THE CONSEQUENCES OF CANNIBALISM IN THE STOCK-RECRUITMENT
RELATIONSHIP OF PLANKTIVOROUS PELAGIC FISHES SUCH AS *ENGRAULIS*

by

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INTRODUCTION

Recruitment in clupeoid fishes is usually highly variable (see Sharp, this volume, also Cushing, 1971; Cushing and Harris, 1973). This variability obscures the nature of the underlying relationship between the expected value (in the statistical sense) of recruitment and the abundance of the parental stock. A wide variety of mathematical models of the relationship have been proposed, but in very few cases have empirical observations been sufficient to justify a choice between models. While greater awareness of "The Stock Recruitment Problem" has been gained in the last two decades, remarkably little progress has been made in solving it. As a case in point, the classic debate between Frances N. Clark and John C. Marr (Clark and Marr, 1955) regarding density dependence versus independence in the stock-recruit-relationship of the Pacific sardine (*Sardinops sagax caerulea*) is being renewed in discussions regarding management of the northern anchovy (*Engraulis mordax*) fishery which succeeded it in California.

No doubt, given a long time series of data, empirical stock-recruitment models can be developed. However, in management's quest for maximizing consumptive benefit from most of these fisheries, we are faced with two problems: 1) an incorrect interim choice of management strategy is likely to terminate collection of the necessary data due to collapse of the fishery; and 2) overly conservative management is usually unacceptable due to pressing social and economic needs which can be met by fishery expansion. In this context, we cannot simply choose to wait until sufficient data have been accumulated to justify a particular empirical model; given the natural variability of recruitment, this approach could require more than a century. The alternative is to attempt to elucidate the mechanisms determining recruitment, and to construct rational "cause-and-effect" models.

This paper examines one cause-and-effect mechanism which leads to a characteristic family of stock-recruitment curves. While it is often difficult to demonstrate specific density dependent mechanisms by which clupeoid populations are regulated (albeit weakly), cannibalism is indisputably such a mechanism. The following discussion of cannibalism includes a variety of species, but the clearest and most complete information is available for the genus *Engraulis*.

THE RICKER CURVE

Ricker (1954) developed what has come to be known as the "Ricker curve" to describe a stock-recruitment relationship wherein initial production of offspring is proportional to stock size, but their subsequent mortality rate is also proportional to adult stock size. One common form of the Ricker curve is:

$$R = aSe^{-bS} \qquad (1)$$

where R is recruitment, and S is spawner abundance. Fitted coefficients a and b reflect density independent and dependent factors respectively. In particular, coefficient b describes the proportionality between spawner abundance and the instantaneous coefficient of mortality of offspring up to the age of recruitment. Two mechanisms by which mortality is likely to be proportional to parental abundance are 1) cannibalism by the parents themselves (ibid), and 2) food limitation, whereby the length of time spent in some vulnerable stage is proportional to the initial number in this stage, and the mortality rate is constant over this time (Chapman, 1973). *Engraulis* eggs and yolk sac larvae would only be subject to cannibalism, but feeding larvae are conceivably subject to both density denendent mechanisms.

The food limitation mechanism is difficult to study. Probably the first step would be to demonstrate the existence of sufficiently small coherent patches of larval fish food such that predation by the larvae is a significant determinant of the density of food in the patch. Current thinking (Lasker, 1978) is that favourable food patches are very large with respect to distances travelled by larvae, i.e. larval ambits. An alternative possibility which is presently being investigated (J. Trent, Scripps Institution of Oceanography, personal communication) is that larvae are able to successfully feed on the cloud of plankton that surrounds particles of "marine snow". The size of these food patches is sufficiently small that feeding by larval fish could affect local food density. This mechanism will not be discussed further here.

Cannibalism has been the rationale for using the Ricker curve in models of several engraulid and clupeid populations, but its appropriateness has not been justified quantitatively; cannibalism has not been shown to be of sufficient magnitude to account for an appropriate portion of the mortality of spawning products. More often the Ricker curve is used because it appears to fit the data. Schaaf and Huntsman (1972) fit a Ricker curve to Atlantic menhaden (*Brevoortia tyrannus*) data with no discussion of an underlying mechanism. Murphy (1966, 1967) fitted Ricker curves to Pacific sardine data, citing cases of cannibalism by that and other species of *Sardinops*.

Gulland (1973) suggested that the Ricker model may be appropriate for the Peruvian anchoveta (*Engraulis ringens*), again based on non-quantitative considerations of cannibalism. Gulland suggested that mortality from cannibalism could, in principle, be determined from detailed examination of stomach contents. At the Third Session of the Panel of Experts (Instituto del Mar del Peru, 1973), J. Csirke presented a Ricker curve fit to catch per unit effort (CPUE) indices of adult and recruit abundances, but the mechanisms were discussed in only general terms. Interestingly, nearly all of the data points fell on the descending limb of the stock-recruitment curve. This tendency for recruitment to decline at increasing stock sizes clearly dictated rejection of a monotonically increasing stock recruitment curve such as that developed by Beverton and Holt (for a comparison of Ricker and Beverton-Holt curves, see Ricker 1973, 1975).

Csirke (1980) modified the usual Ricker curve in order to better distinguish between density dependent and independent mechanisms assumed to underly the model. Density independent processes were assumed to be a function of anchoveta stock abundance as calculated by cohort analysis (VPA). He realized that density dependent processes indeed were a function of density (biomass per unit volume or area) rather than overall abundance. Csirke's method

of quantifying this difference was ingenious; he utilized CPUE as an index of density, effectively taking advantage of the very problem which has made CPUE a poor index of abundance of pelagic fishes. Csirke's model will be discussed further in a later section. As before, Csirke assumed that cannibalism is the most likely mechanism determining the shape of the stock-recruitment relationship. He cited several reports of stomach contents, some of which indicated extensive consumption of spawning products.

QUANTIFICATION OF CANNIBALISM

Until recently quantification of the impact of cannibalism has been difficult because little was known about egg production. Hunter and Goldberg (1980) have resolved this problem by histological analysis of anchovy gonads. The frequency of occurrence of one-day-old post-ovulatory follicles led them to conclude that *E. mordax* spawned every 6 to 8 days during the peak of the season. This allows daily production to be compared with estimated consumption of spawning products over a similar period. Hunter and Kimbrell (In press) have attempted such calculations. Based on a mean of 5.1 eggs per stomach and an instantaneous coefficient of gastric evacuation of 0.701/hr., they estimated daily consumption to be 85.8 eggs, or 5.1 eggs/g of fish weight. This compares with an average batch fecundity of 29.7 eggs/g for all fish (including males).

If we think of cannibalism as analogous to fishing, the catch equation describes the relationship between consumption ("catch"), initial abundance and rates of mortality. Thus we have

$$C_c = E_0 F_c (1 - e^{-(F_c + M)t_e})/(F_c + M) \qquad (2)$$

where C_c is daily egg consumption per gram of adults (5.1 eggs/g)

E_0 is daily egg production per gram of adults (29.7 eggs/g)

F_c is coefficient of mortality due to cannibalism

M is coefficient of mortality due to other causes, and

t_e is length of time eggs are subject to mortality, i.e. time to hatching

Two estimates of instantaneous coefficient of total mortality (Z) for anchovy eggs are available. Hunter and Kimbrell used an estimate given by Smith and Lasker (1978) of about 53%/day (Z = 0.775). This is an average over the years 1951 through 1969 and includes a wide range of anchovy abundances. The second estimate of Z is based on extensive sampling of egg abundance-at-age (Stauffer and Picquelle, 1980). This estimate of Z = 0.39 is somewhat lower and is associated with a level of anchovy abundance similar to that presumed to exist in 1976 and 1977 when Hunter and Kimbrell obtained their samples. Under typical conditions (ca. 15°C), anchovy eggs hatch in about 2.5 days (Theilacker, this volume). For purposes of the present calculations, I assume that a single day's consumption of eggs from the past three days' cohorts is equivalent to the consumption over three days of a single cohort. For the larger estimate of Z (Smith and Lasker, 1978), F_c is 0.153, and accounts for 20% of total mortality. The smaller estimate of Z gives an F_c of 0.108, accounting for 28% of total mortality.

These estimates of F_c allow evaluation of the significance of cannibalism to the stock-recruitment relationship of anchovy. The Ricker curve (Equation 1) has a maximum when S = 1/b (Ricker, 1973). At this stock size the density dependent term is e^{-1}, and the survival rate from density dependent sources of mortality is 36.8%. If cannibalism is the only source of density dependent mortality, recruitment is maximal when

$$\int^{t_R} r_c(t) \, dt = 1 \qquad (3)$$

That is, when the age specific coefficients of density dependent mortality ($F_c(t)$) integrated over the time from spawning to recruitment (t_R) is equal to unity. If the integral exceeds unity, recruitment will decrease because of density dependent effects. This provides a convenient reference level for assessment of density dependent effects. If we evaluate the above integral over the egg stage alone (2.5 days), we obtain values of 0.383 and 0.270 for our two estimates respectively. Thus, in the egg stage alone, this accounts for one-third of the "reference" level of density dependent mortality.

Similar calculations are difficult to make for larvae. Hunter and Kimbrell (in press) report that anchovies digest small larvae beyond recognition in 30 min., so the apparent residence time is very short. Also, with digestion proceeding this rapidly, many larvae could be decomposed between the time the adult is captured and when the preservative effectively stops digestion. For example, midwater trawls for adult *E. mordax* are often 20 mins., in duration, and retrieval of the net takes another 20 mins. By the time the samples are preserved, at least 30 mins. have elapsed since the average time of capture. This indicates that only the larger larvae could resist digestion long enough to be observed, which is consistent with reported stomach contents. If cannibalism on larvae is to be quantified, rapid sampling methods will have to be developed. One possibility is a preservation system acting in the cod end of the sampling net.

In the absence of quantitative data on larval mortality caused by cannibalism, I offer the following speculation. The instantaneous coefficient of total mortality of *E. mordax* larvae has been estimated by Smith and Lasker (1978) as 0.14, and by Hewitt (In press) as 0.16. This is considerably lower than estimated egg mortality rates (also see Jones and Hall, 1974); it seems reasonable that rates of cannibalism will decrease similarly. Anchovy eggs and larvae are patchily distributed at all ages; however, patchiness is minimal at an age of about 18 days (Hewitt, In press). Dispersion may help decrease the rate of cannibalism, as the schools of adult anchovies orient preferentially to concentrations of food. However, anchovy larvae are susceptible to cannibalism for many weeks. The one measurable anchovy larva encountered by Hunter and Kimbrell (In press) was 17 mm, which corresponds to a likely age of over 30 days based on the growth curve given by Hunter (1976). If the average daily coefficient of mortality due to cannibalism were as low as 0.02, its action over 30 days would account for enough additional density dependent mortality to reach or exceed the "reference" level of 1.

The only comparable observations (i.e. quantified and taken during the spawning season) for the Peruvian anchoveta are reported by Rojas and Ochoa (1973). Rojas and Ochoa did not encounter anchovy larvae in the anchoveta stomachs, but did encounter 235 anchoveta eggs in 95 stomachs taken at four stations (I have omitted their station 52 in which the stomachs were nearly empty). The average stomach therefore contained 2.5 anchoveta eggs, or about one-half that observed by Hunter and Kimbrell. Rojas and Ochoa hypothesized a minimum feeding rate of three times per day, which is considerably less than Hunter and Kimbrell's gut evacuation rate would suggest. However, Rojas and Ochoa also indicated that phytoplankton may be digested more rapidly than zooplankton, and feeding rates could be generally higher for phytoplankton. Because *Engraulis* eggs are of a size that is usually consumed by filter-feeding (O'Connell, 1972; Hunter and Kimbrell, in press), we may expect higher rates of cannibalism when adults are filter-feeding upon phytoplankton. Because no egg production rate estimates are available for the Peruvian anchoveta, no firm conclusions can be drawn from Rojas and Ochoa (1973).

MODELS OF CANNIBALISM

Effective rates of cannibalism are undoubtedly influenced by a wide variety of factors, such as adult size, distribution and behaviour, adult and larval food quality and concentration, and abiotic factors such as mixing and temperature. It would be premature to attempt to treat all of the possible factors in a cannibalism model, given our present limited knowledge. Rather we may gain an indication of the nature, direction, and perhaps magnitude of these influences based on very simple models. These simple models may also provide some insight as to appropriate management of cannibalistic planktivores.

Hunter and Kimbrell (In press) argued that a random filtering model could not describe the apparent consumption rate of eggs. Under simple assumptions of habitat volume and egg density, they found that an anchovy would have to randomly filter from 17 to 25 h/day, which they interpreted as indicating non-random, selective feeding behaviour. This does not mean that we should not begin a modelling effort with a random filtering model. Contrary to Hunter and Kimbrell, a random filtering model may be sufficient to approximate the effects of cannibalism as a regulatory mechanism. It would certainly form a reasonable point of departure for construction of cannibalism models based on non-random filtering behaviour.

The following models assume the time of year to be the spawning season. Many stochastic considerations will be omitted so as to limit the scope of the discussion to the fundamental framework. Initially, the models will consider only local dynamics. A more integrative view is presented in the discussion following development of the models.

Random filtering model for eggs

A cohort of eggs will be subject to mortality from cannibalism, with rate coefficient F_c, and to the rest of natural mortality, including predation and starvation, with rate coefficient M, as in Equation (2). The rate of cannibalism is given by

$$F_c = Nvp/V \qquad (4)$$

where N is number of adult fish (cannibals)
   v is average volume of water filtered per fish per unit time
   p is fraction of time spent filtering, including fraction of habitat occupied by eggs,
and V is habitat volume

The egg mortality rate is therefore given by

$$dE/dt = -E(M + F_c)$$

or

$$dE/dt = -E(M + Nvp/V) \qquad (5)$$

Upon integration we obtain the number of eggs (E_h) surviving the period in the egg stage (t_e), i.e. the number of eggs that hatch.

$$E_h = E_o e^{-(M + Nvp/V)t_e} \qquad (6)$$

The initial abundance of eggs (E_0) is the product of the number of fish and the average individual fecundity (f), including males and prespawners. This gives

$$E_h = fNe^{-(M + Nvp/V)t}e \tag{7}$$

This equation has the form of a Ricker curve (Equation 1)

where
$$a = fe^{-Mt}e$$

$$b = vpt_e/V$$

and number of eggs hatching is analogous to recruitment.

In modelling the events influencing the abundance and survival of pelagic fish larvae, initial conditions must include the number of eggs effectively hatched into the larval environment, which will be called "effective fecundity". Effective fecundity (E_h) can be divided into pre-spawning and post-spawning components. "Virtual fecundity" is the number of eggs released into the environment, and as Tsukayama and Alvarez (this volume) have shown, this component can be a compensatory function of population size, i.e. $E_0 = f(N)N$. The second component involves the subsequent survival of spawning products. Natural mortality and cannibalism will reduce the number of eggs which actually hatch to produce larvae. Again, cannibalism clearly leads to compensatory changes in effective fecundity as a function of population size or density.

As stated previously, the Ricker curve has a maximum when the density dependent exponent is equal to unity. Thus effective fecundity will be maximal when

$$Nvpt_e/V = 1$$

or

$$Nvpt_e = V \tag{8}$$

That is, effective fecundity is maximal when the local population filters a volume of water equivalent to the habitat volume exactly once during the length of time it takes the eggs to hatch. Note that the location of the maximum is independent of natural mortality, although the value of the maximum is not.

Note that intensity of cannibalism is associated with fish density (N/V) rather than abundance alone. The density of fish which maximizes effective fecundity according to this model can be compared with actual fish densities. This provides an independent test of whether cannibalism is likely to be an important factor in population regulation. Johannesson and Vilchez (this volume) give most of the information necessary to perform the calculations. They base their biomass estimates on anchoveta averaging 6.7 g. Leong and O'Connell (1969) estimate that an *E. mordax* of this size would filter 1.64 l/min, and I will assume that this is valid for *E. ringens* as well. If time to hatching is 2.5 days, each fish would be capable of filtering 5900 l in this period. One metric ton would contain 150 000 fish, so one ton could filter 0.88×10^9 l in 2.5 days. Johannesson and Vilchez report that most of the biomass was detected in the upper 40 m of the water column. One square nautical mile at this depth would contain 1.37×10^{11} l. If filtering were random and continuous over the entire 2.5-day period (p = 1.0), maximum effective fecundity would correspond to a density of 156 tons/mile^2. Johannesson and Vilchez found average anchoveta densities of 600 or more tons/mile^2 in the years 1973, 1976 and 1978. Local densities reached much higher levels, occasionally exceeding 2000 tons/mile^2. Even if p is small, cannibalism is likely to have a significant effect on the proportion of anchoveta eggs being hatched.

Recruitment model

As was discussed previously, cannibalism continues for at least one month following hatching, although the rate may be lower. Whereas the anchovy feeds on eggs by filter feeding, larvae are of a size which is captured by biting (Leong and O'Connell, 1969; O'Connell, 1972; Hunter and Kimbrell, in press). The ratio of biting to filtering activity varied with the relative abundance of large and small food particles. O'Connell (1972) estimated that the ratio of particle sizes in southern California waters suggested that biting activity could exceed 50% of the total feeding activity. While individual fish did not tend to alternate feeding modes when faced with a mixture of particle sizes, fish at the front of the school showed more biting activity, while fish at the rear of the school showed more filtering activity. Although it may be attractive to model biting and filter feeding as mutually exclusive events (the time spent consuming larvae cannot be spent consuming eggs, and vice-versa), a more practical approach is to assume that a school consumes all eggs and larvae in its path. Either approach requires more knowledge of school sizes and behaviour than is presently available.

If a model incorporating cannibalism on larvae were to be constructed, it would be analogous to the egg model (Equation 7). Larval life may be divided up into three periods: t_e is the length of the egg period, t_1 is the length during which larvae are subject to cannibalism, and t_r is remaining time to recruitment. Each period has a natural mortality coefficient, M_e, M_1 and M_r respectively. The model would now give expected recruitment (R) as a function of population size and density:

$$R = fNe^{-(M_e t_e + M_1 t_1 + M_r t_r)} e^{-pn(vt_e + ct_1)/V} \tag{9}$$

where c is rate of cannibalism on larvae. Recruitment will be maximized when

$$Np(vt_e + ct_1) = V \tag{10}$$

This is analogous to Equation (8), and may be interpreted similarly. If the appropriate unit of cannibalistic activity is the school rather than the individual fish, then recruitment will be maximal when a volume of water equivalent to the habitat volume is swept once by the schools over the period from spawning to end of vulnerability ($t_e + t_1$), assuming p=1. If the speed and average cross-sectional area of schools were known, it would be possible to attempt calculations similar to those for eggs.

Evaluation of terms

The recruitment model (Equation 9) contains three terms bearing on recruitment strength: fecundity, density independent mortality, and density dependent mortality. These terms are clearer if we transform the equation by taking logarithms:

$$\log_e(R/N) = \log_e f - \Sigma M_i t_i - (vt_e + ct_1)pN/V \tag{11}$$

Here the coefficient of density independent mortality has been generalized to $\Sigma M_i t_i$, where an arbitrary large number of stages replace the three simplified stages in Equation 9.

Relative roles of the three terms in determining recruitment can be evaluated by considering probable values in Equation (11). Hunter and Goldberg (1979) estimate the batch fecundity of female *E. mordax* to be 389 eggs/g. If half the fish are female and they average 17 g, the average batch fecundity is 3 300 egg/fish per spawning batch. If females spawn once every 6-8 days during the spawning season (ibid), perhaps 15 batches are spawned, giving a total fecundity of 50 000 egg/fish for the year. Thus $\log_e$ is approximately 11. The pre-

vious discussion of density dependent mortality indicates that we should expect this coefficient to be approximately 1. For a short-lived fish such as *Engraulis*, the adult natural mortality rate commonly exceeds 50% annually. At 50%, the replacement level of recruitment is equal to the spawning stock, so $\log_e (R/N) \approx 0$. The only remaining value is $\Sigma M_i t_i$ for which there is no direct measure; however, it must be approximately 10 for Equation (11) to balance.

These values indicate that the ratio of density independent to density dependent factors (neglecting density dependent effects on fecundity) is 10 to 1. The preponderance of density independent influences tends to mask the relatively weak regulation of stock abundance. This is consistent with the large variability characteristic of clupeid and engraulid stocks. The large contribution of density independent variability does not allow the population to equilibrate at a stable level. Rather, equilibrium takes the form of a probability distribution of abundances centred about a mean value (see MacCall 1980, Sharp this volume). A production or equilibrium yield curve may be derived, but it should be used with caution: it must be interpreted in a probabilistic rather than deterministic sense.

Equation (11) also provides a framework for consideration of variability in recruitment. For a given population size, fecundity and density dependent mortality have fixed average values, with variability being dependent on environmental conditions. The probability distribution associated with the density independent term will tend to characterize recruitment at all population sizes. A variation in any $M_i t_i$ will have an equivalent effect on recruitment independently of the stage (i) in which it occurs. The final convolution of the probability distributions of $M_i t_i$ for all i may be complicated. For example covariance is possible, as in the case where the high density of esculent particles required for successful first feeding will tend to increase the probability of subsequent successful feeding and survival.

Alternatively, it may be possible to define a number of stages for which the probability distributions of $M_i t_i$ are independent. The sum of several such random variates ($\Sigma M_i t_i$) may approach a normal probability distribution according to the Central Limit Theorem. If variability in density independent mortality dominates overall variability, we would expect $\log_e (R/N)$ to approach a normal distribution. Recruitment itself would tend to be distributed log-normally about its expected value for a given stock size. There is little direct evidence to demonstrate the true probability distribution of recruitment; indeed, the proper regression function is seldom clear. Use of log-log transformation often yields a constant variance of recruitment over a wide range of stock sizes, giving some support to the hypothesis of log-normality.

DISCUSSION

These models employ parameterizations which simplify complicated conditions and processes. The following discussions are centred on various types of considerations and their associated parameters.

Effects of fish size

Whereas fish size has not explicitly appeared in these models, several parameters can conveniently be expressed as power functions of fish weight or length. Leong and O'Connell (1969) estimated that the volume of water filtered by *E. mordax* per unit time increases approximately as the square root of fish weight. Hunter and Macewicz (1980) have estimated that batch fecundity increases as the 1.6 power of ovary-free female weight of *E. mordax*. Collins (1969) fitted allometric weight-length curves for *E. mordax*, obtaining exponents very near 3.0 for anchovies from southern California, but exponents were smaller (2.7 to 2.8) for fish from central California. If we standardize these variables to length of southern California anchovies, weight increases as the 3.0 power, filtration volume increases as the 1.5 power, and fecundity increases as the 4.8 power.

These relationships allow the model to be expressed in terms of biomass rather than numbers of fish. Biomass (B) is given by number of fish multiplied by their average weight (w), so $N = Bw^{-1}$. For example, the above filtration volume relationship can be substituted in Equation (8) to give maximum effective fecundity as a function of fish weight and biomass:

$$B/V = \sqrt{w}/apt_e \qquad (12)$$

where a is a constant of proportionality in the filtration volume relationship. This indicates that optimum density of biomass is proportional to the square root of the average fish weight, or the 1.5 power of average fish length. In other words, if anchovies are physically large, a larger equilibrium biomass would be expected than if they are physically small. As corollary, insofar as a fishery reduces the average age, and therefore the average size, the optimum density of the resource itself may be diminished. This argument holds only for the filter feeding mode of cannibalism (eggs). Leong and O'Connell (1969) estimated that particulate feeding rate increased as the 1.1 power of anchovy weight. This relationship is more appropriate to cannibalism of larvae, and the analog of equation (12) would indicate that the relationship is nearly independent of fish size.

Habitat volume and fish density

The preceding models have been restricted to local effects. The overall stock-recruitment relationship is an integrative average over extensive geographic and temporal variability. Neither the population (density dependent effects) nor environmental conditions (density independent effects) are uniformly distributed. While effective fecundity and production of larvae is likely to conform to a Ricker curve for a local area, the overall stock-recruitment relationship will be different. Ricker (1975, p. 294) states that nonuniformity of spawner distribution is likely to result in a flatter dome and more gently inclined descending limb than the simple Ricker curve would indicate. Johannesson and Vilchez (this volume) clearly show the extent of this nonuniformity: "estimates derived from the 7302 cruise data showed that 55% of stock biomass was concentrated in only 13% of the total area of distribution. Likewise, during the cruise 7603, 36% of the biomass fell within only 3.4% of the total area." It may be worthwhile to undertake a simulation study to examine possible shapes of stock-recruitment curves arising from observed patterns of stock distribution.

Habitat volume is essentially composed of three dimensions: alongshore, inshore-offshore, and vertical depth. The first two can be combined as a geographic area inhabited by the stock. Engraulid and clupeid fishes often show a characteristic pattern of changes in distribution with changes in population size. Murphy (1977) states "all or nearly all of the (clupeoid) stocks contract their feeding and spawning range as the population is reduced". Specific examples of this pattern are given by Smith (1972) for *E. mordax*, and Santander (this volume) for *E. ringens*.

The relationship of this pattern to reproduction may be elucidated by the following model. Consider a set of n discrete parcels of water V_i, i = 1...n. The first parcel corresponds to the centre of population distribution, and subsequent parcels are at progressive distances from the centre. I assume that density independent mortality is least (i.e. conditions are most favourable for larvae) at the centre, and that conditions are progressively less favourable at greater distances from the centre. Within each parcel the stock-recruitment relationship is a Ricker curve (Equation 1), and each parcel has a density independent survival rate a_i which decreases in value as i increases ($a_i > a_{i+1}$). The total population ($N_{tot} = \Sigma N_i$) is distributed among the parcels, and each parcel has a coefficient of fish concentration $c_i = N_i/N_{tot}$. Coefficients of concentration are estimated from the distribution of population among the parcels.

Given the above model, I wish to estimate the vector of coefficients of concentration which will maximize recruitment for the entire stock, and to examine how this vector changes with population size. Without actually solving the equations, I will offer a heuristic argument that this model generates distribution patterns similar to those observed for clupeoids. At very low population sizes, most of the population will be in the first parcel, where reproduction will be the most successful. As the population size increases, density dependent mortality will reduce the per capita recruitment rate in the first parcel until combined mortality rates in the first parcel are equal to the density independent mortality rate in the second parcel. At this point the population will begin expanding into the second parcel. Each successive parcel will be similarly occupied. At each level of N_{tot} the vector of c_i will be such that the sum of density dependent and density independent mortality rates (i.e. the total mortality rate) will be the same for all parcels. Under this condition there is no reproductive advantage in migrating to another parcel. There should be some level of N_{tot} which maximizes total recruitment. Above this population size maximum recuitment would be obtained by shunting the excess spawners to the least favourable area (increasing c_n) but this will not happen as long as fish individually attempt to maximize their own reproduction.

As a result of this pattern of distribution, average fish density increases relatively more slowly than total population size. This suggests that clupeoid stock-recruitment relationships may be better described by a generalized Ricker curve such as

$$R = aNe^{-bN^c} \tag{13}$$

where $0 < c < 1$. When c = 1, a Ricker curve results. As c becomes smaller, the ascending limb becomes steeper, and the peak becomes broader with a progressively shallower descending limb. Csirke's (1980) stock-recruitment model is nearly equivalent to equation (13). Catch per unit effort (C/f) for pelagic fishes may commonly behave as a power function of stock abundance,

$$C/f = aN^\beta \tag{14}$$

where $\beta < 1$ (MacCall, 1976; Ulltang, 1976; Gulland, 1977). Thus Csirke assumes that β is a useful approximation of c in equation (13). It should also be noted that MSY will be overestimated if stock-recruitment data are fit by a Ricker curve (c = 1) when the actual relationship is characterized by c < 1. This is because the latter curve has a less pronounced peak.

I have hypothesized that habitat volume changes with population size in order to maximize individual reproduction. The mechanisms by which habitat volume changes are not known. One likely possibility is a tendency for adults to follow gradients of increasing food concentration. Without specifying any actual processes, it is safe to say that population expansion and contraction may occur by partially different mechanisms. For example, random diffusion will increase the range of fish as age increases. There is considerable evidence that older anchovies are distributed more widely than young anchovies in southern California (Mais, 1974). Larval drift patterns may result in some areas receiving more recruits than others, resulting in a tendency to contract toward these areas. If there are different mechanisms for expansion and contraction, and if the balance of effects determines the stock distribution, then habitat volume for the same total population size is likely to be characteristically different for increasing and decreasing trends in abundance. Thus, we may expect to see a "hysteresis" in the trajectory of population sizes over a cycle of decrease and increase. The concept of a single underlying stock-recruitment curve may be inappropriate.

Another consequence of the above geographic model is that the apparent overall stock-recruitment curve varies with the pattern of fishery removals. Segments of the population residing in the central "most favourable" areas will be reproducing closer to the peak or on the descending limb of their local stock-recruitment curves, while peripheral segments will be reproducing on the ascending limb of their stock-recruitment relationships. This indicates that fishery removals from the periphery may reduce recruitment proportionally to the fishery harvest, while removals from the centre may have little effect or may even increase recruitment. The most productive pattern of fishing should be to fish central areas of high density, and to discourage fishing at the edges of the population. Dispersion and migration of the fish will tend to reduce the relative benefit of this geographic fishing strategy.

The preceding discussion has not addressed the aspect of depth as a determinant of habitat volume. Over much of the range of the Peruvian anchoveta, maximum habitable depth is determined by low oxygen concentration. Limiting concentrations of oxygen may be as shallow as 10 to 20 m in inshore areas off northern Peru (see Richman and Smith, in press). The depth and intensity of oxygen depletion is a function of the rate at which organic material falls out of the overlying water. By consuming large amounts of primary and secondary production in the surface waters, the anchoveta may reduce the rate of detrital fallout, thereby depressing the depth of limiting oxygen concentration. Thus, within a given geographic area, increasing density of anchoveta may result in increased habitat volume, and increased reproductive rate due to decreased intensity of cannibalism.

Effects of food and feeding behaviour

Intensity of cannibalism is closely linked to the feeding behaviour of adults. The following discussion examines this relationship from three standpoints: responses to food abundance and to food composition, and non-random feeding behaviour. These considerations affect the value of parameter p, the effective time spent feeding.

Clearly, the amount of time spent feeding will decrease as food abundance increases (O'Connell 1972). The relationship between these two variables is poorly known because of our lack of knowledge of digestion patterns. Hunter and Kimbrell (In press) assumed a constant rate of gut evacuation, but their data appear to support the existence of an initial period of reduced gut evacuation, perhaps lasting 1 hour. Such a delay would increase the average residence time from 1.4 hours to 2.4 hours, decreasing estimates of total consumption by 40%. Rather than a continuous feeding model, Rojas and Ochoa (1973) appear to support a batch-feeding model. Until gut evacuation patterns are better known, it is difficult to compare gut contents with concentration of food in the environment in order to estimate volume of water swept or length of time spent feeding.

Bakun and Parrish (this volume) have compared oceanographic characteristics of the Peru and California currents with respect to larval habitat. Their discussion indicates that Peruvian conditions are favourable to formation of microlayers of larval food (see Lasker, 1978) because the ratio of wind mixing to upwelling decreases toward the equator. To this I would add that the high densities of food may result in less water being swept during feeding, and a lower *per capita* rate of cannibalism (b in Equation 1), so the peak of the Ricker curve occurs at a higher density of anchoveta than for the northern anchovy off California. Also, because food density may vary on a local scale, it may be appropriate to modify the geographic model presented earlier so that coefficients of density dependence (bᵢ) also vary among water parcels.

El Niño conditions may pose a compounded problem for the anchoveta. Not only may the density of spawners be high due to crowding into areas of upwelling (i.e. N/V is high), but if food abundance is low, the fish will spend more than a usual proportion of their time feeding (p is high). This combination may result in greatly reduced recruitment due to intense cannibalism. It may be appropriate to harvest these El Niño-induced inshore concentrations of anchoveta in order to increase recruitment. However, if density independent mortality of larvae is high, it may be more appropriate to maximize adult survival to the following year.

Adult *E. mordax* will feed either by biting or filtering depending on the size of food particles and their relative abundance (O'Connell, 1972). Thus eggs will tend to be cannibalized in the presence of phytoplankton, which is filtered, and larvae will tend to be cannibalized when in the presence of adult zooplankton, which is bitten. Rojas and Ochoa (1973) suggest that digestive rates may be higher for phytoplankton than for zooplankton, in which case the fraction of time spent feeding (p) would be higher in the presence of phytoplankton.

For the purposes of the following discussion, random feeding implies that feeding activity is independent of the abundance of eggs or larvae in the water. Hunter and Kimbrell may have prematurely dismissed the utility of simple random filtering models. They argue that the assumption of random filtering necessitated an unrealistically large proportion of time be spent to give the rate of egg cannibalism that they observed. However, if the mean residence time of eggs in the anchovy gut is 2.4 hours rather than 1.4 hours (see above), estimated daily consumption, and accordingly estimated fraction of time spent filtering (17h) would decrease by 40% (10h). Hunter and Kimbrell's second argument was based on their estimate that 17% of daily egg production was consumed by cannibalism. If we substitute the values of F_c derived earlier in this paper (0.108 to 0.153), which are more appropriate to the calculation, the length of time spent filtering will drop by 10% to 36% from the 25 hours they estimated. These lengths of time spent filtering (10 to 22 h/day) are consistent with O'Connell's (1972) calculations of the length of time necessary to obtain a daily food ration by filtering in areas of food abundance off southern California.

Non-random feeding behaviour is more strongly indicated by Hunter and Kimbrell's comparison of mean number of eggs per stomach and egg density in the same area as determined by towed plankton nets. Consumption of eggs increases as the 1.6 power of egg abundance, although the true functional shape of the relationship is unclear. It seems reasonable to hypothesize that at low egg concentrations consumption by filter feeding is incidental, whereas at higher concentrations eggs may contribute to the stimuli which elicit filter feeding.

Non-random feeding is more likely as food patchiness increases. Lloyd's (1967) "mean crowding" is a measure of the density of individuals within a patch and is therefore closely related to the stimuli eliciting feeding by adult anchovies (Leong and O'Connell, 1969; O'Connell, 1972). Mean crowding decreases as overall population density decreases, while patchiness (Lloyd, 1967) is a measure of mean crowding relative to mean density. Hewitt (in press) has examined these aspects of the spatial pattern of $E.$ $mordax$ larvae, and has shown that Lloyd's patchiness decreases from 10 to 8 during the first three days following hatching. From spawning to a corresponding total age of six days, numerical abundance decreases by about 75% (M_e = 0.4, M_1 = 0.1, t_e = 2.5). Assuming that the patchiness of eggs is the same as newly hatched larvae, the combined result is an approximately 80% decrease in mean crowding over the first six days of life. Thus, any potential tendency for concentrations of eggs or larvae to elicit a feeding response by adults should diminish rapidly with time. Correspondingly, random feeding models of cannibalism may provide sufficiently good approximations that non-randomness can be ignored or can be parameterized by an increase in the proportion of time spent feeding (p).

SUMMARY AND CONCLUSIONS

Major points discussed in this paper were:

1)   The Ricker curve often has been used to describe clupeoid stock-recruitment relationships, but quantitative justification has been lacking.

2)   Cannibalism is an important regulatory mechanism if $F_c t \geq 1$, where F_c is the coefficient of cannibalistic mortality and t is the length of time eggs and larvae are subject to cannibalism.

3)   Quantitative information on stomach contents and spawning rates of *E. mordax* indicate that $F_c t$ is in the range of 0.27 to 0.38 for anchovy eggs.   Further cannibalism on larvae may be of reduced intensity, but the total effect indicates that cannibalism is sufficiently intense to be a regulatory mechanism.

4)   Cannibalism on eggs is represented by a random filtering model.   The rate of cannibalism is proportional to adult abundance and is inversely proportional to habitat volume: stock density rather than stock size is the important consideration.

5)   Acoustic surveys of Peruvian anchoveta have shown densities sufficiently high that cannibalism is likely to have had a significant effect on net egg production.

6)   Rates of cannibalism on larvae are not known.   A complete stock-recruitment model cannot yet be calibrated with respect to cannibalism.

7)   Evaluation of terms in a complete stock-recruitment model for *E. mordax* indicates that total coefficients of density independent and density dependent mortality are approximately 10 and 1 respectively.   The preponderance of density independent influences tends to mask the relatively weak regulation of stock abundance.   Clupeoid stock-recruitment and production curves must be interpreted in a probabilistic rather than a deterministic sense.

8)   If the intensity of density independent mortality is a random variable, and is independent for several different life stages, recruitment may tend to be distributed lognormally about its expected value.

9)   Biomass density giving maximum net egg production is proportional to the square root of average adult fish weight.

10)   The rate of cannibalism on larvae, for a given level of biomass, is nearly independent of average adult fish size.

11)   Because clupeoids expand and contract their ranges with changes in abundance, adult fish density is not proportional to stock size.   The standard Ricker model is not appropriate;   a generalized Ricker model such as $R = aN \, EXP(-bN^c)$ is more realistic, where $0 < c < 1$.   The standard Ricker model ($c=1$) will overestimate the maximum sustainable yield from clupeoid stocks.

12)   Contraction and expansion of range with changes in total abundance is predicted by a geographic model wherein spawners cannibalize their young, density independent survival of young decreases toward the periphery of the range, and spawners distribute themselves so as to maximize individual reproduction.   As adult density in the most favourable area increases, cannibalism causes the total larval mortality rate to increase until peripheral, poorer areas become equally attractive spawning locations.

13) The optimal distribution of spawners results is a constant total mortality rate of offspring throughout the inhabited range. This mortality rate is equal to the density independent mortality rate at the edge of the range.

14) This geographic model suggests that harvests taken from the center of the range will have a smaller impact on abundance than harvests taken from the periphery of the range.

15) If Peruvian anchoveta consume sufficient production to decrease the rate of detrital fallout, it may cause a deepening of the level of limiting oxygen concentration. A larger anchoveta stock may thereby increase its own habitat volume, and in turn increase its own reproductive potential.

16) Rates of cannibalism are likely to depend on the size and abundance of adult food organisms. The *per capita* rate of cannibalism may be lower for *E. ringens* than for *E. mordax* because the high density of food off Peru may result in less time being spent feeding.

Cannibalism is one of the important mechanisms tending to regulate the highly variable abundance of clupeoids such as *Engraulis*. An initial framework was constructed which allows integration of life history information, physiology, behaviour, and quantitative ecology into a theory of clupeoid population dynamics. Further work can proceed in many directions; perhaps the most important is to incorporate environmental variability in order to fully describe the volatility of clupeoid populations. Finally, a number of speculations and hypotheses have been presented. Some of these may be tested in the field or laboratory.

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