

QUANTIFYING NATURAL SELECTION ON BODY SIZE FROM FIELD DATA: WINTER MORTALITY IN *MENIDIA MENIDIA*

STEPHAN B. MUNCH,^{1,3} MARC MANGEL,² AND DAVID O. CONOVER¹

¹Marine Sciences Research Center, State University of New York, Stony Brook, New York 11794-5000 USA

²Department of Applied Mathematics and Statistics, Jack Baskin School of Engineering, University of California, Santa Cruz, California 95064 USA

Abstract. Analyses of changes in size distributions over time frequently suggest that mortality rates depend on body size. Such observations, however, are probably confounded with changes in size due to growth. We describe a parametric method by which the size dependence of both mortality and growth may simultaneously be inferred from pairs of size distributions collected at different times. The method is tested in a Monte Carlo study and found to have sampling properties similar to those of other methods that require more data.

Survival of the first winter of life appears to be size dependent in a diverse array of taxa, although few prior studies have accounted for growth. Analysis of sizes of *Menidia menidia* (Atlantic silverside) from three different latitudes revealed that changes in size distributions through winter resulted from growth in southern populations and mortality in the north. Winter mortality was better described by a power function of size than an exponential. Allometric exponents increased with latitude and were greater than predicted from metabolic- or starvation-based models. The steepness of the estimated survivorship curves imply that winter mortality in *M. menidia* is more consistent with a threshold effect perhaps attributable to offshore migration.

Key words: *Atherinidae*; *Atlantic silverside*; *Bergmann size clines*; *body size*; *latitudinal gradient*; *maximum likelihood*; *Menidia menidia*; *Monte Carlo simulation*; *selection*; *size-dependent mortality*; *winter mortality*.

INTRODUCTION

Substantial advances have been made in the measurement of selection in wild populations (e.g., Lande 1979), and the techniques developed are well suited to the study of selection on phenotypes that remain constant through a study interval. However, there are many traits of interest in ecology and evolutionary biology that do not remain constant through significant periods in the life history. Body size, for example, is an important determinant of fitness (Roff 1992), but one that constantly changes through the course of development. Because the distribution of such dynamic traits may change for a variety of reasons in wild populations, the measurement of natural selection on dynamic traits in the field is fraught with obstacles. We present a novel method for the estimation of selection on dynamic traits. The method is then applied to selection on body size during the first winter of life, a period of time when both size-dependent mortality and growth are possible.

Survival of the first winter is thought to be a pivotal determinant of cohort abundance in many taxa. Juvenile Soay sheep, mule deer, and several bird species experience mortality rates as high as 70% over their first winter (Massemin and Handrich 1997, Loison et al. 1999, Milner et al. 1999). Turtles, green anoles, and many species of fish also experience substantial first-winter mortality (Toneys and Coble 1979, Distler et al. 1998, Bodie and Semlitsch 2000, Nagle et al. 2000). Field studies typically show an increase in mean size and a decrease in variance from beginning to end of winter, usually interpreted as mortality of smaller individuals (Toneys and Cobble 1979, Miranda and Hubbard 1994, Milner et al. 1999, Nagle et al. 2000). Accordingly, larger individuals are more likely to survive periods of exposure to winter conditions in laboratory experiments (Oliver et al. 1979, Post and Evans 1989, Hurst and Conover 1998). Because growth through the first year is density dependent in many species, the size dependence of first-winter mortality may be a mechanism contributing to density-dependent population dynamics (Johnson and Evans 1990, Milner et al. 1999). Predictive population dynamics models should therefore incorporate the effects of winter. A well-defined functional relationship among size, winter duration/severity, and survival is needed to do so.

Size-dependent winter mortality may play an important role in the evolution of body size and growth

Manuscript received 6 March 2002; revised 10 October 2002; accepted 29 October 2002; final version received 16 December 2002. Corresponding Editor: S. Nylin.

³Present address: Department of Applied Mathematics and Statistics and Center for Stock Assessment Research, Jack Baskin School of Engineering, University of California, Santa Cruz, California 95064 USA.

E-mail: zasummen@aol.com

rate in temperate animals. Adult body size tends to increase with latitude in a pattern known as Bergmann's Rule (Lindsey 1966). The genetic capacity for growth also increases with latitude in many temperate species (Conover and Shultz 1995). Because temperature and the seasonal opportunity for growth decrease with latitude, this pattern of local adaptation in growth is referred to as countergradient variation (Levins 1968). Both Bergmann's rule and countergradient variation may be explained, in part, by a latitudinal gradient in the size dependence of first-winter mortality (Conover 1992). Although Bergmann's Rule is well documented and the evolution of juvenile growth rate has received increasing attention in recent years, few (if any) studies have examined the size dependence of winter mortality at multiple latitudes.

Conover and Present (1990) reviewed data on the mean size of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae), before and after winter. At all latitudes, the mean size of this annual estuarine fish species increased from beginning to end of winter and the magnitude of this increase was strongly tied to latitude. These data suggest that the size dependence of winter mortality increased with latitude. However, it is unclear how much of the change in mean size was due to growth vs. mortality at any latitude (Post and Evans 1989).

Although there is a well-developed literature on estimating mortality and growth from size distributions (e.g., Banks et al. 1991, Wood 1994) these methods require more data than are typically available in studies of winter mortality. In *M. menidia* and many other species, winter migrations (Conover and Murawski 1982) make multiple censuses impossible. We developed a new method based on paired size distributions, collected before and after winter, and tested its performance in a Monte Carlo study. We then applied our method to size distributions of *M. menidia* from three latitudes to test the hypothesis that the changes over winter represent growth at low latitudes and mortality at high latitudes.

METHODS

The model

For simplicity, we refer throughout to collections made before winter as "autumn" and after winter as "spring," regardless of date of collection. Our goal was to obtain estimates of winter mortality as a function of body size from a pair of autumn and spring size distributions, given that some growth may have occurred. If we knew how winter growth depended on body size, we could simply predict the spring size of the individuals collected in autumn. We then could estimate relative survivorship from the numbers in each predicted spring size class divided by the numbers in the observed spring size classes (Fig. 1). The ratio of the number of individuals in the corresponding size

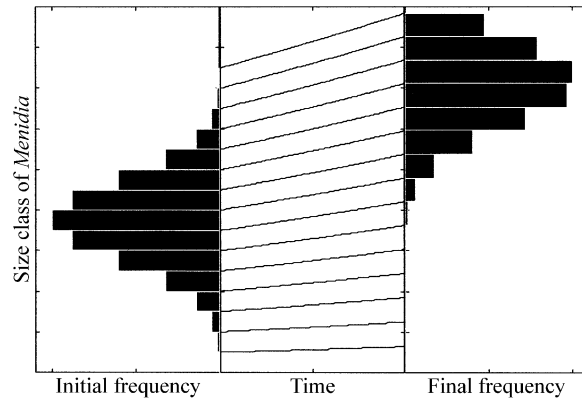


FIG. 1. A hypothetical example. The size distribution before winter (left) was sampled from a normal distribution ($\mu = 7.5$, $\sigma = 2$). The center panel shows corresponding trajectories for each size class under allometric growth ($g_1 = 0.0025$, $g_2 = 0.15$, $t = 100$ days). The size distribution after winter (right) is determined by the number of fish in each size class before winter and survival under exponential mortality ($m_1 = 0.025$, $m_2 = 2$).

classes (spring/autumn) is an estimate of survival, assuming that growth over winter is solely a function of size. Although we do not know the size dependence of growth, the estimation of survival from corresponding size classes before and after winter forms the basis of our method.

We assume that the rate of growth through the winter $G(x)$ is allometric. That is,

$$G(x) = g_1 x^{1-g_2} \quad (1)$$

where x is body size and g_1 and g_2 are the parameters governing growth. Allometric growth results in size trajectories that are nearly exponential to nearly linear for g_2 in $(0, 1)$. For $g_2 > 1$, small individuals grow faster than large ones and size trajectories converge, resulting in decreasing variance in size over time and giving the appearance of mortality.

Survival (S) of individuals growing along a given size trajectory is given by

$$S = \exp \left[- \int_{t_0}^{t_1} m[x(t)] dt \right] \quad (2)$$

where $m(x)$ is the instantaneous rate of mortality for individuals of size x , t_0 and t_1 are the start and end of winter, and x_0 and x_1 are the individuals' sizes at those times. Because our observations are on sizes, we make the change of variables from time to size ($dt = dx/G(x)$) and Eq. 2 becomes

$$S = \exp \left[- \int_{x_0}^{x_1} \frac{m(x)}{G(x)} dx \right]. \quad (2a)$$

We consider two models for the size dependence of mortality through the winter. Specifically,

exponential mortality:

$$m(x) = \exp(m_1 - m_2x) \tag{3a}$$

allometric mortality: $m(x) = m_1x^{-m_2}$. (3b)

Although both models appear in the size-dependent mortality literature, the allometric mortality model (Eq. 3b) seems to be the most generally accepted (Petersen and Wroblewski 1984, McGurk 1986, Pepin 1993). Parameter estimation for both models is somewhat simplified by the fact that evaluation of the integral in Eq. 2a can be carried out explicitly for each (see Appendix).

Statistical approach

Although several prior methods treat the initial size distribution as given (e.g., Wiegand et al. 2000), the number of individuals in each size class is only an estimate of the actual number, both before and after winter. The first step is to choose appropriate size classes for the autumn distribution. The choice of bin width (size intervals on which the histogram is constructed, Δx) represents a trade-off between sampling error in the numbers of individuals (decreases as Δx increases) and uncertainty in the size of individuals within the class (increases as Δx increases). We used $\Delta x = 2(\text{IQR})n^{-1/3}$ as suggested by Friedman and Diaconis (1981), where IQR is the interquartile range of the autumn sample and n is the sample size. This bin width is nearly optimal for normal size distributions and is robust to modest departures from normality.

Our algorithm for finding the growth and mortality parameters, which we describe in detail, can be summarized as follows:

- 1) Construct a histogram for the observed autumn sizes based on near optimal bin widths, including several (~10) extra classes at the extreme sizes.
- 2) Choose an initial set of growth and mortality parameters.
- 3) Based on the current choice of growth parameters and autumn size classes, predict corresponding size classes for the spring sample and tabulate numbers of individuals in each.
- 4) Calculate the likelihood.
- 5) Choose new growth and mortality parameters to improve the likelihood.

Repeat steps 3–5 until the maximum likelihood is obtained.

If the expected number of individuals in size class i is λ_i in autumn, then the expected number of individuals in the corresponding spring size class is $\bar{S}_i\lambda_i$, where S_i is the fraction of individuals in the size class that survive the winter. The observed number in each size class is assumed to be Poisson distributed; the probabilities of observing a_i individuals in autumn and b_i individuals in spring are each given by

$$P(a_i | \theta) = \exp(-\lambda_i)\lambda_i^{a_i}(a_i!)^{-1}$$

$$P(b_i | \theta) = \exp[-\lambda_i\bar{S}_i(\theta)][\lambda_i\bar{S}_i(\theta)]^{b_i}(b_i!)^{-1}.$$

Assuming that the observations in each size class in autumn and spring are independent, the probability of observing the pair of samples before and after winter is

$$P(a_i, b_i | \theta) = \exp\{-\lambda_i[1 + \bar{S}_i(\theta)]\}\lambda_i^{a_i+b_i}\bar{S}_i(\theta)^{b_i}(b_i!a_i!)^{-1} \tag{4}$$

where $\theta = \{g_1, g_2, m_1, m_2\}$ is a vector of growth and mortality parameters. Because the location and width of the corresponding size interval in spring depends on the growth parameters, b_i is a function of θ . Consequently, the apparent average survival of individuals in the size interval depends on both the growth and mortality parameters and is now written as $\bar{S}_i(\theta)$. Dividing the autumn size distribution into N size classes, the likelihood (L) of observing the entire distribution is the product of Eq. 4 taken over each pair of corresponding size classes, i.e.,

$$L(\theta, \lambda, c) = \prod_{i=1}^N \exp\{-\lambda_i[1 + c\bar{S}_i(\theta)]\} \times \lambda_i^{a_i+b_i}[c\bar{S}_i(\theta)]^{b_i}(a_i!b_i!)^{-1} \tag{5}$$

where $\lambda = \{\lambda_1 \dots \lambda_N\}$ and a constant c has been included to account for the possibility that the fraction of the population sampled in the autumn is different than that in the spring. Because we cannot distinguish between sampling and overall mortality, this method can only provide estimates of relative survival. Given a set of growth and mortality models, we find the best model by maximizing $\ln(L)$ over choices of λ , c , and θ . For each of the λ_i 's, an explicit solution exists. Specifically,

$$\lambda_i = \frac{a_i + b_i}{1 + c\bar{S}_i(\theta)} \tag{6}$$

which can be interpreted as a weighted mean of the numbers of individuals observed in size class i before and after winter. Note that if there is no mortality and the same fraction of the population is sampled both times (i.e., $c = S = 1$), λ_i is simply the average number in the size class before and after winter. Further, c can be rapidly obtained from the following recursion equation:

$$c_{\text{new}} = \left[\sum_{i=1}^N \frac{\bar{S}_i(\theta)(b_i + a_i)}{1 + c_{\text{old}}\bar{S}_i(\theta)} \right]^{-1} \sum_{i=1}^N b_i \tag{7}$$

which is derived by setting $\partial \ln L / \partial c = 0$ and solving for c . The remaining parameters (θ) were obtained using a Nelder-Mead simplex algorithm implemented in MATLAB (version 5.2; MathWorks 1998). The likelihood surface for the model is fairly rugose, with many local maxima. To circumvent problems associated with this, we started the fitting algorithm from 500 random

TABLE 1. Sampling locations for *Menidia menidia*, sampling dates, and input parameters.

Site	Sample dates		Winter duration (d)	Bin widths [†] (mm)
	Autumn	Spring		
Annapolis River, Nova Scotia (NS)	29 Sep 1987	30 May 1988	244	3.72
	26 Sep 1988	3 Jun 1989	250	4.05
Great South Bay, New York (NY)	27 Oct 1987	27 Apr 1988	183	4.49
	25 Oct 1988	18 Apr 1989	175	4.31
Edisto River, South Carolina (SC)	1 Dec 1987	30 Mar 1988	120	2.76
	28 Nov 1988	20 Mar 1989	112	3.30

[†] Size intervals used to construct histograms of *Menidia* body size.

points within the plausible parameter space and chose the highest likelihood from among the results.

Monte Carlo simulation

To test the ability of our method to estimate accurate parameter values, we conducted a Monte Carlo simulation. The simulation consisted of generating 1000 replicate data sets for each mortality model assuming allometric growth. For each replicate, the autumn sample consisted of observations drawn from a normal distribution with mean 60 and standard deviation 8, chosen to mimic the observed sizes of *Menidia* before winter. The inverse transformation method (Ross 1997) was used to generate each spring sample, which consisted of observations from the distribution obtained by modifying the autumn normal frequencies by size-specific survival and growth as previously outlined. For each replicate, $L(\theta)$ was maximized to find the growth and mortality parameters for both mortality models. The mean, cv, and bias of the parameter estimates were calculated for comparison with previous methods. To address how the performance of the model is affected by sample size, the simulation was repeated for samples of 75, 150, 300, and 600 observations drawn from the autumn and spring size frequency distributions.

In addition to the precision of the parameter estimates, the ability of the model to discriminate between changes in size distributions associated with growth vs. mortality is also of interest. That is, how often will rapid growth and low mortality be mistaken for slow growth and high mortality? To address this, we repeated the simulations for three cases: (1) rapid growth, low mortality; (2) moderate growth, intermediate mortality; and (3) slow growth, high mortality. In each case, the parameters were chosen such that the mode of the spring size distribution was fixed at 90 mm.

From these samples, we determined the probability of correctly identifying the case from which the size distribution was sampled based on the predicted survival and growth of an individual of average initial size. Classification was based on dividing the space of possible survival and growth values into logarithmically equal bins and tabulating frequencies in each bin. The bin frequencies were used to estimate two probabilities: (1) the probability that a distribution sampled

from a particular class was correctly classified, and (2) the probability that distributions classified as cases 1, 2, or 3 were, in fact, sampled from the corresponding cases.

Winter mortality in *Menidia menidia*

Menidia menidia is one of the most abundant fishes along the east coast of North America (Bayliff 1950). It has a simple annual life cycle, the timing of which is strongly tied to temperature and photoperiod. Consequently, growth and reproduction occur at temperatures of 12–30°C regardless of latitude (Conover and Present 1990). *M. menidia* were sampled just before and just after winter at three latitudes in 1987 and again in 1988 (Table 1). The sites were Annapolis River, Nova Scotia (NS; 44°40' N), Great South Bay, New York (NY; 42°45' N), and Edisto River, South Carolina (SC; 33°20' N). These locations span most of the current range of latitudes over which *M. menidia* is found (Johnson 1975). Between 300 and 500 fish were captured by beach seining at each site. For further details on the collection methods, refer to Billerbeck et al. (1997). Size distributions of *Menidia* were broader at high latitudes before winter; bin widths for each site and year are shown in Table 1. For each pair of autumn and spring size distributions, we estimated the maximum likelihood parameters for each mortality model.

Because the correct model for the size dependence of mortality in *Menidia* is unknown, we wanted to determine whether one model fit the data significantly better than the other. The two mortality models can be thought of as specific cases of a more general model for the size dependence of mortality, i.e., $dm(x)/dx = -m_2x^q m(x)$ where q is set to 0 for exponential mortality and to -1 for allometric mortality, they may be compared by a likelihood ratio test with one degree of freedom. In order to test the hypothesis that changes in the size distributions were due to growth in the south and mortality in the north, we conducted a series of likelihood ratio tests (Hilborn and Mangel 1997) comparing the effects of growth and mortality for each latitude. The significance of the size dependence of mortality was tested by comparing the full model (i.e., both mortality and growth) to the best model obtained by setting m_1 and m_2 equal to zero. Similarly, the sig-

TABLE 2. Results of Monte Carlo study for $N = 300$ *Menidia menidia*.

Parameter	CV of predicted value	Bias (%)
Exponential mortality		
g_1	0.24	5.50
g_2	0.23	3.93
m_1	0.37	4.45
m_2	0.20	1.96
Allometric mortality		
g_1	0.21	3.82
g_2	0.20	0.82
m_1	0.23	4.20
m_2	0.38	2.27

Notes: In both models, g_1 and g_2 are the slope and exponent for the allometric model. For exponential mortality, m_1 is a scaling factor, and m_2 determines the size dependence of mortality. For allometric mortality, m_1 and m_2 are the slope and exponent, respectively.

nificance of growth over the sampling period was assessed by setting $g_1 = g_2 = 0$.

RESULTS

Monte Carlo simulation

The fitting method adequately recovered the parameters from which each sample was drawn with very small bias for samples of 300 individuals. Typical results for samples of 300 individuals are given in Table 2. Although the bias increased as sample size decreased, the estimated bias was always $<15\%$. The cvs for the growth parameters are within 26% and improved only modestly with increased sample size (Table 3). The cvs of the mortality parameters were much more strongly influenced by sample size, with substantial gains in precision up to sample sizes of ~ 300 individuals. The two parameters for the growth model were strongly negatively correlated ($r = -0.66$) and the two mortality parameters were strongly positively correlated ($r = 0.75$), implying a fairly flat likelihood surface in each of these directions. This is to be expected because there are only two samples from which to estimate growth and mortality.

Once the maximum likelihood parameter estimates were obtained for each sample, the predicted survival and growth of an individual of average initial size was used to evaluate the probability of mistaking growth and mortality. We focus here on classification as one

of three cases: (1) rapid growth, low mortality; (2) moderate growth, intermediate mortality; and (3) slow growth, high mortality. Given the case from which the sample was drawn, the probability of correctly reclassifying a size distribution was 0.97, 0.88, and 0.99 for cases 1, 2, and 3 respectively. On the other hand, given that a sample was observed in a given case, the probability that this post hoc classification was correct was 0.99, 0.99, and 0.90 for cases 1, 2, and 3, respectively.

Winter mortality in *Menidia menidia*

The method reproduces the pre- and postwinter size distributions of *Menidia* quite well (Fig. 2). The resulting likelihoods for each model at each location and year are reported in Tables 4 and 5. Overall, the allometric mortality model fit the observed size distributions best. The total log-likelihood (summed over all locations and years) for allometric mortality (6118.75) is significantly greater ($P < 0.0001$) than that for the exponential model (6106.85). Within years, the allometric mortality model was significantly better than the exponential model in 1987–1988, while in 1988–1989 there was no significant difference. Although parameters and P values for the exponential mortality model were different from those of the allometric model, all qualitative results were identical and the remainder of the discussion is limited to the allometric mortality model.

Growth was significant for all populations in 1987–1988 whereas in 1988–1989, growth was only significant in South Carolina, SC (Table 4). In all instances, growth rate was very slow and nearly proportional to length (i.e., $g_2 < 0.1$; Table 5). Over winter 1987–1988, the greatest change in size due to growth occurred in New York, NY, whereas in 1988–1989, it was maximal in SC. Survival was significantly size dependent for NS (Nova Scotia) and NY in each year, but independent of size in SC (Table 4). The estimated relative survivorship (Fig. 3) was steep for Nova Scotia *M. menidia* in both years and a substantial portion of the observed autumn size distribution was predicted to have near-zero survival. There was also substantial interannual variation in the survivorship curves for each population, although the survivorship curves for NS were more similar across years than were the curves for NY. These differences among years could not be accounted for by differences in overwinter growth alone: holding

TABLE 3. Coefficients of variation as a function of sample size for the exponential mortality and allometric mortality models for *Menidia menidia*.

Sample size (no. fish)	Exponential mortality				Allometric mortality			
	g_1	g_2	m_1	m_2	g_1	g_2	m_1	m_2
75	0.25	0.24	0.60	0.34	0.26	0.25	0.34	0.52
150	0.22	0.21	0.46	0.25	0.23	0.21	0.28	0.42
300	0.24	0.23	0.37	0.20	0.21	0.20	0.23	0.38
600	0.18	0.18	0.25	0.13	0.19	0.18	0.17	0.26

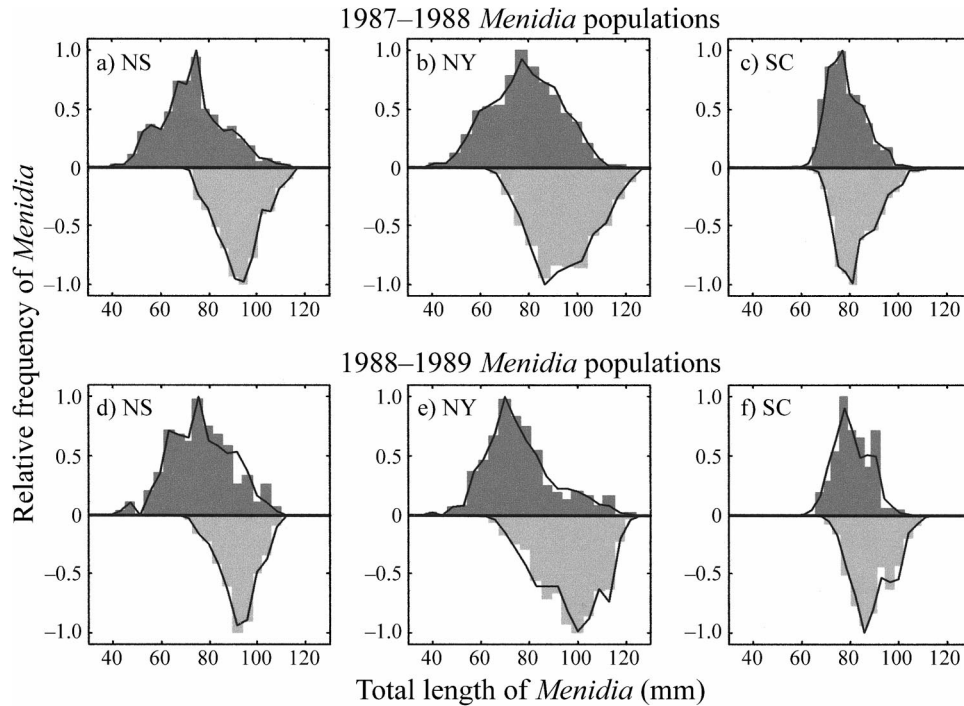


FIG. 2. Observed and predicted size distributions for the allometric mortality model. Each panel shows the relative frequency, i.e., observed/maximum(observed) of fish in autumn (dark, upward bars) and spring (light, downward bars). The lines indicate the distributions predicted by the best-fit model (parameters are shown in Table 4). The fit to the left-hand tail of each autumn distribution should be ignored in evaluating model performance because predicted abundance in size classes with near-zero survival are determined solely by the number before winter (see Eq. 6). Location abbreviations are: NS, Annapolis River, Nova Scotia; NY, Great South Bay, New York; SC, Edisto River, South Carolina.

growth parameters constant across years did not eliminate differences in relative survival.

DISCUSSION

The method described in this paper deals with the problem of estimating the size dependence of mortality when growth may also be a function of body size. This problem, however, is not restricted to growth and mortality, but applies to any trait that changes naturally over time and is simultaneously subject to selection. The progression of individuals among age classes or ontogenetic stages is the most obvious example. Although this has previously been dealt with in the literature (e.g., Caswell 2001) other factors such as seasonal changes in energy content or the timing and mag-

nitude of reproductive effort have not. Methods such as the one presented in this paper should be of great use in the analysis of natural selection on dynamically changing traits.

Analyses of size distributions may be separated into two categories: those based on mixture models (MacDonald and Pitcher 1979, Schnute and Fournier 1980) and those based on the McKendrick-VonFoerster (MVF) partial differential equation model (Banks et al. 1991, Wood 1994, Smith et al. 1998). The mixture model methods typically decompose a set of multimodal frequency distributions collected at an annual time increment into component distributions, allowing single cohorts to be tracked through time. Methods based on the MVF model (also referred to as the Sinko-

TABLE 4. Negative log likelihoods and probabilities for the allometric mortality model.

Site and year	Full model	No-growth model	<i>P</i>	No size selection	<i>P</i>
NS 1987–1988	966.48	962.87	0.027	917.37	0.000
NS 1988–1989	336.09	336.09	1.000	284.27	0.000
NY 1987–1988	1847.38	1838.24	0.000	1830.31	0.000
NY 1988–1989	1164.51	1164.51	1.000	1138.00	0.000
SC 1987–1988	1266.36	1256.75	0.000	1265.99	0.690
SC 1988–1989	537.93	532.86	0.006	535.24	0.068

Note: *P* values are based on χ^2 with *df* = 2 and indicate the probability that the improvement in the full model, by the addition of the missing term (growth or mortality), is due to chance.

TABLE 5. Significant parameters for the allometric mortality model.

Site and year	$g_1 (\times 10^4)$	$g_2 (\times 10^2)$	$m_1 (\times 10^2)$	m_2	c
NS 1987–1988	0.36 (0.31, 0.53)	5.68 (1.2, 10.27)	2.17 (2.13, 2.22)	8.77 (8.41, 9.2)	6.54
NS 1988–1989	NS	NS	3.08 (2.97, 3.19)	4.93 (4.69, 5.18)	36.53
NY 1987–1988	5.89 (5.87, 6.34)	1.94 (1.75, 4.27)	2.25 (2.2, 2.32)	12.53 (11.69, 13.61)	1.23
NY 1988–1989	NS	NS	5.17 (4.91, 5.45)	2.68 (2.55, 2.81)	33.35
SC 1987–1988	4.44 (4.04, 5.03)	1.09 (-0.32, 5.13)	NS	NS	1.41
SC 1988–1989	7.00 (6.97, 7.03)	9.16 (9.02, 9.36)	NS	NS	1.83

Notes: Only significant parameters are shown. Confidence intervals (in parentheses) are determined from the likelihood profile. Parameter values have been multiplied by factors of 10 where noted in column heads. See Fig. 2 for the site abbreviations.

Streifer [1967] model) track changes in frequency distributions directly and may be subdivided further into nonparametric and parametric methods.

Several authors have developed nonparametric methods for the general problem of determining growth and mortality rates as functions of both size and time (Banks et al. 1991, Wood 1994). These studies construct approximate solutions to the MVF model using nonparametric (e.g., spline) surfaces chosen to minimize squared deviations from a set of 10 or more size frequencies. Because our data were limited to pairs of size frequencies, there is insufficient information to

generate meaningful nonparametric surfaces. Our approach, however, is analogous to a parametric MVF model such as those used by Smith et al. (1998) and Wiegand et al. (2000). In a thorough analysis, Smith et al. (1998) specified models for growth and mortality as functions of size, and fit a steady-state (i.e., constant recruitment, constant size frequency) MVF model to a series of 30 or more size frequencies. Using samples of 400 size frequencies, their method produced estimates with variability and bias comparable to ours (Smith et al. 1998). Smith et al. (1998) incorporated growth increment data gathered under laboratory conditions to improve parameter estimates. Our use of paired size distributions separated by a known time interval allows the assumption of steady state to be relaxed and estimates to be obtained in the absence of laboratory data on growth.

Our Monte Carlo simulations demonstrate that reasonably precise parameter estimates may be obtained from the sort of data typically collected in studies of winter mortality. In all methods, however, mortality is far more difficult to estimate than is growth. Our method could readily be extended to the analysis of multiple frequency distributions, but will be of particular value when only two distributions are available. However, the approach developed here requires that there be a set of reasonable candidate functions from which to choose in describing changes in the size distribution over time; in situations where the data are sufficient, the nonparametric methods may be preferred.

In previous studies of winter survival, it has been difficult to distinguish between size-dependent growth and mortality based on size frequency distributions collected before and after winter. These studies have typically been limited to observations about changes in the mean and variance of size distributions before and after winter (e.g., Toneys and Coble 1979, Hurst and Conover 1998). In situations where the possibility of growth can be rigorously ruled out, changes in the size

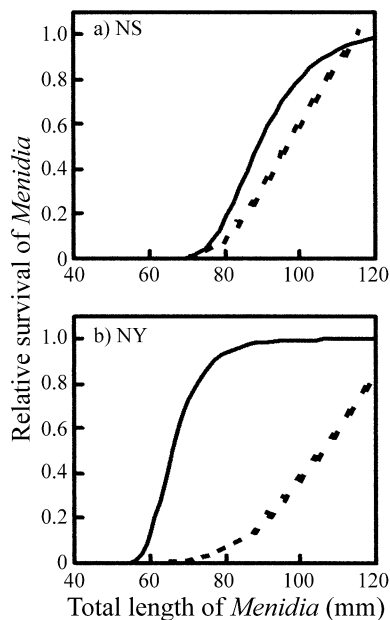


FIG. 3. Predicted survivorship curves for (a) Nova Scotia and (b) New York *Menidia* populations. Curves indicate survivorship over the winter of 1987–1988 (solid lines) and 1988–1989 (dashed lines). Overwinter survival for South Carolina study populations was independent of size.

distribution may confidently be attributed to mortality. However, because growth may be size dependent such that growth trajectories converge over time and the variance in size consequently decreases, changes in mean and variance are often insufficient to establish the size dependence of mortality. Post and Evans (1989) advocated the use of Q-Q plots to help distinguish growth from mortality, but noted that the results were equivocal. Application of our method allows the effects of growth and mortality to be accounted for simultaneously. For the purpose of studying winter survival in *M. menidia*, we limited our analysis to one growth model and two plausible mortality functions commonly applied in the literature. The allometric growth assumption allows growth curves to be nearly linear to nearly exponential, and allows size trajectories to converge or diverge. Because growth over winter is likely to be quite limited, this should be a reasonable approximation. Analyses of the size dependence of mortality during other life history stages have shown that mortality is either exponential (Wang and Hayward 1999) or allometric with body size (Petersen and Wroblewski 1984, Pepin 1993). The assumption that mortality over the first winter also decreases with body size is supported by the observation that most previous studies (Conover and Present 1990, Hurst and Conover 1998, Loison et al. 1999, Nagle et al. 2000), have reported shifts in size distributions that imply selection against smaller individuals. In the present study, winter mortality in *M. menidia* in NS and NY was best described by the allometric mortality model. However, previously reported allometric exponents range from 0.75 to 1.2 (assuming that body mass is proportional to cubed length; Petersen and Wroblewski [1984], Pepin [1993], Lorenzen [1996]) for mortality during the growing season or across species. The allometries that we have found are much steeper (2.68–12.53), implying that the size dependence of winter mortality is fundamentally different from mortality observed throughout the growing season.

It is commonly thought that because winter is a period of low productivity, starvation is the primary source of winter mortality in fishes (Cunjack 1988). Johnson and Evans (1996) suggest that because mass-specific lipid reserves scale as $W^{0.57}$ and mass-specific metabolism scales as $W^{-0.25}$, the time to starvation should scale as $W^{0.82}$, implying that the allometric exponent (in terms of length) for first winter mortality should be ~ 2.4 . For *M. menidia*, the allometry of energy reserves varies with latitude, with estimates of 4.05, 5.18, and 5.73 for SC, NY, and NS, respectively (Shultz and Conover 1997, 1999). There is also some interpopulation variability in standard metabolic rate; ~ 1.96 for SC and 2.24 for NS after conversion to length (Billerbeck et al. 2000, Munch and Conover 2002). The expected starvation allometry for *M. menidia* of different latitudes would be ~ 2.09 in SC and 3.49 in NS, with NY being intermediate. These starvation expo-

nents are substantially lower than the mortality exponents observed in this study, except for those from NY 1988–1989. Massemin and Handrich (1997) and Hurst et al. (2000) have argued that lipid reserves alone cannot explain the observed size dependence, and our results support this.

Several alternative mechanisms have been demonstrated to play an important role in winter mortality. Lethal exposure to low temperatures, increased susceptibility to predation and disease, loss of osmoregulatory function, and size-dependent migration success are potential mortality sources, either alone or in combination. The extreme steepness of the mortality allometries that we observed suggests a threshold effect. One possibility is that migration success is strongly tied to body size. Both NS and NY *Menidia* migrate offshore prior to winter (Conover and Murawski 1982), whereas SC *Menidia* remain inshore throughout the winter. The fact that in both years winter survival was independent of body size in SC, whereas it was strongly size-dependent for NS and NY, suggests that size-dependent migration success may play an important role in winter survival.

Size dependence of winter survival has important implications for the evolution of body size and growth for local populations. Several authors have noted that Bergmann size clines commonly observed in ectotherms may be explained by size-dependent winter survival (Conover and Present 1990, Bodie and Semlitsch 2000). Accordingly, *M. menidia* from Nova Scotia are somewhat larger at maturity than are their southern conspecifics (Conover and Present 1990). In Nova Scotia, winter mortality was consistently strongly size selective; fish smaller than 70 mm were unlikely to survive the winter. In New York, the survivorship curve was steeper than in NS in 1987–1988, but less steep in 1988–1989. Because no evidence has been found for latitudinal differences in the size dependence of mortality during other seasons (Lorenzen 1996), first-winter mortality is likely to be the chief agent of size selection with a latitudinal gradient.

In temperate species, the duration of the growing season is strongly tied to latitude such that increased size at high latitudes must be achieved by faster growth. In fact, *Menidia* from Nova Scotia grow 2–3 times faster than South Carolina *Menidia* in a common environment (Present and Conover 1992, Billerbeck et al. 2000). Conover (1992) argued that northern *Menidia* have evolved rapid growth rates in order to survive the winter. Our results support the hypothesis that both Bergmann size clines and countergradient variation in juvenile growth may be the result of a latitudinal gradient in the size dependence of first-winter mortality in *Menidia*.

ACKNOWLEDGMENTS

We thank Robert Armstrong and Tom Hurst for useful discussion. Thanks also to Bob Cerrato and three anonymous reviewers for comments on previous drafts of this manuscript.

This publication was supported by the National Sea Grant College Program of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration under award NA86RGO056 to the Research Foundation of the state university of New York for New York Sea Grant. This work received additional support from the Ocean Sciences division of the National Science Foundation, grant number OCE-0081916. The views expressed herein do not necessarily reflect the views of any of these organizations.

LITERATURE CITED

- Banks, H. T., L. W. Botsford, F. Kappel, and C. Wang. 1991. Estimation of growth and survival in size-structured cohort data: an application to larval striped bass (*Morone saxatilis*). *Journal of Mathematical Biology* **30**:125–150.
- Bayliff, W. H. 1950. The life history of the Atlantic silverside, *Menidia menidia*. Publication Number 90. Chesapeake Biological Laboratory, Solomons Island, Maryland, USA.
- Billerbeck, J. M., G. Orti, and D. O. Conover. 1997. Latitudinal variation in vertebral number has a genetic basis in the Atlantic silverside, *Menidia menidia*. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1796–1801.
- Billerbeck, J. M., E. T. Schultz, and D. O. Conover. 2000. Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. *Oecologia* **122**:210–219.
- Bodie, J. R., and R. D. Semlitsch. 2000. Size-specific mortality and natural selection in freshwater turtles. *Copeia* **732**–739.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.
- Conover, D. O. 1992. Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology* **41**:161–178.
- Conover, D. O., and S. Murawski. 1982. Offshore winter migration of the Atlantic silverside, *Menidia menidia*. *Fishery Bulletin* **80**:145–149.
- Conover, D. O., and T. Present. 1990. Countergradient variation in growth-rate: compensation for length of the growing-season among Atlantic silversides from different latitudes. *Oecologia* **83**:316–324.
- Conover, D. O., and E. T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology and Evolution* **10**:248–252.
- Cunjack, R. A. 1988. Physiological consequences of overwintering in streams: the cost of acclimatization? *Canadian Journal of Fisheries and Aquatic Sciences* **45**:443–452.
- Distler, J. K., M. E. Dorcas, J. Gibbons, K. Kandal, and K. R. Russell. 1998. Winter mortality in the green anole, *Anolis carolinensis* (Lacertilia: Poychridae). *Brimleyana* **25**:140–143.
- Friedman, D., and P. Diaconis. 1981. On the maximum deviation between the histogram and the underlying density. *Zeitschrift für Wahrscheinlichkeitstheorie und verwandte Gebiete* **58**:139–167.
- Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey, USA.
- Hurst, T. P., and D. O. Conover. 1998. Winter mortality of young-of-the-year Hudson river striped bass (*Morone saxatilis*): size dependent patterns and effects on recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1122–1130.
- Hurst, T. P., E. T. Shultz, and D. O. Conover. 2000. Seasonal energy dynamics of young-of-the-year Hudson River striped bass. *Transactions of the American Fisheries Society* **129**:145–157.
- Johnson, M. S. 1975. Biochemical systematics of the atherinid genus *Menidia*. *Copeia* **662**–691.
- Johnson, T. B., and D. O. Evans. 1990. Size-dependent winter of young-of-the-year white perch: climate warming and invasion of the Laurentian Great Lakes. *Transactions of the American Fisheries Society* **119**:301–313.
- Johnson, T. B., and D. O. Evans. 1996. Temperature constraints on overwinter survival of age-0 white perch. *Transactions of the American Fisheries Society* **125**:466–471.
- Lande, R. 1979. Quantitative-genetic analysis of multivariate evolution applied to brain-body size allometry. *Evolution* **33**:402–416.
- Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.
- Lindsey, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. *Evolution* **20**:456–465.
- Loison, A., R. Langvatn, and E. J. Solberg. 1999. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* **22**:20–30.
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology* **49**:627–647.
- MacDonald, P. D., and T. J. Pitcher. 1979. Age-groups from size frequency data: a versatile and efficient method of analyzing distribution mixtures. *Journal of the Fisheries Research Board of Canada* **36**:987–1001.
- Massemin, S., and Y. Handrich. 1997. Higher winter mortality of the Barn Owl compared to the Long-eared Owl and the Tawny Owl: influence of lipid reserves and insulation. *Condor* **99**:969–971.
- MathWorks. 1998. MATLAB version 5. 2. MathWorks, Natick, Massachusetts, USA.
- McGurk, M. D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Marine Ecology Progress Series* **34**:227–242.
- Milner, J. M., D. A. Elston, and S. D. Albon. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *Journal of Animal Ecology* **68**:1235–1247.
- Miranda, L. E., and W. D. Hubbard. 1994. Length dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. *Transactions of the American Fisheries Society* **123**:80–87.
- Munch, S. B., and D. O. Conover. 2002. Accounting for local physiological adaptation in bioenergetic models: testing hypotheses for growth rate evolution by virtual transplant experiments. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:393–403.
- Nagle, R. D., O. Kinney, J. D. Congdon, and C. W. Beck. 2000. Winter survivorship of hatchling painted turtles (*Chrysemys picta*) in Michigan. *Canadian Journal of Zoology* **78**:226–233.
- Oliver, J. D., G. Holeton, and K. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Transactions of the American Fisheries Society* **108**:130–136.
- Pepin, P. 1993. An appraisal of the size-dependent mortality hypothesis for larval fish: comparison of a multispecies study with an empirical review. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2166–2174.
- Petersen, I., and J. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* **41**:1117–1120.
- Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences* **46**:1958–1968.
- Present, T., and D. O. Conover. 1992. Physiological basis of latitudinal growth differences in *Menidia menidia*: variation

- in consumption or efficiency? *Functional Ecology* **6**:23–31.
- Roff, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman and Hall, New York, New York, USA.
- Ross, S. M. 1997. *Introduction to probability models*. Sixth edition. Academic Press, San Diego, California, USA.
- Schnute, J., and D. Fournier. 1980. A new approach to length–frequency analysis: growth structure. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:1337–1351.
- Shultz, E. T., and D. O. Conover. 1997. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). *Oecologia* **109**:516–529.
- Shultz, E. T., and D. O. Conover. 1999. The allometry of energy reserve depletion: test of a mechanism of size-dependent winter mortality. *Oecologia* **119**:474–483.
- Sinko, J. W., and W. Streifer. 1967. A new model for age-size structure of a population. *Ecology* **48**:910–918.
- Smith, B. D., L. Botsford, and S. R. Wing. 1998. Estimation of growth and mortality parameters from size frequency distributions lacking age patterns: the red sea urchin (*Strigyllocentrotus franciscanus*) as an example. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1236–1247.
- Toneys, M. L., and D. W. Coble. 1979. Size-related first winter mortality of fresh water fishes. *Transactions of the American Fisheries Society* **108**:415–419.
- Wang, Y., and M. Haywood. 1999. Size-dependent natural mortality of juvenile banana prawns *Penaeus merguensis* in the Gulf of Carpentaria, Australia. *Marine and Freshwater Research* **50**:313–317.
- Wiegand, T., S. Milton, K. Esler, and G. Midgley. 2000. Live fast, die young: estimating size–age relations and mortality patterns of shrub species in the semi-arid Karoo, South Africa. *Plant Ecology* **150**:115–131.
- Wood, S. N. 1994. Obtaining birth and mortality patterns from structured population trajectories. *Ecological Monographs* **64**:23–44.

APPENDIX

An analytical integration of size-dependent mortality (Eq. 2a) is available in ESA's Electronic Data Archive: *Ecological Archives* E084-051-A1.