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FROM EGG SURVEYS TO ECOSYSTEM MODELS: BIOLOGICAL ASSUMPTIONS IN FISHERIES MANAGEMENT

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ABSTRACT

The biological assumptions associated with fishery management are discussed within the framework of three problems of increasing complexity. The first is the use of egg or larval surveys to estimate spawning biomass and the associated questions about modelling aggregation. The second is management of krill in the Antarctic and the relationship between catch per unit effort and stock abundance. The importance of behavioral models in fishery management is discussed. The third topic is the management of multiple pelagic species in California coastal waters and the need for the development of community ecology models for the California Current.

Introduction

The title of this section, "Critique of assumptions in biological analysis", suggests consideration of the effect of assumptions about the biology of the organism on the success of management . A fishery is a complex bio-socio-economic system involving at least the following components: the fish stock itself, a fishing fleet, processors, consumers, managers and research biologists. It is thus difficult to separate "biological" assumptions from a mix of assumptions that are analytical, economic, sociological and political. To begin, then, we could ask why there is even a need for a discussion of biological assumptions. Virtually all fisheries across the world are managed in some way, and the list of management failures certainly exceeds the list of management successes. In most of this paper, I will deal with explicit assumptions about the role of biology in fisheries management. Even so, it is worthwhile to begin by considering some implicit assumptions. Examples of such implicit assumptions, and alternate assumptions, are the following:

- Effort determines catch. *Alternate assumption*: Over the short term, catch or catch per unit effort (CPUE) in a particular period determines effort in the next period.

- Catch per unit effort is proportional to stock level. *Alternate assumptions*: i) CPUE has little or nothing to do with stock level or ii) CPUE is a nonlinear function of stock level.

- The migratory nature of fish is important for management purposes and thus requires international management of fishery resources. *Alternate assumption*: In most cases, we can ignore the migratory nature of fish when developing management plans.

- A thorough understanding of the sources of year to year fluctuations in stock abundance levels will lead to improved management. *Alternate assumption*: We can do just as well with a good stock assessment early in the season and a target escapement.

- Biology and economics are all that is needed for successful management. *Alternate assumption*: Physical oceanographic factors are most important in fishery management.

The intent of this list is to provoke the reader: the alternate assumptions may be no better than the ones usually used, but it is important to recognize at least what the assumptions are and to try to understand why they are used and what the implications are.

Most of the this paper will be concerned with a discussion of the role of models of the biology of the system under consideration. Although the models that are discussed in this paper are mainly mathematical ones, it is usually true that as soon as management of a fishery is attempted, a model is implicitly present. The model may be qualitative -- and it may even be only in the manager's head -- but it is still a model. Part of the role of analysis in such a situation is to characterize the model using quantitative methods, so that the basis of the model can be understood. The questions then become: how important is the biological basis of this model, how valid are the assumptions of this model, what kind of management can be done in light of limited biological knowledge, and how important is good biological knowledge for management? In the literature associated with pest management problems, there has been recent discussion about the need for ecological understanding --

see, for example, Barfield and O'Neil (1984) whose paper is entitled "Is an ecological understanding a prerequisite for pest management?". One of the purposes of a workshop such as this one is the development of similar discussion for fisheries management.

In this paper, three examples from the specific to the general are chosen for discussion and analysis. The first example is that of egg or larval surveys used for management purposes. In this case, the question is how one models the aggregation or contagion of the eggs or larvae and how important is the choice of a particular model for the analysis of the management question. The second example is management of krill in the Antarctic. This is a "predator-prey" system at many trophic levels and has received considerable attention in the past (e.g., May *et al.* 1979). Here, I stress the importance of behavioral modelling for management. The third example is a discussion of management in the California current ecosystem. The question that I address here is the need for and the possibility of a model of the entire ecosystem (see Riffenburgh 1969).

The approach taken here is an "operational" one, in the sense that the purpose of modelling for management is to aid in management decisions, in contrast to modelling for general intuitive understanding, biological understanding, or modelling for the study of complex mathematical phenomena (although each of these is a valid activity, and typically a lot of fun). With the operational approach, assessment of the biological assumptions is connected closely with how well one can do the job. That is, the value of a biological assumption must be judged in terms of how well the appropriate management problem is handled using this assumption.

Egg Surveys

The problems discussed in this section are connected to the "management" of Pacific sardine (*Sardinops sagax*) in California waters. "Management" is in quotation marks because at the current time (early 1987) there is hardly any directed fishery (1000 ton limit) for sardine. Yet, the sardines were once a major fishery species, and the role of management is to restrict fishing until the sardine population recovers from its current level of somewhere between 10,000 and 25,000 tons to levels commensurate with opening serious directed fisheries on sardines .

The Pacific sardine population has declined from an estimated level of 2 to 5 million tonnes adult spawning biomass (in the early part of this century) to less than 10,000 tonnes adult spawning biomass (in the 1960's) -- for more details see Smith (1978) or Wolf and Smith (1985). Current California law, enacted in 1974, prohibits a fishery if the biomass is below 20,000 tons, allows a fishery with a quota of 5% of the spawning biomass if the biomass exceeds 20,000 tons, and mandates that in each year the Department of Fish and Game shall determine whether this critical biomass level has been reached (see Wolf and Smith, 1985, 1986 for more details). This situation is atypical in fishery management. Usually the problem facing by managers and analysts is to

demonstrate that a problem exists or will occur unless action is taken. In the case of California sardine, the problem is already well recognized and the management question is when can action be taken? For the time being, at least, the management objective is thus relatively simple: to determine whether or not the spawning biomass exceeds 20,000 tons; and if it does, to recommend a quota for the fishery. This situation also highlights the issue of the transfer of scientific information from the scientist or analyst to the manager. The law mandates the critical level (20,000 tons) and the quota (5%), but these values are determined -- at least in principle -- by scientific analysis. It is often assumed that the flow of information from scientists to managers is smooth and essentially perfect, but this need not be the case, especially in economically valuable situations. Continued analysis of the methods of the transfer of information between scientists and managers in a fisheries is warranted.

The determination of the relatively low level of spawning biomass of sardine is not an easy task because of the pelagic nature of the fish -- the potential habitat occupies a considerable area. There are few methods that can be used to directly census the spawning population with any level of accuracy. The scientists assigned the assessment problem thus chose to use egg surveys as a means of estimating the size of the spawning biomass (see Lasker 1981, 1985 or Smith and Richardson 1977 for general information on egg surveys of pelagic fish stocks). Sardine eggs have, in fact, been studied for many years (e.g. Sette and Ahlstrom 1948 or Taft 1960), and as early as 1955 egg data and fecundity estimates were used to estimate spawning stock size (see Taft 1960 for a discussion).

One way of determining spawning biomass from egg surveys would be the development of an "egg simulator". The coastal region near California would be divided into cells and we would let **B**(i,t;y) denote the spawning biomass in the i^{th} cell at the start of week t in year y. We would then need to include assumptions about: i) spawning behavior (e.g. what fraction of the spawning biomass produce eggs each week), ii) stock motion, iii) stock fecundity, iv) year-to-year dynamics of adult biomass. This model would then be used to detemine a spatial distribution of eggs; superimposed on this spatial distribution would be an egg sampling scheme. We would use the simulation to determine the relationship between eggs encountered and spawning biomass. The difficulty with such an approach is that we must make many assumptions in order to get the simulation working. Parameters would have to be estimated, and some major features (e.g. characteristics of motion) are known to be very poorly modelled. Parsimony is an excellent property of models, and this one doesn't have it. The discussion, however, does highlight that egg survey methods will always have many stated and unstated biological assumptions. This is not necessarily bad, but it indicates the difficulties whenever we attempt to infer backwards from fertilization success in a small region to spawning biomass.

The *egg production method* (EPM) estimates spawning biomass by the following equation (Hewitt, Bindman and Lo 1984, Wolf and Smith 1985, 1986):

$$B = PAkW / RFS \qquad [1]$$

where **B** is the estimate of spawning biomass, **P** is the daily egg production per unit area of sea surface, **A** is the area of the survey, **W** is the average weight of mature females, **R** is the fraction of the females in the population, **F** is the fecundity measured by the number of eggs per batch, **S** is the fraction of females spawning per day and **k** is a conversion factor. (The units of these quantities are, for the purposes of this discussion, not important.)

In order to answer the management question put to them, Wolf and Smith (1985, 1986) have turned equation (1) around, using the following reasoning: We wish to know whether or not the spawning biomass exceeds a critical level B_c. Associated with this critical level is a certain critical area occupied by the spawning biomass. This area is obtained by solving equation [1] for **A**:

$$A_c = B_c RFS / PkW \qquad [2]$$

The following argument is then made: if eggs are found in an area exceeding A_c, then the spawning biomass is assumed to exceed B_c.

In the actual survey operation, CalCOFI (California Cooperative Oceanic Fisheries Investigations) sites are sampled at an intrasite distance of 4 n mi off shore and 10 n mi along shore; so that each site is assumed to represent 40 n mi^2. The sampler used at the sites has an area of .05 m^2, so that samples taken at different sites are assumed to be completely independent. If in the survey, **S** sites were observed to have eggs at them, then when using the *inverse egg production method* (IEPM), we associate an area 40S n mi^2 with the spawning biomass. If 40S exceeds the critical area, then we assume that the spawning biomass exceeds the critical level.

Let us examine some of the assumptions in this model. The IEPM is based on the premise that we are taking a "snapshot" of the population during the survey; hence the linear relationship between biomass and egg production is used. The implicit assumption of the IEPM is that we can use a distribution over space at one time to back calculate spawning biomass. There are five parameters that enter into the determination of the critical area (other than the critical biomass -- which is a legislated parameter, based on the transfer of scientific information to lawmakers). These are average female weight, batch fecundity, sex ratio, egg production and fraction of females spawning. Wolf and Smith (1985) indicate fair confidence in values of average female weight (120 gms), sex ratio (0.5) and batch fecundity (32,000 eggs/female/batch). Less certain are the values of egg production and spawning fraction. They quote CalCOFI surveys from 1951-1959 and more recent work by R. Hewitt that give a range of egg production of 1.5 to 5.0 eggs/.05 m^2/day. (Also see

Lo, 1984 for more information about anchovy egg production.) Spawning fractions for other species are given by Wolf and Smith as ranging from .02 to about .15 females/day. Wolf and Smith thus report a range of values of the critical area, determined mainly by the combination of egg production (high - 5.0 eggs or low - 1.5 eggs/0.5 m^2/day) and the fraction of females spawning (they used .02, .05, .10, and .15). The range of critical area turns out to be 141 n mi^2 to 3528 n mi^2; the arithmetic average of these values is about 1200 n mi^2. Wolf and Smith (1985, 1986) use the value A_c = 500 n mi^2 in analyzing the results of an egg survey cruise in 1985 and making management recommendations. Thus, they implicitly assumed that certain values of egg production and spawning fraction were more likely than other values. Other biological assumptions that enter their analysis are the independence of fecundity and spawning biomass and the independence of spawning fraction and spawning biomass. These assumptions are made, presumably, because of inability to collect data that could lead to any quantifiable relationships. The most variable of the parameters that enters into the IEPM computations is the estimate of the rate of egg production. The reason for the great variability is that eggs are spawned in extremely dense patches, which are slowly dispersed by oceanic turbulence. The estimate of egg production rate is then determined by back extrapolation of a mortality curve (see Smith 1973 for a discussion of mortality and dispersal of sardine eggs and larvae). Regarding this biological assumption, it is very reasonable to assume that the eggs are spawned in dense patches, and then slowly disperse and die as time since spawning progresses. This back extrapolation requires previous surveys that were temporally coincident with spawning. A concluding assumption, and one that is essential for the success of the IEPM, is that the survey interval and spawning period overlap.

Recently, I have been examining somewhat different models for estimating spawning biomass from egg surveys. These models are especially concerned with the spatial distribution of eggs and how that distribution can be characterized and used to assess spawning biomass. The models that are being considered are a class of spatial "point processes"; that is, they are stochastic models that associate a value (in this case the number of eggs) to a certain point in space and time (in this case one of the CalCOFI sites at the time of the survey). The models are also "contagious" in the sense that there are two parameters that enter into the probability distribution and by adjusting these two parameters we can make the variance of the distribution exceed the mean by virtually any desired amount. (An introduction to some of the ideas about point processes is found in Diggle 1983 and many of the distributions described below are discussed in more detail in Johnson and Kotz 1969).

One example of this kind of distribution is the negative binomial with parameters **m** and **k**. That is, let **X** denote the number of eggs at a particular station; given that the station is indeed a spawning habitat. Then according to the negative binomial (NB) model:

Prob(X = x|station is a habitat) =

$$(\Gamma(x + k)/ x!\,\Gamma(k))\ \{k/(k + m)\}^{k}\ \{m/(k + m)\}^{x} \qquad [3]$$

where $\Gamma(k)$ is the gamma function. The mean of X is $E\{X\} = m$ and the variance is $Var\{X\} = m + m^2/k$, so that for a given value of the mean, by making k particularly small one can make the variance exceed the mean by a considerable amount. Paul Smith (Southwest Fisheries Center, La Jolla) estimates that k for sardine eggs runs between .09 for eggs that are recently spawned, .18 for eggs that are about 1.5 days old, and .27 for eggs that are about 2.5 days old; so that small values of k predominate.

Now, if the number of eggs at a station that is a habitat follows the NB distribution (3), the probability of getting no eggs in a sample is simply:

Prob{ X = 0| station is a habitat} =

$$\{\, k / (k + m)\,\}^{k} \qquad [4]$$

and this can be considerable, even if m is large. For example, if k = .09, the probability of getting X = 0 for a variety of values of m is shown below:

log(m)	Prob{X = 0}
0	.799
1	.734
2	.672
3	.614
4	.562
5	.513

That is, even if the mean of the particular negative binomial distribution is e^5, there is still about a 50% chance that the value of X is 0, when the station is a habitat for the spawning stock. Of course, if the station is not a habitat for the spawning stock, then the probability of getting 0 eggs in the sample is 1.

The NB distribution has been used in ecology, and particularly in fisheries, for a long time and has been recently attacked as a model of spatial pattern. (A sampling of papers describing the use of the NB distribution is: Bissell 1972, Bliss and Owen 1958, Cassie 1962, Debouzie and Thioulouse 1986, Dennis and Patil 1984, Hewitt 1981, Mead 1974, Taylor 1953, Taylor 1971, Zahl 1977, and Zweifel and Smith 1981). One of the strongest attacks on the use of the NB model, particularly the use of "blind assumptions" about the value of k is found in Taylor *et al.* (1979) and Perry and Taylor (1986) who argue forcefully that k is a function of m. They suggest:

i) Using Taylor's power law (Taylor 1971) in which the sample variance is related to the mean by $s^2 = am^b$ with s^2 the sample variance, **m** the sample mean, and **a, b** parameters; and

ii) Finding moment estimate for **k** to obtain

$k(m) = 1/[\, am^{b-2} - m^{-1} \,]$. Thus, we determine the functional form for the overdispersion parameter, as a function of the mean.

There is no doubt that the NB is limited in what it can be used for because of the interaction of spatial scales of the sampler and the sampled organism and by pattern of the organism (see Debouzie and Thioulouse, 1986 for an example of the problem), but the real issue comes back to the essential question posed at this workshop: What is one trying to do with this "contagious distribution" and can it do the job ?

Before addressing that issue, it is worth noting that there are other contagious distributions which, although it seems that they have not appealed to ecologists, are equally appealing as the NB. For example, one could consider a Neyman type-A distribution for which

Prob{ X = x | station is a habitat} =

$$\sum_{j=1} \{\exp(-\lambda)\, \lambda^j / j!\} \exp(-j\theta)\, (j\theta)^x / x! \qquad (5)$$

where λ and θ are parameters. In this case, the mean of X is $\lambda\theta$ and the variance of X is $\lambda\theta(1+\theta)$, so that the variance can also be made as large as desired, relative to the mean. The probability of a zero term for the Neyman type-A distribution is then

Prob(X = 0 | station is a habitat) =

$$\exp(-\lambda(1 - e^{-\theta})) \qquad (6)$$

Other possible contagious distributions are described in Mangel (1986) and Mangel and Smith (1988) and include the Polya (urn model) and a zero/random model in which one parameter determines whether a station has any positive number of eggs. If it does, the number of eggs is then determined randomly (i.e. according to a Poisson distribution). The NB model was presumably popular in the past because of its analytical tractability. In the future, as desktop computers become more readily available and more powerful, it is likely that these other distributions will be more commonly used.

Regardless of which contagion model is chosen, none of them will be "right" -- all models are approximations of reality. So, we return to the question of what will be done with the model? For the egg surveys in particular, presence-absence sampling methods are excellent. The idea behind such methods is that rather than deal with egg counts at a particular station we simply observe the presence or absence of eggs. This means that the only term

of the contagion model that is needed is the one that gives Prob(X =0). The models that I have been studying assume that not all stations are spawning habitats in the year that the egg survey is taken, so that the probability of obtaining no eggs in a sample from a particular site is based on two terms: the first is the probability that a station is not a spawning habitat, in which case the probability of $X = 0$ is identically 1; the second is the probability that a station is a habitat times Prob(X =0 | station is a habitat), given by an equation similar to (4) or (6). In these models, the overdispersion parameter **k** may indeed be a function of the mean and the probability p_i that the i^{th} site is a habitat can also be a function of the mean **m**. Neither complicates the conceptual approach. These models are an extension of the "Δ -method" described by Pennington (1983); also see Aitchison (1955) for one of the seminal papers in this area. In particular, I suggest that

i) We could use some method analogous to the one proposed above to determine the functional form of **k(m)**. (Although for sardines, the data in Smith and Richardson (1977) suggests that **k** is constant)

ii) The ecological theory of habitat choice can be used to determine the functional form of $p_i(m)$ (e.g. Southwood 1977 or Rosenzweig 1987) .

iii) One of the most important issues for future consideration is the field determination of habitat boundaries (e.g. McCoy *et al.* 1986) and habitat selection (Rosenzweig 1981, 1985; Rosenzweig and Abramsky 1985).

The data for this method then consist of the fraction of sites at which eggs were present. From these data, we estimate the mean **m** of the NB distribution. By assuming a linear relationship between the spawning biomass and the mean **m**, it is possible to make inferences about the spawning biomass from the presence-absence data. The linearity between adult biomass and mean number of eggs per haul is assumed on the basis of previous data -- see Zweifel (1973), MacCall (1979) or Figure 6.3 in Rothschild (1986) .

Although the NB distribution can be criticized as a "general" model in ecology, my own experience in this particular example is that whether one uses the negative binomial, Neyman type A, Polya or Zero-Random distribution is not particularly important. From the viewpoint of criticizing biological assumptions, it is surely true that none of these models describes what is actually happening. Yet, we can still obtain a management answer with some confidence even though the particular biological model is, to a large extent, fabricated. I would thus argue that what is being done with the models is sufficiently robust to modelling details that the answers are relatively insensitive to the biological correctness of the particular model of aggregation. The approach described in this section is also particularly well suited for incorporating other kinds of information about egg distributions, and for using egg surveys as prior distributions if fishing surveys are conducted (see Mangel and Smith 1988). An alternate approach to this problem might be to estimate

density of spawning biomass directly, using distance between stations with eggs, as described in Delince (1986).

In concluding this section, it is worthwhile to discuss some of the other biological assumptions and questions associated with this problem. Perhaps the most important is the interaction of spatial scales. One of the assumptions underlying either the inverse egg production method or the probability methods based on contagious distributions is that samples taken at different sites can be treated as independent random variables. This need not be so, but the interaction of the various spatial scales -- the spawning stock, the egg patch, the sampler itself,and the survey design -- needs to be considered in more detail. Smith (1978) provides a lucid discussion of the biological effects of different scales and Smith and Hewitt (1985) describe some observations in which the scale of the egg patch and the sampling scale interact. (Some other papers on this general topic are Gerritsen and Strickler 1976, Wiebe 1971, and Wiebe and Holland 1968).

Another implicit assumption in either the inverse egg production method or the probability models is that we can identify the spawning habitat clearly. As Southwood (1977) suggests, habitat may in fact be the "templet for ecological strategies" and yet methods for identifying habitat boundaries are in their infancy (see, e.g. McCoy *et al.* 1986). The assumption that the egg survey is within the spawning habitat is a crucial one and may drive all of the results if one is not careful. For example, one can always add zeroes to the data by sampling for eggs in areas that are not spawning habitats. The assumptions about interaction of spatial scales and identification of habitat are, in my opinion, much more important for this particular problem than the choice of model to describe patchiness.

In the future, it may be possible to employ methods from geophysical analysis ("kriging" and other techniques -- see Ripley 1981 for a general discussion or Stolyarenko 1986 for a specific fishery application) to obtain more or less continuous distributions of stock levels and/or egg levels.

Management of Krill in the Antarctic

Preventing the depletion of Antarctic krill recently has become a topic of considerable interest. For example, Butterworth (1986) devotes an entire section to krill stocks in a paper on Antarctic marine ecosystems management. He writes: "To prevent substantial depletion of the krill standing stock by human exploitation is a priority. This objective could be expressed as follows: the standing stock of krill in each designated management area must not be permitted to fall to less than an agreed proportion of its current level" (Butterworth 1986, p. 40). He then discusses the selection of appropriate management areas and means for monitoring krill stocks. The direct method uses hydroacoustic surveys of the krill stocks; this method will not be discussed here. Rather, attention will be given to the indirect method, the use of catch

per unit effort (CPUE) as an indication of krill abundance, and to the biological assumptions underlying this use of CPUE.

The Antarctic krill are part of a complex multispecies and multitrophic level ecosystem. There are at least four trophic levels: the prey of krill, the krill, nonhuman consumers of krill (whales, seals, marine birds) and humans. The management question is really not only how much krill should be left for marine animals, but what kind of spatial and temporal pattern of remaining krill is needed for them and how do we insure that this pattern is achieved? There is a natural tension between the fishing activities of humans and the foraging activities of the animals.

One approach to this complex ecosystem is the development of a multispecies management model. May *et al.* (1979) do this using what are essentially Lotka-Volterra equations. Such models can be used to assess qualitative features of an ecosystem but it is difficult to use them for quantitative prediction. The biological assumptions underlying these models can be attacked so easily that it is not even worth doing (Kingsland 1985 provides a very interesting history of the Lotka-Volterra class of models). An alternate approach is taken by Laws (1977) who provides a relatively coarsely grained picture of seasonal changes of ice pack, zooplankton volume (including species other than krill), and feeding activity of the main consumers of krill. Laws's work shows a need for understanding some of the behavioral patterns of krill and their predators if one wishes to get at the assessment of krill stocks.

Multispecies management models are extremely interesting from a number of different points of view but suffer because of the complexity of the models and the quality of the biological assumptions that underly them. In a review of a conference on tropical multispecies models, Pauly (1982) wrote that there were many models but "scanty data" and that "ecological theory, as it presently stands, has generated too many untestable hypotheses and uses too many unquantifiable parameters to be of great use to fishery biologists." In the past few years, a number of authors have tried to rectify some of these difficulties (e.g. Getz *et al.* 1985 or May 1984). Newman (1984) gives a discussion of management techniques of Antarctic resources and, in particular, lists some of the details about the logistic problems and expense of direct sampling of krill stocks.

We are thus led to indirect methods for the assessment of krill stocks. The use of CPUE is based on the biological-operational assumption that catch rate C is proportional to a measure of effort E and average population level N:

$$C = q(E)\,N \qquad [7]$$

where the proportionality function $q(E)$ may be nonlinear. In the simplest case we have $q(E) = q_0 E$, where q_0 is a constant. There are two ways to view the biological assumptions underlying equation [7]. The first is a statistical viewpoint: How does we assess [7] statistically? For example, fishery data are often collected according to geographic region (e.g., 1^o by 1^o squares), but how is this distribution related to the way that the stock under consideration

distributes itself? Just the question of how to combine CPUEs from different geographic regions is an interesting and difficult one (see, e.g. Quinn *et al.* 1982 for a discussion). A simple example will suffice. Suppose that the stock under consideration is composed of two sub-stocks so that $N = N_1 + N_2$ where N_i is the substock in region i. Assuming that q_i and E_i are the catchability and effort in region i and a completely linear model, the total catch is

$$C = q_1E_1N_1 + q_2E_2N_2 \qquad [8]$$

The CPUE based on total catch and total effort is

$$CPUE = (q_1E_1N_1 + q_2E_2N_2)/(E_1 + E_2) \qquad [9a]$$

while the CPUE determined by summing CPUEs over regions is

$$CPUE = q_1N_1 + q_2N_2 \qquad [9b]$$

Even these simple quantities are not easily connected with total population unless efforts and catchabilities are clearly quantified and understood. Measuring fishing effort and catchability are notoriously difficult endeavors. The ultimate conclusion of this kind of an approach, however, is often the statement "if we could just collect enough data to do good statistical analysis, everything would be fine". Hedgpeth addressed this attitude in 1957, when he wrote:

> Too many ecologists, especially fisheries workers, employ statistical procedures without any clear idea of what they mean and, what is worse, often apply them to data which are of doubtful biological validity. For example, the idea that the size of a large fish school may be estimated by the tagging and recapture method without any reference to the schooling behavior of the fish is inexcusably bad biology and a squandering of public funds. Adequate statistical procedures are tedious and time consuming, and it would be well to spend a comparable amount of time at the outset in working out an adequate sampling technique (Hedgpeth 1957).

When doing biostatistics, we need to think about biology as well as statistics.

A second approach is to ask the following question: What is the underlying biology that would make CPUE linear in N? There is increasing evidence that in a number of fisheries that catch is not directly proportional to stock but that

$$C = q(E)\, N^{\beta} \qquad (10)$$

where the parameter β is less than 1 (examples are given by MacCall 1976, Murphy 1977 and Ulltang 1980). CPUE is no longer a direct measure of population size. If we assume that it is -- that is, force catch divided by effort to be proportional to N -- then the catchability coefficient becomes a function of population size with the somewhat undesirable property that catchability increases with decreasing population size.

The relationship between CPUE and population size has been studied for many years (Ricker 1940, Paloheimo and Dickie 1964) and there is a considerable body of recent work on the relationship (Bannerot and Austin 1983, Clark and Mangel 1979, Cooke 1985 a, b; Cooke and Beddington 1984; Dupont 1983; Fox 1974, Mangel 1982, 1986; Peterman and Steer 1981; Richards and Schnute 1986; Steele, 1984; and Zahl 1982 a, b). The general gist of the theoretical work is this: for pelagic schooling fisheries in which search for schools occupies a considerable portion of the operating time, the relationship between CPUE and N is virtually always going to be nonlinear. For demersal bottom fisheries in which fishing is essentially all of the operating time, the relationship between CPUE and N is more likely to be linear. Special mention must be given to the work of Richards and Schnute (1986) who performed an experimental test of the relationship between CPUE and stock abundance by using a submersible to make visual estimates of the rockfish density in the Strait of Georgia (British Columbia) and compared these estimates with CPUE from fishing. They found a strict proportionality relationship between CPUE and stock abundance of the major species (quillback rockfish *Sebastes maliger*) and that CPUE was a poor abundance index when combined across species. The actual relationship of CPUE and N thus depends upon a number of biological and operational factors, including the schooling behavior of the species of interest, the abundance of the species of interest, and the search and harvest operations of the fishing fleet. The papers of Clark and Mangel (1979) and Mangel (1982) are indicative of the importance of schooling behavior to stock assessment. These papers are concerned with the purse seine fishery for yellowfin tuna, which are usually caught in aggregations on the surface of the ocean. Two mechanisms for the aggregation of tuna to the surface are identified. In the first, the movement of tuna from a subsurface, nonvulnerable population to the surface (where fishing occurs) is proportional to the difference between surface and subsurface population levels. In the second case, movement to the surface occurs as long as the surface population is below its carrying capacity. In the first case, CPUE gives an indication of stock abundance but in the second case there is essentially no connection between CPUE and N until the stock has crashed (in which case N = CPUE = 0). Without knowing the behavioral mechanism of school formation and surface aggregation, one must be very careful in the analysis of catch and effort data. Thus to assume that CPUE is a good indicator of population size, for the purposes of management, may be highly unjustified biologically.

Krill in the Antarctic are observed in a number of different kinds of physical structures. The major ones are (Kalinowski and Witek 1982, 1985)

i) *Concentrations*: These are collections of krill with a spatial scale of 1 to 100 km with surface densities of at least 10 g/m^2; ii) *Swarms*: These are the most commonly found krill structure, typically with a spatial scale of 10 -100 m and surface densities of 10 - 10000 g/m^2; iii) *Layers*: These are collections that may exceed 1000m as a spatial scale, may be 100 m thick and have krill densities of 10 -100 g/m^2 and iv) *Superpatches*: These are rare aggregations with spatial scales of the order of more than a km and many hundreds of meters thick with densities of the order of 100-1000 g/m^2. Fishing for krill is done almost exclusively on the larger aggregated forms. Immediate questions come to mind, such as what causes the patchiness, what is the temporal and spatial scale of the patchiness (e.g. Mackas *et al.* 1985), and what is the effect of the patchiness on population assessment and sampling (e.g. Jillet and Zeldis 1985 or Omori and Hamner 1982). The nagging problem of scales arises here too. The spatial scales range from the individual krill (10 cm) to superpatches (1000 m). The different spatial scales also have correspondingly different temporal scales.

Concerning the relationship between CPUE and stock abundance, Butterworth (1986) writes:

> The relationship between CPUE and krill biomass needs special investigation, particularly the quantification of possible non-linear effects, such as catchability increasing as biomass decreases. In a species such a krill, which shows marked swarming behavior, this effect may well be substantial.
>
> Empirical determination of the non-linear effects is not appropriate. Probably only a substantial biomass decrease would provide the necessary data. Instead, attempts should be made to develop a model of the fishing operation that provides quantitative prediction of the nonlinear effects...It is important to construct the basis for such a model at an early stage, because non-standard data may need to be collected along with CPUE statistics.
>
> (Butterworth 1986, pg. 41).

If the "biological" assumption that CPUE is proportional to stock abundance is at least temporarily dropped because of its possible weaknesses, we can then ask how the first step in Butterworth's program is taken. In particular, what are some of the biological bases on which the model that predicts the nonlinear effects should be developed? In light of the theoretical papers mentioned previously, we could begin to phrase the question in the following way: Is the Antarctic krill fishery more like a pelagic schooling fishery or more like a demersal trawl fishery? In connection with this question, I wish to discuss one particular area which has often been notably lacking in

the development of management models. This area is behavioral ecology. (Virtually unique exceptions are Pope (1980) and the ICLARM Conference Proceedings "Fish Behavior and Its Use in the Capture and Culture of Fishes" edited by Bardach *et al.* (1980), and O'Hara (1986). Hamner (1985) gives a particularly eloquent argument for the importance of ethological and behavioural considerations when investigating marine zooplankton.)

I mentioned earlier that krill show marked swarming behavior and it is likely that certain types of krill behavior make them susceptible to fishing in the same way that the aggregation of eggs during spawning makes egg surveys feasible. We need to develop models that involve the search for concentrations of krill swarms, and then the search for swarms within concentrations. In order to do this, we must consider at least two kinds of behavioral questions. The first is the behavior of the fishing fleet -- particularly search and capture operations. The second is the behavior of the krill species, in particular how aggregation and life cycle are connected to vulnerability by fishing. It is conceivable that such behavioral models could also be used to assess the spatial distribution of the krill (e.g. Clutter 1969). It is thus possible that what have previously been viewed as "basic" studies of krill biology and behavior (e.g. Marr 1962, Ivanov 1970, Macintosh 1972 or Ettershank 1984) can provide at least a guide to the kinds of behavioral models needed for the development of better assumptions about the relationship between CPUE and stock abundance. Without the use of such behavioral models, the assumption that CPUE is proportional to stock abundance -- although it is easy to use -- may lead to really disastrous management consequences. A start (suggested by A. MacCall) is to assume a nonlinear relationship CPUE = aN^{β}, then to estimate the the parameters a and β (e.g. by catch at age analysis -- but what if the data are not available?) and then use this empirical relationship in management. Use of a nonlinear, empirical relationship is most likely to be superior to the linear assumption, but leaves open the question of the biology underlying the nonlinearity.

Most existing management models treat the biology of the organism as a "black box", but we need to begin understanding the behavior of organisms if we wish to draw as much information as possible from our survey and fisheries data.

A Model of the California Current Ecosystem

The California current runs between Punta Eugenia in Baja California and Vancouver Island. Chelton *et al.* (1982), Hickey (1979) and Parrish *et al.* (1981) provide excellent descriptions of the physical oceanography of the California current. In this section, I examine the kinds of biological assumptions and information needed to model the fisheries for pelagic species in the California current and discuss whether the appropriate data can be collected. The most successful "ecosystem model" in fishery research at the current time is a model of the North Sea. This model, however, has a number

of particular properties which make it hard to translate to other systems. In this section, I advocate the need for research into the community ecology of the California current, rather than advocating a particular approach to the development of an ecosystem model for the California Current.

In November, 1983, a workshop was held at the Southwest Fisheries Center (La Jolla, Ca.) with the purpose of generating a management information document for the major species in the coastal pelagic fisheries of California. MacCall (1984a, 1984b) gives an excellent description of the issues . The major commercial species are the northern anchovy, Pacific sardine, Pacific mackerel, jack mackerel, Pacific bonito, and market squid. (There are about 500 different species of fish found in the California current.) The six major commercial species are tied together in relatively complex food webs. Figures 1 and 2 show the food webs in Monterey Bay and a simplified version of the food web relating the six coastal pelagic species of interest. Note that another implicit biological assumption is made when we consider figures such as these: The figures are drawn from the perspective of the adult animal. Food webs based on other life stages might look quite different. The interaction and ecology of these species is complicated as well. For example, it is possible that on relatively long time scales, sardine and anchovy "replace" each other in the coastal waters of California. (Figure 3 shows data on scale deposition rates that suggest this concept). The disappearance of sardine in the late 1940s may thus be tied to long term ecological factors that we still do not understand.

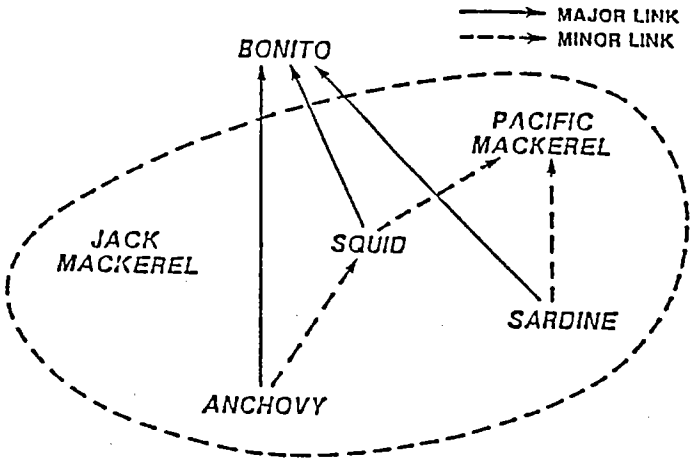

FIGURE 1. Simplified food web (from the adult perspective) for the major pelagic species in the California current (take from MacCall 1984a). The arrows show the direction of energy transfer. Major links are indicated by solid lines, minor links are indicated by dashed lines. The vertical position indicates the relative trophic level of the interaction. The species in the ellipse feed extensively on euphausids.

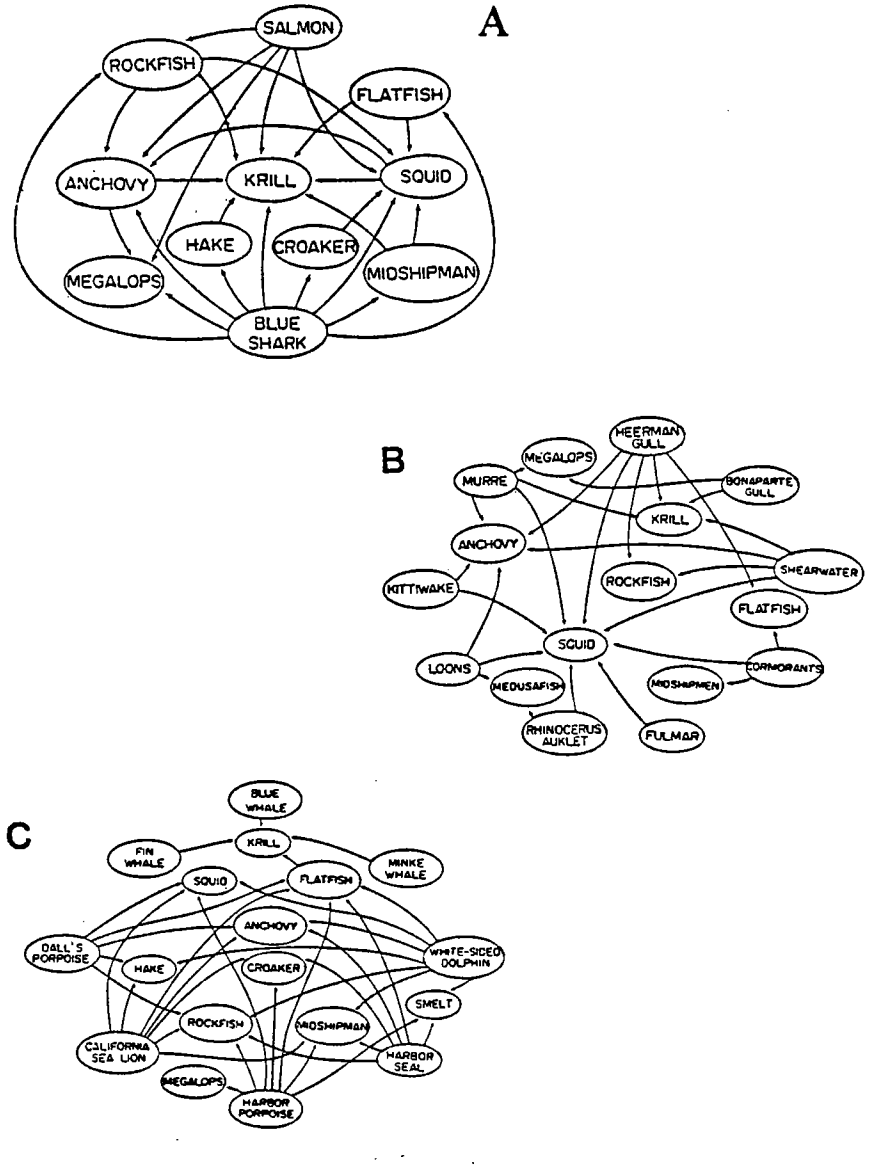

FIGURE 2. Three food webs in Montery Bay (taken from MacCall 1984a, who took it from Morejohn *et al.* 1978). a) The food web for commercially important or abundant fish. b) The food web for seabirds and commercially important or abundant fish. c) The food web for marine mammals and commercially important or abundant fish.

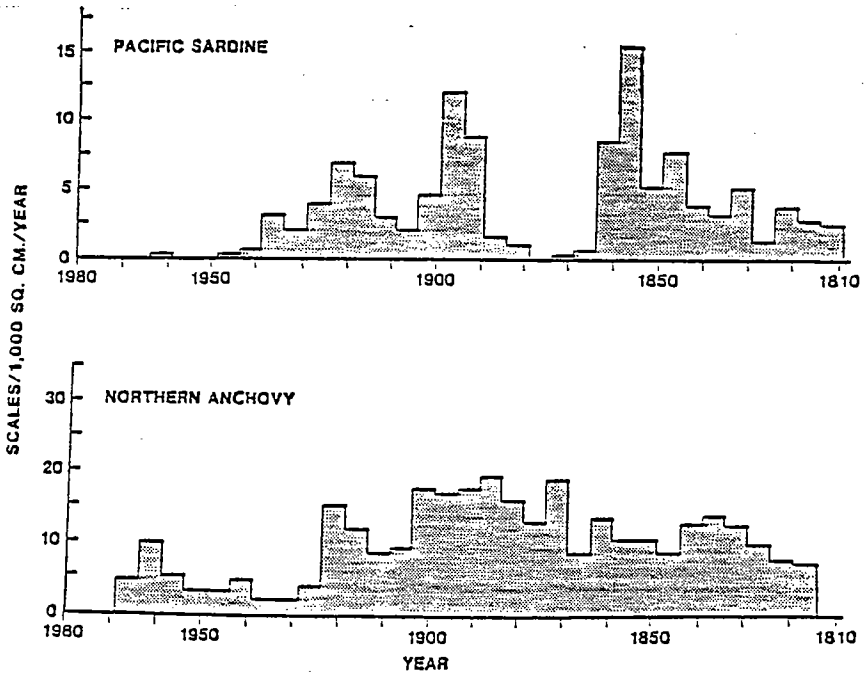

FIGURE 3. Deposition rates for sardine and anchovy scales in sediments in the Santa Barbara Basin (taken from MacCall 1984a, who took it from Soutar and Isaacs 1974.) Data such as these suggest the possibility of long term interchanges of species.

The 1983 workshop participants identified a number of questions and issues that pertain to the management of the California coastal fisheries. The first five of these questions, in rank order, are :

1. What is the potential yield of the stocks?

2. What is the economic importance and contribution of the species complex to each segment of the fishery?

3. Are our methods of estimating abundance adequate for management?

4. What is the fishery development potential -- not only yield but in kinds of fisheries?

5. Is multi-species management worthwhile? If so, how does it differ from existing methods?

The "existing methods" mentioned in question 5 refer to single species management currently in place for each of the six main species shown in Figure 1. The current management of each species is described in pages 60 ff of MacCall (1984a.) Multispecies management is discussed in MacCall (1984a), in particular the length of fishing seasons and interaction of the legal and natural fishing seasons and various kinds of harvest limits (optimal yields and quotas). The potential of a combined-species quota system as a management tool still needs to be properly assessed. Two multi-species quota systems are discussed briefly in MacCall (1984a, p. 65). The need for further development of multispecies management concepts appears clearly in MacCall (1984), as well as in Wilomovsky (1985), where the formalization of decision algorithms and risk levels in fishery management is discussed.

I believe that in order to develop management schemes that might in some sense be considered scientific, rather than political or reactive, we need to understand the community ecology of the California current system. The types of questions that one needs to ask and answer are: Why are certain species found together (i.e. what causes species assocations), what causes geographic separation of species, and how do we quantify these relationships? The usual approaches to community ecology (Diamond and Case (1986) or Pimm (1984) say) are not very helpful in addressing the crucial issues in the California current. Ricklefs' (1987) recent article is a notable exception.

There is one simplified model of the California current ecosystem (Riffenburgh 1969). Riffenburgh explicitly considers sardine and anchovy and their predators and prey, so that the food web is somewhat reduced. He develops a Markov chain model for the population dynamics and tries to use this model to understand the cause of the collapse of the Pacific sardine fishery and to show how a combined sardine-anchovy-hake fishery could be managed.

The physical properties of the California current are highly variable (Hickey, 1979; Parrish *et al.* 1981; Winant and Bratkovich 1981) and any attempt to model the ecosystem must surely take such physical variability into account. The paper of Parrish *et al.* (1981) explicitly deals with the interaction of physical processes (in particular, transport mechanisms) and reproductive success of fish in the California current (also see Cushing 1982, Frye 1983, Lemke 1977 and Pritchard *et al.* 1971 for related discussions). Recent work on the physical structure of the California current is described in Chelton *et. al.* (1987). It may be that as our ability for extended range forecasting of weather increases (e.g. Reinhold 1987), the understanding of the interaction of physical and biological factors will also increase. An ecosystem model for the California current must deal with the following features. The system is "open" in the sense that the populations move freely across spatial boundaries. There is considerable interaction between physical and biological factors (e.g. see Chelton *et al.* 1982 for evidence in support of this hypothesis). The spatial and temporal distribution of prey species must be modelled (e.g. Arthur 1976, 1977;

Sheldon and Parsons 1967, Wickett 1967) and methods for determining the patterns of community structure (Helfman 1978) and the boundaries of the habitat (Ricklefs 1987) must be developed. Methods for assessing the levels of each stock and the spatial and temporal overlap between stocks must be developed. (Recall that for a stock such as sardine, which is spread over considerable geographic range, there is essentially no reliable method for direct stock assessment when the stock level is very low . How do we deal with the "minor" species in the ecosystem?)

It appears that the relevant data on physical attributes and on distributions of prey items are available. The data on the interaction of the six major species within the ecosystem are not so good -- we are forced to deal with a range of hypotheses concerning the biological interactions. The potential yield from attempting such a model has two aspects. First, there may indeed be improved management if the multi-species ecosystem is understood better. Second, the development of a model for the California Current ecosystem would lead to a better understanding of the biological interactions between the species, a deeper understanding of the community structure and sources of diversity in the California current, and thus possibly to a better assessment of the biological assumptions in fisheries management.

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Comments on Biological Assumptions in Fishery Management

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Professor Marc Mangel's paper concerns several biological analyses and their assumptions. The assumptions upon which biological analyses are founded have been of considerable interest to me for some time. Not only are the assumptions themselves of interest but, in particular, the effects of their failure on the ensuing fishery management advice and the implemented fishery management programs, since assumptions by their very nature are doomed to some degree of failure. Aside from the obvious intellectual aspect of assumptions being appealing foci of research, there is a very practical reason for my interest -- it is my very firm conviction that fishery managers must be held accountable for their decisions, and this requires that the decision environment be transferred accurately and completely.

There are several ways that a paper could tackle the topic of this session. For example, one could make an immense list of all the assumptions in biological analyses. I think it is important to note that these assumptions are by nature statistical, mathematical, sociological, economic and political as well as biological. Mangel also makes this point. They could then be classified into the typical four functional groups as follows:

1. Model Structure

2. Data Collection and Processing

3. Parameter Estimation

4. Advice Formulation and Transfer

plus those that interact among the groups. Instead of using a functional grouping, one could also accumulate the assumptions according to the specific biological analysis to which they pertain -- this to a large degree is the

approach taken in the paper by of Megrey and Wespestad (this volume). Alternatively, one could choose some common characteristic of all biological analyses, classify it by some measure of degree and discuss the associated assumptions -- this is essentially the approach taken by Mangel.

In reality, no one ever constructs the full list of assumptions, and the papers in this session are no exception. Regardless of the approach, one usually selects a set of assumptions within a given grouping believed to be the most important. Therefore, as a final alternative one could group assumptions according to a priority set of substantive classes. My top five substantive assumption classes are as follows:

1. The existence of equilibrium;

2. The existence of a stock-recruitment relationship;

3. The relationships among the control variables, the observational variables and the fishing mortality rate;

4. The relationships between a stock and its exogenous environment; and

5. The relationship between advice and uncertainty.

For these classes, the usual or "state-of-the-art" assumptions are:

1. Equilibrium exists;

2. Recruitment is independent of stock size or its characteristics over the range of interest;

3. The relationships among the control variables, observational variables and fishing mortality are linear;

4. There are no exogenous relationships that can not be represented as random, independent errors with zero means;

5. One must "prove" an effect of fishing before giving advice to take some management action or before management action is taken even if advice is given to do so.

Mangel uses three examples which range from the specific to the complex to illustrate his view of the assumptions associated with biological analyses in fishery management. His first example demonstrates how uncertainty can be incorporated in management action (substantive class 5) using California sardine egg sea surveys. He also mentions most of the plethora of biological, statistical and mathematical assumptions needed to get from a proximal measure of local sardine egg fertilization to a measure of

sardine spawning biomass, and he discusses a different model for making the estimates.

In his second example, Mangel directly addresses the assumptions associated with substantive class 3 in using catch per unit effort data from the Antarctic krill fishery to index changes in the krill population. He makes the particular observation that substantial research in the field of behavioral ecology may be needed in order to resolve this class of assumptions adequately. This is an important point, one that could be crucial to understanding how fishery systems will behave under management.

Mangel addresses substantive class 4 with his last example using an overview of a California Current ecosystem model. It is important to develop criteria for the success of ecosystem models, i.e. modeling should have a purpose from which such criteria can be derived. Mangel adequately discusses how the model could be used in answering management questions.

Finally, I would like to comment about the theme of the workshop. It seems to me that there are really no primary biological objectives in fishery management. The real objectives in fishery management are economic and social. There are, of course, biological constraints to how a fishery system can behave with or without management but these are not objectives. I also distinguish a secondary objective, say avoiding some biological constraint by some margin with some degree of certainty. One can legitimately argue over the timeframe to use in determining which path or set of alternatives is optimal or over how certain one wants to be in achieving specific attributes in the fishery. All too frequently, however, objectives with longer timeframes and higher degrees of certainty are confused with or are actually termed as being "biological." Apparently in doing so the proponents hope to obtain some deference to the motherhood concept and the opponents hope for denigration because of it -- both just make it more difficult to resolve the issue.