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Multi-objective assessment of conservation measures for the European eel (*Anguilla anguilla*): an application to the Camargue lagoons

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The European eel (*Anguilla anguilla*) stock has declined since the early 1970s and is currently considered to be outside safe biological limits. The European Commission has proposed a regulation (COM 2005/472 final) to establish measures for the recovery of the stock, with the aim of achieving an escapement to the sea of 40% of the adult eel biomass (with respect to undisturbed conditions) from each river basin. The proposed regulation imposes an effective reduction of fishing activities until implementation of an approved eel management plan. We use a demographic model, explicitly accounting for age, length, and sex structure, and important features of the continental phase of eel life cycle, to assess the effectiveness of the proposed regulation. We explore alternative management options with reference to the Camargue (southern France) eel population. Using multi-criteria methods, we compare different fishing policies with respect to two potentially conflicting objectives: preserving a sufficient spawner escapement and guaranteeing an acceptable harvest to fishers. We show that the current fishery is inefficient and that appropriate management policies (such as limiting the fishing season and increasing the mesh size of fishing gear) are likely to have a doubly positive effect, by achieving the conservation target of the regulation and increasing fisher revenues.

Keywords: *Anguilla anguilla*, conservation plans, demographic models, European eel, multi-objective analysis, Pareto analysis, sustainable fisheries.

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Introduction

Available information on the status of the European eel *Anguilla anguilla* stock and its fisheries supports the view that the stock has declined severely in most of its distribution area. The stock is currently considered to be outside safe biological limits, and current fisheries are not sustainable (Dekker, 2003a, b; ICES, 2003). The decline is likely to be caused by a number of factors, the relative importance of which is still debated: oceanic climate change, water pollution and contamination, habitat loss, overexploitation at all developmental stages, and human-caused transfer of parasites and diseases (Castonguay *et al.*, 1994; Robinet and Feunteun, 2002; Dekker, 2003b; Knights, 2003; Palstra *et al.*, 2005, 2006).

The development of active conservation policies has been recognized as a fundamental task for the maintenance of the European eel stock and the sustainability of a huge number of small-scale fisheries depending on its commercial harvest (Dekker, 2003a). An EU Regulation for the recovery of the European eel stock was proposed in 2005 by the European Commission and is currently under discussion. The main point of the proposed regulation is the establishment of eel management plans at a river basin scale, with the aim to "achieve the objective of a 40% escapement of adult silver eel from each river basin (measured with respect to undisturbed conditions)" (CEC, 2005). One option in the proposal is to impose the closure of the fishery in a river basin for 15 d each month until the relevant Member State has implemented an approved eel management plan aimed at achieving the 40% escapement objective.

The choice of conservation measures to ensure eel survival rests with Member States. Possible conservation measures that could form part of eel management plans include a reduction of yellow eel fishing effort, a reduction of silver eel fishing effort during autumn to facilitate the downstream migration of adult eels, increases in restocking, improvements in water quality, modifications to water management aimed at improving eel migration, reduction of recreational fishing, and assisted migration. Social and economic consequences of different choices among proposed measures should be assessed on a local scale. The key element of the proposal is that "a failure to act will result in a disappearance of all eel fishing and aquaculture sectors if the stock decline continues" (CEC, 2005).

As anticipated, the proposal generated great concern among fishers. Along the Mediterranean coasts of France, the European eel is the most important species of fish from a socio-economic

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viewpoint (Loste and Dusserre, 1996). Its artisanal fisheries account for some 70% of total revenues of professional fishers (Lefebvre *et al.*, 2003). Eel catches from French Mediterranean lagoons peaked in the 1970s and started dropping in the mid-1980s. By the early 1990s, they had reached a minimum, where they remain to this day (COGEPOMI, 2006). Local fishers claimed that the decline should not be ascribed to fishing pressure, but rather to habitat loss, pollution, and climate change. A recent ICES report argued, in contrast, that overfishing might have had a major impact also in the Mediterranean Sea (ICES, 2005). Also, fishers declared that the objective of a 40% escapement of mature eels is already met in southern France, because many coastal streams are not being exploited.

To assess the effectiveness of the proposed EU Regulation and its impact on the existing fishing activities, it is necessary to (i) evaluate the present status of local stocks, (ii) estimate their abundance under undisturbed conditions, and (iii) assess the potential effects of different conservation measures. As alternative management strategies may have different ecological and socio-economic consequences, the effectiveness of measures to be implemented need to be evaluated according to at least two (potentially contrasting) criteria: preservation of a sufficient spawner escapement, and maintenance of an acceptable harvest by fishers.

Here, we use an updated version of the demographic model proposed by De Leo and Gatto (1995) to assess the consequences of different management policies on the status of the Camargue eel stock. De Leo and Gatto's (1995) model is here modified to account for the specific characteristics of the Camargue eel population, then used to estimate the output of silver eels from the lagoons and the harvest by local fishers corresponding to different mesh sizes of nets and levels of fishing effort. Finally, a Pareto analysis is performed to identify the fishing policies that provide the best compromise between the two conflicting objectives of maximizing the escapement of silver eels and maximizing the harvest.

Material and methods

Study site

The Camargue water system (Rhône River delta, southern France) consists of two major watersheds (Figure 1): the Impériaux lagoon (4600 ha) and the Vaccarès lagoon (6400 ha). The lagoons are isolated from the two arms of the Rhône River (Grand Rhône and Petit Rhône) and from the Mediterranean Sea by dykes. Water flow between the lagoons and the sea is regulated by sluice gates at Grau de la Fourcade, near Saintes Maries de La Mer. Water management is aimed mainly at maintaining low water levels inside the lagoons (to prevent the flooding of Saintes Maries de La Mer and to ensure the drainage of cultivated land) and low levels of salinity (to avoid damage to rice fields).

Demographic model

De Leo and Gatto (1995) developed a size- and age-structured demographic model for the European eel population of the Comacchio lagoons (Po River delta, northern Italy). The model is based on a multiple classification of individuals by sex, size, and age class. It was successfully used to describe the demography of the local eel stock and to perform a bioeconomic analysis of the silver eel fishery in the same lagoons (De Leo and Gatto, 2001). The model accounts for the main features of the eel life cycle: strong sexual dimorphism, high plasticity in body growth, and size-dependence of differentiation and the maturation processes. Body growth was described by a classical von Bertalanffy curve, with different parameters for females and males. Here, we use a modified version of De Leo and Gatto's (1995) model, suitably adapted to account for the peculiarities of the Camargue eel population and for some features which were not included in the original model (interannual variability of glass eel recruitment, and density-dependent juvenile survival). To describe body growth, we use the model proposed by Melià *et al.* (2006) for the Camargue eel population, which accounts for delayed sex

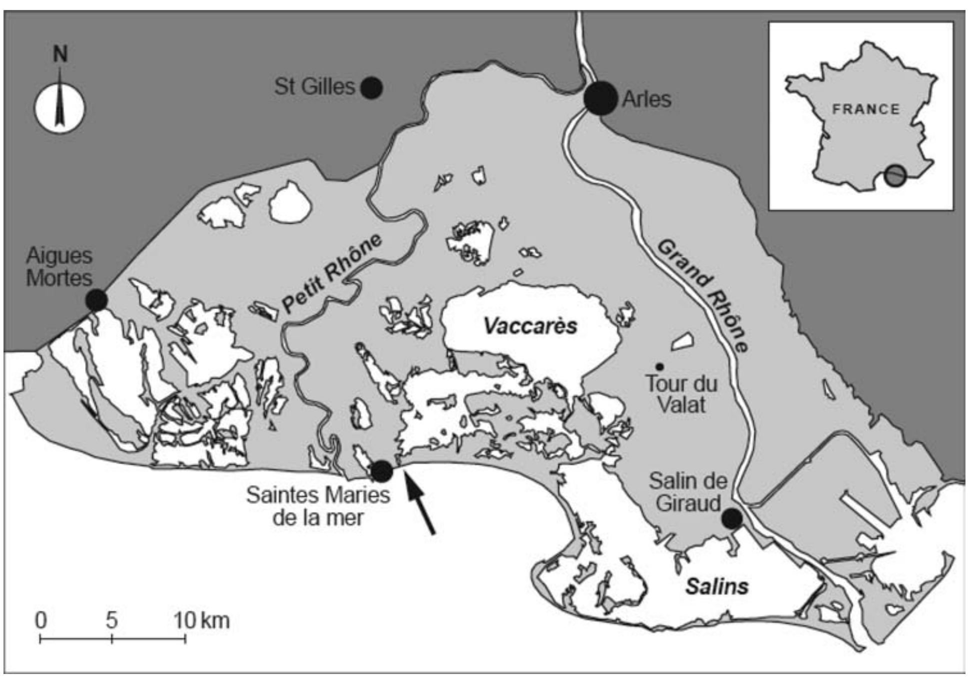

Figure 1. The Camargue water system. The arrow indicates the position of the Fourcade sluice gates.

differentiation by adopting three distinct growth curves for undifferentiated, female, and male eels. Then, we link sexual maturation to body length through a sigmoid curve (De Leo and Gatto, 1995), adapted to the Camargue by Bevacqua *et al.* (2006).

As the total number of glass eels entering the Camargue water system each year is unknown, we assume it to be proportional to the annual catch per unit effort (cpue) of glass eels. Experimental catches of glass eels were made periodically between 1993 and 2003 by the Tour du Valat Biological Station (using a fry net with a 0.5 mm mesh and a 20 m leading net) to monitor recruitment variability. As fluctuations in glass eel abundance are strongly dampened in the yellow eel population, we assume a density-dependent survival rate from the glass eel to the elver stage (small, sexually undifferentiated yellow eels of ~65–75 mm). This is in accord with previous work reporting evidence of density-dependent juvenile survival in the European eel (Vøllestad and Jonsson, 1988; De Leo and Gatto, 1996). Therefore, we link elver abundance to glass eel cpue through a Beverton–Holt function. To represent natural mortality, we use the relationship proposed by De Leo and Gatto (1995), which links the survival rate to eel age through a Weibull function. As for fishing mortality, we assume the rate to be proportional, through a catchability and a selectivity coefficient, to the fishing effort.

The effectiveness of the fishing device used in Camargue, the so-called capétchade (an eel pot with a 40 m guiding net, called a paradière), is linked to eel body length and mesh size through a selectivity curve (Figure 2), obtained from the method proposed by De Leo and Gatto (1995). The average monthly fishing effort during the past decade was reconstructed on the basis of information gathered by the Tour du Valat Biological Station and is shown in Figure 3. Mathematical details on the formulation of the model are provided in the Appendix. The model was calibrated by fitting the simulated length structure and biomass of the catch to that observed by the Tour du Valat Biological Station during the period 1993–2003. Data were aggregated into 50-mm length classes, and into trimesters. Also, because silver eels in the catch constituted a small fraction of the total catch, maturation categories (yellow/silver) were pooled, and sex categorization (undifferentiated/male/female) was maintained.

Management scenarios

The model allowed us to estimate the present structure of the Camargue eel population and provides us with a tool to predict its fate under different scenarios. To this end, we ran the model from the present state of the stock on by feeding it with a constant eel input (958 000 elvers year^{-1}), corresponding to the median recruitment estimated by the model for the years 1993–2003. To characterize candidate management policies, we consider two decision variables: the mesh size of fishing devices, and the fishing effort. The nets currently used in the Camargue have a 6 mm (knot-to-knot) mesh in derogation to the national law that enforces a 10 mm mesh size for the eel fishery in the rest of France. The selectivity of a 6 mm mesh size is zero for eels with total length <100 mm, and becomes 100% for fish >176 mm (Figure 2). As Camargue eels reach this length after ~1 year's growth in the lagoons (see Figure 5 of Melià *et al.*, 2006), 6 mm capétchade nets are definitely highly selective, especially if it is considered that in most northern European countries, fishing devices start being effective only at sizes >300 mm. For these reasons, we analyse the consequence of increasing mesh size up to 24 mm.

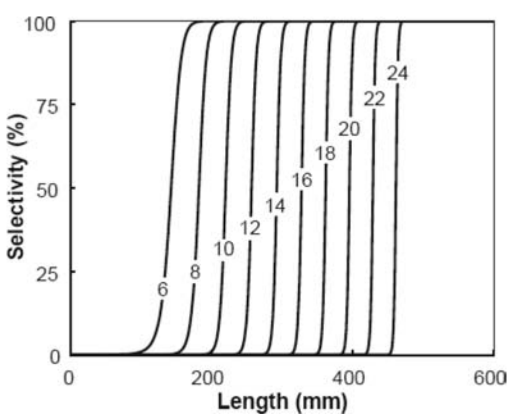

Figure 2. Selectivity of capétchade nets with different mesh sizes.

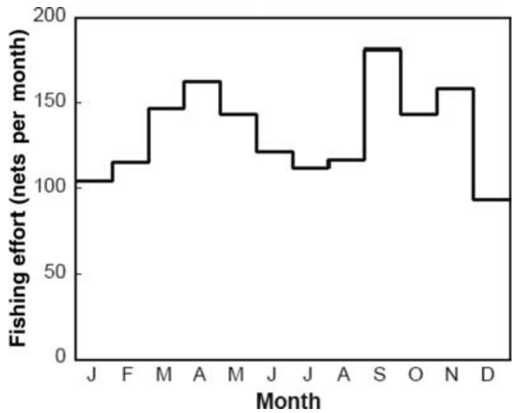

Figure 3. Average fishing effort in the Camargue lagoons by month, 1993–2003.

For fishing effort, we consider six effort-limitation rules, representing different management alternatives:

(i) to maintain the present fishing effort (baseline scenario);

(ii) to completely close the fishery (an approximation of undisturbed conditions);

(iii) to halve the present fishing effort by imposing a 15-d closure each month (the original EU proposal in the absence of approved management plans);

(iv) to impose a seasonal summer closure (following fishers' practice to reduce fishing effort then);

(v) to impose a seasonal autumn closure (to facilitate downstream migration of adult eels);

(vi) to impose a seasonal winter closure (following fishers' practice to reduce fishing effort then).

The model was run over a 7-year period (i.e. from 2003 until 2010). As the maximum residence time of an eel in the Camargue lagoons is ~6 years (Melià *et al.*, 2006), this time horizon is sufficient to ensure that the population structure has approximately reached the regime.

Multi-objective analysis

By running the model with different values of decision variable, we evaluated the performances of all management policies resulting from a combination of mesh sizes of 6–24 mm with the different effort limitation rules listed above. The performance of each policy was evaluated with respect to two potentially conflicting objectives: to maximize spawner output from the lagoons, and to maximize the harvest by Camargue fishers. Although, with our model, optimal management of the fishery with respect to maximizing spawner output alone is straightforward (the spawning output is at a maximum when the fishing effort is zero), the same does not hold for the maximizing the harvest. On the other hand, if the stock is exploited beyond its productive limits, because the effort is too high or the mesh size too small, the fishery may become inefficient. The maximum harvest is usually achieved at intermediate exploitation levels (Clark, 1990). Therefore, to identify the best management policies with respect to the socio-economic objective, we looked for the optimum mesh size corresponding to the different effort-limitation rules considered.

Then, to highlight possible trade-offs between the two objectives and to determine the management policies providing the best compromise between them, we performed a multi-objective analysis. Multi-objective analysis provides a useful framework for the development of realistic management policies in fisheries when multiple and conflicting objectives are to be considered (Enriquez-Andrade and Vaca-Rodriguez, 2004), and has been used to rationalize the management of a range of fisheries (Sylvia, 1992; Pan *et al.*, 2001; Enriquez-Andrade and Vaca-Rodriguez, 2004). Following classical theory for multi-objective analysis, we identify the Pareto-efficient alternatives, i.e. the management policies for which it is not possible to modify decision variables to improve one performance indicator (for instance, the abundance of the spawner output) without worsening at the same time the other performance indicator (i.e. catch abundance). Then we excluded all Pareto-dominated policies, i.e. those management alternatives for which there existed at least another feasible policy that guaranteed both a larger harvest and a better spawner output. The non-dominated policies identify the so-called Pareto boundary. Hereafter, we use the term "optimal" to refer to the best performing policies with respect to a single objective, and we denote as "Pareto-efficient" those policies belonging to the Pareto boundaries determined through the multi-objective analysis.

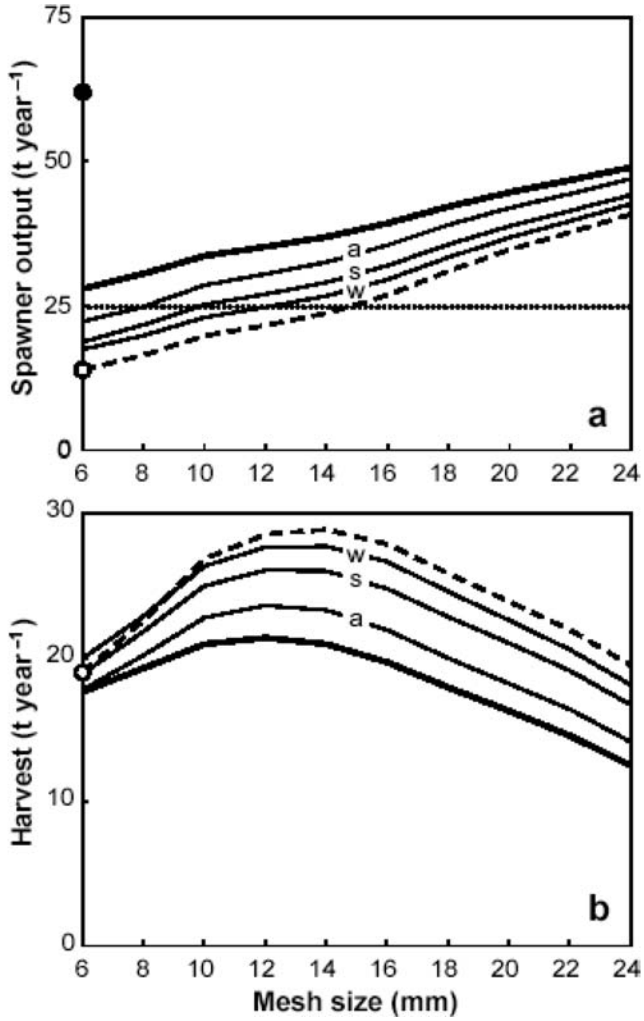

Figure 4. Performances of different fishing policies as determined by different mesh sizes: (a) spawner output, and (b) total annual harvest. Dashed lines represent current levels of fishing effort, bold lines represent halved effort (a 15-d monthly closure), and thinner lines depict seasonal closures (s, summer; a, autumn; w, winter). The filled circle represents complete closure, and the open circle the current fishery. The horizontal dotted line indicates 40% of the spawner output in undisturbed conditions. Recruitment was assumed to be constant and equal to the median of that observed between 1993 and 2003.

Results

Single-objective analysis

Figure 4 shows the effect of different fishing policies on the local stock with respect to the two objectives, considered one at a time. Under the hypothesis that recruitment remains constant and equal to the median of the past 11 years, and assuming that the closure of every fishing activity provides a reliable proxy for the undisturbed conditions referred to by the regulation proposal, we estimate a maximum potential spawner output of about 62 t (this estimate could be higher if an increase in the spawning stock positively affects reruitment, and if such benefits are taken into account in the calculations). However, the annual output of silver eels under the present fishing pressure is estimated to be ~14 t. Under the current management system, the spawner output would therefore be only 22% of the potential output, far below the conservation target of the regulation (40% of the potential output), i.e. ~25 t.

The spawner output (Figure 4a) increases almost linearly with the mesh of the fishing gear, at least in the range of mesh sizes considered. To ensure achievement of the conservation target under the current level of fishing effort, the mesh of the nets should be increased from the present 6 mm to at least 16 mm. Alternatively, a 50% reduction in effort would guarantee the required escapement even if the mesh size remained unchanged. Among seasonal effort-reduction policies, the most effective is the closure of the fishery in autumn, which preserves silver eels from being captured just before leaving for the ocean.

Annual catches (Figure 4b) are estimated to stabilize, given the present fishing effort, mesh size, and a constant recruitment, at ~19 t year^{-1}. However, an increase of the harvest to 29 t year^{-1} (under the same effort) could be achieved by increasing the mesh size to 16 mm. This would indeed shift the fishing pressure from younger, undifferentiated eels <200 mm to older fish

Table 1. Optimal and Pareto-efficient mesh sizes (in mm) corresponding to different effort-limitation rules (see text), as obtained with the single-objective (maximizing harvest) and the multi-objective (maximizing harvest and spawner output) analyses, respectively.

Effort-limitation rule	Optimal mesh size (single-objective)	Pareto-efficient mesh range (multi-objective)
(a) Baseline scenario	14	14–24
(b) Complete closure	–	–
(c) 15-d closure	12	20–24
(d) Summer closure	12	16–24
(e) Autumn closure	12	16–24
(f) Winter closure	14	22–24

Note that scenario (b) (complete fishery closure) is Pareto-efficient (and obviously does not depend on mesh size) and has no interest for the single-objective analysis, because harvest is zero. In contrast, a 14-mm mesh (although optimal/Pareto-efficient) does not respect the EU conservation target under the baseline scenario.

>300 mm (Figure 2). Our analysis shows that for all the fishing strategies considered, the optimal mesh size (with respect to maximizing catches) would be between 12 and 14 mm (Table 1). Within this range, all effort-limitation rules would guarantee better catches than present management. Above a mesh size of 14 mm, catches are expected to decrease, but to remain greater than those predicted under current management scenarios, for mesh sizes up to 16–24 mm (depending on effort).

Multi-objective analysis

Changing fishing effort with respect to the present level obviously has an opposite effect on spawner output and catch: spawner stock always decreases with increasing fishing effort, whereas catch increases with fishing effort (in this case, it is the constant recruitment assumption that supports the continuous increase in catches). Similarly, spawner output and catch react differently to changes of the fishing gear, the former increasing with mesh size, and the latter being a unimodal function of mesh size. The results of the multi-objective analysis can help decision-makers understand the trade-off between the two objectives. Figure 5 shows the performances of the fishing policies considered above in relation to the two objectives. It is evident that there is a range of Pareto-efficient policies (summarized in Table 1), corresponding to different effort-limitation rules and mesh sizes. The current fishery is clearly inefficient, because there are several policies, also outside the Pareto-set, providing both better catches and greater adult escapement. Whatever the effort, the minimum mesh necessary to achieve efficiency is always ≥14 mm (Table 1). This corroborates the belief that the current mesh is far too selective to preserve the reproductive potential of the eel population. It is of note that a simple reduction in fishing effort, not associated with the development of a specific management plan, would achieve the conservation target, but would be unfavourable to fishers, whose catches would be reduced with respect to present management.

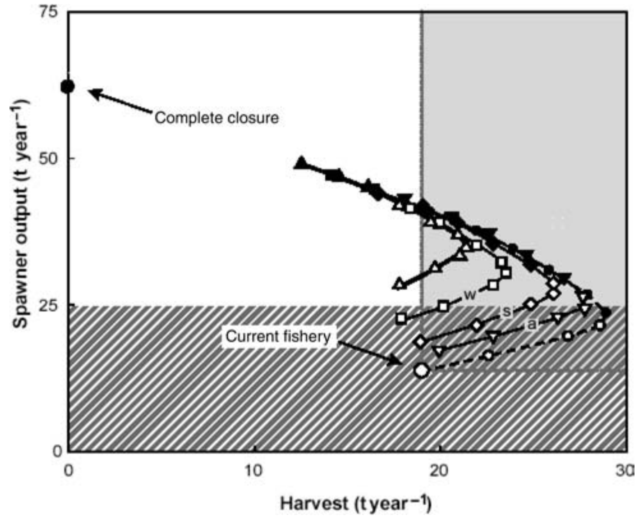

Figure 5. Pareto analysis with respect to the two management objectives (maximizing spawner output, and maximizing catches). Each symbol represents a management policy (effort-limitation rule plus mesh size). Filled symbols refer to Pareto-efficient policies (Pareto boundary), open symbols to non-efficient policies, the dashed line connecting the circles is the current fishing effort, the heavy line connecting normal triangles is the halved effort (a 15-d monthly closure), and the thin lines connecting inverted triangles, diamonds, and squares refer to seasonal closures (a, autumn; s, summer; w, winter). Policies within the shaded area dominate the current fishery with respect to both objectives, whereas the hatched area identifies non-feasible policies, i.e. those not respecting the conservation target.

Transition regime

The predictions of harvest and spawner output reported above refer to a regime situation, provided that recruitment remains constant through time. However, increasing the mesh from the current to a larger size would certainly cause a temporary decline in catches, until juvenile eels (currently the main target of the fishery) have grown to the minimum size retained by the new mesh size. To assess the impact of this phenomenon on the fishery, we focus on the dynamics of the catch during the transition. Figure 6 shows estimated catches between 1999 and 2003 and those predicted between 2004 and 2010 under three different policies, respectively, aimed at: (i) maintaining current exploitation levels (both effort and mesh size), (ii) maximizing the catch while respecting the conservation target of the regulation (current effort, 16 mm mesh size), and (iii) maximizing the spawner output without decreasing the catch of the regime (summer closure, 22 mm mesh size). Monthly catches are characterized by extremely broad fluctuations between 1999 and 2003, attributable to the combined effect of recruitment variability and the seasonal fluctuations in fishing effort. In contrast, predicted catches between 2004 and 2010 show only seasonal fluctuations, because recruitment is supposed to remain constant from year to year. Moreover, annual catches between 1999 and 2002 were influenced by two exceptional recruitments, in 1998 and 2000.

At current levels of exploitation, annual catches are expected to decrease from about 32 t in 2003 (and a median catch of 45 t year^{-1} between 1999 and 2003) to about 19 t. Under the second scenario, catches are expected to remain below those obtained under current levels of exploitation during the first 2

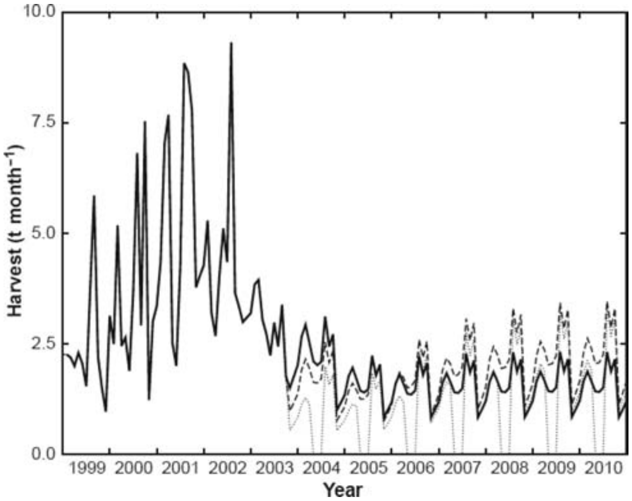

Figure 6. Estimated (1993–2003) and predicted (2004–2010) monthly harvest during the transition towards different regimes determined by different management scenarios. Solid line, current fishery; dashed line, maximum harvest compatible with EU adult-escapement targets; dotted line, maximum adult escapement not affecting current annual catches.

years (−5.4 and −1.7 t, respectively), but to exceed 20 t year^{-1} by the third year after changing the mesh size. In the long term, the second management scenario would produce an annual catch of about 29 t. Under the third scenario, catches would undergo a marked decrease during the first 3 years (−15.2, −8.5, and −5.5 t, respectively), and reach a catch of 19 t year^{-1} only after roughly 7 years, with an overall loss to the fishery of some 39 t before the end of the transition.

Discussion

The results of our analysis support the view that, at present, the Camargue eel fishery is inefficient with respect to the two objectives of maximizing spawner output and catches.

In fact, the use of highly selective fishing devices such as those employed by Camargue fishers decreases productivity by focusing the fishing pressure on younger eels. The goal to guarantee a 40% escapement of adult eels from the Camargue lagoons could be achieved without significant changes in the productivity of the fishery, provided that a suitable management policy is adopted.

One wonders what the reasons are for this inefficiency, in particular considering that the current mesh size is far below the minimum allowed by French law. A major cause is that the current mesh allows fishers also to catch small fish species, such as the sandsmelt *Atherina boyeri* (30–70 mm long). Although eels are still the target of the fishery, the declining catch during the past two decades may have induced fishers to decrease the mesh size to compensate for their reduced harvest, causing a further increase in the fishing pressure on eels. Moreover, there could be a market demand for catches containing small eels to be resold to aquaculture plants, in France and elsewhere. A comprehensive analysis of the eel market would provide a better understanding of fisher behaviour and possibly influence the range of acceptable management policies. Decision-makers should take into account these issues when trying to identify feasible ways to increase the efficiency of the local fishery.

Our results suggest that an effort-limitation rule based on a 15-d fishery closure each month would have a very positive effect on spawner output. However, it would have a negative effect on fisher revenues if no action were taken to impose the use of fishing devices with a larger mesh. Also, strict monitoring of fishing effort by local authorities would be necessary to ensure that effort does not intensify during periods when fishing is allowed, to compensate for losses during the closures. A seasonal closure of the fishery is likely to be easier to manage than intermittent monthly closures. In any case, the analysis shows that decision-makers can choose among a number of management policies that should achieve the regulation's objectives, while concurrently increasing the catch significantly.

In our analysis, we assumed recruitment to remain constant, consistent with the available data from the Camargue, which do not suggest any decline since the early 1990s. However, the effectiveness of different management policies will depend critically on the actual number of elvers settling in the lagoons each year. If recruitment decreases appreciably in future, the conservation target of the regulation might become unattainable even if the fishery were to be closed completely and permanently. In contrast, a substantial increase in recruitment might allow fishers to meet the target even without changing the current fishing policy, at least if density-dependent effects are limited to juvenile survival and do not have appreciable effects on older stages (as assumed in our model). In this case, the results of the Pareto analysis are indeed independent from the level of recruitment, because all scenarios are equally affected by a change in its magnitude.

Another critical point of the EU's regulation proposal is how to assess the "undisturbed conditions" that set the benchmark for the conservation target. The regulation makes a generic reference to "the absence of human activities affecting the fishing area or the stock". Such a pristine state, however, seems quite impractical to determine. If we refer to the pre-industrial era, we would lack any reference data. ICES (2006) suggests, when possible, using historical abundance data from the 1950s to the 1970s (depending on the specific stock) to set a reference point for undisturbed conditions. For sites where no historical data are available, such as the Camargue lagoons, the availability of a demographic model is of basic importance to assessing the dynamics of local populations in the absence of exploitation with respect to differing levels of recruitment. It is important to note, however, that fishing is not the only source of disturbance (although anthropogenic impacts in the Camargue natural reserve are likely to be relatively small compared with other environments). Hence, fishers might try to shift the attention onto alternative conservation measures, aimed at improving environmental conditions (such as a different management of sluice gates regulating water exchanges with the sea) rather than at rationalizing fishing. However, the efficiency of a fishery depends only on the choice of an appropriate fishing policy.

Our results refer to a brackish water system that forms only a part of a wider river basin, that of the Rhône River. The guidelines emerging from this study cannot be extended simply to the management of the whole basin without more investigation. However, correct management of the lagoons would have a positive impact on the spawner output of the whole basin and on local economy. Although the ideas analysed here are based on a detailed understanding of eel demography in the Camargue lagoon, the mathematical model we have derived can be adapted to simulate eel population dynamics in other coastal lagoons and rivers, provided the necessary data for calibration are available. Also, the multi-objective approach can be extended easily to include a complete bioeconomic analysis, integrating demographic knowledge and socio-economic information (such as market prices and fishing costs). For these reasons, the conceptual framework proposed here can provide a useful tool to reveal existing trade-offs between conservation and production objectives and to evaluate different exploitation policies from contrasting viewpoints.

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References

Bevacqua, D., Melià, P., Crivelli, J., De Leo, G. A., and Gatto, M. 2006. Timing and rate of sexual maturation of European eel in brackish and freshwater environments. Journal of Fish Biology, 69: 200–208.

Castonguay, M., Hodson, P. V., Couillard, C. M., Eckersley, M. J., Dutil, J. D., and Verreault, G. 1994. Why is recruitment of the American eel, *Anguilla rostrata*, declining in the St Lawrence river and gulf. Canadian Journal of Fisheries and Aquatic Sciences, 51: 479–488.

Clark, C. W. 1990. Mathematical Bioeconomics: the Optimal Management of Renewable Resources, 2nd edn. Wiley-Interscience, New York.

COGEPOMI. 2006. Programme de gestion de l'anguille sur les lagunes méditerranéennes 2006–2008. Direction Régionale de l'Environnement Rhône-Alpes Bassin du Rhône-Méditerranée, Lyon, France.

CEC. 2005. Proposal for a Council regulation establishing measures for the recovery of the stock of European eel. COM (2005) 472.

De Leo, G. A., and Gatto, M. 1995. A size and age-structured model of the European eel (*Anguilla anguilla* L.). Canadian Journal of Fisheries and Aquatic Sciences, 52: 1351–1367.

De Leo, G. A., and Gatto, M. 1996. Trends in vital rates of the European eel: evidence for density dependence? Ecological Applications, 6: 1281–1294.

De Leo, G. A., and Gatto, M. 2001. A stochastic bioeconomic analysis of silver eel fisheries. Ecological Applications, 11: 281–294.

Dekker, W. 2003a. On the distribution of the European eel (*Anguilla anguilla*) and its fisheries. Canadian Journal of Fisheries and Aquatic Sciences, 60: 787–799.

Dekker, W. 2003b. Did lack of spawners cause the collapse of the European eel, *Anguilla anguilla*? Fisheries Management and Ecology, 10: 365–376.

Enriquez-Andrade, R. R., and Vaca-Rodriguez, J. G. 2004. Evaluating ecological tradeoffs in fisheries management: a study case for the yellowfin tuna fishery in the eastern Pacific Ocean. Ecological Economics, 48: 303–315.

ICES. 2003. Report of the ICES/EIFAC Working Group on Eels. ICES Document CM 2003/ACFM: 06.

ICES. 2005. Report of the ICES/EIFAC Working Group on Eels. ICES Document CM 2005/I: 01.

ICES. 2006. Report of the Joint EIFAC/ICES Working Group on Eel (WGEEL), 23–27 January 2006, Rome, Italy. ICES Document CM 2006/ACFM: 16.

Knights, B. 2003. A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the northern hemisphere. Science of the Total Environment, 310: 237–244.

Lefebvre, F., Acou, A., Poizat, G., and Crivelli, A. 2003. Anguillicolosis among silver eels: a 2-year survey in 4 habitats from Camargue (Rhone Delta, South of France). Bulletin Francais de la Peche et de la Pisciculture, 368: 97–108.

Loste, C., and Dusserre, K. 1996. La pêche sur l'étang de Bages-Sigean. Evolutions de 1985 à 1995. CEPRALMAR Report, Montpellier. 100 pp.

Melià, P., Bevacqua, D., Crivelli, A. J., De Leo, G. A., Panfili, J., and Gatto, M. 2006. Age and growth of the European eel *Anguilla anguilla* in the Camargue lagoons. Journal of Fish Biology, 68: 876–890.

Palstra, A. P., Cohen, E. G. H., Niemantsverdriet, P. R. W., van Ginneken, V. J. T., and Van Den Thillart, G. 2005. Artificial maturation and reproduction of European silver eel: development of oocytes during final maturation. Aquaculture, 249: 533–547.

Palstra, A. P., van Ginneken, V. J. T., Murk, A. J., and van den Thillart, G. 2006. Are dioxin-like contaminants responsible for the eel (*Anguilla anguilla*) drama? Naturwissenschaften, 93: 145–148.

Pan, M. L., Leung, P. S., and Pooley, S. G. 2001. A decision support model for fisheries management in Hawaii: a multilevel and multiobjective programming approach. North American Journal of Fisheries Management, 21: 293–309.

Robinet, T. T., and Feunteun, E. E. 2002. Sublethal effects of exposure to chemical compounds: a cause for the decline in Atlantic eels? Ecotoxicology, 11: 265–277.

Sylvia, G. 1992. Concepts in fisheries management—Interdisciplinary Gestalt and socioeconomic policy models. Society and Natural Resources, 5: 115–133.

Vøllestad, L. A., and Jonsson, B. 1988. A 13-year study of the population dynamics of the European eel *Anguilla anguilla* in a Norwegian river: evidence for density-dependent mortality, and development of a model for predicting yield. Journal of Animal Ecology, 57: 983–997.

Appendix

Here, we provide a concise description of the model structure, in particular the equations of the submodels describing juvenile mortality from the glass eel to the elver stage, recruitment of elvers to the lagoons, body growth and sex differentiation, sexual maturation, and natural and fishing mortality of yellow and silver eels.

Recruitment

Recruitment to the Camargue lagoons has been monitored since 1993 by the Tour du Valat Biological Station. The absolute number of juveniles entering into the lagoons (G) cannot be measured directly in the field, but the observed annual cpue of glass eels can be used as a recruitment indicator. Observed fluctuations in the adult population are much reduced compared with those of juveniles, suggesting density-dependent survival from glass eel to elver. As cannibalism by adult eels on juveniles can be excluded on the basis of analyses of gastric contents (AJC., unpublished data), and no overcompensation effects have been observed in the Camargue population, we express recruitment at the elver stage (E) as a Beverton–Holt function of glass eel cpue C:

$$E = \frac{\alpha C}{\beta' + C},$$

where $\beta' = \beta/\kappa_R$. Calibration of the model (see main text) provided an estimate of α (8.97×10^6 net-months) and β' (14.22 eels net^{-1} month^{-1}).

Body growth and sex differentiation

We describe body growth with the model proposed by Melià *et al.* (2006) for the Camargue population, which accounts for sexual dimorphism and sex differentiation using three distinct growth curves for undifferentiated eels, males, and females:

$$L(x) = \begin{cases} L_0 + (L^* - L_0)\dfrac{1 - \exp(-k_U x)}{1 - \exp(-k_U x^*)} & \text{for } x \le x^* \text{(undifferentiated)} \\ L_{\infty F} - (L_{\infty F} - L^*)\exp(-k_F(x - x^*)) & \text{for } x > x^* \text{(females)}, \\ L_{\infty M} - (L_{\infty M} - L^*)\exp(-k_M(x - x^*)) & \text{for } x > x^* \text{(males)} \end{cases}$$

where L_0 is the length at metamorphosis to elver, L^* and x^* length and age at sexual differentiation, k_U, k_F, and k_M the Brody growth constants for undifferentiated eels, females, and males, respectively, and $L_{\infty F}$ and $L_{\infty M}$ the asymptotic mean lengths of females and males, respectively (see Melià *et al.*, 2006, for further detail and parameter estimates).

Sexual maturation

Following De Leo and Gatto (1995), we link sexual maturation to body length by assuming that the silvering rate is a sigmoid function of eel length L:

$$\gamma(L) = \frac{\gamma_{max}}{1 + \exp[(\lambda - L)/\eta]},$$

where γ_{max} is the maximum silvering rate, λ the average length at maturation, and η a shape parameter. Here, we use the curves calibrated by Bevacqua *et al.* (2006) for the Camargue eel population. These retain the formula proposed by De Leo and Gatto (1995), but with different parameter sets accounting for the differences between the two sexes and for monthly variations in silvering rates (see Bevacqua *et al.*, 2006, for further detail and parameter estimates).

Natural mortality

Under the hypothesis that density-dependence acts only in the early life stages, and that yellow and silver eel survivorship depends only upon age, we use the model proposed by De Leo and Gatto (1995), describing adult annual survivorship σ as function of age x:

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

where b and c are scale and shape parameters, respectively, of a Weibull age-at-death distribution. Although the De Leo and Gatto (1995) demographic model had an annual step, ours has a step of 1 month. Assuming that natural mortality acts only during spring and summer (De Leo and Gatto, 1995), we spread its effect over a 6-month span, from April to September.

Fishing mortality

We assume the rate of fishing mortality to be proportional, through a catchability coefficient q and a selectivity coefficient φ (depending on eel length, L) to the fishing effort E, measured as the number of nets multiplied by the fishing time:

$$F(L, t) = q\,E(t)\varphi(L).$$

Selectivity φ is linked to body length through the sigmoid model proposed by De Leo and Gatto (1995):

$$\varphi(L) = \frac{1}{1 + \exp[(\bar{A} - \rho^{-1} a L^{b-1})/\zeta]},$$

where $\bar{A}$ is the average section retained by the mesh of the net (29.07 mm^2 for the fishing device used by Camargue fisher, the so-called capétchade), ρ the relative density of an eel (assumed to be 1 g cm^{-3}), a and b the parameters of the length–weight relationship (estimates for the Camargue population are provided by Melià *et al.*, 2006), and ζ a shape parameter (=3.5 mm^2 for the capétchade). Calibration of the model (see main text) provided an estimate of q of 6.13×10^{-4} net^{-1} month^{-2}.

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