AGGREGATION OF FISH THROUGH VARIABLE DIFFUSIVITY

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ABSTRACT

It is argued that the commonly used model for the dispersal of tagged fish may be inappropriate; for yellowfin tuna at least, it is unable to reproduce the observed spatial variation of abundance. An alternative model, in which the local environment affects both the local population dynamics and the dispersal of fish, is presented.

Fishing is introduced using a simple bioeconomic model; the effect on the distribution of the population is surprising. Routine management questions such as maximizing production become difficult, if not impossible, within this heterogeneous model. Of particular interest are the interactions between a region of high production and its surroundings: at steady state with low rates of exploitation, there is net emigration from areas that can sustain larger populations, but the direction of net migration reverses as fishing pressure increases. Interaction between zones where different technologies are applied is investigated.

Skellam (1951) suggested adopting a diffusion model for the dispersion of inert particles for describing the motility of living organisms, based upon their random motion. Beverton and Holt (1957) put it within a fisheries context, and Jones (1959 and 1976) explained its use in detail. The method is simple: a velocity vector is determined for each recovery, the mean of these is calculated, the differences between each vector and their mean are obtained, and finally the mean of the squares of these residuals is calculated. This term, the "diffusion coefficient" or "diffusivity", a^2, and the mean velocity vector, v, are used to characterize the movements of entire populations. The first governs the dispersion of a population while the second parameterizes any directed, often seasonal, migration.

If there is no directed migration then, for a fish with constant range, the effective area searched per unit time is determined solely by a^2. Analysis of tagging experiments in the eastern Pacific Ocean have not yet shown clear seasonal direction in movements of either yellowfin, *Thunnus albacares*, or skipjack tuna, *Katsuwonus pelamis*, in this area (Hunter et al. 1986). Directed migration, v, is not explicitly incorporated into the model presented, but could be.

Previous mathematical models for the dispersion of fish have assumed the coefficient of diffusion to be constant, so that the rate of transport due to dispersion is proportional to the gradient of abundance. Bayliff and Rothschild (1974) and Bayliff (1979, 1984), however, reported that estimates of a^2 varied by between one and two orders of magnitude for both yellowfin and skipjack tuna in the eastern Pacific. There appeared to be some pattern to these results; for instance, close to islands and shallow banks, where it has been suggested that prey is more abundant (Sund et al. 1981), a^2 was often less. However, there has been no attempt to formulate the pattern formally, and variations in measured coefficients of diffusion have been treated simply as noise or errors of measurement.

Taking a typical value for the coefficient of diffusion leads to a problem in the case of yellowfin tuna; any single value for a^2 estimated from tagging experiments predicts an almost homogeneous distribution. This is not observed; catch rates tend to be high where prey are believed to be abundant (Sund et al. 1981). Spatial variability of production is unlikely to be sufficient to maintain the variability of abundance that is demonstrated by variability in catch between areas.

This inconsistency does not arise with a variable coefficient of diffusion. Kareiva and Odell (1987) considered a diffusion process for ladybugs preying upon aphids in which the probability of course reversal was increased when the aphid had recently eaten. They showed that this foraging mechanism concentrated predators in areas of high prey density. A similar mechanism is suggested for pelagic fish; if the coefficient of diffusion is a function of local habitat then distributions of tuna can be more realistically simulated. The mechanism involves den-

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sity dependence of the relevant organism, but only indirectly because the density is moderated by the local environment.

For apex predators, such as yellowfin and skipjack tuna, the quality of their environment is determined primarily by the availability of prey; the local degree of saturation by predators is determined by the availability of prey. Saturation is defined as the biomass of predators divided by the maximum that the locality could sustain; thus it is dependent upon the intrinsic richness of the locality and the number competing for those riches. For any particular area, an increase in predators will decrease the availability of prey; this will, in turn, reduce the quality of that area for those predators.

THE MODEL

The biomass of a particular species at any point (x,y) may be modelled:

$$\frac{dA(x,y)}{dt} = F(A(x,y)) + \frac{\partial^2}{\partial x^2}\left(\frac{a^2}{4}A(x,y)\right) + \frac{\partial^2}{\partial y^2}\left(\frac{a^2}{4}A(x,y)\right) - qE(e,y)\,A(x,y). \qquad (1)$$

That is to say, the rate of change of the local biomass with time, t, is determined by the production function, $F(A(x,y))$; the catch equation, where q is the catchability coefficient and $E(x,y)$ is the fishing effort expended; plus the diffusion of fish into or out of the locality in both the x and y directions. The key parameter governing diffusion is a^2. It is either constant, or a function of local biomass and carrying capacity; variables that were also in the domain of F.

The production of biomass is modelled using a modification of the Schaefer (1954) model:

$$F(A(x,y)) = A(x,y)\left(r'\left(1 - \frac{A(x,y)}{K'(x,y)}\right) - M\right) \qquad (2)$$

where $r' = r + M$ and $K'(x,y) = ((r + M)/r)\,K(x,y)$. The modification simply separates natural mortality, M, from the intrinsic growth rate: the modified form uses the gross, rather than net intrinsic growth rate, r. The form of $F(A(x,y))$ is unchanged; the function was rewritten so that birth and death processes would be more explicit. In particular, the carrying capacity is unchanged, as can be checked by multiplying through the above expression for $F(A(x,y))$ by r', and substituting for $K'(x,y)$.

The term a^2 may be a constant, D, or proportional to the local abundance divided by the local carrying capacity. That is to say, unless constant,

$$a^2(x,y) = DA(x,y)/K(x,y).$$

Effort was determined by a simple bioeconomic equation taken from Clark (1985):

$$\frac{dE(x,y)}{dt} = \alpha(pqA - c)\,E(x,y), \quad \text{if } E > 0; \qquad (4)$$

$$= 0 \text{ otherwise.}$$

p represents the price per ton received by fishermen, c is the cost to the fishermen of each unit of effort, and α is the proportion of profits reinvested. An implicit assumption is perfect liquidity, i.e., that a loss immediately causes a reduction in effort of the same magnitude as the increase created by a profit.

Equation (1), which represents the kernel of the model, is a nonlinear partial differential equation; it might be possible to solve it analytically, but it is difficult. Solutions were found numerically by iterating explicitly using finite differences.

The 5 million square nautical miles of the range of yellowfin tuna within the eastern Pacific is represented by a grid of 20 × 20 cells, each cell representing an area of approximately 2 degrees in both latitude and longitude. The northern and southern edges of the model grid were joined, as were the western and eastern edges; forming a torus and circumventing any boundary problems. Parameter D was set at 0.08, equivalent to 1,000 square nautical miles per day, a number within the mid range of those found by Bayliff (1984).

The carrying capacity for the region as a whole, and the intrinsic natural rate of increase, were obtained by fitting a Schaefer (1954) model to catch and effort data for this entire region.[2] This gave an annual value for r of 1.61, and an estimate for the carrying capacity of the entire region of 431,000 tons (IATTC in press). The annual rate of natural mortality was estimated at 0.8 by Hennemuth (1961). The catchability coefficient, q, is the probability that a particular fish will be caught by a unit

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of effort given that the effort and fish are in the same area, so q has dimension of (1/area). The estimated value of 0.000039 (IATTC in press) for the entire fishery was therefore multiplied by the number of cells, 400, to obtain the q for each cell.

The price of fish, p, was set at \$1,200 per ton, which approximated that of the last half of 1987 (Parks et al. 1988). The cost of a unit of effort, c, was estimated by assuming that in 1987 there existed an economic equilibrium, that is the fishermen just covered their costs in this year but made no net profits. If that were the case, the cost of a unit of effort would be simply the total catch times the price divided by the total effort for that year. This gives c to be approximately \$24,000 per days effort, which was used as the initial value for this parameter when exploitation was included. To evaluate the effect of different restraints upon fishermen in different areas, c was in some cases made position dependent. The proportion of profits reinvested in effort, α, was set arbitrarily at 0.2.

For the initial run all but two cells had carrying capacities set at 1,000 tons; the two exceptions, positioned at (10,5) and (10,10) were given carrying capacities of 10,000 tons. This range of a factor of 10 for the capacities was chosen because it corresponds with the range shown by annual productivity over the region (Berger et al. 1987). The total carrying capacity specified within the model, 418,000 tons, was close to that estimated for the fishery. The abundance for each cell was initially set at the local carrying capacity, except for the cells with the higher capacities where the abundance was 0.8 of that, to speed convergence. Every run of the model was continued until a steady state was evident; the possibility of multiple steady states, implicit in such a nonlinear model was not investigated.

RESULTS

The equilibrium distribution of abundance at zero exploitation was calculated for constant a^2. The abundance of tunas was little higher in the cells of high capacity than elsewhere. This was true even when the "hot" cells were given capacities 100 times that of the others, and when a^2 was reduced by a factor of 10, well below any observed value.

It was believed that if the area of the region of increased capacity were greater, then the leakage of extra production of fish would be less from that region, and a significant local increase in abundance might be seen. By analogy with a coal fire, individual coals cool quickly, but if they are grouped together, they have proportionately less surface area and so cool more slowly. The local increase in abundance was greater when the area of higher capacity was expanded, but most of the increased production of the local area still diffused away. The region of higher capacities was increased to 3 × 3 cells and even 5 × 5 cells, but there still was not the sort of variation in abundance that one can infer from catch records. Variations of the same order as appear to occur in the ocean were not found until a^2 was allowed to vary with the degree of saturation of the local carrying capacity.

Figure 1a shows the distribution of fish when

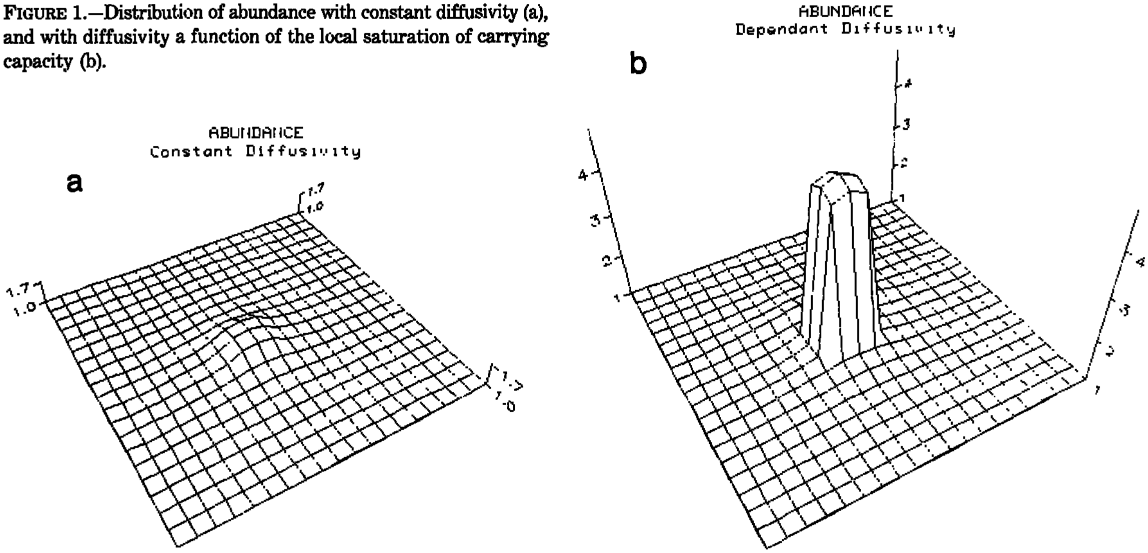

FIGURE 1.—Distribution of abundance with constant diffusivity (a), and with diffusivity a function of the local saturation of carrying capacity (b).

a^2 is constant, and there are 9 cells with carrying capacities 10 times that of the rest. These 9 cells are arranged in a square; the distribution of fish is almost constant. Compare this to Figure 1b, where a^2 is proportional to the degree of saturation of the local capacity. Varying the diffusivity in this way allows the fish to aggregate substantially. This heterogeneity may be maintained even if the cells with higher capacities are not contiguous, as in Figure 2a. The proportion of the biomass in each cell that originated in one of the two anomalous cells is shown in Figure 2b. The data for Figure 2b were prepared by keeping separate account of biomass produced in the two anomalous cells. This

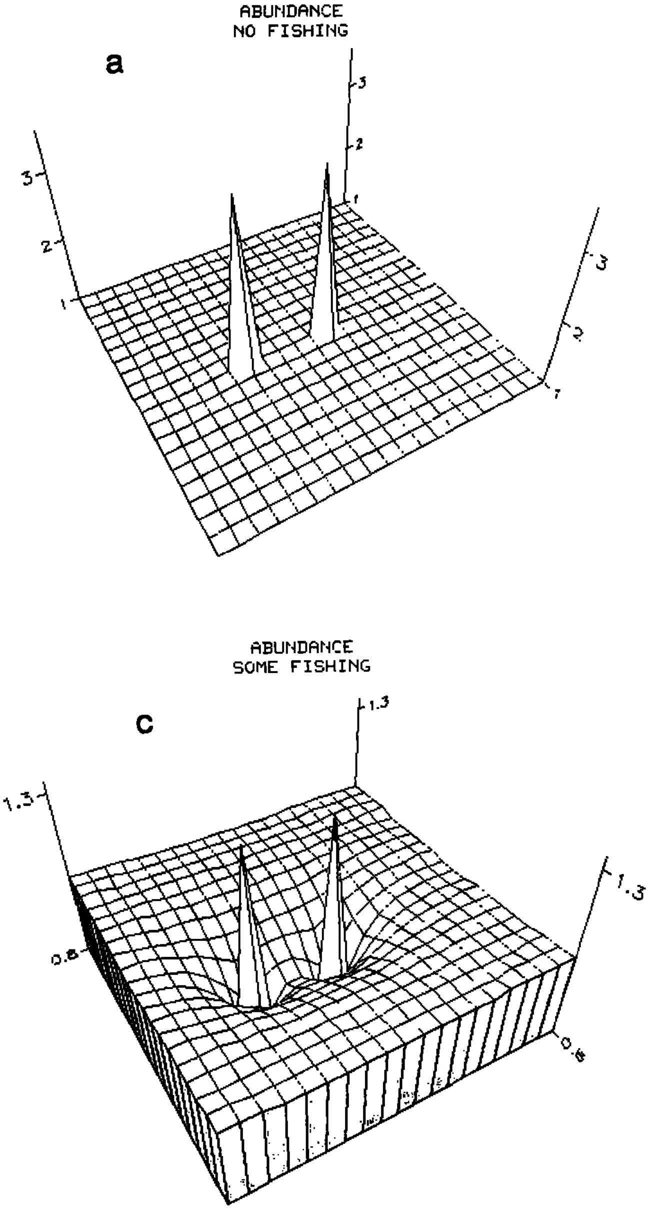

FIGURE 2.—Dependent diffusivity: distribution of fish when there is no fishing (a), and the proportion of the local biomass which originated within the two 'hot spots' (b). Fishing affects both the overall

biomass diffused and died as the rest, in proportion to its abundance; production was determined by the total biomass but ascribed according to location.

Fishing has an effect upon the distribution of fish; the effect is at first surprising (Fig. 2c). A relatively high cost per unit of effort constrains effort; a profit is possible only in those cells with the highest concentrations of fish. In such cells the effort increases until a profit is no longer realized. The abundance has then been reduced to a level that can sustain existing fishing operations, but the catch rate offers no incentive for further investment. From the equation for effort (Equation (4)), the equilibrium

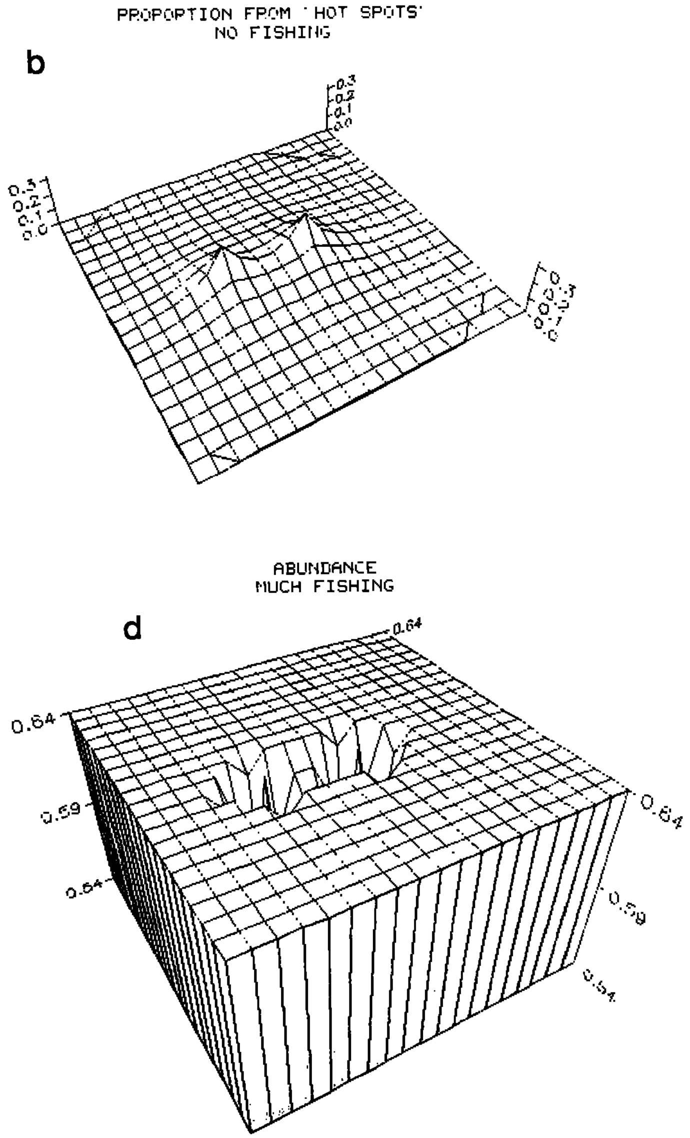

FIGURE 2.—*Continued*—abundance and its distribution (c). Halving the cost of effort halves the level to which the fishery can reduce local populations, and the area of fishing expands to most of the region (d).

abundance of fish in the absence of movement, A^*, would be $A^* = c/pq$. If, say, the cost of fishing, c, is reduced by half, it becomes profitable to increase the effort until the concentration of fish is half of what it was (Fig. 2d). Note also that this reduction in cost allows parts of the region with lower carrying capacities to be exploited. The term A^* determines the maximum equilibrium concentration of fish, and effort increases locally until the abundance of fish is reduced to that level. Effort has a levelling effect upon abundance; it is greatest in the cells with the greatest capacity. In the area immediately surrounding these cells of high capacity, which contain the maximum density, the abundance of fish falls to a minimum because of movement to the cells of high capacity. At this minimum fishing is unprofitable (less than A^*), so there is no exploitation in this area.

It was suggested earlier that regions surrounding islands might consist of enhanced habitat. Cells of higher carrying capacities may contain an island or group of islands with economic conditions significantly different from the rest of the region. The economic parameters need to be different for these cells. This is simply done; the model allows consideration of the effects of economic changes, both local and global, upon the fishery throughout the whole region.

A single island was considered; the island and its waters were assumed to be synonymous with a single cell having a capacity 10 times that of any other cell within the entire 20 × 20 cell region. Three regimes of fishing were considered: low exploitation with the cost of a unit of effort set at $24,000; a regime twice as intensive as a result of halving the cost of effort; and a mixed regime where the single cell of high capacity was exploited according to the parameters of low exploitation, while elsewhere the parameters were as for high exploitation. This could be thought of as a paradigm of development of the fishery if one is careful to ensure that units of effort from different types of fishing are comparable in that they have an equivalent effect upon the target population. It takes many days for a trolling boat to equal the impact a purse seiner has in one day.

The first regime might represent a relatively low level of technological development where further fishing becomes uneconomical while fish are still relatively abundant. Changes in technology might reduce the cost of effort, leading to the second regime with the cost cut by half. The model is such that effort increases everywhere while the abundance of fish is more than half of the previous maximum, and continues to increase until the abundance falls to that level. The mixed regime might represent the case where the higher technology could not be used close to the island because of technical considerations, such as lack of depth for purse seiners, or political ones, such as the prohibition of such fishing to protect artisanal fishermen.

Table 1 shows the effect on catches and sustainable effort of these changes in technology or policy. Technological advancement temporarily increases profits, which leads to greater effort and a decline in catch per unit effort (CPUE). For the parameters used here, the long-term effect of higher technology is to increase the effort expended within the island's waters by 20%, but the CPUE is halved; hence the local catch decreases substantially. Effort is sustainable offshore with the change to the model, and the catch from the newly exploited area is much higher than the total catch which was previously taken only from the island's waters. If the new technology were kept from the island's waters, then the original CPUE could be maintained only by halving the original local effort. Thus, if the new technology were introduced to the high seas, one would expect half as many artisanal boats to be viable, and these boats would catch about half of what had been taken from their waters. If the managers of the island's waters chose to maximize catch by allowing access to the new technology, they could still only stabilize the catch at 60% of what it had been before the advent of the high-seas fleet.

TABLE 1.—Effort and catches at equilibrium under different economic conditions. CPUE at high exploitation is half that at low exploitation.

	Low rate of exploitation	High rate of exploitation	Mixed rates of exploitation
Effort/catch within hot spot	2.03/40.6	2.43/24.3	1.01/20.2
Total effort/catch elsewhere	0.0/0.0	38.53/385.3	39.29/392.9

DISCUSSION

Although I feel certain that constant diffusivity is an inappropriate model for tunas, there may other models at least as appropriate as that presented here. (See Okubo (1980) for an extensive review of diffusion within models of ecology.) If the basic structure of the model were correct; the assumption that a^2 is a linear function of local saturation might not be. The structure of the model is testable;

in particular it predicts that heavy fishing will enhance immigration. In a practical model, one might use a^2's directly when possible and find a convenient empirical function for indirect estimation of a^2 at other times.

The dimensions of a^2 are (distance^2/time); a^2 can be thought of as the average distance moved before taking another direction, multiplied by the mean speed over that interval (Beverton and Holt 1957). Even at constant speed, an individual fish can reduce its a^2 simply by changing course more frequently, so the fish could maintain an almost constant position if it were to change direction frequently enough. The upper limit is determined by the fish's ability to hold a course. Walker et al. (1985) showed that yellowfin tuna can detect a geomagnetic field and suggested that they might use it for navigation. This appeared incongruous in a fish whose direction at any time is said to be random. But, if it allows each fish to hold any random course longer, then it allows the fish to get away from an area it has found to be unsatisfactory. Fish in an isolated undesirable area will all be, in a sense, navigating away from that area, but in different directions; that is why the population in that area does not exhibit any directed migrations; they all cancel each other.

Given that there is heterogeneity in the distribution of prey, it is not surprising that predators have evolved towards matching that distribution. A fish cannot know where the greatest concentrations of prey are and then navigate to them, but it can reduce the chances of leaving a favorable region and increase its search area when hunting is poor. A tuna varying a^2 inversely with habitat quality has advantage over any with constant a^2. In poor habitat the fish has high a^2, and its net movement over any period is greater. Upon entering a more favorable area, a^2 drops, and the fish weaves a more intertwined track over a smaller area. Thus the individual spends more time in the more favorable areas; a population of such individuals accumulates in the better habitat without any directed migration.

The most patently unrealistic aspect of this model is its topology, that of a torus. This is a convenience chosen to avoid boundary conditions at the spatial limits of the model and to avoid speculating about an additional mechanism that maintains the fish within those limits. Specifying more realistic boundary conditions might include seasonal changes in the positions of those boundaries.

A species constrained within such plastic boundaries would demonstrate seasonal changes in distribution, and tagging would suggest directed movement. But, no long-range directed navigation would be necessary. At one end of their distribution, as the boundary of intolerable conditions encroaches, fish might retreat, or simply die. Elsewhere the population might simultaneously be expanding by the chance movement of individuals into freshly habitable waters.

For those species whose directed movements are real, one can simply add a term, v, to the model. Determining the (time varying) values for this might require more tagging effort than that required simply for evaluating a^2.

There is probably some autocorrelation in the direction of movement of the fish, but this would not affect the conclusions drawn from this model. Individuals emanating from a point source at first show a clear orientation away from this source; if each individual's course exhibits autocorrelation, then this orientation persists but diminishes through time. Eventually the individuals lose their orientation to the source, and direction is independent of position. The void initially created at the source is filled, and the simpler diffusion equation may be considered an acceptable model for describing the distribution of individuals (Skellam 1973).

In a more realistic model, the topography of the environment would be very complicated, with variation at many scales. This model is a very inexact description of the population it purports to describe (yellowfin tuna in the eastern Pacific), but habitat dependent diffusion may be applicable to other regions and other species. Kleiber[3] has shown that the simple diffusion model is also inadequate for skipjack tuna in the western Pacific. Beamish and McFarlane (1988) suggested that the dispersal of adult sablefish may be affected by the local density. Sablefish are much more sedentary than tunas; Beamish and McFarlane estimated that local fluctuations of abundance are determined by recruitment of juveniles and by fishing.

Scientists who have examined data for tunas tagged close to islands refer to two populations: one which remains associated with the islands, which must have a low a^2; and one that breaks away, which necessarily has a higher value for a^2. Individuals that leave one island are, of course, still susceptible to "capture" by another island, or perhaps a shallow bank. The model described here suggests

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[3] Pierre M. Kleiber, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1988.

that the difference in a^2's is more an effect than a cause of their positions.

Figure 2b makes an important point. Although, in the absence of fishing, the anomalous cells (the "hot spots") act as a net source of fish to the entire region of the model, there is still much mixing of fish into these sources. The importance of mixing depends upon the rate of dispersal of fish, mortality rate, and the distance involved. In this case, it is clear that it would be foolhardy, having divided the region into "substock areas", to then try to manage these areas in isolation.

The effect, seen in Figures 2c and 2d, that fishing has of creating a minimum in the abundance close to the maximum, needs to be explained further. Figure 2a shows the steady-state abundance before any extraction of fish; the net flux through each cell is zero. The probability that a given individual within each cell migrates must be inversely proportional to the number of others within that cell, as otherwise the total emigrating would not be constant for all cells. Let us suppose that fishing starts in just one cell, that with most fish. The balance of migration is temporarily disturbed. Fish move in at the same rate as before but, because there are now fewer fish inside than there were, there is less emigration from that cell. This causes a net flow towards the cell that is being fished despite the fact that this cell still contains more fish; the variability of a^2 allows flow "uphill", against the gradient in abundance. The flow to the cell being fished causes the abundance to drop in its neighbors, which then stimulate a net flow from cells more distant from the fishing. A dynamic equilibrium is established when the amount removed by fishing is met by a balance of local production and net immigration to the cell of exploitation. This immigration is fed by the rest of the region, where carrying capacity is constant and flow is "downhill". The transport of fish towards exploitation is maintained by a gradient of abundance and amplified by the differences in a^2 created by that gradient. Fishing at the places of highest capacity makes them sinks for the entire region, drawing fish in from everywhere. The ability of a fishery to mold the topography of the abundance may lead to a founder effect in (model) fisheries. An established fishery will depress the abundance in the surrounding region, which may make fishing uneconomical. This might not have been so if fishing had started simultaneously.

There is no clear evidence, as far as I am aware, that abundance minima surround areas of exploitation. It is the bane of fisheries science that little information is obtainable from marginal areas; most of our information comes from fishermen who do not generally choose to work where they expect fewer fish. In a more realistic model, with habitats changing realistically (time-scales of a few hours), the system may rarely be near equilibrium. This, and the fact that there is variability on very different scales in space as well as time, make it unlikely that the simple topography illustrated here would be seen in practice. Indeed, most fishermen would suggest that the spatial and temporal topography of abundance is extremely complicated. The variability of q, the notional catchability coefficient, may be due to changes in the degree of aggregation of the fish. Too disperse and the fish may not be economic to catch. Too aggregated and a few boats might be fortunate, but they would be overwhelmed and unable to fully exploit what they had found.

Migration of fish between different fishing areas tends to diminish the attraction of catch reduction as a management tool to a manager responsible for just one of those areas; high rates of exploitation effectively enlarge the range of the fishery. With a^2 a function of the immediate environment, the effect is enhanced; reducing the catch reduces immigration and enhances emigration.

Within the Schaefer (1954) model, biological production is highest at half the carrying capacity. Figure 2a shows that the abundance at the hot spots, while higher than elsewhere, is less than 40% of the carrying capacity of those spots. In this sense the populations of fish at the "hot spots" are below optimum, even before any fishing takes place. Fish are exported to the surrounding region, increasing the abundance there to more than the local carrying capacity. Thus the surrounding region has negative net production. Maximizing local production everywhere is impossible, and working out the distribution of effort that would lead to maximum overall production would be difficult. Harvesting outside of the hot spots would reduce the abundance of fish at these hot spots and so reduce the productivity there still further. Regardless, it is unrealistic to suppose that a total ban on fishing where catch rates are highest is feasible, or even desirable. The economic portion of this model allows us to investigate the effects of intrinsic change and less intrusive management.

Table 1 indicates that the effects of an increase in power of the fishery may not be positive in a region where the fishery is viable before the change. Here power denotes the technology that allows fishing to be viable at a particular index of abundance of fish. Reducing the cost, as was done explicitly within the model, has the same effect as increasing catchability or, perhaps through improved handling and distribution of the fish, raising the price. Whatever the reason, increasing power allows fish to be profitably caught when there are fewer of them. This enables fishing to take place at locations other than the hot spot, but the change reduces the catch at the hot spot even though effort there increases. There is the familiar reason of local overexploitation, but also the reduction in fish elsewhere decreases the flow of fish to the hot spot. If the hot spot contains an island with a government that can create local restrictions on effort, the local catch rate could be held at the original level only by drastically reducing the effort to far less than that of the original local fishery. This might prove a difficult choice for a small island dependent upon fishing.

CONCLUSION

A constant value for a^2 creates an unrealistic, almost homogeneous distribution of fish. A variable a^2 allows fish to spend more time in good habitats. They can vary a^2 by changing direction more or less frequently. Preliminary observations indicate that a^2 does vary as this notion predicts.

Fishing, by removal of competing individuals, increases the potential production of a surviving individual; thus the habitat appears enhanced and migrants are more likely to stay. In this way fishing has an impact far beyond its location. The catch rate close to an island is partially sustained by tapping the resources from the contiguous region. An effect of a high-seas fleet is to reduce the gradient of habitat saturation from what would occur if there were only fishing close to islands; thus the relationship between a high-seas fleet and artisanal inshore fishery is clearly competitive.

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LITERATURE CITED

BAYLIFF, W. H.

1979. Migrations of yellowfin tuna in the eastern Pacific as determined from tagging experiments initiated during 1968–1974. Inter-Am. Trop. Tuna Comm., Bull. 17:445–506.

1984. Migrations of yellowfin and skipjack tuna released in the central portion of the eastern Pacific Ocean, as determined by tagging experiments. Inter-Am. Trop. Tuna Comm., Intern. Rep. 18, 107 p.

BAYLIFF, W. H., AND B. J. ROTHSCHILD.

1974. Migrations of yellowfin tuna tagged off the southern coast of Mexico in 1960 and 1969. Inter-Am. Trop. Tuna Comm., Bull. 16:1–64.

BEAMISH, R. J., AND G. A. MCFARLANE.

1988. Resident and dispersal behaviour of adult sablefish (*Anaplopoma fimbria*) in the slope off Canada's west coast. Can. J. Fish. Aquat. Sci. 45:152–164.

BERGER, W. H., K. FISCHER, C. LAI, AND G. WU.

1987. Ocean productivity and organic carbon flux: Part 1 Overview and maps of primary production and export production. Scripps Inst. Oceanogr., SIO Ref. 87-30, 67 p.

BEVERTON, R. J. H., AND S. J. HOLT.

1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric., Fish Food (G.B.), Ser. II, 19, 533 p.

CLARK, C. W.

1985. Bioeconomic modelling and fisheries management. John Wiley and Sons, N.Y., 291 p.

HENNEMUTH, R. C.

1961. Year class abundance, mortality and yield-per-recruit of yellowfin tuna in the eastern Pacific Ocean, 1954–1959. Inter-Am. Trop. Tuna Comm., Bull. 6(1):1–51.

HUNTER, J. R., A. W. ARGUE, W. H. BAYLIFF, A. E. DIZON, A FONTENEAU, D. GOODMAN, AND G. R. SECKEL.

1986. The dynamics of tuna movements: an evaluation of past and future research. FAO Fish. Tech. Pap. 277, 78 p.

IATTC.

In press. Annual report of the Inter-American Tropical Tuna Commission 1987.

JONES, R. J.

1959. A method of analysis of some tagged fish returns. Cons. Perm. Int. Explor. Mer, J. 25(1):58–72.

1976. The use of marking data in fish population analysis. FAO Fish. Tech. Pap. 153, 42 p.

KAREIVA, P., AND G. ODELL.

1987. Swarms of predators exhibit "prey taxis" if individual predators use area restricted search. Am. Nat. 130(2):233–270.

OKUBO, A.

1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, N.Y., 213 p.

PARKS, W., P. DONLEY, AND S. HERRICK.

1988. The tuna industry in 1987. Tuna Newsl. 89:1–6. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla.

SCHAEFER, M. B.

1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-Am. Trop. Tuna Comm., Bull. 1(2):25–56.

SKELLAM, J. G.

1951. Random dispersal in theoretical populations. Biometrika 38:196–218.

1973. Diffusionary processes in population biology. *In* M. S. Bartlett and R. W. Hiorns (editors), the mathematical theory of the dynamics of biological populations, p. 63–85. Acad. Press, N.Y.

SUND, P. N., B. BLACKBURN, AND F. WILLIAMS.
1981. Tunas and their environment in the Pacific Ocean: a review. Oceanogr. Mar. Biol. Annu. Rev. 19:443–512.

WALKER, M. M., J. L. KIRSCHVINK, AND A. E. DIZON.
1985. Magnetoreception and biomineralization of magnetite fish. *In* J. L. Kirschvink, D. S. Jones, and B. J. Macfudden (editors), Magnetite and magnetoreception in organisms, p. 317–337. Plenum Publ. Corp.