12. THE STOCK/RECRUITMENT RELATIONSHIP

12.1 CLASSICAL S/R CONSIDERATIONS
12.2 THE STABILITY OF RECRUITMENT
12.3 TOWARDS MODELLING RECRUITMENT

The stock and recruitment problem may be considered as the search for the relationship between parental stock size and the subsequent recruitment in numbers or the year class strength (cf. Section 8.3). This is a central problem of fish population dynamics, since it represents nature’s regulation of population size, whether or not the populations are being exploited.

This chapter presents some considerations on the stock/recruitment (S/R) relationship problem although it does not present methods to solve actual problems. The reason why the S/R relationship is given this kind of treatment is not that the subject is less important, but rather that really convincing models to handle the problem have not yet been developed.


To present the S/R relationship an exceptionally clear example has been chosen (Fig. 12.0.1). It deals with the false trevally (Lactarius lactarius) in the Gulf of Thailand (Pauly, 1980a). In this case there appears to be a well defined relationship between recruitment and spawning stock size. However, as already mentioned in Section 8.3 (Fig. 8.3.2) this is not a typical example of an S/R plot.

Fig. 12.0.1 Stock and recruitment plot for the fake trevally (Lactarius lactarius) in the Gulf of Thailand (from Pauly, 1980a)
Fig. 12.0.2 shows the S/R plot for herring (*Clupea harengus*) in the North Sea for the years 1949-1978. The estimates of stock sizes and recruitment (numbers of one year old fish) are derived from VPA (cf. Section 5.1). This example is more representative for S/R plots in general.

**Fig. 12.0.2 Stock and recruitment plot of North Sea herring (*Clupea harengus*). Number of one year old herring vs spawning stock biomass. Data derived from VPA (reproduced from Beyer and Sparre, 1983)**

Obviously, there can be no recruits if no adult fish are left to mature, spawn and produce eggs which hatch and grow to become recruits. The females of most fish species are extremely fecund, producing thousands, even millions of eggs during their adult life. This enormous fecundity has led many fishery biologists to believe that even a very small parental stock should be able to rebuild the stock after each spawning season. It was assumed that features of the abiotic environment (e.g. oceanographic conditions) were the major factors determining how many of the spawned eggs would survive to become recruits. They believed that the spawning stock biomass (biomass of mature fish) was virtually an irrelevant factor for the determination or recruit numbers, except in cases of stock sizes close to zero. This lack of an S/R-relationship was suggested, for example by Beverton and Holt (1957) (see also Beverton, 1963). Later works (e.g. Parrish, 1973 and Saville, 1980) suggest that many fish stocks do display an S/R-relationship. It has been suggested that most of the fish stocks that collapsed in recent decades suffered from recruitment overfishing (cf. Section 8.3) (Murphy, 1966, 1977; Saville, 1980).

However, S/R relationships generally cannot be established directly by plotting the number of recruits (or some index of recruitment) on spawning stock biomass. Rather, it is necessary to simultaneously account for an S/R relationship and the biotic and/or abiotic factors which may affect it. Csiszko (1980) demonstrated a strong effect of oceanographic conditions on the recruitment of the Peruvian anchovy.

**12.1 CLASSICAL S/R CONSIDERATIONS**

It has been observed for many fish stocks that the mean recruitment level is almost constant in a large intermediate domain of variation of the parental stock (see Figs. 12.0.2 and 12.1.1). In the case of the North Sea herring (Fig. 12.0.2) it has been estimated that this intermediate range comprises at least an interval corresponding to \(10^{12}-10^{13}\) eggs. The mean recruitment level is about \(8*10^9\) one year old fish. Thus
the probability of an egg developing into a one year old recruit is about 0.0001.

**Fig. 12.1.1** The basic form of a recruitment curve. The shaded distribution indicates variation in recruitment about the mean level.

**Fig. 12.1.2** Ricker curve fitted to the spawning stock biomass and recruitment of southern bluefin tuna. Data derived from cohort analysis (reproduced from Murphy, 1982, with permission)

It should be noted that this low rate of survival has nothing to do with fishing, since we are considering mortality in the pre-exploited stage of the life-history (the fish younger than Tr, cf. Section 4.1). The effect of fishing is a reduction of the spawning potential (i.e. growth overfishing, cf. Section 8.2), not of the recruitment. It is only when the rate of fishing is increased beyond a certain level that recruitment is affected (i.e. recruitment overfishing, cf. Section 8.3). In the case of North Sea herring, such a transition from growth overfishing seems to have taken place somewhere in the seventies. But, in principle, we do not know very much about the proper location of this transition zone in the recruitment graph. There is only one thing that is known for certain and that is the point of extinction. We know little about the other extreme of the recruitment curve. Beverton and Holt (1957) suggest the following type of S/R relationship:

\[
R = \frac{E}{E + gR_{max}} \times R_{max} \tag{12.1.1}
\]

where \(g\) is a parameter and where the number of recruits, \(R\), increases towards an asymptotic level, \(R_{max}\), when the egg production, \(E = \text{(number of females) } \times \text{(average egg production)}\), increases. This model is derived from a simple density-dependent mortality model:

\[
\frac{dN(t)}{dt} = -M(t)\times N(t) \text{ and } M(t) = m1 + m2\times N(t) \tag{12.1.2}
\]

where \(N(t)\) is the number of survivors at age \(t\), \(M(t)\) the rate of natural mortality of juveniles and \(m1\) and \(m2\) are parameters. Thus, the more survivors there are at age \(t\), the higher their mortality. This mechanism evens out the differences in survival caused by other, biotic or abiotic, factors.

It can be shown (Beverton and Holt, 1957) that Eq. 12.1.1 is the solution to the differential equation 12.1.2.

This is an example of a model describing "density dependent mortality". Density dependent mortality may be explained by food competition. If food is limited the number of starvation deaths becomes a function of the number of specimens which have to share the food.

The characteristic shape of the Beverton and Holt S/R curve is shown in Fig. 12.1.1. The S/R plot of Fig. 12.0.2 is difficult to describe by a curve, but if a curve were fitted it would be of the Beverton and Holt type.

Ricker (1954) suggested a different mathematical model for the S/R-relation-ship (see Fig. 12.1.1):

\[
R = R1 \times E \times \exp(-R2\times E) \tag{12.1.3}
\]

where \(R1\) and \(R2\) are parameters.
In this model the number of recruits decreases from a maximum level (of $R1/(e^{R2})$ when $E = 1/R2$) towards zero as the production of eggs, $E$, increases. The recruitment decline is explained by cannibalism of the young by the adults. These matters are described more fully by Ricker (1954, 1975).

The eye-fitted curve in Fig. 12.0.1 is a Ricker type of S/R relationship. However, the descending part of the curve is based on only one point. A few more observations for large spawning stocks may change the picture. Fig. 12.1.2 shows a Ricker curve fitted to data for southern bluefin tuna (*Thunnus maccocyii*) (Murphy, 1982). This example also illustrates the difficulties often encountered when trying to fit an S/R curve. As Murphy (1982) says about this plot: "there appears to be an underlying density dependent relationship overlaid by considerable environmental variability".

Essentially, the Bevorton and Holt model says that above a certain level of spawning stock there is no relationship between parent stock and recruitment, whereas the Ricker model says that this relationship exists for all sizes of the spawning stock, and that there is an optimum spawning stock size (cf. Fig. 12.1.1).

Deriso (1980) and Schnute (1985) suggested a general stock/recruitment model:

$$R = R1*E*[1 - R2*R3*E]^{1/R3}$$

where $R1$, $R2$ and $R3$ are parameters. For large values of the "shape" parameter $R3$, the above model reduces to the Ricker model as we then get

$$R = R1*E*exp(-R2*E)$$

If $R3 = -1$ we get the Beverton and Holt model by redefining the parameters to $R1 = 1/g$ and $R2 = 1/(g*Rmax)$ as

$$R = R1*E/[1 + R2*E] = (R1/R2)/(E + 1/R2)$$

Most available data on stock and recruitment refer to the medium range of variation in the spawners. It is here that most species appear to maintain a constant mean recruitment level and this constitutes the motivation for the assumption of constant recruitment in classical fish population dynamics. The most remarkable fact, perhaps, is that recruitment shows only relatively small variations about this mean level considering the great reduction in numbers from the egg stage until maturity (Ursin, 1982)

### 12.2 THE STABILITY OF RECRUITMENT

Table 12.2.1 gives relative recruitment variations for eleven commercially important North Sea species in the period 1963-75 (Ursin, 1982). The table is derived from VPAs from various ICES working group reports. We see for example, that the cod year classes show a factor of six in their variation from the weakest to the strongest.

To consider this variation range in the light of the range of population reduction of cod during the first year of life we may apply the following consideration as an approximation of the situation in the seventies. The mature stock comprises about 200,000 tonnes of cod, half of which are females. Once a year each female spawns 10% of her body weight as eggs, giving a total annual production of 10,000 tonnes of eggs or $2*10^{13}$ eggs, since each egg weighs about 0.5 mg wet weight. The mean recruitment level, however, is only $2*10^{8}$ one year old fish. Thus on the average only one egg out of 100,000 survives and grows into a one year old cod. The factor of six
in recruitment variation implies that the probability of a fish dying in the first year of life at most changes from 0.999,997 for a bad year class to 0.999,983 for a good year class, or in other words the probability of a fish surviving changes from 0.000,003 to 0.000,017.

We could also consider stability in terms of recruitment to the mature stock. During her lifetime a female cod must produce an average of one mature female and one mature male. Only extremely small deviations from this magic number 2 are feasible if the cod stock is to remain at approximately the same level, as it apparently has done for the last 150 years or more.

Table 12.2.1 Recruitment variation in North Sea fish stocks 1963-1975. Numbers adjusted to a value of 100 for the most outstanding year class of each species. "Ratio" is the ratio between the numbers in the strongest and the weakest year class (after Ursin, 1982)

<table>
<thead>
<tr>
<th>year class</th>
<th>gadoids</th>
<th>flatfish</th>
<th>clupeids</th>
<th>others</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>cod</td>
<td>haddock</td>
<td>whiting</td>
<td>saithe</td>
</tr>
<tr>
<td>1963</td>
<td>52</td>
<td>1</td>
<td>14</td>
<td>17</td>
</tr>
<tr>
<td>1964</td>
<td>49</td>
<td>1</td>
<td>26</td>
<td>23</td>
</tr>
<tr>
<td>1965</td>
<td>70</td>
<td>2</td>
<td>30</td>
<td>18</td>
</tr>
<tr>
<td>1966</td>
<td>63</td>
<td>12</td>
<td>37</td>
<td>50</td>
</tr>
<tr>
<td>1967</td>
<td>20</td>
<td>100</td>
<td>100</td>
<td>51</td>
</tr>
<tr>
<td>1968</td>
<td>19</td>
<td>6</td>
<td>33</td>
<td>55</td>
</tr>
<tr>
<td>1969</td>
<td>82</td>
<td>2</td>
<td>30</td>
<td>29</td>
</tr>
<tr>
<td>1970</td>
<td>100</td>
<td>14</td>
<td>33</td>
<td>29</td>
</tr>
<tr>
<td>1971</td>
<td>18</td>
<td>21</td>
<td>68</td>
<td>30</td>
</tr>
<tr>
<td>1972</td>
<td>35</td>
<td>4</td>
<td>90</td>
<td>40</td>
</tr>
<tr>
<td>1973</td>
<td>31</td>
<td>21</td>
<td>63</td>
<td>100</td>
</tr>
<tr>
<td>1974</td>
<td>51</td>
<td>40</td>
<td>92</td>
<td>27</td>
</tr>
<tr>
<td>1975</td>
<td>27</td>
<td>9</td>
<td>37</td>
<td>50</td>
</tr>
<tr>
<td>Ratio</td>
<td>6</td>
<td>100</td>
<td>7</td>
<td>6</td>
</tr>
</tbody>
</table>

This approximate one-for-one replacement between successive generations holds at least as long as the mature stock is within the medium range of variation as referred to above. Thus, whether we are considering a situation of heavy fishing, where the mature female cod on the average lays about two million eggs in its short lifetime, or whether we are considering an average production of 40 million eggs per female at a low fishing level, the number 2 still holds.

We do not know what causes this enormous reduction in numbers from the egg stage and leads to the fine adjustment of the number of recruits to the number of mature fish. Note in passing that the North Sea haddock and Norway pout show a remarkable instability in recruitment (see Table 12.2.1). It could be that stabilizing mechanisms do not exist in the North Sea for these two species.

12.3 TOWARDS MODELLING RECRUITMENT

It is difficult to attack the recruitment problem in a sensible way by means of
statistical tools only because of the small amount of useful data that in general seem to be available. We only achieve one new data point per species each year. Thus, to explain recruitment variability such as the occurrence of extremely strong year-classes, we may advance a great variety of conflicting hypotheses, all of which lead to different conclusions but none of which can be rejected on the basis of the available data.

The situation is no better with respect to explanations of recruitment stability. It is not possible to discriminate between empirical recruitment models such as those given by Eqs. 12.1.1 and 12.1.3. Neither is it possible beforehand to sort out irrelevant mechanisms of mortality regulation by means of data. Apparently we need to build more biological knowledge on the causes of natural mortality in the first year of life into the recruitment models. See also Sinclair (1988).