# AGGREGATION AND FISHERY DYNAMICS: A THEORETICAL STUDY OF SCHOOLING AND THE PURSE SEINE TUNA FISHERIES[1]

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## ABSTRACT

This paper describes mathematical models of exploited fish stocks under the assumption that a certain portion of the stock becomes available through a dynamic aggregation process. The surface tuna fishery is used throughout as an example. The effects of aggregation on yield-effort relationships, indices of abundance, and fishery dynamics are discussed. The predictions of the theory are notably different from those obtained from general-production fishery models, particularly in cases where the available substock has a finite saturation level. Possible effects include fishery "catastrophes" and lack of significant correlation between catch-per-unit-effort statistics and stock abundance. Various management implications of the models are also discussed.

The relationship between fishing effort, catch rate, and stock abundance is of fundamental importance to the management of commercial fisheries. To a first approximation, it is usually assumed that catch per unit effort ($C/E$) is proportional to stock abundance ($P$), with a fixed constant of proportionality (catchability coefficient), $q$:

$$C = q\,EP, \qquad (1)$$

where $C$ denotes catch per unit time and $E$ denotes fishing effort. By combining this relationship with an appropriate model of population dynamics, one obtains a dynamic fishery model which can then be used as a basis for management policy (Schaefer 1957).

The form of Equation (1) is predicated on certain underlying assumptions pertaining to the fishing process, particularly a) that fishing consists of a random search for fish and b) that all fish in the stock are equally likely to be captured. More precisely, by introducing an explicit stochastic model of the fishery based upon such assumptions, one can deduce Equation (1) for the expected catch rate $C$. But such models can also be employed to investigate the consequences of alternative, and possibly more realistic, assumptions. For example,

stochastic models of purse seine fisheries, incorporating detailed descriptions of the operation of fishing vessels, have been discussed by Neyman (1949), Pella (1969), and Pella and Psaropulos (1975). On the other hand, the effects of concentration of fish and of fishing effort have been studied by Calkins (1961), Gulland (1956), and others.

In this paper we discuss fishery models in which the assumption of equal availability of all portions of the stock is relaxed. Specifically, we are concerned with fisheries that exploit aggregations of fish; these aggregations are assumed to constitute a dynamically changing substock of the entire population. Although a general class of such models could be developed, we shall restrict the discussion here to the case of the tuna purse seine fisheries, in which aggregation apparently occurs through the process of surface school formation. Several alternative models of the interchange process between surface and subsurface tuna subpopulations will be presented, and the effects of the surface fishery will be investigated for each model. Evidence arising from studies carried out at the Inter-American Tropical Tuna Commission (Sharp 1978), and at the Southwest Fisheries Center, National Marine Fisheries Service, shows that yellowfin tuna, *Thunnus albacares*, captured in surface schools in the eastern tropical Pacific Ocean do in fact spend part of their time below the surface. Little seems to be known, however, about the dynamics of the interchange process; our analysis of alternative models indicates that such knowledge could become crucial to the management of the fishery.

Fisheries for various other pelagic, schooling species, such as anchoveta, herring, and mackerel, also appear to involve aggregative processes. Several of these fisheries have in fact experienced collapses which are qualitatively similar to those predicted by our aggregation models.[4] Other mechanisms, however, may be involved in these fisheries, including: predation (Clark 1974); competitive exclusion (Murphy 1966); increased catchability (Fox[5]); depensation in stock-recruitment relationships (Clark 1976). In some cases, stocks have failed to recover following a collapse, even when fishing has been greatly curtailed (Murphy 1977). Dynamic behavior of this kind is not consistent with any of the traditional models employed in fishery management.

On the other hand, discontinuous behavior of continuous nonlinear systems is a well-known phenomenon in applied mathematics. Thus the term "bifurcation" refers to such discontinuous changes induced by continuous parameter shifts in explicit mathematical models. More recently the subject "catastrophe theory" has been developed as an abstract approach to these phenomena (Thom 1975; Zeeman 1975; see also the report in *Science* by Kolata (1977)).

A discussion of catastrophe theory as it applies in the fishery setting appears in Jones and Walters (1976). Indeed these authors assert that "... the tropical tuna fisheries have almost certainly moved into a cusp region, ... where small changes in investment policy or failure to rapidly adjust catch quotas could lead to fishery collapse." (Jones and Walters 1976:2832). Since no specific biological (or technological) catastrophe-inducing mechanism has been suggested by Jones and Walters, their assertion stands only as a plausible conjecture—a warning that possible nonlinear system effects ought to be investigated more fully.

In this paper we shall investigate in some detail the interactions between the schooling behaviour of tuna and the operation of the purse seine fishery. Since current knowledge about the schooling strategy of tuna is limited, we shall construct a variety of models in order to investigate the possible effects of and interactions with the fishery. In particular, we shall discuss the following topics:

1. yield-effort relationships,
2. indices of stock abundance,
3. fishery dynamics,
4. management implications.

The results turn out to be highly, perhaps surprisingly, sensitive to the assumptions and parameters of our models. Of particular importance is the way in which the size of surface tuna schools depends upon the overall abundance of tuna. If it is the case that school size (as unaffected by the fishery) is relatively independent of total tuna abundance, then our models indicate the possibility (under certain additional conditions) of a catastrophic collapse of the tuna fishery as the intensity of fishing passes some critical level. That such a prediction could arise from a potentially biologically realistic tuna model was completely unexpected at the beginning of the study, in spite of the theoretical investigations mentioned above.

Another significant result of our analysis is that, under our model assumptions, the catch-per-unit-effort (CPUE) statistic may constitute an extremely unreliable index of stock abundance. The bias may be in either direction depending on the model adopted—CPUE may severely either underestimate or overestimate the decline in abundance as the fishery develops, while in other cases CPUE may quite accurately represent abundance.

Following the description and analysis of our various models, we shall present some simple simulated development paths for the tuna purse seine fishery, based upon the models. The first simulation that we performed utilized our best guesses as to realistic parameter values. In this simulation the fishery experiences a catastrophic collapse when effort is increased to 18,000 standardized vessel days per annum. The decline of the tuna population itself occurs quite gradually, but is not reflected by any significant decline in catch or in CPUE, until the fishery is virtually destroyed. In other words, the collapse of the fishery involves not an abrupt change in the stock, but rather an abrupt change in the input-output relationship.

## TUNA PURSE SEINE FISHERY

The commercial fishery for tuna in the eastern tropical Pacific Ocean began in the years following World War I, the two main species taken being yellowfin tuna and skipjack tuna, *Katsuwonus*

*pelamis*. Annual catches in the between-war period rose to a total of about 70,000 short tons. Following World War II "there was a great upsurge in the fishery" (Schaefer 1967:89), which has continued to the present time, see Figure 1. The entire period has also seen a progressive expansion of the fishery into the offshore waters, concomitant with progressive developments in technology. Of particular significance is the switchover from bait boats to purse seiners, which occurred in the early 1960's and has resulted in substantial continuing increases in the catch of yellowfin tuna. Much of this increase has resulted from the offshore fishery on porpoise-associated tuna schools.

The purse seine tuna fishery operates by locating schools of tuna at or near the surface of the sea. The main types of schools encountered are: a) non-porpoise associated schools (pure yellowfin tuna, pure skipjack tuna, or mixed schools) and b) porpoise schools (yellowfin tuna only). Schools of tuna that are not associated with porpoise are sometimes associated instead with concentrations of floating debris ("log schools"). Management of the yellowfin tuna fishery has been complicated by the controversial problem of limiting the incidental kill of porpoise, but this question will not concern us here.
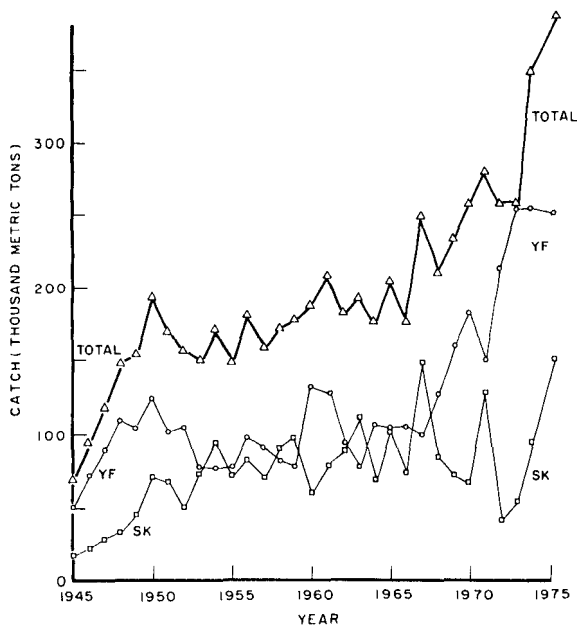


FIGURE 1.—Annual catches of yellowfin (YF) and skipjack (SK) tuna in the eastern tropical Pacific Ocean, 1945-75.

Schools of tuna are normally located by visual search, often by noting the presence of flocks of sea birds. After sighting and approaching a school, the vessel attempts to capture tuna by setting its purse seine net about the school. During a set on porpoise schools, speedboats may be lowered into the water to assist in concentrating the porpoise so that the school can be encircled by the net. Of the daylight hours spent on the fishing grounds, perhaps 70% are spent in searching for schools and 30% on setting of nets.

According to biological observations (Sharp 1978), only a portion of the total tuna population is available to the fishery, as schooled fish, at any given time. It appears that the magnitude of this available portion may be related to environmental conditions, particularly the depth in the ocean of certain thermal isoclines. Furthermore, it seems evident that there must exist a dynamics of school formation and exchange. The fishery interacts with this dynamic process by removing some of the schools. To our knowledge, the implications of such a dynamic availability phenomenon have not been previously investigated in detail.

Since present knowledge about the schooling strategy of tuna is limited, we shall discuss a coterie of submodels for the formation of schools. The models have been chosen in an attempt to "bracket" the possible range of schooling strategies; a wide variety of alternative models could obviously also be set up (see Appendix B).

We next describe a submodel for the purse seine fishery. In order to keep the length of this paper within bounds we discuss only a single fishery submodel, in which vessels search at random for randomly distributed surface schools. Finally we introduce our submodel of tuna population dynamics, which will be the standard Schaefer model. In the main body of the paper we employ the continuous-time version of the Schaefer model, but a discrete-time version will be discussed in Appendix A.

In Appendix B we describe several more detailed models pertaining to the schooling strategy of tuna, using techniques known from chemical kinetics. This approach yields as special cases the two submodels described in the text proper and also gives rise to a number of interesting new details.

Although the background of our schooling and fishery models is stochastic, we concern ourselves only with expected values, so that the analysis remains essentially deterministic. (Explicit

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stochastic considerations are taken up in a forthcoming paper by Mangel.[6]) Two important omissions from our models are: a) age structure and b) spatial distribution of the tuna population; the multispecies aspect is also not covered. These omissions were dictated by our desire to concentrate on the novel features of our work, viz the schooling strategy and its implications. Further research will be required (probably based primarily on simulation techniques) if more sophisticated, disaggregated models are to be studied.

## SCHOOL FORMATION SUBMODELS

We imagine a given number, $K$, of school "attractors," such as porpoise schools, or collections of floating debris. (Our models also apply to nonporpoise and nonlog schools provided that the exchange process between subsurface and surface schools satisfies the appropriate hypotheses, see Equations (10).) Tuna from an underlying, or "background," population associate with these attractors according to one of the submodels A or B below; the attractors are independent of one another and do not interchange associated tuna. Let $N$ denote the number of tuna present in the background (subsurface) population. The number of tuna in an individual generic school is denoted by $Q = Q(t)$. (A full list of variables and parameters is given in Table 1.)

### Model A

Tuna associate with a given attractor at a rate $\alpha N$ proportional to the background population, and dissociate at a rate $\beta Q$ proportional to the current school size:

$$\frac{dQ}{dt} = \alpha N - \beta Q. \qquad (2)$$

(The dissociated tuna return to the background population, see Equation (15).) For fixed $N$ the resulting equilibrium school size $Q^*$ is given by

$$Q^* = \frac{\alpha N}{\beta}. \qquad (3)$$

If $Q(0) = Q_0$, Equation (2) has the solution (for fixed $N$):

[6]Mangel, M. 1978. Aggregation, bifurcation, and extinction in exploited animal populations. Cent. Nav. Prof. Pap. 224. Center for Naval Analyses, 1401 Wilson Boulevard, Arlington, VA 22209.

TABLE 1.—Basic parameters and variables of the models. Symbols endemic to the appendices are given below.

| Item | Meaning | Units of measurement |
|---|---|---|
| **Parameters:** | | |
| $\alpha$ | schooling rate per attractor | day$^{-1}$ |
| $\beta$ | deschooling rate | day$^{-1}$ |
| $Q^*$ | maximum equilibrium school size | tons |
| $b$ | catchability of attractors | (standard vessel day)$^{-1}$ |
| $K$ | number of attractors | — |
| $x_0$ | capture ratio | — |
| $r$ | intrinsic growth rate | day$^{-1}$ |
| $\bar{N}$ | carrying capacity | tons |
| **Variables:** | | |
| $Q$ | school size | tons |
| $t$ | time | days |
| $N$ | subsurface tuna population | tons |
| $E$ | fishing effort | standardized vessels |
| $Y$ | catch rate | tons × (day$^{-1}$) |
| $S$ | surface tuna population | tons |
| $S^*$ | carrying capacity of $S$ | tons |
| $\theta$ | net rate of transfer | tons × (day$^{-1}$) |
| $G$ | growth rate | tons × (day$^{-1}$) |
| **Appendix A:** | | |
| **Parameters:** | | |
| $T$ | length of fishing season | days |
| $\bar{P}$ | carrying capacity | tons |
| $g$ | growth parameter | (day$^{-1}$) |
| **Variables:** | | |
| $R$ | recruitment | tons |
| $P$ | escapement | tons |
| **Appendix B:** | | |
| **Parameters:** | | |
| $\gamma$ | number of core schools per complex | — |
| $S_0$ | weight of core schools | tons |
| **Variables:** | | |
| $T$ | number of core schools | — |
| $C$ | number of complexes | — |

$$Q(t) = Q^* (1 - c_0 e^{-\beta t}), \qquad (4)$$

where $c_0 = 1 - Q_0/Q^*$.

Thus in model A, the equilibrium size of schools is directly proportional to the background tuna population. (Since we treat the number of attractors, $K$, as fixed, we do not discuss the possibility that school size could also depend on $K$.)

### Model B

In this alternative submodel, we assume that the maximum school size is a constant, $Q^*$, which is independent of the background tuna population. Equation (2) is replaced by

$$\frac{dQ}{dt} = \alpha N \left(1 - \frac{Q}{Q^*}\right) \qquad (5)$$

where $Q^* =$ fixed maximum school size.

Thus we now have (for fixed $N$)

$$Q(t) = Q^* - (Q^* - Q_0)e^{-\alpha Nt/Q^*}. \qquad (6)$$

As will be seen in the sequel, the characteristics of our purse seine fishery model are severely inflenced by the choice of the schooling submodel A or B. Which of these submodels more accurately reflects the actual schooling strategy of tuna is a question we are not qualified to answer.[7] It may be the case that neither extreme (school size $Q^*$ strictly proportional to tuna abundance $N$ in submodel A, and $Q^*$ strictly independent of $N$ in submodel B) is realistic. For example, school size may saturate for large $N$, but exhibit density dependence at low $N$, giving rise to a combination of models A and B. Submodels involving more general links between $Q^*$ and $N$ could easily be constructed, but we will not attempt to work through the details here. A more general class of schooling submodels is discussed in detail in Appendix B.

Let us remark here that models A and B assume in effect a uniformly distributed "background" tuna population. The models discussed in Appendix B assume instead that the background population consists of "core" schools; according to Sharp (1978) the latter assumption is more realistic. In certain cases the core-school models reduce to the models A and B described above.

## MODEL OF
## THE PURSE SEINE FISHERY

We shall use a simple Poisson model to describe the process whereby the fishing fleet searches for schools of tuna. The hypotheses underlying this model are well known (see, e.g., Ludwig 1974) and will not be specified here. Let us note, however, that our model pertains to a single type of school (e.g., porpoise school, log school); a more refined model might allow for a random intermingling of school types. A nonrandom distribution of school types, on the other hand, would lead to the as yet unsolved problem of attributing allocation of effort by fishing vessels.

The probability that the fishing fleet locates exactly $K$ school attractors with the expenditure of $t$ days of searching effort, is given by

$$P_k(t) = \frac{(\lambda t)^k}{k!} e^{-\lambda t} \qquad (7)$$

where $\lambda = (a/A)K$
$a$ = area searched per day
$A$ = total area of fishing ground
$K$ = number of school attractors.

If searching effort is properly standardized, we will have

$$a/A = bE,$$

where $E$ = effort
$b$ = a constant.

Hence

$$\lambda = b\,E\,K. \qquad (8)$$

The average number of attractors located by the fleet in time $t$ is

$$\bar{k} = \lambda t = bEKt.$$

Thus the total catch rate of tuna, $Y$, is given by

$$Y = bEK\chi_0 Q \qquad (9)$$

where $\chi_0$ = capture ratio (average fraction captured when a school is encountered).

Let $S(t)$ denote the total number of tuna present at time $t$ in surface schools: $S = KQ$. Our model then implies that

$$\frac{dS}{dt} = \begin{cases} \alpha KN - \beta S - b\chi_0 ES & \text{(Model A)} \\ \alpha KN(1 - S/S^*) - b\chi_0 ES & \text{(Model B)} \end{cases} \qquad (10)$$

where $S^* = KQ^*$ represents the total "carrying capacity" of the surface school attractors. (Note that, replacing $\alpha KN$ by $\rho N$ = flow rate from subsurface to surface populations, we could simply adopt Equation (10) as the basic hypothesis of our model, eliminating any particular assumption regarding the attractive mechanism for surface schools.)

Let us assume for the moment that an equilibrium is achieved rapidly in the surface fishery, relative to adjustments in the underlying population $N$. (The dynamics of the underlying popula-

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[7]Broadhead and Orange (1960) imply that $Q^*$ is nearly constant, although it may in some cases be slightly density dependent. However, for skipjack tuna, in the eastern Pacific, school size and population size as indexed by CPUE are highly correlated (but the two estimates are not independent). J. Joseph, Director of Investigations, Inter-American Tropical Tuna Commission, La Jolla, CA 94720, pers. commun. July 1978.

tion will be modeled below.) Setting $dS/dt = 0$, we obtain the following "catch equations":

$$Y = \begin{cases} \dfrac{b\chi_0\alpha KEN}{\beta + b\chi_0 E} & \text{(Model A)} \\[2em] \dfrac{b\chi_0\alpha KQ^*EN}{\alpha N + b\chi_0 Q^* E} & \text{(Model B)} . \end{cases} \qquad (11)$$

These equations appear not to be of a standard form, as encountered either in ecology (where $Y/N$ would be termed the "functional response," see Fujii et al. ), or in economics (where $Y$ would be termed the "production function" of the fishery, see Clark 1976, sec. 7.6), or in the fisheries literature (Paloheimo and Dickie 1964; Rothschild 1977). This unfamiliarity is perhaps to be expected since, as far as we know, the peculiar "skimming" process of the purse seine fishery has not previously been modeled. Equations (10) are however closely analogous to the Michaelis-Menten equation of enzyme kinetics (White et al. 1973) as might be expected from the observation that the attractors serve to "catalyze" the purse seine fishery, see Appendix B.

Regarding the catch Equations (11), let us observe that both submodels exhibit a saturation effect with respect to fishing effort $E$, whereas only submodel B exhibits a saturation effect with respect to tuna abundance $N$. For a fixed background population level $N$, the catch rate $Y$ bears an asymptotic relationship with fishing effort $E$. For small $E$ we have, from Equations (11):

$$Y \approx \begin{cases} \dfrac{b\chi_0\alpha NK}{\beta} E & \text{(Model A)} \\[1.5em] b\chi_0 Q^* KE & \text{(Model B)} . \end{cases} \qquad (12)$$

Since $Q^* = \alpha N/\beta$ in Model A, these expressions are in fact the same for the two submodels, and concur with the standard Schaefer fishery production function. For large $E$ we have

$$\lim_{E \to \infty} Y = \alpha NK = Y_\infty \qquad (13)$$

[8]Fujii, K., P. M. Mace, and C. S. Holling. 1978. A simple generalized model of attack by predator. Unpubl. manuscr., 39 p. University of British Columbia, Institute of Animal Resource Ecology, Vancouver, B.C., Canada V6T 1W5.

for both submodels. For submodel B we also have (for fixed $E$)

$$\lim_{N \to \infty} Y = b\chi_0 KQ^*E \qquad \text{(Model B).} \qquad (14)$$

## FISHERY DYNAMICS

As our submodel of population dynamics of the subsurface tuna population, we adopt the familiar Schaefer logistic model (Schaefer 1957):

$$\frac{dN}{dt} = rN(1 - N/\overline{N}) - \theta \qquad (15)$$

where $r$ = intrinsic growth rate
$\overline{N}$ = environmental carrying capacity
$\theta$ = net rate of transfer to the surface population.

The net rate of transfer, $\theta$, is obtained from Equations (2) and (5):

$$\theta = \begin{cases} \alpha NK - \beta S & \text{(Model A)} \\ \alpha NK(1 - S/S^*) & \text{(Model B).} \end{cases} \qquad (16)$$

Our dynamic models of the surface tuna fishery then consist of the simultaneous system of Equations (10) and (15). For convenience we rewrite the two systems as follows:

$$\text{Model A:} \quad \left. \begin{aligned} \frac{dS}{dt} &= \alpha KN - \beta S - b\chi_0 ES \\ \frac{dN}{dt} &= G(N) - (\alpha KN - \beta S) \end{aligned} \right\} \qquad (17)$$

$$\text{Model B:} \quad \left. \begin{aligned} \frac{dS}{dt} &= \alpha KN(1 - S/S^*) - b\chi_0 ES \\ \frac{dN}{dt} &= G(N) - \alpha KN(1 - S/S^*) \end{aligned} \right\} \qquad (18)$$

where $G(N) = rN(1 - N/\overline{N})$. $\qquad (19)$

Although the difference between these two models may appear minor, their qualitative behavior turns out to be quite dissimilar. Their behavior is also quite different from the standard Schaefer model (Schaefer 1957). As indicated by results discussed in the appendices, however, the qualitative behavior of the above models seems to be characteristic of a wide variety of alternative

models of both population dynamics and the school-formation process. We next discuss the behavior of our models in detail.

## Model A

Figure 2(a) and (b) show the system of solution trajectories $(N(t), S(t))$ for the Equation system (17), for the two cases

$$\alpha K < r \text{ and } \alpha K > r$$

respectively. The system has a unique stable equilibrium at the point $(N_\infty, S_\infty)$; the corresponding sustained yield from the fishery is given by

$$Y = b\chi_0 E S_\infty.$$



(a) $\alpha K < r$



(b) $\alpha K > r$
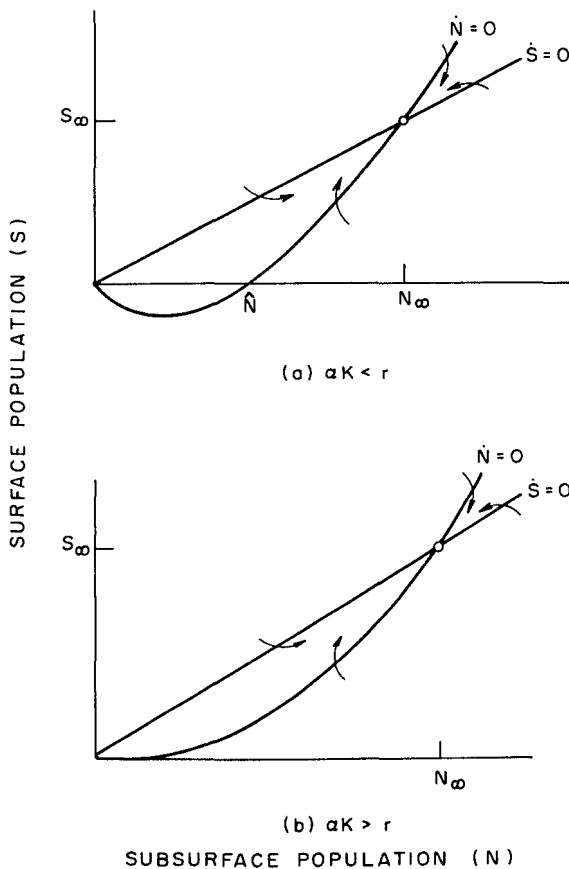
SUBSURFACE POPULATION (N)

FIGURE 2.—Trajectory diagram for model A: a stable equilibrium exists at the point $(N_\infty, S_\infty)$. Case (a): intrinsic schooling rate less than intrinsic growth rate; population cannot be depleted below $\hat{N}$ by surface fishery. Case (b): intrinsic schooling rate greater than intrinsic growth rate; population can theoretically be fished to arbitrarily low levels (see also Figure 3).

In these Figures, the effect of an increase in the effort parameter $E$ is to rotate the isocline $\dot{S} = 0$ in a clockwise direction, thus decreasing both population levels $N_\infty$ and $S_\infty$. The corresponding yield-effort curves are shown in Figure 3(a) and (b) respectively.

The shape of these yield curves is easily explained. Note from Equations (16) that the constant

$$\rho = \alpha K$$

represents the maximum net rate at which the subsurface population $N$ aggregates to the surface; this may be referred to as the "intrinsic aggregation rate" (or "intrinsic schooling rate" in the present model). If the intrinsic aggregation rate $\rho$ is less than the intrinsic growth rate $r$ (see Figures 2(a), 3(a)), then the population cannot be exhausted by the surface fishery; in this case $N \to \hat{N} > 0$ and $Y \to \hat{Y} > 0$ as effort $E \to \infty$. (Figure 3(a) shows yield increasing to a maximum level and then declining as effort increases. This situation arises if $\hat{N} < \bar{N}/2$, i.e., if $\rho > r/2$; otherwise, $Y$ simply increases to an asymptotic value $\hat{Y}$.)



(a) $\alpha K < r$
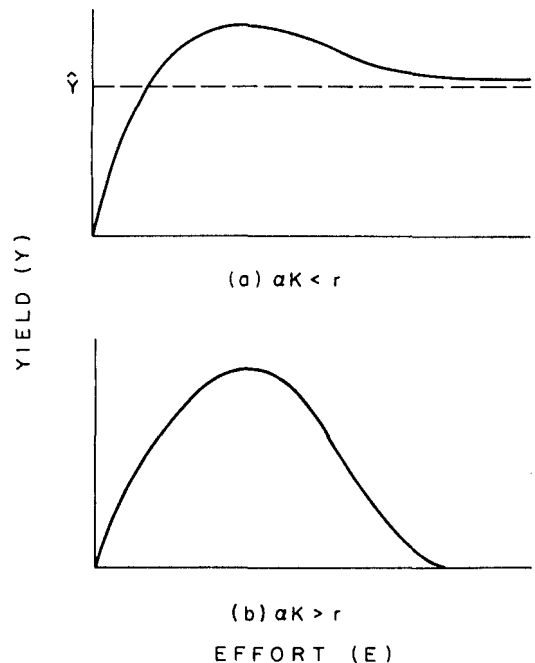


(b) $\alpha K > r$

EFFORT (E)

FIGURE 3.—Equilibrium yield-effort curves for model A. Case (a): intrinsic schooling rate less than intrinsic growth rate; yield approaches a positive asymptotic value as effort approaches infinity. Case (b): intrinsic schooling rate greater than intrinsic growth rate; yield approaches zero at finite effort level.

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On the other hand, if $\rho > r$ (Figures 2(b), 3(b)) then exhaustion is possible at sufficiently high levels of effort. This case is similar to the Schaefer model.

For model A, CPUE is a seriously biased index of total stock abundance. The instantaneous CPUE is, of course, simply an index of abundance for the surface population. Sustained CPUE progressively overestimates the decline in abundance at high levels of effort. Conversely, particularly if the aggregation rate is large, CPUE may underestimate the decline in abundance at intermediate levels of effort. It is clear in general that no simple transformation of the CPUE index can provide an unbiased estimator of abundance, for this model. Any fishery exploiting a substock of a biological population necessarily provides only partial information concerning total abundance; in the event that the fishery itself affects the relationship between the substocks, the interpretation of a time series of catch-effort data becomes extremely difficult.

To summarize, if the present model realistically represents the process of aggregation (via surface schooling) of tuna, then CPUE data may ultimately overestimate the decline in abundance of tuna. Management policy based on such data may then be unduly restrictive. The situation may be very different, however, if model B is the more realistic representation. We now turn to this case.

## Model B

The solution trajectories of Equations (18) are illustrated in Figure 4(a) and (b), again corresponding to the cases $\alpha K < r$ and $\alpha K > r$ respectively. The corresponding yield-effort curves are shown in Figure 5.

In case (a), $\alpha K < r$, the system has a unique stable equilibrium $(N_\infty, S_\infty)$. As in model A, we have $N_\infty \rightarrow \hat{N} > 0$ as $E \rightarrow +\infty$. The yield-effort curve for this case has the same shape as for model A.

A new phenomenon arises, however, in the case that $\alpha K > r$. For small $E$ (see Figure 4(b)) there now exist two stable equilibria, at $(N_\infty, S_\infty)$ and at $(0,0)$, separated by a point of unstable equilibrium. As $E$ increases, the stable and unstable equilibria coalesce and then disappear, leaving only the stable equilibrium at $(0,0)$. In mathematical terminology, the Equation system (18) undergoes a "bifurcation" at the critical effort level $E = E_c$ where the two equilibria coalesce. The graph of sustainable yield vs. effort (Figure 5(b)) becomes
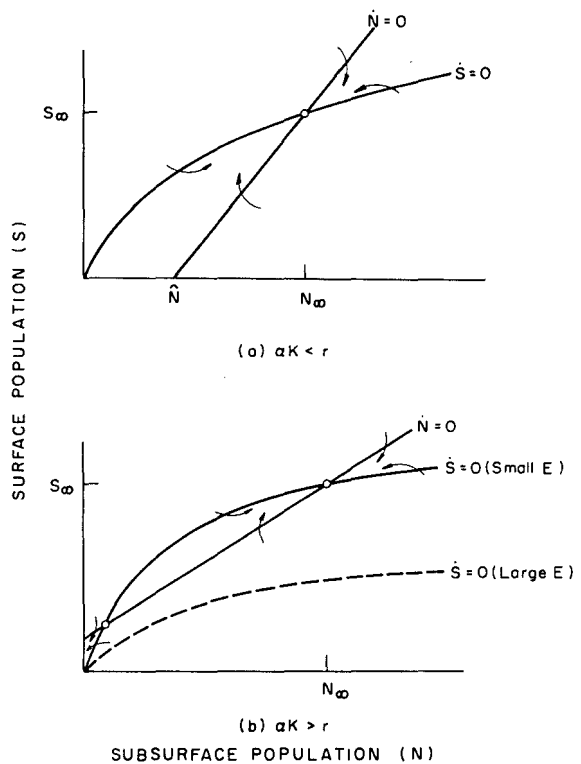


FIGURE 4.—Trajectory diagrams for model B: a stable equilibrium exists at point $(N_\infty, S_\infty)$; in diagram (b) an unstable equilibrium also exists for small E, but both equilibria disappear for large E. Case (a): intrinsic schooling rate less than intrinsic growth rate; population cannot be depleted below $\hat{N}$ by surface fishery. Case (b): intrinsic schooling rate greater than intrinsic growth rate population can theoretecally be shed to arbitrarily low levels; the transition from $N = N_\infty^-$ to $N = 0$ is "catastrophic"; see also text and Figure 5(b).

multivalued for this case. Model B exhibits an explicit mathematical "catastrophe."

The significance of multivalued yield-effort curves for fishery management has been discussed by Clark (1974, 1976); see also Anderson (1977). As effort $E$ expands from a low level, the catch follows the upper stable branch (Figure 5(b)), possibly with some lag. But once $E$ exceeds the critical level $E_c$, sustainable yield drops discontinuously to zero and the fish population goes into a steady decline. Subsequent decreases in effort do not necessarily result in recovery of the fishery, which may become "trapped" at a position of low abundance. This behavior is characteristic of the "catastrophe" situation (here the so-called "fold" catastrophe (Zeeman 1975)). In general, once a catastrophic jump has occurred, a large-scale change in the control variable (effort) is required
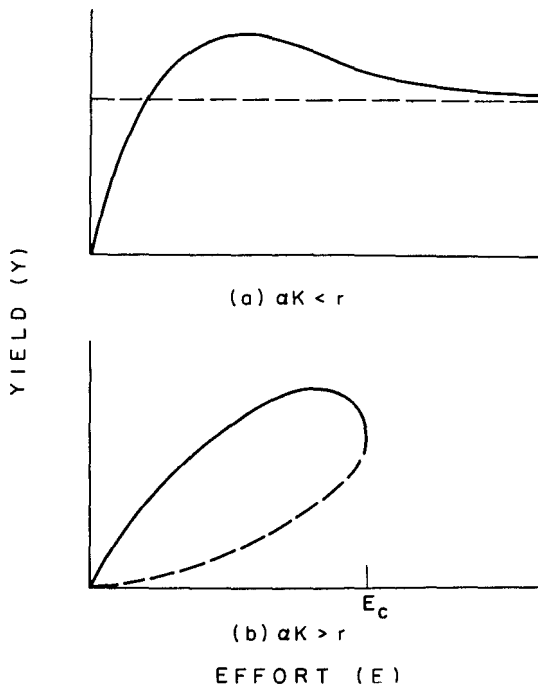
FIGURE 5.—Equilibrium yield-effort curves for model B. Case (a): intrinsic schooling rate less than intrinsic growth rate; yield approaches a positive asymptotic value as effort approaches infinity. Case (b): intrinsic schooling rate greater than intrinsic growth rate; yield undergoes a catastrophic transition when effort exceeds critical level $E_c$.



FIGURE 6.—Catastrophic surface ($\Sigma$) corresponding to model B: This surface describes the equilibrium population level (N) as a function of effort (E) and intrinsic schooling rate ($\alpha$K). Path I represents the development of the fishery, as effort increases, in the case that $\alpha$K < r, while Path II corresponds to the case $\alpha$K > r. In the latter case the fishery experiences a catastrophic collapse at point P.

in order to return the system to the original stable equilibrium.

The behavior of our model (submodel B) can be described in terms of Figure 6, in which the horizontal plane represents the "control space," with effort $E$ as the basic control and intrinsic schooling rate $\alpha K$ as a parameter (which in some cases might also be subject to manipulation, or to stochastic variation). The vertical axis represents subsurface stock size $N$. The surface $\Sigma$ is the locus of equilibrium solutions for our model.

Two possible paths for the development of the fishery are also shown in Figure 6. (Simulated versions of these paths will be presented below.) Path I, corresponding to Figure 5(a), occurs if $\alpha K < r$; here there is a steady decline in the equilibrium population level $N = \hat{N}$ as the effort parameter increases. (If $E$ varies rapidly over time, then equilibrium conditions will not prevail, and the actual development path will diverge from Path I lying on $\Sigma$. Figure 6 is still useful for understanding the dynamics in this case, however.)

Path II, with $\alpha K > r$, behaves similarly to Path I

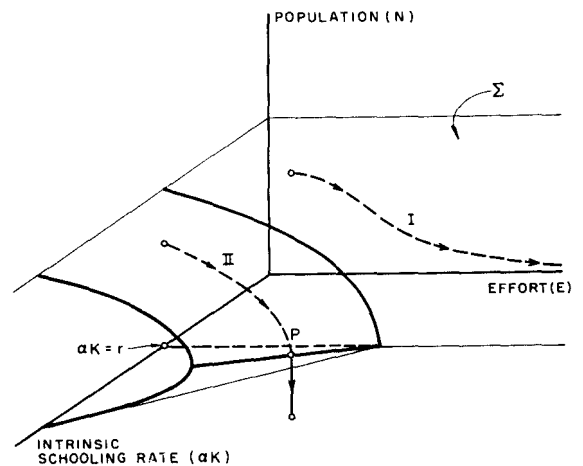for small levels of effort, but then suddenly falls over the "edge" of the catastrophe surface $\Sigma$, at point $P$. (Notice that for $\alpha K > r$ the surface $\Sigma$ folds under itself, the upper sheet $N = \hat{N}$ and the lower sheet $N = 0$ being stable equilibria, while the middle sheet $N = N^\dagger$ is unstable. This surface shape is the typical "cusp" catastrophe of Thom 1975.)

The management implications of the theory will be discussed later; the question of robustness of the models will be taken up in the appendices.

Figure 6 stresses the significance of the parameter $\rho = \alpha K$ for the interactive dynamics of aggregation and fishing. For tuna, $\rho$ may be age-dependent, as suggested by the differences in age distribution between longline and purse seine catches. Also, as noted previously, $\rho$ may vary over time and space as a result of environmental gradients. The theoretical consequences of such complexities have yet to be investigated (Mangel see footnote 6).

A "cusp" catastrophe surface similar to that depicted in Figure 6 can also be used to describe the response of the tuna fishery to simultaneous exploitation of the surface schools and the subsurface (background) population. If a given level of fishing mortality $f_s$ is applied to the subsurface population, the effect will be to replace our dynamic Equation (15) by

$$\frac{dN}{dt} = rN(1 - \frac{N}{N}) - f_s N - \theta$$

$$= (r - f_s) N (1 - \frac{r}{r - f_s}\frac{N}{N}) - \theta.$$

Thus the net biological growth rate becomes $r - f_s$ and the condition for catastrophic behavior in submodel B becomes

$$\alpha K > r - f_s.$$

If we now consider effort $E$ in the surface fishery and mortality $f_s$ in the subsurface fishery as control variables (now assuming $\alpha K$ = constant), it is clear that the surface of equilibrium $N$-values has the same nature as shown in Figure 6. Thus while the surface fishery might be "subcatastrophic" in the absence of any subsurface fishery, the development of the latter might transform the system into a catastrophic region.

One further possibility is worth noting. As remarked earlier, the schooling behavior of tuna may be influenced by environmental factors, particularly the depth of certain thermal isoclines. If so, the system might switch randomly between catastrophic and noncatastrophic states. Under these circumstances the fishery might exist for sometime at a level of stable sustained yield, but could suffer a catastrophic collapse induced by unusual, or unusually protracted environmental conditions.

The practical importance of these possibilities is increased by the fact that CPUE is likely severely to misrepresent the decline in abundance of the tuna population. In the first simulation reported below, for example (Figure 7), CPUE falls by only 20% even though the tuna population declines by over 99%.

## A SIMULATED CATASTROPHE

Figures 7 and 8 show the outcome of two simulations based on submodel B. (These simulations employed the discrete-time version of the population-dynamics submodel, as described in Appendix A. Qualitatively the results are the same as for the continuous-time model.) The following parameter values were utilized:

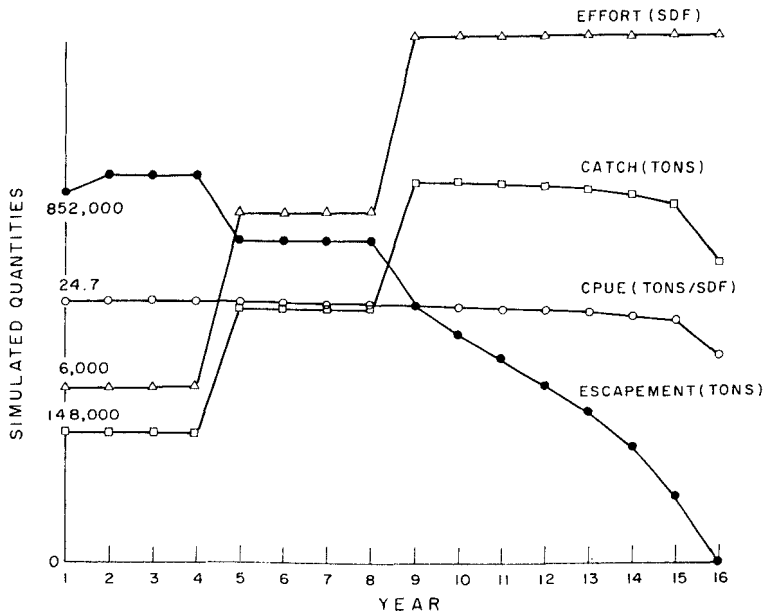$$K = 5,000 \text{ attractors}$$
$$\chi_0 = 0.5$$



FIGURE 7.—Simulation results: model B, "catastrophic" case. Effort (measured in standardized days fishing (SDF)) is increased at years 1, 5, and 9. The final effort level produces a catastrophic but gradual decline in the tuna population, which is not "picked up" by the catch-per-unit-effort (CPUE) index until the population has been essentially eliminated. (Scales for the four curves are linear but not related; see initial values shown.)
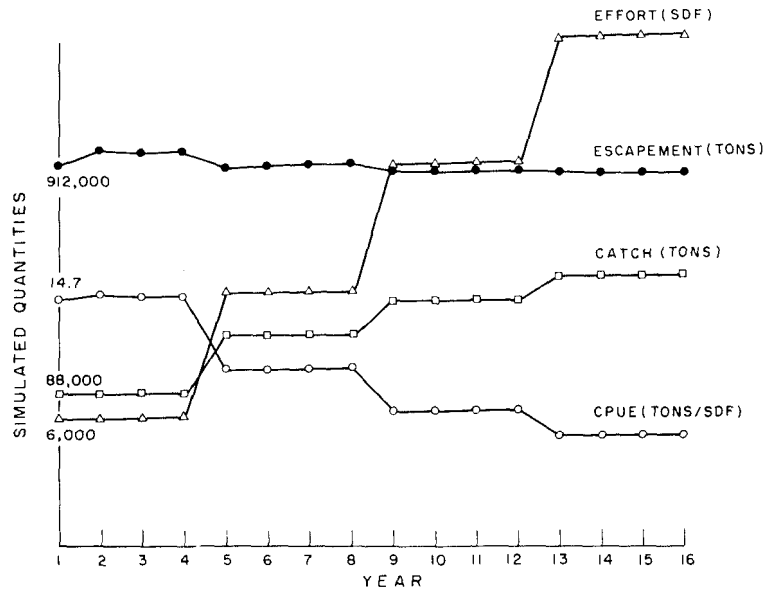
FIGURE 8.—Simulaion results: Model B, noncatastrophic case. In this case, CPUE (catch per unit effort) seriously overestimates the decline in tuna abundance. SDF = standardized days fishing.

$$Q^* = 50 \text{ tons}$$
$$b = 2 \times 10^{-4} \text{ per vessel day}$$
$$r_{\underline{a}} = 1.5 \text{ per annum}$$
$$N = 10^6 \text{ tons.}$$

In the first simulation (Figure 7) we set $\alpha = 10^{-5}$, implying an intrinsic schooling rate of 5% per day. Since this is well in excess of the intrinsic growth rate of 0.11% per day, a catastrophe is observed. In the second simulation (Figure 8) we set $\alpha = 1.5 \times 10^{-7}$, implying an intrinsic schooling rate of 0.075% per day, which is below the intrinsic growth rate.

In Figure 7, effort is fixed at 6,000 vessel days for years 1-4, then 12,000 vessel days for years 5-8, and finally 18,000 vessel days for all later years. The escapement population stabilizes at about 890,000 tons by year 4, and stabilizes again at about 735,000 tons by year 8. However in years 9-17 the effort level is above $E_c \cong 15,000$ vessel days, and the population is steadily reduced, ultimately to a level <100 tons. Although the population decline itself occurs gradually, neither catch nor CPUE shows any marked decline until the tuna population has crashed. For example, the decline in catch (and CPUE) in year 14 is 2.5% relative to the level for year 1, and in year 15 is 5.4% relative to the same level. Even in year 16, when the tuna population is virtually destroyed, the catch (and CPUE) falls by only 20%.

The same effort profile was used in the simulation shown in Figure 8, except for an additional increase in effort at year 12. In this simulation, CPUE declines significantly, but the population level is only slightly reduced. The biological explanation lies in the low rate of schooling in comparison with the first simulation. Because of this low schooling rate, increased effort mainly has the effect of reducing the surface population, and (at the levels shown here) has little effect on the subsurface population. This also explains why CPUE is much lower, at any fixed $E$, than in the first simulation.

Finally, Figure 9 shows the results of a simulation based on submodel A, using the same parameter values as for Figure 7. This simulation indicates that, as expected, submodel A behaves quite similarly to traditional fishery models.

## MANAGEMENT IMPLICATIONS

The models described above, and in the appendices, indicate that traditional methods of fishery management may be inappropriate in cases where aggregation processes significantly affect the fishery. On the one hand, such processes may be the source of bias in CPUE indices of stock abundance. On the other hand, these processes may also lead to a catastrophic relationship between fishing effort and sustainable yield. The latter situation will be especially serious in the event that CPUE underestimates declines in abundance.

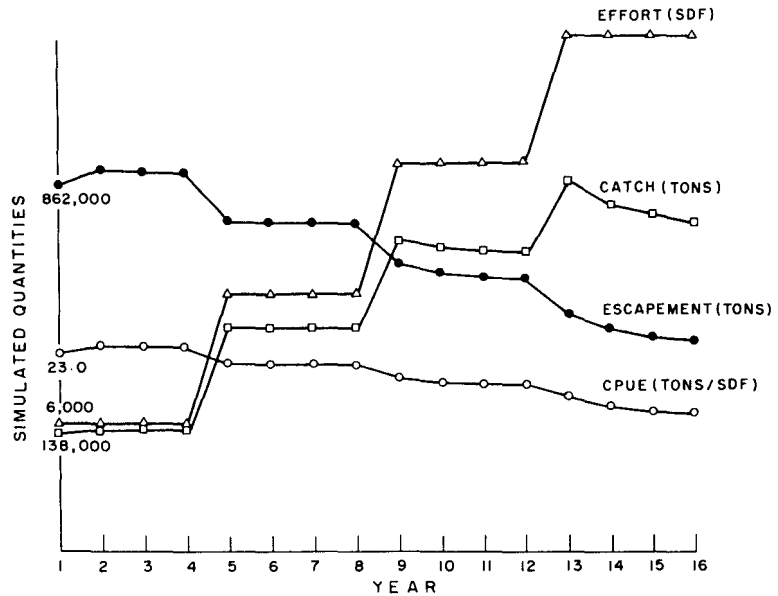In addressing the management implications of

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FIGURE 9.—Simulation results: Model A. The behavior of the model is similar to that of traditional fishery models. SDF = standardized days fishing; CPUE = catch per unit effort.

these theoretical results, for a particular fishery, we face two main problems. First, what is the likelihood that the fishery in question does involve an aggregation process, and if so, that catastrophic conditions may prevail? (We remark again that catastrophic conditions may be the result of processes other than aggregation.) Secondly, given that such conditions may exist, what are the implications for management policy?

If an aggregation process is known to exist, our models suggest that the next question that ought to be addressed is whether aggregation is density dependent, and if so, to what extent it depends on population abundance? Also, the rate parameters of the process should be determined. Unfortunately this information may be extremely difficult to obtain, and the question arises whether inferences can be drawn from data supplied by the fishery, such as catch-effort data, school size, density of schools, size composition of catches, and so on.

For example, if aggregation is density dependent, then the size of the aggregated (surface) population will decrease with the size of the residual (subsurface) population. For the case of tuna, either the number or the size of schools (or both) should decrease as the fishery develops. But the converse implication cannot be made: school size and/or number may decrease merely because the surface population is reduced by fishing pressure. Unless a direct, independent abundance estimate of the subsurface population is available,

the interpretation of such fishery data may remain ambiguous.[9]

The possibility that aggregation may lead to catastrophic yield-effort relationships lends a sense of urgency to the question of achieving a fuller understanding of the dynamics of the aggregation process. But whenever such catastrophic relationships seem possible, for whatever reason, a conservative approach to management appears appropriate. In view of the uncertainties involved, quotas should probably be established at a level lower than the estimated maximum sustainable yield. Furthermore, since depletion may nevertheless occur unexpectedly, emphasis should be placed on achieving a high degree of controllability of the fishery. To a certain extent this necessity has been recognized by the Inter-American Tropical Tuna Commission, the Director of Investigations now being empowered to close the yellowfin tuna fishery in the event of a sharp decline in CPUE. However, if the decline were truly "catastrophic," more drastic measures, such as a moratorium of some duration, might become necessary. Although the possibility may seem remote at present, we feel that further attention

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[9]Various alternative indicators of depletion, involving size composition of the catch and the results of cohort analysis, are in fact employed by the Tuna Commission and have demonstrated no severe change that can be attributed to the fishery. The validity of such indicators should not be affected by the presence of an aggregation process, but we have not attempted to extend our model to include cohort structure.

needs to be given to these problems. Experience gained from other fishery failures suggests that control may be extremely difficult to achieve unless expansion of the fishing industry is kept under control. For domestic fisheries operating within 200-mi zones, such control is now a possibility. For international pelagic fisheries, such as the tropical tuna fisheries, however, the problem of entry limitation remains unresolved.

## ACKNOWLEDGMENTS

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# APPENDIX A

The purpose of these appendices is to test the robustness of our models, by introducing alternative submodels for population dynamics (Appendix A) and for the schooling process (Appendix B). In this appendix we replace the continuous-time Schaefer model by a discrete-time stock-recruitment model. We postulate a fishing season of given length, during which the stock is fished down, followed by an interim season which results in the replenishment of the stock. The purpose of this exercise is not particularly to provide a more realistic model of tuna population dynamics, but simply to enquire whether our main results are independent of the type of model employed. (See Clark 1976, chapter 7, for a general discussion of models of the sort considered here.)

Our alternative Model A is governed by the equations

$$\left.\begin{aligned}\frac{dS}{dt} &= \alpha KN - \beta S - b\chi_0 ES \\[1mm] \frac{dN}{dt} &= -(\alpha KN - \beta S)\end{aligned}\right\} \quad 0 \leqslant t \leqslant T \quad \text{(A1)}$$

$$N(0) = R, \ S(0) = \alpha KR/\beta \qquad \text{(A2)}$$

where $R$ denotes recruitment prior to the fishing season, and $T$ denotes the length of the fishing season. In Equation (A2) we also assume, for simplicity, that the surface population $S$ reaches equilibrium with $N$ before the fishing season begins.

Let $P = N(T)$ denote escapement at the close of the fishing season. From the linearity of Equations (A1) it follows that $P$ is a linear function of $R = N(0)$:

$$P = C_E \cdot R \qquad (C_E = \text{constant} < 1). \quad \text{(A3)}$$

Clearly $C_E$ is a decreasing function of $E$; it is easily seen that

$$\lim_{E \to +\infty} C_E = \exp(-\alpha KT). \qquad \text{(A4)}$$

If $G(P)$ now denotes the stock-recruitment function, the coupling between successive years is given by the equations

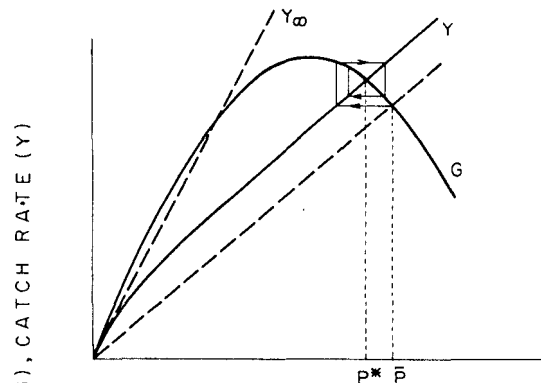$$\left.\begin{aligned}R_{k+1} &= G(P_k) \\[1mm] P_k &= C_E R_k\end{aligned}\right\}. \qquad \text{(A5)}$$

If, for example, $G(P)$ is quadratic:

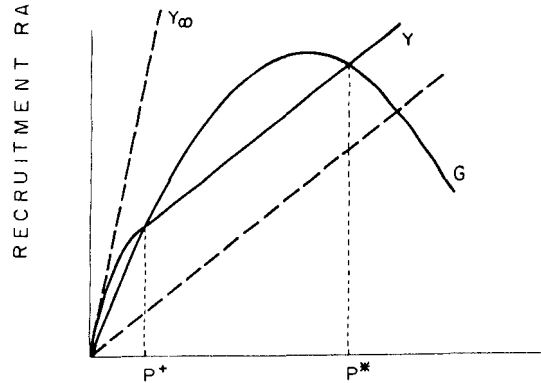$$G(P) = gP(1 - P/\bar{P}), \qquad \text{(A6)}$$

the equilibrium escapement level $P_\infty$ is easily calculated:

$$P_\infty = \begin{cases} \bar{P}(1 - 1/gC_E) & \text{if } gC_E > 1 \\ 0 & \text{if } gC_E \leqslant 1. \end{cases}$$

Exhaustion of the stock by the surface fishery is thus possible if and only if



FIGURE 10.—Fishery dynamics for the discrete-time models; schooling model B. $G$ = net population growth curve; $Y$ = catch curve; $Y_\infty$ = limiting position of $Y$; $P^*$ = population equilibrium for given $Y$. Case (a): intrinsic schooling rate less than intrinsic growth rate; escapement population cannot be reduced below level $\hat{P}$ by surface fishery. Case (b): intrinsic schooling rate greater than intrinsic growth rate: population can be fished to arbitrarily low levels; $P^+$ denotes an unstable equilibrium. (The corresponding yield-effort curve is similar to Figure 5(b).)

$$\exp (\alpha KT) > g,$$

i.e., if and only if the intrinsic schooling rate (over the duration of the fishing season) exceeds the intrinsic growth rate.

It is also clear that the yield-effort curves for this model have the same appearance as in Figure 3. Hence the behavior of the two models is closely analogous; bifurcations do not arise.

The discrete-time version of model B is obtained by replacing the expression $(\alpha KN - \beta S)$ in Equation (A1) by $\alpha KN(1 - S/S^*)$. This gives rise to a nonlinear escapement-recuitment relationship

$$P = \Psi_E(R).$$

It can be shown (we omit details) that

$$\lim_{R \to 0} \Psi_E'(R) = \exp(-\alpha KT)$$

$$\lim_{E \to \infty} \Psi_E(R) = \exp(-\alpha KT) \cdot R$$

$$\lim_{R \to \infty} (R - \Psi_E(R)) = b\chi_0 S^* TE.$$

The resulting dynamics can be described in terms of Figure 10. If $\alpha KT < \sigma = \ln g$ the model is noncatastrophic (Figure 10(a)), having a single equilibrium $P^*$ (escapement) which approaches $\hat{P} > 0$ as $E \to +\infty$. (If $g > 2$ the equilibrium at $P^*$ may be unstable, even "chaotic," for small $E$ (May 1974), but this possibility will not concern us here.) But if $\alpha KT > \sigma$ a second, unstable, equilibrium $P^+$ emerges, and a bifurcation occurs at some critical effort level $E = E_c$.

To summarize, this appendix has demonstrated that the qualitative predictions of our schooling strategy models are independent of the basic population dynamics of the tuna population. Although we have explicitly established this fact only for two specific models, it should be clear that the theory will remain valid for a large variety of other models, including alternative forms of the growth and stock-recruitment functions and including delayed-recruitment models as well as cohort models. In all cases, the nature of yield-effort curves will depend critically upon a) the relationship between intrinsic schooling rate and biotic potential and b) the schooling strategy of tuna to the extent that school size is sensitive to the total tuna population.

## APPENDIX B

In this appendix, we present two detailed, kinetic models of the schooling behavior of tuna and tuna-porpoise complex formation. The models are more general that either model A or model B, which are in fact special cases of the models developed in this appendix. Since our basic assumptions are quite different from those used in the body of the paper, it is interesting that equivalent results can be obtained, at least in special cases.

The models are based on the following assumption: in some large area of ocean, $\Omega$, there are $T(t)$ core tuna schools and $K(t)$ "attractors" (porpoise schools or logs) at time $t$. We assume that the core schools move independently of each other and that the motion is random.

We first assume that when an attractor and $\gamma$ ($\gamma \geq 1$) tuna schools "collide" (i.e., come within some critical distance), a tuna-attractor complex is formed. Let $C(t)$ denote the number of tuna-attractor complexes at time $t$. The fishery is assumed to fish only on these complexes. We shall postulate different mechanisms of complex formation and analyze the resulting kinetic equations. The kinetic equations are derived assuming a law of "mass action" similar to the one used in chemical kinetics (Moore 1972).

We shall not consider the mechanism by which the core tuna schools are formed. Whenever it is necessary for the analysis, we shall assume that the number of core schools has a logistic growth function. This assumption is derived by firstly assuming that the biomass of tuna, $N(t)$, has a logistic growth function. Namely, if no fishing occurred and no complexes formed:

$$\frac{dN}{dt} = rN(1 - N/N_0) \qquad \text{(B1)}$$

where $N_0$ is the carrying capacity of $\Omega$, in terms of biomass of tuna. Let $S_0$ denote the weight of a core school. Then we have

$$\frac{dT}{dt} = rT(1 - T/T_0) \qquad \text{(B2)}$$

where $T(t) = N(t)/S_0$ is the number of core schools at time $t$.

A model in which the tuna-attractor complex is formed by one collision between $\gamma$ tuna schools and one attractor is first analyzed. Submodel A of the paper is a special case of this model. We show that

the harvest rate is a nonlinear function of effort and saturates as $E \rightarrow \infty$. Consequently $Y/E$ is not a valid biomass estimate. We discuss other possible biomass indices, the behavior of $T(t, E)$ as a function of effort and the sensitivity of the results to the parameters which appear in the kinetic equations.

Next, a multistep complex formation process is considered. A two-step model is analyzed in full detail. Submodel B is contained as a special case. In addition to exhibiting all of the features of the one-step model a multistep mechanism may lead to "catastrophic" behavior. The catastrophic behavior was not built into the model but arises naturally from the dynamics.

The models presented in this appendix (particularly the multistep model) are based on what appear to be reasonable assumptions about the schooling behavior of tuna and formation of the complexes.

The ultimate behavior of the system (fishery + tuna + porpoises) does not appear to be an artifact of the models, but a result of the basic assumptions that the tuna form into schools and that the fishery seeks tuna schools associated with attractors. In fact, Thom's (1975) theorem on the structural stability (robustness) of unfoldings asserts that small modifications of our models will not alter the qualitative behavior.

The analysis of discrete-time versions of our models is relatively intractable. Numerical studies are underway. We do not expect the results will be qualitatively different from the continuous-time results. The analysis presented in Appendix A supports this expectation.

We have not included spatial effects (e.g., diffusion) in our kinetic equations. The addition of diffusion greatly complicates the analysis of the kinetic equations. However, preliminary work based on the recent theory of Aronson and Weinberger (1975) has been carried out, treating the kinetic equations with spatial dependence. We expect that if diffusion is added to the models in this appendix, the transitions between high and low tuna steady states may occur at effort levels lower than those predicted by the models without diffusion.

## Single-Step Collision Model

In this model we assume that $\gamma$ tuna schools collide, at once, with one attractor to form a complex:

$$K + \gamma T \underset{\beta}{\overset{\alpha}{\rightleftharpoons}} C. \tag{B3}$$
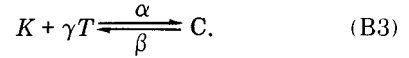
The rate constants $\alpha$, $\beta$ measure the association and dissociation rates of the complex. The complexes are fished at a rate $bE$ with capture ratio $\chi_0$:

$$C \xrightarrow{\chi_0 bE} K + \text{harvest of } \gamma \text{ schools.} \tag{B4}$$
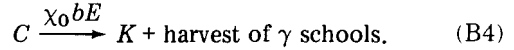
Equation (B3) indicates that $\gamma$ schools must be present for a complex to form. In particular, if $\gamma > 1$ this model does not allow for the formation of "partial" complexes, with fewer than $\gamma$ tuna schools in the complex. It is clear that this assumption is restrictive; later we relax it and allow for complexes with $1, 2, \ldots, \gamma$ tuna schools.

The kinetic equations corresponding to Equations (B3) and (B4) are

$$\dot{T} = g_T - \alpha K T^\gamma + \beta \gamma C \tag{B5}$$

$$\dot{K} = g_K - \alpha K T^\gamma + \beta C + bE\chi_0 C \tag{B6}$$

$$\dot{C} = \alpha K T^\gamma - \beta C - bE\chi_0 C ; \tag{B7}$$

in Equations (B5) and (B6) $g_T$ and $g_K$ are the tuna and attractor growth functions, respectively ($g_K = 0$ for logs).

The term proportional to $T^\gamma$ arises in the following way. Consider a small area of ocean, $a$. The probability, $p$, that a tuna school is in $a$ should be proportional to $a/\Omega$ and to $T$:

$$p = k\frac{a}{\Omega} \cdot T = \tilde{k}T. \tag{B8}$$

If a complex containing $\gamma$ tuna schools is to form, $\gamma$ schools must be in $a$. Since the tuna schools move independently and randomly, the probability of finding $\gamma$ schools in $a$ is proportional to $p^\gamma = \tilde{k}^\gamma T^\gamma$. (A more precise analysis would lead to $\tilde{k}T(T - 1)(T - 2)\ldots(T - \gamma + 1)$ instead of $\tilde{k}T^\gamma$, since once a school is in a specified area of ocean, there remain $T - 1$ schools to be distributed over the ocean. Once the location of two schools has been specified, there remain $T - 2$ schools, etc. When $T$ is large, as we are assuming, $\tilde{k}T^\gamma$ is a good approximation to the exact expression.)

The steady-state number of complexes is determined by setting $\dot{C} = 0$. We obtain

$$C = \frac{\alpha K T^\gamma}{\beta + bE\chi_0}. \tag{B9}$$

The instantaneous rate of harvest, $Y$, is the product of (the number of complexes) × (the encounter rate $bE$) × (the capture ratio $\chi_0$) × (the number of schools per complex). Thus

$$Y = \frac{bE\chi_0 \gamma \alpha KT^{\gamma} S_0}{\beta + bE\chi_0}. \qquad (B10)$$

If $\gamma = 1$, Equation (B10) becomes

$$Y = \frac{bE\chi_0 \alpha KTS_0}{\beta + bE\chi_0} \qquad (B11)$$

which is, with the exception of $S_0$, identical to Equation (11A). The additional factor $S_0$ arises here because we are considering numbers of tuna schools, whereas model A of the main part works directly with tuna biomass.

Model A is thus a subcase of the model in this section. Hence, we have provided a second physical picture for the mechanism which generates model A used in the paper.

Equation (B11) exhibits a saturation as $E$ increases and is similar to results obtained in the Michaelis-Menten approach to enzyme kinetics (White et al. 1973). This is not unexpected, since our models are based on the assumption that the attractors "catalyze" the fishery.

The tuna and attractor steady states are determined from the steady-state versions of Equations (B5) and (B6). Adding Equations (B6) and (B7) gives

$$g_K = 0, \qquad (B12)$$

which we assume has a solution $K = K_c$. (Note that this model does not allow for the loss of attractors due to fishing.) The steady-state tuna population satisfies

$$0 = g_T - \alpha KT^{\gamma} + \beta\gamma \left[\frac{\alpha KT^{\gamma}}{\beta + bE\chi_0}\right] \qquad (B13)$$

or

$$g_T = \alpha KT^{\gamma}\left[\frac{bE\chi_0 - \beta(\gamma - 1)}{\beta + bE\chi_0}\right]$$

$$= \alpha KT^{\gamma} f(E,\gamma). \qquad (B14)$$

Since the case in which $\gamma = 1$ was analyzed in the body of the paper, we shall not consider that

case here. We shall briefly consider the case of $\gamma \geqslant 2$. This case may be of little interest in the actual tuna fishery, but there may be other instances where $\gamma \geqslant 2$ is interesting (e.g., animal populations).

When $E$ is small, so that $bE\chi_0 < \beta(\gamma - 1)$, the coefficient $f(E,\gamma)$ is negative. Equation (B14) has a graphical solution sketched in Figure 11. The steady-state tuna level, $T_s$, is greater than the "natural level" $T_0$, but this is explained as follows. At any time there are a certain number of tuna schools bound in the complexes. The remaining, uncomplexed, tuna achieve the steady state level $T_0$. The total number of tuna, however, is $T_0$ plus the number in the complexes.

As $E$ increases, a level of effort is reached so that $f(E,\gamma) = 0$. At this point, Equation (B14) becomes

$$g_T = 0. \qquad (B15)$$

The tuna level is at the natural steady state, because tuna are removed from the complexes as quickly as they enter the complexes.

As $E$ increases further, $f(E,\gamma) \to f_\infty$, where $f_\infty = 1$ is the limit as $E \to \infty$ of $f(E,\gamma)$. Equation (B14) becomes

$$g_T = \alpha KT^{\gamma}. \qquad (B16)$$
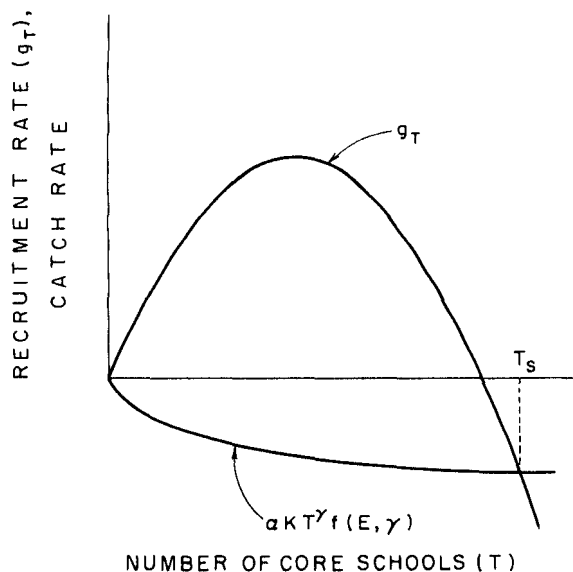
The graphical solution of Equation (B16) is



FIGURE 11.—Graphical determination of the steady-state tuna population ($T_s$) for the one-step kinetic model, when the natural dissociation rate is greater than fishing mortality (see text).

sketched in Figure 12. When $\gamma \geqslant 2$, it is impossible to overfish the tuna into extinction (compare Figure 12 with Figure 2, which corresponds to the case $\gamma = 1$). The reason for this behavior is that, as the tuna level decreases, the rate of formation of complexes, $\alpha K T_\gamma$, decreases much more rapidly since $\gamma \geqslant 2$. When $T$ is small, it is unlikely that a complex will form. This result should be contrasted with the case of $\gamma = 1$, in which is it possible to overfish the tuna to extinction.

From Equation (B10) we have

$$Y/E = \frac{b\chi_0 \gamma \alpha K T^\gamma S_0}{\beta + b E \chi_0} . \qquad (B17)$$

Thus, if $\beta >> bE\chi_0$ we obtain

$$T^\gamma \propto Y/E \qquad (B18)$$

so that

$$T \propto (Y/E)^{1/\gamma}. \qquad (B19)$$

Thus $(Y/E)^{1/\gamma}$ is a possible biomass index, if $\beta >> bE\chi_0$.

If $bE\chi_0 >> \beta$, then

$$Y/E \approx \frac{\gamma \alpha K T^\gamma}{E} S_0. \qquad (B20)$$

In this limit a possible biomass index is $(Y)^{1/\gamma}$. Thus, the catch itself is a biomass index.
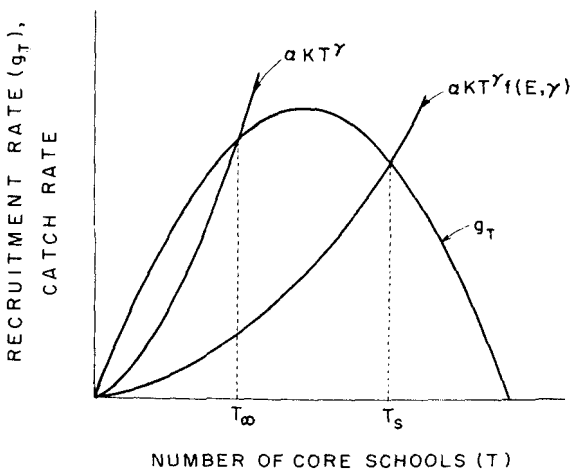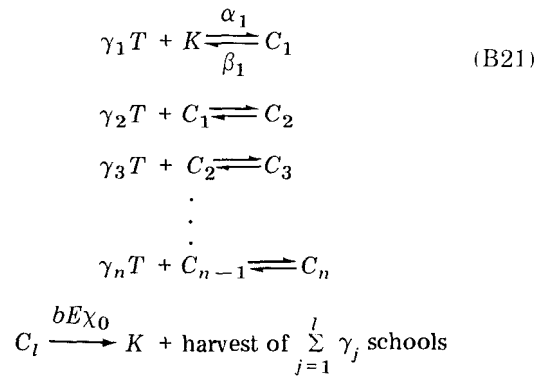


FIGURE 12.—Graphical determination of the steady-state tuna population $(T_s)$ for the one-step kinetic model, when fishing mortality is greater than the natural dissociation rate (see text).

In the intermediate region $\beta \approx bE\chi_0$ it appears that no simple biomass index is available.

The determination of the appropriate biomass index depends upon the size of $bE\chi_0/\beta$. This is a natural measure since it compares the rate at which complexes are dissociated due to fishing with the natural dissociation rate $\beta$.

## Multistep Collision Model

The model in the last section is somewhat unrealistic in that the complex with $\gamma$ tuna schools is formed only if the $\gamma$ schools collide simultaneously with an attractor. Hence, the model did not allow for complexes with $\gamma - 1, \gamma - 2, \ldots, 1$ tuna school per complex. A more realistic model is one in which the tuna-attractor complexes form by a multistep mechanism:

$$\gamma_1 T + K \underset{\beta_1}{\overset{\alpha_1}{\rightleftharpoons}} C_1 \qquad (B21)$$

$$\gamma_2 T + C_1 \rightleftharpoons C_2$$

$$\gamma_3 T + C_2 \rightleftharpoons C_3$$

$$\vdots$$

$$\gamma_n T + C_{n-1} \rightleftharpoons C_n$$

$$C_l \overset{bE\chi_0}{\longrightarrow} K + \text{harvest of } \sum_{j=1}^{l} \gamma_j \text{ schools}$$

where $l = 1, \ldots, n$.

More detail could be added, e.g., when a complex $C_l$ is fished, $j = 1, \ldots, l$ tuna schools might be removed with probabilities $p_{lj}$. When all $\gamma_k = 1$, Equation (B21) is undoubtedly the most realistic model presented here. (Since the probability that two core schools are added at the same instant is essentially zero, the idea of stepwise addition of schools seems justified.) The kinetic equations corresponding to the reactions in Equation (B21) are (for $\gamma_j = 1$ for all $j$)

$$\dot{T} = -T \left\{ \alpha_1 K + \sum_{j=2}^{n-1} \alpha_j C_{j-1} \right\} + \sum_{j=1}^{n} \beta_j C_j + g_T(T)$$

$$\dot{C}_1 = \alpha_1 KT - (\beta_1 C_1 + bE\chi_0 C_1 + \alpha_2 C_1 T) + \beta_2 C_2$$

$$\dot{C}_n = \alpha_n C_{n-1} T - (\beta_n C_n + bE\chi_0 C_n$$
$$+ \alpha_{n+1} C_n T) + \beta_{n+1} C_{n+1} \quad (n \geqslant 2) \quad (B22)$$

$$\dot{K} = -\alpha_1 KT + bE\chi_0 \left\{ \sum_{j=1}^{n} C_j \right\} + \beta_1 C_1 + g_K(K).$$

Steady states of the system are obtained if we set the left-hand sides in Equation (B22) equal to zero. We then find that the steady states are determined by:

$$C_1 = \frac{\alpha_1 KT + \beta_2 C_2}{\beta_1 + bE\chi_0 + \alpha_2 T}$$

$$C_n = \frac{\alpha_n C_{n-1} T + \beta_{n+1} C_{n+1}}{\beta_n + bE\chi_0 + \alpha_{n+1} T} \quad (n \geq 2) \qquad \text{(B23)}$$

$$g_K(K) = 0$$

$$0 = -T \left\{ \alpha_1 K + \sum_{j=2}^{n-1} \alpha_j C_{j-1} \right\} + \sum_{j=1}^{n} \beta_j + g_T(T).$$

Equations (B22) and (B23) seem to represent a fairly realistic model of the fishery dynamics. A full analysis of these equations would be quite illuminating. However, as it is, the analysis of this model quickly becomes intractable. In order to illustrate the behavior of this model, we will analyze the case $n = 2$ (for arbitrary $\gamma_1$, $\gamma_2$):

$$K + \gamma_1 T \xrightleftharpoons[\beta_1]{\alpha_1} C_1$$

$$C_1 + \gamma_2 T \xrightleftharpoons[\beta_2]{\alpha_2} C_2$$

$$C_1 \xrightarrow{bE\chi_0} K + \text{harvest of } \gamma_1 \text{ tons} \qquad \text{(B24)}$$

$$C_2 \xrightarrow{bE\chi_0} K + \text{harvest of } \gamma_1 + \gamma_2 \text{ tons.}$$

The results of the analysis of three-(or higher)step mechanisms should be similar to the analysis of the two-step mechanism.

The multistep model provides a picture of the tuna-porpoise bond which appears to be relatively realistic. For example, we may imagine that the first $\gamma_1$ schools are bound strongly to the complex ($\alpha_1$ large, $\beta_1$ small) and that the next $\gamma_2$ schools are bound less strongly ($\alpha_2 < \alpha_1$, $\beta_2 > \beta_1$). Sharp's (1978) discussion of the effect of the thermocline on the tuna-porpoise association supports this model. In particular, it seems likely that the $\alpha_i$ and $\beta_i$ depend upon the location of the thermocline.

The kinetic equations corresponding to the multistep model are

$$\dot{T} = g_T - \alpha_1 T^{\gamma_1} K - \alpha_2 T^{\gamma_2} C_1 + \beta_1 C_1$$
$$+ \beta_2 C_2 + \gamma_1 \beta_1 C_1 + \gamma_2 \beta_2 C_2 \qquad \text{(B25)}$$

$$\dot{K} = g_K - \alpha_1 T^{\gamma_1} K + \beta_1 C_1 + bE\chi_0(C_1 + C_2)$$
$$\text{(B26)}$$

$$\dot{C}_1 = \alpha_1 T^{\gamma_1} K - \beta_1 C_1 - \alpha_2 C_1 T^{\gamma_2}$$
$$+ \beta_2 C_2 - bE\chi_0 C_1 \qquad \text{(B27)}$$

$$\dot{C}_2 = \alpha_2 C_1 T^{\gamma_2} - \beta_2 C_2 - bE\chi_0 C_2 . \qquad \text{(B28)}$$

In the steady state, we have

$$C_2 = \frac{\alpha_2 C_1 T^{\gamma_2}}{\beta_2 + bE\chi_0} . \qquad \text{(B29)}$$

Adding the steady-state version of Equations (B25)-(B28) gives

$$g_K = 0 \qquad \text{(B30)}$$

which we assume has the solution $K = K_e > 0$. The steady-state version of Equation (B27), using Equation (B29), is:

$$0 = \alpha_1 KT^{\gamma_1} - \beta_1 C_1 - \alpha_2 C_1 T^{\gamma_2} - bE\chi_0 C_1$$
$$+ \alpha_2 \beta_2 T^{\gamma_2} C_1 / (\beta_2 + bE\chi_0)$$

which can be solved to give the steady-state level of $C_1$ complexes:

$$C_1 = \frac{\alpha_1 KT^{\gamma_1}}{\beta_1 + \alpha_2 T^{\gamma_2} + bE\chi_0 - \alpha_2 \beta_2 T^{\gamma_2} / (\beta_2 + bE\chi_0)} .$$
$$\text{(B31)}$$

The instantaneous harvest rate is given by:

$$Y = bE\chi_0(\gamma_1 C_1 + (\gamma_2 + \gamma_1) C_2) S_0 \qquad \text{(B32)}$$

$$= \frac{bE\chi_0 S_0 \alpha_1 KT^{\gamma_1}}{\beta_1 + \alpha_2 T^{\gamma_2} + bE\chi_0 - \alpha_2 \beta_2 T^{\gamma_2} / (\beta_2 + bE\chi_0)}$$

$$\times (\gamma_1 + \gamma_2 \alpha_2 T^{\gamma_2} / (\beta_2 + bE\chi_0)) . \qquad \text{(B33)}$$

Note that if we set $\beta_1 = \beta_2 = 0$ and $\gamma_1 = \gamma_2 = 1$, Equation (B33) becomes

$$Y = \frac{bE\chi_0 S_0 \alpha_1 KT}{bE\chi_0 + \alpha_2 T} \times (1 + \alpha_2 T / bE\chi_0). \quad (B34)$$

With the exception of the multiplicative term $(1 + \alpha_2 T/bE\chi_0)$, Equation (B34) is equivalent to Equation (11) (model B) in the body of the paper. We shall show that the model presented in this section contains model B as a special case and also exhibits "abrupt" transitions, between multiple steady states.

As $E \rightarrow \infty$, the harvest rate saturates and

$$Y \rightarrow Y_\infty = \alpha_1 \gamma_1 S_0 K_e T^{\gamma_1}. \quad (B35)$$

Hence, when $E$ is large, $(Y)^{1/\gamma_1}$ is a biomass estimate.

When $E$ is small, Equation (B33) becomes

$$Y \approx \frac{bE\chi_0 S_0 \alpha_1 KT^{\gamma_1}}{\beta_1} \left( \gamma_1 + \frac{\gamma_2 \alpha_2}{\beta_2} T^{\gamma_2} \right), \quad (B36)$$

which can be written as

$$Y/E \approx h_1 T^{\gamma_1} + h_2 T^{\gamma_1 + \gamma_2} \quad (B37)$$

where $h_1 = \dfrac{b\chi_0 S_0 \alpha_1 K \gamma_1}{\beta_1}, \quad h_2 = \dfrac{h_1 \gamma_2 \alpha_2}{\gamma_2 \beta_2}. (B38)$

Unlike the one-step model, in the multistep model $Y/E$ is not a useful biomass estimate at any level of effort.

The steady-state tuna level is determined from the steady-state version of Equation (B25). After Equations (B29) and (B32) are used for the values of $C_1$ and $C_2$ and the resulting expression is simplified, we obtain

$$g_T = \alpha_1 T^{\gamma_1} K \frac{\Delta(\alpha, \beta, E, T)}{\rho(\alpha, \beta, E, T)} \quad (B39)$$

where $\Delta = (\gamma_1 + 1) [\beta_1 \beta_2 + \beta_1 bE\chi_0]$

$$+ (\gamma_2 - 1)\beta_2 T^{\gamma_2}$$

$$+ \beta_2 bE\chi_0 + (bE\chi_0)^2 \quad (B40)$$

$$\rho = \beta_1 \beta_2 \quad (B41)$$

$$+ bE\chi_0(\beta_1 + \beta_2 + bE\chi_0 + \alpha_2 T^{\gamma_2}).$$

Because $\Delta$ and $\rho$ are so complicated, Equation (B39) is difficult to analyze as it stands. To simplify the analysis, we assume that $\beta_1 = \beta_2 \approx 0$. Physically, this means that the rate of dissociation of complexes due to fishing is much greater than the natural dissociation rate of complexes. Since our major interest is in the qualitative behavior of Equation (B39), this assumption seems acceptable.

If $\beta_1 = \beta_2 = 0$, Equation (B39) becomes

$$g_T = \frac{\alpha_1 T^{\gamma_1} KbE\chi_0}{bE\chi_0 + \alpha_2 T^{\gamma_2}}, \quad (B42)$$

which can be analyzed. We denote by $f(E, \gamma_1, \gamma_2, T)$ the right-hand side of Equation (B42). The solutions of Equation (B42) will be discussed according to the values of $\gamma_1$ and $\gamma_2$. A complete analysis of Equation (B42) is very involved. We shall present a partial analysis, in order to illustrate the types of behavior which may occur. We first consider the case in which $\gamma_1 = \gamma_2 = 1$. Equation (B42) becomes

$$g_T = \frac{\alpha_1 KbE\chi_0 T}{bE\chi_0 + \alpha_2 T}, \quad (B43)$$

which is analogous to Equation (11B) of the body of the paper. Consequently, we shall not pursue the analysis here. In the analysis of Equation (11B), we showed that Equation (B43) may have multiple steady states. As effort increases, a transition between the steady state where the tuna level is high and the steady state where $T = 0$ is possible if $\alpha_1 K > g_T'(0)$ (the "catastrophe" condition).

In the one-step model, a complex containing two tuna schools was formed only if the two schools, at once, came into close contact with an attractor. That model did not exhibit multiple steady states, or even the possibility of overfishing the tuna into extinction.

On the other hand, if the complex that contains two schools is formed by a stepwise process, so that schools are added to an attractor one at a time, "catastrophic" behavior and extinction of the tuna are possible.

Sudden transitions in population (catastrophes) are usually difficult to predict. However, the model presented here leads to a natural measure of overfishing. From Equations (B29) and (B31), when $E$ is large we have

$$C_1 \sim \frac{1}{bE\chi_0} \qquad C_2 \sim \frac{1}{(bE\chi_0)^2} . \qquad \text{(B44)}$$

Consequently, if overfishing is occurring, the number of complexes with two tuna schools is much less than the number of complexes with one school. As effort increases further, the fishery will find more and more attractors without any associated tuna schools. Such observations should act as a warning that the tuna are being over-exploited. We note that it is possible that CPUE will not decrease, even though the number of tuna schools per complex is decreasing (see Figure 7).

A host of complex solutions and bifurcations can be determined if the values of $\gamma_1$, $\gamma_2$ are not 1. Since $\gamma_1 > 1$, $\gamma_2 > 1$ do not have an immediately obvious interpretation for fishery dynamics, we will not consider those cases here.

In this Appendix, we have taken an approach to modelling the fishery that is substantially different from the approach in the main part of the paper. The results obtained here complement the main results, and extend them. We have shown that models A and B presented in the paper arise as special cases of the kinetic models in this Appendix. It is clear that these models could be greatly elaborated and many other details explored.