PN ABK-249
75234

WORKING PAPER SERIES

FISHERIES STOCK ASSESSMENT

TITLE XII
Collaborative Research Support Program

Fisheries Stock Assessment CRSP Management Office
International Programs, College of Agriculture
The University of Maryland, College Park, Maryland 20742

In cooperation with the United States Agency for International Development (Grant No. DAN-4146-G-SS-5071-00) the Fisheries Stock Assessment CRSP involves the following participating institutions:

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The University of Rhode Island—International Center for Marine Resource Development
The University of Washington—Center for Quantitative Sciences
The University of Costa Rica—Centro de Investigación en Ciencias del Mar y Limnología
The University of the Philippines—Marine Science Institute (Diliman)—College of Fisheries (Visayas)

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WORKING PAPER SERIES

Working Paper No. 69

PRELIMINARY MODEL DEVELOPMENT FOR CORAL REEF FISH ASSEMBLAGE RECOVERY FROM BLAST FISHING

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June, 1990

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The Fisheries Stock Asssessment CRSP (sponsored in part by USAID Grant No. DAN-4146-G-SS-5071-00) is intended to support collaborative research between U.S. and developing countries' universities and institutions on fisheries stock assessment and management strategies.

This Working Paper has been produced by The University of Rhode Island research component in collaboration with the University of the Philippines and in association with the International Center for Living Aquatic Resources Management. Additional copies are also available from the CRSP Management Office and from:

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ABSTRACT

The importance of coral reef and shallow tropical coastal areas for studies related to biodiversity is indicated. A continuous time Markov chain model for the recolinization of perturbed areas is developed and described. The application of this model to previous data on recolonization of benthic invertebrates gave results identical to the deterministic model of McArthur and Wilson (1967) for island biogeography. However, the stochastic nature of the new model is believed to provide more realism in application than the deterministic model previously developed. This latter model can be applied to data now being gather in a coral reef environment in the Philippines.

INTRODUCTION

Wilson (1989) has clearly pointed out the current global decline in biological diversity and the probable grave consequence of its loss. He also emphasized the fact that the task of studying biodiversity is still in an early stage of development. The report of the National Science Board (1989) referred specifically to marine biota and quoted Ray (1988) who suggested that disturbance and degradation of coastal zones is occurring as rapidly as tropical forest destruction. The Board also indicates that biological diversity is highest in the tropics and that these are the areas of highest risk. A specific example is provided by coral reefs which can be both highly diverse and extremely fragile.

Over two-thirds of the surface of planet earth is ocean, and the biota of the earth's oceans are essential to the structure and function of the global ecosystem. Although the global coastal zone covers only about 8 percent of the earth's surface (Ketchum, 1972), more than 50 percent of the entire human population lives within or very near it. In addition, about 90 percent of the total annual yield of living marine organisms is taken from the coastal zone. The biological diversity of the zone is very high, as attested to by the fact that of all living species of chordates, the class Osteichthys (bony fishes) contains the greatest diversity of species, more than 18,000 in contrast to a total of about 4,000 species of mammals. Tropical coral reefs and shallow coastal areas (especially in Southeast Asia) contain the most diverse fish communities in the world. It is clear that more attention needs to be focused on tropical coastal areas and coral reefs as centers of biological diversity, not only because they contain large numbers of species but also because these fragile environments are being increasingly affected by man's activities.

This project's overall objectives involve developing and testing new methodologies for detecting and assessing changes in biodiversity of tropical coral reef and shallow marine communities affected by destructive fishing methods, with special reference to blast fishing. The latter term refers to the use of various type of explosives for the capture of fish.

Blast fishing is one of the most common among illegal fishing activities in the Lingayen Gulf, the Philippines. Blast fishing is also common in other tropical third world. It poses a threat to the fishing industry due to the possibility of indiscriminate destruction of marine resources and the coralline environment. Studies are in progress to monitor the temporal recovery of areas affected by blast fishing, and to study the species composition and the size distribution of coral fish assemblages and the recovery rate of the coral reef environment.

This report is restricted to the conceptual development and description of a model for the recovery of fish assemblages or coral communities affected by blast fishing or other perturbations. The model is believed to be a refinement and extension of the original model described by McArthur and Wilson (1967) and applied by Saila (1975) for the recolonization of macroinvertabrates on dredged material which had been dumped in Rhode Island Sound.

MODEL ASSUMPTIONS

Consider a relatively large tropical coral reef area that has been significantly perturbed by some means, such as blast fishing, and has suffered substantial damage to its fish population. As the perturbed area recovers certain species of fish will begin to re-enter from the perimeter region, assuming the habitat is suitable. Evidence from

tropical reef studies indicates that this re-entry may be done primarily by juvenile fish or from their pelagic larval phase. It seems unlikely to expect large scale re-entry into this area by adult reef fish, since many species of reef fish tend to spend their entire life within very restricted areas (Sale et al., 1984). Hence, the availability of early life history stages may play a large role in the rate at which this re-entry occurs (Williams 1980: Victor 1982; Doherty 1983). A mathematical model describing the movement of species in and out of a perturbed area, such as a recovering blast site, would be of use in predicting its eventual state. In particular, inferences could be drawn from such a model about the number of species expected in the repopulated area as a function of recovery time. In addition, these results would indicate whether or not there are significant differences in the diversity and relative abundance of species in the repopulated site as compared to an equivalent pristine area. Use of a stochastic model permits such statistical comparisons.

Suppose there is a potential pool of P species of fish in the surrounding area. Assume the arrivals and departures of species into the depleted area are random. This assumption is based on the consideration that knowing the time since the last arrival or departure is of little or no value in predicting the time of the next event. Even in the extreme case of predator-prey relationships, the point in time that the predator species is aware of the presence of the prey species and subsequently enters this area, is random. It is also possible for a predator species to enter this area before a prey species is present. After a species has re-entered this area there may be several reasons for its departure/extinction from this area. For example, perhaps not enough fish from a given species have entered to create a necessary mass for survival. In addition a given species may not be able to locate a suitable food source or habitat and hence, some will not remain in this area. Intense competition amongst the species already present or the arrival of predators could also create an inhospitable

environment resulting in predation mortality or departure. All of these factors can be considered random in their occurrence. Hence, the arrivals and departures of a species in this area are Poisson events, which implies that the time between an arrival, or similarly a departure, is exponentially distributed. Note that the rate of arrivals should be dependent on the number of species already in the recovering site. Also, from the above discussion we would expect many species that enter this area to go extinct shortly after their arrival. This agrees with the usual behavior of an exponential model which likewise has a high occurrence of early failures. Moreover, as the number of species in the site increases, we would concurrently expect an increase in the extinction rate. The model to be described satisfies these characteristics.

It is recognized that the theory of island biography as developed originally by MacArthur and Wilson (1967) and this work which are closely related, may be oversimplifications in several respects. Variability within defaunated areas, dispersal across variable habitat gradients (β-diversity factors) and sequences of equilibria over time are not explicitly considered. However, we believe that all models are simplifications of reality, but the addition of stochasticity to the original model provides a practical advantage in its real world application.

MODEL DESCRIPTION

Let X_i, $i = 1, ..., P$, represent the time until the ith species enters the area. Then each X_i is an independent continuous random variable that is exponentially distributed. We will assume that each species is equally likely to enter this area and hence, that the average entry rate for each species is a constant, λ, i.e., X_i has a density function, $\lambda \exp(-\lambda t)$. We can now determine the distribution for the entry of a species

when n species have already migrated into the recovery area. Note that when a species is in the system i.e. the recovery area, it is temporarily taken out of the pool of potential species. Hence, when n species are in the affected area, P-n different species can potentially enter the system. Next order the random variables $X_1, \ldots, X_{p-n}$ and denote the ordered random variables by $X(1),\ldots, X(P-n)$ where $X(1) < \ldots < X(P-n)$. Thus, $X(1)$ represents the minimum time until another species enters and is the minimum of P-n exponentially distributed random variables. Therefore, $X(1)$ is exponentially distributed with mean $(P-n)\,\lambda$, which we shall denote by λ_n.

Again, assuming that n species are in the system, we next determine the distribution for the departure/extinction time. Let Y_i represent the time that the ith species remains in the repopulated area, $i = 1,\ldots,n$. We will assume that the rate at which any individual species leaves this area, μ, is constant. Since we have assumed that a species leaving an area is a random event, then each Y_i is exponentially distributed with density function $\mu \exp(-\mu t)$. Now, when n species are in the system, let $Y(1),\ldots,Y(n)$, represent the ordering of the random variables Y_i $i = 1,\ldots, n$. Hence, $Y(1)$ denotes the time when the first of these species leaves this area. Again, since each Y_i is exponentially distributed then so is $Y(1)$ with mean, $1/n\mu$. For consistent notation, we shall denote $n\mu$ by μ_n. We also note that when a species leaves the recovery area, it returns to the pool of species in the perimeter region. Hence, the number of potential species has increased to $P- n+1$. It is of interest to observe that under these assumptions, both λ_n and μ_n are linear functions of n, the number of species in the system.

Let us further consider the situation when n species, $n = 1,\ldots,P$, have entered the recovery area. We will refer to the process of repopulation as being in state n. We will assume that at most a single arrival and/or single departure can occur during a

small time period of length Δt. Hence, if the system is in state n at time t, the probability of a single arrival or departure in the interval $(t, t+\Delta t)$ for small Δt are $\lambda_n \Delta t$ and $\mu n \Delta t$, respectively. The probability of more than one arrival or more than one departure during a small time interval, ΔT, is $0(\Delta t)$ where:

$$\lim_{\Delta t \to 0} \frac{0(\Delta t)}{\Delta t} = 0$$

Thus, we have described a continuous-time Markov chain with states (0,1,...,P) for which transitions from state n can only be to state n-1 or n+1 in a small interval of time Δt.

Let $p_n(t)$ represent the probability of being in state n at time t. Then, we can obtain the following differential difference equations for $p_n(t)$ from the forward Chapman-Kolmogrov equations:

for n = 0,

$$\frac{dp_o(t)}{dt} = -\lambda_o p_o(t) + \mu_1 p_1(t) \qquad (1)$$

for $n \geq 1$,

$$\frac{dp_n(t)}{dt} = -(\lambda_n + \mu_n) p_n(t) + \lambda_{n-1} p_{n-1}(t) + \mu_{n+1} p_{n+1}(t) \qquad (2)$$

For the long-run behavior of our system, we derive the steady state solutions to these equations. In particular then, the derivative of $p_n(t)$ would be zero and hence, $p_n(t)$ would be a constant which we shall denote by p_n. The steady state solutions for these equations are well known and are given by:

$$p_n = \prod_{i=1}^{n} (\lambda_{i-1} / \mu_i) p_o \tag{3}$$

For our particular case, $\lambda_{i-1} = P - (i-1)\lambda$ and $\mu_i = i\mu$ which implies that p_n is:

$$p_n = \left(\prod_{i=1}^{n} (P - i + 1)\lambda / i\mu\right) p_o \tag{4}$$

or simply

$$p_n = \binom{P}{n} (\lambda/\mu)^n p_o \tag{5}$$

We can solve for p_o by applying the identity:

$$\sum_{n=0}^{P} p_n = 1 \tag{6}$$

which yields

$$p_o = (\mu / \mu + \lambda)^P \tag{7}$$

However, we can gain additional insight into the system by returning to equations (1) and (2) and investigating the expected state of the system at time t.

$$M(t) = \sum_{n=1}^{P} n\, p_n(t) \tag{8}$$

Taking the derivative with respect to time and substituting equation (2) into the summation yields the following linear differential equation (see appendix 1 for details):

$$M\ (t) = P\lambda + \mu)\, M(t) \tag{9}$$

If immediately after a perturbation the system is in state n_o, then we may use the initial condition, $M(O) = n_o$, to determine the solution to (9) as:

$$M(t) = (P\lambda / \lambda + \mu)\,[1-\exp\{-\lambda + \mu)t\}] + n_0 \exp\{-(\lambda + \mu)t\}. \qquad (10)$$

In most situations, it would be reasonable to let $n_0 = 0$ in equation (10), yielding:

$$M(t) = (P\lambda / \lambda + \mu)\,[\,1 - \exp\{-(\lambda + \mu)t\}] \qquad (11)$$

Figure 1 indicates the general shape of M(t) which would be controlled by the parameters λ and μ.

As $t \to \infty$ in (11), the steady state value for the expected state of the system is simply:

$$E(n) = P\lambda / (\lambda + \mu) \qquad (12)$$

Since M(t) is a monotone increasing function, we can determine the time until the system is within a specified bounded region of the steady state value. In particular, using equation (11) we can find the time $t_B = -(\lambda + \mu)^{-1} \ln(1-B)$ such that for $t \geq t_B$, then $M(t) \geq B\,(P\lambda / (\lambda+\mu))$. For example, if B equals .95 then for: $t \geq t_{.95} = 2.996\,(\lambda + \mu)^{-1}$, we have $M(t) \geq .95\,(P\lambda / \lambda + \mu)$.

To find the variance:

$$V(t) = \sum_{n=0}^{P} (n - M(t))^2\, p_n(t) \qquad (13)$$

we shall again take the derivative with respect to time. This results in:

$$V'(t) = \sum_{n=0}^{P} (n - M(t))^2\, p_n'(t), \qquad (14)$$

since $\Sigma\ (n - M(t))\ p_n(t) = 0$. Substituting (1) and (2) into (14) and after some manipulations (see appendix 2) we obtain the linear differential equation:

$$V'(t) = -2\,(\lambda + \mu)\,V(t) + P\lambda + (\mu - \lambda)\,M(t), \tag{15}$$

which can be solved to yield:

$$V(t) = [P\lambda / 2(\lambda + \mu)] - [(\lambda - \mu)\,P\lambda/(\lambda + \mu)^2]\,\{1/2 - \exp-(\lambda + \mu)t\} + c\exp-2(\lambda + \mu)t \tag{16}$$

Again if we let $V(0) = 0$ then we can solve for c. However, we are more interested in the variance as $t \to \infty$ which yields the steady state variance as:

$$V(n) = P\lambda\ \mu / (\lambda + \mu)^2 \tag{17}$$

Before applying these outcomes to an example, we note that for our values of λ_n and μ_n, the results obtained for the mean and variance agree with results from the generalized model suggested by Mac Arthur and Wilson (1967) and the model described by Goel and Richter-Dyn (1974). Further, the expected value generated by our stochastic process is equivalent to a deterministic model suggested by MacArthur and Wilson. The obvious advantage to a stochastic model is that it allows a probabilistic range of values for the model parameters, and permits critical statistical comparisons over time or space.

Let us now apply this model to a case reported by Saila (1975) for a dredge spoil site and its surrounding area. A reasonable estimate of the number of invertebrate species in the surrounding area is $P = 150$. In the first sample from this area 32 species of benthic organisms were noted. Two years later 55 species were present. It was also observed that 9 of the original 32 species found were no longer in this area, indicating that over the two year period an additional 32 species had actually entered

the area. Hence, from this data an estimate of λ, the arrival rate per species is given by $\lambda = 16/(150 - 32) \approx .14$. Similarly, μ, the extinction rate per species (present in the system) is $\mu = 4.5 / 32 = .14$. Fig. 1 illustrates the application of these data and the derived model.

Using these values for λ and μ in equation (12) and (17), the expected number of species in the repopulated area at steady state is 75 species with a standard deviation of 6.12. Hence for this distribution, which can be shown to be symmetrical and mound shaped, the empirical rule indicates that with .95 probability, the number of species at steady state should be between 63 and 88 species. Using our expected value of 75 species, we can predict that it would take a minimum of 10.7 years to achieve this expected value. As mentioned earlier, due to the agreement of the expected value, M(t), with the deterministic model of MacArthur and Wilson used by Saila, we find the mean and years to achieve this value are identical to this earlier work.

This model remains to be further tested with emprical data derived from perturbed areas in the Philippines, and other approaches to modeling are also under active consideration.

ACKNOWLEDGEMENTS

The authors would like to extend thanks to Dr. Sonia P. Formacion, University of The Philippines, College of Fisheries, in the Visayas for her perceptive review of an early draft of this material, which brought to our attention the model development of Goel and Richter-Dyn. This work was sponsored by the U.S. Agency for International Development under Grant No. DAN-4024-6-SS-9113-00.

Appendix 1

We take the derivative of $M(t) = \sum_{n=1}^{P} n\, p_n(t)$ to get

$$M(t) = \sum_{n=1}^{P} n\, p_n(t)$$. Substituting (2) yields

$$M(t) = \sum_{n=1}^{P} - (\lambda_n + \mu_n)\ n\ p_n(t) \ +$$

$$\sum_{n=1}^{P} \lambda_{n-1}\ n\ p_{n-1}(t) \ +$$

$$\sum_{n=1}^{P} \mu_{n+1}\, n p_{n+1}(t)$$

$$= \sum_{n=1}^{P} - (\lambda_n + \mu_n)\ n\ p_n(t) \ +$$

$$\sum_{n=1}^{P} \lambda_{n-1}\,(n-1)\, p_{n-1}(t) + \sum_{n=1}^{P} \lambda_{n-1}\ p_{n-1}(t) \ +$$

$$\sum_{n=1}^{P} \mu_{n+1}\,(n+1)\, p_{n+1}(t) - \sum_{n=1}^{P} \mu_{n+1}\, p_{n+1}(t)$$

Let $i = n-1$. Then $n = 1$ implies $i = 0$ and $n = p$ implies $i = p-1$.

Similarly let $i = n+1$ then $n = 1$ implies $i = 2$ and $n = p => i = p+1$.

Making these index changes and regrouping yields:

$$M'(t) = -\sum_{n=1}^{P} \lambda_n\, n\, p_n(t) \ + \sum_{n=1}^{P-1} \lambda_i\ i\ p_i(t)$$

$$-\sum_{n=1}^{P} \mu_n\ n\ p_n(t) \ + \sum_{i=2}^{P+1} \mu_i\ i\ p_i(t)$$

$$+ \sum_{i=o}^{P-1} \lambda_i\ p(t) - \sum_{i=2}^{P+1} \mu_i\ p_i(t)$$

$$= \sum_{i=o}^{P-1} \lambda_i \; p_i \; (t) \; - \sum_{i=1}^{P+1} \mu_i \, p_i \, (t)$$

Note $\lambda_p = o$ and $\mu_{p+1} = o$, so we can re-arrange the upper summation limits to give:

$$M'(t) = \sum_{i=o}^{P} \lambda_i \, p_i \, (t) \; - \sum_{i=1}^{P} \mu_i \, p_i \, (t)$$

Letting $\lambda_i = (P\text{-}i)\,\lambda$ and $\mu_i = \mu i$ we obtain

$$M'(t) = P\lambda \sum_{i=o}^{P} p_i(t) \; - \lambda \sum_{i=o}^{P} i \, p_i(t) - \mu \sum_{i=o}^{P} i \; p_i(t)$$

$$= P\lambda - (\lambda + \mu) \; M(t)$$

Appendix 2

$$V(t) = \sum_{n=o}^{P} [n-M(t)]^2 \; p_n(t)$$

$$V(t) = \sum_{n=o}^{P} [n-M(t)]^2 \; P_n(t)$$ Substituting (1) and (2)

yields:

$$V(t) = - \sum_{n=o}^{P} (\lambda_n + \mu_n) \; (n-M(t))^2 \, p_n(t)$$

$$+ \sum_{n=o}^{P} \lambda_{n-1} \; p_{n-1}(t) \; (n-M(t))^2$$

$$+ \sum_{n=o}^{P} \mu_{n+1} \; (n-M(t))^2 \; p_{n+1}(t)$$

$$= - \sum_{n=o}^{P} (\lambda_n) + \mu_n \; (n-M(t))^2 \; p_n(t)$$

$$+ \sum_{n=o}^{P} \lambda_{n-1} \; ([(n-1) - M(t)] + 1)^2 \; p_{n-1}(t)$$

$$+ \sum_{n=o}^{P} \mu_{n+1} \; ([(n+1) - M(t)] - 1)^2 \; p_{n+1}(t)$$

$$= - \sum_{n=o}^{P} \lambda_n \, (n-M(t))^2 \, p_n(t)$$

$$+ \sum_{n=o}^{P} \lambda_{n-1} \; ((n-1) - M(t))^2 \; p_{n-1}(t)$$

$$+ 2 \sum_{n=o}^{P} \lambda_{n-1} \, ((n-1) - M(t)) \, p_{n-1}(t)$$

$$+ \sum_{n=o}^{P} \lambda_{n-1} \; p_{n-1}(t)$$

$$- \sum_{n=o}^{P} \mu_n (n - M(t))^2 p_n(t)$$

$$+ \sum_{n=o}^{P} \mu_{n+1} ((n+1) - M(t))^2 p_{n+1}(t)$$

$$-2 \sum_{n=o}^{P} \mu_{n+1} \quad ((n+1 - M(t) \quad p_{n+1}(t)$$

$$+ \sum_{n=o}^{P} \mu_{n+1} P_{n+i}(t)$$

$$= 2 \sum_{n=o}^{P} \lambda_{n-1} ((n-1) - M(t)) p_{n-1}(t)$$

$$+ \sum_{n=o}^{P} \lambda_{n-1} p_{n-1}(t)$$

$$- 2 \sum_{n=o}^{P} \mu_{n+1} ((n+1) - M(t)) p_{n+1}(t)$$

$$+ \sum_{n=o}^{P} \mu_{n+1} p_{n+1}(t)$$

Let $i = n-1$ then $n = o$ implies $i = -1$, and $n = P$ implies $i = P-1$.

Also for $i = n+1$, then $n = o$ implies $i-1$ and $n = P => i = P+1$.

Re-indexing yields (note $\lambda-1 \; p_{-1}(t) = 0$, also $\lambda_p = 0$)

$$V'(t) = 2 \sum_{i=o}^{P} \lambda_i (i - M(t)) p_i(t)$$

$$+ \sum_{i=o}^{P} \lambda_i p_i(t)$$

$$-2 \sum_{i=1}^{P} \mu_i (i - M(t)) p_i(t)$$

$$+ \sum_{i=1}^{P} \mu_i \, p_i \, (t)$$

Substitute $\lambda = (p-i)\,\lambda$ and $\mu_i = \mu i$ and obtain

$$V'(t) = 2\,P\,\lambda \sum_{i=o}^{P} (i - M(t))\, p_i(t) - 2\,\lambda \sum_{i=o}^{P} i(i - M(t))\, pi\,(t)$$

$$+ \; P\lambda \sum_{i=o}^{P} p_i(t) \quad - \; \lambda \sum_{i=o}^{P} i\, p_i(t)$$

$$- 2\,\mu \sum_{i=1}^{P} i\,(i - M(t))\, p_i(t)$$

$$+ \mu \sum_{i=1}^{P} i \;\; p_i(t)$$

But $\sum_{i=o}^{P} i\,(i - M(t))\, p_i(t) = V(t)$ and hence:

$$V'(t) = -2\,(\lambda + \mu)\, V(t) + P\,\lambda + (\mu - \lambda)\, M(t)$$

which is a linear differential equation.

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