

**"Fifth Course on Mathematical Ecology  
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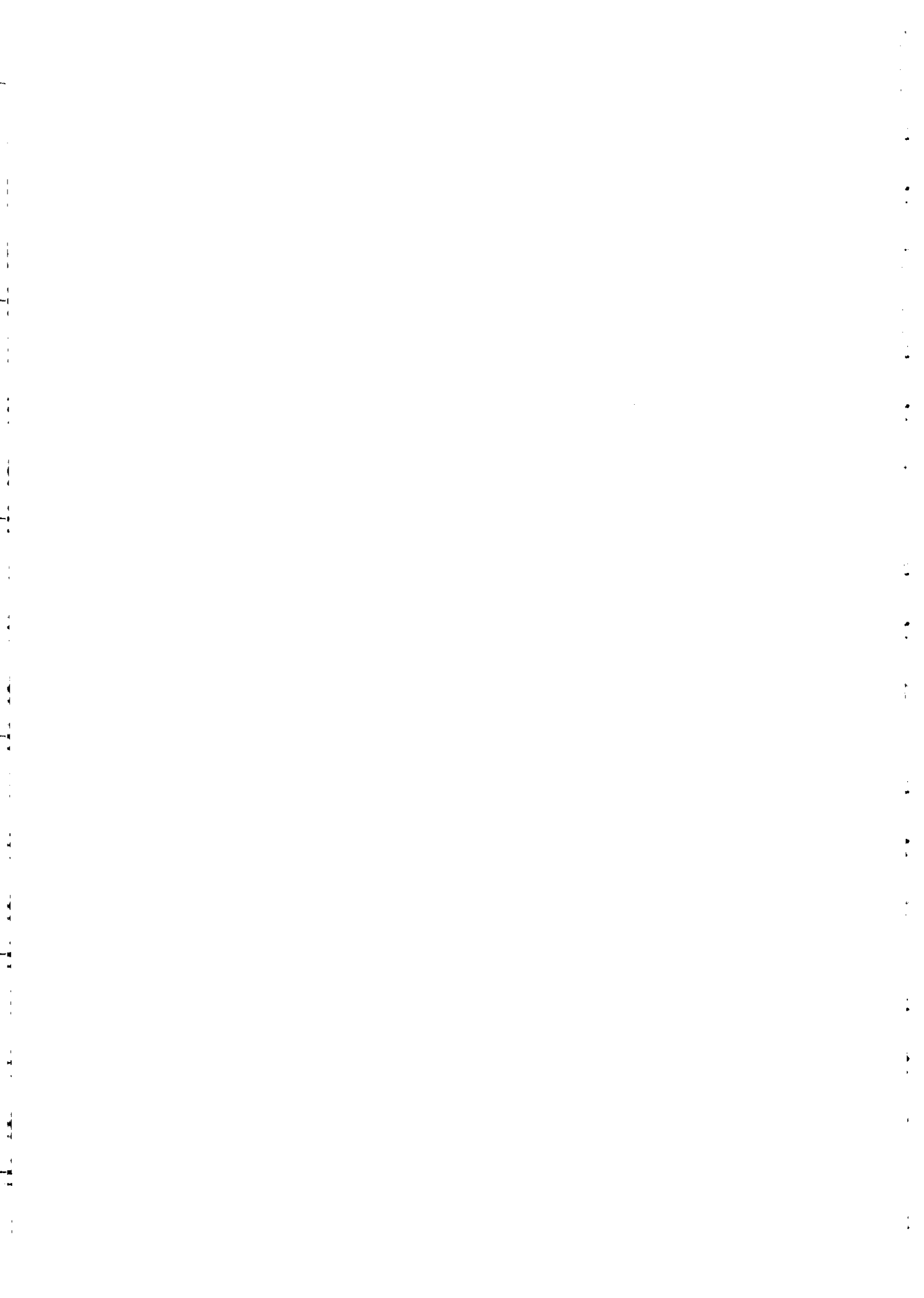
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**TRENDS IN VITAL RATES OF THE EUROPEAN EEL;  
EVIDENCE FOR DENSITY DEPENDENCE?**

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## TRENDS IN VITAL RATES OF THE EUROPEAN EEL: EVIDENCE FOR DENSITY DEPENDENCE?<sup>1</sup>

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**Abstract.** We used a population model to investigate possible density-dependent processes in the European eel (*Anguilla anguilla* L.). We derived this model to include fundamental features of this catadromous fish that have been historically neglected, such as high plasticity in individual growth, length-dependent sexual maturation, sexual dimorphism, and skewed sex distributions. Populations were sampled three times in the Valli di Comacchio lagoons during 1974 through 1989, a period during which both commercial yield and density declined. A bootstrap procedure permitted us to estimate demographic parameters and evaluate their uncertainty. With the model we could estimate eel recruitment to lagoons and the density of prereproductive eels per length and age class, especially useful information because these data cannot be collected directly. With the exception of age 1, survival increased as density declined. In addition, as density declined, the proportion of females and female body size, as well as age and length of both sexes at sexual maturity, increased. Density-dependent processes, such as competition for limited food and space, and trade-offs between reproductive success and survival provide a parsimonious explanation (though not one we could test) for these shifts in population parameters.

**Key words:** *Anguilla anguilla*; density dependence; eel; fish density decline; fishery management; fish population modeling; life history strategies; sex ratio; sexual dimorphism and maturation; statistics, nonparametric; survival.

### INTRODUCTION

How density dependence operates in fish populations is critical for the management of commercially exploited species. Most literature focuses on stock-recruitment relationships of the type described by Ricker (1954) or Beverton and Holt (1957), but the path by which density affects the rate of increase of a population can be quite varied and may involve only selected specific components of a fish life history (juvenile and adult survival, fecundity, body growth). Density-dependent processes in fish decline with age; density effects on adult fish rarely have been detected (Cushing 1975). That density dependence is usually restricted to early life stages is supported by some authors (Elliott 1989, Persson and Greenberg 1990, Dawson 1991, Jenkins et al. 1991), but not by others. For instance, density dependence has been documented in older fish, but not in yearlings, for 10 lakes and reservoirs in Idaho (Rieman and Myers 1992). At times density influences juvenile stages unconventionally, as when survival is unaffected by density, but time to maturity increases with increasing density (Jones 1987, Armstrong et al. 1989). Further, some authors have documented the relationship among fish density, diet, and somatic growth (Barlow 1992, Diehl 1993, Garman

and Moring 1993, Newman 1993). In practice, generalizations are lacking and, as such, we require insight into how density dependence acts in fish populations.

Here we search for evidence of density dependence in the demographic parameters of the European eel (*Anguilla anguilla* L.), a fish characterized by remarkable complexity in its life history and by few existing data. Our interest is twofold. On the one hand, because eels are commercially exploited, information on their demography might improve management. On the other hand, a scientific interest exists because the factors regulating the dynamics of eel populations do not seem to be those traditionally considered by stock-recruitment models: competition does not appear to modify mortality patterns in the early life stages, but rather to influence adult survival, sex ratio, and rate of somatic growth, while promoting selection for early maturation. One of the most important studies on eel vital rates is by Vøllestad and Jonsson (1986) who analyzed the life history of this catadromous fish in the Imsa River (Norway). Herein, we review Vøllestad's hypotheses and explore whether the juvenile and adult survival, the rate of body growth, the rate of metamorphosis from prereproductive to reproductive adult, and the sex ratio of European eel are influenced by density. To this purpose we studied the eel population of the Valli di Comacchio lagoons (northern Italy). This fishery provided  $\approx 15 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  until the mid 1970s and then declined to the current level of  $\approx 6 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ . Lagoon man-

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agers responded by stocking different numbers of juveniles into different lagoons. Declining catch was believed to result from a decline in natural recruitment, though this has never been quantified.

Both the decline of eel recruitment and the restocking program represent a unique opportunity to test the demographic response of the European eel to an important variation in fish density occurring not under laboratory conditions, but in a natural environment and on a large scale. In a previous work (De Leo and Gatto 1995), we presented a detailed model of eel population dynamics that was used to estimate the basic demographic rates of the European eel from the data collected in 1989 by Carrieri et al. (1992) in the Comacchio lagoons. Here we use the same model to estimate recruitment abundance, eel density in the prereproductive stage, and the demographic rates from another data set, collected between 1974 and 1976 when density was much higher. Also, we reconsider the 1989 data by discriminating between two low-density situations: one with high and one with low stocking.

A nonparametric technique (bootstrapping) provided estimates of model parameters. Vital rates derived for the three reference cases were then compared by using a randomization test performed on the bootstrap distributions. These comparisons suggest that the data sets have important differences and that variation in eel density may have a profound impact on the life history of the European eel.

#### GENERAL INFORMATION AND DATA

##### Study site

The Valli di Comacchio (10 400 ha) are three shallow lagoons located near Ferrara, northern Italy. The Comacchio fishery has been operating for centuries taking advantage of the autumn–winter migration of European eels to the ocean. Valle Campo, the smallest (1600 ha) of the three, is completely separated from the other two; Valle Magnavacca and Valle Fossa di Porto are largely connected and are usually treated for management purposes as a single wide water body (8800 ha). Several species thrive in the Valli, but the fishery has always been dominated by *Anguilla anguilla*, which comprises up to 90% of fishery yield in mass.

##### European eel life history

About 8–12 mo after the metamorphosis from the larval to the glass eel stage (Tesch 1977), elvers enter the lagoons through the sluice gates in late spring and remain in this environment for a number of years as yellow eels. Most elvers are not sexually differentiated; differentiation takes place usually within 1–2 yr. Yellow eels feed and grow in the lagoons until they metamorphose into silver eels whereupon all silver eels migrate to the ocean (Sargasso Sea) for spawning. During migration, which occurs mostly between October and December, all the sexually mature individuals are

caught at the sluice gates by means of special devices called lavorieri, a series of V-shaped screens, which select all lengths typical of silver eels. Therefore, the Valli catch is practically the whole silver population, whereas yellow eels are not caught at the fishing stations. Annual recruitment in Comacchio is not related to the abundance of mature individuals in the three lagoons. In fact, the European eel can be regarded as one population with almost complete panmixia even though the population is distributed over most of the northern hemisphere waters between 30° W and 45° E in its nonreproductive life stages. The overall spawning stock is thus represented by all the silver eels that successfully migrate from Europe and North Africa to the common area in the Sargasso Sea; the actual recruitment to Comacchio lagoons consists only of the fraction of glass eels that reach the North Adriatic coast as they migrate to feeding sites. Due to declining catches, fishery managers have recently supplemented natural recruitment with stocking. Every year since 1978,  $\approx 7.5$  kg/ha of French and Spanish elvers have been introduced into Valle Campo; only  $1.4$  kg·ha<sup>-1</sup>·yr<sup>-1</sup> have been stocked at the other site (Valle Magnavacca and Valle Fossa di Porto).

#### MATERIAL AND METHODS

The Comacchio lagoons have been extensively studied over the past 20 yr (Colombo 1972a, b, Rossi and Colombo 1979, Gatto et al. 1982, Rossi et al. 1986). All observations confirm the distinctive features of the species *Anguilla anguilla* both at physiological and population level. First, growth is extremely variable (Rossi and Colombo 1976b); same-age eels exhibit quite variable lengths. Second, strong sexual dimorphism exists; females are usually larger than males of similar age (Rossi 1979). Third, the sex ratio varies in time and is considerably skewed towards females (Rossi and Colombo 1976a). This is possible because sex differentiation is determined phenotypically as heteromorphic chromosomes related to sex do not exist in *Anguilla anguilla* (Sola et al. 1980, Wiberg 1983). Finally, sexual maturation depends upon body length rather than age (Rossi and Colombo 1976a, Vøllestad 1986a, Vøllestad and Jonsson 1986, Vøllestad 1992). For males, metamorphosis from the yellow (immature) to the silver (mature) stage occurs at  $\approx 38$ –45 cm; in females, size at metamorphosis occurs over 40–90 cm. All males migrate to the sea within 4–7 yr, whereas some yellow females can attain considerably older ages (9–13 yr) without undergoing metamorphosis to the silver type (Rossi 1979, Gatto and Rossi 1979, Rossi et al. 1987/1988, Carrieri et al. 1992).

Our analysis has been based on three sampling campaigns carried out by researchers of the Dipartimento di Biologia Evolutiva, University of Ferrara: one in 1974–1976 (Rossi 1979, hereafter referred to as Data set 74–76) and the other two in 1989 (Carrieri et al. 1992), respectively in Valle Campo (Data set VC89)

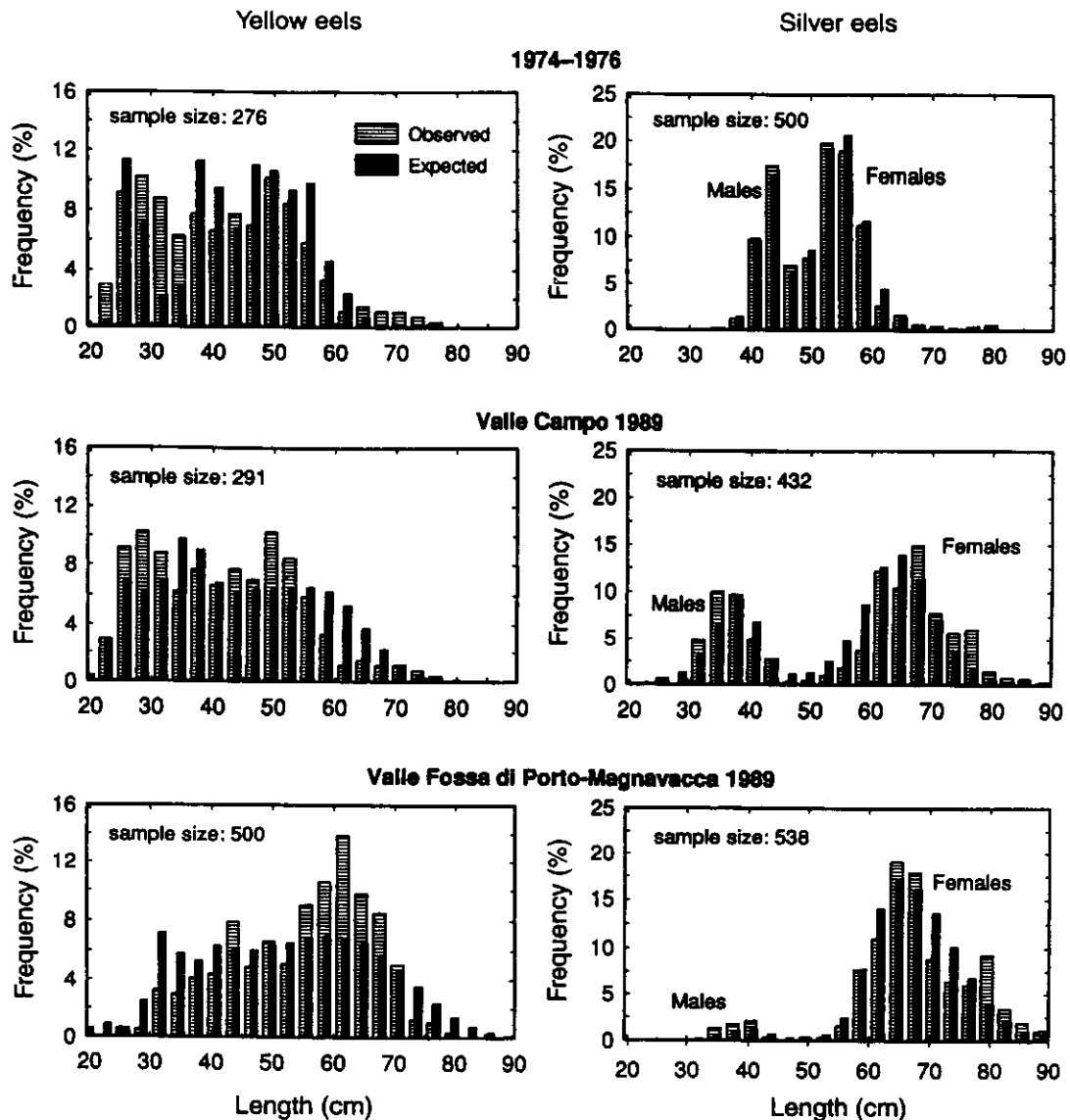


FIG. 1. Observed vs. expected size distributions of yellow and silver eels for three data sets collected in the Comacchio lagoons during 1974–1976, at Valle Campo in 1989, and at Valle Fossa di Porto-Magnavacca in 1989, respectively. Expected distributions are computed independently for each data set by the best fitting size- and age-structured demographic model.

and in Valle Fossa-Magnavacca (Data set VFM89). Silver eel samples have been extracted from the autumn catch on the basis of a stratified sampling design described elsewhere (Carrieri et al. 1992, De Leo and Gatto 1995). Yellow eel samples were collected by means of trawl nets (15-mm mesh size) in 1976 and fyke nets (8-mm mesh size) during spring 1989. The stratification for yellow eels was similar to that for silver eels. While the absolute density of the silver eels is known for each lagoon, because all of these fish are trapped in the lavorieri, this is not true for yellow eels because the fraction of the population actually captured is unknown.

*Data set 74–76.*—Five hundred silver eels were randomly sampled, after stratification, from the 1974 autumn catch at the lavorieri (Carrieri et al. 1992). A trawl net (15-mm mesh size) was used to sample 276 yellow eels during autumn 1976. Specimens collected in the three lagoons were originally pooled into two groups of yellow and silver eels, respectively (Rossi 1979). Each individual was weighed ( $\pm 5$  g), measured ( $\pm 5$  mm), and sexed. Females comprised  $\approx 69\%$  of the silver eels and 82% of the elvers with a resulting size distribution (Fig. 1). Age was determined by otolith examination on subsamples of 207 males (51 yellow and 156 silver eels) and 474 females (130 yellow and

344 silver eels). Age was calculated starting from the glass eel stage (Tesch 1977). Age at recruitment in the lagoons was conventionally set to 1 yr (Gatto and Rossi 1979).

*Data set VC89: Valle Campo.*—Four hundred thirty-two silver eels were randomly sampled after stratification of the 1989 autumn catch at the lavorieri (Carriero et al. 1992). By using fyke nets (8-mm mesh size) 1241 yellow eels were caught in spring 1989, and a random sample of 291 individuals was removed after stratification. Each specimen was measured and a sample of the measured fish (290 yellow eels, 300 silver females, and 88 silver males) was weighed; age was determined by otolith examination on 44 yellow males and 153 females (81 yellow and 73 silver eels). The size structure of silver eels has a marked bimodal shape (Fig. 1); smaller silver females were always larger than the largest silver males. Therefore, the fraction of silver females (67%) was computed from the normalized frequency distribution of lengths as the histogram area corresponding to typical female sizes (>43 cm). Sex ratios of juvenile yellow eels were determined by inspecting the gonads in a random sample of 18 eels aged 2–4 yr caught in spring 1989 (fraction of females = 77.7%). Sex was not determined for older yellow eels and juvenile sex ratio cannot simply be extended to older age classes.

*Data set VFM89: Valle Fossa-Magnavacca.*—We randomly sampled 538 silver eels after stratification of the autumn catch at the lavorieri (Carriero et al. 1992). By using fyke nets (8-mm mesh) 1449 yellow eels (513 kg) were caught in spring 1989, and a random sample of 500 individuals (175.5 kg) was removed after stratification. Each specimen was measured and a sample of the measured fish (367 yellow eels, 512 silver females, and 16 silver males) was weighed. Age was determined by otolith examination on 18 yellow males and 292 females (185 yellow and 107 silver eels). Size structure is reported in Fig. 1. The proportion of females in the silver eel stock (96%) was computed in the same way as for the previous data set. Sex ratios of juvenile yellow eels were determined by gonad inspection in a random sample of 39 eels aged 2–4 yr caught in spring 1989 (fraction of females = 97.4%).

#### THE DEMOGRAPHIC MODEL

De Leo and Gatto's (1995) size- and age-structured model is an extension of Kirkpatrick (1984) and Schnute's (1987) theory, which explicitly includes stochasticity in individual growth and both age- and size-dependent parameters. Our model includes two novelties. First, it accounts for some fundamental features of the life cycle of catadromous species neglected in previous studies, such as sexual dimorphism, high variability in body growth, size-dependent sexual maturation, and age-dependent natural mortality. Second, the mathematical approach is quite flexible compared to that of Kirkpatrick (1984) and Schnute (1987). In fact, their

theoretical framework for constructing and analyzing size-dependent models provides a set of equations that are analytically tractable in a closed form. However, this tractability is achieved by means of some critical hypotheses about the shape of the net-selectivity curves, the analytical expression of the mortality function, and the structure of the stochastic growth model. In our work we follow Deriso and Parma's suggestion to "let the computer add the numbers" (Deriso and Parma 1988:1055) and provide a flexible framework in which realistic assumptions concerning net selectivity, growth, survival, and sexual maturation can be made.

We first subdivide the population into distinct cohorts of individuals. Each cohort was characterized by a continuous distribution of individuals over the complete range of sizes. A set of recursive equations specifies, on a discrete-time basis, the demographic fate of individuals in a cohort according to their age and size distribution. In this sense, the model is intermediate between classical matrix models and more involved partial differential equation models, combining the computational ease of the former with the flexibility of the latter. More precisely, the model relies on four main assumptions concerning body growth, size distribution at recruitment, survival, and metamorphosis.

The first and basic assumption is that the variability in body growth, as expressed among individuals, is already operating at the age of recruitment  $x_0$  (the so-called assignment-at-birth model by Kirkpatrick 1984). Therefore the actual length  $l(x)$  of an individual at age  $x$  is the product of the expected length  $L(x)$  at age  $x$  and a growth factor  $g$  randomly assigned to each fish. In the specific cases examined here,  $g$  is distributed according to a lognormal distribution function with unitary median. A von Bertalanffy growth equation was used (Table 1), in which  $L_0$  (the length of elvers at metamorphosis from the glass stage) was assumed to be 75 mm (per D'Ancona 1959, 1960, Vøllestad and Jonsson 1986), while  $k$ ,  $L_\infty$ , and the variance of  $g$  were estimated from available data after a logarithmic transformation.

The second assumption is that the size of a newly recruited individual (age  $x_0$ ) at time  $t$  is a random variable with (known) probability density. This density is implicitly defined by the previous assumption, i.e., it is lognormal with median  $L(x_0)$  and variance derived from the variance of  $g$ .

The third basic assumption concerns survivorship. First, natural mortality during winter is neglected; compared to summer mortality, when high water temperature and oxygen deficit in the brackish environment cause a large number of fish to die (Vøllestad 1986b, Rossi et al. 1987/1988, De Leo and Gatto 1995), winter mortality is low. Second, summer survival is assumed to be age dependent. Here, we use a Weibull distribution of the age at death (Pinder et al. 1978), which is characterized by two parameters: the scale and the shape parameter, respectively denoted by  $b$  and  $c$ . The Weibull distribution

TABLE 1. Parameters ( $\pm 1$  SE) of logarithmic regressions of mass ( $w$ , g) vs. length ( $L$ , cm) and length ( $L$ , cm) vs. age ( $x$ , yr) for the three data sets, describing growth parameters of the European eel.

Data source	Regression of mass vs. length: $w(L) = \alpha L^\beta$			Regression of length vs. age: $L(x) = L_\infty(1 - e^{-kx}) + L_0e^{-kx}$		
	Sample	$\beta$	$\ln \alpha$	Sample	$L_\infty$ (cm)	$k$ (per yr)
Data set 74-76	Yellow eels (males + females)	$3.272 \pm 0.031$	$-7.601 \pm 0.114$	Silver and yellow males	$44.9 \pm 0.6$	$0.40 \pm 0.017$
	Silver females	$2.983 \pm 0.062$	$-6.296 \pm 0.249$	Silver and yellow females	$59.6 \pm 1.6$	$0.282 \pm 0.019$
	Silver males	$2.171 \pm 0.135$	$-3.237 \pm 0.507$			
Data set VC89	Yellow eels (males + females)	$3.368 \pm 0.033$	$-7.942 \pm 0.129$	Silver and yellow males	$42.8 \pm 1.5$	$0.31 \pm 0.09$
	Silver females	$3.089 \pm 0.050$	$-6.714 \pm 0.209$	Silver and yellow females	$69.62 \pm 1.3$	$0.30 \pm 0.036$
	Silver males	$3.115 \pm 0.100$	$-6.852 \pm 0.361$			
Data set VFM89	Yellow eels (males + females)	$3.362 \pm 0.028$	$-7.961 \pm 0.113$	Silver and yellow males	$43.7 \pm 2.3$	$0.32 \pm 0.06$
	Silver females	$3.134 \pm 0.042$	$-6.847 \pm 0.179$	Silver and yellow females	$79.4 \pm 1.7$	$0.20 \pm 0.009$
	Silver males	$2.965 \pm 0.449$	$-6.281 \pm 1.628$			

Note: Data set 74-76: eels sampled in the three lagoons between 1974-1976; VC89: eels sampled in Valle Campo in 1989; VFM89: eels sampled in Valle Fossa di Porto-Magnavacca in 1989.

is rather flexible and can possess either positive or negative skewness. The corresponding annual survival can hence decrease or increase with age when  $c$  is respectively  $>$  or  $< 1$ ; it is constant when  $c = 1$ . These patterns correspond to Type I, II, and III survivorship curves, respectively (Pearl 1928, Deevey 1947).

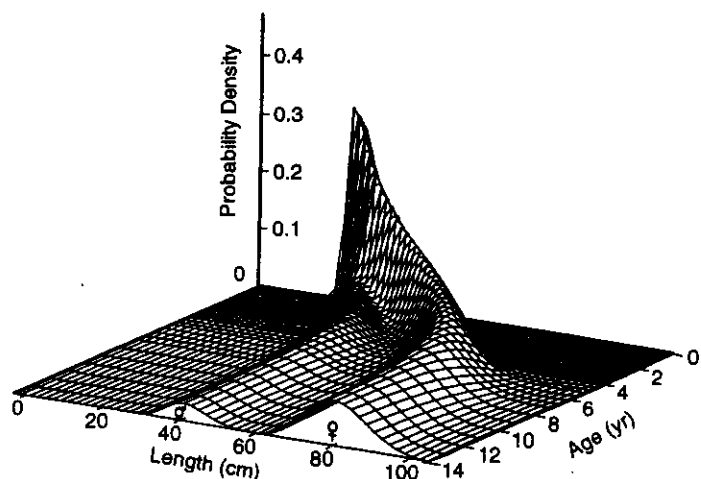
The last basic assumption is that sexual maturation depends upon the length  $l$  of individual fish (as documented for eels by Vøllestad and Jonsson 1986, Vøllestad 1992). Let  $\gamma(l)$  be the expected fraction of fish of length  $l$  that reaches sexual maturity. As for eels, there is evidence that  $\gamma(l)$ , the fraction of maturing yellow eels, is increasing and sigmoidal. Specifically, the following metamorphosis function was used:

$$\gamma(l) = \frac{\gamma_{\max}}{1 + \exp\left(-\frac{l - \lambda}{\eta}\right)} \quad \gamma_{\max}, \lambda, \eta > 0 \quad (1)$$

where  $\gamma_{\max}$  ( $\leq 1$ ) is the maximum rate of metamorphosis,  $\lambda$  is a semisaturation constant, and  $\eta$  is a parameter inversely proportional to the slope of the metamorphosis curve at  $l = \lambda$ . Therefore, for positive  $\lambda$  and  $\eta$ ,  $\gamma(l)$  increases with eel length and levels off to  $\gamma_{\max}$  for large values of  $l$ .

Based on the above assumptions, we wrote recursive equations that allow the time propagation of the initial size distribution of newly recruited individuals (see De Leo and Gatto 1995 for details). Marked sexual dimorphism of eels required separate distributions for females and males (see Fig. 2 for an example). As an approximation, we considered eels as already differentiated at recruitment. Sex ratio at recruitment was set equal to that observed for each data set within the juvenile age classes. Accordingly, growth curves  $L(x)$ , growth factors  $g$ , and metamorphosis functions  $\gamma(l)$  were assumed to differ for the two sexes. In contrast,

FIG. 2. The propagation of eel size structure within a cohort of same-aged individuals. The vertical axis represents the probability density of an eel being of length  $l$  at age  $x$ . The size distribution of females initially overlaps that of males, but with increasing age, the cohort size structure attains a typical bimodal shape, the larger mode corresponding to females. The inclusion of a lognormally distributed growth factor accounts for the dispersion of eel sizes on wider and wider intervals.



males and females were assumed to share the same survivorship function, which was a function of age alone. Note that there is no clear evidence either against or in favor of sex and length as further determinants of eel survival (Tesch 1977, Vøllestad and Jonsson 1986). Thus, our hypothesis is mainly dictated by a principle of economy to keep the model as manageable as possible without sacrificing its precision. As an alternative, we considered a model where eel survival depended upon length only, but found no advantage in terms of fit to the available data.

The model provides detailed information on biomass and abundance for each gender, size, and age group and allows for estimation of the size structure of immature and mature fish, in our case yellow and silver eels, respectively. While the length distribution of silver eels can be directly compared to data, it cannot for yellow eels. In fact, the data were collected by using trawls in 1976 and fyke nets in 1989, two types of fishing gear that are size-selective (Rossi 1979, Carrieri et al. 1992). To account for net selectivity as a function of size, we used the data from a mark-recapture experiment performed by Rossi et al. (1987/1988) in the Comacchio lagoons in 1982. The yellow eel size structure thus was modified via the estimated selectivity functions before testing the model against data (see De Leo and Gatto 1995 for details).

#### MODEL CALIBRATION

Three coefficients  $\gamma_{MAX}^F$ ,  $\lambda^F$ , and  $\eta^F$  of the metamorphosis function were estimated for females. For males, only  $\lambda^M$  and  $\eta^M$  required estimation, because  $\gamma_{MAX}^M$  equaled unity, as all surviving males eventually reached sexual maturity (Gatto and Rossi 1979). The survivorship curve has two unknown parameters  $b$  and  $c$ . Recruitment abundance  $R$  had to be estimated as well.

Altogether, model calibration required that eight unknown parameters be estimated. A set of estimates is derived for each data set independently. Recruitment, as well as the other parameters of the model, was assumed constant through time within each data set. This is obviously a critical assumption, as there is evidence that natural recruitment can vary year to year (Vøllestad 1986b, Vøllestad and Jonsson 1988). Unfortunately, recruitment abundance has not been monitored in any of the published studies on the Comacchio lagoons. Thus, the simplest assumption is that, within each data set, recruitment in year  $t$  is distributed around a constant average value:  $Rec(t) = \epsilon_t R$ , where  $\epsilon_t$  is a random factor with unitary geometric mean and reasonably small variance. The estimate of  $R$  from the data set 74–76 was taken as representative of the high density situation, whereas estimates from data sets VC89 and VFM89 were considered as representative of the 1989 low-density situation with high and low stocking, respectively. Estimated values of  $R$  accounted for both natural recruitment and stocking.

The calibration procedure benefits from the fact that length distributions (from now on denoted as  $\pi^Y$  and  $\pi^S$  for yellow and silver eels respectively) do not depend upon recruitment abundance under time-invariance assumption (De Leo and Gatto 1995). Thus, model parameters were estimated in two steps: (1) first, we derived the expected value of all parameters except  $R$  by minimizing the following square deviation:

$$\Xi(\gamma_{MAX}^F, \lambda^F, \eta^F, \lambda^M, \eta^M, b, c) = \int (\pi^Y - \hat{\pi}^Y)^{2m} dl + \int (\pi^S - \hat{\pi}^S)^{2m} dl \quad (2)$$

where  $\pi^Y$  and  $\pi^S$  are the observed size structures of yellow and silver eels combined over sexes (Fig. 1),  $\hat{\pi}^Y$  and  $\hat{\pi}^S$  are the expected counterparts computed with the model, and  $m$  is a positive integer. The optimal values of  $\gamma_{MAX}^F$ ,  $\lambda^F$ ,  $\eta^F$ ,  $\lambda^M$ ,  $\eta^M$ ,  $b$ , and  $c$  were obtained for each of the three samples by using the downhill simplex method to minimize  $\Xi$  (Press et al. 1988);  $m$  was set equal to two, a fair compromise between convergence speed and goodness-of-fit to size-distribution tails; (2) then, after having estimated these parameters, we computed the recruitment abundance  $R$  for each data set to match the mean observed catch of silver eels in the corresponding period, that is, 14.5 kg/ha in 74–76 and 6.15 kg/ha in 1989 for both Valle Campo and Valle Fossa-Magnavacca. A golden-section algorithm (Press et al. 1988) was used to derive  $R$ . The size structure of yellow and silver populations, previously estimated for each data set, was used along with the corresponding length-mass relationships reported in Table 1 to compute an estimate of the recruitment biomass (De Leo and Gatto, 1995).

A bootstrap procedure (Efron 1982), which closely followed the original sampling design (Pelletier and Gros 1991, Carrieri et al. 1992), was implemented to evaluate uncertainty in parameter estimation (De Leo and Gatto 1995). To increase confidence in our estimator, we recombined the data 1000 times for each sample. Convergence of the downhill simplex algorithm was relatively fast for each recombination, but the high number of replicates made the calibration procedure a quite long process;  $\approx 10$  h of computing time on a Workstation HP-720 were necessary to complete the overall bootstrap calculation for each reference sample. A bias-adjusted expected value (Meyer et al. 1986), the coefficient of variation, a bias-corrected 90% confidence interval (Efron 1982), and the skewness of model parameters were obtained for each sample by using the frequency distributions of the 1000 bootstrap replicates.

The knowledge of the distribution of the eight basic parameter estimates made it possible to derive the main statistics of a number of important indices and vital rates that are of more immediate understanding and practical usage. In particular, by using the recruitment estimate, the expected size distributions of yellow males and females, and the length-mass relationship, we obtained the absolute density and biomass of yellow



eels. This is of particular interest because it cannot be established directly from sampling. Furthermore, the frequency distribution of annual age-specific survivals was derived for each data set by using the 1000 bootstrap pairs of parameters  $b$  and  $c$ . The same approach was used to compute the frequency distribution of length-specific metamorphosis rates.

Estimates of these vital rates for each data set were then compared in pairs by using a randomization test performed on the bootstrap distributions (Edgington 1987). A typical hypothesis we tested was that the expected value of a parameter estimated from data set  $j$  ( $j = 74-76, VC89, VFM89$ ) was significantly greater (smaller) than the expected value of the same parameter obtained by using another data set. The procedure was based on the following simple scheme (Manly 1991): (1) a value  $\theta_j^*$  of the parameter to be tested is randomly selected from the bootstrap distribution obtained by using the first data set; (2) a second value  $\theta_k^*$  ( $k \neq j$ ) is randomly selected from the other bootstrap distribution; (3) the difference between  $\theta_j^*$  and  $\theta_k^*$  is then computed. The scheme (1-3) is replicated a large number of times (10 000). Finally, the significance level  $P$  is computed as the fraction of times the difference between  $\theta_j^*$  and  $\theta_k^*$  is strictly negative (positive).

A Behrens-Fisher  $t$  test was used to compare the average body sizes and the parameters of length-mass and age-length relationships estimated for each data set. A Kolmogorov-Smirnov (K-S) test was used to test the goodness-of-fit of recruitment bootstrap distributions to normal and lognormal distributions. In reporting our results, we use the criterion  $P < 0.05$  for significance, unless specified otherwise.

## RESULTS

### Body growth

Average body lengths  $l$  of silver eels differed among the three data sets. For females,  $l_{74-76} < l_{VC89} < l_{VFM89}$  ( $P < 0.001$ ); for males,  $l_{74-76} > l_{VC89}$  ( $P < 0.001$ ) and  $l_{74-76} > l_{VFM89}$  ( $P < 0.001$ ), while the average lengths for VC89 and VFM89 did not differ. Similar differences held true also for body mass.

The relationship of total length ( $l$ , in centimetres) vs. mass ( $w$ , in grams) was computed for yellow eels, silver females, and silver males for each of the three data sets (Table 1). Yellow eels and silver females in 1989 were slightly heavier than those of the same length in 1974-1976, while eel weight in Valle Campo and Valle Fossa-Magnavacca was similar. In contrast, silver males were remarkably heavier for their length in 1974-1976 than in the two 1989 data sets.

The parameters  $k$  and  $L_\infty$  of the length-age relationship were estimated by using nonlinear least squares with a logarithmic transformation of the von Bertalanffy curve (Table 1). The asymptotic lengths  $L_\infty$  of females differed in the three samples, with  $L_{\infty(74-76)} <$

$L_{\infty(VC89)} < L_{\infty(VFM89)}$  ( $P < 0.001$ ). No other differences among samples occurred.

### Demographic parameters

The estimates of model parameters are shown in Table 2. A correlation analysis on the bootstrap replicates of each sample suggests moderate cross-dependence between some of the model parameters (particularly between  $b$  and  $c$ , with correlation  $\approx 0.8$  for the three data sets), but correlations were very small in most cases and rarely significant. Therefore, the problem of minimizing the objective function (Eq. 2) is well posed and the demographic model was not overparameterized with respect to available data. The expected size distributions, corresponding to parameter estimates reported in Table 2, are plotted against observed ones (Fig. 1) suggesting a good fit to the available data.

### Recruitment

The bootstrap distributions of recruitment abundance were plotted for the three samples (Fig. 3). Corresponding statistics (expected value, coefficient of variation, 90% confidence intervals, and skewness) are reported (Table 2). The frequency distribution of  $R$  was fitted by a normal curve in the case of data set 74-76 (K-S test,  $d = 0.0099$ ), while a lognormal distribution was more appropriate for data set VC89 (K-S test,  $d = 0.032$ ). Recruitment in Valle Fossa-Magnavacca (data set VFM89) was even more skewed than in Valle Campo but the K-S test for the lognormal function was not significant.

A randomization test revealed that the expected value of recruitment abundance in the mid 1970s (case 74-76) was larger than that attained at the end of the 1980s both in Valle Campo ( $P < 0.001$ ) and in Valle Fossa-Magnavacca ( $P < 0.001$ ). In terms of biomass, our recruitment estimate was 17.2 kg/ha for the mid 1970s, and 4.3 kg/ha for Valle Campo and 1.2 kg/ha for Valle Fossa-Magnavacca at the end of the 1980s. The differences between Valle Campo and Valle Fossa-Magnavacca seem to reflect the different stocking policies in the two lagoons (high stocking at Valle Campo, low stocking at Valle Fossa-Magnavacca).

### Yellow eel density

The calibration procedure allowed the estimation of the absolute density of yellow eels, which could not be inferred directly from samples. As expected, the mid 1970s were characterized by high density (3388 eels/ha, 149 kg/ha) and 1989 by low density (Valle Campo [VC89]: 597 eels/ha, 55 kg/ha, Valle Fossa-Magnavacca [VFM89]: 308 eels/ha, 65 kg/ha). In addition, the model produced detailed estimates of both abundance and biomass per sex, age, and size class. To summarize these features of the population, we have pooled age classes 2-6 yr in a juvenile age group and age classes 7-15 yr in a prereproductive age group (Table 3). As expected, elvers and juveniles were char-

TABLE 2. Main statistics of the 1000 bootstrap estimates of model parameters for each data set, describing population parameters of the European eel.

Data source		$b$	$c$	$\gamma_{MAX}^f$	$\lambda^f$	$\lambda^M$	$\eta^f$	$\eta^M$	$R$
Data set 74-76	EV	0.97	0.64	0.34	52.6	42.5	1.90	1.26	1806
	CV (%)	22	11	28	2	1	22	15	23
	CI	(0.68, 1.37)	(0.52, 0.75)	(0.21, 0.49)	(50.9, 54.4)	(42.2, 43.5)	(1.20, 2.58)	(0.96, 1.58)	(1132, 2496)
	SK	1.12	0.16	1.09	0.36	0.30	-0.07	0.05	0.07
Data set VC89	EV	0.66	0.43	0.33	63.3	39.4	4.1	2.97	306
	CV (%)	42	24	30	4	5	23	22	28
	CI	(0.18, 1.16)	(0.28, 0.61)	(0.18, 0.55)	(59.5, 67.8)	(36.9, 42.9)	(2.68, 5.68)	(2.06, 4.15)	(173, 404)
	SK	0.410	0.312	0.608	0.005	1.013	0.167	0.832	0.650
Data set VFM89	EV	1.06	0.32	0.14	59.2	40.5	2.01	3.1	106
	CV (%)	44	24	28	1	6	20	25	57
	CI	(0.26, 1.80)	(0.20, 0.46)	(0.08, 0.21)	(58.1, 60.6)	(37.2, 43.3)	(1.42, 2.70)	(2.13, 4.19)	(52, 203)
	SK	-0.11	0.24	0.17	0.03	1.013	0.74	0.832	2.00

Notes: Bias-adjusted expected value = EV, coefficient of variation = CV, bias corrected 90% confidence interval = CI, and standardized skewness = SK. Data set 74-76: eels sampled in the three lagoons in 1974-1976; VC89: eels sampled in Valle Campo in 1989; VFM89: eels sampled in Valle Fossa di Porto-Magnavacca in 1989. See Results for description of parameters.

acterized by high densities for 74-76 and low density for VFM89, with VC89 being intermediate. However, these marked differences were not found for prereproductive adults.

#### Survival

Estimates of age-specific annual survival were computed for the three data sets (Table 4). As the Weibull parameter  $c$  is  $<1$  for all data sets (Table 2), survival increased with age from  $\approx 30\%$  in elvers to 80-90% in the oldest animals. For each data set the expected elver (age 1) survival was significantly smaller than that of older animals. The same held true for juveniles aged 2 yr. A randomization test revealed that elver survival was roughly equal for all three data sets. On the other hand, for eels older than 1 yr estimates of survival in 1974-1976 were always smaller ( $P < 0.001$ ) than the same-age-class estimates in 1989 for both data sets (VC89, VFM89). Annual survivorship estimates in Valle Fossa-Magnavacca were always greater than in Valle Campo, but the differences were not significant.

#### Age and size at sexual maturity

Length-specific metamorphosis rates were computed for the three data sets (Fig. 4). The maximum rate of metamorphosis  $\gamma_{MAX}^f$  was significantly smaller for VFM89 than for 74-76 and VC89. A randomization test, performed on the bootstrap replicates of the metamorphosis curves, revealed that the fraction of females metamorphosing at some specific length can differ among data sets (Fig. 5). In particular,  $\gamma^f(l)$ , for both 74-76 and VC89, was larger than for VFM89 at any relevant length ( $>45$  cm), while positive differences between 74-76 and VC89 were significant between 48 and 60 cm, namely the range comprising all sexually mature females in 1974-1976. The shape of the metamorphosis curve affects the average length and age of the prereproductive yellow females; the mean age at sexual maturation, corresponding to parameter esti-

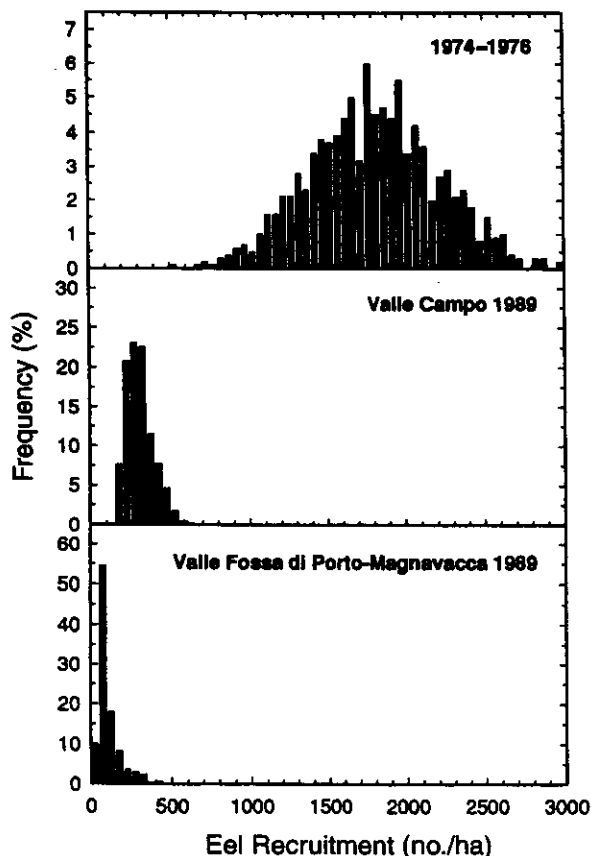


FIG. 3. Frequency distributions of European eel recruitment (no./ha) resulting from the 1000 pseudo-values obtained by bootstrapping the three data sets collected in the Comacchio lagoons during 1974-1976, at Valle Campo in 1989, and at Valle Fossa di Porto-Magnavacca in 1989, respectively.

TABLE 3. Estimates of absolute density of yellow eels (prereproductive stage) obtained by calibrating the model on each data set.

Age	Yellow eel density					
	74-76		VC89		VFM89	
	no./ha	kg/ha	no./ha	kg/ha	no./ha	kg/ha
Elvers (Age 1)	1806.2	17.21	306.4	4.27	105.7	1.17
Juveniles (Age 2-6)	1475.2	108.20	244.1	33.05	136.2	22.1
Prereproductive adults (Age 7-15)	107.0	24.03	47.2	17.58	66.3	41.21

Note: Data set 74-76: eels sampled in the three lagoons in 1974-1976; VC89: eels sampled in Valle Campo in 1989; VFM89: eels sampled in Valle Fossa di Porto-Magnavacca in 1989.

mates of Table 2, was 6.3 yr in 1974-1976, 7.3 yr in Valle Campo 1989, and 9.3 yr in Valle Fossa-Magnavacca 1989.

Estimation of the metamorphosis rate for males (Fig. 4) seems to be slightly more accurate in 1974-1976 than in 1989. The slope of the metamorphosis curve (inverse of parameter  $\eta$ ) was significantly lower in 1989. Hence, in 1989 males started metamorphosing to the silver stage at distinctly smaller sizes than in 1974-1976. In fact, Fig. 5 shows that  $\gamma^M(l)$ ,  $l < 42$  cm, was significantly smaller in 1974-1976 than in 1989.

#### DISCUSSION

The model fit the silver eel size distributions reasonably well, whereas it fit yellow eel distributions less well for all three data sets. This is not surprising. In fact, silver eels were randomly sampled in autumn catch, a time when the catch represents the whole sexually mature population. Conversely, data on yellow eels were affected by higher uncertainty due to the difficulty of collecting large samples over 10 000 ha.

TABLE 4. Annual survival resulting from the bootstrap distribution estimation procedure applied to each data set.

Age	Annual survival (% $\pm$ 1 SE)		
	74-76	VC89	VFM89
1	36.0 $\pm$ 4.8	30.3 $\pm$ 5.4	36.4 $\pm$ 6.3
2	56.9 $\pm$ 2.7	66.6 $\pm$ 5.2	77.6 $\pm$ 5.4
3	62.8 $\pm$ 3.0	73.7 $\pm$ 5.2	83.6 $\pm$ 4.5
4	66.2 $\pm$ 3.3	77.8 $\pm$ 5.2	86.7 $\pm$ 4.0
5	68.6 $\pm$ 3.5	80.4 $\pm$ 5.1	88.6 $\pm$ 3.6
6	70.4 $\pm$ 3.6	82.2 $\pm$ 5.0	89.9 $\pm$ 3.4
7	71.9 $\pm$ 3.7	83.6 $\pm$ 4.9	90.9 $\pm$ 3.2
8	73.1 $\pm$ 3.8	84.7 $\pm$ 4.8	91.7 $\pm$ 3.0
9	74.1 $\pm$ 3.9	85.7 $\pm$ 4.7	92.3 $\pm$ 2.8
10	74.9 $\pm$ 3.9	86.4 $\pm$ 4.6	92.8 $\pm$ 2.7
11	75.7 $\pm$ 4.0	87.2 $\pm$ 4.5	93.3 $\pm$ 2.6
12	76.4 $\pm$ 4.0	87.9 $\pm$ 4.4	93.6 $\pm$ 2.5
13	77.0 $\pm$ 4.0	88.0 $\pm$ 4.4	94.0 $\pm$ 2.4
14	77.5 $\pm$ 4.0	88.0 $\pm$ 4.4	94.2 $\pm$ 2.3
15	78.0 $\pm$ 4.0	88.0 $\pm$ 4.4	94.5 $\pm$ 2.2

Note: Data set 74-76: eels sampled in the three lagoons in 1974-1976; VC89: eels sampled in Valle Campo in 1989; VFM89: eels sampled in Valle Fossa di Porto-Magnavacca in 1989.

Moreover, trawl and fyke net catches may be affected by eel activity, which is influenced by water temperature, wind, atmospheric pressure, cloud coverage, moon phases, and other factors (Vøllestad 1986b). Despite these caveats, overall model performance seems reasonably good, allowing us to analyze those factors that contribute to eel demography.

First, net natural recruitment has declined to a scant kilogram per hectare in the last 10-15 yr. Large-scale, long-term fluctuations arising from regulation mechanisms, independent of the local phenomena occurring in Comacchio, cannot be ruled out (Tesch 1977, Carrieri 1982). Yet, strong evidence exists that natural recruitment from sea to lagoons was affected seriously by past management in Comacchio lagoons. First, canals connecting the sea to the lagoons have not been dredged for years. Therefore, silting and clogging hampered the natural recruitment of elvers from the Adriatic Sea. Second, during 1978 through 1982, a regional law allowed fishermen to catch elvers by using huge square nets directly in the canals. Artificial stocking, which was mainly practiced in Valle Campo, only partially counteracted the decline in natural recruitment.

Coincident with this decline, the shape of recruitment distribution has changed during 1974 through 1989, displaying an increasing skewness. If we assume that the variance of  $R$  partially derives from actual recruitment variability rather than just from uncertainty in parameter estimation, our findings are basically in accordance with other empirical observations (Allen 1973, Hennemuth et al. 1980, Garrod 1983) and with theoretical arguments (Ricker 1954, Armstrong and Shelton 1988, Fogarty et al. 1991). Low recruitment abundance implies a low degree of independence among individuals which results in highly skewed log-normal-like distributions; conversely, high abundance promotes independence and, consequently, symmetric, normal distributions (Shelton 1992).

Declining recruitment during 1974 through 1989 was the main factor accounting for the decline of both yellow and silver eel abundance in the Comacchio lagoons. Samples in the Valli di Comacchio in 1974-1976 and in 1989 are therefore representative of three

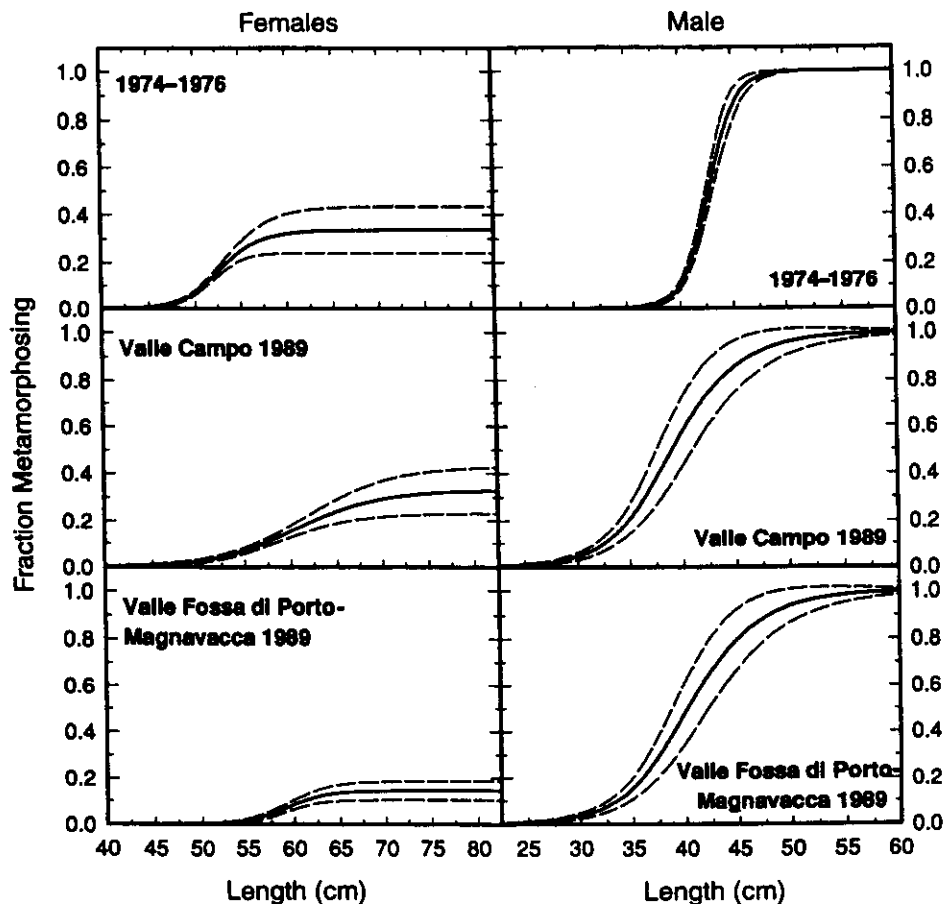


FIG. 4. Expected length-specific metamorphosis rate ( $\pm 1$  SE) for female and male eels resulting from the bootstrap distribution of model parameters for the three data sets collected in the Comacchio lagoons in 1974–1976, at Valle Campo in 1989, and at Valle Fossa di Porto-Magnavacca in 1989, respectively.

different density conditions: (1) a high-density population with no stocked fish (data set 74–76); (2) a low-density population with high elver restocking (VC89), and (3) a low density population with low elver stocking (VFM89). Our results point out significant differences among the vital rates corresponding to these three situations. Whether these differences can be actually ascribed to density dependence is difficult to say. Below, we analyze different components of eel life history and suggest mechanisms that may explain observed patterns.

#### Survival and body growth

Survival of juveniles and prereproductive adults increased during 1974–1976 to 1989, as eel density decreased, in contrast to claims that eel survival in the Valli di Comacchio has not changed in the last 15 yr (Rossi et al. 1987/1988). Even though our model did not include any explicit relationship between survival and food availability, the simultaneous reduction of mortality and fish density may be interpreted as evidence of reduced competition for resources and space.

Eels strongly compete for food and space (Tesch 1977), with dominant individuals growing faster and submissive ones likely incurring higher mortality. Because the prey-size spectrum is incredibly large, food choice shows a marked correlation with body size, with smallest eels (up to 20–30 cm) eating mainly insect larvae, intermediate eels eating snails, mussels, and crustaceans (in particular *Crangon crangon* and *Palaemon* sp., Rossi et al. 1987/1988) and larger eels (>50–60 cm) feeding preferentially on fish (in particular *Atherina boyeri*, *Aphanius fasciatus*, *Polatoschiustus* sp., Rossi et al. 1987/1988). Clearly, fish meals are not advantageous to small eels. However, Tesch (1977) observed that if strong competition for food reduces the abundance of insect larvae and small crustaceans, smaller eels begin to eat fish; when this occurs, reduced body growth can be expected. Accordingly, analysis of eel stomach contents in the Comacchio lagoons (Rossi et al. 1987/1988) showed that in the 1970s, when eel density was high, diet was indeed dependent on fish, while in the 1980s, when density was low, eels mainly foraged on crustaceans. The shift in diet during the

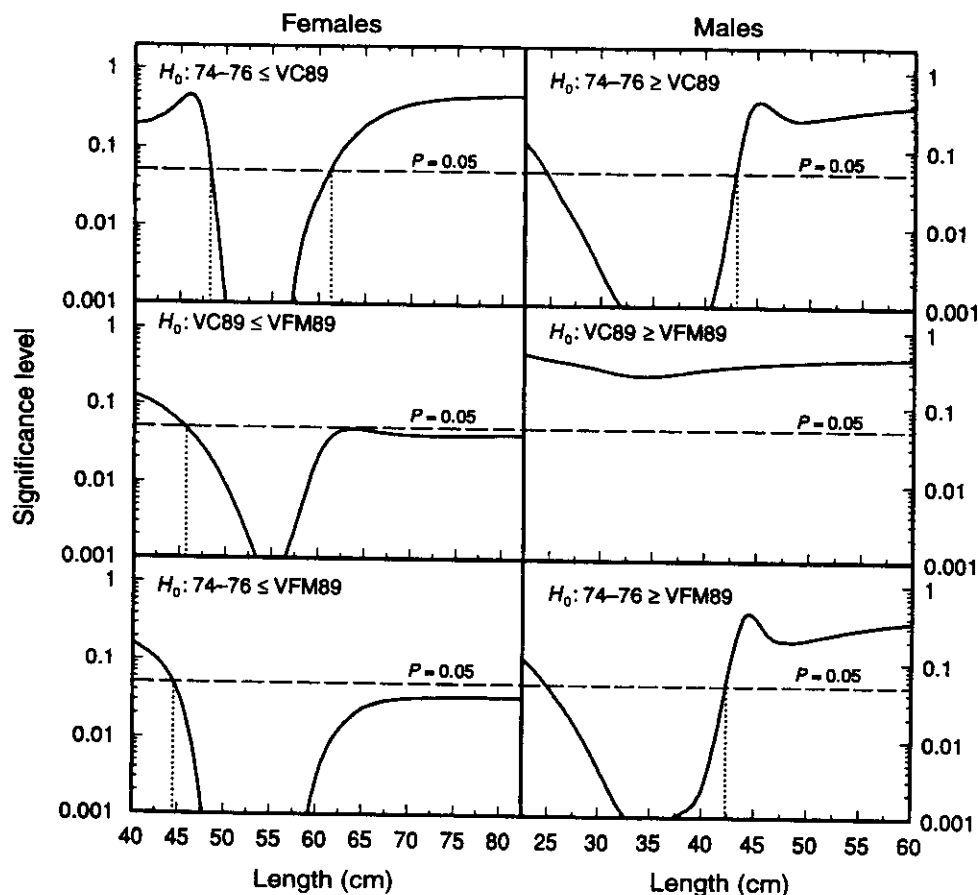


FIG. 5. Results of a randomization test on the difference of the expected values of length-specific metamorphosis rates in the three data sets collected in the Comacchio lagoons during 1974–1976, at Valle Campo in 1989, and at Valle Fossa di Porto-Magnavacca in 1989, respectively. The solid line indicates the significance level  $P$  of the null hypothesis  $H_0$  at any length. Whenever the solid line is below the dashed line,  $H_0$  is rejected.

studied period has been paralleled by a corresponding change in body size, as previously observed by Tesch (1977) in other sites; our data indicate that in the 1974–1976 high-density population, when diet was largely based on fish, the average eel size was smaller than in the 1989 low-density population. Thus, our data suggest that competition for food may actually apply, although other environmental factors accounting for the observed trends cannot be ruled out.

For elvers, survival did not change during 1974–1989. Density dependence in the early stages of continental life has been commonly observed in many fish populations and in the specific case of the European eel (Vøllestad and Jonsson 1988). Whether a 10-fold variation in recruitment density may or may not affect elver survival through food limitation is a matter of debate. Conceivably, environmental changes may have overridden any density dependence as primary productivity increased in the Comacchio lagoons between 1975 and 1989. Dissolved and suspended nutrients (nitrites, nitrates, and phosphates) approximately tripled (Regione Emilia Romagna 1984) and phytoplankton

(mainly diatoms), which was scarce in 1970 (Boni and Somma 1970) and 1974 (Cognetti et al. 1975), increased rapidly at the end of the 1970s with chlorophyll  $a > 150 \text{ mg/m}^3$  in the spring–summer season. Ensuing anoxia may have negatively influenced elvers in particular, as the oxygen requirement is higher for young, fast-growing eels than for adults.

#### Sex ratio and sexual maturation

For all data sets, sex ratios were skewed towards females, in agreement with observations on other eel populations (Frost 1945, 1950, Vøllestad and Jonsson 1986). However, the fraction of females was highly variable in Comacchio, ranging from 69% in 1974–1976 to 96% for VFM89. Sex determination is certainly metagamic, that is, sex is established by environmental and/or ecological factors (Sola et al. 1980, Wiberg 1983). The fraction of females increases with decreasing densities in our model, which agrees with other observations both in intensive rearing ponds and in natural environments (Colombo and Rossi 1978, Vøllestad and Jonsson 1986). As decreasing density is ac-

accompanied by variation in body growth, the effect of density on sex determination could be indirect; namely, faster growing eels would become female and slower growing eels would become male (Parsons et al. 1977). However, this mechanism could not explain the high fraction of males (70–90%) usually observed in intensive rearing ponds (Egusa and Hirose 1973, Egusa 1979), where males kept at very high density reach growth rates comparable to those of females in natural environments.

Metamorphosis curves of males and females have changed during 1974–1989. In both sexes a minimum size at maturity is needed to cope with the stress of migration to the spawning area (eels do not feed after metamorphosis) and the development of sexual products. The life schedules of females and males differ, as females metamorphose at older ages and larger sizes than males. Males invest much less energy in gonadal maturation than females, the gonad mass of mature males rarely reaching 15% of their body mass, whereas females attain ~60% (Boëtius and Boëtius 1967, 1980, Larsson et al. 1990). The current hypothesis is that a smaller energy requirement and the absence of size-dependent mate selection by females (Vøllestad and Jonsson 1986) may allow males to use a time-minimizing strategy, as concluded by Vøllestad (1992) for the European eel and by Helfman et al. (1987) for the closely related American eel. According to these authors, males will metamorphose as soon as they reach the minimum length that guarantees a successful migration, because any further delay simply increases the probability of dying while waiting. However, our results show that the average length of silver males was not constant during 1974–1989; silver males were distinctly larger in 1974–1976 than in 1989 when fish density was lower. Moreover, in 1974–1976 their size distribution partially overlapped that of silver females, while in 1989 the smaller females were always larger than the larger males. Therefore the time-minimizing strategy proposed by Vøllestad (1992) cannot fully explain our data on silver males.

For females, we find that the eel density decline was paralleled by both an increase in length at metamorphosis and a decrease in the maximum rate of metamorphosis. Thus, females, though growing faster, required more time to mature at low density than at high density. Variation of metamorphosis rates in the three data sets may be ascribed to a trade-off between reproduction and survival (Stearns 1992); Vøllestad and Jonsson (1986) point out that even a small increase in length may result in a substantial gain in reproductive output, because gonad mass and fecundity increase exponentially with eel size (Wenner and Musick 1974). Therefore, females would feed in the lagoons up to an optimal age of sexual maturity, at which an increase in fecundity as a result of increase in body size is no longer sufficient to compensate for the decline in survival caused by waiting another year (Roff 1982, Jons-

son et al. 1984). If the reproductive gain obtained by postponing reproduction is low compared with the chance of dying, reproduction should occur as early as possible. Indeed, our results show that in 1974–1976, a period characterized by high density, high mortality, and slow growth, females metamorphose to the silver stage as soon as they reach a minimum length that guarantees successful migration and reproduction. On the contrary, our results for Valle Fossa-Magnavacca in 1989 suggest that very low eel density, high growth, and high survival are associated with protracted pre-reproductive stage and large size at metamorphosis.

#### CONCLUSION

We have analyzed the life history of European eels under three density regimes, pointing out significant differences among the estimated vital rates. Although we suggest that density-dependent mechanisms explain the observed trends, we cannot provide unequivocal evidence that these factors drive eel population dynamics. With our modeling approach we have estimated vital rates that are not directly measurable. In turn, relevant comparisons among data sets are possible by jointly using a rather unconventional model of fish demography and modern, time-consuming, nonparametric statistics. Although the model has been developed for eel populations, our procedure is sufficiently flexible to be easily extended to other fish populations in which recruitment is independent of parental stock. In our opinion, increasing availability of inexpensive computing will render this and similar approaches more common.

Our eel model is not exempt from weaknesses. Variable environmental factors surely affect the population dynamics of this catadromous fish, but, unfortunately, their influence on eel demography is poorly documented. We are thus aware that the weakest assumption of our application is the time invariance of model parameters within each of our three periods, particularly the assumption of constant recruitment. However, the available data did not allow for a more realistic assumption. Future field studies will be more valuable if they attempt to determine the size structure through a time period comparable to the average life-span of the European eel. Further, a possible relationship among density, food abundance, and components of eel life history should be explicitly tested by means of suitable field experiments. Despite these reservations, we believe that our approach, which makes joint use of age- and size-structured demography, modern nonparametric statistics, and the availability of cheap computing, represents a nontraditional way for making detailed comparisons among different data sets of a fish population.

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