
Abstract.— Models used by fisheries managers and population ecologists to analyze or predict the size-frequency distribution of populations usually incorporate assumptions concerning recruitment and mortality, and individual growth that provide mathematical simplicity, but also constrain the shapes of size distributions. In this paper we derive a predictive model for size-frequency distributions which assumes constant recruitment and mortality, and Brody-Bertalanffy growth, then examine the effects of specific violations of these assumptions on the potential shapes of size distributions. Although bimodal and strongly unimodal size-frequency distributions are not possible under these assumptions, the model indicates that specific age-related changes in the mortality rate (Z) and the growth coefficient (K) are required to obtain these distributions. Shifts in Z/K with age from growth-dominated ($Z/K < 1$) to mortality-dominated ($Z/K > 1$) usually result in strongly unimodal size-frequency distributions. Stable bimodal distributions require shifts from mortality-dominated to growth-dominated conditions via age-related changes in Z , K , or both. Non-equilibrium conditions or events such as pulses in recruitment or mortality can also modify size-frequency distributions, but these effects are usually transient. These results indicate that inferences concerning the demographic dynamics of a population may be derived simply by observing the shape of its size-frequency distribution.

Inferring Demographic Processes from Size-Frequency Distributions: Simple Models Indicate Specific Patterns of Growth and Mortality

James P. Barry

Mia J. Tegner

A-001 Scripps Institution of Oceanography
La Jolla, California 92093

Population ecologists and wildlife managers are often interested in identifying spatial and temporal patterns of growth and mortality in order to understand the dynamics of populations. Because of logistic or other constraints in their abilities to directly quantify mortality and growth, however, ecologists often rely on the analysis of size distributions to infer these parameters (Cassie 1954; Beverton and Holt 1956; Ricker 1958, 1975; Ebert 1973; Van Sickle 1977b; Pauly and Morgan 1987). A population's size-frequency distribution (hereafter referred to as size distribution or size structure) results from its recent history of recruitment and mortality, integrated with the growth rates of individuals. Temporal or spatial changes in the size structure of a population must therefore reflect changes in one or more of these parameters. For example, red sea urchins *Strongylocentrotus franciscanus* are long-lived and have size distributions that are relatively stable through time, but vary in space due to geographic changes in recruitment and mortality related to the distribution of predators and dispersal of larvae (Tegner and Barry Unpubl.). In some locations urchins have persistently bimodal size structures, while in others, the population is unimodal or amodal.

Techniques for size-frequency analysis usually combine models of the growth rates of individuals with

mortality rates to describe observed size-frequency distributions. Because growth and mortality both affect the shape of the distribution, knowledge of one parameter may allow deduction of the other from the shape of the size-frequency distribution. Since growth, mortality, and recruitment can vary considerably, as well as independently of one another, analyses of size distributions typically utilize several simplifying assumptions.

In this paper, we show that although simplified models commonly employed for growth and mortality result in a limited range of size structures, they can nonetheless be indicative of the demographic patterns of populations. Thus, examination of size-frequency distributions may allow reasonable inferences concerning the dynamics of a population. In particular, bimodal size distributions, that are "impossible" under typical model assumptions but are typical of red urchins in the Southern California Bight, must arise from particular patterns of age or size-specific changes in demographic parameters. In order to generate these size structures, assumptions concerning constant mortality and growth coefficients are not tenable.

The most basic assumption of most models is that the population is stable and has a stationary age structure. Thus, recruitment is taken to be invariant from year to year, or continuous, and mortality rates are presumed

constant over time. In addition to these assumptions, the population is usually required to conform to strictly deterministic equations that describe growth and abundance. Often, mortality rate is also assumed to be independent of age (Green 1970, Ebert 1973), resulting in a type II survivorship curve (Deevey 1947). Growth rates of individuals are frequently assumed to fit a Brody-Bertalanffy function (von Bertalanffy 1957, Ricker 1975) in which size increases at a rate proportional to the distance from the maximum size. For models in which one or another of these assumptions is relaxed, see Van Sickle (1977a,b), DeAngelis and Mattice (1979), DeAngelis and Coutant (1982), and several papers in Pauly and Morgan (1987).

The applicability of these simplifying assumptions varies considerably among species and populations. For some species (e.g., certain long-lived fishes of arctic lakes), age structures are stable and size distributions are stationary, with fairly constant recruitment from year to year (Johnson 1976). For many species, however, the assumption of a stable age structure is unrealistic, due to considerable interannual variability in recruitment to the zero age class (Johnson et al. 1986, Pearse and Hines 1987, Raymond and Scheibling 1987, Barry 1989). For red urchins, although recruitment varies between years, the shape of its size distribution is characteristically constant from year to year (Tegner and Barry Unpubl.). The assumption of an age-invariant mortality rate is also probably unwarranted for many, if not, most species. A more common pattern is high juvenile mortality, followed by high adult survival (type III survivorship). Models incorporating these simplifying, but perhaps unrealistic, assumptions (discussed above) can, nevertheless, be of value in identifying patterns of individual growth as well as in estimating recruitment and mortality for the population. In many cases these properties may otherwise be unobtainable.

In this paper we are concerned with population dynamics that result in a bimodal distribution of sizes. Bimodal size distributions have been reported for several species, and are of considerable interest (Johnson 1976; Tegner and Dayton 1977, 1981; Shelton et al. 1979; Timmons et al. 1980; Stein and Pearcy 1982; Wilson 1983; Pollard 1985; Page 1986; Tegner and Barry Unpubl.), especially for populations that are apparently stable. Intuitively, bimodality may develop and persist under equilibrium conditions by a combination of rapid growth of individuals to adult size and high survival rates. Thus, a mode of juveniles may be distinct from an adult mode comprised of several age classes that overlap in size, with relatively few intermediate-sized, rapidly growing individuals. DeAngelis and Mattice (1979) and Power (1978) suggested that bimodality may arise from this sort of "pileup" of individuals at

larger size classes due to a decrease in growth rate at adult size, even with constant mortality. Mortality decreases the number of older individuals, but a large number are left clustered near the upper size limit. Here we show that bimodal size structure must develop from particular patterns of age-specific growth, mortality, or both, that are not possible with commonly employed models. Specifically, bimodality can develop only from an increase in survivorship with age or an increase in the growth coefficient with age, or both. Even though simple models are limited in their range of size distributions, we can use these models to identify deviations from them that are necessary or sufficient to produce particular size distributions, such as bimodal or strongly unimodal distributions.

Derivation of a simple size-frequency model

The change in abundance of a cohort can be represented as,

$$\frac{dN}{dt} = -ZN \quad (1)$$

where N is the number of individuals alive in the cohort at time t , and Z is the instantaneous mortality rate for the population. Assuming that Z is constant over time and independent of age and size, this equation can be integrated to obtain a simple decreasing exponential function for the number of individuals versus time,

$$N_t = N_0 e^{-Z(t-t_0)} \quad (2)$$

where t_0 is the time of recruitment or birth and N_0 is the abundance of the population at time t_0 . The equation can be simplified slightly by defining abundance in terms of age rather than time; age (τ) equals $t - t_0$, or time since recruitment. Hence, equation (2) becomes

$$N_\tau = N_0 e^{-Z\tau} \quad (3)$$

If we now assume that the population is stable, with constant recruitment, this function describes both the time series of abundance for a single cohort and the stable age structure of the population.

Brody-Bertalanffy growth is characterized by exponentially decaying growth in size, with no lag during early life. The general form of this deterministic equation is

$$S_t = S_\infty(1 - be^{-K(t-t_0)}) \quad (4)$$

where S_t is the size of an individual at age τ (i.e., at time t after t_0 , the time of birth or recruitment), S_∞ is

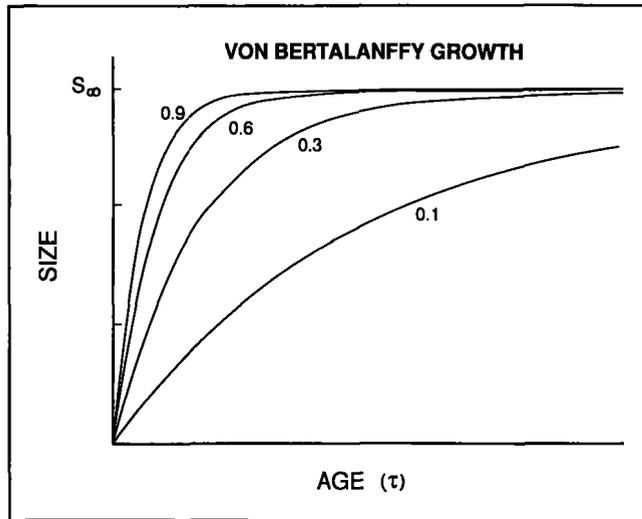


Figure 1

Brody-Bertalanffy growth for various values of the Brody growth coefficient K . Values of K are listed adjacent to each curve.

the maximum size, b is a scaling factor to account for a size at recruitment larger than 0 (for a recruitment size of 0, $b = 1$), and K is the Brody growth coefficient (Ricker 1975) which constrains the shape of the function. Higher values of K result in a more rapid approach to asymptotic size (Fig. 1). If b is considered to be unity and age (τ) rather than time is used, the equation simplifies to

$$S_\tau = S_\infty (1 - be^{K\tau}). \quad (5)$$

Assuming these functions adequately describe the mortality and growth schedules of the population, we can combine equations (3) and (5) to derive an expression for the size-frequency distribution of the population. By definition, the number of individuals alive in an age interval τ_1 to τ_2 in equation (3) is equal to the number in the corresponding size interval S_1 to S_2 , as determined by equation (5).

$$N_S d\tau = N_\tau dS_\tau$$

and rearranging,
$$N_S = N_\tau \frac{d\tau}{dS_\tau}. \quad (6)$$

Because we assume these relationships to be strictly deterministic, we can solve equation (5) for τ

$$\tau = -\frac{1}{K} \ln \left(1 - \frac{S_\tau}{S_\infty} \right). \quad (7)$$

Next, we form the first derivative of equation (7) with respect to τ , yielding

$$\frac{d\tau}{dS_\tau} = \frac{1}{KS_\infty \left(1 - \frac{S_\tau}{S_\infty} \right)}. \quad (8)$$

Combining equations (6), (3), (7), and (8) yields an expression for number as a function of size,

$$N_S = N_0 e^{\frac{Z}{K} \ln \left(1 - \frac{S_\tau}{S_\infty} \right)} \cdot \frac{1}{KS_\infty \left(1 - \frac{S_\tau}{S_\infty} \right)}$$

which simplifies to:

$$N_S = \frac{N_0}{KS_\infty} \left(1 - \frac{S_\tau}{S_\infty} \right)^{\left(\frac{Z}{K} - 1 \right)}. \quad (9)$$

This size distribution function (9) describes population abundance as a function of size, rather than age, for any conditions of constant mortality (Z) and growth coefficient (K). By evaluating its first derivative at $dN/dS = 0$, we can identify conditions necessary for the existence of a zero slope (modes or troughs) in the size distribution. This derivative is

$$\begin{aligned} \frac{dN}{dS} &= \frac{N_0}{KS_\infty} \left(\frac{Z}{K} - 1 \right) \left(1 - \frac{S_\tau}{S_\infty} \right)^{\left(\frac{Z}{K} - 2 \right)} \left(-\frac{1}{S_\infty} \right) \\ &= \left(\frac{Z}{K} - 1 \right) \frac{-N_0}{KS_\infty^2} \left(1 - \frac{S_\tau}{S_\infty} \right)^{\left(\frac{Z}{K} - 2 \right)}. \end{aligned} \quad (10)$$

The conditions where $dN/ds = 0$ are:

$$N_0 = 0 \quad : \text{trivial}$$

$$S_\tau = S_\infty \quad : \text{trivial}$$

$$S_\infty = \infty \quad : \text{trivial}$$

$$Z = K \quad : \text{growth is balanced by mortality.}$$

The only non-trivial condition where the size-frequency function has a slope of zero is when $Z = K$. In this case all size classes are equally abundant, since the solution to equation (9) indicates that when $Z = K$, N_S is constant and independent of S_τ . Therefore, there are no conditions of growth and mortality that are capable of producing a bimodal distribution when using these simplifying assumptions. Thus, the hypothesis that bimodality arises from rapid growth to adult size

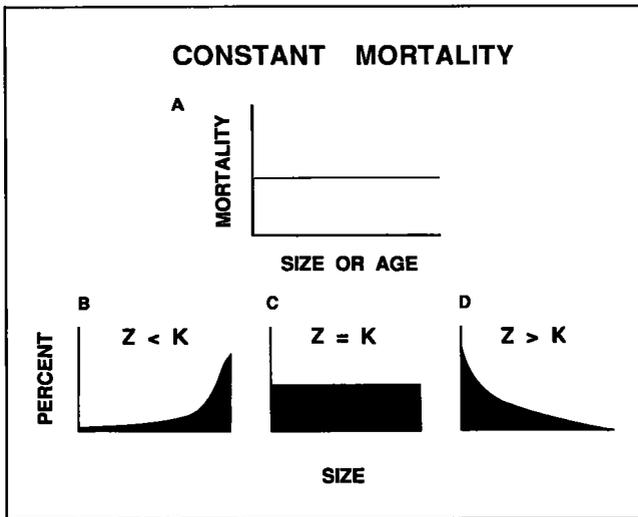


Figure 2

Hypothetical size-frequency distributions for populations exhibiting constant mortality and von Bertalanffy growth. (A) Mortality (Z) is constant for all sizes. The growth coefficient (K) is also assumed to be a constant. Due to these assumptions, the shape of size-frequency distributions are limited to those general forms presented in b-d, according to the relative magnitudes of Z and K . (B) Z is less than K over all S . (C) Z equals K . (D) Z is greater than K .

and high (constant) survivorship (Van Sickle 1977a, Power 1978, DeAngelis and Mattice 1979), is not adequate, assuming simple Brody-Bertalanffy growth and constant mortality under steady-state conditions. There must be a more complicated age dependence of growth rate, or an age dependence of mortality, to account for a bimodal stable size distribution.

Because the signs of N_0 , S_r , S_∞ , and K are all positive, the sign of dN/dS in equation (10) is determined by the first term ($Z/K-1$). If Z is greater than K , the slope is negative and the size structure is dominated by juveniles (Fig. 2). When Z is less than K , the slope is positive, up to S_∞ , and the population is dominated by adults. These can be termed mortality-dominated and growth-dominated populations, respectively.

Effects of age-related rates of growth and mortality

Let us now relax the assumption that K and Z are independent of age. Age-specific variation in these coefficients can result in a bimodal or unimodal size distribution, depending upon the relative magnitude of K and Z . The derivations of similar models for age-varying K and Z are more complicated, but we can evaluate the effect of such changes simply by considering a combination of size distributions generated with

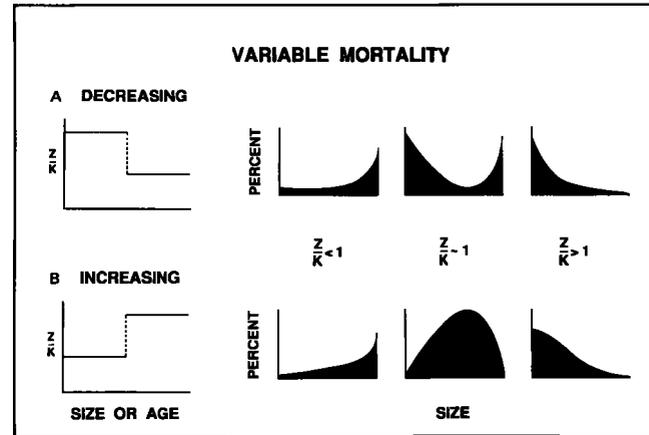


Figure 3

If the assumptions of constancy for Z and K are violated, the shape of a size distribution varies according to the pattern of the violation. The figures on the left-hand column indicate a shift (step function) in the relative values of Z and K , with age or size. The figures in the three right columns show the general shape of the size-frequency distribution for the specified conditions, created by combining the predicted size distributions for before and after the change in K or Z . (Row A) For a decrease in the ratio of Z/K with larger size, bimodality is possible, depending upon the magnitude of Z and K . When Z is near in value to K , and Z/K shifts from greater than to less than unity, bimodality is likely. For cases where Z is always greater than K or less than K , the size-frequency distribution is dominated by juveniles, or adults, respectively. (Row B) For an increase in Z/K , the size distribution may be unimodal with a mode in any position, but cannot be bimodal. For each of the three right columns, the appropriate value of Z/K for the interval S_0 to S_∞ is indicated.

different values for one or both of these coefficients. The important implications remain unchanged. If K or Z changes with size such that the ratio of Z/K shifts from greater than to less than unity as size increases, the slope of the size distribution will change from negative to positive: conditions required for a bimodal distribution (Fig. 3). In contrast, a shift from growth-dominated ($Z/K < 1$) to mortality-dominated ($Z/K > 1$) conditions produces a strongly unimodal pattern, with the position of the mode determined by the size where $Z = K$.

Obviously, variation in the ratio of Z/K can arise from size or age-specific changes in the value of Z , K , or both. Although Bertalanffy-type growth curves assume K to be independent of age, the growth intervals of species are frequently shown to exhibit variations in K with age, with K commonly decreasing slightly with age (Ricker 1975). For example, decreases in K with size or age are evident from the increasing slope of Walford plots for sea urchins *Strongylocentrotus purpuratus* presented by Russell (1987). Estimates of K from Russell's Figure 3 decrease from approximately 0.5 to 0.05 from small to large urchins at most locations. Assum-

ing the reported instantaneous mortality rates ($Z \approx 0.1$) to be constant, the age-specific Z/K ratio indicates that the size-specific population dynamics switch from growth-dominated ($Z/K < 1$) to mortality-dominated ($Z/K > 1$), which might account for the observed strongly unimodal size-frequency distributions. Other species of urchins (Tegner and Dayton 1977, 1981; Himmelman 1986; Tegner and Barry Unpubl.) as well as many species of long-lived arctic fishes (DeAngelis and Matice 1979) exhibit bimodal size-frequency distributions and must, under steady-state conditions, undergo a shift from mortality-dominated to growth-dominated population dynamics.

In that the growth rates of individuals usually decrease with age (Ricker 1975, but see Campbell 1979, Himmelman 1986), the most likely cause of persistently bimodal size distributions under steady-state conditions is an even greater decrease in the mortality rate of large individuals. A reduction in mortality, assuming a constant or slightly decreasing growth coefficient, could allow Z/K to shift from >1 to <1 : conditions necessary for bimodality.

Evidence for lower mortality with larger size or age is common. Many species exhibit type III survivorship curves of decreasing mortality with age (Deevey 1947, Odum 1971, Wilson and Bossert 1971). For example, because lobsters preferentially consumed small-sized red urchins *Strongylocentrotus franciscanus* (Tegner and Levin 1983) and sheephead *Semicossyphus pulcher* repeatedly select smaller *S. franciscanus* when offered a choice of sizes (Tegner and Dayton 1981), predation mortality apparently decreases with size (= age) in urchins. In addition, geographic differences in the size structure of red urchins are related to the distribution of predators, with bimodal size-frequency distributions found where these predators are most abundant (Tegner and Barry Unpubl.). Intraspecific competition for resources and high adult survivorship appear to limit the growth or survival rates of juveniles or both for arctic fishes (Johnson 1976), green sea urchins (Himmelman 1986), as well as forest trees (Harper 1977), often leading to a bimodal distribution of sizes; however, bimodality in these populations may arise from stochastic, age-specific changes in growth (DeAngelis and Coutant 1982).

Unstable or non-equilibrium conditions

There are conspicuous alternative causes of bimodal size-frequency structures for populations with unstable or non-stationary age compositions. In particular, species that have seasonal recruitment and live for only two years (e.g., blue crabs; Hines et al. 1987) have persistent, but recruitment-controlled bimodality. For

longer-lived species, relaxation of the assumptions of a stable age structure and stationary size distribution allow for transient, but perhaps persistent, variations in age and size structures due to temporal variation in recruitment and mortality. Interannual variation in recruitment, to a population normally dominated by an adult mode, can skew the age structure and occasionally produce a mode of juveniles, thereby resulting in bimodality. This feature will, however, deteriorate as the juveniles grow and merge into the adult mode. Similarly, a mortality-dominated population can become bimodal when a large pulse of juveniles grows to adult size, before being eventually depleted by mortality. In both cases bimodality is a transient feature of the size structure. How long it will persist is determined by the rapidity with which individuals grow to asymptotic size as well as the range of variation in recruitment. Recruitment pulses leading to unstable size and age distributions have been reported for several species (Hjort 1914, 1926; Ebert 1983; Cowen 1985; Johnson et al. 1986; Paine 1986; Pearse and Hines 1987; Raymond and Scheibling 1987).

Variation in growth and mortality within an age cohort, due to stochastic processes and genetic variability, can disrupt the deterministic character of growth and survivorship processes leading to a highly variable age and size structure, even within a single cohort. Intraspecific competition for resources can induce bimodality within a single cohort if growth to a particular size confers a great competitive advantage, leading to even more rapid growth (DeAngelis and Coutant 1982). For example, if recruitment by juveniles into the adult size classes is regulated by stochastic processes that provide limiting resources to a few juveniles upon the removal of adult individuals, the size structure of a cohort may become bimodal. This is apparently typical of arctic fishes (Johnson 1976), large-mouth bass (Shelton et al. 1979; Timmons et al. 1980), green sea urchins (Himmelman 1986), stalked barnacles (Page 1986), and many species of forest trees (Harper 1977).

Value of simple size-frequency distribution models

As shown in this analysis, even very simple models of size-frequency distributions, with perhaps unrealistic assumptions, can provide valuable information concerning the growth and mortality schedules of populations. Although the range of potential size structures is constrained by model assumptions such that bimodal size distributions, or unimodal distributions with the mode centered away from S_0 or S_∞ , are not possible, we can still utilize these models to identify likely

patterns of age-related mortality and growth; "impossible" size-frequency distributions are indicative of specific violations of the assumptions. Even though model assumptions impose severe restrictions upon the shape of size distributions, the shape of an observed distribution, coupled with marginal information concerning recruitment and growth for the species, can be used to infer age-related changes in growth, mortality, or both, leading to better directed research efforts on the population. This is particularly important for species such as red urchins which show strong geographical variation in their population dynamics (Tegner and Barry Unpubl.); fishery managers often must rely on easily collected size-frequency information to infer demographic parameters, rather than costly population studies at several locations.

Acknowledgments

We thank P. Dayton, J. Enright, C. Lennert, A. McCall, T. Ragen, W. Stockton, G. Sugihara, W. Wakefield, W. Wright, and an anonymous reviewer for advice and editorial help. This research was sponsored in part by the National Science Foundation, National Sea Grant College Program, Department of Commerce, under grant NOAA 04-8-MO1-189, project number R/F-36, through the California State Resources Agency. The U.S. Government is authorized to reproduce and distribute for governmental purposes.

Citations

- Barry, J.P.**
1989 Response of a marine annelid to winter storms: an analog to fire-adaptation in plants? *Mar. Ecol. Prog. Ser.* 54:99-107.
- Beverton, J.H., and S.J. Holt**
1956 A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 140:67-83.
- Campbell, R.N.**
1979 Ferox trout, *Salmo trutta* L., and charr, *Salvelinus alpinus* (L.), in Scottish lochs. *J. Fish. Biol.* 14:1-29.
- Cassie, R.M.**
1954 Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. Mar. Freshwater Res.* 5:513-522.
- Cowen, R.K.**
1985 Large scale patterns of recruitment by the labrid, *Semioscyphus pulcher*: Causes and implications. *J. Mar. Res.* 43:719-742.
- DeAngelis, D.L., and C.C. Coutant**
1982 Genesis of bimodal size distributions in species cohorts. *Trans. Am. Fish. Soc.* 111:384-388.
- DeAngelis, D.L., and J.S. Mattice**
1979 Implications of a partial-differential-equation cohort model. *Math. Biosci.* 47:271-285.
- Deevey, E.S., Jr.**
1947 Life tables for natural populations of animals. *Q. Rev. Biol.* 22:283-314.
- Ebert, T.A.**
1973 Estimating growth and mortality rates from size data. *Oecologia (Berl.)* 11:281-298.
1983 Recruitment in echinoderms. *In* Jangoux, M., and J.M. Lawrence (eds.), *Echinoderm studies*, p. 169-203. A.A. Balkema, Rotterdam.
- Green, R.H.**
1970 Graphical estimation of rates of mortality and growth. *J. Fish. Res. Board Can.* 27:204-208.
- Harper, J.L.**
1977 Population biology of plants. Acad. Press, NY, 892 p.
- Himmelman, J.H.**
1986 Population biology of green sea urchins on rocky barrens. *Mar. Ecol. Prog. Ser.* 33:295-306.
- Hines, A.H., R.N. Lipcius, and A.M. Haddon**
1987 Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 36:55-64.
- Hjort, J.**
1914 Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer* 20:1-228.
1926 Fluctuations in the year classes of important food fishes. *J. Cons. Perm. Int. Explor. Mer* 1:1-38.
- Johnson, D.F., L.W. Botsford, R.D. Methot, Jr., and T.C. Wainwright**
1986 Wind stress and cycles in Dungeness Crab (*Cancer magister*) catch off California, Oregon, and Washington. *Can. J. Fish. Aquat. Sci.* 43:838-845.
- Johnson, L.**
1976 Ecology of Arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest territories. *J. Fish. Res. Board Can.* 33:2459-2488.
- Odum, E.P.**
1971 Fundamentals of ecology, 3d ed. W.B. Saunders Co., Toronto, 574 p.
- Page, H.M.**
1986 Differences in population structure and growth rate of the stalked barnacle *Pollicipes polymerus* between a rocky headland and an offshore oil platform. *Mar. Ecol. Prog. Ser.* 29:157-164.
- Paine, R.T.**
1986 Benthic community-water column coupling during the 1982-1983 El Niño: are community changes at high latitudes attributable to cause or coincidence? *Limnol. Oceanogr.* 31:351-360.
- Pauly, D., and G.R. Morgan**
1987 Length-based methods in fisheries research. ICLARM Conference Proceedings 13. Int. Cent. Living Aquat. Resour. Manage., Manila, Philippines, and Kuwait Inst. Sci. Res., Safat, Kuwait, 468 p.
- Pearse, J.S., and A.H. Hines**
1987 Long-term population dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline. *Mar. Ecol. Prog. Ser.* 39:275-283.
- Pollard, J.E.**
1985 *Isopodichnus*, related arthropod trace fossils and notostracans from Triassic fluvial sediments. Fossil Arthropods as living animals. *Trans. R. Soc. Edinb.* 76:273-286.
- Power, G.**
1978 Fish population structure in arctic lakes. *J. Fish. Res. Board Can.* 35:53-59.

Raymond, B.G., and R.E. Scheibling

1987 Recruitment and growth of the sea urchin *Strongylocentrotus droebachiensis* (Müller) following mass mortalities off Nova Scotia, Canada. *J. Exp. Mar. Biol. Ecol.* 108:31-54.

Ricker, W.E.

1958 Handbook of computations for biological statistics of fish populations. *Fish. Res. Board Can. Bull.* 119, 300 p.

1975 Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board Can. Bull.* 191, 382 p.

Russell, M.P.

1987 Life history traits and resource allocation in the purple sea urchin *Strongylocentrotus purpuratus* (Stimpson). *J. Exp. Mar. Biol. Ecol.* 108:199-216.

Shelton, W.L., W.D. Davies, T.A. King, and T.J. Timmons

1979 Variation in the growth of the initial year class of largemouth bass in West Point Reservoir, Alabama and Georgia. *Trans. Am. Fish. Soc.* 108:142-149.

Stein, D.L., and W.G. Pearcy

1982 Aspects of reproduction, early life history, and biology of macrourid fishes off Oregon, U.S.A. *Deep-Sea Res.* 29:1313-1329.

Tegner, M.J., and J.P. Barry

Unpubl. Size structure of red sea urchin (*Strongylocentrotus franciscanus*, Agassiz) populations in southern California: Effects of growth, recruitment, predation, and oceanography.

Tegner, M.J., and P.K. Dayton

1977 Sea urchin recruitment patterns and implications of commercial fishing. *Science (Wash., DC)* 196:324-326.

1981 Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Mar. Ecol. Prog. Ser.* 5225-5268.

Tegner, M.J., and L.A. Levin

1983 Spiny lobsters and sea urchins: analysis of a predator-prey interaction. *J. Exp. Mar. Biol. Ecol.* 73:125-150.

Timmons, T.J., W.L. Shelton, and W.D. Davies

1980 Differential growth of largemouth bass in West Point Reservoir, Alabama-Georgia. *Trans. Am. Fish. Soc.* 109: 176-186.

Van Sickle, J.

1977a Analysis of a distributed-parameter population model based on physiological age. *J. Theor. Biol.* 64:571-586.

1977b Mortality rates from size distributions. *Oecologia (Berl.)* 27:311-318.

von Bertalanffy, L.

1957 Quantitative laws in metabolism and growth. *Q. Rev. Biol.* 32:217-231.

Wilson, E.O., and W.H. Bossert

1971 A primer of population biology. *Sinauer Assoc., Sunderland, Massachusetts*, 192 p.

Wilson, G.D.

1983 Variation in the deep-sea isopod *Eurycope iphthima* (Asellota, Eurycopidae): depth related clines in rostral morphology and in population structure. *J. Crust. Biol.* 3:127-140.