Conflicting objectives in trophy trout recreational fisheries: evaluating trade-offs using an individual-based model

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Abstract: Standard fisheries models, based on average population metrics, are inadequate for analyzing recreational fisheries where fishing is size-selective and management objectives are related to preserving population size structure. We developed a framework for policy analysis of size-based harvest strategies in recreational fisheries. The framework combines a mixedeffects body growth model and an individual-based harvest model to describe the relationship of growth, mortality, and size structure. Fishery performance is quantified with indicators directly associated to catch-related components of anglers' satisfaction: yield (kg), population size, and availability of trophy-size fish. We applied our analyses to the steelhead (*Oncorhyn-chus mykiss*) fishery in the Santa Cruz River (Patagonia, Argentina). Large declines in trophy-size fish are to be expected at fishing mortalities much too low to cause a sizeable decline in recruitment from virgin values. When somatic growth is density-independent, harvest occurs at the expense of other indicators associated with the quality of fishing experienced by individual anglers. Size limits provide a tool to better accommodate harvest without compromising fishing quality. When preserving population size is favored over preserving trophy-size fish, minimum size limits constitute the best policy overall, whereas maximum size limits are best when the emphasis is on preserving trophy-size fish.

Résumé : Les modèles standards de pêche, basés sur les métriques moyennes de la population, sont inadéquats pour analyser les pêches sportives dans lesquelles la pêche est sélective en fonction de la taille et les objectifs de gestion cherchent à conserver la structure en taille de la population. Nous avons mis au point un cadre pour l'analyse des politiques des stratégies de capture en fonction de la taille dans les pêches sportives. Le cadre combine un modèle à effets mixtes de croissance corporelle et un modèle de récolte basé sur l'individu afin de décrire la relation entre la croissance, la mortalité et la structure en taille. La performance de la pêche est déterminée à l'aide d'indicateurs directement associés aux composantes reliées à la capture dans la satisfaction des pêcheurs sportifs, soit le rendement (kg), la taille de la population et la disponibilité de poissons de taille trophée. Nous avons appliqué nos analyses à la pêche de truites arc-en-ciel anadromes (Oncorhynchus mykiss) de la rivière Santa Cruz (Patagonie, Argentine). On peut s'attendre à de forts déclins des poissons de taille trophée à des mortalités dues à la pêche beaucoup trop faibles pour causer une diminution substantielle dans le recrutement par rapport aux valeurs originales. Lorsque la croissance somatique est indépendante de la densité, la récolte se fait aux dépens des autres indicateurs associés à la qualité de la pêche perçue par les pêcheurs sportifs individuels. Les limites de taille représentent un outil pour mieux accommoder la récolte sans compromettre la qualité de la pêche. Lorsqu'on favorise le maintien de la taille de la population plutôt que la préservation des poissons de taille trophée, les limites de taille minimale constituent la meilleure politique globale, alors que les limites de taille maximale sont plus appropriées lorsque l'emphase est sur la préservation des poissons de taille trophée.

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Introduction

The potential of recreational fishing to adversely impact fish populations has gained recognition in recent years, pointing to the need for more effective management strategies for these fisheries (Post et al. 2002; Cooke and Cowx 2004,

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2006). Unlike commercial fisheries, which are commonly assessed and managed by sophisticated methods, specific approaches for recreational fisheries are much less developed. It is not uncommon to import regulations from other recreational fisheries of the same species, with little specific support for them (Redmond 1986; Brousseau and Armstrong 1987; Radomski et al. 2001). There is a clear need for analytic frameworks that recognize the realities and specific management objectives of recreational fisheries.

In developing such frameworks, three specific characteristics of recreational fisheries need to be considered. First, most recreational fisheries are fully open access, with universal rights to buy a license and fish (Cox and Walters 2002). Unlike many commercial fisheries, regulating fishing effort through the number of licenses sold is not an option; realized effort is highly variable and dependent on a combination of factors, such as the interest drawn by the fishery and its accessibility as determined by costs, facilities, and geographical location (Cox and Walters 2002). In such fisheries, catches can only be indirectly regulated by setting limits to the operation of individual anglers: creel limits, closed seasons, gear restrictions, area closures, catch-and-release regulations, and size limits (Noble and Jones 1999).

Second, the objectives of recreational fishing are complex and cannot be expressed in terms of maximizing the harvest in kilograms or dollars, but are more closely associated to the overall quality of the fishing experience. We focused our analyses on fisheries such as trout fisheries, where the interest of users is largely directed at entertainment, and quality fishing involves satisfying a diverse array of anglers' desires and expectations (Radomski et al. 2001; Johnston et al. 2010). For instance, in many trout fisheries worldwide, anglers' motivations are often related not only to the quality of the fishing itself (e.g., catch rate or the size of the fish caught), but also to variables associated with recreational value beyond the fish populations, such as scenic value, the quality of lodging, etc. (Vigliano et al. 2000; Hutt and Bettoli 2007). Mapping the perceptions of recreational anglers into quantitative indicators of quality and defining clear management objectives are not easy tasks because solutions depend on the type of anglers involved and their values and motivations (Fedler and Ditton 1994; Peterson and Evans 2003; Johnston et al. 2010).

Third, the expectations of multiple users may be conflicting in nature. Clearly, allowing harvest for those anglers who take their catch home and preserving high catch rates of large fish for those practicing strict catch-and-release fishing are conflicting management goals. A central objective of modern fisheries science is to clearly expose such trade-offs between alternative management objectives, providing managers with tools to decide where to operate along the tradeoff (Walters and Martell 2004). The recognition of trade-offs among management objectives is emerging as a major issue in the study of recreational fisheries. As Pitcher and Hollingworth (2002, p. 13) state, "the generally unrecognized reason for failures in sport fishery management....is that there is no Holy Grail of an optimal solution".

The three specific characteristics of recreational fisheries described above have been widely recognized in the specific literature, but formal analyses of trade-offs or general principles for managers to operate within these trade-offs given the regulatory tools at hand do not exist. To provide such an analysis, our first specific objective is to develop different indicators of performance that reflect the diversity of management objectives in recreational fisheries and use a simulation model to explore their response to different management strategies. We combine typical fishery indicators (yield in numbers and in biomass, spawning biomass, recruitment rate) with others more specifically related to the quality of recreational fishing (average fish size, probability of catching a trophy-size fish). Models traditionally used to analyze recreational fisheries regulations consider the average growth of fish (e.g., Clark et al. 1980; Taylor 1981; Jensen 1981). Such models cannot accurately assess the effects of size-selective harvesting on population size structure (Sainsbury 1980; Parma and Deriso 1990). We develop an individual-based model (IBM) of recreational fishing that explicitly incorporates individual variation in growth, therefore allowing a more realistic representation of size-dependent processes in the life history and in the fishery.

Our second specific objective is to use our model to analyze the trade-offs between yield in biomass, expected harvest rate, and the probability of catching a trophy-size fish when different fishing rates and size-limits regulations are applied, including minimum and maximum size limits and harvest slot size limits (Noble and Jones 1999). Based on these results, we discuss the general value of size regulations to accommodate take-fishing while maintaining the quality of fishing through the preservation of large fish.

Finally, our third objective is to evaluate the robustness of the conclusions derived from a per-recruit analysis to the existence of density dependence in the stock-recruitment relationship. Per-recruit analyses examine how growth, natural mortality, and fishing interact to determine the most appropriate fishing strategy, without considering the possibility of changes in recruitment (and reproductive capacity) due to change in stock size. Considering that for the majority of continental fisheries no time series of abundance data are available to allow estimation of stock-recruitment parameters (Pitcher and Hollingworth 2002; Radomski 2003), our underlying goal is to assess the ability of per-recruit analyses to capture essential features of trout recreational fishery management, without the need to explicitly consider the effects on recruitment.

To anchor our analysis on realistic biological and management reference points, we use as a case study the steelhead (sea-run rainbow trout, Oncorhynchus mykiss) fishery in the Santa Cruz River of southern Patagonia, Argentina (Pascual et al. 2001). Several characteristics of this population make it well suited for our analyses. Santa Cruz steelheads (SCS) are highly iteroparous anadromous trout, reaching large sizes through multiple yearly ocean migrations throughout their life cycle (Riva-Rossi et al. 2007). SCS undergo exposure to the fishery on entering the river to overwinter or spawn every year (Riva-Rossi et al. 2007). The SCS fishery is still developing, providing adequate estimates of run structure, size structure, and somatic growth for the unfished state. Because it is an exotic trout, uniquely found in this river, with a marine diet dominated by highly abundant zooplankton (Ciancio et al. 2008a), we expect density-dependent effects in the ocean to be weak and, therefore, growth to be largely invariant with density (an assumption of our model). The fishery is becoming a destination for national and international flyfishers, with a growing provision of lodging and guiding services, and also accommodates more traditional local fishers that keep fish for consumption. Anglers are restricted to fish with a single hook, and there are daily and a seasonal creel limits of one and two individuals above 550 mm, respectively. Determining allowable rates of fishing mortality dominates the management agenda for this resource. The SCS fishery provides a good model for other sea-run trout fisheries in Atlantic river basins of southern Patagonia, such as sea trout (sea-run brown trout, Salmo trutta) in the Gallegos and Grande rivers (Ciancio et al. 2008b), with similar biological characteristics and management requirements.

Materials and methods

Our IBM has two main components. The first one, a von Bertalanffy growth model (VBGM) with individual var-

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Parameter	Value
Finite rate of natural mortality	A = 0.309
River entry or vulnerability to fishery (%)	Age $3 = 40$; age $4 = 50$; age $5-13 = 100$
Age-specific maturation (%)	Age $3 = 20$; age $4 = 70$; age $5-13 = 100$
Parameters length-mass function	$a = 0.000007 \text{ (g·mm}^{-b}); b = 3.0736$
Mean parameters for VBGM	$L_{\infty} = 750.69 \text{ (mm)}; k = 0.4893 \text{ (year}^{-1}); t_0 = 1.1864 \text{ (year)}$
Standard deviation and correlation of growth parameters	SD(l) = 65.24; $SD(t) = 0.2867$; $cor(l,t) = 0.274$
Residual variance in growth model	$\operatorname{Var}(\varepsilon) = 13.8943$
Slope of linear relationship between natural mortality and size	$c = 0.18 \; (\mathrm{mm}^{-1})$

 Table 1. Model parameters.

Note: Rates are expressed as proportion or percentage calculated on an annual basis. VBGM, von Bertalanffy growth model.

iation, is used to simulate individual growth trajectories representing population-level variability in growth. Growth parameters of individual fish are random variables that deviate from the population means. The second component, an individual-based yield-per-recruit (YPR) model, represents the history of a cohort over time as individuals grow and experience natural mortality, maturation, river–ocean migrations, and in-river fishing mortality. Different size regulations and fishing rates are introduced as size-specific probabilities of individual fish being harvested in a particular year. The final outcomes of the model are the total number of fish surviving and total number harvested, together with their size and mass distributions. Spawning biomass is calculated as a function of maturation and individual mass.

Case study and basic data

The Santa Cruz is the second largest river of Argentinean Patagonia (50°S, 70°W; average discharge 690 m³·s⁻¹; SSRH 2005). It flows for 382 km across the Patagonian plateau to drain into the Atlantic Ocean (Pascual et al. 2001).

The general life history plan of SCS has been described by Pascual et al. (2001), Riva-Rossi et al. (2003), and Riva-Rossi et al. (2007), based on samples of adults collected with gillnets and by anglers during the spawning migration (period 2000–2008) and from radiotelemetry studies. Recreational fishing takes place for the most part close to the estuary, around the town of Piedra Buena, when SCS enter the river from the ocean in March-April. Spawning occurs between August and October, primarily in locations along the mainstem river. Most individuals have a 2-year freshwater residence (few fish smolt at ages 1 or 3). Fish are fully vulnerable to the in-river fishery and mature at age 5, with partial vulnerability and maturation at ages 3 and 4. We used direct aging of fish caught in-river, supported by scale pattern analysis, to estimate that 40% of fish become vulnerable to the fishery at age 3 and 30% more at age 4 (Table 1). However, not all fish that enter the river mature; only 20% of vulnerable fish at age 3 mature, (i.e., 8% of age-3 fish), and at age 4, 70% of all vulnerable and immature fish mature (Table 1). The oldest fish registered was 11 years old and had spawned in 8 consecutive years. Finite rate of natural mortality (A) was estimated by catch curve analysis assuming that the current age structure is close to that of the virgin population (Table 1). For aging and growth analysis (next section), we used scales extracted from an area below the posterior margin of the dorsal fin and above the lateral line. Complementary, fish were measured (fork length, FL, mm), weighed (g), and sexed.

Analysis of growth

Individual growth trajectories were obtained through backcalculated size-at-age from scale measurements on fish with the predominant 2-year freshwater residency. Annual marks (annuli) were recognized using general criteria for temperate fish (Tesch 1971) and experience with SCS (Riva-Rossi et al. 2007). The radii corresponding to different annuli were measured from the nucleus and along the longitudinal anterior axis of the scale. Age and radii measurements were recorded for a total of 135 individual fish caught between May 2004 and November 2005. The biological intercept backcalculation method was employed to estimate lengths-at-age for each individual (Campana 1990):

(1)
$$FL_i = FL_c + \frac{(r_i - r_c)}{(r_c - r_0)} \times (FL_c - FL_0)$$

where FL_i is the estimated fork length at age *i*, FL_c is the fork length at capture, r_i is the scale radius at age *i*, r_c is the scale radius at capture, and FL_0 and r_0 are the fork length and scale radius, respectively, at the start of proportionality between the somatic growth and the scale growth. We used 30 mm and 0.07168 mm as values of FL_0 and r_0 , respectively. These values represent the mean fork length at scale formation and the mean scale radius measured from the focus to the first circulus, both obtained on hatchery fish (J. Lancelotti, CENPAT-CONICET, Puerto Madryn, Argentina, personal communication, 2005).

A VBGM curve (Quinn and Deriso 1999) was fitted to the individual profiles of marine growth (excluding freshwater ages 1 and 2) using nonlinear mixed-effects models (Davidian and Giltinan 1995; Pinheiro and Bates 2002) as previously done by Schaalje et al. (2002) and Escati-Peñaloza et al. (2010). Mixed-effects models facilitate the incorporation of different sources of growth variability by including "fixed effects", associated with the population means, and "random effects", associated with individual variability. Under this method, growth parameters of each individual fish are expressed as the sum of a population mean parameter (fixed effect) and an individual deviation (random effect) (Lindstrom and Bates 1990):

(2)
$$L_{ij} = (L_{\infty} + l_i) \times \left\{ 1 - e^{-(K+k_i) \times [age_{i,j} - (t_0 + t_i)]} \right\} + \varepsilon_{ij}$$

where L_{ij} represents length at age *j* for the *i*th fish; L_{∞} , *K*, and t_0 are the VBGM population mean parameters (fixed effects); and l_i , k_i , and t_i are individual deviations (random effects) from the VBGM population mean parameters for the *i*th fish, assumed to be normally distributed, with zero mean

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and variance–covariance matrix Σ , a 3 × 3 matrix with diagonal elements var(*l*), var(*k*), and var(*t*₀) and off-diagonal elements given by cov(*l*,*k*), cov(*l*,*t*), and cov(*k*,*t*). The term ε_{ij} represents process stochasticity assumed to be normally distributed with zero mean and variance–covariance matrix $\sigma_{\epsilon}^2 \Lambda$.

The Akaike information criterion (AIC) and the likelihood ratio test (LRT) (Burnham and Anderson 1998) were used to asses several nested VBGMs of varying statistical complexity in random effects. Parameters and their variance–covariance matrix were estimated using maximum likelihood methods implemented in the nlme library (Pinheiro et al. 2009) in R software (R Development Core Team 2009). Alternative mixed-effects models, based on the Richards, Logistic and the Gompertz growth models, were fitted to the individual length data, but the VBGM was favored by an AIC analysis.

Individual-based demographic model

We built an individual-based version of the generic agestructured YPR model (Quinn and Deriso 1999) and implemented it in Visual Basic for Applications (Microsoft Excel). In IBMs, each individual can be assigned different status or characteristics (age, sex, maturity, social status) and it is tracked through time (DeAngelis and Gross 1992; Grimm and Railsback 2005). In our case, the model incorporates individual variability in growth and the associated probability of harvest as a function of individual size.

A run of our model consisted of a Monte Carlo simulation of the history of a cohort of 300 000 fish through time, from age 3 (recruits, R) to age 13, under a given exploitation scenario (see below). Each of the 300 000 fish was assigned its own set of growth parameters, $L_{\infty i}$, K_i , and t_{0i} , based on the mixed-effects model (previous section). These values were drawn from a multivariate normal distribution with mean vector μ (population mean parameter) and variance-covariance matrix Σ (for the "best model"; previous section). At each age or time step, each fish was exposed sequentially to five stochastic processes: growth, river entry and vulnerability to the fishery, maturation, angling, and natural mortality. Fish grew according to the VBGM (eq. 2), based on their individual set of parameters, plus a normal random residual $(0, var(\varepsilon))$. For each fish and remaining processes, a random uniform number (0, 1) was drawn to decide whether the event (i.e., vulnerability, maturation, catch, or natural death) occurred or not. For our base runs, we used age-dependent probabilities for vulnerability and maturation and an invariant probability of death by natural causes (Table 1).

For a given age, all vulnerable fish are equally likely to be caught (with probability equal to the fishing rate), but only those within the size limits are sacrificed, while the others are assumed to be released and to survive. Therefore, whereas fishing rate is age- and size-independent, realized catch is age-dependent through the vulnerability-at-age function (Table 1), and harvest (i.e., sacrificed fish) is size-dependent through the size-limit regulation. Several simulation experiments were conducted, each one consisting of a given management scenario of size limits and fishing rate (details below). Different indices of fishery performance and population status were calculated for each management scenario.

YPR is the total harvest (kg) per recruit, calculated as the sum of the individual masses of fish harvested over the 10

time steps divided by *R*. Individual masses are a power function of individual length (parameters in Table 1):

$$(3) \qquad W = a \times L^b$$

Relative run size is the number of surviving fish entering the river summed over all ages relative to the corresponding number for an unfished stock. It provides an index of population–run size per recruit under different harvest strategies, assumed to be proportional to the expected catch in numbers per unit of effort by an average fisherman.

Relative average size of fish is the average size of all vulnerable surviving fish summed over all ages, relative to the corresponding value for the unfished stock. It provides an index of the average size of fish an angler can expect to catch.

Relative abundance of trophy-size fish is the number of vulnerable surviving fish summed over all ages, larger than a trophy size of 760 mm (90th percentile of virgin stock), computed relative to the corresponding number in the unfished stock. It provides a relative index of the probability for an angler to catch a trophy-size fish.

Relative spawning biomass (S/B_0) is the sum (over all ages) of the individual masses of all surviving mature fish, computed relative to the corresponding number in the unfished stock. It provides an index of eggs per recruit.

Relative recruitment (R/R_0) is the recruitment expected from the spawning biomass remaining after harvest, computed relative to its value for the virgin population and for different scenarios of population "productivity" (unknown for SCS). Relative recruitment (R/R_0) as a function of relative spawning biomass was modeled by a Beverton–Holt stock– recruitment relationship reparameterized in terms of a productivity parameter known as "steepness" (*h*), corresponding to the relative recruitment when S/B_0 is equal to 0.20 (Mace and Doonan 1988):

(4)
$$R/R_0 = \frac{S/B_0}{\alpha + \beta \times S/B_0}$$

(5)
$$\alpha = \left(\frac{1-h}{4\times h}\right)$$

(6)
$$\beta = \frac{5 \times h - 1}{4 \times h}$$

Steepness values for salmonids were obtained from a metaanalysis of spawner-recruit time series for many species and families conducted by Myers et al. (1999). The estimated median value of steepness for salmonids was 0.85, with 20th and 80th percentiles of 0.8 and 0.89, respectively. We calculated relative recruitment based on these median and percentile values, in addition to lower, more conservative steepness values of 0.6 and 0.7.

The first index of fishery performance, YPR, is expressed in mass units (kg). Meanwhile, the remaining five indices are all dimensionless, expressed as relative values with respect to the corresponding value for the unfished population.

Management scenarios

We examined the performance of different combinations of size limits and fishing rates by conducting two sets of simula-

Table 2. Simulated management scenarios.

	Scenario		
Harvest control	1: Variable fishing rate	2: Variable size limit	
Minimum size limit (mm)	550	300 to 900 (step 10)	
Maximum size limit (mm)	900	300 to 900 (step 10)	
Annual fishing rate	0.05 to 0.40 (step 0.05)	0.10	

Note: Shaded cells represent management controls that stayed fixed, while unshaded cells represent variables that were changed across simulations. For Scenario 1 (variable fishing rate), the step between fishing rates was 0.05; a maximum size limit of 900 mm implies that the only effective restriction is in the minimum size limit. For Scenario 2 (variable size limits), the step between sizes was 10 mm, and all possible combinations of maximum and minimum size limits (each defining a slot) were evaluated (see text for details). Annual fishing rate is expressed as proportion captured per annum.

tions (Table 2). In the first set, referred to as "variable fishing rate", we simulated the current minimum size limit for SCS (550 mm) at different fishing rates (from 5% to 40% by 5% increments). In the second set, called "variable size limits", we kept fishing rate at 10% and changed the size limits using all combinations of minimum and maximum size-limit regulations within the range 300–900 mm, by steps of 10 mm. For practical purposes, and because virtually no fish grow larger than 900 mm, setting an upper size limit of 900 mm is equivalent to a minimum size regulation. Similarly, few vulnerable fish are smaller than 300 mm, and setting a lower size limit of 300 mm is equivalent to maximum-size regulations. Combinations with lower limits higher than 300 and upper limits lower than 900 provide harvest-slot regulations.

Generalization of results

Our base model includes individual variability only in growth, but assumes that other parameters, such as natural mortality, river entry, or maturation are independent of fish size. Whereas these parameters may be affected by size in fish (reviewed by Rose et al. 2001), we have no data to support any specific parameterization of such relationships. To explore the sensitivity of our results to departures from those basic assumptions, we performed an additional set of simulations, similar to those in the variable size limits (Table 2), but with natural mortality varying with size. We made natural mortality of individual fish a linearly decreasing function of the individual asymptotic size (i.e., larger fish have higher survival):

$$7) \qquad A_i = A - c \times (L_{\infty i} - L_{\infty})$$

where A, the mean natural mortality, is equal to that of our base case (30.9% per year; Table 1), L_{∞} is the mean parameter for the population, and $L_{\infty i}$ is the corresponding parameter for the individual fish *i*, equal to $(L_{\infty} + l_i)$, and *c* was chosen to ensure a significant level of individual variation in natural mortality; the 5th and 95th percentiles of the individually assigned mortalities (A_i in eq. 7) were 12% and 50%, respectively (Table 1). This formulation of size-dependent natural mortality would represent better the apparent faster growth of older fish in our samples (Fig. 1).

Modifications in the mortality assumption affected the size structure of simulated populations. Because we defined trophy size as the 90th percentile of the size distribution of the unfished stock (760 mm in our base case), we recalculated the trophy size for the size-dependent mortality scenario to ensure consistency in results involving the corresponding fishery performance indices.

Results

IBM for somatic growth

The reconstructed trajectories of size-at-age show a significant individual variability in growth, whereas individual trajectories have similar shape (Fig. 1*a*). Our model captures the individual differences in growth as individual variation in the parameters of the VBGM. Convergence problems were encountered every time we tried to incorporate individual variability in the *K* parameter independently of the starting values (Table 3). The LRT and AIC values indicated that among the remaining models, model 3 (random effects on L_{∞} and t_0) had a significantly better fit than alternative, more restrictive formulations (Table 3, parameters in Table 1):

(8)
$$L_{ij} = (L_{\infty} + l_i) \times \{1 - e^{-K \times [age_{i,j} - (t_0 + t_i)]}\} + \varepsilon_{ij}$$

This model provided an adequate representation of the individual growth trajectories (Fig. 1*b*). The few old fish in our data set (six fish older than age 8), however, are larger at older ages than the average length predicted by the mixedeffects model (Fig. 1*a*), hinting at a possible negative relationship between size and mortality (see below).

Effects of increasing fishing rate on different fishery indicators

We explored the per-recruit effects of increasing the annual fishing rate while maintaining the current minimum size limit of 550 mm on relative run size, relative abundance of trophysize fish, relative average fish size, and yield in mass (Figs. 2a-2d). Relative run size declined moderately with fishing rate (about 20% reduction for a 20% fishing rate; Fig. 2a), while the number of fish larger than 760 mm in the run declined sharply (about 60% reduction for a 20% fishing rate; Fig. 2b). The average fish size in the run was largely insensitive to fishing rate (Fig. 2c). In general, fishing rates of 10% had minimal effects on average size, moderate effects on run size, and strong effects on the abundance of trophy-size fish (reduction of 40%). Meanwhile, yield in biomass per recruit increased monotonically with fishing rate (Fig. 2d), exhibiting a clear trade-off with the other indicators of fishing quality.

Increasing fishing rates significantly reduced relative

Fig. 1. von Bertalanffy growth model fitted by treating individual differences as random effects. (*a*) Dashed lines are observed individual growth trajectories, the solid line is predicted mean size-at-age, and the shaded area represents the 5% and 95% quantiles calculated from simulated growth trajectories. (*b*) Scatterplot of observed size-at-age versus predicted size-at-age values.



spawning biomass (about 30% reduction for a 20% fishing rate; Fig. 2*e*). However, the expected reductions in relative recruitment resulting from these spawning levels and for typical steepness values reported for salmonids were marginal. Even for values of steepness that could be considered low for salmonids (h = 0.6), recruitment was not reduced by more than 20% under fishing rates as large as 40% per year. Therefore, most effects on fishery performance are to be expected from postrecruitment impacts of fishing. Hence, perrecruit analyses (e.g., Figs. 2a-2d) largely capture the effects to be expected from fishing, particularly for low fishing levels such as those that would be applicable if the recreational quality of the fishery, as expressed by availability of trophysize fish, were to be preserved (<10% decline).

Size limits, trade-offs, and fishery performance

Considering the fast deterioration of fishing quality with fishing rate, we next explored the value of size-limit regula-

Table 3. Results of model selection.

Model		Fit and selection		
No.	Random effects	LL	LRT	AIC
1	L_{∞}, K, t_0	NC	NC	NC
2	L_{∞}, K	NC	NC	NC
3	L_{∞}, t_0	-1850.733		3715.466
4	L_{∞}	-1900.391	3 vs. 4***	3810.781
5	t_0	-1944.494	3 vs. 5***	3898.988
6	<i>K</i> , <i>t</i> ₀	NC	NC	NC
7	Κ	NC	NC	NC

Note: LL, log-likelihood; LRT, likelihood ratio test; AIC, Akaike's information criterion; NC, no convergence; ***, p < 0.0001 (3 vs. 4: $\chi^2 = 99.3149$, df = 2; 3 vs. 5: $\chi^2 = 187.5214$, df = 2).

tions for improving fishery performance. We applied a 10% fishing rate to various retention size slots and looked at changes in relative run size, relative abundance of trophysize fish, and YPR (Fig. 3). All three indices varied markedly with changing size limits. In general, and as expected, restricting slot sizes resulted in increased run size and abundance of trophy-size fish, with reductions in yield. However, the different shapes of the response surfaces suggest that given the unavoidable trade-off between fish removal and preservation of large fish in the population, there may be room for improvement in overall performance relative to the current regulation.

Trade-offs are better explored by plotting two value measures against one another (Walters and Martell 2004). Overall, the trade-offs between run size and yield and between abundance of trophy-size fish and yield have a similar shape (Fig. 4). The current minimum size limit of 550 mm provides near-to-maximum yield but, being very liberal and providing very little size selectivity in harvest, results in substantial reductions in run size and abundance of trophy-size fish. Both quality indicators could be considerably enhanced by setting more stringent size limits. Meanwhile, alternative size limits perform very differently under the two trade-offs considered. In the trade-off between run size and yield, minimum sizelimit regulations lie along a Pareto Frontier (Walters 1986; Walters and Martell 2004) — a convex trade-off curve at the outer boundary of feasible solutions where no further improvement can be made on one axis without negatively impacting the other (Fig. 4a). Harvest strategies on this boundary provide better solutions to the trade-off than any other alternative strategy. Maximum size regulations, on the other hand, provide the poorest solutions to this trade-off, and slot sizes have intermediate performance. The relative performance of minimum and maximum size limits is inverted when the trade-off between the abundance of trophysize fish and yield is considered (Fig. 4b). Although some slot regulations perform better than maximum size limits, the improvement is marginal. Maximum size limits provide close-to-best solutions for this trade-off. Minimum size regulations, on the other hand, provide the poorest performance.

Overall, these results indicate that for a given yield level, minimum size regulations are best at maintaining large runs and maximum size regulations are best at preserving large fish. Because no harvesting strategy simultaneously provides optimal solutions to the trade-offs between yield and run size and between yield and abundance of trophy-size fish, man-

Fig. 2. Effects of increasing fishing rate on different performance indicators for a minimum size limit of 550 mm: (*a*) relative run size, (*b*) relative abundance of trophy-size fish, (*c*) relative average size of fish, (*d*) yield-per-recruit (YPR), (*c*) relative spawning biomass, and (*f*) relative recruitment (steepness for salmonids from Myers et al. (1999): solid line median (h = 0.85), short dashed line 20th percentile (h = 0.89); more conservative steepness values: long dashed line (h = 0.7) and dot-dashed line (h = 0.6)).



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agement options need to be considered by conditioning on two of the indicators and finding the optimum with respect to the third indicator. For instance, if fishing quality is favored over yield, we may select the strategy that maximizes yield among the subset of strategies that keep run size and the abundance of trophy-size fish above a certain minimum acceptable level. If, for example, the goal is to keep run size and abundance of trophy-size fish at 90% of virgin values, a subset of size limit options can be identified (shaded area in Fig. 4). Within that subset, a maximum size limit of 630 mm maximizes yield. Whereas keeping run size at 90% of virgin values would allow for higher yields (as large as 0.448 kg per recruit), keeping the abundance of trophy-size fish at 90% of virgin values imposes a more stringent constraint, limiting maximum yield to 0.263 kg per recruit. An overall optimum, given the constraints, is obtained with a slot size of 500-680 mm (Fig. 4), but the improvement in yield with respect to a maximum size limit of 630 mm is not large (0.077 kg).

Size-dependent natural mortality

The trade-offs between fishery quality indicators were not substantially modified when natural mortality was assumed to decrease with size (Fig. 5). It must be understood that the change in the mortality assumption modified not only the size structure of the unfished stock, but also its size in total number of fish. Absolute run size, YPR, and numbers of trophy-size fish, therefore, varied accordingly. However, by expressing fishery performance indices of run size and trophy-size fish as relative values with respect to those of the unfished stock, we were able to look at the general shape of the trade-offs. Results indicate that whereas the specific values of YPR emerging from different size regulations change somewhat with respect to those in the base case

Fig. 3. Performance of various size-limit regulations under 10% fishing rate. Shown are isopleths for three indicators: (*a*) relative run size, (*b*) relative abundance of trophy-size fish, and (*c*) yield-per-recruit (kg). Relative run size and relative abundance of trophy-size fish are in relation to the virgin stock. Solid circle (\bullet) represents a minimum size limit of 550 mm (current regulation for SCS).



(Fig. 4), the main features of the trade-offs were kept. Namely, the shape of the trade-offs is virtually the same and the relative impact of the current size regulations, as well as minimum and maximum size-limits regulations on the three fishery indicators, remain unchanged.

Discussion

We developed a general framework to analyze the value of alternative management strategies in recreational fisheries, which captured the complexities associated with multiple objectives and to individual-based population demographic processes.

To measure performance we used a suite of indicators of population state and fishing quality that capture essential drivers of anglers' satisfaction. Arlinghaus (2006) found that German anglers attach relatively little importance to catch motives during interviews; however, their realized satisfaction with the fishing experience is still mainly catch-dependent. We believe this is true for many trout and other game fisheries around the world. In such fisheries, catch-related, activity-specific components of anglers' satisfaction (those related to the fishing activity itself as compared with those common to all outdoor recreation activities), such as the number of large fish, the number of consumable fish, or the quantity of fish bites, comprise a most important part of overall satisfaction (Arlinghaus 2006). These catch-dependent components are summed up by three fishing quality indicators, namely YPR, run size, and the availability of trophysize fish.

In a classic paper, Jensen (1981) analyzed the harvest of large or "trophy fish" based on an average-growth in a YPR model. Harvest in numbers of old fish (those ages with average length above some defined trophy size) was used as the response variable, and harvest rate and age of first capture were the controls. But because size in fish is not only associated with age but with individual growth rates, the abundance of large fish is only loosely correlated with the abundance of old fish. In addition, average-growth models cannot capture the compounded effect on size structure of selectively removing fish with different growth rates (Sainsbury 1980; Parma and Deriso 1990) by applying different size regulations. Combining mixed-effects growth models and individualbased harvest models provides a full description of the relationship of growth, mortality, and size structure (including the provision of trophy-size fish), as well as a general frame**Fig. 4.** Performance of various size-limit regulations under 10% fishing rate when natural mortality is constant: trade-offs between (*a*) yield-per-recruit and relative run size and (*b*) yield-per-recruit and relative abundance of trophy-size fish. Each point corresponds to a specific size-limit regulation, identified by the following symbols: (\bullet) minimum size limit, (\bigcirc) maximum size limit, (\cdot) harvest slot size limits, (grey \diamond) minimum size limit of 550 mm (current regulation for SCS), (\blacktriangle) maximum size limit that maximizes yield (630 mm), and (∇) harvest slot size limits that maximizes yield (500–680 mm). Shaded area identifies the subset of size limits that maintains run size and abundance of trophy-size fish within 90% of their virgin values.



work for policy analysis of size-based harvest strategies and objectives in fisheries.

By applying this framework to a case study, we were able to derive some general principles to support the management of recreational fisheries. Moderate levels of harvest produced negligible changes in average size, total abundance, and even recruitment rate, but resulted in important reductions in the abundance of trophy-size fish. In developing recreational fisheries, anglers and managers are likely to notice a decline in catch rates of trophy-size fish before declining run size or overall catch rates. This is consistent with our experience in Patagonia, where anglers report the reduction in size as a primary problem and the reduction in numbers as less of a concern (Pascual et al. 2002; Casalinuovo et al. 2002; Vigliano et al. 2008). It is also consistent with previous work where no apparent changes in total densities of fishes were detected between fished and unfished sections of Spanish rivers that showed sharp differences in age structure and life span (Braña et al. 1992).

The recognition in recent years of the potential of recreational fishing to adversely impact fish populations has led many authors to emphasize the need to limit fishing effort (Post et al. 2002; Walters and Martell 2004). The fact that trophy fishing is so sensitive to harvest indicates that keeping large fish may only be possible through very low take levels. Whereas controlling fishing effort appears as the most direct way to reduce fishing mortality, catch-and-release practices provide an alternative. It must be understood, however, that hooking mortalities incurred under strict catch-and-release policies may not be insignificant when fishing pressure is high (up to 10%, from a meta-analysis conducted by Bartholomew and Bohnsack 2005). In intensively exploited recreational fisheries, the effectiveness of catch-and-release strategies is inevitably linked to low levels of postrelease mortality (Coggins et al. 2007; Pine et al. 2008).

As traditional tools to manage recreational fisheries have proven unable to limit fishing effort, the addition of fish has been regarded as a possible tool to compensate for the effects **Fig. 5.** Performance of various size-limit regulations under 10% fishing rate when natural mortality is size-dependent: trade-offs between (*a*) yield-per-recruit and relative and (*b*) yield-per-recruit and relative abundance of trophy-size fish. Each point corresponds to a specific size-limit regulation, identified by the following symbols: (\bigcirc) minimum size limit, (\bigcirc) maximum size limit, (\cdot) harvest slot size limits, (grey \diamond) minimum size limit of 550 mm (current regulation for SCS). Shaded area identifies the subset of size limits that maintains run size and abundance of trophy-size fish within 90% of their virgin values.



of fishing. Stocking is one of the most common practices, if not the most common, used in inland fisheries management today (Cowx 1994; Welcomme 2001). However, most stocking programs are conducted without a clear definition of objectives or without a proper assessment of potential or actual success (Cowx 1994). Our results show that large declines in fishing quality can be expected at fishing mortalities that are much too low to cause a sizeable decline in recruitment from virgin values. Thus, quality overfishing in these fisheries, a problem closely related to growth overfishing, could occur even with healthy levels of recruitment. In such cases, stocking of young fish at stages previous to those at which population bottlenecks operate would fail to produce any major improvement of fishing quality. Stocking could even have negative population-level impacts if somatic growth or mortality at juvenile stages were density-dependent (Ali et al. 2003).

Trade-offs among management objectives are particularly important in recreational trophy fisheries for trout. When somatic growth is density-independent, fish harvest occurs at the expense of other indicators associated with the quality of fishing experienced by individual anglers (e.g., trophy-size fish, number of bites); best fishing occurs at virgin stock levels. Harvest and fishing quality are conflicting objectives.

Meanwhile, our results illuminate some general management approaches to deal with conflicting objectives. Size limits provide a tool to better accommodate harvest without compromising fishing quality. For a given yield, minimum size regulations are best at maintaining larger runs, and maximum size limits are best at preserving large fish. Harvest slots provide some marginal improvements over maximum size limits to preserve large fish. However, slots are more difficult to assimilate by anglers and also more difficult to implement (Pierce and Tomcko 1998). For our case study, and we suspect that for recreational trout fisheries in general, the difficulties of implementing slot limits, together with their small marginal gain over maximum size limits, may lead managers to discard their use. In summary, the relative value of minimum or maximum size limits in trophy-size fisheries will depend on whether management is targeted towards preserving run-size or trophy-size fish. When preserving run size is favored over preserving trophy-size fish, minimum size limits constitute the best policy overall, whereas maximum size limits are best when the emphasis is on preserving trophy-size fish.

The balance among complexity, data availability, and generality needs to be considered when using models in general (Levins 1966) and IBMs in particular. IBMs provide a highly flexible tool for simulating individuals and populations, incorporating aspects usually ignored in analytical models (e.g., variability among individuals), and have the advantage that they are closer in details to real systems (Grimm and Railsback 2005). In fact, there is virtually no limit to the degree of complexities in relation to individual responses that they could accommodate. But this great flexibility comes at a cost; they can easily become too complex and difficult to analyze and understand (Grimm 1999; Grimm and Railsback 2005), and they can hide general, important patterns and loose generality (Levin and Pacala 1997). We kept the complexity of our model within the limits imposed by data availability. Nevertheless, it is pertinent to analyze how different simplifying assumptions in our model may compromise the robustness and generality of our results.

Our base model includes individual variation in growth, but does not consider concomitant variations in natural mortality or maturation. Our second round of simulations had natural mortality modeled as a function of each individual's maximum size. This simulation exercise shows that our general results regarding the shape of the trade-offs and the relative value of alternative management strategies for given management goals are quite robust to violation of the assumption of size-invariant mortality. Maturation, on the other hand, does not affect per-recruit fishery performance indices; therefore, most of our results are independent of the assumptions about the relationship between body size and maturation.

Another assumption in our model is that growth of adult, vulnerable fish is density-independent. This is a reasonable assumption in our case, but may not be so for populations where adults are affected by crowding (Rose et al. 2001). The extent to which density dependence could lessen the direct impact of the harvest on population size structure is of course casespecific. While consideration of density-dependent growth is beyond the scope of this paper, it would be straightforward to conduct such an analysis with our IBM approach.

From a methodological viewpoint, our results indicate that if preserving the abundance of trophy-size fish is a determinant goal, per-recruit analysis may capture the essence of the harvest problem without the need to consider stock-recruitment processes. This is because harvest rate must be kept at values that are low relative to those that are expected to impact recruitment. Long time series of population abundance and recruitment are rarely available for recreational fisheries (Pitcher and Hollingworth 2002; Radomski 2003); thus, it is encouraging that management guidelines can be derived from per-recruit analyses based solely on life history parameters.

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