COEXISTENCE OF COMPETITORS IN A STOCHASTIC
ENVIRONMENT: THE STORAGE EFFECT

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The pre-reproductive, or juvenile stages of an organism, are often the most
precarious. These are the stages in the life cycle that are most subject to the
vagaries of the environment, while potentially reproductive adults tend to have
both higher average survivorship and more predictable survivorship. It follows
that recruitment to the adult population is often much more variable than adult
survivorship. This difference in variability is increased in some species by a
tendency of adults to reduce reproductive effort when conditions are poor thus
increasing their own survivorship or enhancing later reproductive success (Murdoch
1966, Goodman 1974, Nichols et al. 1976, Tyler and Dunn 1976).

High variability in recruitment, together with both less variable and high
adult survivorship is a characteristic feature of many populations of commercially
exploited fishes (Gulland 1982). The low adult death rates mean that the adult
population can be maintained for a long time by a single large recruitment event.
Essentially, the adult population stores up recruitment events subject to a yearly
discount equal to the adult death rate. As a consequence, the adult stocks are
not nearly so variable as the sporadic recruitment might suggest. The interaction
between variable recruitment and high, less variable, adult survivorship that leads
to these population characteristics will be called the *storage effect*. The
storage effect is present whenever recruitment is variable and generations overlap,
but the effect is strongest for long-lived species.

Variable recruitment and long-lived adults are also features of perennial
plant populations (Harper 1977, Grubb 1977, Hubbell 1980) but the consequences of
the storage effect for these populations is not nearly so well documented.

For a guild of competing species, the storage effect can have quite surpris-
ing consequences: it can be the mechanism of coexistence. Chesson and Warner
(1981) investigated the storage effect in the lottery model of competition for
space among reef fishes. Only in the presence of both variable recruitment and
overlapping generations was coexistence possible; that is, the storage effect was
found to be essential for coexistence. Is this result merely a special feature of
the lottery model or can it apply more generally? To answer this question I shall
discuss a general mathematical model incorporating the storage effect. I shall
then go on to consider a variety of examples that may be useful in applications,
and which illustrate the generality of situations where the storage effect may
promote coexistence of competing species. A companion paper (Warner and Chesson,
manuscript) discusses the biological implications of the storage effect, and

suggests procedures for testing the hypothesis that storage is indeed the mechanism of coexistence in field situations.

1. THE GENERAL MODEL

    To model the storage effect, let $X_i(t)$ be the population density of adults of species i at time t; δ_i is the adult death rate and $R_i(t)$ is the per capita recruitment rate during $(t, t+1)$. It follows that

$$X_i(t+1) = (1-\delta_i)X_i(t) + R_i(t)X_i(t). \tag{1}$$

In this equation $R_i(t)$ will generally depend on $X_i(t)$, the other species present in the system, and the state of the environment, $E(t)$, during $(t, t+1)$. Thus we have

$$R_i(t) = f_i(E(t), X_1(t), \ldots, X_k(t)), \tag{2}$$

where f_i is some function. For simplicity the death rate δ_i is assumed to be constant, but, as can be seen from Chesson and Warner (1981) and Chesson (1982), δ_i may vary with the environment without substantially altering the conclusions below. Moreover the death rates can be made to depend on population densities to a limited degree. However, in general we shall think of the adult death rates as small and relatively constant while the recruitment rates are highly variable.

    To analyze the model we define

$$\rho_i(t) = R_i(t)/\delta_i. \tag{3}$$

Species i increases when $\rho_i(t) > 1$ and decreases when $\rho_i(t) < 1$. Persistence of species i depends on its mean instantaneous growth rate at low density, Δ_i, which is given by the formulae

$$
\begin{aligned}
\Delta_i &= E \log X_i(t+1)/X_i(t) \\
&= E \log \{1 + \delta_i[\rho_i(t)-1]\},
\end{aligned}
\tag{4}
$$

evaluated for $X_i(t) = 0$. If $\Delta_i > 0$ then species i persists in the sense of invasibility (Turelli 1978), i.e., species i tends to increase from low values. Invasibility often implies persistence in the more satisfactory sense of stochastic boundedness or "s.b. persistence" (Chesson 1978, 1982). S.b. persistence means that $X_i(t)$ is stochastically larger than some positive random variable U, uniformly in t, in symbols

$$P(X_i(t) > x) \geq P(U > x).$$

To determine invasibility by calculating Δ_i it is usually assumed that $(E(t),X_1(t),\ldots,X_k(t))$ approaches some stationary process when $X_i(t) = 0$; and the expected value is taken for the stationary distribution, or more commonly, for some approximating distribution. In this study the stationary distribution is not always available but we do find stationary lower bounds to $\rho_i(t)$ which allows us to deduce conservative conditions for invasibility. If these conservative conditions are satisfied, and the lower bound to $\rho_i(t)$ is an independent and identically distributed (i.i.d.) function of $E(t)$, then Theorem 5.1 of Chesson (1982) can be modified to prove s.b. persistence for the regular examples given below. However, in general, we shall be content to show that a species satisfies the invasibility criterion.

To determine invasibility, we note from Chesson (1982) that

$$\Delta_i \geq \delta_i E[\log \rho_i | \rho_i > 1] P(\rho_i > 1) + \log(1 - \delta_i) P(\rho_i < 1). \tag{5}$$

It follows that Δ_i will be positive whenever

$$E[\log \rho_i | \rho_i > 1] \geq c(\delta_i) P(\rho_i < 1)/P(\rho_i > 1) \tag{6}$$

where

$$c(\delta_i) = -\log(1 - \delta_i)/\delta_i \tag{7}$$

and $c(\delta_i)$ is close to 1 for small δ_i.

The expression (6) provides a highly conservative yet very useful criterion for persistence in the sense of invasibility. Note that the criterion does not depend on the magnitude of ρ_i, the ratio of the recruitment rate and death rate, during periods of population decrease. Referring to periods of population increase and decrease respectively as favorable and unfavorable, we see that the criterion (6) depends only on the mean magnitude of $\log \rho_i$ during favorable periods and on the frequency of these periods relative to unfavorable periods. Thus a species can persist provided only that some of its favorable periods are sufficiently favorable (as measured by $\log \rho_i$) relative to their frequency of occurrence. This is the storage effect in operation: large recruitment events are stored in the adult population reducing the significance of the actual magnitude of $\log \rho_i$ during unfavorable periods. A general tendency for population increase can be maintained by favorable periods alone.

The magnitude of $\log \rho_i$ during unfavorable periods becomes important when criterion (6) is not satisfied. If the unfavorable periods are not greatly unfavorable then persistence can occur with substantially poorer favorable periods than suggested by (6). Precise relationships between mean favorability, variance in favorability and adult death rate, can be found from an obvious reinterpretation

of the figures in Chesson and Warner (1981).

The fact that a species may persist by having only occasional good recruitment periods has important consequences for a set of interacting species. If the interactions are negative, so that not all species can have favorable periods simultaneously, coexistence may nevertheless occur. Each species simply needs to experience favorable periods that are sufficiently favorable relative to their frequency of occurrence. Such periods may be brought on by fluctuations in the environment, or by fluctuations, which may or may not be environmentally induced, in other species.

We now illustrate these ideas with a variety of specific examples. Additional examples can be found in Ellner (1983) and Shmida and Ellner (1983).

(i) The multispecies lottery model.

This first example shows that the storage effect may promote coexistence not just in a two-species system, as shown by Chesson and Warner (1981), but in systems with many species.

In the lottery model of Chesson and Warner each adult individual holds a unit of space, called a "home" which may be a defended territory (e.g., some reef fishes) or simply room to grow (e.g., trees or bushes). The total number of homesites available is assumed fixed and sites become available to new recruits only by death of adults. Thus the amount of space becoming available during $(t,t+1)$ is $\Sigma \delta_i X_i(t)$. The $\beta_i(t)X_i(t)$ juveniles of species i compete for this space with juveniles of all species. The outcome is assumed to be a random or biased random division of space among the individuals of the k species. In the slightly simpler completely random case we have

$$R_i(t)X_i(t) = \sum_{j=1}^{k} \delta_j X_j(t) \cdot \frac{\beta_i(t)X_i(t)}{\sum\limits_{j=1}^{k} \beta_j(t)X_j(t)} \qquad (8)$$

The parameters $\beta_i(t)$ representing birth and survivorship to the age of recruitment, are assumed functions of the environment $E(t)$. The process $E(t)$ is assumed to be stationary in all examples, and for proofs of stochastic boundedness we make the stronger assumption that it is an i.i.d. process. Formula (8) involves the implicit assumption that the total number of juveniles exceeds the available space, and hence that all space is filled at each recruitment period. Measuring density as the proportion of space that a species occupies, it follows that $\Sigma_{i=1}^{k} X_i(t) = 1$.

For species i at zero density, $\rho_i(t)$ $(= R_i(t)/\delta_i)$ is given by

$$\rho_i(t) = \frac{\sum\limits_{j\neq i} \delta_j X_j(t)}{\delta_i} \cdot \frac{\beta_i(t)}{\sum\limits_{j\neq i} \beta_j(t)X_j(t)} \tag{9}$$

$$\geq \frac{\min\limits_{j\neq i} \delta_j}{\delta_i} \cdot \frac{\beta_i(t)}{\max\limits_{j\neq i} \beta_j(t)} \tag{10}$$

The general result (6) implies that species i will persist if $\rho_i(t)$ takes on values that are sufficiently large relative to their frequency of occurrence. The inequality (10) thus shows that the species will coexist if each species has periods when its birth rate, $\beta_i(t)$, is sufficiently superior to the birth rates of the other species. Thus coexistence results from sufficient variability in the birth rates of each species relative to the others. Moreover since (10) is independent of the population densities it is an i.i.d. process when $(\beta_1(t),\ldots,\beta_k(t))$, $t = 0,1,\ldots$ is an i.i.d. sequence of random vectors. It follows that each species will be s.b. persistent when there is sufficient variability in birth rates.

Although inequality (10) helps show that coexistence will occur with sufficient variability it does not give a very useful indication of the amount of variation necessary. It suggests that the necessary variation increases quite sharply as the number of species increases, however the equality (9), which gives a much better indication, suggests a substantially milder increase in the necessary variability. For $\rho_i(t)$ to be large in (9), $\beta_i(t)$ has to be large relative to, not the maximum birth rate for the other species, but to a weighted average of their birth rates, the weights being the species' densities.

Coexistence results from a sufficient storage effect in the multispecies lottery model; the storage effect is also necessary for coexistence. When generations are nonoverlapping, equation (6) of Chesson and Warner (1981) shows that the species with the largest value of $E \log \beta_i(t)$ eventually dominates the system. In a constant environment, the species with the largest value of β_i/δ_i, is the only one that persists.

(ii) The lottery model with vacant space.

The application of the previous model may be restricted by the assumption that the total number of juveniles surviving to the recruitment stage always exceeds the available space. To remove this assumption for the two-species case we let $Y(t) = 1 - X_1(t) - X_2(t)$, the amount of unoccupied space. The recruitment term, $R_i(t)X_i(t)$, of the lottery model is modified to

$$\min\left\{\beta_i(t)X_i(t),\ [Y(t)+\delta_1 X_1(t)+\delta_2 X_2(t)]\frac{\beta_i(t)X_i(t)}{\beta_1(t)X_1(t)+\beta_2(t)X_2(t)}\right\}. \tag{11}$$

In this new model, if there are more juveniles than the space can hold, allocation is at random, otherwise the density of new recruits of species i is simply the density of juveniles.

For $X_i(t) = 0$ we have

$$\rho_i(t) = \min \left\{ 1, \ \frac{Y(t)+\delta_j X_j(t)}{\beta_j(t)X_j(t)} \right\} \frac{\beta_i(t)}{\delta_i} \qquad (12)$$

$$\geq \min \left\{ 1, \ \frac{\delta_j}{\beta_j(t)} \right\} \frac{\beta_i(t)}{\delta_i} \ . \qquad (13)$$

From (13) we see that coexistence will occur if each species has periods when the ratio of its birth rate to its death rate is large both absolutely and relative to the ratio for the other species. This is not much different from the lottery model because the lottery model really only makes sense when $\beta_i(t) \geq \delta_i$. Consequently, when $\beta_i(t)/\delta_i$ is large relative to $\beta_j(t)/\delta_j$, it must also be large absolutely. However the above criterion for coexistence is conservative when there is empty space. Indeed (12) suggests that coexistence will occur under more general conditions, especially if the amount of empty space can be large.

Although we make no attempt to explore more general conditions for coexistence, one thing is clear: the storage effect is essential. To see this consider first the case of a constant environment. For species i to persist $\beta_i/\delta_i > 1$. Thus if both species persist, all space is filled in finite time, and as in the lottery model, the species with the smaller value of β_i/δ_i becomes extinct. When generations are not overlapping

$$X_1(t+1)/X_2(t+1) = (\beta_1(t)/\beta_2(t))X_1(t)/X_2(t). \qquad (14)$$

This equation also holds for the lottery model and it follows that the species with the smaller value of $E \log \beta_i(t)$ becomes extinct. Thus the interaction between variable recruitment and overlapping generations (the storage effect) is essential to coexistence.

(iii) The lottery model with other kinds of competition.

Competition need not be restricted to a single time in the life of an organism. For example in addition to lottery competition for space at settlement, competition among adults may affect reproductive success. Provided this competition among adults does not affect adult death rates, it still fits easily into the general model above. Another interesting possibility involves competition among juveniles before they reach the settlement stage. We model just this latter possibility because the former situation, involving adult competition, can be modeled as a minor modification with very similar conclusions.

To add presettlement competition we do not need to change equation (8) of

the lottery model; we just need to make the $\beta_i(t)$ density dependent as follows, for the two-species case.

$$\beta_i(t) = B_i(t)f_i(B_i(t)X_i(t),B_j(t)X_j(t)). \tag{15}$$

Here $B_i(t)$ is the birth rate and so $B_i(t)X_i(t)$ is the number of juveniles before presettlement competition, while the function f_i represents the fractional reduction in $B_i(t)$ due to this competition. The result, $\beta_i(t)$, is the potential recruitment rate because it is the number that would recruit, per adult, if the space were available.

The interpretation of the model is aided by the following definition of generalized competition coefficients (c.f., Abrams 1975).

$$\alpha_{ij}(\ell_i,\ell_j) = -\frac{\partial}{\partial\ell_j}\log f_i(\ell_i,\ell_j), \quad i \neq j, \tag{16}$$

and α_{ii} is defined analogously. These competition coefficients represent the relative depression of species i juveniles by each additional juvenile of species j and species i respectively. Making the assumptions $f_i(0,0) = 1$, $X_i(t) = 0$, we now obtain

$$\rho_i(t) = \frac{\delta_j B_i(t)}{\delta_i B_j(t)}\, e^{\int_0^{B_j(t)} \alpha_{jj}(\ell,0)-\alpha_{ij}(0,\ell)d\ell}. \tag{17}$$

Inspection of (17) shows that coexistence must always occur if birth rates vary sufficiently in the following sense. Let p and L be fixed positive constants and

$$P(B_i(t) > M,\ B_j(t) < L) \geq p, \tag{18}$$

$i \neq j$; $i, j = 1,2$. By increasing M, variability is increased in the sense of an increase in the difference between the small and large values that the birth rates take on. Expression (18) also insists that some periods of low birth rate for each species coincide with some periods of high birth rate for the other species. With sufficiently high variability (high M) coexistence occurs in this model of general presettlement competition with lottery competition at settlement.

Although we have used a very general definition of high variability it does not cover all cases in which variability may lead to coexistence, especially for particular forms of the model where quite different definitions of high variability can be adequate. The present definition has the property that $EB_i(t)$ will be large when variability is large, however $E\log B_i(t)$ need not be large. Chesson (1982) discusses the relative merits of different ways of defining high variability.

To see what happens in a constant environment we use the general definition of coexistence in terms of an attractor block given by Armstrong and McGehee (1980). In a constant environment we say that the species coexist if there is a positive number ϵ such that both species densities rise above ϵ and remain there, given any positive initial densities. With this definition, a necessary and sufficient condition for coexistence is $\rho_i > 1$, $i = 1,2$. Inspection of (17) is sufficient to give the general features of coexistence in a constant environment. We consider four cases.

(A) $\alpha_{ij} < \alpha_{jj}$, $i \neq j$, $i, j = 1,2$ (intraspecific competition exceeds interspecific competition). Coexistence occurs if $\delta_2 B_1 / B_2 \delta_1 = 1$, but also in many other situations. In general, coexistence is favored by any of the following: $\delta_2 B_1 / B_2 \delta_1$ is near 1; the B_i are large in absolute value; the differences $\alpha_{jj} - \alpha_{ij}$ are large.

(B) $\alpha_{ij} > \alpha_{jj}$, $i \neq j$, $i, j = 12$, (interspecific competition exceeds intraspecific competition). Coexistence never occurs for this case.

(C) $\alpha_{ij} < \alpha_{jj}$, $\alpha_{ji} > \alpha_{ii}$ (species i is a superior competitor). Coexistence can occur if the presettlement competitive advantage of species i is balanced by a large value of $\delta_i B_j / \delta_j B_i$ giving species j an advantage with respect to birth and adult survivorship rates. However it is possible for this ratio to be too large so that species i does not persist.

(D) $\alpha_{ij} \equiv \alpha_{jj}$, $i \neq j$, $i, j = 1,2$ (interpsecific competition equals intraspecific competition). The case is equivalent to the lottery model and so coexistence cannot occur in a constant environment.

Coexistence in a constant environment occurs for subcases of only two of the above cases, however coexistence will always occur in a sufficiently variable environment, as discussed above. Thus a stochastic environment broadens the range of situations in which coexistence can occur.

Although not obvious from our analysis so far, it is not just the stochastic environment that is important but its combination with overlapping generations, i.e., the storage effect. Without overlapping generations coexistence remains impossible in case (D), because this case is equivalent to the lottery model, while in case (B) $\Delta_1 + \Delta_2 = E \log \rho_1 + E \log \rho_2 < 0$, so that it is impossible for both species to satisfy the invasibility criterion. In addition, although it is possible that a stochastic environment could lead to coexistence without overlapping generations for some instances of (A) and (C), these instances necessarily belong to a subset of cases where the storage effect yields coexistence. This follows from the general result for the lottery model (Chesson and Warner 1981), which applies here also,

that smaller death rates favor coexistence.

(iv) The storage effect in a Lotka-Volterra model.

In addition to the storage effect, the above models have all involved lottery competition. To see that lottery competition is not essential to coexistence by the storage effect we now consider a model in which there is no lottery competition. Instead, competition of the Lotka-Volterra kind occurs among juveniles and among adults.

Let $L_i(t)$ be the number of juveniles born to the $X_i(t)$ adults of species i in $(t, t+1)$, then the recruitment term takes the form

$$R_i(t)X_i(t) = \frac{\theta_i(t)L_i(t)}{1+\alpha_{ii}(t)L_i(t)+\alpha_{ij}(t)L_j(t)} . \tag{19}$$

This equation is the hyperbolic form of Lotka-Volterra competition in discrete time (Leslie 1958). It represents the reduction in juvenile survivorship due to competition among juveniles. The parameter $\theta_i(t)$ is per capita juvenile survivorship in the absence of competition; $\alpha_{ii}(t)$ and $\alpha_{ij}(t)$ are the competition coefficients. Although these parameters are possibly time dependent they are assumed to be stationary stochastic processes not involving adult or juvenile densities.

Birth rates of juveniles are affected by competition among adults and the model is completed by the equation

$$L_i(t) = \frac{B_i(t)X_i(t)}{1+\gamma_{ii}(t)X_i(t)+\gamma_{ij}(t)X_j(t)} \tag{20}$$

with the same assumptions as applied to (19) on the time varying parameters.

For species i at 0 density we obtain

$$\rho_i(t) = \frac{\theta_i(t)B_i(t)/\delta_i}{[1+\gamma_{ij}(t)X_j(t)]\left[1+\dfrac{\alpha_{ij}(t)B_i(t)X_j(t)}{1+\gamma_{jj}(t)X_j(t)}\right]} . \tag{21}$$

The behavior of $\rho_i(t)$ depends on the behavior of $X_j(t)$ when $X_i(t) = 0$. Assuming $X_i(t) = 0$, (19) and (20) imply

$$X_j(t+1) \leq (1-\delta_j)X_j(t) + \theta_j(t)/\alpha_{jj}(t). \tag{22}$$

It follows that $X_j(t)$ is bounded by the random variable

$$\xi_j(t) = (1-\delta_j)^t X_j(0) + \sum_{s=0}^{t-1} (1-\delta_j)^s \theta_j(t-s)/\alpha_{jj}(t-s). \tag{23}$$

The significant feature of (23) is that the birth rates are not functionally involved although this does not deny statistical dependence. Substituting in (21) we conclude

$$\rho_i(t) \geq \frac{\Theta_i(t)B_i(t)/\delta_i}{[1+\gamma_{ij}(t)\xi_j(t)]\left[1+\dfrac{\alpha_{ij}(t)B_j(t)\xi_j(t)}{1+\gamma_{jj}(t)\xi_j(t)}\right]} \quad . \tag{24}$$

It follows that if $B_1(t)$ and $B_2(t)$ are large at different times, both $\rho_1(t)$ and $\rho_2(t)$ can take large values. Thus coexistence can occur by the storage effect.

In a constant environment with species j alone, $X_j(t)$ converges to the equilibrium value

$$(\Theta_j B_j/\delta_j - 1)/(\gamma_{jj}+\alpha_{jj}B_j). \tag{25}$$

To see when species i can invade, this equilibrium value is substituted in expression (21) for ρ_i (values of $\rho_i > 1$ indicate invasibility). Inspection of the resulting formula reveals that coexistence can occur if interspecific competition coefficients α_{ij} and γ_{ij} are small while the B_i are large. On the other hand, if the α_{ij} are large, the species cannot coexist for any values of the B_i. While no attempt has been made to delineate precise regions of coexistence, it is clear that the storage effect does indeed lead to a broader range of situations of coexistence: with the storage effect coexistence can occur for any values of the interspecific competition coefficients.

2. SUMMARY

It is not uncommon for the rate of recruitment to an adult population to be much more variable than adult survivorship. If adult survivorship is high, while recruitment is quite variable, the average growth rate of the population will be dependent mostly on the strength of good recruitments and little dependent on the strength of poor recruitments. It is possible that the population is maintained by infrequent strong recruitment events. The interaction between variable recruitment and low adult death rates, that leads to these population properties, is called the storage effect. Because the storage effect can permit a species to have a positive average growth rate if its good recruitments are sufficiently beneficial, independently of the paucity of recruitment at other times, it can promote the coexistence of species that compete quite strongly. For coexistence, each species simply needs periods when its recruitment rate is sufficiently high relative to the frequency of these periods.

Several different competition models are given which illustrate the variety of situations in which the storage effect promotes coexistence.

REFERENCES

Abrams, P. (1975): Limiting similarity and the form of the competition coefficient, *Theoret. Pop. Biol.* 8:356-375.

Armstrong, R.A. and R. McGehee (1980): Competitive exclusion, *Am. Nat.* 115:151-170.

Chesson, P.L. (1978): Predator-prey theory and variability, *Annu. Rev. Ecol. Syst.* 9:323-347.

_____ (1982): The stabilizing effect of a random environment, *J. Math. Biol.* 15: 1-36.

Chesson, P.L. and R.R. Warner (1981): Environmental variability promotes coexistence in lottery competitive systems, *Am. Nat.* 117:923-943.

Ellner, S.P. (1983): Stationary distributions for some stochastic difference equation models, *J. Math. Biol.* To appear.

Goodman, D. (1974): Natural selection and a cost ceiling on reproductive effort, *Am. Nat.* 108:247-268.

Grubb, P.J. (1977): The maintenance of species richness in plant communities: the importance of the regeneration niche, *Biol. Rev.* 52:107-145.

Gulland, J.A. (1982): Why do fish numbers vary? *J. Theor. Biol.* 97:69-75.

Harper, J.L. (1977): *Population Biology of Plants*, Academic Press, London, 892 pp.

Hubbell, S.P. (1980): Seed predation and the coexistence of tree species in tropical forests, *Oikos* 35:214-229.

Leslie, P.H. (1958): A stochastic model for studying the properties of certain biological systems by numerical methods, *Biometrika* 45:16-31.

Murdoch, W.W. (1966): Population stability and life history phenomena, *Am. Nat.* 100:5-11.

Nichols, J.D., W. Conley, B. Batt, and A.R. Tipton (1976): Temporally dynamic reproductive strategies and the concept of r- and K- selection, *Am. Nat.* 110:995-1005.

Schmida, A. and S. Ellner (1983): Coexistence of trophically equivalent plant species, *Vegetatio,* in press.

Turelli, M. (1978): Does environmental variability limit niche overlap? *Proc. Natl. Acad. Sci. USA* 75:5085-5089.

Tyler, A.V. and R.S. Dunn (1976): Ration, growth, and measures of organ condition in relation to meal frequency in winter flounder, *Pseudo-pleuronectes americanus*, with hypotheses regarding population homeostasis, *J. Fish. Res. Board Canada* 33:63-75.