

**"Fifth Course on Mathematical Ecology
including and introduction to Ecological Economics"**

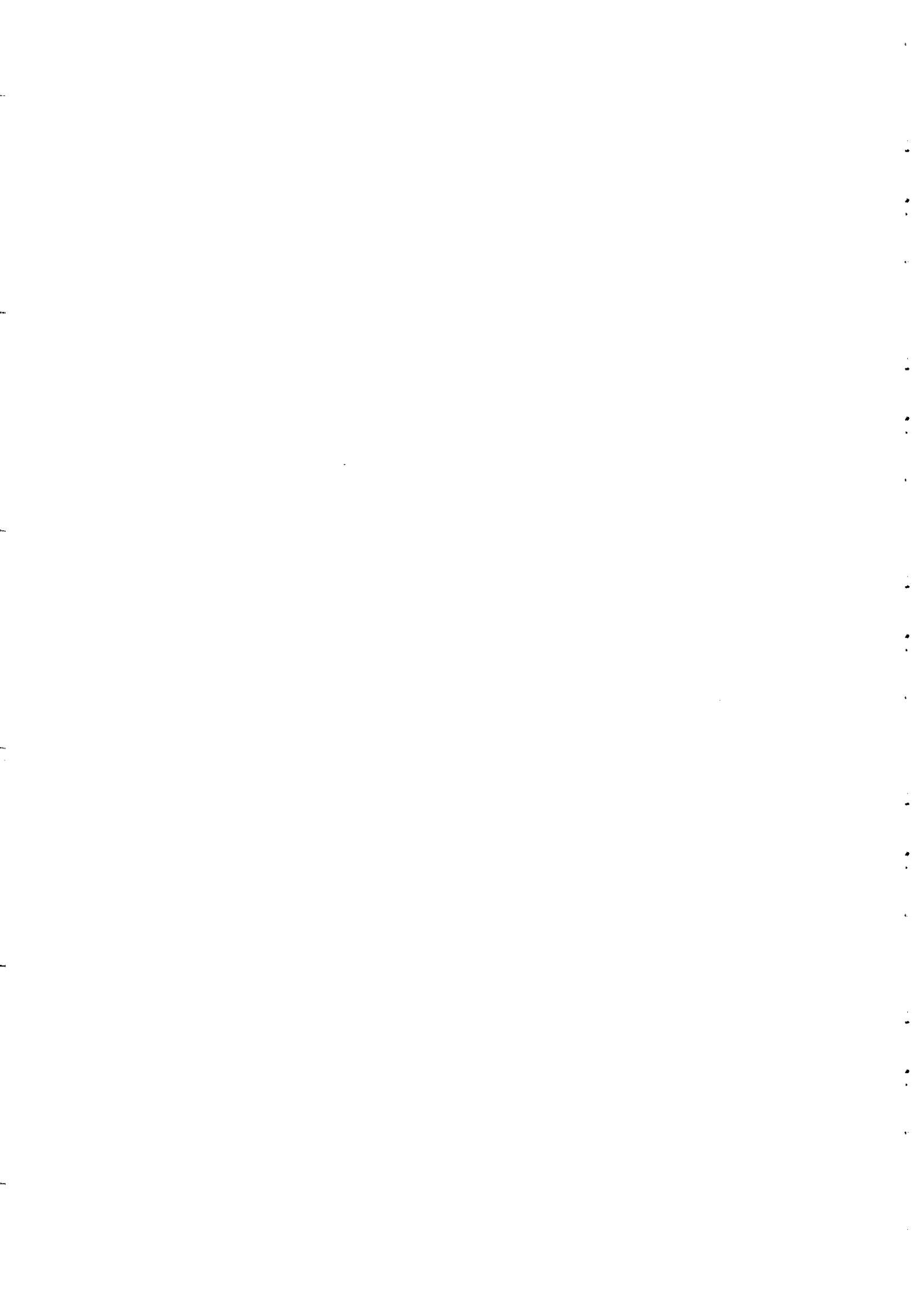
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**A SIZE AND AGE-STRUCTURED MODEL OF THE EUROPEAN EEL
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A size and age-structured model of the European eel (*Anguilla anguilla* L.)

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Abstract: The life cycle of the European eel (*Anguilla anguilla*) presents several distinctive features, such as high plasticity in body growth, marked sexual dimorphism, sex ratio strongly skewed in favor of females and sexual maturation largely dependent upon the size of individuals. A demographic model incorporating all these characteristics is derived on the basis of a multiple classification of individuals by age and size, and variability in individual growth is explicitly included. Existing theory for size-structured stocks is extended to include the dependence of sexual maturation on size, while natural mortality is age specific. Using 1989 population data from Comacchio lagoons (Italy), we estimate mortality and metamorphosis rate and abundance in each age- and size-class for both yellow and silver eels, crucial information for the management of the Comacchio fishery. The use of a nonparametric technique (bootstrapping) yields not only the moments, but also the distributions of these estimates. Validation of the model is performed on the data collected in 1990. The approach adopted is very flexible and different assumptions about survival, sexual maturation, and net selectivity can be easily incorporated in the model.

Résumé : Le cycle vital de l'anguille européenne (*Anguilla anguilla*) présente plusieurs caractéristiques particulières, notamment une croissance corporelle très plastique, un dimorphisme sexuel marqué, un rapport des sexes qui penche fortement en faveur des femelles et enfin une maturation sexuelle qui dépend étroitement de la taille des individus. Nous avons construit un modèle démographique intégrant toutes ces caractéristiques, à partir d'une classification multiple des individus par âge et par taille, et nous tenons compte de façon explicite de la variabilité dans la croissance individuelle. Nous élargissons la base théorique concernant les stocks à structure de taille pour y faire entrer la dépendance de la maturation sexuelle à l'égard de la taille, tandis que la mortalité naturelle est spécifique à l'âge. À partir de données démographiques recueillies en 1989 dans les lagunes de Comacchio (Italie), nous estimons le taux de mortalité et de métamorphose ainsi que l'abondance dans chaque classe d'âge et de taille, pour les anguilles jaunes et argentées, information qui est cruciale pour la gestion de la pêche de Comacchio. L'emploi d'une technique non paramétrique (amorçage) donne non seulement les moments, mais aussi les distributions de ces estimations. Nous avons validé le modèle avec les données recueillies en 1990. L'approche adoptée est très souple, et il est facile d'intégrer au modèle différentes hypothèses sur la survie, la maturation sexuelle et la sélectivité des filets.

[Traduit par la Rédaction]

Introduction

The most commonly used physiological determinant in structured population models is chronological age. Since their introduction by Leslie (1945), "projection matrices" have been widely used by demographers to describe the dynamics of age-structured populations, primarily because they are relatively easy to construct, analyze, and implement

on computers. More recently it has been shown that the use of matrix population models is not restricted to age-structured populations, but can also be applied to those populations whose life cycle is better described in terms of developmental stages or size-classes, rather than age-classes (Lefkovich 1965; Caswell 1989). In many species the ecological consequences of size on vital parameters (e.g., survivorship, fecundity, sexual maturity) are more important than those due to age. The influence of size is particularly important in organisms with high plasticity in body growth. As Caswell states (1986), size dependence per se does not violate the assumption of classical demography: "if size is closely related to age, then a simple mathematical transformation can express size-dependent vital rates as a function of age." But in many species, variability in growth rate makes age a very poor predictor of size. In these cases models of population dynamics should explicitly include reference to size.

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Kirkpatrick (1984) derived a theory for a size-structured fish stock with variable growth rate and size-dependent mortality. In his paper it is shown how the inclusion of variability in individual growth rate can immensely complicate the construction and the analysis of demographic models. For this reason, size dependence is often ignored in practice, although an extensive literature is now available on the subject (Fournier and Doonan 1987; Schnute 1987; Deriso and Parma 1988; Schnute et al. 1989a, 1989b).

Here we present a model of the dynamics of European eel (*Anguilla anguilla*) populations. The interest of this study arises from the fact that the life cycle of this catadromous fish is characterized by several distinctive features, such as a marked sexual dimorphism, a sex ratio strongly skewed in favor of females, high plasticity in body growth, commercial exploitation mainly focused on sexually mature eels, and a recruitment of young eels from the sea that is independent of the phenomena occurring in the lagoon environment where the eel spends the adult, prereproductive stage of its life cycle. As a consequence, few studies on population dynamics of the European eel are available (Gatto and Rossi 1979; Vøllestad and Jonsson 1986). In this paper, we focus on the eel populations of the Valli di Comacchio lagoons (northern Italy). This particular case study is used as a practical testing ground in which a hybrid model is derived on the basis of a multiple classification of individuals by age and size. Schnute's (1987) theory is extended to include the dependence of sexual maturation on size, while natural mortality is age specific, as in classical demography. The basis of our formulation is the subdivision of the population into distinct cohorts of individuals. Each cohort is characterized by a continuous distribution of the individuals over a whole range of sizes, this being a feature shared with more complex continuous-time physiologically structured models (Sinko and Streifer 1967; Metz et al. 1986; Banks et al. 1988, 1991). A set of recursive equations specifies, on a discrete-time basis, the demographic fate of the individuals in a cohort according to their age and size distribution. In this sense, the model is somewhat 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. Indeed, the model can include a great number of physiological traits that influence reproductive and survival success. Despite the great flexibility in treating a variety of factors involved in the development process of a cohort, from a computational point of view, our formulation is only slightly more complicated than the classical matrix formulation.

In the following, we first review some basic facts about eel biology and the fishing activities that take place at Comacchio, and describe the available data (1989 and 1990). Second, we derive a structured population model through the definition of both population variables and submodels describing body growth, sexual maturation, and survivorship. Third, we illustrate the techniques used to estimate unknown parameters from the 1989 data. Estimation is performed by using an optimization algorithm and nonparametric statistics (bootstrapping). Last, we validate the demographic model using the 1990 data.

Available data for the Comacchio eel fishery

The Valli di Comacchio are three shallow lagoons located in northern Italy (Fig. 1). The overall area is about 10 000 h and mean depth about 1 m; salinity ranges between 20 and 35‰ and water temperature fluctuates between 0 and 30°C during the year. Fishery production of the Valli is based on the natural immigration of many euryhaline species (*Dicentrarchus labrax*, *Sparus aurata*, *Liza saliens*, *Zosterisessor ophiocephalus*, *Platichthys flesus*, *Atherina boyeri*). The European eel, however, constitutes the main yield of Comacchio lagoons, with up to 90% of the annual catch by weight.

After metamorphosis from the glass stage (Tesch 1977), the young eels (elvers) enter the lagoons through sluice gates in late spring and remain in this environment for a variable number of years as yellow eels. Here they feed and grow until they metamorphose into silver eels whereupon the animals migrate to the ocean for spawning. During migration, which occurs mostly between October and December, all silver eels are caught at sluice gates by means of devices called lavorieri, a series of V-shaped screens. The yield of the Valli is, therefore, represented by silver eels; yellow eels are only incidentally caught at the lavorieri. Harvested eel biomass has been recorded since 1781: the average yield was more than 14 kg/ha per year until the mid-1970s, but since then it has declined to much lower figures (mean catch from 1977 to 1991 was ca. 6.15 kg/ha; Table 1). The causes of this decline are various. Between 1978 and 1982 the regional government permitted fishing in the canals that connect the lagoons to the sea during the spring, which is the period of elver recruitment. Other likely causes are insufficient dredging of the same canals and declining water quality resulting from organic pollution.

The Valli di Comacchio lagoons have been extensively studied over the past 20 years (Colombo 1972a, 1972b; Rossi and Colombo 1976a, 1976b, 1979; Rossi 1979; Gatto and Rossi 1979; Gatto et al. 1982; Rossi et al. 1986, 1987-1988, 1988; Rossi and Franzoi 1991). The present study is based on sampling carried out by researchers of the Dipartimento di Biologia Evolutiva, University of Ferrara, Ferrara, Italy, between the spring of 1989 and the fall of 1990 (Carrieri et al. 1992), as briefly described below.

The sampling scheme for silver eels takes advantage of the traditional management of the Comacchio fishery. The daily catch is usually held in special tanks kept in water, so that eels can stay alive for several days and sold when the market price reaches its peak. A tank can hold up to 1200-1400 kg, which usually corresponds to a few fishing days. As each tank is weighed, the actual weight of the total autumn catch is known. A number of tanks from different fishing periods were randomly selected for each of the three lagoons and about 50-150 kg of fish were randomly extracted from each selected tank. For each tank, the extracted eels were stratified according to broad size-classes (usually four: (1) <200 g, (2) 200-450 g, (3) 450-650 g, (4) >650 g; see Carrieri et al. 1992 for further details). The strata correspond to different market prices, the price per kilogram being an increasing function of eel size.

A subsample of at least 30–40 specimens was randomly extracted from each stratum, and then each animal was weighed (± 5 g) and measured (± 5 mm). Stratum-specific weighting factors were computed for each selected tank as the ratio of the biomass (kilograms) in the stratum to the biomass of the corresponding subsample. Two further sets of weighting factors were derived on the basis of the actual catch in different fishing periods within each lagoon and of the overall catch in the three lagoons. Frequency distributions of size were finally obtained by multiplying the eel counts in each size-class by the appropriate weighting factors and then summing across all the fishing periods and lagoons. In 1989, 970 silver eels (486 kg) were extracted according to the scheme described above from 7172 kg taken from the autumn catch at the lavorieri (66 900 kg). The following year, 523 silver eels (284 kg) were extracted from 5603 kg taken from the autumn catch (65 000 kg).

As yellow eels are not commercially fished, 2869 specimens (729 kg) were caught in fyke nets (8-mm mesh size) in the spring of 1989 and a stratified random sample of 791 individuals (175 kg) was extracted. In the spring of 1990, 840 yellow eels (318 kg) were extracted from a 1424 kg sample (Carrieri et al. 1992). Stratification was similar to that for silver eels. The main difference is that the total silver eel population from each lagoon is known, because all of these fish are trapped in the lavorieri, while this is not true for yellows that are not commercially fished. Therefore, the size distribution of yellows was derived by using a set of stratum-specific weighting factors, as for silver eels, and a set of weighting factors proportional to the average catch in fyke nets per day and the area of the three lagoons.

The size structure for yellow and silver eels in 1989 and 1990 is shown in Fig. 2. It should be noted that the size structure of silver eels has a marked bimodal shape (Fig. 2b), the smallest silver females being always larger than the largest silver males. Therefore, the fraction of silver females can be easily computed from the normalized size frequency distribution as the histogram area corresponding to typical female sizes (>45 cm). The sex ratio of juvenile yellow eels was derived by inspecting the gonads in a random sample of 57 elvers caught in spring 1989 (M:F = 3:54). Sex was not determined for older yellows and juvenile sex ratio cannot be plainly extended to older age-classes. Age was determined by otolith examination of, respectively, 59 males and 437 females, both yellow and silver, caught between spring 1989 and autumn 1990. It should be noted that age is counted from the date of metamorphosis from the glass to the elver stage. Accordingly, eels sampled in late spring are referred to as being x years old if they have been growing in the yellow stage for x years ($x = 0, 1, 2, \dots$), whereas x^+ refers to eels caught about 6 months later in the commercial fishery. Total length (l ; centimetres) to weight (w ; grams) relationships (Table 2) have been computed for both yellow and silver eels. Age-length data are shown in Fig. 3.

In deriving a model of eel population dynamics the following features are taken into account. (i) There is a marked sexual dimorphism; females are always larger than males

Fig. 1. Map of the study area showing the Valli di Comacchio lagoons.

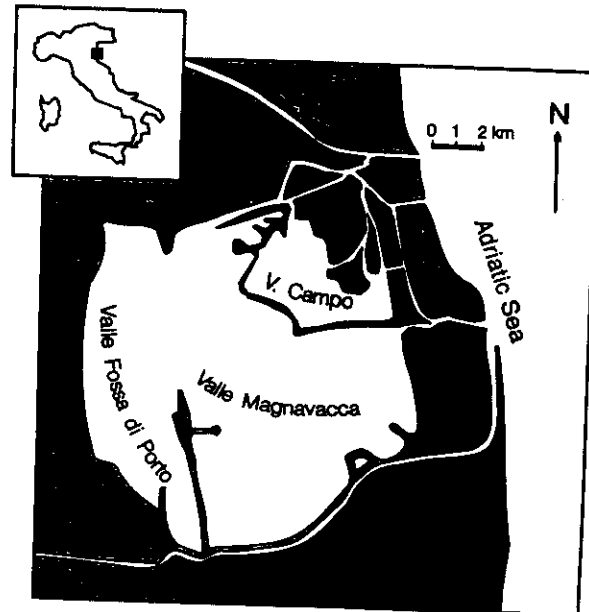
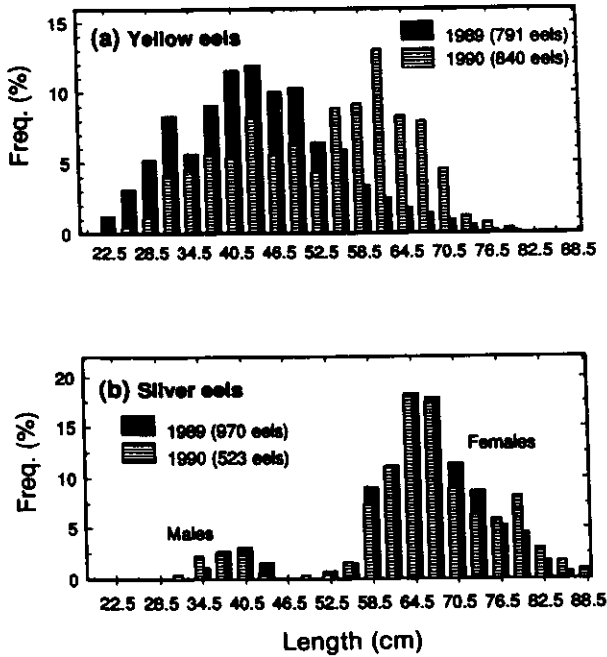


Table 1. Commercial catch of silver eels in the Comacchio lagoon from 1972 to 1991.

Year	Catch (kg)
1972	105 200
1973	156 500
1974	205 400
1975	143 000
1976	116 200
1977	80 200
1978	70 800
1979	66 100
1980	65 000
1981	45 900
1982	43 500
1983	64 600
1984	58 400
1985	35 300
1986	46 000
1987	88 400
1988	87 200
1989	66 900
1990	65 000
1991	39 300

at all ages. (ii) The sex ratio is skewed in favor of females that comprise 90% of eels sampled at the silver stage and roughly 95% of eels at the yellow stage. (iii) Growth is extremely variable among individuals (Rossi and Colombo 1976b), with the size of eels of the same age being scattered over very wide intervals (Fig. 3). (iv) A fraction of

Fig. 2. (a) Size structure of yellow eels resulting from sampling program in spring 1989 and in spring 1990. (b) Size structure of silver eels resulting from sampling the 1989 autumn catch and the 1990 autumn catch.



the female population seems to never reach sexual maturity. In fact, some old yellow specimens (>8–9 years) remain in the lagoons, as shown in several samples collected in 1976 (Rossi 1979; Gatto and Rossi 1979), in 1982–1984 (Rossi et al. 1987–1988), 1989, and 1990 (Carrieri et al. 1992). In contrast, all yellow males are likely to undergo metamorphosis within 4–7 years. (v) The age at metamorphosis is not fixed (Rossi and Colombo 1976a). With respect to the last point, it has been observed that slow-growing eels (both males and females) undergo metamorphosis at older ages, while fast-growing eels reach sexual maturity at younger ages. The emerging evidence (Vøllestad and Jonsson 1986; Vøllestad 1992) suggests that transformation from yellow to silver eels is largely dependent upon body size.

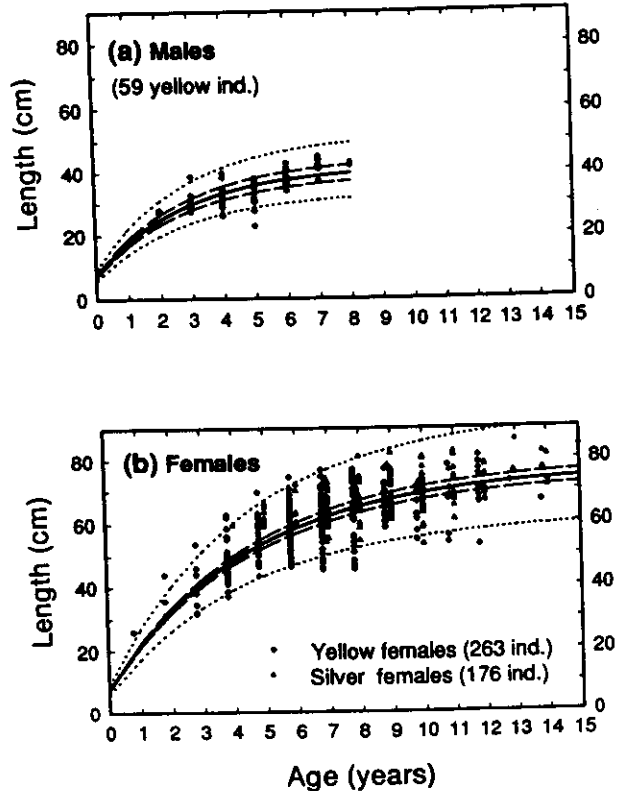
The model

The model derived here relies on the conceptual scheme in Fig. 4. It should be noted that the portion of the eel life cycle that is spent outside the lagoons, i.e., the larval and glass stages (Tesch, 1977), is disregarded, because the recruitment of elvers from the sea is independent of the local phenomena occurring in the lagoons. Attention is focused on population dynamics from the elver stage on.

Population variables

Let l be the size of newly recruited individuals (age x_0) in year t . We suppose it is a random variable with (known) probability density $r(l)$. From now on, size will be assumed

Fig. 3. Age (years) – length (cm) data for (a) 59 yellow males and (b) 439 females (263 yellow + 176 silver). Estimated Von Bertalanffy growth curves (thick line) are plotted along with the 95% confidence intervals (broken lines) and 95% prediction intervals (dotted lines). See Table 3 for regression statistics.



to be length, although a variety of other size indicators such as weight could be used. Therefore, the integral:

$$\int_{l_1}^{l_2} r(l) dl$$

gives the probability of an elver being of a size between l_1 and l_2 ($l_1 < l_2$). If $R(t)$ is the overall number of newly recruited individuals in year t , the expected density $Y(x_0, l, t)$ with respect to l of elvers at time t is given by:

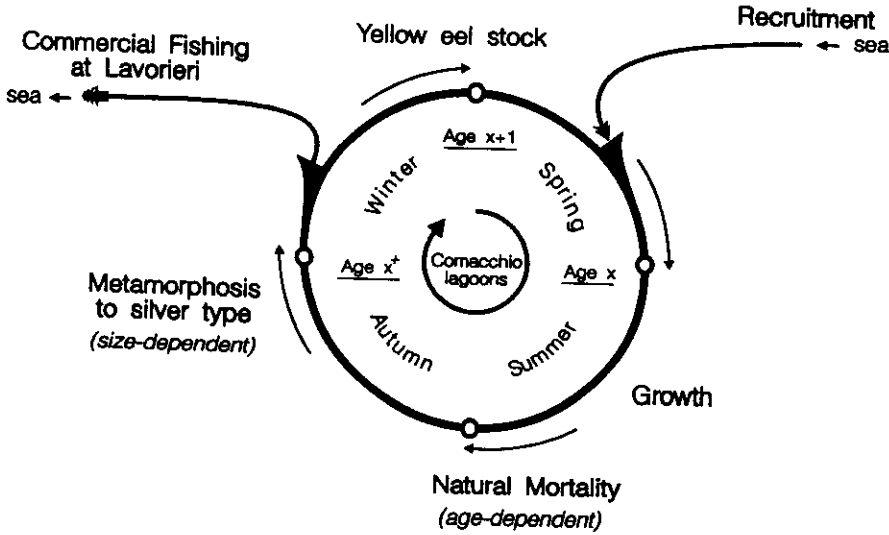
$$Y(x_0, l, t) = R(t)r(l)$$

The size structure of a cohort changes in time as a consequence of growth, survival, and maturation processes. The population variable $y(x, l, t)$ will be used to denote the joint probability density for a yellow eel to be of size l at age x and time t . Unlike r , y is a joint probability function, i.e., the probability that an elver, recruited in year $t - x$, remains in the yellow compartment x years after the transformation from the glass to elver stage and reaches length l . In fact, eels eventually leave the yellow compartment, because either they die (mainly as a consequence of anoxic conditions in summer) or they metamorphose to the silver stage (in autumn).

Table 2. The estimated length (cm) – weight (g) logarithmic relationship, obtained from 579 yellow eels and 669 silver eels, respectively.

	Equation	R ²	F	df	P
Yellow eels (males + females + eivers)	$\ln(w) = 3.37\ln(l) - 7.95$	0.97	21 475	577	<0.001
Silver eels (males + females)	$\ln(w) = 3.18\ln(l) - 7.07$	0.92	8 009	667	<0.001

Fig. 4. Schematic representation of the eel life cycle in the Comacchio lagoons.



The expected density $Y(x, l, t)$, with respect to l , of x -year-old yellow eels at time t is thus given by

$$Y(x, l, t) = R(t - x)y(x, l, t)$$

where $R(t - x)$ is the recruitment at time $t - x$. Therefore, if l_{max} is the maximum length and x_{max} the maximum age, then

$$[1] \quad \Theta(x, t) = \int_0^{l_{max}} R(t - x)y(x, l, t) dl$$

represents the total number of yellows of age x at time t , while

$$[2] \quad \Psi(t) = \sum_{x=x_0}^{x_{max}} \left[\int_0^{l_{max}} R(t - x)y(x, l, t) dl \right]$$

is the total number of yellow eels in the lagoons at time t .

The population variables $s(x, l, t)$ and $S(x, l, t)$ are defined for silver eels by analogy to $y(x, l, t)$ and $Y(x, l, t)$. A variety of parameters can be derived from these population variables. By using the weight-length relationship $w(l)$ (Table 2), it is possible to compute the total biomass of yellow eels at any given age x and time t

$$[3] \quad \int_0^{l_{max}} w_Y(l)R(t - x)y(x, l, t) dl$$

and the overall biomass of silver eels (which coincides with the total catch in the Valli di Comacchio):

$$[4] \quad \sum_{x=x_0}^{x_{max}} \left\{ \int_0^{l_{max}} w_S(l)R(t - x)s(x, l, t) dl \right\}$$

The length structure of both yellow and silver eels can be easily derived from the length structures of the corresponding age-classes and, therefore, the frequency distribution of sizes in year t is simply given by

$$[5a] \quad \pi_l^Y(t) = \frac{\sum_{x=0}^{x_{max}} Y(x, l, t)}{\int_0^{l_{max}} \left[\sum_{x=0}^{x_{max}} Y(x, l, t) \right] dl}$$

$$[5b] \quad \pi_l^S(t) = \frac{\sum_{x=0}^{x_{max}} S(x, l, t)}{\int_0^{l_{max}} \left[\sum_{x=0}^{x_{max}} S(x, l, t) \right] dl}$$

Body growth

To describe age-length data, the Von Bertalanffy growth model has been chosen, among the models listed in Schnute (1981) and Seber and Wild (1989), because it seems to yield the best fit to our data. It is given by

$$[6] \quad L(x) = L_{\infty} - (L_{\infty} - L_0)e^{-kx}$$

Table 3. Results of the age (years) – length (cm) nonlinear logarithmic regression (Von Bertalanffy growth model with a multiplicative error) performed on 59 males and 437 females.

	L_{∞}	k [years ⁻¹]	$\sigma^2_{\ln(g)}$	R^2	df
Males	41.8±2.3	0.35±0.056	0.120	0.901	57
Females	76.2±1.4	0.23±0.010	0.116	0.938	435

Note: The equation was $\ln\{L(x)\} = \ln\{L_{\infty}(1 - e^{-kx}) + L_0 e^{-kx}\} + \ln(g)$.

where k [t^{-1}] is a measure of growth rate, L_{∞} is the maximum reachable length and L_0 is the length of elvers at age 0. As a matter of fact, Eq. 6, being deterministic, is actually a poor descriptor of the age-length data, because eel growth rate is extremely variable among individuals (see Fig. 3). Therefore, some degree of variability should be added to Eq. 6. Kirkpatrick (1984) gives an extensive overview of stochastic body-size growth models. For our purposes it is sufficient to recall that the observed variability may be treated as the expression of genetic differences among individuals, and that these differences are already set at the metamorphosis from the glass to the elver stage (Kirkpatrick refers to this approach as the assignment at birth model). Growth trajectories of eels are, thus, completely determined for the rest of their life. Formally, the actual length $l(x)$ of an individual at age x can be computed:

$$[7] \quad l(x) = L(x)g$$

where $L(x)$ is the expected length at age x given by Eq. 6 and g a growth factor randomly assigned to each eel according to some distribution function. A lognormal distribution of size of individuals within a cohort works well in most cases and is more appropriate than the normality assumption because the latter implies individuals with negative size (as suggested by Kirkpatrick (1984), it should be applied only when the length variance is small relative to the mean).

By definition, g has a unitary geometric mean, while its variance σ_g^2 must be estimated from age-length data. If a logarithmic transformation of Eq. 7 is performed, one obtains

$$[8] \quad \ln(l(x)) = \ln(L(x)) + \ln(g), \quad \ln(g) \sim N(0, \sigma_{\ln(g)}^2)$$

In our case, L_0 has been assumed to be 75 mm, following D'Ancona (1959, 1960) and Vøllestad and Jonsson (1986), while L_{∞} , k and $\sigma_{\ln(g)}^2$ have been evaluated by using a nonlinear least squares estimator (Table 3, Fig. 3) on the available data.

The stochastic growth model is related to the probability density $r(l)$ previously introduced. In fact, $r(l)$ is lognormally distributed with mean and variance given by

$$[9] \quad E[r(l)] = L(x_0), \quad \text{Var}[r(l)] = [L(x_0)]^2 \cdot \sigma_g^2$$

Eel size within a cohort remains lognormally distributed, provided that no other size-dependent processes (such as those relative to sexual maturation) apply. An immediate derivation from Eqs. 6 and 7 shows that (Ricker 1975):

$$l(x + 1) = L_{\infty}(1 - e^{-k})g + l(x)e^{-k}$$

which is a two-parameter relationship between the length $l(x)$ and the subsequent length $l(x + 1)$ 1 year later. In eels growth occurs mostly during the warm summer months with winter growth being negligible. The size at the end of autumn (just before the fishing season) can be thus assumed approximately equal to eel size at the beginning of the following spring, i.e.:

$$[10] \quad l(x^+) = l(x + 1)$$

Following Schnute's notation (1987) for the sake of simplicity, we replace $l(x)$ by l and $l(x + 1)$ by l^+ . The growth model is then stated synthetically as

$$[11] \quad l^+ = g\Lambda + \rho l; \quad \Lambda = L_{\infty}(1 - e^{-k}), \quad \rho = e^{-k}$$

Equation 11 is the keystone that will allow us to propagate in time the probability distribution function of eel size within a cohort, as will be shown in the next section.

Survivorship

Extreme anoxic conditions, which occur frequently in July and August, are the main cause of mortality (Rossi et al. 1987–1988). Conversely, most eels are likely to survive the winter season (unless water temperature falls below 0°C), as they can strongly reduce feeding activities and metabolic rate and enter a state of torpor (Nyman 1972; Sadler 1979; Walsh et al. 1983; Vøllestad 1986b). Therefore, natural mortality during the winter season is assumed to be negligible.

Summer mortality, on the contrary, cannot be neglected. In the most general case, summer mortality may be conceived of as a function of both size and age. Let $\sigma(x, l)$ be the survival from age x to age x^+ and from size l to size l^+ , i.e., the fraction of individuals of age x and size l able to survive from the beginning of spring to the end of summer. We have above defined

$$\int_{l_1}^{l_2} y(x, l, t) dl$$

as the probability that an x -year old yellow eel is between l_1 and l_2 ($l_1 < l_2$) at time t . The same probability at the end of the warm season (age x^+ and time t^+) can be computed as follows:

$$[12] \quad \int_{l_1^+}^{l_2^+} y(x^+, l, t^+) dl = \int_{l_1}^{l_2} \sigma(x, l) y(x, l, t) dl$$

where:

$$[13a] \quad l_1^+ = g_1\Lambda + \rho l_1, \quad l_2^+ = g_2\Lambda + \rho l_2$$

$$[13b] \quad g_1 = \frac{l_1}{L(x)}, \quad g_2 = \frac{l_2}{L(x)}, \quad l_1 < l_2$$

Note that Eqs. 12 and 13 explicitly imply that eel length scatters on wider and wider intervals (Fig. 5), because the size-class (l_1, l_2) is always smaller than (or at most equal to) its projection (l_1^+, l_2^+) 6 months later.

It should be noted that, if no yellow eel of size l underwent metamorphosis during autumn, the joint distribution of age and size at the beginning of the following spring season would simply equal the distribution 6 months earlier:

$$[14] \quad y(x+1, l^+, t+1) = y(x^+, l^+, t^+)$$

because winter growth is assumed to be negligible (Eq. 10). Equations 12–14 allow the temporal propagation of the probability distribution of eel lengths provided there is no metamorphosis.

Whether natural mortality is actually dependent upon eel age or size, or both size and age, is difficult to say. Available data do not shed light on this problem, and no suitable field experiment has been ever done to clarify this point. Because of the lack of information, we will assume an age-dependent survivorship. In particular, age at death is assumed to have a Weibull distribution (Johnson and Kotz 1970; Pinder et al. 1978):

$$Q(x) = 1 - \exp[-((x - x_0)/b)^c], \quad b, c > 0$$

where $Q(x)$ gives the probability of dying before age x and b and c are the scale and shape parameters, respectively, of the Weibull distribution.

Therefore, age-specific survivorship in the interval between x and x^+ can be easily computed as

$$[15] \quad \sigma(x) = \exp\left(\left(\frac{x-x_0}{b}\right)^c - \left(\frac{x-x_0+1}{b}\right)^c\right)$$

The Weibull distribution is rather flexible and can possess either positive or negative skewness. It can be shown (Pinder et al. 1978) that (i) $\sigma(x)$ is a decreasing function of age when $c > 1$; (ii) $\sigma(x)$ is constant when $c = 1$; and (iii) $\sigma(x)$ is an increasing function of age when $c < 1$. These patterns correspond respectively to type I, II, and III survivorship curves (Pearl 1928; Deevey 1947).

Sexual maturity

As already mentioned, the age at metamorphosis is not fixed, with males and females maturing to the silver stage at older ages growing more slowly than those maturing at younger ages (Vøllestad and Jonsson 1986; Vøllestad 1989). On this basis, we will assume that the metamorphosis rate is mostly dependent upon size, and not age. Let $\gamma(l)$ be the expected fraction of yellow eels of size l that undergo metamorphosis to the silver stage in autumn. Then, the probability density function $s(x^+, l, t^+)$ that an elver, recruited in year $t - x$, becomes an x^+ -year-old silver eel of size l can be easily derived from $y(x^+, l, t^+)$:

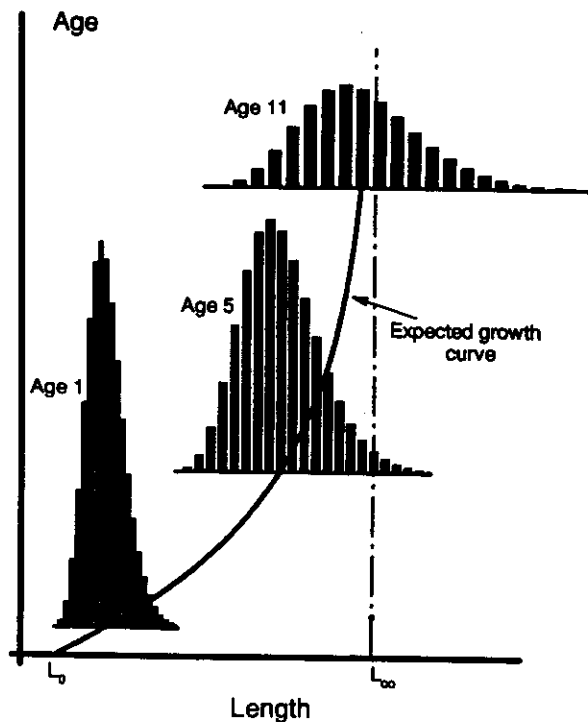
$$[16] \quad s(x^+, l, t^+) = \gamma(l) y(x^+, l, t^+)$$

On the other hand, the probability density of retention in the lagoons as yellow type at the end of the fishing season is

$$[17] \quad y(x+1, l, t+1) = [1 - \gamma(l)] y(x^+, l, t^+)$$

This equation replaces eq. (14) of the previous section where metamorphosis was not accounted for. As sexual

Fig. 5. The evolution of eel size structure within a cohort. L_0 and L_∞ are parameters of the Von Bertalanffy growth curve. The inclusion of a lognormally distributed growth factor determines the dispersion of eel sizes on wider and wider intervals.



maturation is assumed to be size dependent, the probability distribution function of yellow eel size will be altered by this process as soon as yellow eels become large enough to metamorphose to silver type; therefore in the general case, size structure within a cohort will no longer be lognormal.

Because bigger eels are more likely to undergo metamorphosis than the smaller ones, $\gamma(l)$ must be an increasing function of l . Based on the shape of the ascending limb of silver male and female size distributions (see Fig. 2), we have here assumed a sigmoidal metamorphosis function defined by:

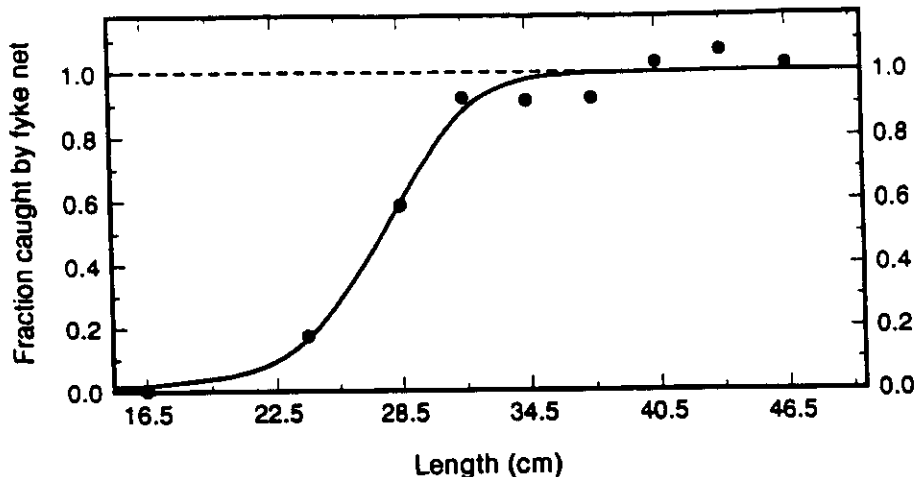
$$[18] \quad \gamma(l) = \frac{\gamma_{\max}}{1 + \exp\left(\frac{l-\lambda}{\eta}\right)}, \quad \gamma_{\max}, \lambda, \eta > 0$$

where γ_{\max} (≤ 1) is the maximum rate of metamorphosis, λ is a semisaturation constant, and η is a parameter inversely proportional to the slope of the metamorphosis curve at $l = \lambda$. When λ and η are positive, $\gamma(l)$ increases with eel size and levels off to γ_{\max} for large values of l .

Net selectivity

The fishing device used to sample yellow eels (fyke net with an 8-mm mesh) is size selective: only larger animals are caught, and most elvers are able to escape through the meshes of the net. Therefore, the length structure derived from 1989 and 1990 data is not the size distribution

Fig. 6. Fyke net selectivity curve (8-mm mesh size) as resulting from a mark-recapture experiment performed in the Comacchio lagoons in 1982 (Rossi et al. 1987-1988). The black dots are the normalized ratios between recaptured and marked eels in each (3-cm-wide) size-class.



π_i^Y computed from $Y(x, l, t)$ (Eq. 5), as the latter refers to all fish living in the lagoons, while the former concerns only the eels captured by fishing gear. A corrected yellow eel size distribution is to be derived to take into account fish liability to capture as a function of size. To this end, we have assumed that the fraction Φ of eels caught in the net is a function of the eel cross section A according to the following equation:

$$[19] \quad \Phi(A) = \frac{1}{1 + \exp\left(\frac{A_{\text{med}} - A}{\zeta}\right)}, \quad A_{\text{med}}, \zeta > 0$$

where ζ (slope of selectivity function) and A_{med} (median cross section) are to be estimated. As our demographic model uses length classes, we need to derive the eel section A as a function of l . To this purpose, note that the weight w (grams) is given by

$$[20] \quad w = \delta A l$$

where δ is the specific weight of eels, assumed to be a constant. The weight-length relationship (Table 2) is

$$[21] \quad w(l) = \alpha l^\beta$$

Matching Eq. 20 with Eq. 21 yields

$$[22] \quad A = \alpha/\delta l^{\beta-1}$$

and Eq. 19 can be rewritten as:

$$[23] \quad \Phi(l) = \frac{1}{1 + \exp\left(\frac{A_{\text{med}} - (\alpha/\delta)l^{\beta-1}}{\zeta}\right)}$$

The value of ζ and A_{med} of Eq. 23 have been estimated from the data of a mark-recapture experiment performed with the same fishing device by Rossi et al. (1987-1988) in the Comacchio lagoons in 1982. The estimated selection curve is shown in Fig. 6.

Therefore, the expected size distribution of yellow eels captured in fyke nets can be computed from the density $Y(x, l, t)$:

$$\pi_i^{Y^*}(t) = \frac{\sum_{x=0}^{x_{\text{max}}} \Phi(l) Y(x, l, t)}{\int_0^{l_{\text{max}}} \left[\sum_{x=0}^{x_{\text{max}}} \Phi(l) Y(x, l, t) \right] dl}$$

Further considerations

Sexual dimorphism

Because of sexual dimorphism, females and males must be represented by different state variables, that is, $y^F(x, l, t)$, $y^M(x, l, t)$, $s^F(x, l, t)$ and $s^M(x, l, t)$ for yellow females, yellow males, silver females and silver males, respectively. Therefore, length and age structure will be different in the two sexes. Females and males share the same survivorship function $\sigma(x)$, while the metamorphosis function $\gamma(l)$ and the expected growth curve $L(x)$ differ in the two sexes. Maximum metamorphosis rate from yellow to silver male has been set equal to 1, because all surviving males eventually reach sexual maturity (Gatto and Rossi 1979).

Time invariance of model parameters

We make the strong assumption that growth, survivorship, and metamorphosis parameters are constant over time. However, the emerging evidence in field ecology is that time invariance is an exception rather than a rule. Actually, we tend to believe that at least recruitment abundance (which we treat as an exogenous parameter, because it is independent of eel abundance in the lagoons) may be variable from year to year (Vøllestad 1986b; Vøllestad and Jonsson 1988). On the other hand, to reconstruct the time series of recruitments is beyond hope, because we lack suitable historical series of length distributions of yellow

and silver eels. Also, the commercial catch, after the dramatic drop at the end of the 1970s, has fluctuated in the last decade (Table 1) around a mean value of about 6.15 kg/ha with a standard deviation of 1.66, which is large but not enormous. Within this context, the unavoidable assumption is that recruitment is distributed around a constant average value $R(t) = \epsilon_t R_a$, where ϵ_t is a random factor with unitary geometric mean. R_a is the parameter we will try to estimate under the further hypothesis that the variance of ϵ_t is not too large. In fact, if this is the case and no disturbance factors have been acting on the population for a number of years, stable age (and stable size) distributions are reached. In other words, population variables may be considered to be substantially stationary, namely

$$y(x, l, t + 1) = y(x, l, t) = y(x, l) \text{ and } s(x, l, t + 1) \\ = s(x, l, t) = s(x, l).$$

In practice, there will be variations from year to year, but these should be small provided the variance of ϵ_t (and of the other parameters) is small. The size structure of both females and males (π_i^Y , $\pi_i^{Y^*}$ and π_i^S) depends upon all model parameters except R_a . In fact, it is easy to prove that

$$[24a] \quad \pi_i^Y = \frac{\sum_x Y(x, l)}{\int \sum_x Y(x, l) dl} = \frac{\sum_x y(x, l)}{\int \sum_x y(x, l) dl}$$

$$[24b] \quad \pi_i^{Y^*} = \frac{\sum_x \Phi(l) Y(x, l)}{\int \sum_x \Phi(l) Y(x, l) dl} = \frac{\sum_x \Phi(l) y(x, l)}{\int \sum_x \Phi(l) y(x, l) dl}$$

$$[24c] \quad \pi_i^S = \frac{\sum_x S(x, l)}{\int \sum_x S(x, l) dl} = \frac{\sum_x s(x, l)}{\int \sum_x s(x, l) dl}$$

where $y(x, l)$ and $s(x, l)$ are computed recursively using Eqs. 9, 12, 13, and 15–18. Consequently, size structure of yellow and silver eels is determined only by the elvers' length distribution $r(l)$ at recruitment (not by the corresponding abundance) and by growth, death, and sexual maturation processes, which have been assumed to be time independent.

Model calibration and validation

A direct comparison of the 1989 and 1990 size distributions (Fig. 2) points out that the histograms of silver eels are quite similar (Kolmogorov–Smirnov test, $D = 0.071$, $p > 0.05$), while those of yellow eels are different (K.S. test, $D = 0.3723$, $p < 0.001$). In particular, the 1990 yellow distribution is skewed in favor of small sizes. The reason for this phenomenon is that during 1989 a considerable number of juvenile yellows (1–3 years old) were stocked into the lagoons in the period following the sampling program. As only a negligible fraction of yellows reach sexual maturity at the typical sizes attained at ages 1^+ , 2^+ , and 3^+ , we can assume that the 1989 size distributions of both silver and yellow eels were not affected by restocking. Therefore, we have proceeded in the following way: the 1989 yellow and silver distributions have been considered stable

distributions (see previous section) and have been used to estimate model parameters; the 1990 data, supplemented with information on restocking, have been used for validating the demographic model.

Unknown parameters

For females, three coefficients, λ_{\max}^F , λ^F , and η^F , of the metamorphosis function are to be estimated, whereas for males λ^M and η^M only, because γ_{\max}^M equals unity. The survivorship curve has two unknown parameters, b and c . The age x_0 at which eels are recruited to the fishery is set to 1 year while the corresponding abundance R_a must be estimated. Altogether, model calibration requires that eight unknown parameters be estimated.

Estimation of unknown parameters

To estimate unknown parameters, the expected length distributions and the expected commercial catch have been compared, respectively, with the observed length distributions of 1989 and the mean yield between 1977 and 1991 (ca. 6.15 kg/ha). As length distributions do not depend on recruitment abundance under the time-invariance assumption, we have first derived the estimates of all parameters except R_a by minimizing the following objective function:

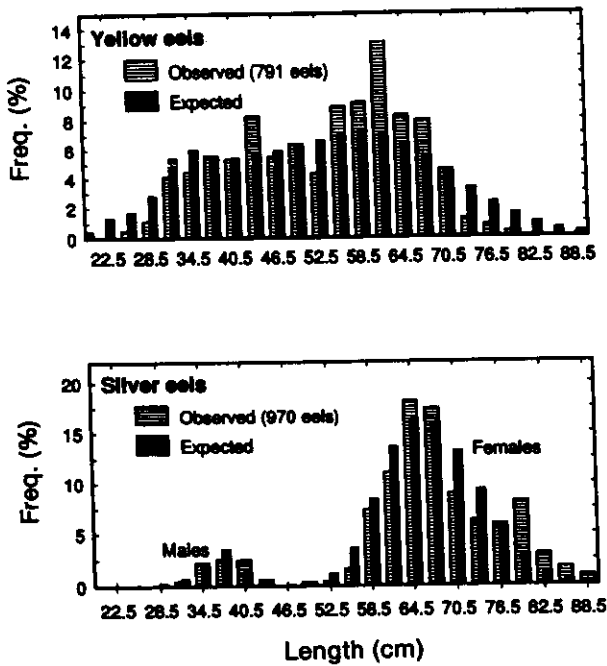
$$[25] \quad \Xi(\gamma_{\max}^F, \lambda^F, \eta^F, \lambda^M, \eta^M, b, c) = \int (\bar{\pi}^{Y^*} - \hat{\pi}^{Y^*})^n dl \\ + \int (\bar{\pi}^S - \hat{\pi}^S)^n dl$$

where $\bar{\pi}^{Y^*}$ and $\bar{\pi}^S$ are the observed size structures of yellow and silver eels, $\hat{\pi}^{Y^*}$ and $\hat{\pi}^S$ are the expected counterparts computed by means of Eqs. 24b and 24c, and n is an even and positive integer. Equations 12, 13, and 15–18 are recursively used to simulate the life cycle of a cohort; in practice, the probability density function $r(l)$ of recruited individuals, estimated from age–length data according to Eqs. 8 and 9, is propagated through ages. Each simulation is run with a different set of values for the seven parameters to be estimated until the best fit to the observed size distribution is obtained. A downhill simplex method (Press et al. 1988) has been applied to find the parameter values that minimize Ξ . An n of 4 is a fair compromise between convergence speed and goodness of fit to size-distribution tails.

Once the optimal value of the first seven parameters has been obtained, the recruitment estimate can be easily computed if one considers that commercial catch is a linear function of R_a under the time-invariance assumption:

$$[26] \quad \text{Catch}(R_a / \hat{\gamma}_{\max}^F, \hat{\lambda}^F, \hat{\eta}^F, \hat{\lambda}^M, \hat{\eta}^M, \hat{b}, \hat{c}) \\ = \sum_{x=x_0}^{x_{\max}} \left\{ \int_0^{l_{\max}} \bar{w}_S(l) [R_a \hat{s}(x, l)] dl \right\} \\ = \left\{ \sum_{x=x_0}^{x_{\max}} \left[\int_0^{l_{\max}} \bar{w}_S(l) \hat{s}(x, l) dl \right] \right\} R_a$$

Fig. 7. Observed versus expected size distributions for 1989. The expected values are computed via the best fitting model.



Therefore, given the value of $\hat{\gamma}_{max}^F$, $\hat{\lambda}^F$, $\hat{\eta}^F$, $\hat{\lambda}^M$, $\hat{\eta}^M$, \hat{b} , and \hat{c} , one can compute the recruitment abundance that provides the mean observed catch (6.15 kg/ha):

$$[27] \quad \hat{R}_a = \frac{6.15}{\sum_{x=x_0}^{x_{max}} \left[\int_0^{l_{max}} \bar{w}_s(l) \hat{s}(x, l) dl \right]}$$

Parameter uncertainty estimation

To evaluate the variance of parameter estimates, nonparametric statistics have been used. Bootstrapping is undoubtedly one of the most widespread computing-intensive techniques recently applied in ecological studies (for an extensive review of methods based on resampling plans see Efron 1982). In the bootstrap procedure, original data are randomly recombined *B* times (replicates), pseudovalues of unknown parameters are computed for each recombination of the original data and the statistics of the parameters of interest are derived from the resulting frequency distributions.

In this study, we basically use bootstrapping procedures with the aim of reproducing sampling variability from the whole population in the lagoons. The simplest way of generating a bootstrap replicate would be to place the original data set of *m* eels (*m* = 970 for silver eels, *m* = 791 for yellows) into a pool and randomly extract *m* animals with replacement. Replacement means that each sampled eel is to be reinserted into the pool before another eel is sampled: thus, any eel of the original data set may be represented more than once in a bootstrap replicate or may not

be present at all. This simple resampling scheme assumes an equal probability of selection of every fish in the catch. This is not true for stratified samples (Efron and Tibshirani 1986), because eels sampled in different strata, fishing periods, and lagoons do not share the same probability of being drawn from the pool. To be consistent with the original sampling design described in the second section, the process of bootstrap replication requires that any eel is drawn with a probability reflecting its subsample and stratum abundances, the different fishing periods, and the catch in the three lagoons. The procedure implemented to accomplish this resampling scheme is described in detail by Pelletier and Gros (1991).

Despite its reputed superiority when compared with other resampling techniques such as jackknifing (Efron 1982), bootstrapping has been applied rarely to parameter estimation in fish dynamics, primarily because it can be tremendously time consuming. The precision of a bootstrap estimate, in fact, strictly depends on how many times the original data are randomly recombined (i.e., how many replicates, *B*, are performed within a bootstrap calculation). Bootstrap estimates will converge to a stable value as *B* becomes large, by the law of large numbers. To have a stable bootstrap estimator, we recombined the data 1000 times (*B* = 1000). About 8 h of computing time on a Workstation HP-720 were necessary to complete the bootstrap calculation. We define $\theta_{i,j}^*$ as the value of the *j*th parameter (*j* = 1, 2, ..., 8) estimated from the *i*th bootstrap replicate (*i* = 1, 2, ..., 1000). The mean value θ_j^B and the variance of the *B* pseudo values $\theta_{i,j}^*$ are

$$\theta_j^B = \frac{1}{B} \sum_{i=1}^B \theta_{i,j}^*$$

$$\text{Var}(\theta_j^B) = \frac{1}{B} \sum_{i=1}^B (\theta_{i,j}^* - \theta_j^B)^2$$

Let θ_j^{true} be the true value of θ_j . As Meyer et al. (1986) state, if the full sample estimator for the original data set, θ_j^{all} , is a biased estimate of θ_j^{true} , then θ_j^B will equally be biased, because it estimates θ_j^{all} , rather than θ_j^{true} . Therefore, a bias-adjusted bootstrap estimate of θ_j^{true} is $\theta_j^{B-adj} = \theta_j^{all} - \theta_j^B$ (see Meyer et al. (1986) for details). A number of statistics (median, mode, skewness, etc.) were then computed from the frequency distributions of the 1000 values ($\theta_{1,j}^*$, $\theta_{2,j}^*$, ..., $\theta_{1000,j}^*$, *j* = 1, 2, ..., 8). Furthermore, a bias-corrected percentile method has been adopted (Efron 1982) to derive the interval between the 5th and 95th percentile values as a candidate for a 90% confidence interval of each parameter.

Model validation

The model has been validated against the data collected in 1990. As anticipated, the 1990 size distributions are influenced by the restocking carried out the year before. According to Carrieri et al. (1992), 35.9 t of elvers were stocked in the lagoons between April and May 1989, soon after the yellow eel sampling described in the second section. The average body weight was 20 ± 7.8 g, with 30% of the specimens being 1 year old, 40% being 2 years old, and 30% being 3 years old. The validation procedure is

Table 4. Main statistics (bias adjusted expected value, SD, bias corrected 5th and 95th percentile, and standardized skewness) obtained from the frequency distributions of the 1000 bootstrap estimates.

Parameters	Expected value	SD	Percentile		Standardized skewness
			5th	95th	
b	0.98	0.54	0.17	1.97	3.77
c	0.30	0.07	0.18	0.43	2.07
γ_{\max}^F	0.12	0.03	0.07	0.17	10.52
λ^F	58.40	0.76	57.30	59.70	11.17
λ^M	39.10	1.63	36.80	42.10	-7.69
η^F	2.40	0.50	1.75	3.25	22.08
η^M	2.80	0.52	1.99	3.69	22.89
R_s	136.80	66.64	70.00	267.78	25.00

Table 5. Correlation matrix of the eight estimates. The significance level corresponding to each correlation coefficient is reported in brackets.

	b	c	γ_{\max}^F	λ^F	λ^M	η^F	η^M	R_s
b								
c	0.552 (0)							
γ_{\max}^F	0.029 (0.355)	-0.450 (0)						
λ^F	0.046 (0.146)	0.090 (0.004)	0.589 (0)					
λ^M	0.015 (0.636)	0.634 (0)	-0.656 (0)	-0.131 (0)				
η^F	0.054 (0.087)	-0.129 (0)	0.496 (0)	0.559 (0)	-0.257 (0)			
η^M	-0.035 (0.274)	0.160 (0)	-0.135 (0)	0.034 (0.284)	0.419 (0)	-0.126 (0)		
R_s	-0.438 (0)	0.313 (0)	0.622 (0)	-0.098 (0.002)	0.590 (0)	-0.186 (0)	0.174 (0)	

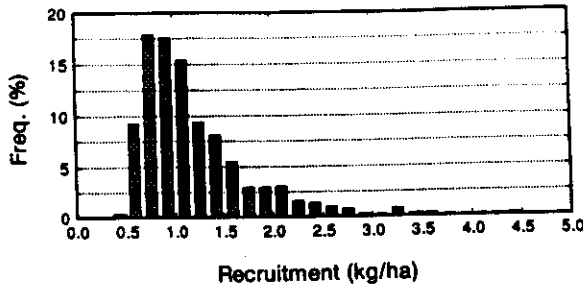
as follows. First, estimates $\hat{Y}(x^+, l, 1989^+)$ of yellow eel abundances in autumn 1989 are obtained by using the model fitted to the 1989 data. By applying Eq. 17 to $\hat{Y}(x^+, l, 1989^+)$ one can then derive the expected distribution and abundance of naturally recruited yellow eels at the beginning of spring 1990. However, this is not sufficient to obtain $\hat{Y}(x^+, l, 1990)$, because the contribution resulting from elver stocking must be accounted for. This contribution can be calculated by using Eqs. 12, 13, and 17 and the estimated vital rates to propagate through time the size distributions and abundances of the three restocked cohorts. In fact, a mark-recapture study conducted by Rossi et al. (1988) indicated that restocked eels adapt to the new environment and exhibit growth, survival, and metamorphosis rates that resemble those of naturally recruited eels. The length distributions resulting from the three cohorts are combined with the size distribution resulting from the natural recruitment, according to the respective abundances in each size-class, to yield $\hat{Y}(x^+, l, 1990)$. The final expected distribution of yellows in the spring of 1990 is obtained by applying net selectivity (Eq. 23) and normalizing. It is

then compared with the sample distribution in spring 1990 to assess on the validation quality. Finally, Eqs. 12, 13, and 16 are applied to $\hat{Y}(x^+, l, 1990)$ to forecast the expected silver eel distribution, which is compared with the observed size structure of the 1990 silver eel catch for further validation.

Results

Expected versus observed size distributions of yellow and silver eels in 1989 are plotted in Fig. 7. The model fits the reference samples quite well, especially the silver distribution. Table 4 reports the bias-adjusted expected values of model parameters along with standard deviations, the bias-corrected 5th and 95th percentile and the standardized skewness, as defined in the previous section. The estimates of λ_{\max}^F , λ^F , η^F , λ^M , η^M , and c can be considered good, because all these parameters have standard deviations of less than 25% of the corresponding average. The expected values of b and R_s are less accurate, a likely consequence of the negligible proportion of elvers in the

Fig. 8. Frequency distribution of eel recruitment (kg/ha) resulting from the 1000 pseudovalues obtained by bootstrapping. Expected recruitment is about 1.2 kg/ha.



yellow sample. The correlation matrix computed from the 1000 bootstrap replicates emphasizes moderate cross dependencies between model parameters (Table 5). The negative correlation (-0.438) between R_w and the scale factor b of the Weibull survivorship curve can be easily explained if one considers that b is positively correlated with survival: small increments of survival, corresponding to larger values of b , imply a larger fraction of eels reaching older stages. Therefore, the estimate of recruitment, computed by means of Eqs. 26 and 27, necessarily decreases so that the same catch of silver eels (6.15 kg/ha) is obtained. A similar remark also applies to the negative correlation (-0.622) between the recruitment and λ_{max}^F , the maximum fraction of yellow eels undergoing metamorphosis: again, if the rate of eels moving from the yellow to the silver compartment increases, R_w must decrease to match the yield of 6.15 kg/ha.

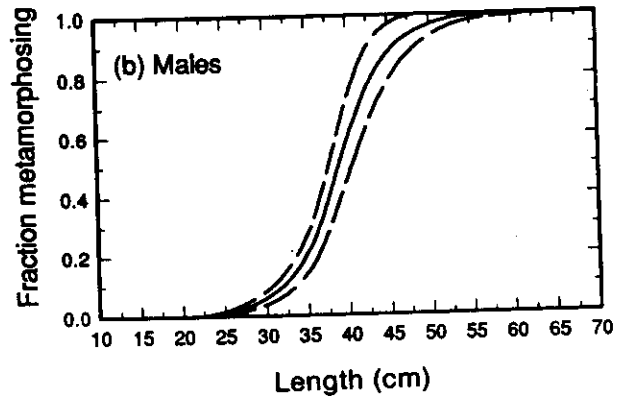
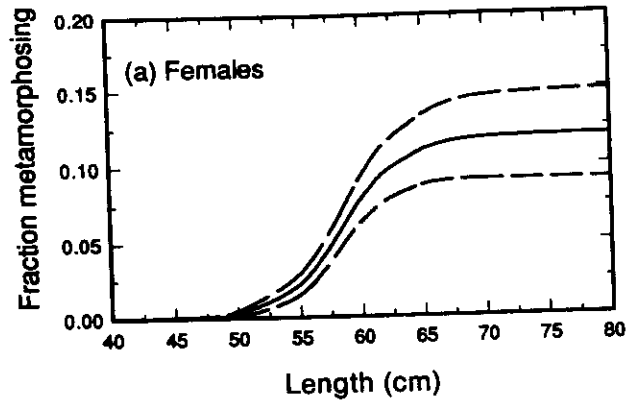
The knowledge of the distribution of the eight basic parameter estimates is rather arid information, but makes it possible to derive the main statistics of a number of important indices and vital rates that are of more immediate understanding and practical use. First, one can obtain recruitment in terms of biomass (per hectare), namely:

$$[28] \quad R_w = \int w_Y(l)[Rr(l)] dl$$

which is a more meaningful figure than abundance. The bootstrap distribution of R_w (Fig. 8) has a rather large variance. In fact, it is made up of two components: one reflects the uncertainty in parameter estimation, and the other is related to the natural variance of recruitment (the variance of the noise factor ϵ_t). It should be noted that recruitment biomass, though fairly uncertain (1.2 ± 0.6 kg/ha; Fig. 8), is one order of magnitude smaller than the estimate obtained by Gatto and Rossi (1979) from the 1974-1976 data collected in the same lagoons (20 kg/ha). This difference actually corresponds to the dramatic drop in commercial catch that occurred at the end of the 1970s as a result of mismanagement of the fishery.

A second piece of information that can be derived from model calibration is the metamorphosis rate at each length. The average metamorphosis curve for females with the bootstrap standard deviation at each size is shown in Fig. 9a. The fraction of eels that reach sexual maturation is virtually negligible for sizes smaller than 55 cm, then it increases and levels off to 0.12 (γ_{max}^F) for sizes over 65 cm. In the case of males (Fig. 9b), saturation of the

Fig. 9. Expected metamorphosis curve (\pm SD) for (a) females and (b) males.



metamorphosis curve is reached for smaller lengths (50 cm). The accuracy of estimation, in terms of percent error with respect to the average metamorphosis rate is different at different body sizes. Note that the estimate of $\gamma^F(l)$ (Fig. 9a) is most accurate for central size-classes (about 60 cm), i.e., in the range comprising the largest fraction of silver eels. In any case, the percent error does not exceed 25% even for larger size-classes.

The other vital rate that follows easily from model calibration is survival at different ages (Fig. 10). Survivorship in the juvenile stage (35% from age 1 to age 2) is much smaller than that in the older age-classes for which it is roughly 90%. Estimates are quite accurate for these age groups, as demonstrated by the small standard deviations. Survival estimates are in agreement with those obtained by Gatto and Rossi (1979) ($\sigma_{x=1,2} = 38\%$, $\sigma_{x>2} = 80\%$) for the 1974-1976 data. A direct comparison with the Vøllestad and Jonsson (1988) estimates for the Imsa River (Norway) is not feasible, as their model is based on age-independent mortality.

Finally, we have evaluated the absolute density (both in terms of abundance per hectare and biomass per hectare) of yellow eels, information of particular interest, because it cannot be measured directly. Abundance of yellow eels is estimated as being 336 individuals per hectare, with

females comprising over 97% of the population. Silver eel abundance (12.1 individuals/ha) is only 3% that of yellows. Yet, the mean weight of silver eels (512 g) is larger than the yellows (188 g), because only the larger animals metamorphose. Therefore, the biomass of silver eels (6.15 kg/ha) is about 10% that of yellow eels (62.38 kg/ha). Further details regarding biomass are reported in Table 6 where we compare the absolute density (kilograms per hectare) of yellow and silver eels per size (Table 6a) and age group (Table 6b). The results can be summarized as follows. The first size (<30 cm) and age group (1–2 years) refer to the prereproductive stage (when no yellow eel undergoes metamorphosis to the silver stage) and comprise less than 5% of the eel biomass. The second and third size groups correspond, respectively, to silver males (30–45 cm) and silver females (>45 cm), because mature males are always smaller than adult females. It is worthwhile to note that both the sexual dimorphism and the allometric relation between size and weight contribute to skew the biomass distribution toward the larger size groups, with eels over 45 cm comprising roughly 90% of the biomass in the yellow stage. The age group from 3 to 7 year olds in Table 6b includes all the silver males, though a consistent fraction of yellow females undergoes metamorphosis from age 5+ on. Therefore, the age structure of silver females overlaps that of silver males such that biomass distributions cannot be completely separated according to this classification. The older age group (>8 years), that consists of only females in both the silver and yellow stages, comprises more than 53% of the total biomass.

The results of model validation are displayed in Fig. 11. As stated before, in deriving the expected size distribution of yellow and silver eels in 1990, we have accounted for the contribution of elvers stocked at the end of April 1989. The model supplemented with the information on restocking fits the reference sample well. As a matter of fact, the introduction of the three cohorts largely affects yellow eel size structure in 1990, skewing the distribution towards the smaller size-classes. On the contrary, 18 months after restocking, the effects on the commercial catch are still hardly detectable, because only a small fraction of the eels introduced in 1989 attain the minimum length required to reach sexual maturation. Only the male distribution seems to be slightly affected, as males undergo metamorphosis at considerably smaller sizes than females.

Discussion

We have derived an age- and size-structured model that mimics the life cycle of eel populations with reasonable detail. Simpler models based on age-classes according to classical demographic theory are unrealistic for eels, because the transformation from yellow to silver stage appears to be largely dependent upon size rather than age, whilst the dispersion of animals of the same age on wide size intervals makes age a very poor indicator of eel length. Our approach is somewhat different from that of Kirkpatrick (1984), Schnute (1987), and Deriso and Parma (1988). In fact, they provide a complete theoretical framework for constructing and analyzing size-dependent models in which the resulting equations are analytically tractable in a closed

Fig. 10. Expected annual survival (\pm SD) as a function of age.

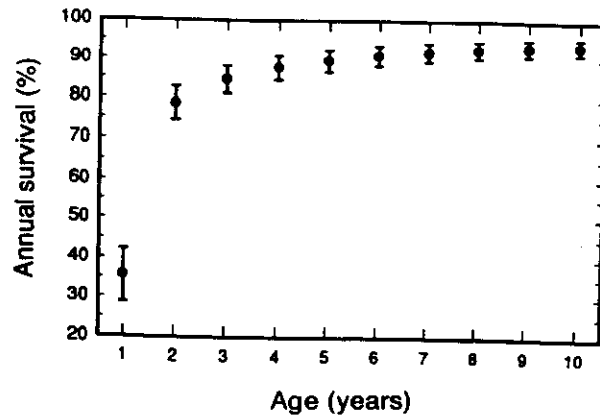
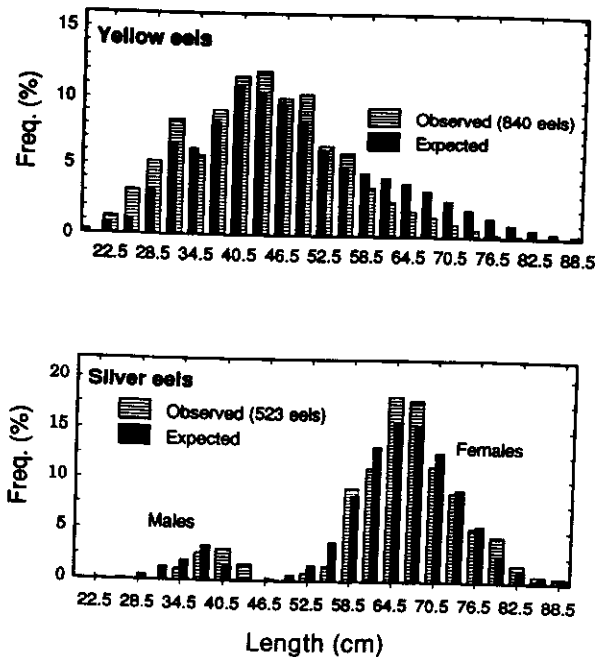


Fig. 11. Observed versus expected size distributions for 1990 (results of validation procedure). Expected distributions for yellow and silver eels are computed by explicitly accounting for elver restocking in April–May 1989, as detailed in the text.



form. The drawback of their approach is that this tractability is achieved by means of some strong 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 fully retain Deriso and Parma's suggestion to "let the computer add the numbers" (Deriso and Parma 1988, p. 1055). Using a few realistic assumptions concerning net selectivity, growth, survival, and sexual maturation, we are able to numerically propagate through time the distribution function of eel sizes by

Table 6. 1989 absolute density (kg/ha) of yellow and silver eels, according to sex and to size and age groups.

(A) Densities by length classes.						
Length (cm)	Yellow (spring)		Silver (autumn)		Yellow	Silver
	Males	Females	Males	Females	Male + female	Male + female
<30	0.09	1.35			1.44	
30-45	0.12	4.68	0.08		4.80	0.08
>45		56.14		6.07	56.14	6.07
Total	0.21	62.17	0.08	6.07	62.38	6.15

(B) Densities by age.						
Age (years)	Yellow (spring)		Silver (autumn)		Yellow	Silver
	Males	Females	Males	Females	Male + female	Male + female
1-2	0.06	3.00			3.06	
3-7	0.15	25.63	0.08	2.19	25.78	2.27
≥8		33.55		3.88	33.55	3.88
Total	0.21	62.17	0.08	6.07	62.38	6.15

Note: Figures for yellows refer to spring (age x), those for silver eels to autumn-winter (age x^+).

recursive equations that update the distribution of lengths in any age class.

The model has been applied to the eel fishery of the Valli di Comacchio lagoons. Estimation of model parameters from 1989 data has led to the evaluation of natural survivorship, the rate of metamorphosis from yellow to silver type, and absolute abundance and biomass in each age- and size-class of each sex, for both yellow and silver eels. A similar assessment was previously carried out by Gatto and Rossi (1979) for the same fishery on the basis of the 1974-1976 catch data, by Vøllestad (1986a) for Hallangspollen Bight (Norway) and by Vøllestad and Jonsson (1988) for the Imsa River fishery (Norway). However, these authors used classical age-class models and did not provide validation, as we do here by using the 1990 data. Parameter uncertainty has been estimated via bootstrapping. It is worth noting that this statistical procedure (or similar resampling plans), although time-consuming, is to be recommended whenever nonanalytic models or analytic models of even moderate complexity are used. In fact, in these cases finding analytical properties of the estimators used to fit the data is beyond hope.

The weakest assumption of the present application is perhaps the time invariance of natural recruitment abundance. Unfortunately, the influence of the environment on recruitment and the effects of varying recruitment on population dynamics are scarcely documented for eel populations. Therefore, we had to exploit the available data, using only 1 year for calibration and one for validation. Future field studies will be of significantly increased value if they attempt to determine historical series of either natural recruitment or yellow and silver eel size structures. Despite these reservations, the model yields reasonable

estimates of the expected recruitment and its variability. The bootstrap distribution shape of natural recruitment (Fig. 8) is highly skewed and lognormal-like in accordance with both empirical studies (Allen 1973; Hennemuth et al. 1980; Garrod 1983) and theoretical arguments (Ricker 1954; Walters and Hilborn 1976, Peterman 1978; Hollowed et al. 1987, Evans and Rice 1988; Armstrong and Shelton 1988; Fogarty et al. 1991; Shelton 1992) about the recruitment distribution of marine fishes.

The assumption of constant recruitment is, however, specific to this application, being a consequence of the relative scarcity of data actually available to fit the model. As a matter of fact, the set of equations that specify cohort dynamics has been derived with no reference to the time invariance of natural recruitment. The introduction of patterns or trends in recruitment is straightforward, as we have shown in the validation section where the contribution of a number of restocked fish cohorts has been explicitly considered. More generally, the model presented in this paper is quite flexible: survival, sexual-maturity and net-selectivity functions can be modified to satisfy more realistic assumptions or to test new hypotheses on the dynamics of the population at hand; ancillary data, such as sex ratios, can easily be used to improve the fitting of the model to data. Moreover, the model allows for the investigation of a variety of management policies, from fish restocking to the exploration of a range of fishing efforts and the use of different fishing gears, with size-dependent net selectivity, catch cost, and selling price being explicitly considered. Lastly, the computer code has been implemented on a workstation, much like a deterministic abundance model and is easily upgradable and portable to other hardware platforms with moderate effort.

We are quite confident that the conceptual framework used for modeling the specific case of European eel demography can be easily extended to a variety of other species in which plasticity of body growth leads to a wide spectrum of organism sizes within cohorts of individuals of the same age. Size dispersion over ages is remarkably important whenever success in reproduction, survival, predation liability, or any other trait happens to be affected by size rather than age. Therefore, differences in size among individuals of the same age should be explicitly acknowledged and accounted for, rather than ignored and averaged over. From a practical point of view, size determination involves simply weighing or measuring individual organisms, whereas age determination is more complicated and involves counting periodic marks of otoliths or scales. As a result, supplementing data on age structure with data on size structure comes at no cost and it is certainly wasteful to neglect these very useful data.

It should be finally noted that, while our model retains the power of more complex partial differential equation models to simulate continuous size distributions, the mathematical framework here derived allows for a straightforward extension to an individual-oriented formulation in which many different individuals, each with its own characteristics, are simulated simultaneously with a Monte-Carlo-like approach (De Angelis et al. 1993). In such a case the distribution of sizes can be derived as the sum of the simulation of many individuals. The demographic consequences of small population size, environmental stochasticity, and complex individual behaviors can be investigated provided Eqs. 7, 12, 13, 16, and 17 are replaced by their suitable individual-oriented counterparts, with growth factors and sexual maturation and survival probabilities being drawn for each individual from the respective probability density functions estimated on available data. Whether the individual-oriented approach, which is surely even more computer intensive than ours, can provide real advantages for fishery management is certainly an issue that deserves being debated and investigated.

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Appendix 1.

Glossary of functions and parameters. This appendix describes and summarizes all notation used in the paper. Numbers in parentheses refer to equations where the symbol is defined or used.

A	cross section of a yellow eel (19)
A_{med}	semisaturation constant of the net selectivity function (19)
B	number of bootstrap replicates
b, c	scale and shape parameters of the Weibull mortality function $Q(x)$ (15)
F, M	superscripts specifying parameters for females and males
g	growth factor (a random variable log-normally distributed with unitary mean and variance σ_g^2) (7)
k	slope parameter of the Von Bertalanffy growth curve (8)
l	eel body size

l^+	eel size in autumn (given its size in the previous spring was l)	δ	eel specific weight (20)
l_{\max}	maximum body size	ε_t	random factor, with unitary geometric mean, that modulates the mean recruitment abundance R
$L(x)$	mean body size at age x	ζ	slope parameter of the net selectivity function (19)
L_{∞}	asymptotic body size (8)	η	slope parameter of the metamorphosis function $\gamma(l)$ (18)
L_0	mean body size of elvers at age 0 (8)	θ_j	j th unknown parameter ($j = 1, 2, \dots, 8$) of the demographic model
m	number of eels in the sample	θ_j^*	value of the j th parameter ($j = 1, 2, \dots, 8$) estimated from the i th bootstrap replicate ($i = 1, 2, \dots, 1000$)
n	power of the objective function (25) in the estimation procedure	θ_j^B	mean value of the j th parameter ($j = 1, 2, \dots, 8$) estimated from its bootstrap distribution
$Q(x)$	probability of dying before age x	θ_j^{true}	true value of θ_j
$r(l)$	probability distribution function of recruitment with respect to size	θ_j^{all}	full sample estimate of j th parameter for the original data set
$R(t)$	number of elvers recruited in year t	$\theta_j^{\text{B-adj}}$	bias-adjusted bootstrap estimate of θ_j^{true}
R_e	expected number of elvers	$\Theta(x, t)$	expected number of yellow eels of age x in year t (1)
R_w	expected biomass of newly recruited individuals (28)	Λ	$= L_{\infty}(1 - e^{-\lambda})$ (11)
$S(x, l, t)$	expected number of silver eels of age x and size l in year t	λ	semi-saturation constant of the metamorphosis function $\gamma(l)$ (18)
$s(x, l, t)$	probability that an elver recruited in year $t - x$ will be an x -year-old silver eel of size l in year t	$\Xi(\theta_j, j = 1, 2, \dots, 8)$	objective function used in the estimation procedure (25)
t	beginning of year t (spring)	$\pi_1^Y(t)$	frequency distribution of sizes of yellow eels in year t (5, 24)
t^+	beginning of the fishing season of year t (late Autumn)	$\pi_1^{Y^*}(t)$	frequency distribution of sizes of yellow eels captured in fyke nets in year t (5, 24)
$w(l)$	generic length-weight relationship	$\pi_1^S(t)$	frequency distribution of sizes of silver eels in year t (5, 24)
$w_Y(l), w_S(l)$	length-weight relationship for yellow eel and silver eels, respectively (26-28)	ρ	$= e^{-t}$ (11)
x	age of an eel in spring	σ_g^2	variance of g (9)
x^+	age of an eel in autumn	$\sigma_{\ln(g)}^2$	variance of $\ln(g)$ (8)
x_0	age at recruitment	$\sigma(x)$	survival between age x and age x^+ (15)
x_{\max}	maximum age	$\Phi(A)$	net selectivity as a function of eel cross section (19)
$Y(x, l, t)$	expected number of yellow eels of age x and size l in year t	$\Psi(t)$	expected number of yellow eels in the lagoon in year t (2)
$y(x, l, t)$	probability that an elver recruited in year $t - x$ will be an x -year-old yellow eel of size l in year t		
α, β	parameters of the length-weight relationship (21)		
$\gamma(l)$	fraction of yellow eels of size l undergoing metamorphosis to the silver stage (16-18)		
γ_{\max}	maximum rate of metamorphosis (18)		

