

A STOCHASTIC BIOECONOMIC ANALYSIS OF SILVER EEL FISHERIES

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Abstract. Catadromous species such as the eel often present several distinctive features (high plasticity in somatic growth, size-dependent sexual maturation, strongly skewed sex ratio, variable recruitment) that make their management quite complex. Fisheries usually operate in lagoons where effort is exerted on the sexually mature individuals migrating back to the sea, or on the young prereproductive individuals feeding in the lagoons, or on both. The aim of this work is to investigate the possibility of improving the economic return of the most typical catadromous fish, the European eel *Anguilla anguilla*, by exploring which fraction of prereproductive individuals should be caught every year, and whether declining recruitments from sea should be supplemented by restocking young eels (called elvers). Eel population dynamics is described through a demographic model based on a multiple classification of individuals by age and size and which explicitly includes environmental stochasticity and variation in model parameters. The model has been calibrated on the data from the most important Italian eel fishery located in the Comacchio lagoons, where only the migrating, mature eels are traditionally harvested. Different policies in terms of fishing effort, net selectivity, and restocking density have been analyzed by using the simulation model. Optimal management has been assessed with reference to the average net economic return under different discount rates. A Monte Carlo approach has been used to evaluate the variability of the mean economic benefit. Our model predicts that substantial improvement, relative to the traditional harvesting policy, can be achieved by restocking elvers, while catching yellow eels with fyke nets allows only for minor improvements of economic return. A sensitivity analysis shows that these results hold for different discount rates and for realistic variations of harvesting costs, but if the present price gap between yellow and silver eels were to increase, yellow eel fishing would be unprofitable. Also, elver restocking should be performed only in low-density populations. Otherwise the density-dependent increment in natural mortality may overcompensate the benefits of restocking. The conceptual framework used for modeling the specific case of European eels demography is very flexible and can be easily extended to a variety of other catadromous species.

Key words: *Anguilla anguilla*; bioeconomic analysis; Valli di Comacchio lagoons; catadromous species; environmental stochasticity; European eel; fishery management; harvesting costs and demographic rates; Monte Carlo simulation and bootstrapping; optimal management; population dynamics.

INTRODUCTION

The management of euryhaline species is particularly important, because many fish species of commercial interest in coastal areas or brackish waters are catadromous, i.e., they reproduce in the sea but spend part of their life cycle in fresh or brackish waters before migrating back to the sea for spawning. Actively fished catadromous species are the gray mullets (such as the ubiquitous flat-headed gray mullet *Mugil cephalus*, the thick-lipped gray mullet *Chelon labrosus*, the thin-lipped gray mullet *Liza ramada*, and the golden gray mullet *Liza aurata*); the bass (*Dicentrarchus labrax*); the flounder (*Platichthys flesus*), and the gilthead (*Sparus aurata*). But probably the best known among ca-

atadromous species is the eel. Commercial fisheries of eels are present almost everywhere in the world: *Anguilla anguilla* is fished in most of the European coasts, including Italy, Spain, Portugal, France, England, Germany, and Norway (Vøllestad and Jonsson 1992). *Anguilla australis* is fished in Australia (Skehan and DeSilva 1998), while *Anguilla rostrata* is a species of commercial interest on the East coast of North America (Maine–Florida), with annual catches of 3.84×10^3 – 16.45×10^3 kg during 1970–1995 and valued at US\$1.17–5.49 million (Atlantic States Marine Fisheries Commission 1997). The number of reported shipments of live American eels exceeded US\$10 million in 1995, with 36.6% of shipments to Asian ports, 47.4% to European ports, and 16.2% to North American ports. The country with the longest history of eel culture (with the exception of the Comacchio lagoons in Italy) is Japan, where *Anguilla japonica* has been farmed commercially for 150 yr and, on a subsistence basis, for

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centuries longer. Commercial eel fisheries became very important in Taiwan following World War II. In eastern Asia, the production of intensive aquaculture, which depends upon wild-caught young eels, measures $>150 \times 10^6$ kg (Moriarty and Dekker 1997).

For catadromous species, the recruitment of fries or elvers in a specific brackish system may be partially or totally independent of the stock of mature individuals in the same system, as the actual spawning stock may be made up of fishes migrating from other unexploited geographical areas (Bardach et al. 1972). Therefore, unless the overall population is heavily exploited, the dynamics and management of a specific local population might be described via models that do not account for fertility, but only for cohort dynamics according to age-dependent mortality and body size growth. The model for eumetric fishing developed by Beverton and Holt (1957) for populations with constant recruitment is probably the best known of this kind. Unfortunately, there are many problems in applying the Beverton-Holt theory to catadromous species. First of all, recruitment may be highly variable from year to year. This weakens the classical results of Beverton-Holt theory, which was derived for a single cohort in a purely deterministic framework, or for stationary populations. Second, different fishing gear must be used depending on the fraction of the population being fished, namely the sexually mature individuals that migrate back to the sea for spawning, or the prereproductive stage, or both. Therefore, the Beverton-Holt theory needs to be adjusted to this specific case. Third, body size may be extremely variable at each age, thus making age a very poor indicator of fish length or mass. This point has serious implications on both population dynamics and fishery management. In fact, some demographic parameters (such as fertility or time of sexual maturation) are more likely to be size dependant rather than age dependent. Therefore, a description of population dynamics that does not take fish size into account may simply miss an important piece of its demography. The knowledge of size structure can also be critical for deriving optimal management strategies, because fishing gear is usually size-selective as opposed to age selective. Moreover, it is often the case that fish price per unit mass is not constant, but increases with body size.

Another matter of concern for many catadromous species is that, in extensive environments such as lagoons, there is often little or no possibility of controlling food, water temperature, predators, and parasites (Bardach et al. 1972). Growth rates and survivorships are strongly sensitive to the physical and biological environment where the population lives and can be quite variable from year to year (Hofmann and Powell 1998). Therefore, management strategies devised on the basis of population dynamics models should explicitly consider environmental variability as well as uncertainty in parameters estimation, as these

factors can dramatically affect the actual outcome of a bioeconomic analysis (Hilborn and Ludwig 1993). Fortunately, demographic uncertainty can be easily included (Mangel 1985, Walters 1986, Hilborn 1987) to produce estimates, not just of the mean expected economic return, but also of its variability. Nonparametric techniques, such as Monte Carlo simulations and bootstrapping, can be very powerful in this respect (Meyer et al. 1986), because they can provide flexible and robust methods for evaluating the economic performance of a fishery in a variable environment.

Here, we develop these ideas with reference to the fishery of the European eel (*Anguilla anguilla*) of the Comacchio lagoons. It is a very interesting testing ground for the analysis of optimal exploitation policies of structured populations in a variable environment, because this population is fairly well known, as it has been studied for decades (Colombo 1972a, b, Rossi and Colombo 1979, Gatto et al. 1982, Rossi et al. 1987/1988). The Comacchio eel fishery of the Comacchio lagoons has a particular historical and ecological importance. It has been the most important in the Mediterranean sea for longevity, fishing area, and landed biomass. It has been operating for several centuries exploiting the free services provided by nature, namely the natural recruitment of elvers (the young eels) from the sea into the lagoons, the growth of prereproductive individuals (the so-called yellow eels) inside the lagoons, and the natural migration of the reproductive adults (silver eels) from the lagoons to the sea. The yield of the Comacchio fishery has been traditionally represented only by silver eels, which are caught during migration at the sluice gate connecting the lagoons to the sea. Archeological sites show that the eel fishery of the Comacchio lagoons was already exploited in the Roman period. The local economy thrived throughout the centuries, deeply interwoven with the fabric of the lagoons' natural environment. Up to the middle 1970s, the eel fishery had been very productive, with an annual yield of >15 kg/ha. But starting from the middle 1970s, the catch dropped to a few kilograms per hectare and has not recovered since. The ultimate reasons for this decline are still largely unknown, even though they must be somehow related to a general reduction of natural recruitment in the North Adriatic Sea, which might be partially dependent upon local phenomena occurring in the lagoons (De Leo and Gatto 1996). Comacchio managers responded to the drop in commercial catch by starting a program of elver restocking in the second half of the 1980s. As the amount of elvers restocked in each of the three lagoons was highly variable from year to year, the benefits of this policy have never been fully understood. Similarly, the effectiveness of fishing a suitable fraction of yellow eels has never been tested in practice, although this management scheme is common in other Italian lagoons.

In this work, we assess whether the status of the traditional silver eel fishery can be improved by im-

plementing yellow eel fishing and/or elver restocking. While previous studies of eel population dynamics, carried out by Gatto and Rossi (1979) for the same fishery, Vøllestad and Jonsson (1986) for Hallangspollen bight (Norway), and Vøllestad and Jonsson (1988) for the Imsa River fishery (Norway), were based on classical age-structured models, which do not fully account for the complexity of the eel's life cycle, the present analysis is performed by using a detailed model of eel population dynamics. It is based on a multiple classification of individual by age, size, and sex. The central assumptions are that sexual maturation is a function of eel body size and natural mortality is a function of age. We presented the model in a previous paper (De Leo and Gatto 1995). Estimation of model parameters from data collected in 1989 and 1990 by Carrieri et al. (1992) allowed us to evaluate natural survivorship; the rate of metamorphosis from yellow to silver type; and abundance and biomass per age, size class, and gender (De Leo and Gatto 1995). A nonparametric calibration procedure (bootstrapping) allowed the estimation of the expected value of demographics rates along with their probability distributions. These demographic results are the basis for the stochastic bioeconomic analysis of the Comacchio fishery over a range of management strategies.

The work is organized as follows. In the first part of the paper, we briefly review the basic information required to understand the subsequent bioeconomic analysis, namely the eel's life cycle in the Comacchio lagoons, the available data and the main feature of the demographic model. Then, we outline a number of management schemes corresponding to different harvesting regimes for yellow eels (in terms of effort and mesh size of the fishing gear) and to different policies of elver restocking. We briefly describe how the catchability coefficient, the selectivity of the fishing gear, and the costs per unit effort have been estimated. We then define the indicators of economic performance used to evaluate the different harvesting and stocking policies. As environmental variability affects the production of the lagoons, we use information on the probability distribution functions of model parameters (De Leo and Gatto 1995) to explicitly track year-to-year variations in commercial catch and economic return. On this basis, we derive optimal management policies and then conduct a sensitivity analysis with respect to different discount rates, fishing costs, market prices, and demographic rates corresponding to different eel density. The different management alternatives are finally discussed in the light of these results.

BACKGROUND INFORMATION

Eel life cycle and the Comacchio lagoons

The Valli di Comacchio are three shallow water lagoons of ~10 000 ha located in northern Italy (Fig. 1). Eel recruitment in Comacchio is not related to the abun-

dance of mature individuals in the three lagoons. In fact, although the population is distributed over most of the northern hemisphere waters between 30° W and 45° E in its nonreproductive life stages, the European eel can be regarded as one population with almost complete panmixia. The overall spawning stock is thus represented by all the silver eels that successfully migrate from Europe and North Africa to a common area in the Sargasso Sea; recruitment to the Comacchio lagoons consists only of the fraction of elvers that reach the North Adriatic coast as they migrate to feeding sites. The elvers enter the lagoons through the sluice gates and remain in this environment for a variable number of years as yellow eels. Here they feed and grow as yellow eels until they metamorphose into silver eels and migrate to the ocean for spawning. Time to sexual maturation changes with respect to gender and population density (De Leo and Gatto 1996): in 1989, the mean age of silver females was ~9 yr and that of males, ~5 yr. During migration, which occurs mostly in winter during October–February, silver eels are *all* caught at the sluice gates by means of special devices called “lavorieri,” which consist of a series of V-shaped screens. Therefore the annual yield of Comacchio is represented by the overall silver eel population, while yellow eels are only incidentally caught at the fishing stations.

Available data

The present study is based on data sampled in several field experiments performed by researchers of the Dipartimento di Biologia Evolutiva, University of Ferrara during 1976–1990. A detailed description of the available information is reported in Carrieri et al. (1992) and De Leo and Gatto (1995, 1996). Data gathered in 1989 and 1990 have been used to calibrate and validate the model. In autumn 1989, a stratified random sample of 970 silver eels (486 kg) was extracted from the autumn catch at the lavorieri (66 900 kg). As yellow eels are not commercially fished, 2869 specimens (729 kg) were caught by fyke nets (the traditional fishing gear for eels) in the spring of 1989, and a stratified random sample of 791 individuals (175 kg) was extracted. The lengths and masses of all specimens were measured (in units of centimeters and grams, respectively). Age and sex ratios for yellow and silver eels were determined only from subsamples. In the spring of 1990, 840 yellow eels (318 kg) were extracted from a 1424-kg sample (Carrieri et al. 1992) and then measured for length and mass. We refer to De Leo and Gatto (1995) for further details.

Market prices per unit mass depend upon the developmental stage and size of eel. As reported in Table 1 (1990 prices), silver eels are always more valuable than yellow eels. Moreover, the price per unit mass increases with eel size. All fishing activities are managed by a single public company (Consorzio Azienda Speciale Valli di Comacchio [Si.Val.Co.]). The gross

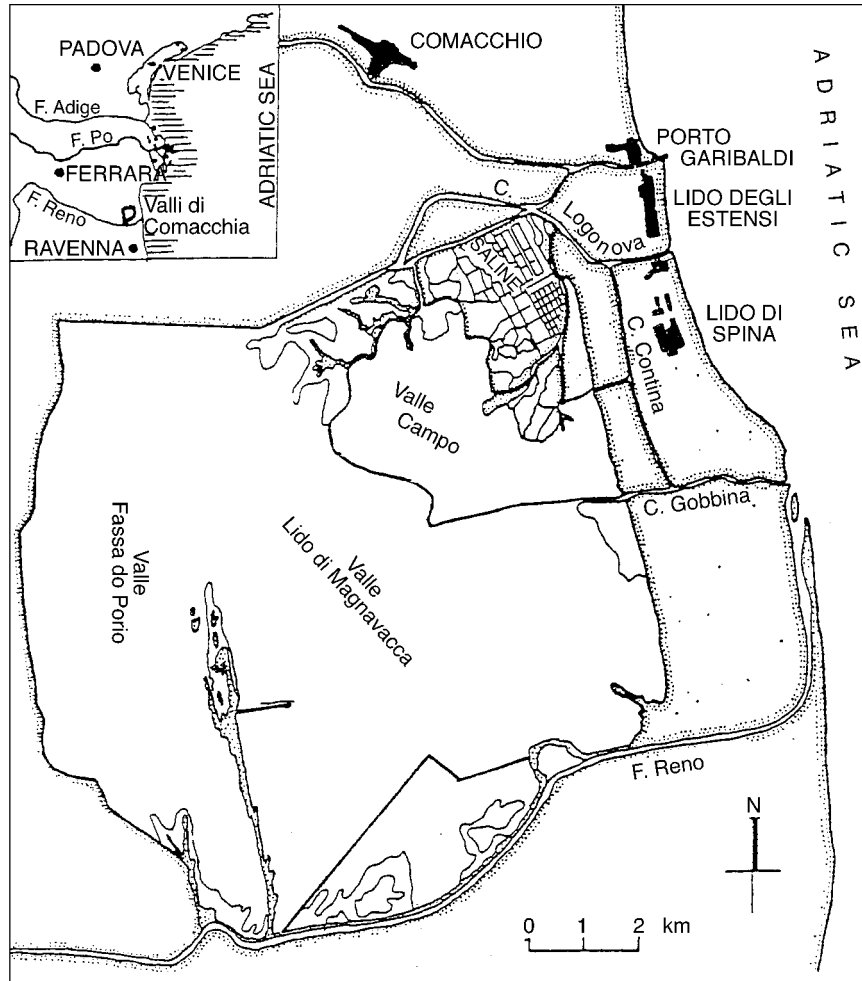


FIG. 1. The Valli di Comacchio lagoons, Italy.

economic return from eels (other fish species are harvested in the lagoon) was $\sim 1 \times 10^9$ Italian lire in 1990. Unfortunately, a detailed report of management costs has never been made available, although the company

is known to generate negligible or negative profit since the decline of the silver eel catch.

DEMOGRAPHIC MODEL

The demographic model used in this work has been presented in detail elsewhere (De Leo and Gatto 1995); here, we review only its essential features to understand how the mathematical framework has been used to assess the effectiveness of different management strategies. De Leo and Gatto's (1995) size- and age-structured model is based on a multiple classification of individuals by gender, size, and age class. The model explicitly includes stochasticity in individual growth by using the so-called "assignment-at-birth" model derived by Kirkpatrick (1984). Therefore, the actual length $l(x)$ of an individual at age x is the product of the median length $L(x)$ at age x and a growth factor g randomly assigned to each fish. The growth factor g is distributed according to a lognormal distribution function with unitary median and has been estimated by fitting a Von Bertalanffy growth equation to age-length

TABLE 1. Mean prices (given in 1990 Italian lire/kg [IL/kg]) of yellow and silver eels.

Mean eel mass (g)	Yellow eels (IL/kg)	Silver eels (IL/kg)
0-50	0	0
50-70	0	0
70-100	0	0
100-130	8 000	10 500
130-150	9 500	12 000
150-175	10 000	12 500
175-225	10 000	12 500
225-270	12 000	14 000
270-400	13 000	15 500
400-600	13 500	15 500
600-800	13 500	15 000
800-1000	13 000	15 000
1000-1200	13 000	14 500

data for each sex. Correspondingly, the size of a newly recruited individual (age x_0 , which is conventionally set to 1 yr; Gatto and Rossi 1979) is a random variable having a lognormal probability density with median $L(x_0)$. Length–mass relationships were also derived for both yellow and silver eels.

Other important aspects of eel vital rates accounted for by the model are as follows:

1) Natural mortality: It is assumed to be age dependent, according to a Weibull distribution of the age at death (Fig. 2a) and is thus characterized by two parameters, one for scale (b) and the other for shape (c); mortality is concentrated mainly in summer.

2) Sexual maturation: As suggested by Vøllestad and Jonsson (1986), the rate of sexual maturation is assumed to be a sigmoidal increasing function of size (Fig. 2b). The expected fraction of yellow eels of size l undergoing metamorphosis to the sexually mature silver stage, $\gamma(l)$, is characterized by three parameters (De Leo and Gatto 1995): γ_{\max} (≤ 1), the maximum rate of metamorphosis (which is set to 1 for males); λ , a semi-saturation constant; and η , a parameter inversely related to the slope of the metamorphosis function at $l = \lambda$.

3) Sexual dimorphism and sex ratio: Separate probability distributions have been used for females and males to account for sexual dimorphism. Accordingly, different growth curves $L(x)$, growth factors g , and metamorphosis functions $\gamma(l)$ have been assumed for the two sexes. On the contrary, males and females are assumed to share the same survivorship function. The fraction of females at recruitment has been set equal to the observed value (94%).

A set of recursive equations, reported in De Leo and Gatto (1995), propagates over time the probability density distribution of body sizes of a cohort of newly recruited individuals. Survival, the metamorphosis function for males, that for females, and natural recruitment were estimated by De Leo and Gatto (1995, 1996) by using data sampled in 1989 and 1990. To evaluate uncertainty in parameter estimation, a bootstrap procedure (Efron 1982), which closely follows the original sampling design (Pelletier and Gros 1991, Carrieri et al. 1992), was implemented by recombining the data 1000 times (De Leo and Gatto 1995). 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 computed by using the frequency distributions of the bootstrap replicates. The main results are reported in Table 2. Fig. 2a, b shows the annual survival and metamorphosis function. The mean expected recruitment is 136 ± 66 individuals/ha, or equivalently 1.2 ± 0.6 kg/ha; its probability distribution is shown in Fig. 2c. The abundance of yellow eels in each age and size class has also been estimated with the model and is reported in Table 3. This information is of particular interest because, while silver eel abun-

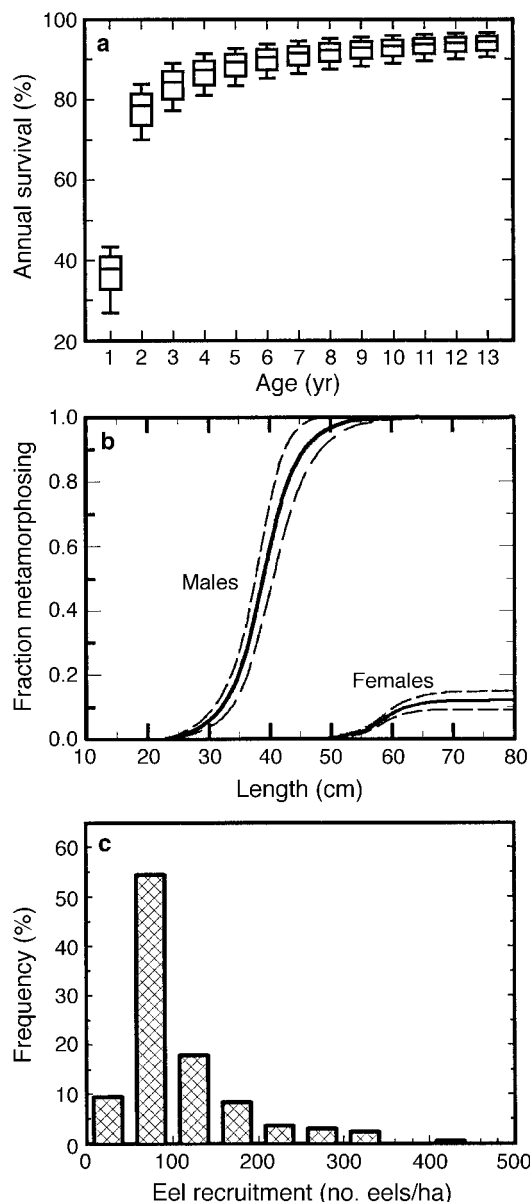


FIG. 2. (a) Age-specific survival estimates (median, 5th, 25th, 75th, 95th percentiles) resulting from the bootstrap distribution of model parameters. (b) Expected length-specific metamorphosis function (± 1 SE) for males and females. (c) The bootstrap probability distribution of natural recruitment. All these parameters have been estimated from 1989 data by using a nonparametric procedure (bootstrapping) reported in De Leo and Gatto (1995) and validated against 1990 data.

dance per age and size class was easily estimated from catch data, that of yellow eels was never established directly from sampling.

Environmental variability and uncertainty in parameter estimation have been simulated by running the demographic model several times with values of natural recruitment, survival rate, and metamorphosis rate randomly drawn from the 1000 bootstrap replicates de-

TABLE 2. Model parameters used to simulate eel population dynamics.

Parameters	Expected value	1 SD
b	0.98	0.54
c	0.30	0.07
γ_{\max}^F	0.12	0.03
λ^F	58.40	0.76
λ^M	39.10	1.63
η^F	2.40	0.50
η^M	2.80	0.52
R	136.80	66.64

Notes: Parameters b and c are the scale and shape parameters of the Weibull survival function, respectively; γ_{\max}^F , λ^F , and η^F are the coefficients of the metamorphosis function for females, and λ^M and η^M are those for males (γ_{\max}^M is known to equal unity); R is the natural recruitment. The values of these parameters have been estimated from 1989 data by using a nonparametric procedure (bootstrapping) reported in De Leo and Gatto (1995), and then validated against 1990 data.

rived in De Leo and Gatto (1995). A matter of concern is whether the procedure of utilizing the bootstrap distribution of model parameters is reasonable for the purpose of estimating the statistical significance of the economic performance under different management policies. In general, the variance of demographic parameters is composed of two components: one reflects the uncertainty and/or errors in parameter estimation; the other is related to the natural variability of the parameters to be estimated, namely recruitment, mortality, and sexual maturation (the environmental stochasticity component). Unfortunately, we were not able to discriminate between the two of them, but from a management perspective this limitation should not be considered dramatic. Management decisions need to be taken on the basis of the best available predictions and their uncertainty, whatever the source of this uncertainty. A realistic bioeconomic assessment must account for both the variability of the environment and the prediction power and precision of the model used to forecast the future population dynamics.

A further concern is whether the data used to identify the model were nevertheless sufficient to provide information on environmental variability. Of course, the ideal thing would be to have a long time series of data. Unfortunately, size distributions were measured for two years, and the model was calibrated against these data only (Spring 1989, Winter 1989–1990, Spring 1990, and Winter 1990–1991). However, to temper this concern, one should consider that the size distributions for yellow and silver eels used for calibration comprised several cohorts (eels can be ≤ 15 yr old) and are therefore representative of several years of eel history and recruitment into the lagoons. Therefore, we are confident that the bootstrap estimates do convey information on between-years variability, as well.

MANAGEMENT POLICIES

The model we describe allows us to explore the consequence of changes in the traditional management of

the fishery, according to which only silver eels are harvested by using lavorieri. In particular, we want to investigate whether the profitability of commercial harvest can be improved by (1) allowing a suitable quota of yellow eels to be caught by fyke nets every year before they die or metamorphose to silver eels, and (2) increasing the recruitment by restocking elvers. Interest lies in the first policy, because yellow eel harvesting is a common practice in other Italian lagoons where the traditional fishing technique of Comacchio for silver eels (the lavorieri) is not used. The second policy, elver restocking, has been irregularly implemented for a few years during the 1980s–1990s, although its effectiveness has never been quantitatively tested.

Yellow eel fishing

The fishing season for yellow eels is assumed to last one month and start in late winter/early spring, right at the end of the silver eel fishing season. In this sense, yellow eel fishing should briefly extend the traditional fishing season and follow the seasonal pattern of market demand, which peaks in middle winter. Since the yellow eel fishing season does not overlap with the silver eel fishing season, which occurs in winter, in the following we will refer to the yellow eel season as the spring fishing season and to its catch as the yellow eel spring catch to distinguish it from the silver eel winter catch.

Yellow eels are fished by fyke nets. Given the size of the lagoons (10 000 ha), a maximum number of 500 fyke nets can be realistically considered. The number of yellow eels caught in one day is here assumed to be proportional, through a coefficient q , to the abundance of yellow eels in the lagoon, the number E of fyke nets (fishing effort) and their selectivity $\Phi_m(l)$ (a function of eel size l and mesh size m), namely,

$$\sum_{x=1}^{15} \int qE\Phi_m(l)Y(x, l, t) dl \quad (1)$$

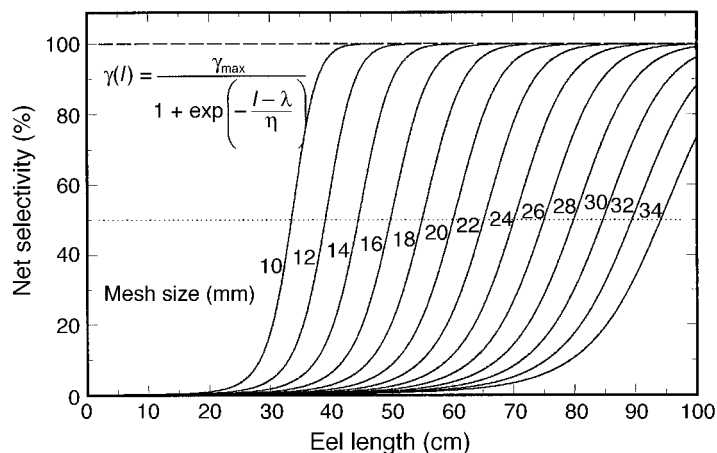
where $Y(x, l, t)$ is the number of yellow eels of age x and size l in spring of year t , and 15 yr is the maximum

TABLE 3. Expected eel density (kg/ha) of yellow and silver eels in 1989, according to sex, size, and age groups.

Measure- ment	Yellow eels (spring)		Silver eels (autumn)	
	Male	Female	Male	Female
Length (cm)				
<30	0.09	1.35
30–45	0.12	4.68	0.08	...
>45	...	56.14	...	6.07
Total	0.21	62.17	0.08	6.07
Age (yr)				
1–2	0.06	3.00
3–7	0.15	25.63	0.08	2.19
≥ 8	...	33.55	...	3.88
Total	0.21	62.17	0.08	6.07

Note: Figures for yellow eels refer to spring (age x); those for silver eels refer to autumn–winter (age x^+).

FIG. 3. Selectivity curves of fyke nets as a function of eel length for mesh sizes 6–34 mm (as indicated by numbers in the interior of the figure).



age. The catchability coefficient q can be considered as the probability that an eel encounters one of the fyke nets, and the selectivity function $\Phi_m(l)$ as the probability that an eel encountering a net with mesh size m is actually caught.

This policy is thus characterized by two decision variables: (1) the mesh size m , which determines net selectivity; and (2) the number E of fyke nets used (i.e., the fishing effort). The overall yellow eel biomass caught in 30 d at the beginning of spring of year t can be computed as follows (see the Appendix for further details):

$$YC_m(t) = \sum_x \int \{1 - [1 - qE\Phi_m(l)]^{30}\} Y(x, l, t)w(l) dl \quad (2)$$

where $w(l)$ is the mean mass of an eel of size l .

Selectivity of the fishing gear.—Fyke net selectivity (Φ) obviously depends upon the size of the mesh, because larger mesh sizes allow for the selection of larger individuals only. As explained in De Leo and Gatto (1995), we have thus assumed that the fraction Φ of eels caught in the net is an increasing saturating function of the eel's size. The selectivity $\Phi_m(l)$ is reported in Fig. 3 for different mesh sizes m .

Catchability coefficient of fyke nets.—To estimate the catchability coefficient q (namely, the fraction of yellow eels caught in one day by one fyke net), we have used information on yellow eel catch in 1989–1990 and the estimated yellow eel abundance in the same years. During March–April 1989, in Valle Magnavacca, one of the Comacchio lagoons, 580.8 kg were caught in 23 d by using one fyke net, i.e., 23.6 kg/d. During the same season in 1990, 921.6 kg were caught in 36 d, namely 25.6 kg/d. We have thus assumed that one fishing gear catches on average ~ 25 kg/d. Since in 1989 Comacchio lagoons were harboring $\sim 623\,800$ kg of yellow eels (De Leo and Gatto 1995) as shown in Table 3, the catchability coefficient q of fyke nets has

been computed as the ratio between the mean fyke net catch and total abundance, namely,

$$q \cong 25/623\,800 = 4 \times 10^{-5}.$$

Harvesting costs per unit effort.—As yellow eels are not commercially fished in the Comacchio lagoons, to derive yellow eel fishing costs, we have interviewed the director of Consorzio Azienda Speciale Valli di Comacchio (G. Cavallini) and extrapolated results from other brackish water bodies where fyke nets are used to fish commercial species. Nine workers (three for each of the three lagoons) can manage ~ 100 fyke nets: they have to set the fyke nets in the lagoons at the beginning of the spring fishing season, check them on a regular basis, and land the daily catch. The gross wages per person for the fishing season is $\sim 4.5 \times 10^6$ 1999 Italian lire (IL). One hundred fyke nets cost $\sim 50 \times 10^6$ IL and may last ~ 5 yr before being replaced; therefore, their annual cost can be assumed to be 10×10^6 IL. The cost of 100 fyke nets and labor sum to 50.5×10^6 IL for the fishing season. Therefore, cost per unit effort is about $\sim 0.5 \times 10^6$ 1999 IL. As the data used to calibrate the model were sampled during 1989–1990, and thus reflected eel dynamics and their density in those years, we have scaled fishing costs to 1990 IL by using a 1.4 conversion factor provided by the Italian Institute of Statistics. Thus, we assume a cost per fyke net of $\sim 0.34 \times 10^6$ IL. As this figure may be affected by uncertainty or variations of the actual cost of labor force and/or fishing gear, we have performed a sensitivity analysis of the net economic return over a wide range of fishing costs per fyke net, namely from 0 – 1×10^6 1990 IL.

Elver restocking

Elvers cost $\sim 14\,000$ IL/kg (1990 prices). Elvers are usually caught on the Atlantic coast in Portugal or France where they are taken by the Gulf Stream from the Sargasso Sea. A fraction of restocked elvers ($\sim 20\%$) dies right after the introduction into the la-

goon, because of the stress of transportation and differences in water salinity and temperature (Rossi et al. 1988).

Two scenarios are analyzed. In the first one, all restocked elvers are assumed to be 1-yr-old and indistinguishable from natural recruitment, thus sharing the same size distribution, growth rate, survival, and metamorphosis function. However, an analysis performed by Carrieri et al. (1992) revealed that the age and size structure of restocked elvers can be quite different from that of naturally recruited elvers: in 1990 a considerable fraction of stocked elvers had a mean body size similar to that of local 1-yr-old individuals, but was actually aged 2–4 yr. These specimens thus lie in the left tail of the size distribution of their naturally recruited siblings at any given age. Such slow-growing eels contribute to the catch much less in terms of biomass than the natural recruitment (as reported in Carrieri et al. [1992], it seems that fast-growing elvers are in fact sold preferably to intensive rearing operations where they can guarantee high revenues in a short time). As a consequence, we have analyzed a second scenario of bad-quality elvers, in which the amount of stocked elvers is distributed over different age classes (namely, 40% in age class 1, 30% in class 2, 20% in class 3, and 10% in class 4), with fish belonging to the left tail of the size distribution of their corresponding age class.

OPTIMIZATION CRITERIA

Optimal harvesting has been assessed in terms of annual marginal net economic return (NER), i.e., the difference between extra revenues and extra costs of new fishing policies with respect to traditional management (based only on the silver eel catch at lavorieri). In fact, fishing a lot of yellow eels in spring will obviously reduce the winter catch; only if the overall net benefit of the new policy (yellow eel fishing by fyke nets *plus* silver eel catch at lavorieri) is larger than that of traditional management (silver eel catch *only*), can this policy be justified. Similarly, elver stocking makes sense only if the net benefit of this policy (revenues minus the cost of stocking) is larger than that obtained by doing nothing other than catching silver eels at lavorieri. Details on how to compute annual revenues and costs from the demographic and economic parameters are reported in the Appendix.

Management strategies have been evaluated over a period of 30 yr, and fishing effort and mesh size have been assumed constant during this time. Abundance and age/size structure of the yellow eel stock at the beginning of the simulation has been assumed to coincide with those of the 1990 spring population. To properly discount future benefit, we have calculated the present value of the mean annual net economic return (MANER) as follows:

$$\text{MANER} = \frac{1}{30} \sum_{j=0}^{29} \frac{\text{NER}(j)}{(1 + \delta)^j} \quad (3)$$

where δ is the discount rate and $\text{NER}(j)$ is the net economic return in year j (see the Appendix for further details). To simulate uncertainty in parameter estimation and environmental variability, for each of the 30 yr values of natural recruitment, survival rate, and metamorphosis rate have been randomly drawn from the 1000 bootstrap replicates derived in De Leo and Gatto (1995). For any policy, each 30-yr simulation has been replicated 500 \times to derive statistics on economic performance.

To find the best policy, we have exhaustively explored all realistic values of the fishing effort and mesh size, and we have found the policies that maximize the mean value of MANER over the 500 replicates. Then, a sensitivity analysis of the bioeconomic results was performed with respect to (1) different discount rates, (2) different total costs of effort due to different costs of labor, and (3) different market prices of silver and yellow eels. Finally, we have investigated how MANER is affected by restocking different amounts of elvers.

RESULTS

Yellow eel fishing

The average (computed over the 500 replicates) of the mean annual net economic return (MANER) as a function of fishing effort is reported in Fig. 4, for different mesh sizes and a zero discount rate, along with the 5th and 95th percentiles. The traditional management of Comacchio lagoons (only silver eel winter catch with no restocking) is represented by a zero fishing effort in Fig. 4. The corresponding average mean annual gross economic return (computed over the 500 replicates) is $1012 \pm 66 \times 10^6$ IL. Therefore, annual marginal net economic returns (NERs) are computed as the extra profits with respect to 10^9 IL. Catching yellow eels with an optimal effort can indeed increase the net economic return when intermediate mesh sizes are employed. The improvement is substantial, though not dramatic, if compared with the mean annual gross economic return from silver eel catch. Also, the analysis suggests that yellow eel fishing does not reduce the variability of mean benefit: after 30 yr, the extra benefits are positive, on average, for intermediate mesh size and moderate fishing effort; but, in $\sim 15\%$ of the simulations, the overall return is still $<10^9$ IL, even with the best policy.

The joint effect of different efforts and mesh sizes on the average MANER is reported in Fig. 5. Fig. 5a shows that, for any mesh size, the average MANER first increases with fishing effort, then decreases. Fig. 5b shows the eumetric curve (Beverton and Holt 1957), i.e., the curve that provides the maximum net benefit for any selected fishing effort, when the optimal mesh size is employed. It is clear that, with respect to traditional management, an improvement of the net economic return can be achieved with moderate fishing

FIG. 4. Mean annual net economic return (in millions of 1990 Italian lire and with zero discount rate) as a function of fishing effort (number of fyke nets used), for four different mesh sizes (12, 16, 20, and 24 mm). The thick line indicates the mean annual net economic return averaged over 500 replicates, each of 30 yr (Eq. 6), while the two thin lines indicates the 5th and 95th percentile, respectively.

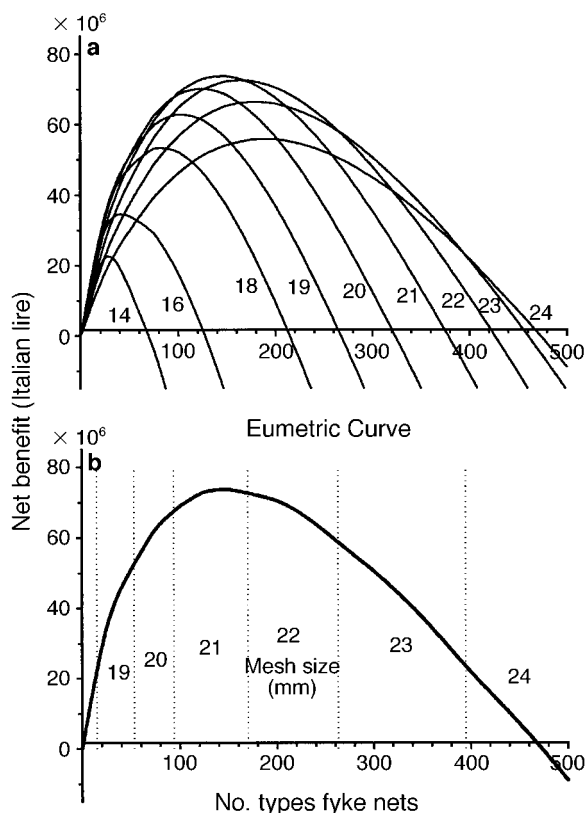
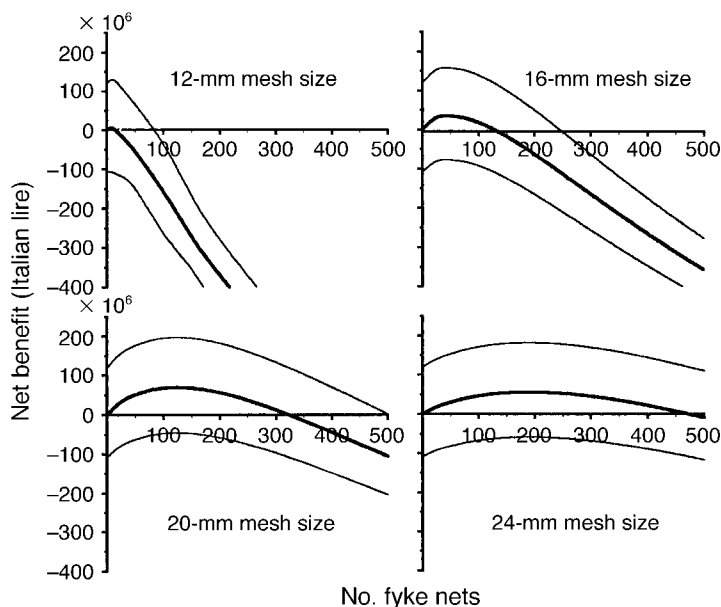


FIG. 5. (a) Mean annual net economic return (MANER; in millions of 1990 Italian lire) for zero discount rate and mesh sizes of 14–24 mm. (b) Corresponding eumetric curve for MANER as a function of fishing effort. Numbers in the interior of the figure indicate the mesh size (mm) that maximizes the mean net economic return.

effort. Best policies are characterized by intermediate mesh size (20–22 mm) and moderate fishing effort (100–200 fyke nets). The maximum expected net benefit (74×10^6 IL) can be achieved with 150 fyke nets and a 21-mm mesh size.

Therefore, the mesh size should be large enough to select only the larger size classes, but not so large (>22 mm) as to require high fishing efforts, whose cost will exceed the revenue from the yellow eel fishery. In fact, yellow eels are always less valued than silver eels. On the other hand, small mesh sizes (<14 mm) are non-optimal for any effort. The reason is twofold. First, fishing too many very small individuals prevents them from growing up into larger eels, and this can even lead to a reduction of the overall harvested biomass (yellow + silver eels catch) with respect to traditional management (i.e., only silver eel fishing). Secondly and most importantly, small yellow eels have little or no value on the marketplace: therefore, when fished at moderate effort, they can increase the overall harvested biomass, but provide little or no income to make up for the reduction of silver eel revenue.

It is to be remarked that optimal policies are heavily affected by the explicit inclusion of economic indicators. In fact, the best policies in terms of economic return imply that ~ 7 – 10% of the standing yellow eel biomass is harvested every year. This effort is substantially smaller than the one maximizing mean harvested biomass. We have calculated that the latter would imply harvesting 40% of the yellow eel biomass in the lagoon, corresponding to >500 fyke nets with large mesh sizes. Therefore, economic considerations may be very important: management policies that maximize yield are not necessarily the most efficient from an economic point of view and are not necessarily more conservative than those maximizing monetary benefits.

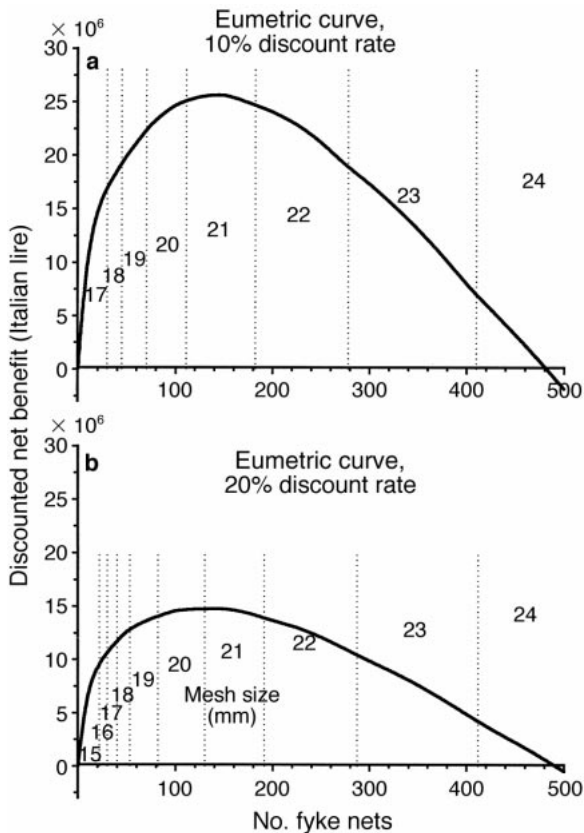


FIG. 6. The eumetric curve of mean annual marginal net economic return (NER) for discount rates of (a) 10% and (b) 20%. Numbers in the interior of the figure indicate the mesh size (mm) that maximizes the mean NER measured in 1990 Italian lire.

Sensitivity analysis

The results are pretty much insensitive even to high variations of the discount rates (0–20%), as shown in Fig. 6: the best policy always requires ~150 fyke nets with a 21-mm mesh size. The only relevant difference is that, if a small fishing effort is implemented (<100 fyke nets), eumetric fishing at high discount rates requires slightly smaller mesh sizes.

As cost per unit effort (0.34×10^6 IL) can be affected by errors in the estimation of the fyke net and labor cost, we have let the cost per unit effort (measured in 1990 lire) range $0-1 \times 10^6$ IL. Eumetric fishing is fairly insensitive to estimation error in fishing costs, as optimal mesh size always ranges 20–24 mm. If the fishing costs per fyke net are $<0.34 \times 10^6$ IL (say, 0.10×10^6 IL) the maximum benefit is obtained with higher fishing effort (300 nets) and larger mesh size (24 mm). On the contrary, a substantial increase of cost per unit effort (e.g., 10^6 IL) shifts the best policy toward smaller fishing effort (50 nets) and smaller mesh size (19–20 mm). Net benefit would not exceed 150×10^6 IL, even if cost per unit effort were zero.

Since silver eel catch is decreasing all over the North

Adriatic Sea, silver eel price may be expected to increase, because the quantity demanded at the current price can exceed the quantity supplied. Actually, in January 1999, market prices of yellow eels were only slightly higher than those of 1990 (a 10% increase), whereas silver eel prices had almost doubled. We have thus analyzed the sensitivity of MANER to an increase of silver eel prices. Our analysis shows that, if the gap between the market price of silver and yellow eels were much larger than in 1990, yellow eel fishing would not be profitable anymore: MANER would be negative regardless of the fishing effort and the mesh size used. This is because fishing yellow eels would prevent them from metamorphosing into much more valuable silver eels.

Elver restocking

The average (computed over the 500 replicates) MANER as a function of density of restocked elvers is reported in Fig. 7a for two different qualities of stocked material, high-quality elvers and low-quality elvers. No restocking corresponds to the traditional management of the Valli di Comacchio. Low-quality elvers also provide an increment of MANER, even though its actual value is always approximately half that corresponding to the same density of high-quality elvers. With respect to the traditional management, elver restocking proves to be effective even at high discount rates: net profit obviously decreases for increasing discount rates, but vanishes only at unrealistically high values of the discount rate, as shown in Fig. 7b. Moreover, the 90% confidence interval in Fig. 7a shows that even stocking only $0.5 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ provides a significantly positive MANER.

Therefore, elver restocking seems to be substantially more effective than harvesting yellow eels, at least for the present, low-density populations. If we assume that no density-dependent phenomena affect eel population dynamics (we will relax this assumption in *Density dependence*), supplementing the decreasing natural recruitment with elver restocking can greatly improve the NER. This is true also for high discount rates, thus showing that the policy is a robust tool for counteracting the current drop in natural recruitment. However, the availability of good-quality elvers is not a trivial problem. A large fraction of old, slow-growing individuals can dramatically reduce the benefits of this policy. If this policy is implemented, a rigorous check of the quality of restocked material should be performed on a regular basis.

DENSITY DEPENDENCE

The core of the bioeconomic analysis has been carried out with reference to the low-density yellow eel population observed in the 1990s. However, in a previous study, De Leo and Gatto (1996) had outlined the possibility of density-dependent feedbacks affecting eel population dynamics during the prereproductive

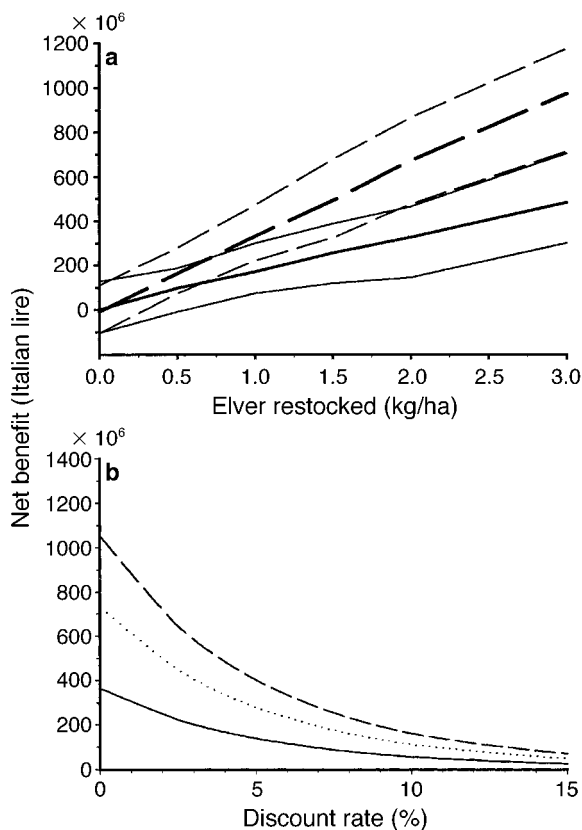


FIG. 7. (a) Mean annual marginal net economic return (NER; bold lines) as a function of different densities of elvers restocked, along with the 90% confidence interval (thinner lines). The dashed line corresponds to high-quality elvers, that is, elvers that share the same survival, growth, and metamorphosis potential of natural recruitment; the solid lines refer to low-quality elvers. (b) Mean annual NER as a function of discount rate for three different restocking densities.

stage of the life cycle: in the middle 1970s, when natural recruitment was estimated to be $15\times$ larger than that of the 1990s and yellow eel abundance $7\times$ bigger, eel mortality was substantially higher than in 1989 and yellow eels metamorphosed at considerably lower size. The effect of this change in vital rates at high eel density deserves to be investigated in a bioeconomic framework. In fact, by substantially increasing yellow eel density through elver restocking, there is the possibility of triggering density-dependent feedbacks that might offset the benefit of elver restocking. Unfortunately, the available data did not allow us to explicitly identify a density-dependent function for such demographic parameters. However, demographic parameters corresponding to the high-density population of the middle 1970s were estimated by De Leo and Gatto (1996). Therefore, to explore what might occur under a high-density scenario, we have performed an extra set of simulations by using these latter estimates of the demographic parameters.

Our analysis shows that, if yellow eel density were

high as it used to be in the middle 1970s, there would be no profit (actually a substantial loss of annual marginal net economic return [NER]) in further incrementing recruitment. Therefore, the amount of elvers to be restocked in the present, low-density situation should not exceed 5–6 kg/ha to avoid negative density-dependent feedbacks due to competition for food and space. A further complication is that sex ratio might be density dependent. In the low-density population of 1989–1990 the fraction of males (which are substantially smaller than females and have little or no market value) was practically negligible (De Leo and Gatto 1996), while at high density the fraction of males in the population may increase up to 30%, as observed in the middle 1970s (Rossi and Colombo 1979). This means that at high density an important fraction of stocked fish will not metamorphose into valuable (yellow and silver) females, with a substantial loss of revenue. This phenomenon has not been explicitly included in the present analysis, but, needless to say, does not encourage a policy of massive elver restocking. Anyway, given the size of the Comacchio lagoons (10 000 ha), it would seem unrealistic to exceed the figure of 5–6 kg/ha.

On the contrary, fishing yellow eels improves the mean annual net economic return (MANER) even when eel density is high. In this case the extra net annual benefit amounts to about $\sim 140 \times 10^6$ IL (when cost per unit effort is 0.34×10^6 IL) which is $\sim 6\text{--}8\%$ of the gross economic return that could be obtained from fishing silver eels only (namely, 1.70×10^6 IL). Optimal fishing would require larger fishing effort (300 nets) and smaller mesh size (18 mm) than in a low-density population. The increase in optimal fishing effort is due to an increase in natural mortality caused by density dependence: as more yellow eels are likely to die before they can metamorphose to the silver stage, it is more profitable to catch a larger fraction of them than to wait for them to turn into more valuable silver eels. The use of a smaller mesh size (compared to that applied in a low-density population) is due to another consequence of density dependence: in a crowded environment, both yellow and silver eels are substantially smaller than in a low-density population (De Leo and Gatto 1996).

CONCLUSIONS

We have presented a detailed bioeconomic assessment of alternative policies to manage traditional silver eel fisheries. The analysis has been performed by using a hybrid model based on a multiple classification of individuals by age and size that allowed us to realistically mimic the complex eel life cycle. We explicitly considered environmental variability and uncertainty in parameter estimation, while analyzing different management scenarios. The bootstrap replicates produced in the calibration phase proved useful to assess uncertainty of future economic performances and to identify

which management policies might lead to benefits that are expected to be significantly positive.

Accounting for size separately from age was crucial to properly include bioeconomic parameters such as size-dependent and stage-dependent market prices and selectivity of fishing gear. As already stressed by Gates (1975) and Richardson and Gates (1986), the omission of population size structure in bioeconomic models may yield policy conclusions that are quantitatively, and in some cases qualitatively, inaccurate. Our analysis shows, for instance, that management policies maximizing yield are radically different than those maximizing economic return. This is because size-specific price differentials can substantially change the economic value of fished biomass, depending upon the actual distribution of the catch in the different size classes. Also, to the extent that both price per kg and mass increase with eel body size, the optimal harvest rule tends to be more conservative (and less sensitive to changes in the discount rate) than is suggested by simpler models that do not account simultaneously for population structure and plasticity in body growth. In fact, even a small increase in eel's length may result in a substantial gain in the economic output, because price increases more than exponentially with eel size, and this can offset the effect of discount rate.

It must be stressed that, if age and body size were strictly related, there would be no problem in expressing size-dependent parameters (such as price and gear selectivity) as a function of age. But variability in growth rate may be so high that this would be practically impossible or highly debatable. For instance, Gatto et al. (1982) applied an age-structured population model to the same Comacchio eel fishery to investigate different fishing rules. Yet, in their work, optimal policies were expressed in terms of age classes to be harvested on the basis of knife-edge fishing gear selectivity. It was thus difficult to translate their recommendations in practice (that is, which mesh size to implement), as fishing gear is obviously a smooth function of body size, not of age. Moreover, the use of age-dependent market prices was questionable. As prices are size-dependent, eel's age is a poor indicator of its body size, and no size dispersion was included in their model. As a consequence, their suggestion of fishing only old specimens (≥ 10 yr of age) seems excessive in the light of our findings and should be replaced as "fishing eels of intermediate size (regardless of their age)".

A number of practical, specific conclusions can be deduced from the bioeconomic analysis of the Comacchio fishery. First, catching also yellow eels in an optimal way can increase net economic return, but the improvement is not dramatic. Second, if fishing yellow eels is implemented, fishing effort should be moderate (~ 8 – 10% of the standing yellow eel biomass), and the mesh size should be sufficiently large to select only intermediate size classes (i.e., 20–22 mm). Third, elver

restocking seems to be substantially more efficient than fishing yellow eels, at least for present low-density populations. Fourth, a comprehensive sensitivity analysis shows that these results are rather insensitive to yellow eels fishing costs; that fishing yellow eels is convenient as long as differences between yellow and silver eels' price are rather small; and that elver restocking is very profitable only when population density is not too high.

We are conscious that these results refer to the management of a local population and should not be generalized, as such, to the entire stock of European eel. Obviously, if managers of all European eel fisheries applied the traditional fishing method implemented in Comacchio, where all the sexually mature eels are caught at the sluice gates by means of *lavorieri*, the Atlantic-wide population would be rapidly overfished. Our results apply as long as there are other unregulated brackish and freshwater systems where mature eels are able to escape fishing and reestablish the spawning stock. On the other hand, the generalized drop of European eels' catch along with that of other related species, such as the American eel (ASMFC 1997), may well be a sign of overexploitation of elver and/or silver eels, loss of suitable habitat due to pollution or land reclamation, lack of up and downstream passages for migrating eels, and impact of the seaweed harvest on the spawning stock in the Sargasso Sea (ASMFC 1997). A large-scale, comprehensive monitoring and management program, as currently pursued by the American Eel Plan Development Team for *Anguilla rostrata*, is thus required to assess the status of the overall European eel population and define a sustainable fishing mortality accounting for the joint impacts of all fisheries and the detrimental effects of other disturbance factors, such as water contamination, habitat loss, and obstacles to migration.

Despite these caveats, we are confident that the conceptual framework used for modeling the specific case of the European eel demography in the Comacchio lagoons can be easily extended to other eel fisheries in Italy (e.g., the lagoons of Valle Nuova, Polesine, Otranto, etc.) and in Europe (Vøllestad and Jonsson 1986, 1988, Amin 1997, Desaunay and Gueault 1997, Holmgren et al. 1997, White and Knights 1997), as well as to other related eel species that are commercially exploited. We believe that our approach, which makes joint use of age- and size-structured demography, modern nonparametric statistics, availability of modern computing power, and basic concepts of fishery economics, is an effective contribution to efficiently managing these important renewable resources.

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APPENDIX

Here we briefly review the equations used to compute the yellow eel catch and the economics indicators. We refer to De Leo and Gatto (1995, 1996) for the complete demographic model used to describe the continental phase of the European eel life cycle (i.e., from the recruitment of elvers to the sexual maturation into silver eel).

YELLOW EEL SPRING CATCH

If yellow eel fishing is implemented, the number of eels harvested can be computed as follows. Let $Y(x, l, t)$ be the joint probability distribution function of x and l for yellow eels, namely the number of x -yr-old yellow eels having size l at the beginning of the spring fishing season in year t . After fishing for one day with E fyke nets of mesh size m , the number of yellow eels left in the lagoon, $Y(x, l, t)_1$, is thus

$$Y(x, l, t)_1 = [1 - qE\Phi_m(l)]Y(x, l, t)$$

where q is the catchability coefficient and $\Phi_m(l)$ the net selectivity.

It follows that 30 d later

$$Y(x, l, t)_{30} = [1 - qE\Phi_m(l)]^{30}Y(x, l, t).$$

The overall yellow eel catch [biomass] is thus

$$YC_m(t) = \sum_x \int \{1 - [1 - qE\Phi_m(l)]^{30}\} Y(x, l, t)w(l) dl$$

where $w(l)$ is the mean weight of an eel of size l .

ECONOMIC RETURN

Revenues deriving from the yellow eel spring catch are computed as follows:

$$\sum_x \int p_Y(l) \{1 - [1 - qE\Phi_m(l)]^{30}\} Y(x, l, t) dl \quad (\text{A.1})$$

where $p_Y(l)$ is the size-dependent market price for yellow eels, as reported in Table 1.

Similarly, revenues deriving from the silver eel winter catch are computed as follows:

$$\sum_x \int p_S(l^+) S(x^+, l^+, t^+) dl \quad (\text{A.2})$$

where $S(x^+, l^+, t^+)$ is the number of x^+ -yr-old silver eels having size l^+ at the beginning of the winter fishing season in year t^+ (the sign “+” indicates that silver eel catch occurs approximately six months after the yellow eel spring catch in year t) and $p_S(l)$ is the size-dependent market price for silver eels, as reported in Table 1.

Fishing costs for yellow eels are computed as the product of price per unit effort times the number E of fyke nets implemented. The cost of elver restocking is computed as the product between elver price per kg and the overall abundance of elver restocked in the Comacchio lagoons in a given year.