

## A Comparison of Length-, Weight-, and Age-Specific Fecundity Relationships for Cunner in Cape Cod Bay

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**Abstract.**—Understanding reproduction and recruitment is essential for the successful conservation of a species. An estimate of the fecundity of cunner *Tautoglabrus adspersus* is critical for assessing population dynamics and perturbation effects. In this study, we estimated length-, weight-, and actual age-specific fecundity relationships for cunner in Cape Cod Bay, Massachusetts. We used the gonadosomatic index to assist with selection of mature, prespawning-size fish for estimating fecundity. We then gravimetrically estimated fecundity for 205 fish 69–185 mm in total length that were collected in May and June 1994. Quadratic models on  $\log_{10}$ -transformed length and weight data each explained 71% of the variance in fecundity, and age data explained 57% of the variance. In a test of age-specific fecundity precision, three age-specific models (actual age, age back-calculated from the von Bertalanffy equation, and a calculated age estimate that was expanded to include additional data) produced consistent fecundity estimates. Finally, a comparison of length-, weight-, and age-specific fecundity relationships showed few differences among the models, suggesting that the more easily obtained length-specific fecundity relationship ( $\log_{10}F = 24.954\log_{10}L - 5.348\log_{10}L^2 - 24.421$ ;  $R^2 = 0.71$ ) is appropriate for future cunner modeling studies.

Accurate fecundity estimates are important for understanding the dynamics of fish populations, predicting trends in population abundance, and estimating spawning-stock biomass (Eldridge and Jarvis 1995). Because reproductive potential influences the ability of a species to respond to abiotic or biotic stresses, knowledge of fecundity is needed to quantify the effects of external stresses (e.g., pollution or overfishing) on the reproductive potential of a species.

Cunner *Tautoglabrus adspersus* is a coastal temperate reef fish that has been used in studies of population dynamics (Levin 1991, 1994, 1996; Tupper and Boutilier 1995, 1997; Levin et al. 1997). Cunner may serve as an ideal indicator of local perturbation (Walton et al. 1978; Williams and Kiceniuk 1987; Mercer et al. 1997) because of a territorial life history characteristic (Green 1975; Olla et al. 1975; Pottle and Green 1979b;

Levin 1991; Tupper and Boutilier 1995, 1997). Though size- and age-specific fecundity have not been estimated for this species (Auster 1989), Williams et al. (1973) indirectly estimated cunner fecundity at 100,000 eggs for a 500-g female.

Life history and reproductive behavior should be considered when estimating fecundity. Cunners have a fairly short spawning season (Pottle and Green 1979a; Martel and Green 1987; Levin et al. 1997), which probably does not allow enough time for immature oocytes to mature, hydrate, and be spawned within the same reproductive season. Therefore, the number of mature or maturing oocytes prior to spawning is probably a good estimate of the potential number of cunner eggs spawned during that reproductive season. For example, in Newfoundland, cunners spawn within a 4- to 6-week period in July and August, most of which occurs within a 2- to 4-week period in July (Pottle and Green 1979a; Martel and Green 1987). In Fishers Island Sound, Connecticut, Dew (1976) observed a short spawning season in June, while in the Gulf of Maine the cunner spawning season occurs in early July (Levin et al. 1997). Therefore, we assumed a priori that a collection of female

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cunners in a variety of sizes before the anticipated peak spawning period would provide an accurate depiction of the potential number of eggs spawned during that reproductive season.

In this study, we estimated the size- and age-specific fecundity of cunners present in inshore waters of Cape Cod Bay, Massachusetts. We did not include the often larger offshore cunners in our estimate (Bigelow and Schroeder 1953). We used the gonadosomatic index (GSI) to help us select only mature cunners for analysis. We then calculated length-, weight-, and age-specific fecundity relationships to determine which measure was the best predictor of egg production. To test the precision of our age-specific fecundity estimate, we compared models that used the actual age estimate and age estimates from lengths derived by the von Bertalanffy growth equation (von Bertalanffy 1938) using samples of different sizes.

### Methods

Cunners were captured in Cape Cod Bay between 1 and 28 June 1994 in fish pots placed at depths of 2–5 m and baited with Atlantic cod *Gadus morhua*. We also used minnow traps and lobster pots with modified vent openings to capture the full size range of inshore cunners. Diver observations ensured all fish sizes at our sites were represented in the collection. Pots were soaked overnight on 17 different occasions off the breakwater of the Pilgrim Nuclear Power Station and on the natural boulder reef near White Horse Beach in Plymouth, Massachusetts. To ensure an adequate size range for fecundity estimates, we collected at least 10 fish in each of 22 5-mm size increments that ranged from 70 to 180 mm. All fish were measured ( $\pm 1$  mm total length [TL]) and weighed ( $\pm 0.001$  g). Staff from the Massachusetts Division of Marine Fisheries (MDMF) extracted sagittal otoliths to assess age (Lawton et al. 1994) and to estimate the parameters of the von Bertalanffy equation using the Fishparm program (Saila et al. 1988). We subsequently used the von Bertalanffy equation to estimate age from length measurements, that is,

$$t = t_0 - \frac{1}{K} \log_e \frac{L_\infty - l}{L_\infty};$$

where  $t$  = age estimated from a given length,  $t_0$  = the hypothetical age when length equals zero,  $K$  = the growth coefficient,  $L_\infty$  = the theoretical maximum fish length, and  $l$  = actual fish length. This equation was later used to test the precision

of the age-specific fecundity estimate. No age-0+ fish were included in the fish collection because we defined the first cohort for this study as age-1 fish, that is, fish 11–12 months old that had been spawned during the previous reproductive season (Jearld 1983). We collected another 35 fish (70–183 mm) on 30 August 1994 (postspawning season) to determine the size range of immature oocytes. We used these data to distinguish immature from mature eggs during egg counts.

Fish ovaries were extracted, weighed ( $\pm 0.001$  g), and preserved in Gilson's fluid, a solution used to harden the eggs and dissolve ovarian tissue (Bagenal and Braum 1971). Ovaries were soaked for at least five months and shaken periodically to help separate the ova (Jessop 1993). The somatic body weight ( $\pm 0.001$  g) of the females was measured and GSI was determined for each fish (Snyder 1983; Wootton 1990; Dee and Parrish 1994) according to the following equation:

$$\text{GSI} = \frac{\text{gonad wet weight}}{\text{somatic wet body weight}} \times 100.$$

Gonadosomatic indices were used in three ways. First, we used a correlation analysis to examine whether gonadal development (GSI) changed with day of collection. Second, we used GSI to determine the size and age of first spawning; fish exhibiting overall lower GSI values in a plot of GSI over the fish size range were considered immature and excluded from the analysis. Third, GSI values of fish collected in late August were used to verify that spawning had ended, and oocyte sizes determined from this sample were deemed representative of immature oocyte sizes.

Fecundity was estimated gravimetrically (Bagenal and Braum 1971; Bagenal 1978) for 205 females. The gravimetric method is considered more precise than the volumetric method, which requires a homogeneous distribution of eggs in a volume of water in order to extract a representative subsample (Snyder 1983). Eggs were first washed and then dried in a drying oven at approximately 85°C for 30–45 min. The total egg mass was then weighed to the nearest 0.0001 g, and three subsamples of 100–1,000 eggs were weighed ( $\pm 0.0001$  g) and counted using a dissecting microscope. An ocular micrometer was used to determine the egg size range from measurements of the smallest and largest eggs during the counts. All eggs larger than 0.05 mm in diameter (dried) were counted. Eggs with a diameter smaller than 0.05 mm were considered immature (based on the

30 August samples) and excluded. If the total number of eggs per unit weight in the subsamples differed by more than 10% of their mean, an additional subsample was taken and the three subsamples that were within 10% of their mean were used in the fecundity calculation (Griswold and Silverman 1992; Jessop 1993). This method assumes that two of the first three samples taken were not anomalies. An additional subsample was required for approximately 15% of the fecundity samples. Finally, the counts were extrapolated as follows to estimate the total number of eggs in the entire ovary:

$$\text{total eggs} = \text{mean} \left( \frac{\text{egg count}}{\text{egg sample wt}} \right) \times \text{total egg wt.}$$

We derived three fecundity relationships, namely, length ( $N = 205$ ), somatic weight ( $N = 205$ ), and actual age ( $N = 177$ ). Variables were  $\log_{10}$ -transformed to improve the fit of the model, to satisfy the assumption of homoscedasticity, and to normalize the residuals. A partial  $F$ -test was used to determine whether a quadratic model explained a significantly higher percentage of the variability than a linear relationship in the length-, weight-, and age-specific fecundity relationships (Kleinbaum et al. 1988).

We compared three age-specific models to assess the precision of the age-specific fecundity estimate. We first examined the method of age estimation on fecundity models using both actual ages ( $N = 177$ ) and ages derived from the von Bertalanffy equation to convert lengths to ages. We compared these two age-specific models to determine whether different size-classes were adequately represented in the actual age-specific fecundity relationship. In a final comparison, we estimated ages of 28 additional fish using the von Bertalanffy equation for which we had length and fecundity estimates but no age data. We included these data in the calculated-age data set to produce a third, "calculated age expanded" model and assessed the consistency of the fecundity relationship by determining whether the increase in sample size resulted in a change in the calculated age-fecundity model.

We compared length-, weight-, and actual age-specific fecundity models by plotting the fitted model curves on a single graph. To compare across models, we standardized the models to a common independent variable by converting both weight and age to length. The original, actual age-specific

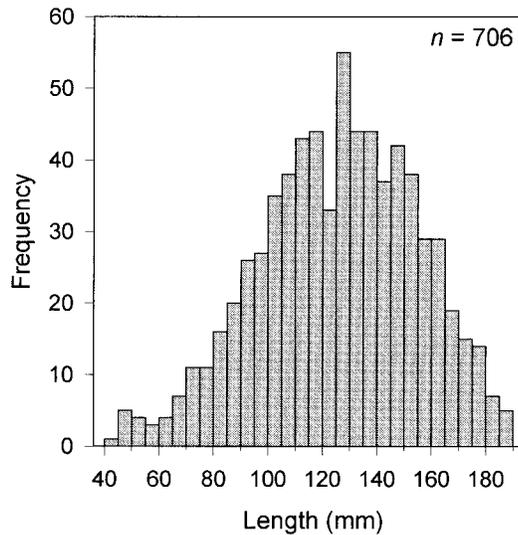


FIGURE 1.—Length-frequency distribution for cunners caught in Cape Cod Bay, Massachusetts, in May and June 1994 from which the fecundity sample was taken.

fecundity model was converted to a length-specific equivalent using the von Bertalanffy equation, and the weight-specific fecundity model was converted using a length-weight regression derived from these data. A back-transformation bias correction (Miller 1984) was used if a considerable bias-reducing adjustment existed. If no substantial differences among the three fecundity models (length, weight, and actual age-specific fecundity) were observed, then the recommended model (i.e., the one that best suited the needs of researchers and managers) was based on two criteria,  $R^2$  and ease of parameter measurement.

## Results

Out of 706 cunners (40–190 mm TL) captured in Cape Cod Bay, Massachusetts, between 25 May and 28 June 1994, a total of 205 females were used in the fecundity analysis (Figure 1). Ninety-five percent of the 205 fish were caught during the first two weeks of June (Figure 2A).

*Gonadosomatic index.*—The GSI varied from 1 to 16 (mean = 8.6) for cunners used in the fecundity analysis (Figure 2A). We detected no relationship between GSI and date of collection ( $r = -0.047$ ,  $N = 210$ ,  $P = 0.49$ ; Figure 2A). The increase in GSI at 65–70 mm (Figure 2B) suggests that this is the size of first spawning (Dee and Parrish 1994). A similar increase in GSI for age-2 fish indicates this is the age of first spawning (Figure 2C). Sex determination, which was only

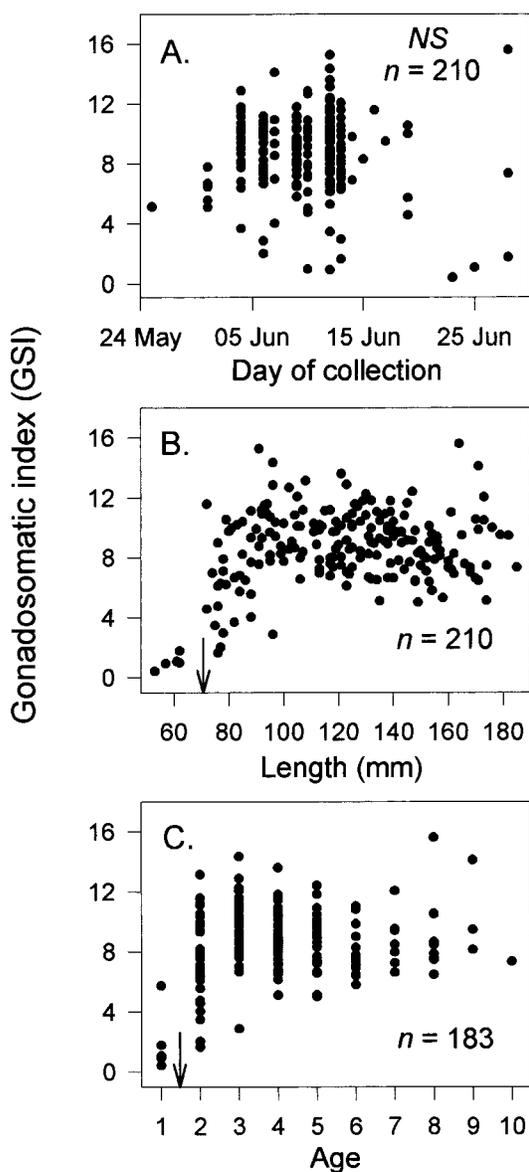


FIGURE 2.—Relationships between gonadosomatic index (GSI) and (A) day of collection, (B) length, and (C) age of female cunners caught in Cape Cod Bay, Massachusetts, in May and June 1994. The first cohort (age 1) consists of fish spawned during the previous reproductive season. Cutoffs for immature fish with low GSI (<65 mm and younger than age 2) are indicated by arrows in B and C. Samples A and B are the same, while C is a subset of the sample where age information exists. NS signifies no significant relationship. No statistics were used in B and C.

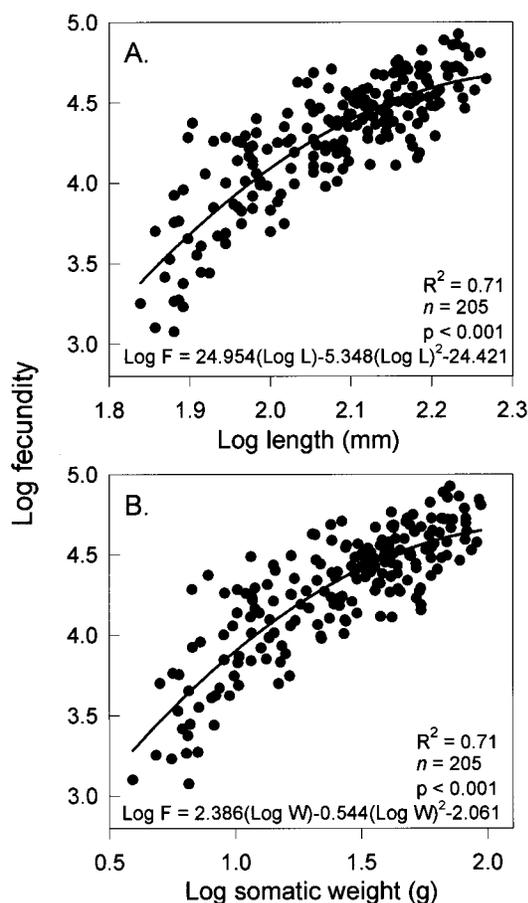


FIGURE 3.—Relationships between fecundity and (A) total fish length and (B) somatic weight for female cunners ranging from 69 to 185 mm and from 3.9 to 94.1 g that were collected in Cape Cod Bay, Massachusetts, in May and June 1994. Data were log transformed to meet statistical assumptions.

possible on 50% of the fish with lengths between 50 and 65 mm, indicated that first spawning occurs when cunners are larger than 65 mm. Thus, immature fish (less than 65 mm and younger than age 2) were excluded from the fecundity analysis. In addition, GSI values for the 14 females (70–182 mm) collected postspawning on 30 August were relatively low; all had GSI values less than 1 (data not shown).

*Fecundity relationships.*—Fecundity increased substantially with small increases in fish length, ranging from 1,192 eggs for a 76-mm fish to 84,403 eggs for a 171-mm fish (Figure 3A). The quadratic form of the length-specific fecundity model explained a significantly higher percentage of the variability than the linear form (Figure 3A;

TABLE 1.—Summary of length-, somatic weight-, and actual age-specific fecundity relationships for adult female cunner caught in Cape Cod Bay, Massachusetts, May–June 1994. Regression equations for length as a function of somatic weight and somatic weight as a function of total fish weight are also shown. The SEs are given for bias-correction adjustments. Variables are as follows:  $F$  = fecundity,  $L$  = length,  $W$  = somatic weight,  $A$  = actual age from otoliths, and  $TW$  = whole fish weight (g). Logarithmic values are base 10.

Variable	Order	Model	Range of dependent variable	$N$	SE	$R^2$	$P$
Length (mm)	1	$\log F = 2.9234\log L - 1.7953$	69–185	205	0.2131	0.680	$\leq 0.001$
	2	$\log F = 24.9539\log L - 5.3481\log L^2 - 24.4211$	69–185	205	0.2050	0.705	$\leq 0.001$
Somatic weight (g)	1	$\log F = 0.9224\log W + 2.9809$	4–94	205	0.2133	0.679	$\leq 0.001$
	2	$\log F = 2.3857\log W - 0.5440\log W^2 + 2.0606$	4–94	205	0.2050	0.705	$\leq 0.001$
Actual age	1	$\log F = 1.4846\log A + 3.4249$	2–10	177	0.2535	0.531	$\leq 0.001$
	2	$\log F = 3.8669\log A - 2.0157\log A^2 + 2.7869$	2–10	177	0.2428	0.572	$\leq 0.001$
Addendum:							
Length–somatic weight	1	$\log L = 0.3123\log W + 1.6384$	4–94	205	0.0155	0.979	$\leq 0.001$
Somatic weight–total weight	1	$W = 0.9014 \cdot TW + 0.0615$	4–106	205	0.0001	0.998	$\leq 0.001$

Table 1;  $\log_{10}F = 24.954\log_{10}L - 5.348\log_{10}L^2 - 24.421$ ,  $R^2 = 0.71$ ,  $N = 205$ , range = 69–185 mm,  $P < 0.001$ ; partial  $F$ -test:  $F = 18.67$ ,  $P < 0.001$ ). For the weight-specific fecundity relationship, somatic weight for fish ranged from 3.916 g to 94.115 g (Figure 3B). The quadratic form also explained a significantly higher percentage of the variability than the linear one (Figure 3B; Table 1;  $\log_{10}F = 2.386\log_{10}W - 0.544\log_{10}W^2 + 2.061$ ,  $R^2 = 0.71$ ,  $N = 205$ ,  $P < 0.001$ ; partial  $F$ -test:  $F = 18.78$ ,  $P < 0.001$ ). The relationship between actual age and fecundity (ages 2–10,  $N = 177$ ) was also better explained by the quadratic model (Figure 4A; Table 1;  $\log_{10}F = 3.867\log_{10}A - 2.016\log_{10}A^2 + 2.787$ ,  $R^2 = 0.57$ ,  $P < 0.001$ ; partial  $F$ -test:  $F = 12.48$ ,  $P < 0.001$ ).

*Comparisons of models.*—In testing the precision of age-specific fecundity, the calculated age-fecundity model did not differ greatly from the actual age-specific model (Figure 4B;  $\log_{10}F = 2.671\log_{10}A - 1.177\log_{10}A^2 + 3.208$ ,  $N = 177$ ,  $R^2 = 0.68$ ,  $P < 0.001$ ; von Bertalanffy parameters used to calculate age were  $t_0 = -1.154$ ,  $K = 0.15$ ,  $L_\infty = 234.7$ ; coefficients of variation [CV = SE/mean] = 22.6%, 16.1%, and 7.2%, respectively;  $N = 267$ ;  $R^2 = 0.83$ ; range, 57–206 mm; B. Kelly, MDMF, personal communication). For the calculated-age-expanded sample, the quadratic model explained 71% of the variation, but in general, the parameters of the model changed little (Figure 4C;  $\log_{10}F = 2.891\log_{10}A - 1.355\log_{10}A^2 + 3.149$ ,  $N = 205$ ,  $P < 0.001$ ).

For a comparison of the length-, weight-, and actual age-specific fecundity models, the derived length–weight regression ( $\log_{10}L = 0.3123\log_{10}$

somatic  $W + 1.6384$ ,  $N = 205$ ,  $R^2 = 0.98$ ,  $P < 0.001$ ) was used to convert the weight-specific fecundity model to its length-specific equivalent (Table 1). The actual age-specific model was converted to its length-specific equivalent by means of the von Bertalanffy equation noted earlier. A back-transformation bias correction was not used since the bias correction only resulted in a 2% increase in the back-transformed length- and weight-fecundity estimates and a 3% increase in the back-transformed age estimate (data not shown). Standard errors are given in Table 1 if back-transformation bias adjustments are desired.

The length-, weight-, and actual age-specific relationships were very similar when the models were converted to length and compared graphically (Figure 5). All models were significant. Length and weight explained 71% of the variance in fecundity, whereas age explained 57% (Figure 5; Table 1).

## Discussion

*Spawning time and assumptions.*—Winter hibernation may produce physiological constraints on cunner reproduction, which could select for a short spawning season. Cunnners hibernate when water temperatures fall below 5–7°C (Green and Farwell 1971; Dew 1976; Pottle and Green 1979a). This hibernation constrains reproduction in two ways. First, spawning is probably inhibited immediately after hibernation due to depleted energy reserves. Pottle and Green (1979a) found that cunnners were active for at least 40 d after hibernation ended and before spawning occurred. Second, survival through winter torpor is probably higher in larger

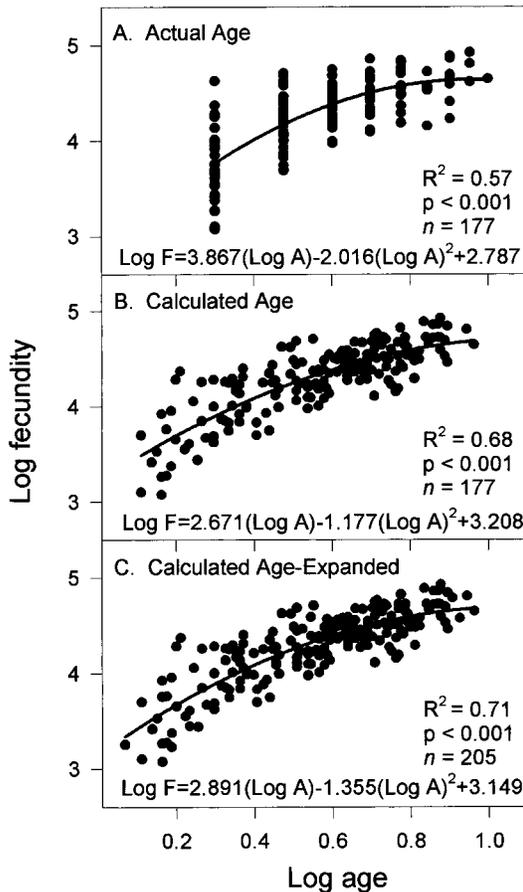


FIGURE 4.—Relationships between fecundity and (A) actual age, (B) age calculated from length using the von Bertalanffy model, and (C) calculated age with the sample increased by 28 fish for which we did not collect age data. Female cunners were collected in Cape Cod Bay, Massachusetts, in May and June 1994. Data were log transformed to meet statistical assumptions.

recruits; winterkills of cunners have been recorded in years of unusually cold weather, and mortality is notably higher for smaller fish during these kills (Bigelow and Schroeder 1953; Green 1974). Cunners may have evolved to spawn early in order to maximize growth between spawning and the subsequent winter hibernation. As a consequence of this short spawning period, we assumed that the number of maturing and mature oocytes present before spawning takes place is an accurate indication of the potential number of eggs spawned during the brief reproductive season.

If the assumption of determinate spawning is invalid, or if favorable environmental conditions result in a prolonged spawning season such that

the number of mature and maturing oocytes before spawning is an inappropriate predictor of the total number of eggs spawned that season (Conover 1985), then our fecundity estimates probably underestimate potential egg production. Estimates of possible oocyte reabsorption at the end of the spawning season would provide a better estimate of true fecundity. Future work on GSI and egg-size distributions, along with histological work on cunners during the spawning season, should help determine the validity of the assumptions used in our fecundity estimates (Hunter et al. 1992).

A fecundity sample should be collected before spawning takes place in order to estimate the total number of eggs spawned in a season. In our study, there were four factors that indicated spawning had not occurred prior to fish collection: GSI, small egg sizes, water temperature, and larvae entrainment sampling at the Pilgrim Nuclear Power Station. First, no relationship existed between GSI and date of collection, as one would find if samples were collected over a time period before, during, and after spawning. Therefore, using the fish collection as a single sample to estimate fecundity seemed appropriate. In addition, the relatively developed ovaries in the fish used for the fecundity estimate had higher GSI values than those in the postspawning (30 August) collection. Second, extruded cunner eggs generally range from 0.75 to 0.85 mm in size (Bigelow and Schroeder 1953); the eggs in our study were small (<0.3 mm), which suggests that spawning had not yet occurred at the time of collection. Third, the water temperature in Cape Cod Bay prior to the June 1994 fish collection averaged 8°C (Anderson 1994; Lawton et al. 1994), well below the temperature threshold (11–12°C) identified as necessary to initiate cunner spawning (Bigelow and Schroeder 1953; Wicklund 1970; Serchuk 1972; Williams et al. 1973). Finally, entrainment sampling every 2–3 d in June and July 1994 at the Pilgrim Nuclear Power Station indicated that cunner spawning had not yet begun at the time of our collection since cunner larvae were absent from ichthyoplankton samples prior to 29 June (Michael Scherer, Marine Research, Inc., personal communication). For these reasons, we believe our sample was collected before spawning had begun.

*Size at maturity.*—Low GSI values and poorly developed gonads in smaller fish suggest that cunners in Cape Cod Bay are immature until age 2 or a size of 65 mm. Wicklund (1970), Pottle and Green (1979a), and Pottle et al. (1981) reported that no cunners under 70 mm spawned. Johansen

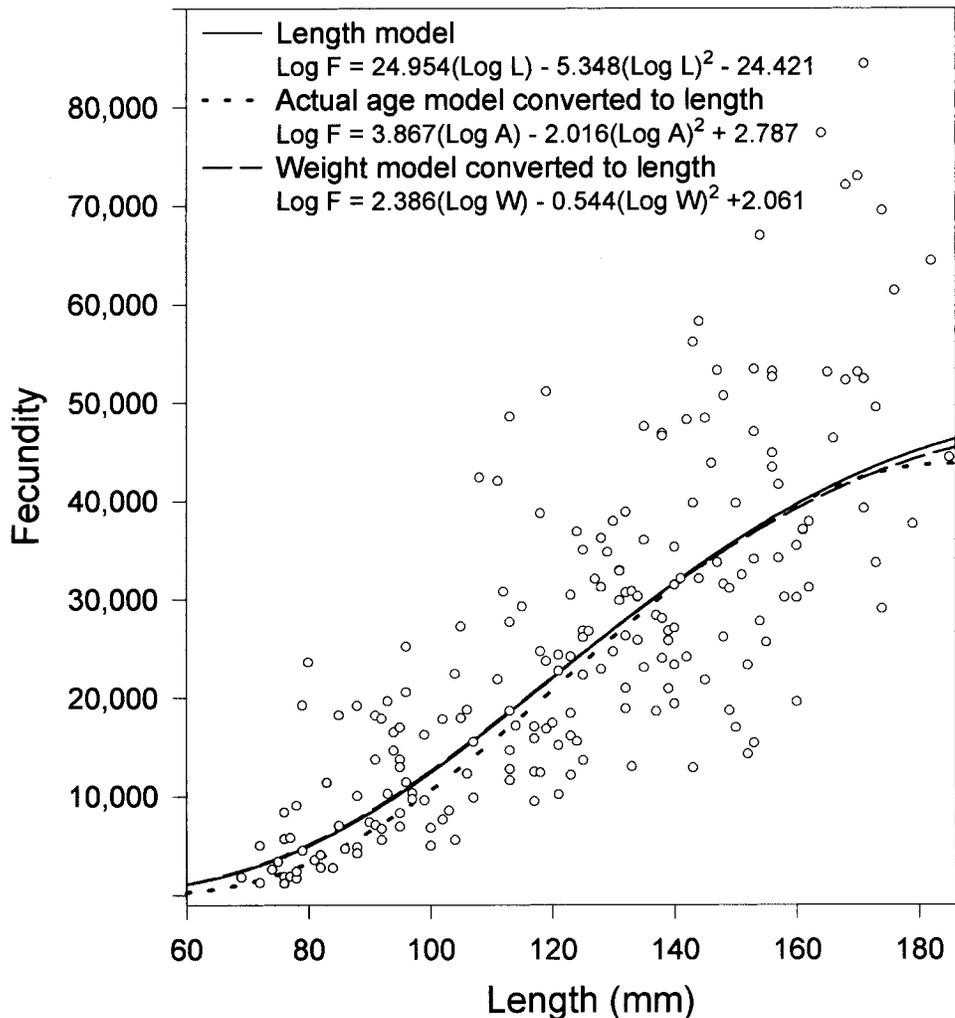


FIGURE 5.—Comparison of the length-, actual age-, and weight-specific fecundity relationships. Each model is converted to a common parameter, length, as described in Methods. Variables are as follows:  $F$  = fecundity,  $L$  = length (mm),  $W$  = somatic weight (g), and  $A$  = age determined from otoliths.

(1925) reported that all fish between 30 and 70 mm (age 1) were immature. Dew (1976) reported that age-1 cunners from Connecticut waters are mature, but the average size at age 1 in that study was much larger (94 mm) than in our sample (63 mm). This size discrepancy could be due to warmer water temperatures, which allow earlier spawning and a longer growing season than is possible for populations north of Cape Cod. We did, however, observe one age-1 fish larger than 65 mm in our sample. The length of the growing season, which can be affected by the annual variability in water temperature, may influence fish size at age and, therefore, fecundity. Spawning of age-1 fish

may play a more important role during a reproductive year with a higher proportion of large, mature age-1 fish. Although large age-1 fish may spawn and annual recruitment may vary, most of the cunners in our sample did not mature until age 2.

*Fecundity sample distribution and statistical analyses.*—Our fecundity samples included most of the inshore adult sizes and age-classes. Fecundity studies are often logistically constrained by the investigator's inability to collect large numbers of fish that are uniformly distributed across a variety of sizes in a relatively small area over a short period of time. Consequently, the accuracy of the

fecundity relationship suffers because of an inadequate number of fecundity estimates for the smaller and larger fish. Fortunately, these logistical constraints did not exert as strong an influence on our collection due to the ease of capturing cunners.

Though most fecundity estimates result in a linear relationship with length when a  $\log_{10}$ - $\log_{10}$  transformation is used (Bagenal and Braum 1971; Clark and Bernard 1992; Griswold and Silverman 1992; Jessop 1993), we found a better fit with the nonlinear quadratic model for  $\log_{10}$ -transformed data. After maturity, cunners possess a very low growth rate ( $k = 0.15$ ), resulting in a small size range (length, 57–206 mm) that spans ten age-classes; this has been determined from otoliths (Lawton et al. 1994) and, to a lesser degree, scales (Serchuk 1974; Dew 1976). We might have detected a linear fecundity relationship in the  $\log_{10}$ -transformed data if our cunners had had a larger size range because length measurements would have had a greater influence on individual fish fecundity estimates (Bagenal and Braum 1971). In addition, we probably would have failed to estimate a significant quadratic model if we had not collected an even distribution of fish sizes in our fecundity estimate.

*Model comparison.*—The small differences between the three age-specific fecundity models (actual age, calculated age, and calculated age expanded) suggest that our fecundity estimate is consistent regardless of the exact data set used. Specifically, similarities between the actual and calculated age-specific models suggest that size-classes were well-represented in our fecundity analysis because the estimate of age was the only factor that differed between these two models; more age estimates were used to determine the parameters of the von Bertalanffy model than were used in the actual age-specific fecundity model (actual age-specific model:  $N = 177$ ; von Bertalanffy model:  $N = 267$ ).

The fecundity models presented here are probably good estimators of fecundity for the size-classes present in the inshore waters of Cape Cod Bay. However, we found higher fecundity relationships than Williams et al. (1973; 200 eggs/g body weight), even though their estimate was based on a single 500-g fish, which is a size rarely seen in inshore waters where cunners are most abundant.

Our length-, weight-, and age-specific fecundity models also resulted in very similar fecundity relationships, indicating that there is consistency in

predicted fecundity among the different metrics used for estimating the fecundity models. Any of these models should be useful in modeling cunner population dynamics or assessing the response to a disturbance; however, the length- and weight-specific models had the closest fits to the data. Consequently, we recommend using the length-specific model, since length data are the simplest and most accurate data that one can collect in the field.

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