measure of recruitment. In most cases this is not possible and scientists providing advice on the status of a stock are in need of an index of year-class strength. Thus, there is a need to identify a stage of the life cycle when the relative strength of a year class is established.

Following Hjort's hypothesis of a critical early life stage during which year-class strength might be established, considerable research effort was directed towards identifying when this might occur as well as the factor(s) that regulated survival (see Chapter 4). In a number of instances, scientists were able to identify an element of the environment that was closely related to the pattern of survival during the course of a study. One factor that received considerable attention was the availability of food following yolk absorption, since failure to successfully feed would likely result in significant mortality because a larva's energy reserves would quickly be exhausted. A demonstration of the significance of such a mechanism would require the observation that a substantial portion of the larval population was subject to starvation. Although starvation does play a role during early life, there is little evidence that a valuable index of recruitment could be derived from estimates of the abundance of the very early larval stages (Leggett & Deblois 1994, see Figure 4.1).

An alternative approach in forecasting recruitment could involve the measurement of an environmental proxy that provides an accurate reflection of the state of the environment in which reproduction and early development take place. Research would identify important environmental factors that affect survival during the egg or larval period. Retrospective analysis can then provide evidence that the strength or occurrence of one or several factors exhibited a correlation with subsequent recruitment. There is substantial risk in taking such an approach, however. For example, a number of studies found that the outflow from the St. Lawrence River, an index of the influx of nutrient-rich waters into the Gulf of St. Lawrence and onto the Scotian Shelf, as well as other environmental indices were closely correlated with the landings of many species in the region. When those relationships were revisited, Drinkwater & Myers (1987) found that a large proportion of them was no longer useful in forecasting recruitment. The reasons for the failure of such environmental proxies to forecast recruitment beyond their period of development probably have more to do with an oversimplification of the complexity of the ecosystem. Many aspects of marine environments undergo changes over decadal time scales. When many aspects are in phase,

certain relationships between the number of recruits and an environmental proxy may arise. On the other hand, as the elements of an ecosystem move out of phase with one another, for whatever reason, proxies may no longer be adequate descriptors of complex interactions. In fact, the use of environmental proxies has probably done more harm than good to the incorporation of knowledge gained from studies of early life stages into the assessment of freshwater and marine fish populations.

The most effective approach to providing an index of recruitment appears to come from indices of abundance immediately before or after the transition away from the planktonic phase of the life cycle, when the animals move into juvenile habitats. As we learned in Chapter 1, transition from the larval to the juvenile period is often associated with important changes in morphology and behavior as well as in niche shifts. For example, the settlement of juvenile plaice (*Pleuronectes platessa*) in the Wadden Sea (Netherlands) is associated with metamorphosis and movement into a benthic habitat where the young fish encounter a new array of prey and predators. One of the key mechanisms determining the strength of a plaice year class appears to be the transport of eggs and larvae from the spawning grounds in the southern North Sea to nursery areas in the Wadden Sea. A reliable estimate of year-class strength (recruitment index) can be obtained from a population survey conducted shortly after larvae settle to the bottom. There can be a variable decline in the number of recruits after settlement because of variations in predation following settlement. There are similar observations for other species that undergo a shift from a pelagic to a benthic or lotic lifestyle. The development of physical and behavioral competence on the part of young fishes appears to be a critical element in reducing their vulnerability to environmental variations and thus making abundance indices of juvenile stages useful tools in population analysis. The case study of Japanese sardine populations in Chapter 11 demonstrates the use of the abundance of age 1 fish entering juvenile feeding areas as a reliable index of recruitment.

5.4 Sample collection

5.4.1 Sampling systems, net avoidance, and extrusion

Population analysis based on the sampling of planktonic fish eggs and larvae faces particularly difficult problems because development is rapid and mortality rates are generally high. This results in substantial changes in the nature of the organisms being sampled over a relatively short time period. Rapid changes in body form (weight and length), swimming capability, and sensory development over the course of the first few weeks of life result in substantial changes in the vulnerability of specimens to collecting gear. The reduction in the number of eggs and larvae over time, their dispersal by currents, and their scarcity relative to other planktonic organisms of similar size requires the development of survey designs and methods that will provide an accurate representation of the population and the changes it is undergoing.

Sampling planktonic fish eggs and larvae is done with nets made of fine mesh. Mesh size depends on the dimensions of the animal to be collected. Devices and methods used to collect fish eggs and larvae represent a balance between the need to collect a sufficient number of animals to obtain a representative sample of the population while attempting to maintain capture efficiency across the range of stages (or sizes) used in the analysis.

When animals are abundant and poor at avoiding sampling gear, such as in the case of eggs and yolk-sac larvae of abundant and fecund species, small devices towed vertically through the water column from a standardized depth may provide an adequate method to sample the population. For example, the CalVET net, a small (25 cm diameter) paired net deployed vertically, is often used in population estimation of anchovies and sardines based on the DEPM. The depth to which the net is lowered is chosen to ensure that most of the eggs or young larvae are included in the collection. Because most planktonic fish eggs are positively buoyant, the vertical distribution of the population can be approximated using knowledge of the buoyancy of the egg and the vertical density structure of the water column.

As the abundance of organisms decreases and their ability to avoid nets increases, the volume of water sampled, as well as the capability to capture specimens, must increase. A common method of sampling early life stages in order to increase the volume sampled and reduce the ability of larvae to avoid the net is to tow the net while the ship is underway. Nets are progressively lowered to a desired depth and gradually retrieved, which results in a saw-toothed profile through the water column, commonly referred to as an oblique tow. The choice of gear type and deployment strategy, which includes towing speed and distance as well as depth of tow, is determined by the need to maintain capture efficiency over a significant portion of the target species' early life. Being able to estimate capture efficiency is particularly important in population analyses aimed at back-calculating the abundance of the youngest age classes, either eggs or hatchlings, since such approaches rely on obtaining an absolute measure of abundance.

In order to estimate capture efficiency, we must be able to determine the probability that an organism will be caught or, alternatively, determine the effective volume sampled by a gear type. The ability of a larva to avoid a sampler will depend on the distance at which it can detect it, and its ability to get out of the path of the gear. This will depend on the distance the larva can cover by swimming at maximum speed in the time available before the sampler reaches the larva (Figure 5.9). It is simple to see that as the sensory (both visual and mechanoreceptors) and motor skills of a larva improve through development, both the perception distance and the maximum swimming speed will increase. Although on the surface this may appear simple to determine, the collection of the information needed to do so is not. To ensure that the probability of capture, or the effective sampling volume, does not decrease too sharply through development, increasing the speed of the sampler or increasing the expanse of the mouth is an obvious solution. Increasing towing speed, however, may also increase the distance at which the net is detected because the pressure wave at the front is more intense, and increasing sample volume may also result in more difficult sample processing.

A more common approach to estimate capture efficiency of larvae is to use the ratio of night-to-day catches. The rationale is that if larvae are relatively inactive and visual cues are eliminated or reduced to minimal levels because of low light, the probability of capture should be maximal. If larvae respond to non-visual cues, this method for estimating capture efficiency will be inaccurate. Nevertheless, by contrasting the night–day catch ratio across age or length classes, one can determine how capture efficiency decreases in older and larger larvae. It is important to note that a catch ratio of 1 does not necessarily imply a capture probability of 1 because small larvae may still be able to avoid the nets to some degree. One possible diagnostic to determine if the catchability of small larvae is nearly 100% involves the use of the catch curve of both eggs and larvae. If there is an abrupt drop in the

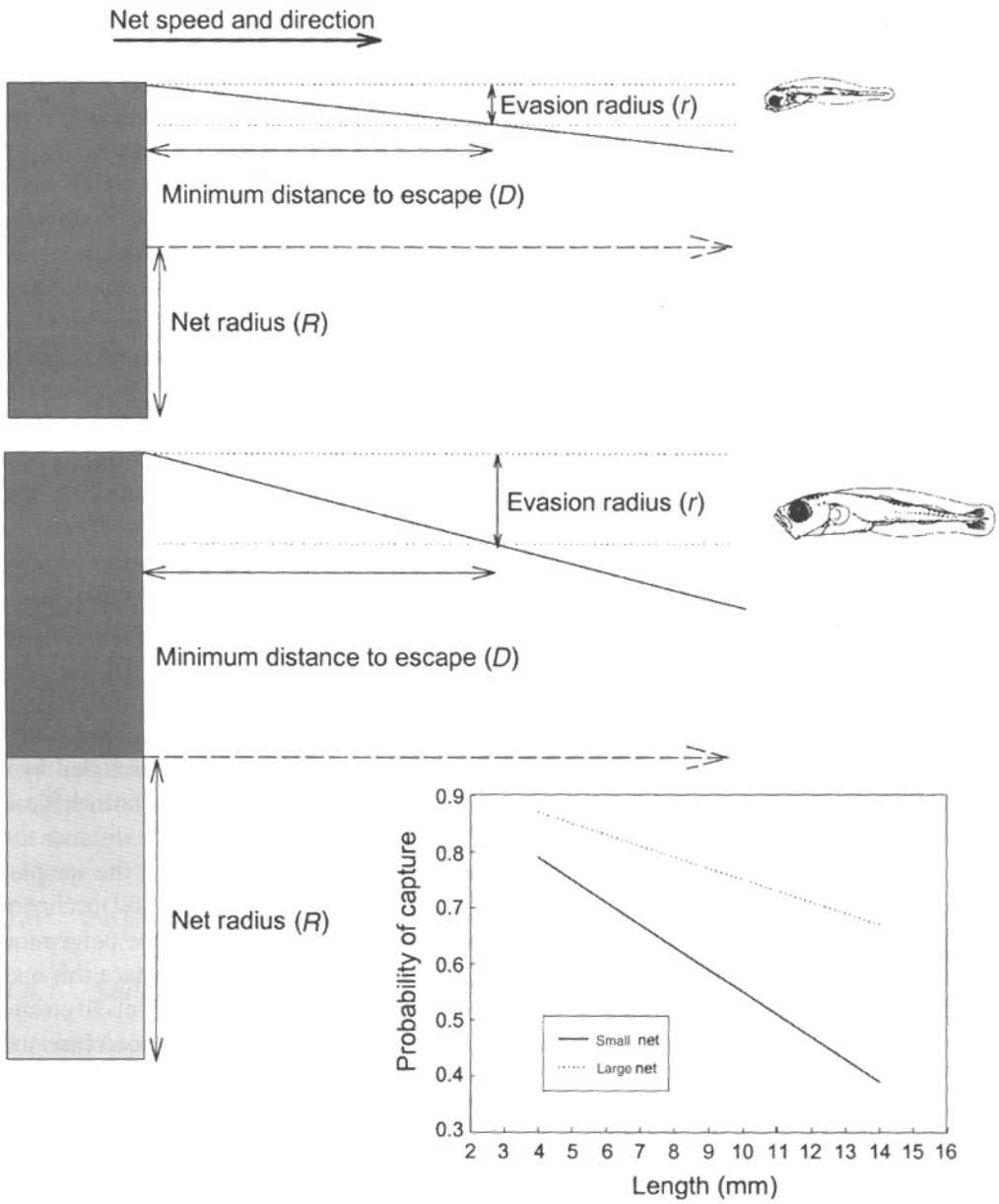

Figure 5.9 Schematic of the elements that determine the vulnerability of larval fishes to plankton nets. The maximum evasion radius is directly related to the maximum swimming speed of a larva, which in turn determines the minimum distance at which a net can be detected. As the length of the larva increases, the maximum evasion radius increases, which results in a decrease in the probability of capture. There are two solutions to reduce the possibility of net avoidance: increasing the net speed or increasing the net radius. The effect of the latter is illustrated in the lower portion of the figure where the lighter shading indicates a doubling of the net radius. Although the maximum evasion radius remains unchanged for either large or small larvae, the likelihood of avoiding the net is decreased because a greater proportion of the net's area is beyond the larva's ability to escape, which results in a greater probability of capture as illustrated in the lower right panel. (Graphic is partly based on Gartz *et al.* 1999.)

number of animals following hatching, this might indicate that catchability is not 100%. Alternatively, there could be an increase in mortality associated with hatching, simply because of physiological demands, or because larvae are being extruded through the mesh of the net. Eggs are more resistant to extrusion than young larvae.

Given the dimensions of planktonic fish eggs and their relatively hard chorion, it is reasonably easy to ensure that they will not pass through the mesh by choosing a spacing that is considerably smaller than the minimum axis. In the case of larvae, extrusion may be important depending on the gear type used. When larvae hatch, their small size may allow them to pass through the mesh. Similar situations may arise for more advanced larvae when sampling with larger plankton nets with wide mesh. The capture efficiency will be dependent on body shape; larvae that have a broad body form for a given length are more likely to be captured than ones that are more elongate.

As sampling moves to later stages of development, such as in the collection of prerecruits, it becomes increasingly difficult to determine capture efficiency. Although the catchability of eggs by plankton nets can be assumed to be near 1 so that estimates of absolute abundance can be considered as accurate, the same cannot be said for late larvae and early juveniles when estimates of abundance become indices.

5.4.2 Sampling variability and patchiness

When a plankton net is towed through the water, the degree to which one sample will resemble the next depends on the time interval and distance between samples and the local patchiness in the distribution of eggs and larvae. Fish eggs and larvae, like most other plankton, are not uniformly distributed through the water at any one site. Most plankton occur in clumps, or patches, whose cohesiveness is dependent on the balance between forces that tend to maintain aggregations, such as convergent currents or active movement to remain close to conspecifics, and those that tend to disperse them, such as current shear.

There is little information available on the scale of patches *per se* but it is worth considering the factors that influence the scale of separation between individual eggs and larvae. The initial scale is determined by the pattern of spawning by the adults. One could consider the mating pair as the smallest level of aggregation (<1 m), most often we can consider spawning aggregations, whether schools of fish or spawning habitats, to be on a scale of tens to hundreds of meters. Even within this spatial scale, the distribution of eggs and larvae is not uniform. A succession of samples taken at a single site reveals that the statistical distribution of catches is typically skewed to the right (Figure 5.10). The frequency of the occasional large catches is dependent on the level of aggregation of the animals within the area sampled and the likelihood that plankton nets will encounter these small patches. As the volume of water filtered by nets is increased, small patches of eggs or larvae are more likely to be encountered and consequently estimates of abundance from large volume samples will have a greater level of precision than those obtained from smaller volumes (Figure 5.10). The catches of other zooplankton of about the same size as ichthyoplankton do not appear to be affected similarly by the volume of the sample, suggesting that the small scale distribution pattern of fish eggs and larvae differs from that of other organisms that occupy a similar trophic level. Unfortunately, there is insufficient information to determine the cause of this apparent difference.

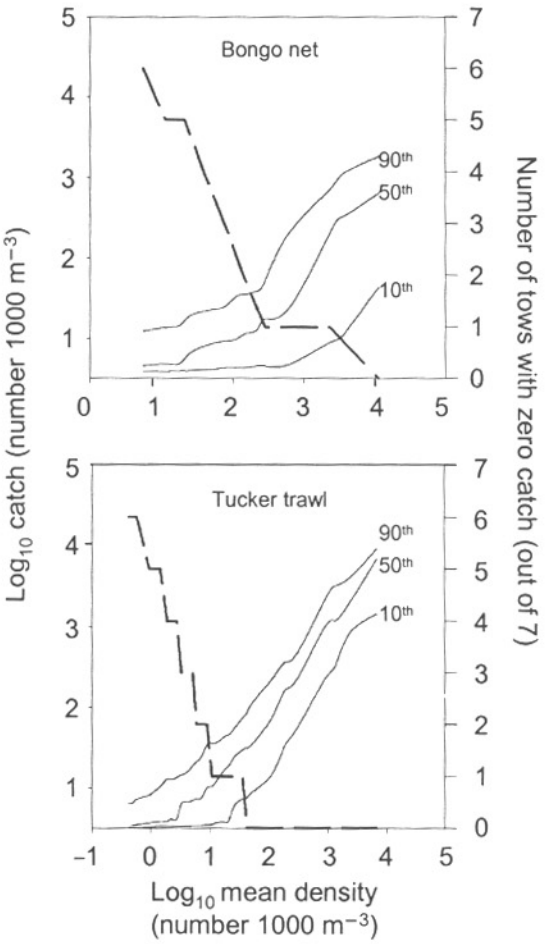

Figure 5.10 Cumulative probability distribution of non-zero catches from two plankton nets, showing the 10th, 50th and 90th percentiles (solid lines), in relation to the mean density of fish eggs and larvae from seven replicate samples at each of four sites (based on data from Pepin & Shears 1997). The bongo net had a 60-cm diameter (area = 0.28 m^2), while the Tucker trawl had a 2-m square frame (area = 4 m^2). Note that the larger net can detect smaller concentrations of larvae, the likelihood of obtaining a zero catch (dashed line) is substantially higher for the smaller bongo net, and the variability in catches (measured here as the distance between the 10th and 90th percentiles) is lower for the Tucker trawl.

Following their release, either as planktonic eggs or as hatchlings from spawning beds, physical forces will begin to transport and disperse the offspring over scales of thousands of meters (Figure 5.11). At the largest scale, the distribution of eggs and larvae will be determined by the size of the population's spawning area, which is an important consideration for survey design. Transport will continue until the young fish become physically competent to carry out directed swimming for a prolonged period of time. The scale of patches may then be dependent on the dominant physical processes of the system in which they are released, such as those defined by eddies, currents, and fronts. Dispersal, on the other hand, may decrease well before that stage of competence because individuals may be capable of forming small local aggregations because of changes in behavior, such as

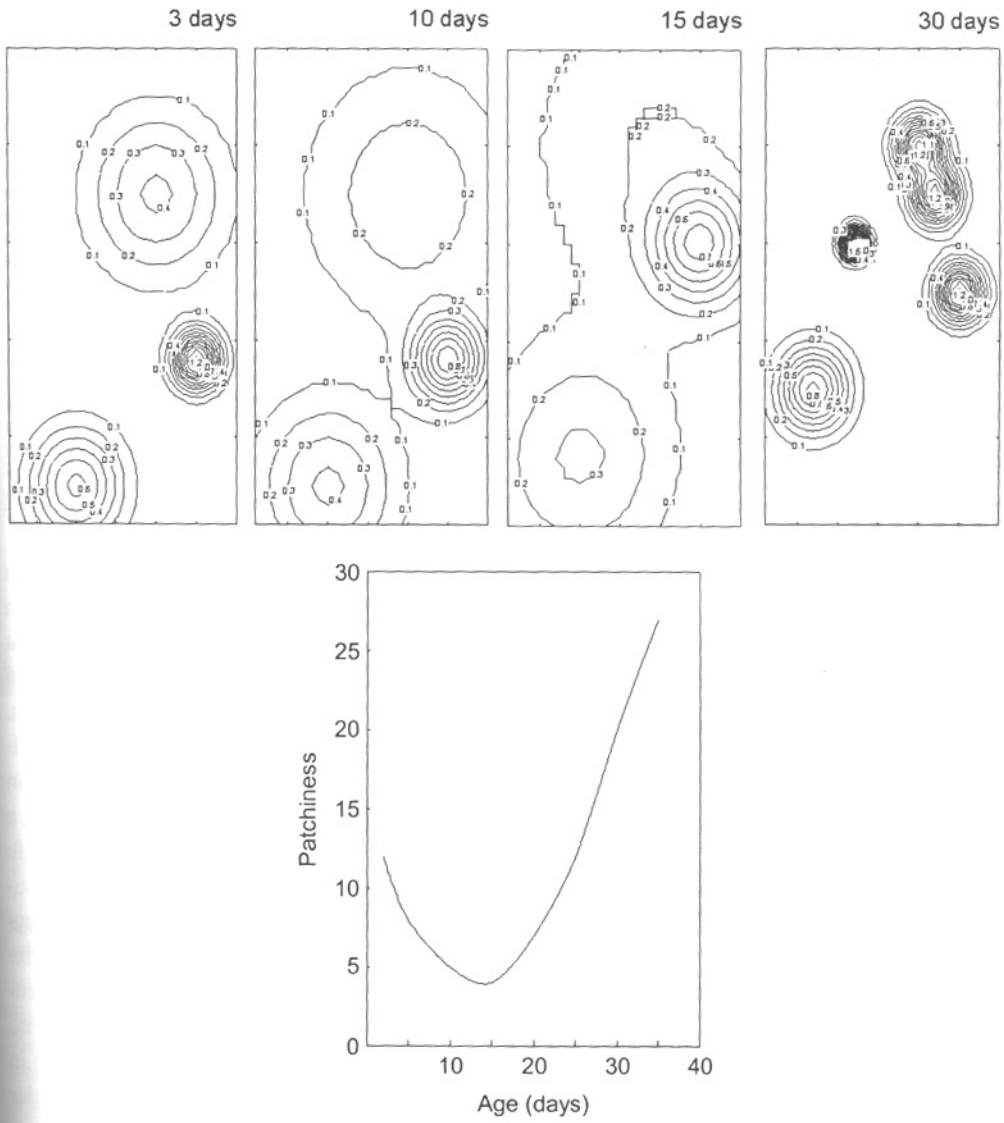

Figure 5.11 Schematic diagram of the changes in distribution and patchiness of planktonic fish eggs and larvae in relation to time since spawning. The contour lines are relative. The pattern shows an increased spread in the distribution associated with a decrease in patchiness. The lower illustration is based on the observations of Matsuura & Hewitt (1995) for the California Current, where the lowest level of aggregation is reached sometime between 8 and 20 days after spawning.

increases in the tendency to school. Biological processes that result in local losses, such as predation by schooling planktivores or the settlement of faster growing individuals, may also begin to counteract physical dispersion forces by reducing the number of eggs or larvae at the scale typical of those processes (100–1000 m). There is no single scale that typifies patch size for early life stages because young fishes are continuously being affected by diverse physical and biological factors. We can safely conclude, however, that the level of aggregation is initially high, and that it will decrease through the early stages because

physical forces dominate until the time when internal and external biological processes allow aggregation to increase once again.

5.5 The role of transport in survey design and interpretation

Because most marine fish eggs and larvae are planktonic, whereby they may have control over their vertical position in the water column but are entirely vulnerable to horizontal currents, transport and dispersal will influence our perception of their distribution and abundance. Surveys are not instantaneous snapshots of environmental conditions and the changes in distribution that take place while sampling is being carried out will have an impact on the accuracy and precision of the information. The size of the area surveyed, the degree to which the strength and direction of currents are known, and how the survey is carried out in relation to that knowledge will ultimately determine the influence that transport and dispersal will have on our perception of the distribution and abundance of early life stages.

It has long been recognized that the early life stages of fishes are highly dependent on ocean currents to determine their drift to, and retention within, suitable environments. The inclusion of the effects of ocean currents in the study of population dynamics, however, is fairly recent and infrequent. The reason is simple, a description of the spatial and temporal patterns of ocean currents is difficult to obtain because of the complex forces driving the circulation. Recent developments in numerical simulation methodology have advanced our basic knowledge of the relationship between early life stages and ocean circulation, but this work is still in its infancy. We can nevertheless take a look at some basic rules to consider when designing a population survey, or any other study that relies on determining the vital rates of early life stages. The section that follows is intended to serve as an intuition-building exercise. The routine application of biophysical modeling to the design and interpretation of plankton surveys is not well developed at this time, but rather is the subject of sophisticated ongoing research.

Take the situation of a population of particles (in our case we can call them fish eggs) centered in the middle of a 10 000-km^2 region we intend to survey (Figure 5.12). If there is no motion and abundance does not change over time, then we will reproduce the pattern in Figure 5.12a reasonably well by sampling stations 10 km apart (Figure 5.12b). But under any survey scheme, currents will alter our perception of the overall distribution and abundance of planktonic organisms. If there is a uniform current flowing toward the east at a speed of 10 cm s^{-1} (Figure 5.12c), then a survey of the area along north-to-south transects starting from the northwest corner of the region (assuming it takes 1 h to sample each station; Figure 5.12b) will give the impression that the particles are more broadly distributed because the center of mass is moving in the same direction as our survey (left to right) (Figure 5.12d). If on the other hand, the survey is conducted along east–west transects (Figure 5.12e), the view of the population's spatial distribution will be substantially different. A clear skew in the distribution will appear because eggs and larvae in the southern part of the region will have moved further east (Figure 5.12f). If we now move to a situation where there is a horizontal gradient in the strength of the current (from 10 to 40 cm s^{-1}) from the north of the region to the southern end (Figure 5.12g), that is to say that there is an increase in the variability within the system we sample, the distortions become even

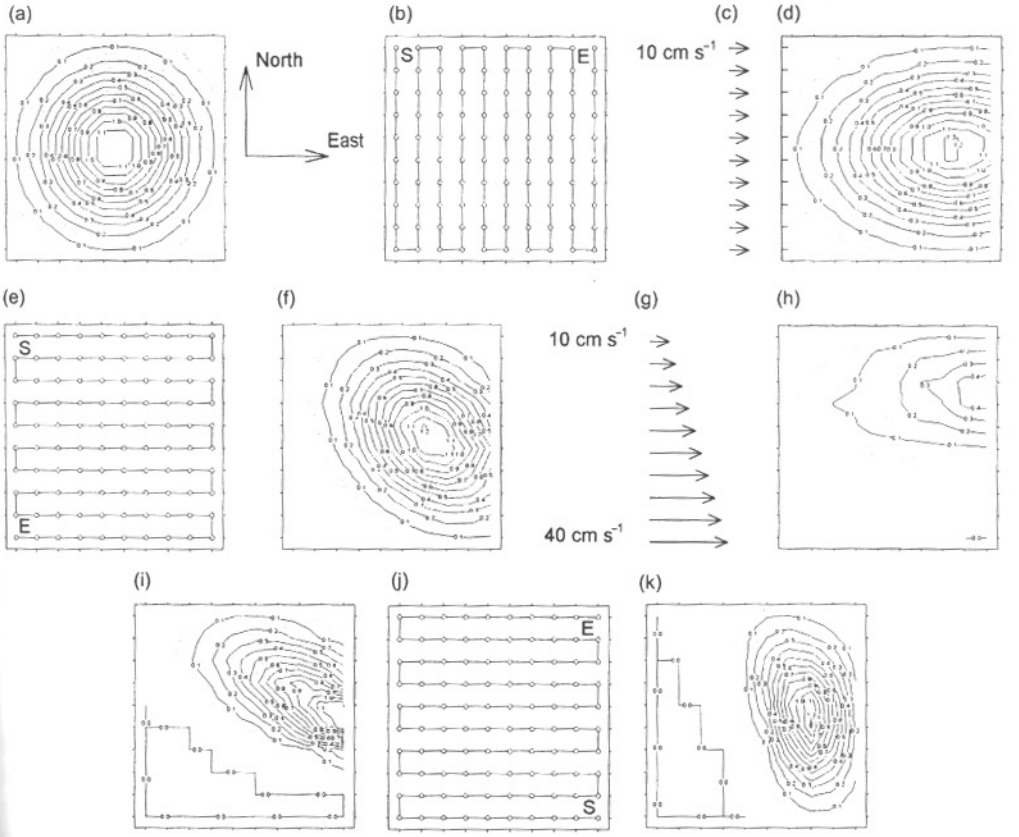

Figure 5.12 Illustration of the effect of currents and the choice of station sequence on our perception of the distribution of passive particles, such as fish eggs, from a "synoptic" survey. The instantaneous production of particles is shown in the top left corner. In this illustration, there is no development or mortality and production of particles occurs only at the start of the simulation. The area under simulation is 10 000 km^2 (100 km on each side) and station spacing in all surveys (b, e and j) is 10 km. The capital letters S and E represent the start and end points of the surveys. The time required to reach each station and perform the sampling is simulated to take 1 h, for a total survey time of a little more than 4 days. (d) and (f) show the perceived distribution of particles given a uniform current of 10 cm s^{-1} (c), for survey sequences (b) and (e), while (h) and (i) show the result for a spatially varying current (g). (k) shows the perceived distribution of particles for the station sequence shown in (j). In all simulations, diffusion is assumed to be negligible.

more pronounced depending on the survey design we apply. If we use north–south transects starting from the northwest corner (Figure 5.12b), the perceived distribution suggests there are relatively few particles in the southern range, due to more rapid advection of particles to the east along the southern edge (Figure 5.12h), and the center of mass is even further to the east, relative to the case with uniform currents. The distortion in the perceived distribution is substantially different when the transects are in a west-to-east direction, and the survey is again started in the northwest corner of the region (Figure 5.12e). Portions of the area that have low current velocity appear to be sampled with less distortion than the portions with high flow rates (Figure 5.12i). If on the other hand, we had started a similar

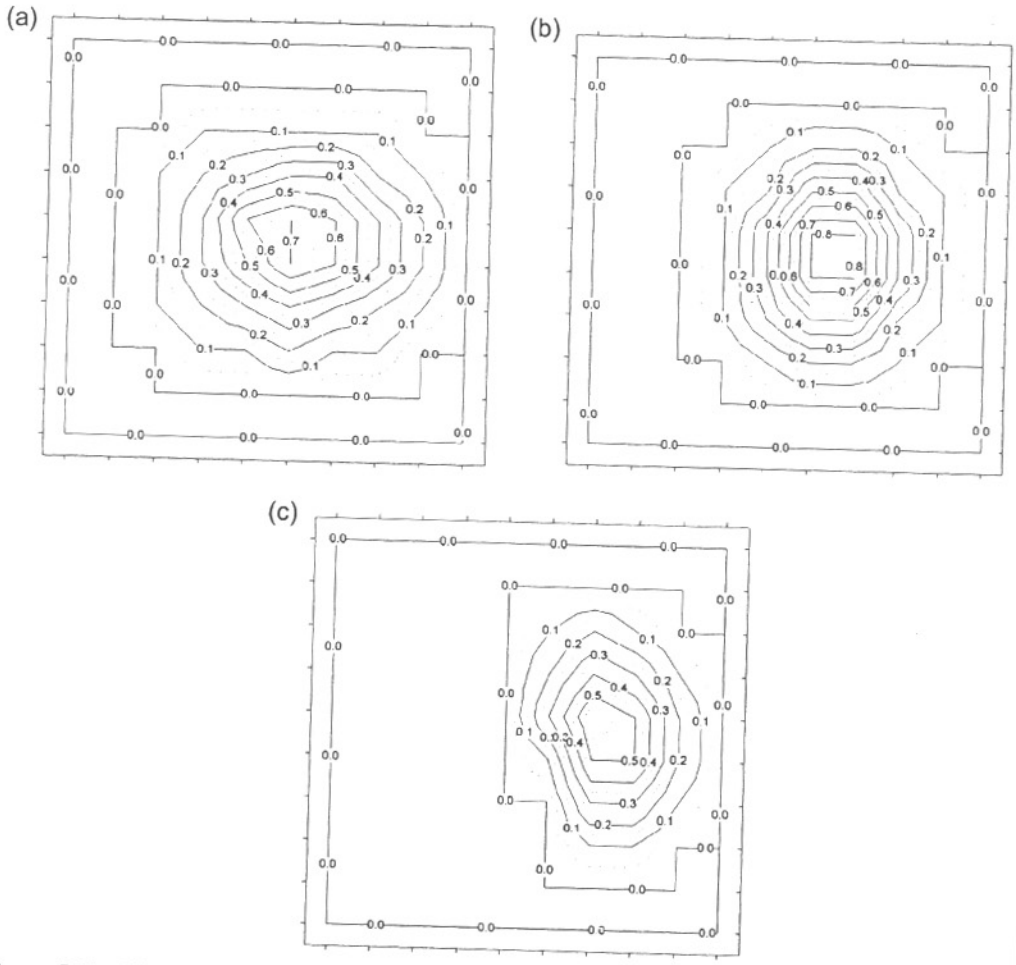

Figure 5.13 Illustration of the perceived distribution patterns of particles for simulations where there is no current (a), a uniform 10-cm s^{-1} current throughout the region (b), and a spatially varying current (c) but with the addition of a spatially uniform mortality rate (Z) of 0.2 day^{-1}. The station sequence in (a) and (b) is the same as shown in Figure 5.12b, while the station sequence in (c) is from Figure 5.12j.

survey in the southeastern corner, using east-to-west transects (Figure 5.12j), then the entire population might have been sampled with less distortion (Figure 5.12k).

The addition of mortality to the population's dynamics causes a distortion in the perceived distribution as areas that are surveyed later suffer greater cumulative loss (Figure 5.13). In the case where there is no drift and a population that is subject to a mortality rate (Z) of 0.2 day^{-1} is surveyed along north-to-south transects as in Figure 5.12b, the center of mass appears to be shifted to the west and the range appears contracted. The interaction of mortality and transport on our perception of the distribution will depend on the magnitude of both factors and the timing of our observations at each site. In essence, a good survey design will cover portions of the area of interest that would likely suffer the greatest losses from the combined factors early in the survey. This example is not based on a true situation but simply serves to illustrate the interaction between survey design and the physical environment on our perception of

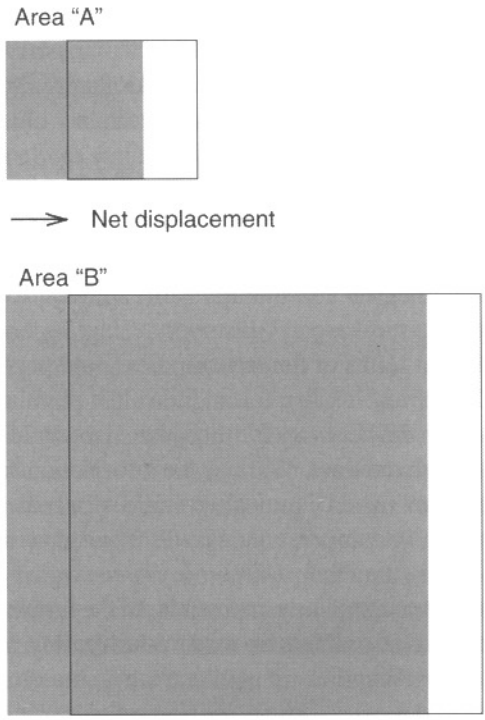

Figure 5.14 Consider two square survey regions, A and B, in which B has 10 times the area of A. Both are to be surveyed simultaneously at times t_1 and t_2. They are subject to a current of the same intensity, which flows from west to east, and results in a net displacement (transport) toward the east equal to the length of the arrow shown between the two areas. Although the level of detail in population distribution measured will be different in the two surveys, because of the time it takes to sample each station, the relative proportion of the water that will have moved out of each area will be substantially different. The shaded grey areas show the original survey regions and the black lines show the position of the projected grids after 12 h. The white portion shows the fraction of the original survey area that would be displaced during that period. Since surveys are generally conducted over the same grid for a given region, the white portion would represent the amount of water (and corresponding eggs or larvae) that would have "emigrated" from the study sites. In the case of the smaller area, 43% of the water would have been advected from the original area while slightly less than 14% of the water from the larger area would have been transported away.

distribution patterns. In most applications of egg or larval abundance or production measurements, the goal is to ensure that the entire distributional area of a population or spawning component is surveyed and delineated by regions with minimal catches so that the impact of transport, either as emigration or immigration, is rendered negligible.

Whether the effect of variations in current strength and direction has an influence on our ability to estimate the abundance of the youngest stages is unclear. It is simple to understand that in a fixed length of time, the loss due to transport will be proportionately greater if a survey is conducted over a small area than over a large one (Figure 5.14). Under this scenario, as long as the time required to survey a region does not increase in direct proportion to the area, the information from a survey conducted over a large area is less likely to be influenced by unexpected variations in currents. Present approaches to measuring or describing the circulation in a region and coupling this with observations of biological

conditions rely on intensive multi-disciplinary research programs. There is still considerable research that needs to be done to understand how our perception of abundance and distribution are influenced by changes in circulation (Helbig & Pepin 1998).

5.6 A final note

Throughout the section dealing with issues important to sampling early life stages, I avoided dealing with specific methodological considerations. In addition to species-specific requirements, there are numerous logistical aspects of surveys, sampling, and laboratory protocols as well as resource availability, in terms of funds, equipment, and personnel that play key roles in determining the specific approach taken for an individual population analysis. One aspect seldom considered explicitly is the necessity for thorough taxonomic knowledge of the species of interest as well as closely related ones. Without the information to unambiguously identify early developmental stages of fishes, abundance indices based on back-calculation may be unreliable. For example, in temperate areas distinguishing the embryonic stages of Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and witch flounder (*Glyptocephalus cynoglossus*) remains nearly impossible. In the future, biochemical approaches may prove useful, however. The problem is made considerably more difficult in tropical ecosystems where taxonomic descriptions of eggs and larvae are often limited because of the large number of closely related species with morphologically similar early life stages.

5.7 Summary

Population analyses that use approaches based on the sampling of early life stages often do so because methods that traditionally rely on surveying the adult population are not possible when trying to determine spawning-stock biomass or an early indication of year-class strength. Consequently, comparing the accuracy of different individual approaches to population assessment is rarely feasible but we can at least contrast their advantages and limitations.

A common method for assessing exploited fish populations involves the use of commercial catch and effort information, which is converted to an estimate of absolute abundance through calibration of catchability using survey indices of adult-stock abundance through sequential population analysis. Calibration can also be done using other indices of abundance, such as those obtained from egg and larval surveys, as is the case for North Sea herring (Heath 1993). Analyses of population abundance based solely on adults depend heavily on accurate knowledge of catchability. In the case of sequential population analysis, abundance estimation is made more complex by the need to have accurate information on commercial catch and effort. Any factor that can lead to inaccurate reports of the actual catch per unit of fishing effort, or changes in fishing behavior caused by changes in the distribution of the target age classes, can lead to errors in the estimate of absolute abundance. In contrast, methods based on sampling early life stages attempt to reduce the number of assumptions by measuring as many of the parameters associated with the assessment as possible. What limits estimates based on early life stages is the level of precision with which

each parameter can be estimated. This is because the error in the estimate of population abundance is based on the sum of the error (variance) in each parameter, and the interdependence (covariance) of these errors. In addition, each estimate based on egg or larval abundance does not build on previous knowledge of the population's state, whereas sequential population analyses can smooth some of the short term variability in estimates of population abundance because each new year's information is not independent of that obtained previously. The result is that population analysis based only on early life stages may exhibit considerable inter-annual variation that can only be reduced by thorough sampling of both adults and offspring. This may not necessarily be considered a disadvantage, however, because approaches such as sequential population analysis tend to underestimate the level of variability in population abundance.

The precision of population estimates is also an issue when we contrast hydro-acoustic integration and early life-history methods, such as the DEPM, both of which provide estimates of absolute abundance. Hydro-acoustic surveys have the advantage that a large area can be surveyed with reasonably high resolution. This is because sampling is continuous along transects and the number of transects can be increased when the ship is not forced to stop on station as frequently as is required when taking conventional biological samples. Furthermore, there are fewer elements to measure when conducting population analysis based on hydro-acoustic surveys, which can result in a greater degree of precision in the estimate of population abundance. On the other hand, hydro-acoustic integration also depends on the calibration of target strength in relation to abundance, which is critical to obtaining a measure of absolute abundance. In the instances where hydro-acoustic integration and early life sampling have been applied to the same population, however, both appear to predict similar changes in abundance indices over time. The general trends in population abundance appear to follow similar patterns even though the year-to-year changes do not exactly correspond.

One situation where the use of early life stages is directly analogous to methods used on adult fishes involves the application of mark–recapture techniques to population estimation. Whereas adults are generally tagged externally, young fishes are marked by chemical immersion (for example, using oxytetracycline or alizarin complexone) in order to "score" the otolith. Otoliths extracted from individuals captured at a later time are then placed under a fluorescent light to assess the existence of a mark. Other ways of marking early life stages include the use of small pit-tags placed in the snout of young fishes, such as salmon alevins, that can subsequently be identified using electronic sensors, or by immersing young fish in fluorescent dyes to mark bone tissue which can be detected easily upon recapture. Mark–recapture studies require that large numbers of marked larvae or young fish be released into the population in order to obtain a sufficiently large number of recaptures, a matter discussed in Section 2.3.1. Assessment of population size can then be carried out using methods identical to those traditionally applied to juvenile and adult populations. The assumptions concerning limited emigration or immigration into the area of interest as well as the lack of differential mortality between marked and unmarked individuals must be satisfied. Application of mark–recapture techniques has been successful in several instances where small local populations appear to remain fairly cohesive, in locations such as small bays, rivers, and estuaries. The concept may not be readily applicable to large populations distributed over a broad geographic area because of the logistics of releasing sufficient numbers of young fish in order to obtain adequate

recaptures (but see the coral reef example mentioned in Section 7.3.7). In most examples where the approach has been successful, the potential for differential mortality could be assessed by sampling soon after the release of marked individuals to determine if substantive losses had taken place. The likelihood of differential mortality appears to be related to the duration of the rearing period prior to release. As the period when young fish are kept in cultured conditions is lengthened, a greater proportion of naïve individuals is produced, possibly because of a lack of appropriate natural stimuli or natural selection.

Approaches based on sampling early life stages are most effective for population assessment when used in conjunction with other sources of information. Their advantages come from the limited number of assumptions they require in contrast to some of the traditional methods that primarily sample adults. Their limitations come from the difficulty in obtaining precise estimates of some elements critical to their application. They are likely to provide a good measure of absolute abundance, however, because they rely on a thorough understanding of the biological characteristics of a species or stock. Therefore, discrepancies with other assessment methods can point to critical gaps in our understanding of the processes affecting a population.

The application of egg or larval production methods has become more widespread because in many instances accurate surveys of adult populations are almost impossible. Population analyses based on early life stages move beyond providing a simple measure of stock size because the basic requirements of such methods rely on observing stock status. We have to consider aspects of both the adults and their offspring in order to appropriately apply the principles on which the approach is based. Population analyses based on early life stages, whether used to estimate spawning-stock abundance or to forecast year-class strength, provide unique information on the biology and processes that affect population dynamics. Estimates of population abundance based on egg or larval production rely on a good understanding of the physiological state of spawning adults and thus provide information on changes in both numbers and reproductive potential of the population. However, these methods can also provide information on the processes that affect year-class strength because the approaches rely on the estimation of development and mortality rates, thereby giving additional insight into the dynamics of the ecosystem in which a stock or species lives.

Additional reading

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Table 7.1 Summary of key physical and chemical habitat variables affecting fish eggs and larvae.

Habitat variable	Effect on eggs	Effect on larvae
Temperature	Affects rate of development and thus incubation period and size at hatching. Eggs are more sensitive to temperature change than adults.	Affects metabolism and thus rates of feeding and growth and stage duration. Temperature also has indirect effects through impact on viscosity and oxygen saturation levels of water. Larvae are more sensitive to temperature change than adults.
Light	Little impact except through possible ultraviolet damage.	Governs daily duration of feeding and depth at which food can be captured. Available light strongly affected by turbidity and color.
Mechanical damage	Potentially serious source of mortality on eggs in shallow water, particularly for broadcast spawners.	Larvae in shallow water are subject to severe mechanical damage, if current or wave action present.
Shelter	Important as protection for eggs from predation and mechanical damage.	Important as protection for larvae from predation.
Current	Potential mortality source for unattached eggs. Provides a renewed oxygen supply to eggs. Can transport pelagic eggs toward nursery sites.	Can transport larvae to nursery sites. Strong currents generally avoided by larvae.
Oxygen	Respiration across chorion is relatively inefficient. More sensitive to low oxygen levels than adults.	The switch from cutaneous to gill respiration and the development of a functional blood oxygen transport system creates a very vulnerable situation during this time. Larvae are very sensitive to low oxygen levels.
Salinity	Affects buoyancy of eggs in marine environment.	Affects buoyancy of larvae in marine environment.
pH	Low pH has a major impact at hatching due to inactivation of hatching enzymes.	Low pH (below 5.5) can reduce larval survival.
Pollutants	Can impact eggs directly or through maternal accumulation. Embryos prior to gastrulation are particularly sensitive.	Yolk-sac larvae are most sensitive to pollutants.