Estimating growth and mortality of juvenile winter flounder, *Pseudopleuronectes americanus*, with a length-based model

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Abstract: This study quantifies the combined effects of density and environmental factors on young-of-the-year (YOY) winter flounder (*Pseudopleuronectes americanus*) in Narragansett Bay, Rhode Island. We used a length-based model to estimate growth and mortality rates from June to October each year from 1988 to 1998. In this model, mortality and growth rates are decreasing functions of length and there is variability in individual growth. Maximum-likelihood methods were used to fit the model to length-frequency data collected by the Rhode Island Division of Fish and Wildlife beach-seine survey in Narragansett Bay during the study years. The monthly mortality rate was density dependent and was positively related to temperature. Growth rate was negatively related to density. There was a significant decline in YOY winter flounder abundance during the period of study. The most recent year of the study, 1998, had the lowest density, lowest mortality, low summer temperature, and high growth rate. Thus, growth and mortality during the juvenile stage do not appear to be limiting the recovery of this depleted winter flounder population.

Résumé : Notre étude vise à quantifier les effets combinés de la densité et des facteurs du milieu sur les jeunes Plies rouges (*Pseudopleuronectes americanus*) de l'année (YOY) de la baie de Narragansett au Rhode Island. Un modèle basé sur les longueurs nous a permis d'estimer les taux de croissance et de mortalité de juin à octobre, chaque année de 1988 à 1998. Dans ce modèle, les taux de mortalité et de croissance sont des fonctions inverses de la longueur et il y a de la variabilité dans la croissance individuelle. Les méthodes de vraisemblance maximale ont servi à ajuster le modèle aux données de longueur/fréquence récoltées lors d'inventaires à la seine de plage par le Rhode Island Division of Fish and Wildlife dans la baie de Narragansett durant les années d'étude. Le taux mensuel de mortalité était relié à la densité et en corrélation positive avec la température. Le taux de croissance affichait une corrélation négative avec la densité. Il y a eu un déclin significatif de l'abondance des jeunes de l'année pendant la période d'étude. Dans la dernière année de l'étude, 1998, la densité et la mortalité étaient à leur niveau le plus bas, la température estivale était basse et le taux de croissance était élevé. Ainsi, la croissance et la mortalité durant la phase juvénile ne semblent pas être les facteurs limitants de la récupération de cette population décimée de Plies rouges.

[Traduit par la Rédaction]

Introduction

Events affecting the growth and mortality of fish during the first year of life greatly influence the strength of the year class. Mortality of marine fishes is much more variable during the first year than during subsequent years (Hilborn and Walters 1992) and is often inextricably linked to the qualities of the environment in which the vulnerable stages of these populations reside. Survival and growth of young-of-the-year (YOY) winter flounder (*Pseudopleuronectes americanus*)

in the northeastern United States have been related to salinity (Armstrong 1997), temperature (Jeffries and Terceiro 1985), dissolved oxygen (Meng and Powell 1999), water quality (Howell 1993; Meise et al. 1999; Meng and Powell 1999), predator abundance (Jeffries and Terceiro 1985; Witting and Able 1995), habitat availability, density of conspecifics, and prey abundance. It is difficult to demonstrate these relationships with field data for several reasons. First, the environmental factor must affect mortality or growth to a sufficient degree that a correlation with mortality or growth

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is detectable, from data with high levels of sampling variability. Traditional methods to examine growth and mortality rates make strong assumptions about the population; they assume the population is closed to recruitment and emigration and that growth and mortality rates remain constant throughout the duration of the study. Finally, a long time series of data must be available so that estimates of growth and mortality rates can be made over a wide range of environmental conditions. We account for these difficulties by using an 11-year time series of data, relaxing assumptions on recruitment during the early summer months and allowing mortality and growth to decrease with increasing length.

Winter flounder spend a significant portion of their lives in inshore waters. With the exception of the population residing on Georges Bank, winter flounder on the U.S. continental shelf undergo a small, onshore–offshore seasonal migration. Adults migrate into deeper offshore water in late spring to early summer and return in fall to spawn in bays and estuaries (Klein-MacPhee 1978; Saila 1961). The juveniles spend the first two years of life in estuaries after which time they join the adults (Klein-MacPhee 1978). The winter flounder population on the northwest Atlantic continental shelf consists of a series of localized spawning subpopulations that exhibit strong fidelity to their natal bays and estuaries (Saila 1961). Separate subpopulations along the southern New England coast include those attributed to Buzzards Bay, Mass., Narragansett Bay, R.I., and the Connecticut River, Conn. These subpopulations intermix in offshore waters during the summer months. For management purposes, these localized populations are grouped into stock complexes.

Winter flounder support a valuable commercial and recreational fishery along the northeastern United States (NEFSC 1999). The southern New England stock complex runs from coastal Massachusetts east and south of Cape Cod to eastern Long Island Sound to the Connecticut River and includes Fishers Island Sound, N.Y. (NEFSC 1999). The southern New England stock complex has been combined with the mid-Atlantic stock complex, which continues from New York south to Delaware. The southern New England – mid-Atlantic stock complex has been heavily exploited in the recent past, which has driven the stock down to low abundance levels (NEFSC 1999). Under the Sustainable Fisheries Act, the National Marine Fisheries Service and the Atlantic States Marine Fisheries Commission enacted a management plan to reduce fishing mortality and to allow the stock complex to increase to levels at which maximum sustainable yield (MSY) is maintainable. The rebuilding process is on track for the southern New England – mid-Atlantic stock complex as fishing mortality has been reduced and the stock is increasing (NEFSC 1999). However, the subpopulation attributed to Narragansett Bay is not following the regional trend. Fishing mortality on the Narragansett Bay component was at or near 1.0 from 1982 to 1993 (Gibson 1998). The fishing mortality rate at which MSY is obtained is estimated to be 0.27 for this population. Fishing mortality of this population has been reduced significantly since then; instantaneous fishing mortality in 1998 was estimated to be 0.39 (Gibson 1998). However, the 1998 Rhode Island Department of Environmental Management, Division of Fish and Wildlife (RIDFW) fall trawl survey, the monthly trawl survey,

and the juvenile beach-seine survey reported the lowest abundance indices of winter flounder on record (Gibson 1998). With the closure of Narragansett Bay to winter flounder fishing in 2000, it is important to examine factors affecting the abundance of the population in addition to fishing mortality.

The purpose of this study was to estimate the summer-to-fall growth and mortality rates of Narragansett Bay YOY winter flounder for the years 1988 to 1998 and to correlate them with environmental factors. The RIDFW has collected juvenile winter flounder length-frequency data during the summer months (June–October) as part of the Narragansett Bay juvenile finfish beach-seine survey. Samples have been taken at selected, fixed stations throughout Narragansett Bay from 1988 to 1998. This type of sampling design is well suited for the estimation of YOY winter flounder abundance and vital rates, as these fish are benthic and reside in the sandy intertidal zone (Tyler 1971). They may shift to deeper or shallower water in response to local environmental conditions, but do not exhibit any large-scale movements from the original site of settlement at the larval stage (Saucerman and Deegan 1991).

Traditional methods for estimating growth and mortality rates (such as catch curve analysis) from data pooled over lengths ignore the decrease in both growth and mortality rates with increasing size. Studies have found juvenile winter flounder growth (Pearcy 1962; Sogard and Able 1992) and mortality (Howell 1993) to decrease with length. The juvenile winter flounder caught during the monthly RIDFW beach-seine survey range in length from about 2 to 30 cm with monthly peak densities between 3 and 7 cm, which correspond to the YOY stage. The distribution of the lengths represented in the sample could be due to protracted spawning, a variable length of time to metamorphosis, differences in growth rates within the population, or a number of other reasons. It is likely that some of the larger fish are age 1.

To estimate length-based growth and mortality rates for each year, we fit these data with a modified version of the length-based model developed by Sullivan et al. (1990). This model allows mortality and growth to decrease with length and for variability in individual growth. The formulation of Sullivan et al. (1990) differs from that of Deriso and Parma (1988) and Quinn et al. (1998) in that it does not track the length frequency of individual cohorts and a gamma distribution is used to model variability in growth. Sullivan et al. (1990) originally applied their model to Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea, *Pseudotolithus typhus* from the Cameroon coast, and *Decapterus russellii* from the Java Sea. Alaska red king crab (*Paralithodes camtschaticus*) data from Bristol Bay have also been fitted with a modification of this model (Zheng et al. 1995). Meise et al. (1999) adapted this model for YOY winter flounder to estimate and compare growth and mortality rates of subpopulations residing in the Connecticut River and New Haven Harbor, Conn., pristine and degraded estuaries, respectively. In the current application, a modified version of this model is used to estimate growth and mortality rates for an 11-year time series. We have tested for a correlation of these rates with density and two environmental variables, temperature and precipitation (as a possible proxy for salin-

ity or stratification). These three variables were selected because there is evidence that they affect vital rates of juvenile winter flounder.

Methods

Data collection

Narragansett Bay, R.I., is an estuary fed by several rivers, the largest of which are the Blackstone (which feeds into the Seekonk River) and the Taunton rivers (Fig. 1). Salinity ranges from 24 to 30 ppt and temperature ranges from –0.5°C to 25°C. The Bay supports a wide variety of marine and estuarine species as well as an active fishing fleet. Monthly samples of juvenile finfish were collected throughout Narragansett Bay from June to October since 1986. In 1986, at the start of the sampling program, 15 stations throughout the Bay were chosen that represented shoreline habitat. In 1998, the survey consisted of 18 stations, as three new stations were added to the sampling program in 1992, 1993, and 1995 to include important juvenile finfish habitat. The data were analyzed using Wilcoxon's rank-sum test (Statistical Sciences 1991) to ensure the average yearly catches from these new stations were not substantially different from the original 15 stations. At each station, one seine haul was conducted with a 61 m × 3.05 m beachseine set from a boat with 0.64-cm mesh size and a 0.48-cm bunt. All finfish caught were enumerated and target species, including winter flounder, were measured to the nearest millimeter. All fish were then returned to the Bay. Sampling was completed over a 5 to 10 day period, during the week of the month when high tide occurred at noon on Wednesday. An estimate of density was calculated based upon the area swept by the beach seine; a standard tow covered approximately 500 m^2.

As only one haul was conducted at each station each month, we summed together the catches from all stations for this study. However, before grouping the samples, we scrutinized two years of data, 1990 and 1992, to ensure there was no apparent difference among stations. To do this, we estimated the growth increment and mortality rates for each station, simply using changes in density (eq. 1) and changes in mean length from one month to the next (eq. 2). We then used stepwise regression analyses in which the growth and mortality rates were predicted from station, month, the logarithm of density, monthly average temperature, length, and growth (for mortality). These analyses showed that temperature and length were the most important predictors of growth in 1990, length and month for growth in 1992, and density and temperature for mortality in 1990 and 1992. The lack of significant differences among stations justified the pooling of data across stations in the subsequent analyses.

Sampling required several days, occasionally spanned the intervening weekend, and did not always occur exactly one month from the previous month's sampling period. To obtain an estimate of the time between samples, we first estimated the mean date (weighted by the size of the catch at each station) the stations were sampled each month and then calculated the time elapsed between the mean sampling dates. As the number of stations sampled increased during the 11-year sampling period, we calculated standardized area swept abundance estimates by summing together the station catches for each month and dividing by the total area swept during the month (number of stations multiplied by 500 m^2 per station). Metamorphosis occurs by the time winter flounder reach 8–9 mm in length (Bigelow and Shroeder 1953) and the juveniles are vulnerable to the beach seine at about 25 mm in total length.

We obtained bottom temperature estimates from the University of Rhode Island Graduate School of Oceanography weekly trawl survey and Providence precipitation from the National Weather Service Web page (http://tgsv5.nws.noaa.gov/er/box).

Model development

Prior to formulating a length-based model, we calculated observed monthly growth and mortality rates directly from the data and tested for a correlation of these rates with average winter flounder length, the logarithm of monthly density, average monthly water temperature, and monthly precipitation. Observed mortality rates were calculated from the negative logarithm of the ratio of subsequent observed monthly abundances (N_t):

$$(1) \qquad Z_{\text{obs},t+1} = -\log\left(\frac{N_{t+1}}{N_t}\right)$$

Observed growth increments were estimated as the difference in average length from one time period to the next.

$$(2) \qquad G_{\text{obs},t+1} = \text{average length}_{t+1} - \text{average length}_t$$

The length-based model calculated the number of individuals that survived and grew into length class l' by the end of the following month:

$$(3) \qquad \hat{N}_{t+\Delta t,l'} = \sum_l P_{l,l'}\,\hat{N}_{t,l}\,e^{-z_l \Delta t}$$

Here, $\hat{N}_{t,l}$ is the predicted abundance at time t of individuals in length class l, z_l is monthly instantaneous mortality for in individual in length class l, $P_{l,l'}$ is the probability that an individual in length class l grows into length l' in Δt time, and Δt is the proportion of the month between subsequent samples. We used 5-mm length classes and a relative abundance estimate for $N_{t,l}$ rather than an absolute estimate. An estimate of the population's total relative abundance at time t would be

$$(4) \qquad \hat{N}_t = \sum_l \hat{N}_{t,l}$$

We assumed that growth follows a gamma distribution, with

$$(5) \qquad P_{l,l'} = \int_{l'_l - l^*}^{l'_u - l^*} \Gamma(x\,|\,\alpha, \beta_l)\,dx$$

Here, α and β_l are the parameters of the gamma function, Γ, l'_u and l'_l the upper and lower limits of the receiving length class l', and l^* the midpoint of length class l. By definition, $\alpha\beta_l$ is the mean growth of an individual in length class l and $\alpha\beta_l^2$ is the variance in growth of an individual in length class l. We assumed that growth followed the time invariant von Bertalanffy model, with the mean monthly growth increment of an individual of length l modeled as

$$(6) \qquad \overline{\Delta l_l} = \alpha\beta_l = (l_\infty - l^*)(1 - e^{-k})$$

where l_∞ is the asymptotic length for winter flounder and k is the Brody growth coefficient. We set the asymptotic length of winter flounder to 46 cm (Klein-MacPhee 1978) and the coefficient of variation (CV) for growth, $\alpha^{-0.5}$, to a constant value of 0.36. This value was consistent with the CV estimated from YOY winter flounder otolith increment widths (Sogard and Able 1992).

Instantaneous monthly natural mortality at length was modeled as a decreasing function of length with

$$(7) \qquad z_l = a\,l^{-c}$$

where a and c are unknown non-negative coefficients (Pepin 1993). If c is zero, then the mortality rate does not decrease with increasing length.

It was not uncommon (6 out of 11 years) for the relative abundance of the June sample to be smaller than that of the July sample. We interpreted this to be due to sampling error and (or) continued recruitment of winter flounder into the intertidal zone during the month of June. To account for error in the June sample, we allowed the model to esti-

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Fig. 1. Map of Narragansett Bay with sampling stations and key locations delineated. The locus map was provided by Environmental Systems Research Institute, Inc. (©1995–1999) and the map of Narragansett Bay was provided by RIGIS (©1990).
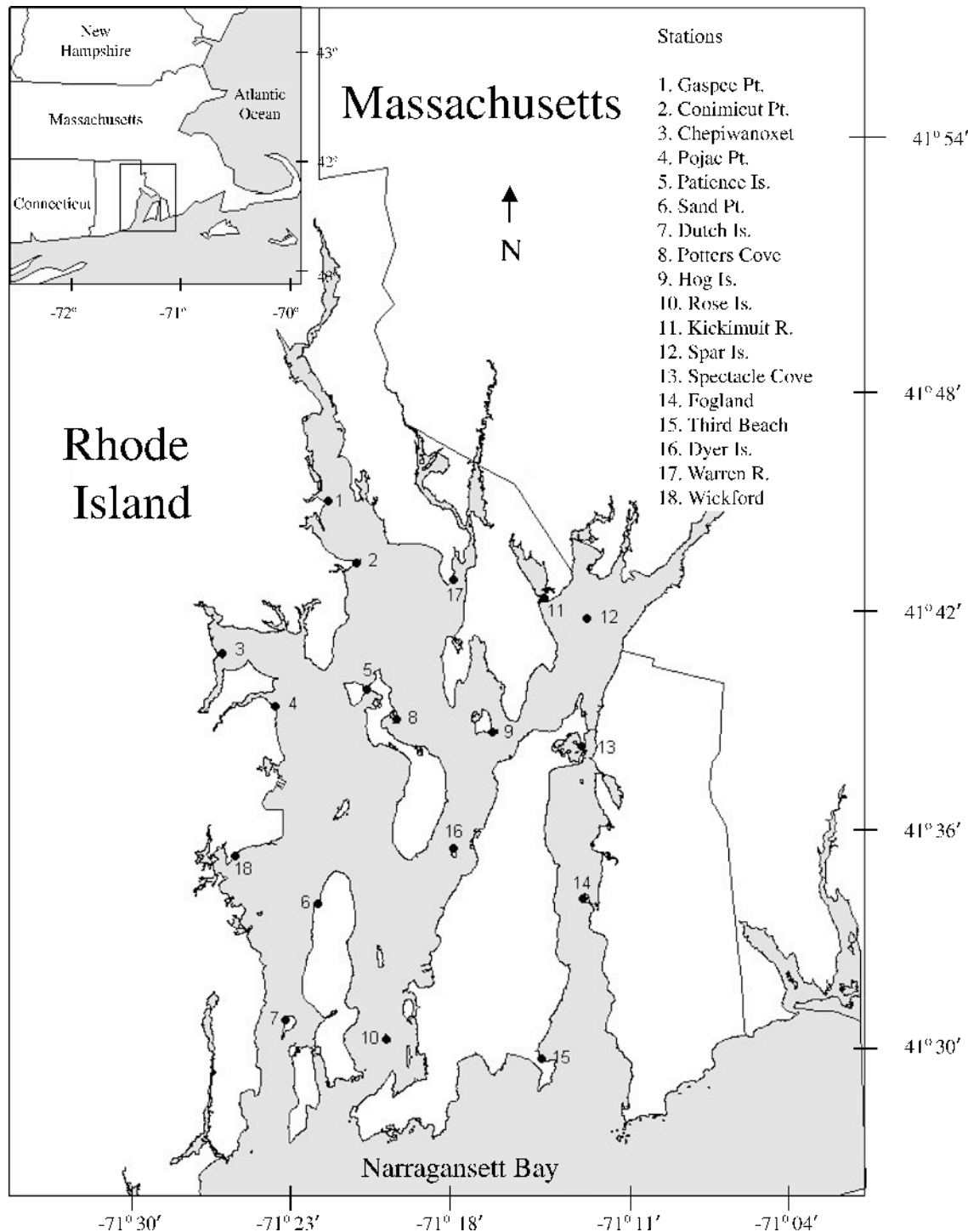
mate the relative abundance in June, while retaining the length-frequency distribution of the sample. Estimating the length frequency of the June sample along with the relative abundance would have overparameterized the model. The model predicted June relative abundance by estimating an additional parameter, m, such that

$$(8) \qquad \hat{N}_{\text{July},l'} = \sum_l m \, P_{l,l'} \, N_{\text{June},l} \, \mathrm{e}^{-z_l \Delta t}$$

This formulation resulted in four parameters to estimate for each

year of data: the Brody growth coefficient, k, the two mortality coefficients, a and c, and the multiplier, m.

Fitting the model

We used maximum likelihood estimation to solve for the four model parameters. The likelihood function that was maximized was of the form

$$(9) \qquad \mathrm{L}(a, c, k, m) = A^f \, B^g \, C^h$$

Each of the three terms in the product, A, B, and C, denotes an assumed form of variability in the model parameters. The first two terms, A^f and B^g, of the objective function incorporate realistic assumptions about the sampling error structure by assuming the error of the total number caught in each sample is lognormally distributed and the length-frequency distribution of each sample follows a multinomial distribution. We express a bivariate normal distribution for the relationship between the mortality parameters a and $\log(c)$ with the term C. The exponents, f, g, and h, are weights for each element of the objective function. In fitting the model, we minimized the negative log-likelihood function

$$(10) \quad \min[-\log(\mathrm{L}(a,c,k,m))] =$$
$$\min[-f\log(A) - g\log(B) - h\log(C)]$$

The term $f\log(A)$ expresses the likelihood of obtaining the observed total monthly catch. We assumed the expected number caught during the July through October survey months was equivalent to the true relative abundance times a lognormally distributed error: $N_t = \hat{N}_t e^{\varepsilon_t}$ Here, ε_t is a random normal deviate with mean 0 and variance σ^2, N_t is the observed relative abundance, and $\hat{N}_t$ is the model-predicted, true population abundance at time t. The negative log-likelihood function of the normal distribution is proportional to the sum of the squared deviations between the observed and predicted values. The model estimated June abundance with the recruitment multiplier, m, which was constrained to be close to 1. This term was incorporated in the objective function under the assumption that the error on the observed June abundance was also lognormally distributed, $\varepsilon_{\mathrm{June}} = \log(N_{\mathrm{June}}) - \log(mN_{\mathrm{June}})$. The resulting term included in the objective function was

$$(11) \quad -f\log(A) =$$
$$f\left[\sum_{t=\mathrm{July}}^{\mathrm{October}} \left(\log(\hat{N}_t) - \log(N_t)\right)^2 + \log^2(m)\right]$$

We further assumed that the observed July to October length-frequency distributions were samples drawn from a multinomial distribution. The probability of obtaining the length-frequency sample observed in month t was equivalent to

$$(12) \quad \frac{\hat{N}_t!}{y_{1t}! \cdot y_{2t}! \cdots y_{nt}!} \cdot p_{1t}^{y_{1t}} \cdot p_{2t}^{y_{2t}} \cdots p_{nt}^{y_{nt}}$$
$$\text{with } \sum_{i=1}^{n} p_{it} = 1 \text{ and } p_{it} > 0$$

where y_{it} is the observed catch of winter flounder of length class i during month t, p_{it} is the model-predicted proportion in length class i during month t, and n is the number of length classes. The model maximized the probability of obtaining the observed length frequency by maximizing the product of these monthly probabilities. In the objective function, the constant terms $\dfrac{\hat{N}_t!}{y_{1t}! \cdot y_{2t}! \cdots y_{nt}!}$ were removed as they were based upon the observed sample, and therefore, did not depend upon the model parameters. The term included in the objective function was

$$(13) \quad -g\log(B) = -g\sum_{t=\mathrm{July}}^{\mathrm{October}} y_{1t}\log(p_{1t})$$
$$+ y_{2t}\log(p_{2t}) + \cdots + y_{nt}\log(p_{nt})$$

To further define mortality and to rein in extreme mortality parameter estimates, we added an additional term to the objective func-

tion, C. The mortality eq. (7) was linearized with a natural log transformation:

$$(14) \quad \log(z) = \log(a) - c\log(l)$$

Standard regression analysis was used to estimate the value of, standard deviation of, and correlation between the mortality parameters $\log(a)$ and c, using 72 independent estimates of mortality at length taken over 6 summers for the juvenile winter flounder population that resided in nearby Niantic River, Conn. (e.g., Northeast Utilities 1993). The penalty term assumed $\log(a)$ and c for the Narragansett Bay population follow a bivariate normal distribution similar to the one determined for the Niantic River population. Estimates for $\log(a)$ and c were improved by restricting them to values close to the minimum of the negative log-likelihood function for the bivariate normal distribution, which was the penalty term used in the model fits:

$$(15) \quad -h\log(C) = \frac{-h}{2(1-\rho)^2} \times \left[\left(\frac{\log(\hat{a}) - \mu_{\log(a)}}{\sigma_{\log(a)}}\right)^2\right.$$
$$\left. - 2\rho\left(\frac{\log(\hat{a}) - \mu_{\log(a)}}{\sigma_{\log(a)}}\right)\left(\frac{\hat{c} - \mu_c}{\sigma_c}\right) + \left(\frac{\hat{c} - \mu_c}{\sigma_c}\right)^2\right]$$

where ρ is the correlation between $\log(a)$ and c from the Niantic River data, $\mu_{\log(a)}$, $\sigma_{\log(a)}$, μ_c, and σ_c are the predicted mean values and standard deviations for $\log(a)$ and c from the Niantic River data, $\hat{c}$ and $\hat{a}$ are the model-predicted values for a and c, and h is the weight for this term relative to the other terms in the objective function and subsumed other constants in the likelihood function. The use of such a penalty term was justified because many years of data were used to parameterize the term and the mortality equation was biologically realistic. For other examples of the use of penalty terms see Fournier and Archibald (1982) and Ludwig et al. (1988).

The two mortality parameters, a and c, were positively correlated; to maintain a similar estimate of mortality while increasing a, the parameter c needed to be increased as well. We reparameterized the model to reduce the covariance among the estimated parameters, thereby making the likelihood surface better conditioned (Draper and Smith 1981). The reparameterized mortality model was $z_l = \varphi_0 x^{-c}$, where $\varphi_0 = a\bar{l}^{-c}$, $x = l/\bar{l}$, and $\bar{l}$ was the mean length in the observed catch for each year. Instead of solving for the mortality parameters a and c directly, we estimated ϕ_0 and c with the model and subsequently used ϕ_0 and c to convert back to a. The parameter ϕ_0 was the monthly instantaneous mortality for the average length winter flounder in a given year and was the mortality parameter used in the analysis of model output.

It is admittedly difficult to determine the best weights for the three terms in the objective function. One approach to determine an appropriate value for f was to find a value that would maintain approximately equivalent weight between the two sources of observation error (NRC 1998). For each monthly sample, we had one density estimate and about 25 length-frequency estimates corresponding to YOY fish (i.e., from 3 to 15.5 in half-centimeter length classes). The probability of obtaining the 25 length-frequency samples was related to the probability of obtaining the sample for length class 1, for length class 2, etc., up to length class 25, a product of 25 probabilities. With g set to 1, setting f to 25, in essence, balanced the two error terms, at least to within an order of magnitude.

It was also important to assess the sensitivity of the model output to a wide range of weight combinations. We fixed g, the weight on the multinomial likelihood term, at 1, and ran the model with a wide range of f and h values. Since the penalty term was used to refine the estimation of mortality, we first explored the sensitivity of the model parameters and fits to various f values, while setting

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the weight on the penalty term to 0. The weights we examined were 0.1, 1, 10, 25, 100, and 1000. Since f was a multiplier for the density term in the objective function, high f values caused an overfitting of the model's predicted monthly densities at the expense of the model fit to the observed length-frequency distribution. As a result, we carefully examined the sensitivity of k to increasing values of f.

Once an appropriate value for f was found, we fixed f to this "best" value and examined a wide range of penalty term weights, h. The weights we examined included 0, 0.001, 0.005, 0.01, 0.05, and 0.1. We determined the best value for h to be the value that both reined in extreme values of the mortality parameters and allowed some deviation from the Niantic River mean values of a and $\log(c)$. We also ensured that the estimates of growth resulting from the final run were not altered substantially from the run with h set to zero.

We examined the sensitivity of the parameters estimated by the model to deviations in the two fixed input parameters, l_∞ and the coefficient of variation of growth. Values examined for l_∞ were 44 and 48 cm, which could represent an error in the assumed l_∞ value of 46. Values tested for the coefficient of variation were 0.27 and 0.42, which represent the values obtained by Sogard and Able (1992) and bound the assumed input value of 0.36.

The length-based model was programmed in S-Plus, a software package that includes many built-in statistical functions (Statistical Sciences 1991). Output from the program included maximum likelihood estimates of k, c, ϕ_0, and m and the associated variance–covariance information matrix of model parameters. Univariate 95% confidence intervals were constructed about ϕ_0 and mean monthly growth rate. Because there was only one free parameter, k, in the von Bertalanffy equation, we used the 95% confidence interval for k to estimate the upper and lower bounds of the average growth increment. We determined whether k and ϕ_0 were correlated with average monthly summer bottom temperature and precipitation (as a proxy for salinity or stratification) and the logarithm of July density. We chose to use the natural logarithm transformation of July density in our analysis, because population density was often found to follow a lognormal distribution. Autocorrelation in the model estimates and the environmental covariates was accounted for in determining statistical significance of the correlations by estimating the "effective" number of degrees of freedom as described by Pyper and Peterman (1998). Regression tree analyses were performed to determine the best predictive model for these vital rates (Venables and Ripley 1999).

Results

Preliminary analyses

The Wilcoxon's rank-sum tests indicated that catches from stations 16 and 17 were not significantly different from the original 15 stations ($p > 0.05$). Conversely, station 18 had significantly higher catches than the original 15 ($p < 0.05$). We included station 18 in our analysis because we deemed that the benefit of using the larger length-frequency sample for these lower abundance years was greater than the possibility that we would misinterpret temporal trends in abundance.

The choice of growth and mortality models used in this analysis was confirmed in a preliminary analysis. Significant correlations were found among observed monthly growth and mortality, monthly average temperature, the natural logarithm of observed monthly density, and monthly mean length. We found that average monthly temperature and mean length had significant, negative correlations with observed growth ($p < 0.001$). A multiple regression model pre-

dicting growth from mean length and temperature explained 38% of the variation in growth increment and both independent variables were significant ($p < 0.05$). Temperature and the natural logarithm of monthly density of winter flounder were significant, positive predictors of observed mortality ($p < 0.05$). A multiple regression model with temperature and log density explained 36% of the variation in observed mortality, and temperature and density were significant ($p < 0.05$). This analysis confirms that our choice of a model structure that allows, but does not force, mortality to decrease with length. Monthly temperature and winter flounder length should be correlated, since both are lowest in the spring. A model design where growth decreases with length allows for a valid test between growth and environmental variables.

Estimates of the parameters for the penalty term in the objective function were obtained from linear regression analysis. The regression of observed Niantic River juvenile natural mortality rates against the natural logarithm of mean length was significant ($n = 72$, $p < 0.05$). The mean values for $\log(a)$ and c were 0.668 and 0.771, their standard errors were 0.350 and 0.276, and the correlation between them was estimated to be 0.967. The 95% confidence contour for $\log(a)$ and c does not include $c = 0$, indicating that Niantic River juvenile winter flounder experienced a significant decrease in mortality with increased length (Fig. 2).

The reparameterization of the function for mortality successfully reduced the covariance between the two estimated mortality parameters. As an example of the effect of the reparameterization, the results of the original model for 1998 showed the covariance between a and c to be 1.045×10^{-3} as estimated by the inverse hessian ($f = 25$, $g = 1$, $h = 0$). The corresponding covariance between ϕ_0 and c with the reparameterized model was -3.4×10^{-5}, a substantial reduction over the original formulation.

Sensitivity analysis

With the objective function weight g set to 1 and h set to 0, f values from 0.1 to 1000 successfully bound plausible estimates for this weight. Plots of individual terms of the negative log-likelihood function at the various weights showed how the lower weights resulted in poorer fits of the model to observed density, especially in 1990, 1994, 1995, and 1998 (Fig. 3a). This plot showed that 10 was a reasonable lower bound for f, as values smaller than this caused this objective function term to increase by a large amount in several years. Similarly, a plot of the difference between $-\log(B)$ at different weights and $-\log(B)$ with the weight set to 0.1 showed how the fit of the model to the observed length-frequency distribution deteriorated as f was increased. In several years (1989, 1993, 1996, and 1998), this difference increased dramatically when f was set to 100 and 1000 (Fig. 3b). These large weights could compromise the estimation of growth. Furthermore, with f set to 25, the growth parameter, k, was not found to deviate greatly from those estimates at low f values, solidifying our choice of 25 as the best value (Fig. 4a).

With f set to 25, examination of the model output under various values of h resulted in our choice of 0.05 as the best value for this weight. When h was set to values below 0.05, the mortality parameter c was estimated to be zero in many

Fig. 2. Comparison of the model-estimated yearly mortality parameters and the 95% confidence contour for the mortality parameters, c and $\log(a)$, with f set to 25 and h set to (*a*) 0.01 and (*b*) 0.05. The contour is generated from mortality estimates of young-of-the-year (YOY) winter flounder in the Niantic River, Conn. X denotes the mean value for c and $\log(a)$ and the years represent the model-fitted parameter values.
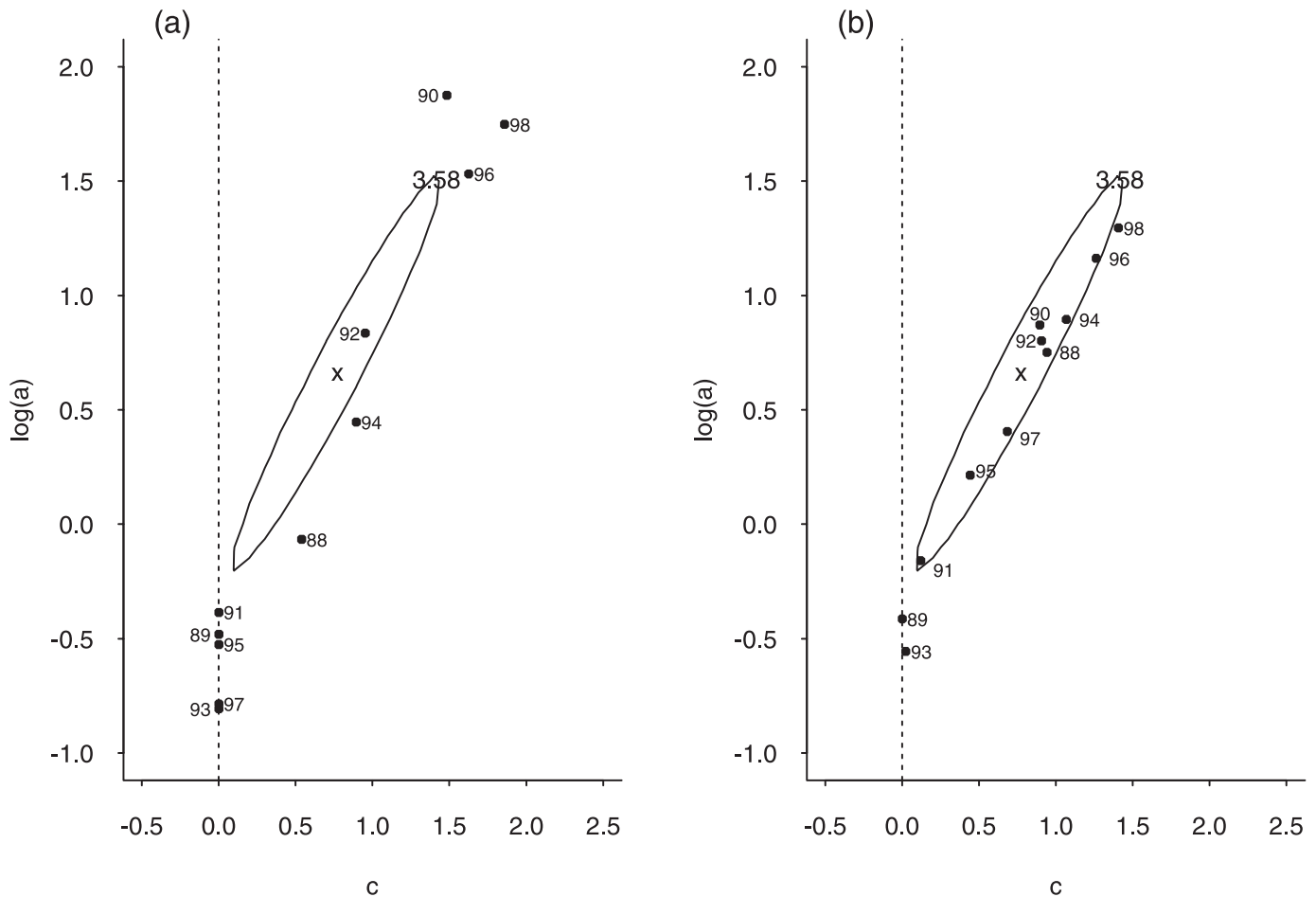
years. For example, c was estimated to be zero in five years, 1989, 1991, 1993, 1995, and 1997, with h set to 0.01 (Fig. 2*a*). With h set to 0.05, $\log(a)$ and c fell within the 95% confidence contour estimated for the Niantic River in 9 of the 11 years, with c estimated close to zero in only two years, 1989 and 1993 (Fig. 2*b*). In most years, the growth estimates with h set to 0.05 did not deviate substantially from those values estimated with h set to 0 (Fig. 4*b*). Two years with the greatest change, 1990 and 1998, were altered by about 0.005 from this baseline estimate of k.

The model estimates of growth and mortality were relatively robust to values assigned to the parameters fixed in the model. Model runs with f set to 25, g set to 1, h set to 0.05, and the coefficient of variation set to 0.27 and 0.42 resulted in quite small changes in the predicted growth and mortality rates. Over this range, k varied by a maximum of 0.0013 and ϕ_0 varied by a maximum of 0.005. With these same objective function weights and l_∞ set to 44 cm and 48 cm, k varied by a maximum of 0.0015 and ϕ_0 by a maximum of 0.003.

Model results

For most years, the model fitted the observed data well,

with f set to 25, g set to 1, and h set to 0.05 (Fig. 5). Certainly some years appeared to have fitted better than the others with 1988, 1989, and 1992 fitting the model well, and 1996 fitting worse. There were no visible patterns in the deviations between the total observed and estimated monthly densities. Due to the inclusion of the recruitment parameter, the June residuals were negative in all but two years (1990 and 1996). Two of the July residuals were negative when the June residuals were negative, indicating no persistent underestimation of abundance in July. The error appears to be partitioned evenly across the months, as the magnitude of the July–October residuals was independent of month. In each year, there were negative July–October residuals.

In several years, however, the length class with maximum density was underestimated in July, indicating that the model regularly underestimated growth from June to July. This may have been due to the model underestimating growth of the smaller fish, which were more abundant in June. Or it could have been due to some other factor controlling growth that was not included in the model but was seasonally correlated. For example, water temperature was considerably cooler in June than in the later months. However, in all years, the predicted length-frequency fitted the data well in at least one

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Fig. 3. Sensitivity of objective function terms to values assigned to the density likelihood term weight, *f*, with *g* = 1 and *h* = 0. (*a*) Value of the density likelihood term, –log(*A*). (*b*) Difference between –log(*B*) at the different weights and –log(*B*) with *f* = 0.1.
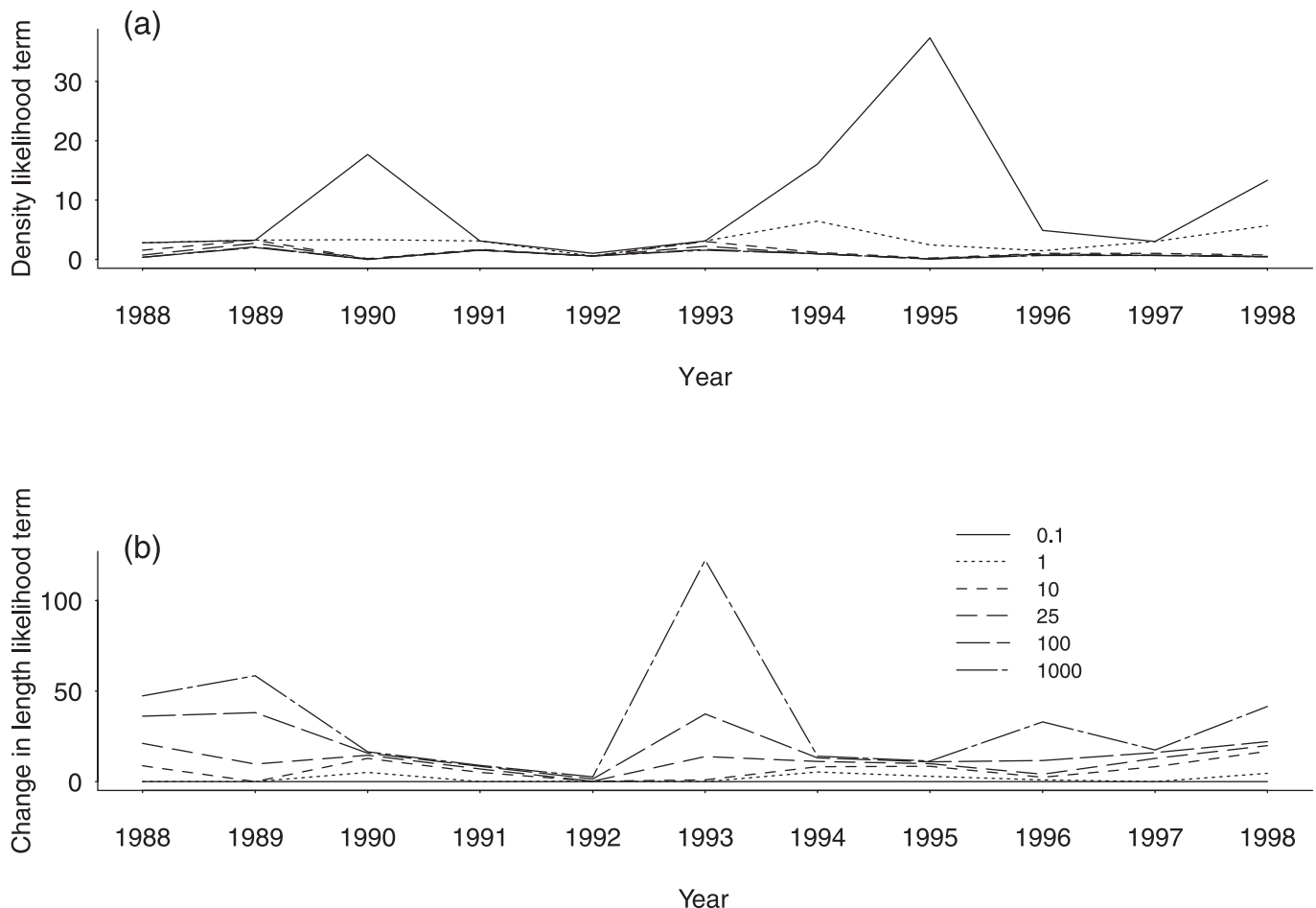
month. For this to happen, the model must overestimate growth in another month. Therefore, the growth parameter estimated by the model most likely provides an average growth in the population for a given year.

The estimated parameters, their standard deviations, yearly mean length, and the yearly environmental variables are provided in Table 1. The growth parameter, *k*, ranges from a low of 0.0071 in 1992 to a high of 0.0274 in 1993. These values correspond to mean growth increments of 0.29 centimeters per month in 1992 to 1.08 centimeters per month in 1993. Mean monthly mortality, ϕ_0, ranged from 0.271 to 0.685, with the upper and lower estimates associated with 1991 and 1998, respectively. The model estimates of the average monthly growth increment and mortality rate and their associated 95% confidence intervals are provided in Figs. 6*a* and 6*b*. The confidence intervals appear relatively tight for growth increments as compared with the intervals for the mortality estimates.

A correlation matrix examining the relationships among model output parameters and environmental variables was constructed. Autocorrelation in the data was accounted for in tests of statistical significance (Pyper and Peterman 1998). The model parameters *k* and ϕ_0 were included along with average precipitation, average temperature, and the logarithm of July observed density (Table 2). This analysis showed that

ϕ_0 was positively related to average temperature and density, indicating that mortality was higher in the warmer years and in the years with high winter flounder abundance (Fig. 7). The growth parameter, *k*, was significantly negatively related to density, indicating that growth was lower in the years with higher density. Density also showed a significant negative correlation with year, which reflects the decline in YOY winter flounder abundance during this period.

The regression tree model for ϕ_0 selected temperature as the best predictor of mortality. Years with average temperature above 18°C had higher estimates of ϕ_0 (Fig. 7). Density was not included in the regression tree model for mortality because of the low number of observations in each group and because density was positively correlated with temperature. Density was the best predictor of growth, as measured by *k*. The regression tree model partitioned the *k* estimates into two groups above and below the threshold density of 0.02·100 m^{-2} (Fig. 7).

Discussion

We have sought reasons for the continued decline of the Narragansett Bay winter flounder population by estimating growth and mortality rates of young-of-the-year from June to October. The model allowed for the incorporation of bio-

Fig. 4. Sensitivity of the growth parameter, *k*, to the objective function weights. (*a*) The model estimates of *k* with *g* = 1, *h* = 0, and varied *f*. (*b*) The model estimates of *k* with *f* = 25, *g* = 1, and *h* set to 0 and 0.05.
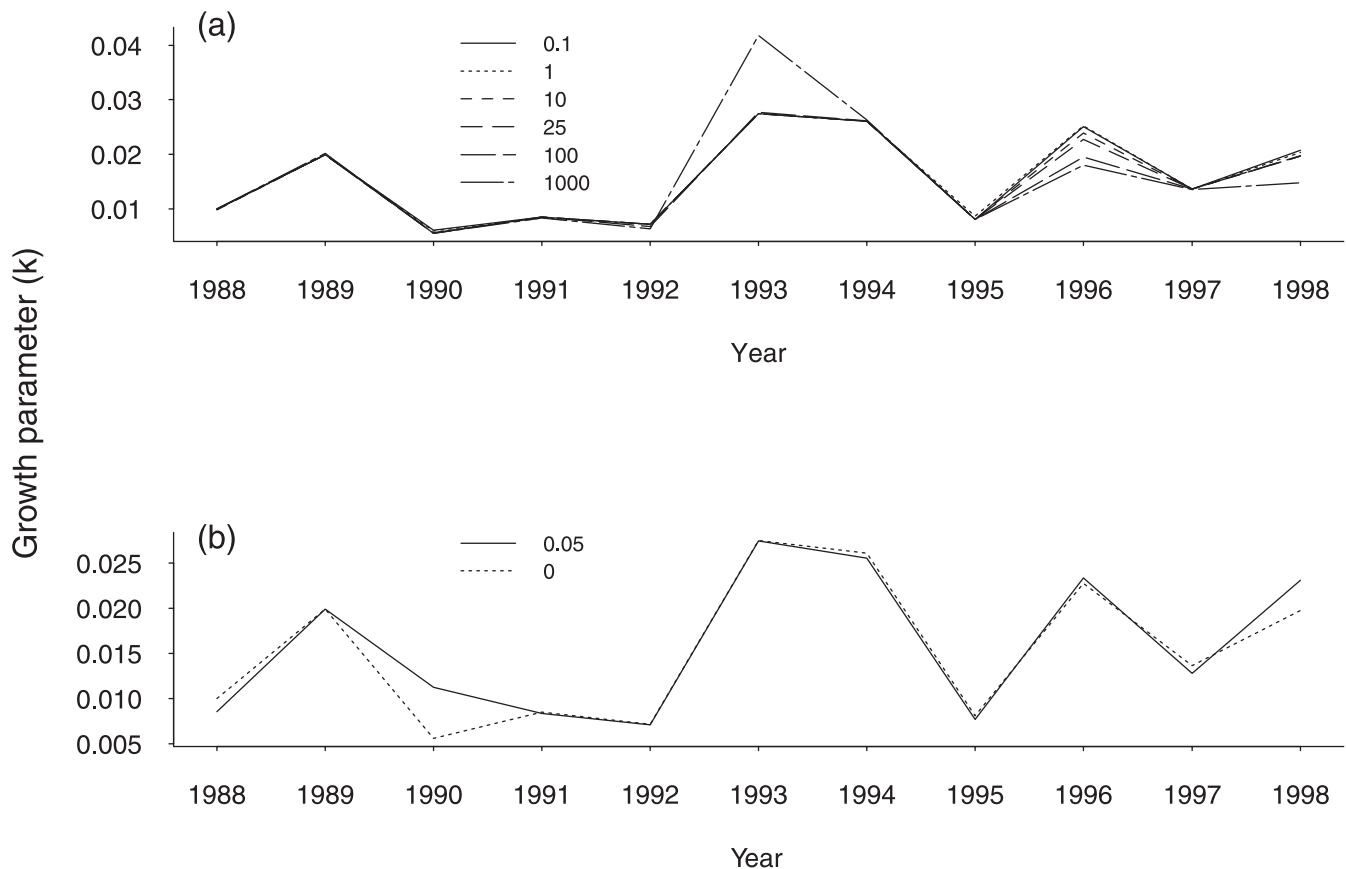
logically realistic processes, such as stochasticity in growth, reduction in growth and mortality as fish length increased, and recruitment of fish from June to July. The structure of the objective function was appropriate because it included realistic assumptions about the error structure of the observed data and resulted in model predictions that adequately fit the observed data. The inclusion of the penalty term for mortality using data from prior winter flounder work on a nearby population allowed us to estimate both mortality parameters and to make fewer assumptions about them.

The assumption that the June sample represents the true length frequency of the population does not appear to have adversely affected the estimates of growth and mortality rates, primarily because we estimated average growth and mortality rates across all months. Furthermore, since recruitment occurred between the June and July samples, we would expect an erroneous use of this assumption to result in an overestimate of abundance in the larger size classes in July because we would expect the new recruits to be in the smaller length classes. This did not appear to be the case; in fact the results showed that the model tended to overestimate abundance in the smaller size classes in July.

The model is relatively insensitive to the reasonable values assigned to the input parameters, l_∞ and the CV of growth, and a sensitivity analysis was performed to determine the best weights for the objective function. The 1990 estimate of *k* exhibited the most sensitivity to the mortality penalty term;

however, without the penalty term the 1990 estimate of *k* was the lowest in the time series. Judging from the comparatively poor fit of the model to the data that year, it may be prudent to treat the results for 1996 with caution. In conclusion, the mortality penalty term was important because it successfully constrained extreme values of log(*a*) and *c* but did not significantly affect the fits of the model output to the data. The penalty term is equivalent to a prior distribution for a parameter in a Bayesian analysis.

This model provided reasonable estimates of growth and mortality rates that compared well with estimates from other winter flounder populations. The mean monthly growth increment of YOY Narragansett Bay winter flounder was found to range between 0.2 and 0.7 cm in 1986 (Buckley and Caldarone 1990). The average growth rate of YOY winter flounder in Rhode Island estuaries in 1962 was 1.05 cm (Mulkana 1966). Growth rates of winter flounder in the Connecticut River were found to range between 0.46 and 0.64 cm·month⁻¹ in 1993 and to range between 0.77 and 1.63 cm·month⁻¹ in 1993 and 1994 in New Haven harbor (Meise et al. 1999). Growth rates of about 0.66–1.8 cm·month⁻¹ for a 3-cm winter flounder were obtained during caging experiments in Narragansett Bay during the summer of 1998 (Meng et al. 2001). Although our data do not include winter flounder less than 4 cm, our model estimates the mean monthly growth increment of a 3-cm winter flounder in 1998 to be 0.98 cm·month⁻¹.

Our mortality estimates were within the range of other

Fig. 5. Monthly observed and model-fitted length-frequency distributions of Narragansett Bay young-of-the-year (YOY) winter flounder for the months July to October in the years 1988 to 1998 with $f = 25$, $g = 1$, and $h = 0.05$. Density estimates are in no.·100 m^{-2}.

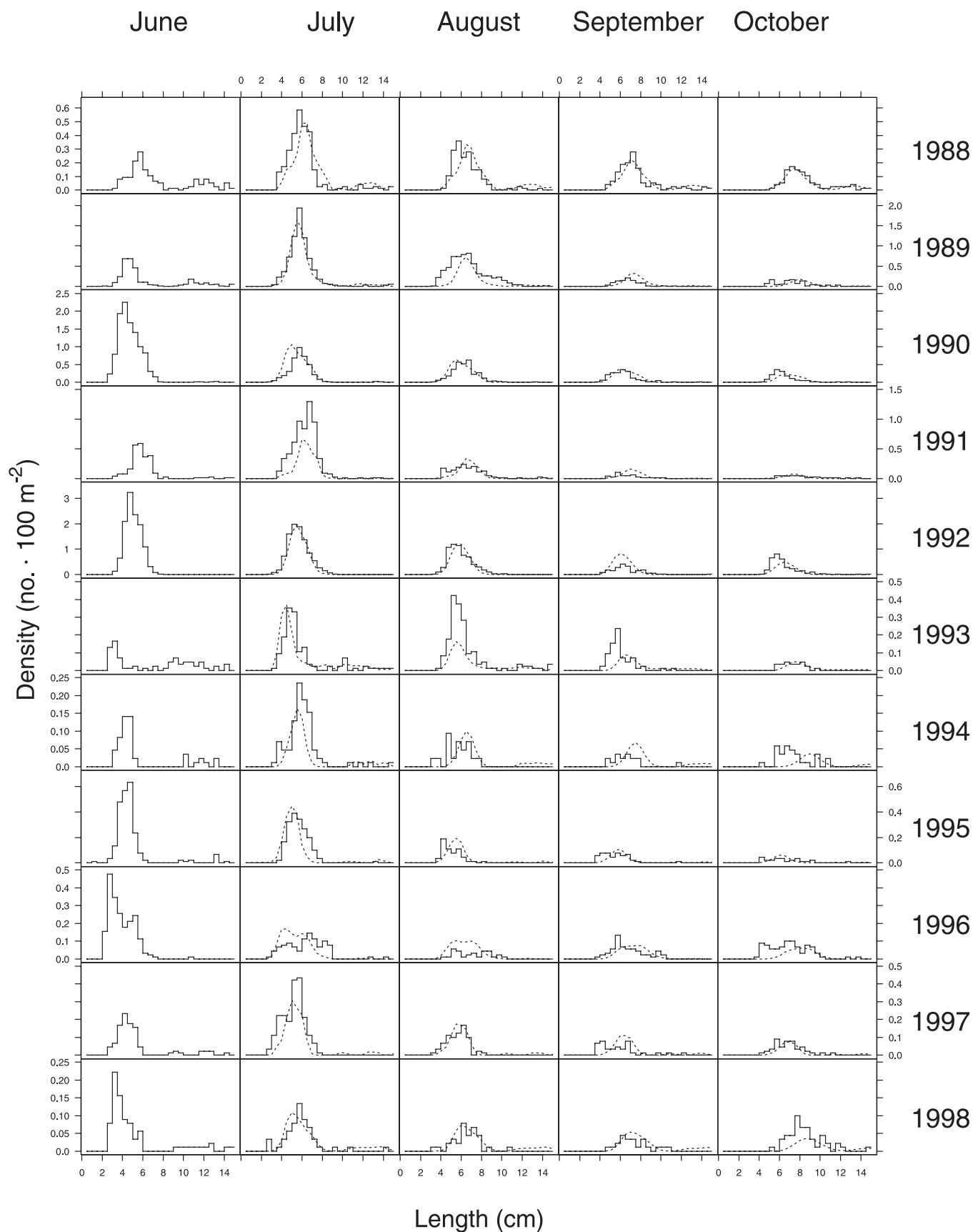**Table 1.** Yearly population mean length, model-predicted values of k, c, ϕ_0, and the multiplier, m, and their standard deviations (SD) with $f = 25$, $g = 1$, and $h = 0.05$, and the environmental covariates.

Year	Mean length (cm)	k Value	k SD	c Value	c SD	ϕ_0 Value	ϕ_0 SD	Multiplier Value	Multiplier SD	Environmental variables July density (no.·m^{-2})	Average temperature (°C)	Average precipitation (mm)
1988	6.91	0.0086	0.0006	0.9416	0.2417	0.3438	0.0387	2.9500	0.2339	0.0289	17.6	69.9
1989	6.25	0.0199	0.0004	0.0000	0.0132	0.6610	0.0342	4.5700	0.3720	0.0727	18.1	152.2
1990	5.38	0.0112	0.0008	0.8955	0.3411	0.5303	0.0489	0.8500	0.0941	0.0427	18.5	65.3
1991	6.30	0.0084	0.0004	0.1195	0.0406	0.6846	0.0392	2.2500	0.2236	0.0655	18.6	100.6
1992	5.57	0.0071	0.0002	0.9063	0.2116	0.4702	0.0408	1.1200	0.1081	0.0970	17.7	106.3
1993	6.31	0.0274	0.0006	0.0234	0.0141	0.5488	0.0318	4.6400	0.3407	0.0149	18.5	50.4
1994	6.10	0.0255	0.0009	1.0682	0.2864	0.3546	0.0387	1.9700	0.1793	0.0101	17.9	90.2
1995	5.22	0.0077	0.0004	0.4429	0.1927	0.5963	0.0359	1.3700	0.1352	0.0186	18.5	80.1
1996	5.48	0.0233	0.0009	1.2617	0.3150	0.3742	0.0424	0.9600	0.0846	0.0103	17.8	107.3
1997	5.42	0.0128	0.0007	0.6830	0.2266	0.4731	0.0366	2.3500	0.2082	0.0203	16.9	64.6
1998	6.34	0.0231	0.0015	1.4073	0.4428	0.2714	0.0393	1.5100	0.1358	0.0059	16.7	123.6

published estimates of juvenile winter flounder mortality. Monthly instantaneous mortality estimates for five populations in Connecticut estuaries were found to range between 0.24 and 1.21 (Howell 1993; Meise et al. 1999). Monthly mortality in the Mystic River estuary was estimated at about 0.31 per month in 1958–1959 (Pearcy 1962). Mortality in New Haven Harbor in 1993 and 1994 was estimated to be between 0.33 and 1.05 (Meise et al. 1999).

Our 11-year time series of winter flounder data provided an excellent opportunity to test relationships between the vital rates of YOY winter flounder and environmental factors, which have been alluded to in the literature. We found YOY mortality to be strongly correlated with temperature and also to be density dependent. A two-factor regression tree model was not feasible given the small number of data points but the combination of density and temperature may perhaps aid in the prediction of mortality. Mortality was estimated to be the highest in 1991, the year with highest average summer temperature and the third highest July density. Furthermore, 1989 ranked second in both mortality and density, with temperature falling in the middle of the range. In 1998, the year with lowest July density, average temperature was also the lowest during the time series, resulting in the lowest estimated mortality rate.

There is strong evidence for density-dependent mortality in 0-group plaice (*Pleuronectes platessa*) populations in European waters (Beverton and Iles 1992). They found that density had a stronger effect on mortality in recently settled populations than during the latter portion of the first year of life. The temperature-dependent effect may be a direct physiological response or an indirect response to a change in other factors, such as higher availability of prey or a lower rate of predation at lower temperatures. It has been hypothesized that the species assemblage in Narragansett Bay changes during colder and warmer years (Jeffries and Terceiro 1985).

The natural logarithm of July observed density was significantly correlated with k, providing a strong indication of density-dependent growth in this population. The estimate of k in 1989 appears to be an outlier in the decreasing plot of k versus density, because July density was the second highest during the time series and k is in the middle of the range. Interestingly, this was the only year in which the mortality parameter, c, was estimated to be zero by the model, indicating

that mortality did not decrease this year with winter flounder length. If indeed c is underestimated for this year, then the higher estimate of k could be attributed to an increase in mortality of the smaller individuals rather than to an increase in the population size structure.

Rose et al. (1996) assumed a curvilinear relationship between growth and temperature for juvenile winter flounder, with optimal growth occurring at about 12.5°C. Monthly average temperatures exceeded this value in all months during the time series. We observed a weakly negative relationship between temperature and the growth parameter, k. We would have expected to observe a decrease in growth rates during warmer years, since Narragansett Bay is close to the southern extent of the species range and because Narragansett Bay experiences high temperatures in some years.

The majority of winter flounder spawn in the upper reaches of the Bay (Keller et al. 1999). Furthermore, during the period 1988 to 1996, as the winter flounder population decreased, the distribution of juvenile winter flounder in Narragansett Bay contracted and became more concentrated in the upper Bay near Gaspee Point (Meng and Powell 1999). This may indicate that the upper Bay contains the most suitable winter flounder nursery habitat. Higher levels of pollutants such as heavy metals have been found in the upper reaches of the Bay (King et al. 1995). Inputs into the Bay are associated with industrial sites along the Taunton and Blackstone rivers and in the vicinity of Providence, the largest city in Rhode Island. Hypoxic and near-anoxic conditions have been found in the upper Bay and in prime winter flounder nursery areas, such as Greenwich Bay (Granger et al. 2000).

With the use of cages, Meng et al. (2001) estimated the growth rates of YOY juvenile winter flounder in the summer of 1998 at three sites located along a northern to southern gradient within Narragansett Bay. This northern to southern range of locations was chosen to represent a possible gradient in habitat quality. In a stepwise regression analysis of habitat variables, the terms included in the final model were location, salinity, dissolved oxygen, and initial fish length. Location explained 40% of the variability in fish growth. Although the fastest growth occurred mid-bay, they found that lower dissolved oxygen levels in the upper bay as the summer progressed negatively affected growth.

If there is an increase in stress owing to environmental

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Fig. 6. Model-predicted mean monthly growth increments (*a*) and mean monthly mortality rates (*b*) with univariate 95% confidence intervals for the years 1988 to 1998.
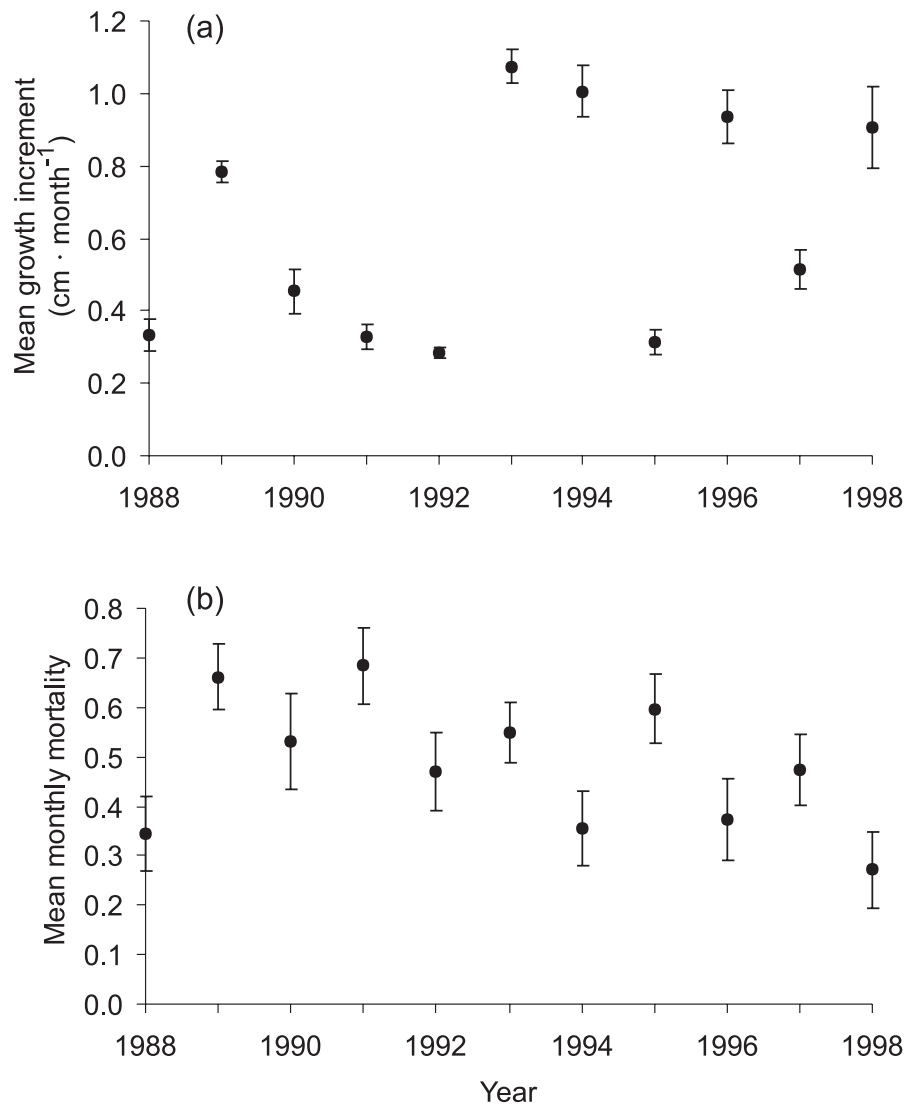

Table 2. Correlations among growth, mortality, and environmental covariates (upper diagonal). The lower left diagonal contains the corresponding probability levels.

	Year	Average temperature	Average precipitation	Logarithm of July density	k	ϕ_0
Year		–0.531	–0.013	**–0.731**	0.369	–0.416
Average temperature	0.114		–0.196	0.415	–0.156	**0.730**
Average precipitation	0.970	0.564		0.174	0.152	0.053
Logarithm of July density	**0.039**	0.204	0.609		**–0.647**	**0.666**
k	0.264	0.647	0.655	**0.031**		–0.332
ϕ_0	0.203	**0.011**	0.892	**0.025**	0.319	

Note: P-values less than 0.05 are in bold.

factors at the head of the bay, it is unfortunate that the historically most densely occupied winter flounder spawning and nursery areas are superimposed on the most stressed habitats. A comparison of YOY winter flounder mortality and growth rates during two summers in relatively pristine and contaminated sites (Connecticut River estuary and New Haven harbor, respectively) indicated that there may be significant difference between the two areas (Meise et al. 1999). Both growth and mortality rates were found to be higher in the contaminated site. The authors attributed their results to differences in predator assemblages, percentages of preferred habitat, and contamination between the estuaries. In New

Fig. 7. Pairwise scatter plots among year, average monthly temperature, average monthly precipitation, July observed density, and the model output estimates of k (for growth) and ϕ_0 (for mortality).
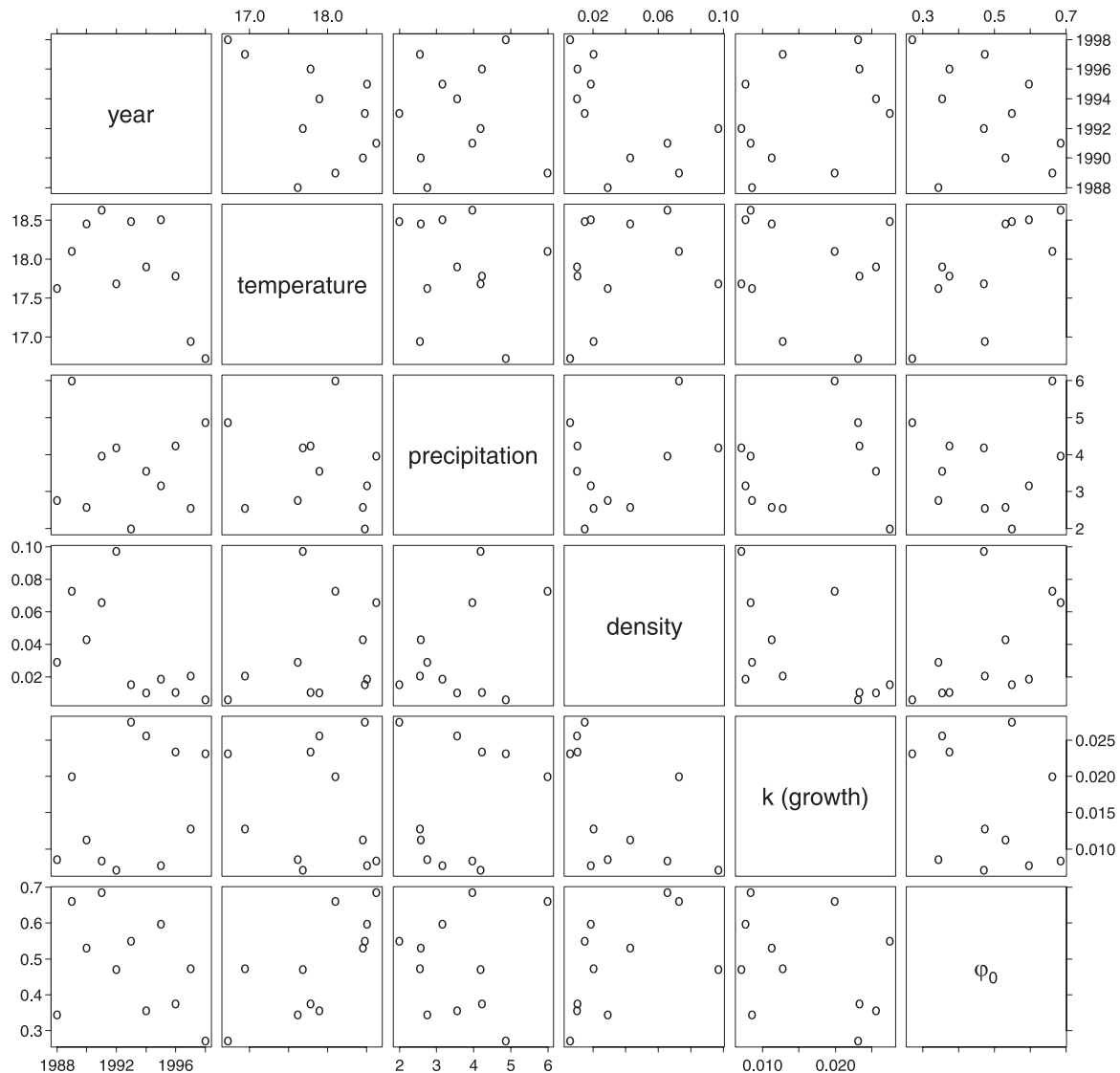
Haven harbor, organic enrichment may lead to increased growth rates, while other pollutants cause higher mortality.

There has been a significant decrease in the abundance of YOY winter flounder during the period 1988 to 1998. However, our results indicate that this decrease is not attributable to increased mortality during the YOY stage, since mortality was shown to decrease during the latter half of the time period and in lower density years. Low densities of winter flounder YOY could be attributable to a low number of eggs spawned (as a result of decreased spawning stock biomass) and (or) poorer survival during the egg or larval stage. To seek answers to the low Narragansett Bay stock biomass, one should take into consideration factors that may influence mortality prior to settlement or the relationship between spawning stock biomass and recruitment.

Acknowledgements

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