

Linking the dynamics of harvest effort to recruitment dynamics in a multistock, spatially structured fishery

Eric A. Parkinson, John R. Post, and Sean P. Cox

Abstract: A freshwater sport fishery that targets hundreds of geographically isolated stocks is simulated by combining a model of angler behavior with a model of rainbow trout (*Oncorhynchus mykiss*) population dynamics. Ideal free distribution (IFD) theory, which suggests that angling quality will be similar on all lakes, is used to drive angler effort distribution. Model parameters are based on creel survey data from 53 lakes and empirical relationships between growth, survival, and density derived from whole-lake density manipulations on nine lakes over a period of 10 years. We compared angling quality, population density, fish size, and yield under unfished conditions, harvest rates that maximize sustained yields (MSY), and an IFD equilibrium driven by angler behavior. The IFD equilibrium rarely maximized yields. Stocks with high MSY angling quality are overexploited at the IFD equilibrium because anglers move to take advantage of exceptional angling opportunities. These stocks would often be viewed as more resistant to harvest pressure because they have higher stock productivities and habitat capacities. However, in our model, they are systematically overharvested because their high fish density attracts excessive angling pressure. Conversely, stocks with low MSY angling quality are underexploited because anglers move to take advantage of better angling quality on other lakes.

Résumé : La combinaison d'un modèle de comportement des pêcheurs à un modèle de dynamique de population de la truite arc-en-ciel (*Oncorhynchus mykiss*) nous a permis de simuler une pêche sportive d'eau douce qui cible des centaines de stocks isolés géographiquement. La distribution libre idéale (IFD), qui suppose que la qualité de la pêche sera la même dans tous les lacs, détermine la répartition des efforts de pêche des pêcheurs. Les variables du modèles sont tirées de statistiques de pêche sportive dans 53 lacs et les relations empiriques entre la croissance, la densité et la survie ont été obtenues par des manipulations de la densité dans neuf lacs entiers sur une période de 10 ans. Nous avons comparé la qualité de la pêche, la densité de la population, la taille des poissons et le rendement de la pêche en l'absence de pêche sportive, ainsi qu'à des taux de récolte qui maximisent le rendement soutenable (MSY) et à un équilibre IFD dû au comportement des pêcheurs. Les stocks avec une qualité de pêche de fort MSY sont surexploités à l'équilibre IFD, car les pêcheurs se déplacent pour jouir des conditions exceptionnelles de pêche. Ces stocks seraient souvent considérés comme plus résistants à la pression de capture parce qu'ils ont une plus forte productivité et font une utilisation plus grande de l'habitat. Cependant, dans notre modèle, ces stocks sont systématiquement surexploités, parce que leurs fortes densités de poissons suscitent une pression de pêche excessive. Inversement, les stocks qui possèdent une qualité de pêche de faible MSY sont sous-exploités, car les pêcheurs se déplacent vers d'autres lacs pour profiter des meilleures conditions de pêche.

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Introduction

A fundamental problem in managing multistock fisheries is that optimal harvest rates often vary substantially among stocks because of variation in stock–recruitment parameters. When multiple stocks are harvested at a single place and time, this variation in optimal harvest rates implies that the

maximum yield of the mixed-stock fishery will be less than the combined maximum yields of the individual stocks (Paulik et al. 1967). If fishers can target individual stocks, the problem of multistock management is substantially reduced and, in theory, maximum yields can be achieved for each stock. In reality, fishery managers rarely have tight control over either the total effort or the allocation of har-

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vesting effort among individually targeted stocks. This raises the possibility that some stocks will be overharvested, even if total effort in the fishery is not excessive.

The two main approaches to the problem of overexploitation have been the biological theory of stock–recruitment relationships (Ricker 1975) and the economic theory of exploitation of a common property resource (Gordon 1954). In general terms, the biological theory of population regulation suggests that there are optimum population levels that will achieve the desired balance between the conflicting goals of maximizing yield or economic value while minimizing risk of collapse (Hilborn and Walters 1992). In sport fisheries, maximum sustainable biomass yields can be replaced by a maximum sustainable benefit, which can be defined as angler effort multiplied by a measure of angling quality. Quantitative models of recruitment dynamics and yield range from simple two-parameter analytic models (Barrowman and Myers 2000) to complex age-structured models (Peterson and Evans 2003; Post et al. 2003).

Economic theory predicts that exploitation will be driven by fishers' expectations of economic returns. The distribution of effort will be determined by the relative economic returns in alternative fisheries (Holland and Sutinen 1999). For commercial fisheries with open access (i.e., effort is not restricted), many authors have recognized that economic forces, poor data, and lack of catch restrictions often result in the severe overharvest of many common property resources (Hilborn 1985; Ludwig et al. 1993). In simple terms, an economic equilibrium results when boats stop entering a fishery because exploitation has driven catch per unit effort (CPUE) down to the point where revenue from sales is equal to the cost of fishing. In many cases, this equilibrium results in excessive fishing effort and depressed fished populations, which, in turn, result in various schemes designed to reduce effort (DeVoretz and Schwindt 1985). The equivalent of an economic equilibrium in a sport fishery occurs when harvest by anglers drives angling quality down to the point where additional anglers stop entering the fishery.

Freshwater sport fisheries are often based on many small, independent population units (stocks in hundreds of lakes) that are tied together into a single fishery by a mobile angling population (Billings 1989; Shuter et al. 1998). In multilake systems, angler movement among lakes is an important factor driving changes in angling quality. The movement behavior of anglers can be modeled using ideal free distribution (IFD) theory, which has been developed by behavioral ecologists to predict the distribution of foragers relative to the distribution of their prey resources (e.g., Gillis et al. 1993; Levin et al. 2000). IFD theory predicts that angling quality should be similar on all lakes. This prediction is based on the belief that differences in angling quality should result in shifts in effort that, at equilibrium, result in a situation where individual anglers cannot experience an improvement in quality by moving to another lake (Cox et al. 2002). Assumptions in IFD theory include zero cost to moving, perfect information about angling quality on all lakes, equivalent costs (e.g., travel time, regulation complexity) on all lakes, and equivalent ancillary benefits (e.g., facilities, aesthetics) on all lakes. In the simplest case, when fish size is not included in either the biological and harvest models, IFD theory suggests that numbers caught per unit of effort

(NPUE) should be the same on all lakes (Cox 2000; Post et al. 2002). However, size structure is clearly an important factor in both angling quality and the dynamics of fish populations. Angling quality can be defined in terms of individual fish size and the total weight of the catch in addition to the number of fish caught. However, various combinations of fish size and NPUE can be defined as equivalent if it can be shown that anglers do not prefer one combination over another (e.g., many small fish versus fewer large fish). External factors, such as aesthetics and facilities, also influence angling quality but are usually assumed to be independent of fish population structure.

In contrast with the homogeneity in angling quality predicted by IFD theory, observations of fish habitat and populations suggest that optimal densities will vary among lakes. For example, the rainbow trout (*Oncorhynchus mykiss*) fishery on the interior plateau of British Columbia, Canada, is supported by many small, independent stocks that vary substantially in both density and size structure. This variation among lakes can be linked to variation in the quality and quantity of stream spawning areas (Larkin 1954) and lake habitat (Northcote and Larkin 1956), which suggests that optimal densities and harvest rates should also differ among lakes. The contrast between variation in optimal densities and the homogeneity predicted by IFD theory implies that the dynamics of the angler effort response will rarely result in optimal harvest rates in fisheries where effort is free to move among biologically independent populations. This contrast reflects the situation for many single-stock fisheries where the economic equilibrium typically does not match the optimum derived from stock–recruitment theory.

In this paper, we explore the dynamic interactions between angler effort and fish populations that vary in biological productivity and examine the implications in terms of harvest. Our goal is to identify conditions that are likely lead to overexploitation in open access fisheries and quantify the gains that might be expected under alternative management policies. We explore these interactions in two stages. First, we develop a simple analytical model to illustrate the general problem. Second, we develop a more complex size-structured simulation model that directly links angling quality (catch rates and fish size) data to angler behavior, biological productivity, and harvest outcomes. We develop and parameterize this simulation model with biological and fishery processes and data from Walters and Post (1993), Post et al. (1999), Cox (2000), and Post et al. (2002).

Methods

Model development and parameterization

Our simulations model a fishery that consists of multiple stocks that are biologically independent but are exploited by a common pool of harvesting effort. Two population models drive the dynamics of fish growth, survival, and reproduction. A simple numerical model is used to illustrate the general behavior of this type of system. A size-structured model provides a more accurate depiction of the demographic and harvest processes that are both strongly size dependent. Model parameters are derived from monoculture, lacustrine rainbow trout populations in British Columbia Management Region 3. In both models, biological differences among pop-

ulations are simulated by varying the maximum rate of increase at low population density (stock productivity) and the maximum population density over a plausible range for monoculture rainbow trout in British Columbia lakes. Angling quality is linked to the fish population model using empirical catchability data. To simulate the effects of mobile effort, we used the IFD prediction that angling quality will be similar on all stocks. The IFD equilibrium is driven by effort that moves among lakes when angling quality is either better (more anglers go to a lake) or worse (some anglers leave) than the average in Region 3. The IFD equilibrium is found by searching for an effort level that produces both the target angling quality and a stable fish population. The same models were used to evaluate the status of the fishery under both minimal and optimal harvest rates. Optimal conditions for each fish population are those that maximize yield.

A simple numerical model

Recruitment was modeled with a Beverton–Holt stock–recruitment relationship between the lake density (fish per hectare) of spawners (N) and recruits (N_1).

$$(1) \quad N_1 = \frac{\alpha N}{(1 + \alpha N/\beta)}$$

The demographic parameters of the fish population are stock productivity (α is the maximum recruits per spawner) and habitat capacity (β is the asymptotic density of progeny produced with very large spawner densities). Parameters were varied over an eightfold range in the case of β (50, 100, 200, and 400 fish·ha⁻¹; Stringer et al. 1980) and a fourfold range for α (2, 4, 8, and recruits·spawner⁻¹; Myers et al. 1999).

With the addition of catchability (q), harvest mortality can be incorporated into eq. 1. If angling effort (E , angler-days per hectare) is constant, harvest rate (HR) is a density-independent function of q and E .

$$(2) \quad \text{HR} = 1 - \exp(-qE)$$

Catchability was set at 0.09 ha·angler-day⁻¹ (Cox 2000).

Since HR is, in effect, a density-independent mortality factor, analytical solutions can be derived for angling quality and yield as functions of effort at the fished equilibrium. Equilibrium spawner numbers at the fished equilibrium (N_e) can be obtained by replacing α and β in eq. 1 with $\alpha' = \alpha(1 - \text{HR})$ and $\beta' = \beta(1 - \text{HR})$ and setting $N_1 = N$.

$$(3) \quad N_e = \beta' - \beta'/\alpha'$$

For particular values of α , β , and HR, substituting eq. 3 into eq. 1 gives recruits at the fished equilibrium (N_{1e}). Yield in the fishery (Y) is the difference between recruits and spawners at the fished equilibrium

$$(4) \quad Y = N_{1e} - N_e$$

and angling quality (NPUE, fish·angler-day⁻¹) is the ratio of Y to effort

$$(5) \quad \text{NPUE} = Y/E$$

Since Y is a function of E , α , β , and q , then equilibrium NPUE can be plotted as a function of E , the demographic parameters α and β , and the constant q . The IFD equilibrium for a given set of demographic parameters occurs where E is such that NPUE equals the regional average (2.07 fish·angler-day⁻¹;

Stone 1988). Given E , then N_e and Y can be calculated for each combination of α and β using eqs. 1–4.

Spawner densities, yields, and harvest rates under maximum sustained yield (MSY) conditions can be derived analytically as functions of α and β (Ricker 1975). Effort at MSY is derived by substituting the MSY harvest rate into eq. 3 and MSY angling quality can then be calculated using eq. 5.

Size-structured demography

The age-structured simulation model runs on an annual time step that mimics the annual sequence of events for rainbow trout in lakes. Rainbow trout spawn in streams where they rear as juveniles for 0–2 years before migrating to the lake and growing to adult size (Northcote 1969). Spawning takes place in May and most of the harvest is taken in May, June, and July. In the simulation model, all newly emerged fry enter the lake in July at a size of 2.6 cm at the start of the annual cycle. Effective density is calculated at this point from the numbers and lengths of fish in each age-class. Growth and survival for the coming year are calculated for each age-class. In May, all fish greater than age 2 mature, and spawning mortality is applied. Egg production is calculated using the lengths after growth and the numbers of mature fish are calculated after size-dependent mortality but prior to spawning mortality and harvest. Harvest is applied to the population in each age-class that remains after the application of spawning and size-dependent mortality. After harvest, the remaining fish graduate into the next age-class and the annual cycle is repeated. Maximum age is 7, which is implemented as 100% spawning mortality at the end of the seventh year of life. The number of newly emerged fry is the product of egg production and egg–fry survival. Egg–fry survival is assumed to be density independent and covers the period from just prior to egg deposition to just after the age-0 fish enter the lake. Stock productivity is varied by assigning a density-independent egg–fry survival that covers an eightfold range (1%, 2%, 4%, and 8%). Using the model, we evaluate the status of populations at equilibrium over a range of stock productivities (analogous to α), habitat capacities (analogous to β), and effort densities. We compare the status in terms of fish densities, growth rates, yields to the fishery, and angling quality for three equilibria. At the unfished equilibrium, a minimal effort (0.001 angler-days·ha⁻¹) is used to establish angling quality. The MSY state is evaluated by searching for the effort that maximizes biomass yield. The IFD state is evaluated by searching for the effort that results in an angling quality equal to that experienced by anglers on Region 3 lakes.

Density-dependant growth is modeled as a function of effective density (ΣL^2) of the fish in the lake rather than more conventional measures such as numerical density (ΣL^0) or biomass density (ΣL^3). Walters and Post (1993) showed that the effective density can be used to represent the total demand for food resources by individuals that vary in size. Using empirical data from lakes that varied in both density and size structure, Post et al. (1999) demonstrated that effective density explains a higher proportion of among-lake variance in growth than either numerical density, which weights small fish heavily, or biomass density, which weights large fish heavily.

Effective density is used to model density-dependant growth using Walford plots that represent annual growth with the equation

$$(6) \quad L_{i+1} = a + bL_i$$

where L_i is the length at age i , a is the Walford intercept, and b is the Walford slope. Assuming that competition among size-classes is symmetrical (i.e., based simply on their capacity to consume food resources), Walters and Post (1993) demonstrated that a varies as a linear function of effective density but b does not. The result is that growth can be described by a series of parallel lines that correspond to variations in density (Fig. 1). As density approaches zero, both growth rate and a approach a maximum. At very high densities, a approaches zero, growth rates are negative, mortality increases, and density falls. An estimate of b (mean 0.71, SE 036) was obtained from Walford plots of multimesh gillnet samples of rainbow trout from 34 lakes in southern British Columbia (B.C. Ministry of Sustainable Resource Management, unpublished data, available at <http://srmapps.gov.bc.ca/apps/fidq/>). Only a few (three to six) age-classes were present in each lake and estimates of b from individual lakes were homogeneous (analysis of covariance (ANCOVA), $p = 0.087$).

If the Walford b is constant, density-dependent growth can be modeled by expressing the Walford a as a function of effective density. The relationship between effective density and the Walford a in eq. 6 was parameterized using a linear regression ($r^2 = 0.82$) fitted through data (Fig. 2) collected by Post et al. (1999).

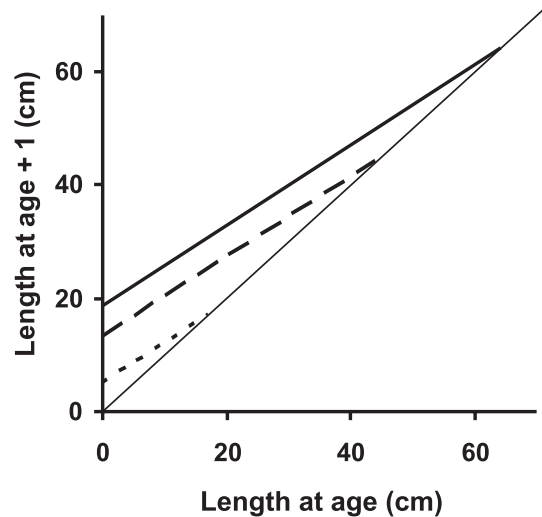
$$(7) \quad a = 18.8 - 2.8 \times 10^{-5} \times D$$

where D is the effective density (square centimetres per hectare) at the start of the year and 18.8 (cm) is the maximum value of a that is observed at very low densities. The maximum growth rate ($a = 18.8$ cm when $D = 0$) is presumably controlled by factors such as the genetic characteristics of the stock and the physical characteristics of the environment (e.g., temperature) rather than food density. The minimum observed growth rate ($a = 5$ cm when density = D_{max}) is presumably controlled by factors such as the minimum length at maturity and the minimum length needed to survive the first winter.

To simulate a range of habitat capacities (analogous to β in eq. 1), we varied the slope of this relationship (eq. 7). The rate at which the Walford intercept a declined with density (i.e., the slope in eq. 7) was set at four multiples (0.25, 0.5, 1, and 2 times) of the slope (-2.8×10^{-5}) estimated from the data in Fig. 2. The minimum value for a (i.e., the intercept in eq. 7) is assumed to be constant, which implies that D_{max} is set at 4, 2, 1, and 0.5 times that observed by Post et al. (1999). The biological interpretation is that, at low habitat capacity, growth will decline rapidly with density (i.e., D_{max} is small) and at the highest habitat capacity, growth declines slowly with density (i.e., D_{max} is large). When combined with the stock productivity range described above, this range of habitat capacity produces densities and size structures that are within the range observed in natural lake populations of rainbow trout in southern British Columbia.

Survival is a function of initial length of cohorts of rainbow trout and the density of fish in the lake (Fig. 3). Rain-

Fig. 1. Density-dependent growth of lacustrine rainbow trout in southern British Columbia as represented by Walford plots when competition among size-classes is symmetric (Walters and Post 1993). The slope (b) of all three lines is 0.71, which represents the average slope from gillnet samples from 34 local lakes and is assumed to not vary with effective density ($\text{cm}^2 \cdot \text{ha}^{-1}$). Maximum growth (thick solid line) represents an extrapolation of the intercept (a) to zero density using the data of Post et al. (1999). At high densities, the minimum growth (dotted line) is limited by the minimum size at maturity and the size needed to survive the first winter. Growth at an effective density of $200\,000 \text{ cm}^2 \cdot \text{ha}^{-1}$ (dashed line) lies between these two extremes. The thin solid line represents the one-to-one relationship. The asymptotic sizes are 64, 17, and 45 cm. If all fish are 30 cm long, $200\,000 \text{ cm}^2 \cdot \text{ha}^{-1}$ is equivalent to about $220 \text{ fish} \cdot \text{ha}^{-1}$ or $68 \text{ kg} \cdot \text{ha}^{-1}$.



bow trout from five size groups were stocked in nine experimental lakes that varied in density among lakes and among years (see Post et al. (1999) for details). The initial size of cohorts was manipulated through a combination of incubation temperature and size selection. Mean lengths of the five groups were 2.6, 3.6, 8.8, 10.4, and 11.9 cm. The range of lengths within each group was <0.5 cm. In the model, as in the empirical data, the observed annual survival for fish of age-class i (S_i) declined exponentially with total density of all age-classes (D) and an exponent (m_i) that is related to size.

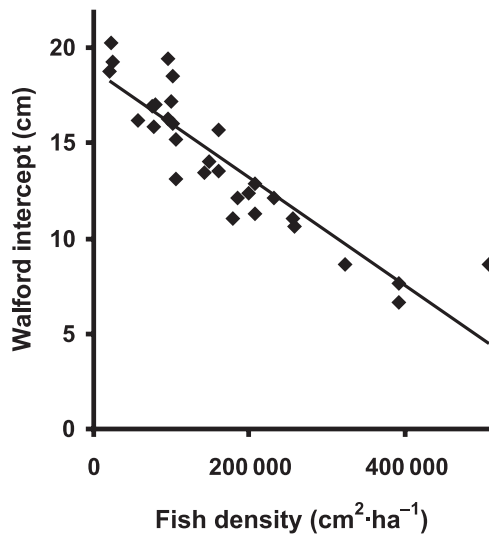
$$(8) \quad S_i = S_{i\max} \exp(-m_i D)$$

This relationship was parameterized using annual survival data for the five size-classes of age-0 and age-1 trout. Maximum annual survival rates were empirically estimated as a saturating function of length at the start of the year (Fig. 4a).

$$(9) \quad S_{i\max} = 0.49 \left[\frac{L_i - 1.81}{1 + 0.49(L_i - 1.81)} \right], \quad r^2 = 0.95$$

where L_i is the length (centimetres) for fish of age i at the start of the year fitted to the intercepts of the empirical relationships between annual survival and initial total density (Fig. 3) for five size-classes of juvenile trout. The empirical relationship between the exponent m_i and L_i was

Fig. 2. Walford intercepts (a in eq. 2) as a function of effective density calculated from the data of Post et al. (1999). Each data point represents the growth of a group of age-0 fish. Lengths at the end of the growing season were estimated directly from field data. Length at age 1 was calculated by adding an increment that represented growth between the end of the growing season and the anniversary of lake entry in early July. This increment was estimated using a relationship between age-1 growth rate ($\text{mm}\cdot\text{month}^{-1}$) and effective density. The Walford intercept for each group is calculated assuming a slope (b in eq. 6) of 0.71 and a length at lake entry of 2.6 cm.



$$(10) \quad m_i = -3.27 \times 10^{-6} \ln(L_i) + 1.21 \times 10^{-5}, \quad r^2 = 0.94$$

where the observed m_i (Fig. 4b) are again derived from survival versus density relationships for five size-classes (Fig. 3). To simulate the effect of different habitat capacities on survival, the m_i derived from the empirical data was multiplied by 0.25, 0.5, 1, or 2. The effect of this is that the density necessary to depress survival to a given value is 4, 2, 1, or 0.5 times the empirical estimate from eq. 10. The biological interpretation is that, at low habitat capacity, survival will decline rapidly with density (i.e., m_i is large) and at the highest habitat capacity, survival declines slowly with density (i.e., m_i is small).

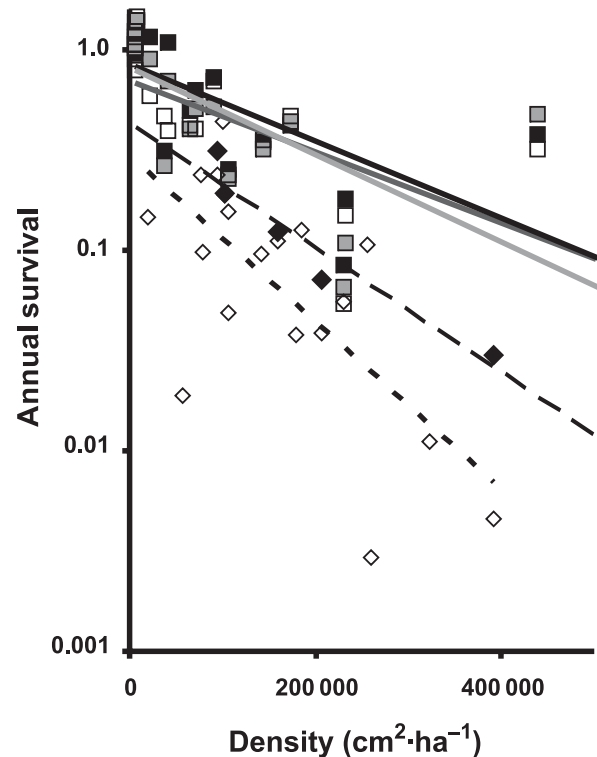
A postspawning survival of 30%, with a maximum age of 7, was chosen to match the age distribution in naturally spawning populations of lightly exploited rainbow trout in British Columbia. Age at first maturity was assumed to be constant at 3 years (Cox 2000). Egg production per mature adult of age i (F_i) was derived data collected by local hatcheries.

$$(11) \quad F_i = \exp[2.9 \ln(L_i) - 10.6], \quad r^2 = 0.92$$

where L_i is the length (millimetres).

The harvest process is modeled in a manner similar to that of Cox and Walters (2002) who analyzed fishing effort, exploitation, and size-selectivity data from eight rainbow trout fisheries in lakes in southern British Columbia. Annual angler effort (E , angler-days per hectare) is a driving variable that is assumed to be constant in a given run. Cox and

Fig. 3. Annual survival of five size-classes of fish as a function of effective density derived from data collected by Post et al. (1999). Each data point represents the survival of a group of age-0 or age-1 fish. Initial lengths of each size-class are 11.9 cm (solid squares, solid line), 10.4 cm (shaded squares, dark shaded line), 8.8 cm (open squares, light shaded line), 3.6 cm (solid diamonds, dashed line), and 2.6 cm (open diamonds, dotted line). Lines fitted through each set of points are of the form $\ln(S_i) = \ln(S_{i\max}) - m_i D$ and have r^2 values that range from 0.31 to 0.92.



Walters (2002) derived a two-parameter fishing mortality rate (f) function of the form

$$(12) \quad f = qvE/(2v + qE)$$

where q is a catchability coefficient and v is the instantaneous turnover rate between pools of available and unavailable fish. This model attempts to account for the fact that catch rates in sport fisheries are somewhat dependent on fish reactivity (i.e., to lures of various types) and the relative distributions of fish and anglers, both of which change (at rate v) over short time scales. Equation 12 is thus an instantaneous fishing mortality rate, which can be used to compute the annual exploitation rate for fully vulnerable fish (U_{\max}).

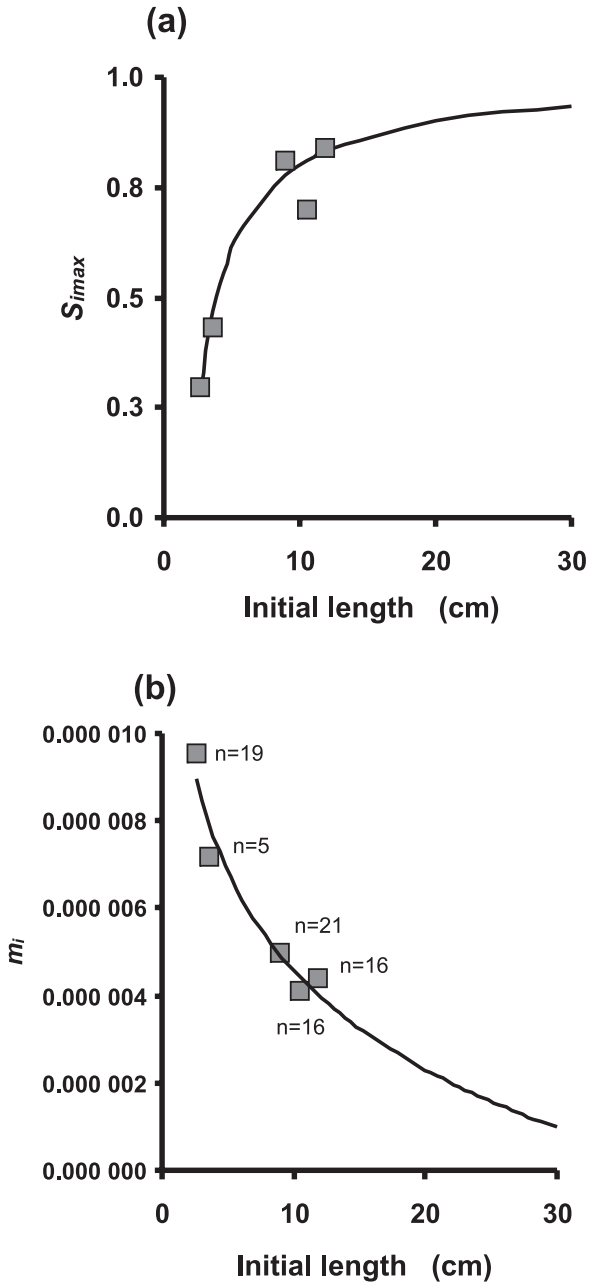
$$(13) \quad U_{\max} = 1 - \exp(-f)$$

Tagging data collected by Cox (2000) indicates that exploitation rate of an age-class (U_i) is a sigmoid function of its length.

$$(14) \quad U_i = U_{\max} \left(\frac{L_i^w}{L_i^w + L_{\text{half}}^w} \right)$$

where L_{half} is the length at which 50% of age-class i fish are vulnerable to harvest and w is the steepness of the curve at

Fig. 4. Relationships between (a) maximum annual survival (S_{imax}) and (b) the rate of change of mortality with density (m_i) and mean initial length as derived from the intercepts and slopes of relationships in Fig. 3. Each point represents a size group where annual survival was repeatedly measured across a range of densities to develop a relationship between initial length and annual survival across a range of densities. In Fig. 4b, the number of survival estimates for each point is given as n .



L_{half} . Except for effort, harvest parameter values are those used by Cox (2000). They are $q = 0.09 \text{ ha}\cdot\text{angler}\cdot\text{day}^{-1}$, $v = 1.61\cdot\text{year}^{-1}$, $L_{half} = 20 \text{ cm}$, and $w = 8$. With these parameters, the maximum exploitation rate at very high effort levels (U_{max}) is 80% (rather than 100%) of the fully vulnerable fish per year. Over the range capacities and egg-fry survivals used in the model, maximum yields in the model are less than the maximum yields ($\sim 120 \text{ kg}\cdot\text{ha}^{-1}$; B.C. Ministry of

Sustainable Resource Management, unpublished data, available at <http://srmapps.gov.bc.ca/apps/fidq/>) observed for lakes in this region.

In the size-structured simulations, the anglers' perception of identical angling quality is defined using an isopleth on a plot of catch rate versus fish size. To empirically describe the trade-off that anglers make between average length and NPUE, we parameterized an isopleth for southern British Columbia interior rainbow trout lakes using mean length and NPUE data collected in a variety of creel surveys over the last 15 years on lakes in Region 3. We excluded three lakes where the number of interviewed anglers was low (<100 angler-hours) and two lakes that were not directly accessible by road. Data from winter ice fisheries were also excluded. The reduced data set from 38 lakes reflects the angling quality conditions experienced by the population of anglers that fish lakes in this general area during the ice-free season. If anglers can move freely among these lakes, IFD theory suggests that a curve fitted through these points can be assumed to represent an isopleth of equivalent angling quality for lakes that differ in fish density and size structure. For comparison, we have also included data from 15 lakes in British Columbia Management Region 5.

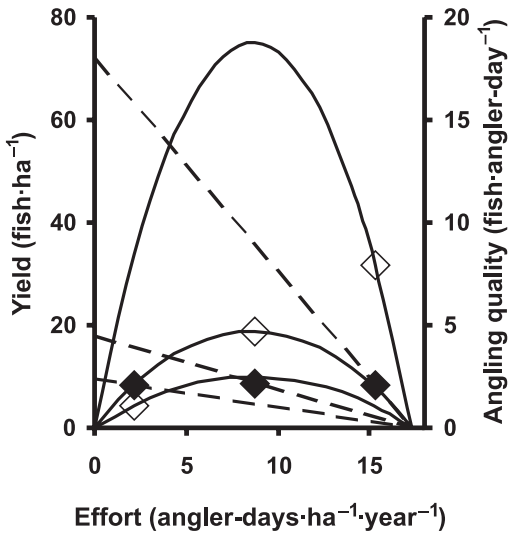
Results

A simple numerical model

The implications of an effort-driven IFD equilibrium can be seen in the relationships of angling quality and yield versus effort (calculated using eqs. 1–5) for three fish populations that vary in habitat capacity (β) but share a common stock productivity (α) and catchability (q) (Fig. 5). At a given level of effort, both angling quality and yield increase with β . In each case, angling quality declines linearly with effort and the IFD equilibrium occurs where this line of declining angling quality intersects the regional average angling quality (Fig. 5). It is important to note that there is no reason to expect that the IFD-driven equilibrium should correspond to the peak of the yield curve (i.e., MSY). The IFD equilibrium is driven by the angling quality experienced by individual anglers rather than the total number of fish captured by all anglers. For high values of β , IFD yields are less than MSY because high densities of fish attract high levels of effort, which result in higher than optimal harvest rates (Fig. 5). For low values of β , IFD yields are also less than MSY because angling quality is not high enough to attract the effort necessary to produce MSY. At very low values of β , effort is expected to be zero, since angling quality at zero effort is less than the regional average.

Similar results are predicted when both α and β vary. MSY increases with both α and β , but yield under the IFD assumption is relatively insensitive to increases in β (Fig. 6a). Since MSY is by definition a maximum, the IFD yields are almost always less than MSY (Fig. 6b). However, this simple model also illustrates that, in many cases, yields are only a fraction of those possible under optimal management control. At low values of α and β , angling quality (Fig. 6b) is not high enough to attract the amount of effort necessary to produce maximum yields. Alternatively, when α and β are high, then angling quality (NPUE) at MSY is much greater than the regional average, which attracts exces-

Fig. 5. Yield (solid lines) and angling quality (broken lines) predicted from the simple analytical model for three populations that share a common stock productivity ($\alpha = 4$ recruits-spawner⁻¹) and catchability ($q = 0.08$ ha-angler-day⁻¹) but vary in habitat capacity ($\beta = 300, 75, \text{ and } 40$ fish·ha⁻¹). For each curve, the IFD equilibrium yield (open diamonds) and angling quality (solid diamonds) have been calculated by assuming that the IFD equilibrium point is where angling quality equals the regional average in British Columbia rainbow trout lakes (2.07 fish-angler-day⁻¹).



sive effort that drives the spawner populations at the IFD equilibrium below MSY levels. These populations are capable of sustaining higher yields but do not do so because of systematic recruitment overfishing.

Angling quality and harvest rates in size-structured populations

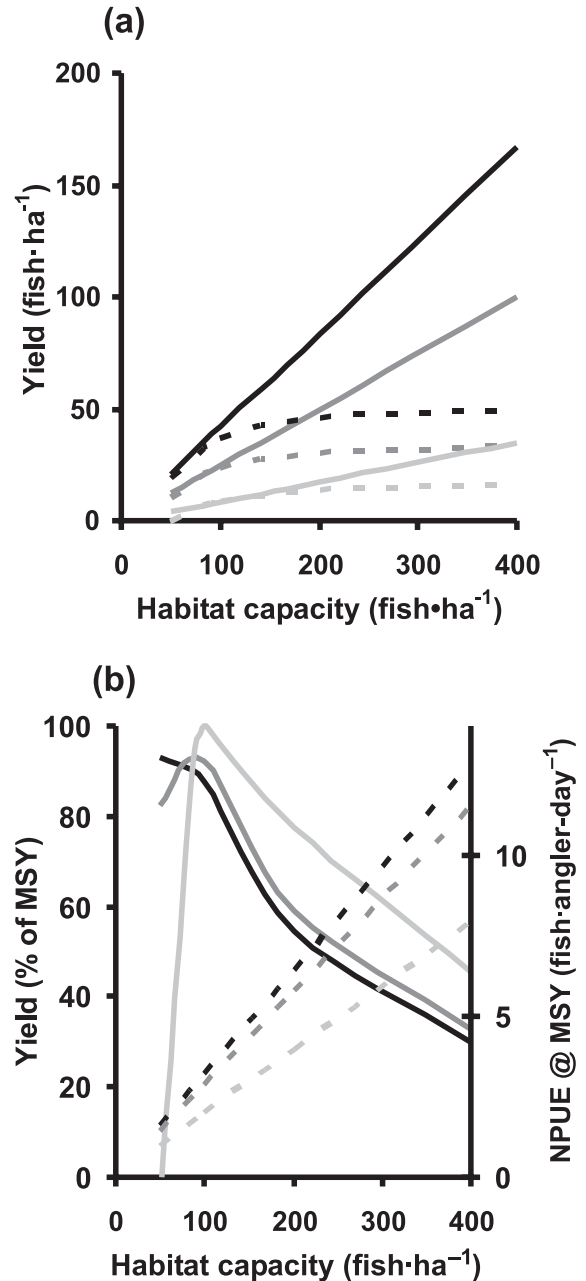
Empirical data on angling quality and effort are consistent with the prediction, based on IFD theory, that angling quality should be similar among lakes within a region but higher on lakes that are farther from population centers. The relationship between catch rate and fish size is significant but differs among regions (ANCOVA, $p < 0.001$) (Fig. 7). Lakes in Region 5, which are farther from British Columbia’s major population center (Greater Vancouver), have a numbers–size trade-off that is similar in form to Region 3, but with higher angling quality. The higher angling quality in Region 5 is associated with a lower density of anglers (8 versus 45 angler-days·ha⁻¹·year⁻¹), higher mean depths (9.9 versus 8.5 m), and lower total dissolved solids (167 versus 191 ppm).

Angling quality in Region 3 can be described as a power function:

$$(15) \quad NPUE = 1\,320\,000 \times L_c^{-4.17}, \quad r^2 = 0.70$$

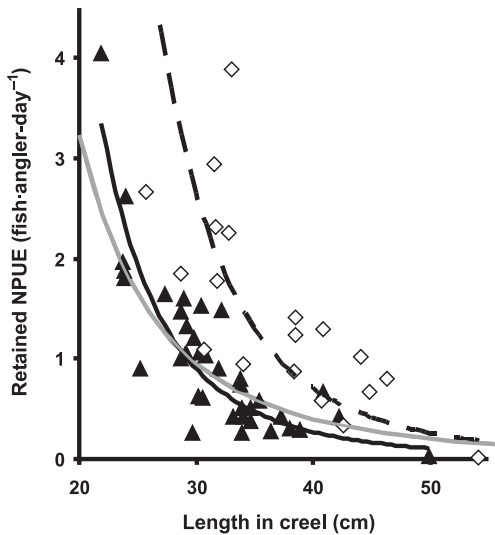
where L_c is the average length of fish in the creel. These parameters are used to define the IFD equilibrium in the size-structured model. This relationship suggests that anglers in Region 3 place a premium on size. When fish are small the observed NPUE is on average higher and when fish are large the observed NPUE is on average lower than that predicted if the numbers–size trade-off was simply proportional to weight (Fig. 7).

Fig. 6. (a) Yield achieved at MSY (solid lines) and at an IFD equilibrium with a target angling quality of 2.07 fish-angler-day⁻¹ (broken lines) and (b) yield at the IFD equilibrium as a percentage of MSY (solid lines) and angling quality at MSY (broken lines) as function of habitat capacity (β). In each case, results for three values of stock productivity ($\alpha = 2, 4, \text{ and } 8$ recruits-spawner⁻¹) are given with darker lines representing higher values of α .



The size-structured population dynamics model produced stable equilibriums in the unfished (pristine) state over the full range of habitat capacity and stock productivity. Density increases with both productivity (egg–fry survival) and capacity (D_{max}) (Fig. 8a). Growth declines with stock productivity because higher density populations grow slower at a given lake capacity (Fig. 8b). Growth does not depend on capacity because the effect of higher densities, at higher habitat capacity, is exactly balanced by the increases in habi-

Fig. 7. Angling quality for 38 lakes in British Columbia Management Region 3 (triangles) and 15 lakes in British Columbia Management Region 5 (diamonds). The solid line is the best-fit power function ($\text{NPUE} = 1\,320\,000 \times L_c^{-4.17}$, $r^2 = 0.70$) for the Region 3 data points. The broken line is a similar power function fitted to the Region 5 points ($r^2 = 0.58$). The shaded line is the best-fit line though the Region 3 data points that assumes a constant weight of fish per day on all lakes.



tat capacity. This outcome results from the direct proportionality between mortality and growth as a function of capacity in eq. 10.

When linked to the population model, the harvest model produces stable equilibriums (with constant effort) and an asymmetrical, dome-shaped yield curve over a range of angler effort (Fig. 9a). The MSY equilibrium (kilograms per hectare) can be estimated from this curve after using the relationship in eq. 15 to express yields in standard units to account for angler preferences for larger fish. Effort levels that result in an angling quality that lies somewhere on the equal quality isopleth (Fig. 7; eq. 15) can be used to define the position of IFD equilibrium (Fig. 9b). The IFD equilibrium conditions involve both a biological equilibrium (i.e., spawners = recruits) and an angler effort equilibrium because a lake is assumed to attract effort if angling quality lies above the angling quality isopleth and lose effort if angling quality is below the isopleth.

The trajectory followed by a hypothetical lake ($D_{\max} = 452\,000 \text{ cm}^2 \cdot \text{ha}^{-1}$, egg-fry survival = 2%) under increasing amounts of effort, expressed in terms of the angling quality at equilibrium, can be used to illustrate the equilibrium process (Fig. 9b). In this case, pristine angling quality consists of an NPUE of just under 4 fish-angler-day⁻¹ for fish that are 28.6 cm long. With increasing effort, density of fish in the lake declines and growth rates improve but the average size of fish is relatively stable because harvest rate is assumed to be a steep, sigmoid function of fish size (eq. 14). NPUE declines rapidly and sustained effort levels that are greater than 15 angler-days-ha⁻¹ drive angling quality below the equal quality isopleth. Harvest pressure alone cannot drive the population to extinction because mortality has been assumed

to be smoothly compensatory and anglers leave the lake if angling quality falls below the isopleth.

A comparison of equilibrium conditions for three system states (pristine, MSY, and IFD) over a range of stock productivity and habitat capacity suggests that large differences can be expected for many combinations. As in the simple numerical model, angling quality under MSY conditions is most strongly depressed (relative to pristine values) for higher productivity stocks but is independent of lake capacity (Fig. 10a). By definition, IFD angling quality is the same on all lakes but, when expressed as a fraction of pristine quality, IFD angling quality is depressed at both higher productivity and higher capacity. High capacity and stock productivity result in high densities of large fish under pristine conditions. As a result, pristine angling quality is very high and the difference between these and the IFD quality (eq. 15) is very large. IFD quality is often less than MSY quality and, in extreme cases, IFD angling quality is a small fraction of MSY angling quality.

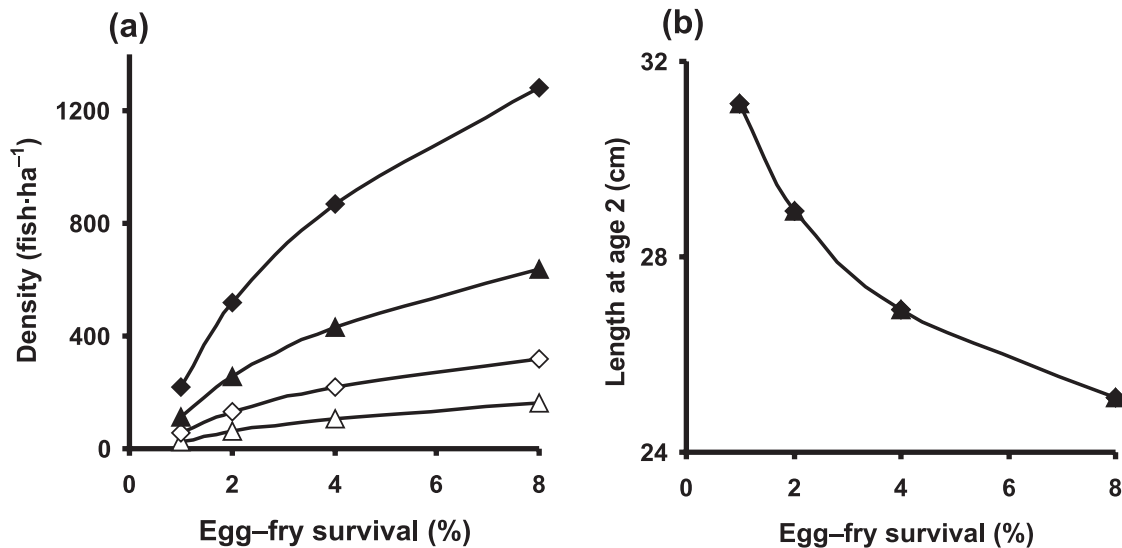
For many combinations of stock productivity and habitat capacity, yields under the IFD equilibriums are substantially less than MSY (Fig. 10b). On low-capacity lakes, yields are low relative to MSY because angling quality at MSY is less than IFD angling quality. As a result, harvest pressure on these lakes at the IFD equilibrium is not high enough to maximize yield. Furthermore, if pristine angling quality is below the equal quality isopleth, angler effort should be close to zero. On lakes with high capacities, angling quality at MSY is well above the equal quality isopleth. Under IFD conditions, this higher quality attracts more angler effort, which depresses spawning populations to below the optimum and results in lower yields because the stock is overfished. IFD yields approximate the MSY only when angling quality at MSY lies close to the equal quality isopleth.

The biological characteristics of the population are also strongly impacted by the high harvest rates that are needed to drive the system to the IFD equilibrium. For the highest lake capacities, growth rates are close to the maximum over the full range of stock productivities (Fig. 10c). These high growth rates are the result of severe depressions in spawner densities to as little as 2% of pristine conditions (Fig. 10d). In general, overfishing at the IFD equilibrium results in much larger changes in biological characteristics and angling quality than those observed in yield.

Discussion

IFD theory predicts patterns in angling quality among lakes and regions that are similar to those that we observed. Within a region, most of the variance in catch rate is explained by differences in fish size and, as a result, angling quality can be described by an isopleth of NPUE versus fish size. The position of individual lakes along this numbers-size isopleth is determined by factors, such as the quality of juvenile habitat, that affect recruitment of trout but are unrelated to angler behavior. In contrast, factors that can be linked to angler behavior, such as travel time to the lake, are expected to affect angling quality. In our study area, angling quality was higher in Region 5, which was farther from the major population center; even though total dissolved solids and mean depth suggested that lake productivity of the lakes in this

Fig. 8. Variation in (a) numerical density and (b) growth among modeled populations of rainbow trout modeled over a range of stock productivity (egg–fry survival) and habitat capacities. Lake capacities are 0.5 times (open triangles), 1 times (open diamonds), 2 times (solid triangles), and 4 times (solid diamonds) the standard capacity derived from the lakes used by Post et al. (1999). These values represent stable equilibriums under unfished (pristine) conditions.



region are about the same as in Region 3. Cox (2000) presented data on this fishery that are consistent with IFD theory; effort densities were linearly related to stocking density in both regions but the effort response per fish stocked was lower in Region 5. The distribution of harvesting effort in other fisheries is also consistent with the predictions of IFD theory (Gillis et al. 1993; Swain and Wade 2003). This dynamic view of angler behavior contrasts with the static portrayal of site selection where angling quality is simply one of many fixed factors that affect fishing site selection by anglers (Hunt and Ditton 1997).

The results of the simple numerical model clearly demonstrate the implications of IFD angler behavior for spatially structured fisheries where stock–recruitment parameters vary among stocks. Variable stock–recruitment parameters imply that optimum densities, and therefore catch rates, should vary among stocks. IFD harvesting behavior implies that actual catch rates, and therefore densities, should be similar, even among stocks that vary dramatically in optimal densities. The net result is that stocks are either underfished, when optimal densities are low, or overfished, when optimal densities are high. This in turn implies that, even if overall effort is not excessive, optimum harvest rates on individual stocks are unlikely to be achieved when anglers are free to move their harvesting effort among stocks.

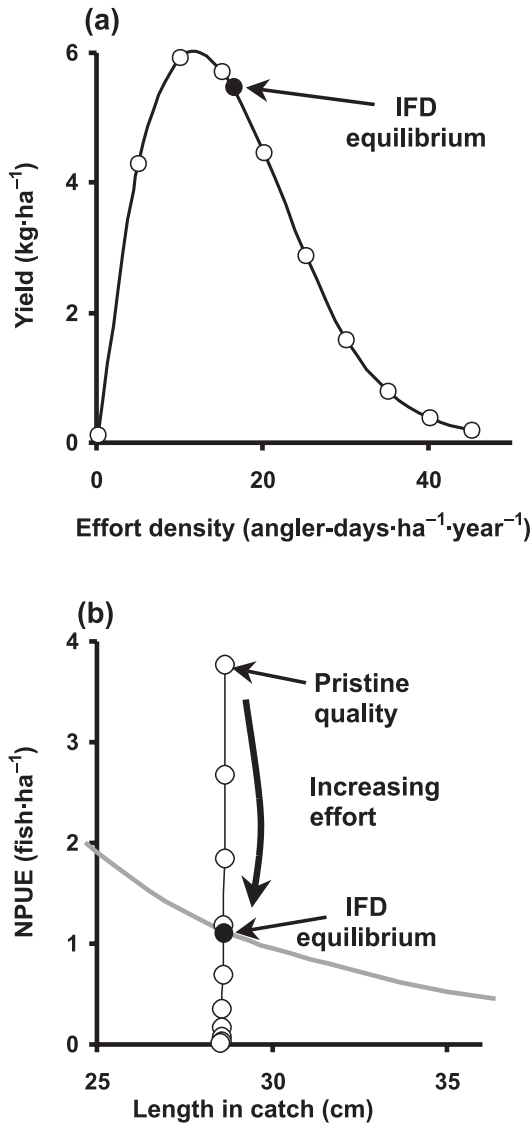
The simple model assumes that catchability is constant with catch rates that are directly proportional to fish density. Empirical data suggest that catchability depends on both fish size and density (Cox 2000; Post et al. 2002). Since catch rate is the key link between recruitment dynamics and harvest dynamics, the implications of relaxing the constant catchability assumption need to be tested. The size-structured model incorporates size- and density-dependent growth, survival, and catchability with outcomes that are similar to those of the simple numerical model. This consis-

tency suggests that our conclusions are relatively robust with respect to model structure.

The process of population regulation in harvested species has typically been considered in isolation from the dynamics of the harvesting effort. Biological management models predict densities and surplus production over a range of harvest rates, but the role of catch rates in determining the level of harvesting effort is rarely incorporated into the dynamics of population regulation. Our model of size-structured trout populations illustrates the effects of angler effort dynamics in a system where the biological mechanisms of population regulation are well documented. An empirical model of the biology, combined with an assumption of simple IFD angler behavior, predicts that open access management will rarely result in optimal populations of rainbow trout in lakes and, in some cases, densities will be depressed to a small fraction of pristine values. Lakes that are naturally capable of supporting high densities of large fish are the most likely to experience severe overfishing but stocks will rarely be driven to extinction if mortality is assumed to be smoothly compensatory. Post et al. (2002) suggested that this may often not be true and discussed a variety of depensatory mechanisms that may make it very difficult for fish stocks to recover after being depressed to very low levels. The focus on high-density, high-productivity populations contrasts with other threats that are generally seen to be more severe for small populations with low productivity (Lande 1993; Caughley and Gunn 1996).

Another clear prediction is that angler effort densities will be variable among lakes that vary in either habitat capacity or stock productivity but that angling quality will be much more uniform (Cox 2000; Post et al. 2002). Moreover, the observed variation in angling quality should be predictable from ancillary variables, such as remoteness, accessibility, or facilities that reflect attractiveness to anglers, rather than

Fig. 9. (a) Yield as a function of effort for a model rainbow trout population. MSY is the peak of this curve. The arrow indicates the approximate position of the IFD equilibrium derived in Fig. 9b. (b) Angling quality (open circles) in a single lake under increasing amounts of effort. The equal quality isopleth (shaded line) is from the relationship described by eq. 15. The point where the two cross is a stable equilibrium driven by angler behavior under an IFD assumption. In both panels, the position of the open circles indicates effort increments of 10 angler-days·ha⁻¹·year⁻¹. In both cases, egg–fry survival is 2%, and capacity is the standard derived from the data of Post et al. (1999).



from characteristics of the lakes that affect the biology of the population. An exception will be lakes with little or no effort where angling quality will be lower than for other lakes. In these cases, angling quality will vary with pristine fish density and size structure, which are in turn a function of stock productivity and habitat capacity.

Both of these results can be generalized to a wide variety of fisheries. The theory behind the dynamics of harvesting effort has been empirically tested in some fisheries (Holland and Sutinen 1999) and it is clear that the effort dynamics

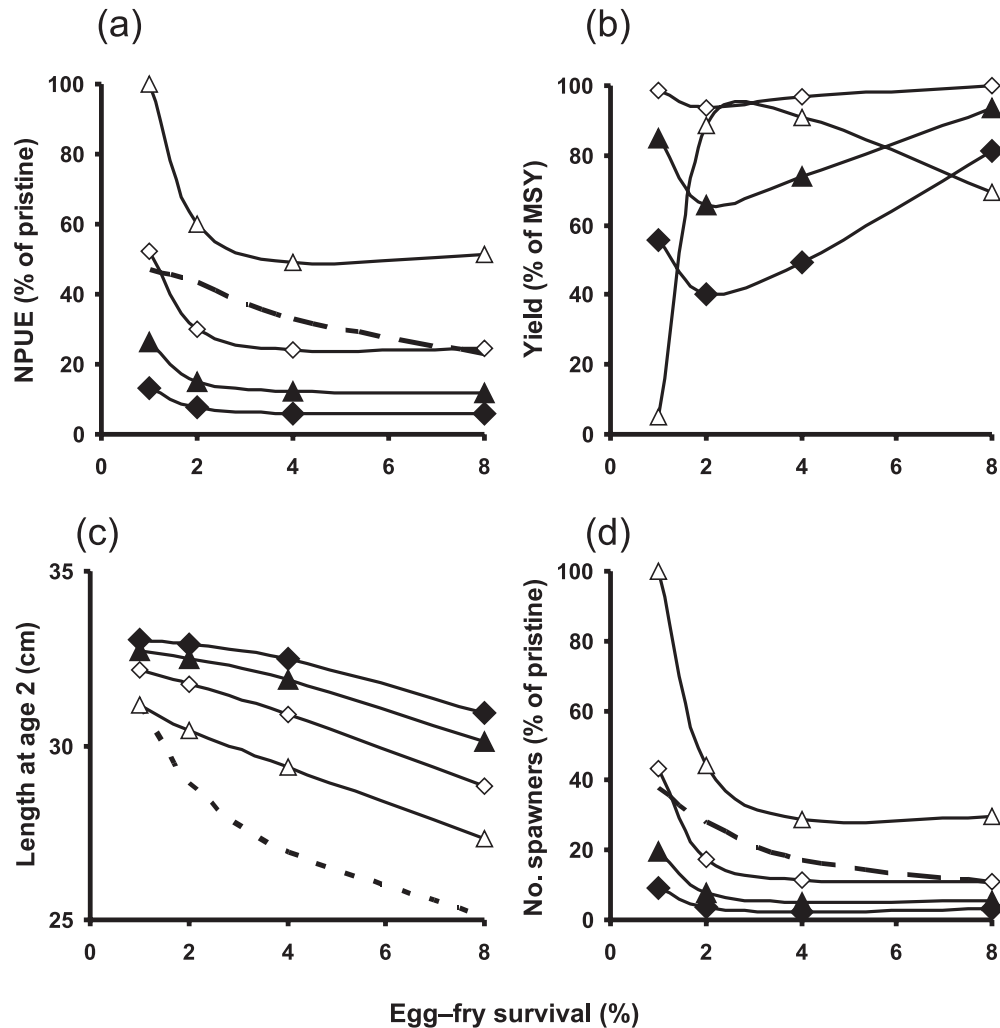
play a critical role in determining current densities in many species. The fact that commercial fisheries with inadequate regulation have depleted many species to a fraction of their former abundance is generally recognized (Pauly et al. 2002) and the role of recreational harvest is now being documented (Post et al. 2002).

Although the process is general, the quantitative outcomes should not be. The position of the equal quality isopleth should vary with the costs of accessing the fishery. In more remote areas, such as Region 5 versus Region 3, we expect that the quality isopleth will be displaced away from the origin. Depletion will be less severe and there will be a greater likelihood that harvest rates will be close to zero because pristine angling quality lies below the isopleth. However, in locations near major population centers, we would predict severe depletion or even extinction of fish stocks when compensatory mechanisms are present (Post et al. 2002). In general terms, we expect that the position of the quality isopleth will be a function of a variety of factors such as remoteness, regulations, facilities, and aesthetics as well as preferences for individual fish species.

The biology of the system will also affect the outcome. In some species, biomass accumulates in older age-classes under pristine conditions and optimal populations consist of relatively high densities of large, old fish. If these high-density populations result in unusually high angling quality, harvesting effort will increase and deplete the stock. In Kananaskis Lake, for example, bull trout (*Salvelinus confluentus*) spawning populations expanded rapidly following the implementation of catch and release regulations that dramatically reduced both the effort and the mortality of captured fish (Mushens et al. 2001). Kananaskis Lake is less than a 2-h drive from the large city of Calgary, Alberta, and bull trout are long-lived salmonids that grow to almost a metre in length. In general, depletion should be expected to be more severe in long-lived, slow-growing species, such as lake trout (*Salvelinus namaycush*) or walleye (*Stizostedion vitreum*), than in short-lived species, such as the rainbow trout in this study.

We recognize the problems associated with focusing on the equilibrium when assessing the outcome of a dynamic process such as angler movements and fish population dynamics. Neither of these processes is expected to be particularly stable. Angler effort and distribution will be perturbed by factors such as the state of the economy, shifting social values, and changes in access to fishing opportunities. Fish populations will be affected by annual fluctuations in weather as well as longer term changes in climate and habitat. As a result, there is no particular reason to expect a system such as the one we have modeled to exist in a state of equilibrium. However, at least some of the processes involved strongly favor equilibrium. Anglers clearly use cues such as new access points, regulation changes, and the experiences of others to quickly focus in on exceptional angling quality that results from perturbations (Johnson and Carpenter 1994). Knowledge of angling quality is not perfect and varies among individuals. Differences in NPUE can be difficult to detect but differences in fish size should be more obvious (Parkinson et al. 1988). However, studious anglers with many connections in the angling community may be adept at de-

Fig. 10. (a) Angling quality (fish·h⁻¹) as a fraction of pristine conditions for the MSY (broken line) and the angler-driven IFD states. (b) Yield (kg·ha⁻¹) under the IFD state as a fraction of MSY. (c) Growth in the pristine (dotted line) and IFD states. (d) Spawner density relative to pristine under the IFD and MSY (broken line) modeled over a range of stock productivity (egg–fry survival) and habitat capacities. In all cases, solid lines represent IFD equilibriums, 0.5 times (open triangles), 1 times (open diamonds), 2 times (solid triangles), and 4 times (solid diamonds) the standard capacity derived from the lakes used by Post et al. (1999). Angling quality is expressed in terms of catch rates of standard-sized fish (~30 cm). Both IFD and MSY yields are expressed in terms of kg 30-cm fish·ha⁻¹. MSY yields, pristine growth rates, and MSY spawner densities do not vary with lake capacity.



protecting transient opportunities with better angling. If these are regular seasonal occurrences, or are predictable from factors such as weather, we expect rapid response to exceptional opportunities.

The implications of IFD angler movement have parallels with the more familiar mixed-stock fishery problem (Paulik et al. 1967). In the conventional mixed-stock fisheries, several stocks are exploited in a single fishery with a single exploitation rate. If they differ in stock productivity, optimal harvest rates will differ among stocks and the combined yield from all stocks is below MSY. In mixed-stock fisheries involving IFD angler distribution, a mobile angler population holds all stocks at similar population densities. If stock productivities or maximum densities vary among stocks, then optimum population densities will differ among stocks and MSY cannot be achieved without restricting angler movement.

A key reason for the disconnection between sport fish management and angler dynamics may be the perception that management can effectively regulate fisheries without directly controlling angling effort. Biological models are often designed to provide reference points for the regulatory process rather than to explore the consequences of ineffective regulation. A variety of models (e.g., Luecke et al. 1994) have considered the effectiveness of alternative regulatory regimes but have not incorporated the dynamics of angler effort. Catch and release regulation is an effective conservation measure but pressure to permit harvesting and nonharvest mortality can both be serious problems when catch rates are high (Nelson 1998; Post et al. 2003). In some cases, the simple observation that anglers are less inclined to fish when catch rates are low has led to the idea that sport fisheries are “self-regulating”, that is, anglers will leave a fishery that has been overharvested and thus allow it to re-

cover (Hansen et al. 2000). Our results suggest that sport fishery management should be refocused onto strategies that deal with the negative consequences of unrestricted growth and movement of effort.

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References

- Barrowman, N.J., and Myers, R.A. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. *Can. J. Fish. Aquat. Sci.* **57**: 665–676.
- Billings, S.J. 1989. Steelhead harvest analysis, 1987–88. *Prov. BC Fish. Tech. Circ.* 85.
- Caughley, G., and Gunn, A. 1996. *Conservation biology in theory and practice*. Blackwell Science, Cambridge, Mass.
- Cox, S.P. 2000. Angling quality, effort response, and exploitation in recreational fisheries: field and modeling studies on British Columbia rainbow trout (*Oncorhynchus mykiss*) lakes. Ph.D. thesis, The University of British Columbia, Vancouver, B.C.
- Cox, S.P., and Walters, C.J. 2002. Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. *N. Am. J. Fish. Manag.* **22**: 21–34.
- Cox, S.P., Beard, T.D., and Walters, C.J. 2002. Harvest control in open-access sport fisheries: hot rod or asleep at the reel? *Bull. Mar. Sci.* **70**: 749–761.
- DeVoretz, D., and Schwindt, R. 1985. Harvesting Canadian fish and rents: a partial review of the report of the Commission on Canadian Pacific Fisheries Policy. *Mar. Resour. Econ.* **1**: 347–367.
- Gillis, D.M., Peterman, R.M., and Tyler, A.V. 1993. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. *Can. J. Fish. Aquat. Sci.* **50**: 323–333.
- Gordon, H.S. 1954. The economic theory of a common property resource: the fishery. *J. Pol. Econ.* **62**: 124–142.
- Hansen, M.J., Beard, T.D., Jr., and Hewett, S.W. 2000. Catch rates and catchability of walleyes in angling and spearing fisheries in northern Wisconsin lakes. *N. Am. J. Fish. Manag.* **20**: 109–118.
- Hilborn, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. *Can. J. Fish. Aquat. Sci.* **42**: 2–13.
- Hilborn, R., and Walters, C.J. 1992. *Quantitative fisheries stock assessment*. Chapman and Hall, New York.
- Holland, D.S., and Sutinen, J.G. 1999. An empirical model of fleet dynamics in New England trawl fisheries. *Can. J. Fish. Aquat. Sci.* **56**: 253–264.
- Hunt, K.M., and Ditton, R.B. 1997. The social context of site selection for freshwater fishing. *N. Am. J. Fish. Manag.* **17**: 331–338.
- Johnson, B.M., and Carpenter, S.R. 1994. Functional and numerical responses: a framework for fish–angler interactions? *Ecol. Appl.* **4**: 808–821.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**: 911–927.
- Larkin, P.A. 1954. Introductions of the Kamloops trout in British Columbia lakes. *Can. Fish Cult.* **16**: 1–10.
- Levin, P.S., Tolimieri, N., Nicklin, M., and Sale, P.F. 2000. Integrating individual behavior and population ecology: the potential for habitat-dependent population regulation in a reef fish. *Behav. Ecol.* **11**: 565–571.
- Ludwig, D., Hilborn, R., and Walters, C. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science (Wash., DC)*, **260**: 17.
- Luecke, C., Edwards, T.C., Jr., Wengert, M.W., Jr., Brayton, S., and Schneider, R. 1994. Simulated changes in lake trout yield, trophies, and forage consumption under various slot limits. *N. Am. J. Fish. Manag.* **14**: 14–21.
- Mushens, C.J., Post, J.R., Stelfox, J.D., and Paul, A.J. 2001. Dynamics of an adfluvial bull trout population following the implementation of catch-and-release only regulations. *In Bull Trout II Conference Proceedings, 17–20 November 1999, Canmore, Alberta. Edited by M.K. Brewin, A.J. Paul, and M. Monita. Trout Unlimited, Calgary, Alta.* pp. 77–78.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**: 2404–2419.
- Nelson, K.L. 1998. Catch-and-release mortality of striped bass in the Roanoke River, North Carolina. *N. Am. J. Fish. Manag.* **18**: 25–30.
- Northcote, T.G. 1969. Patterns and mechanisms in the lakeward migratory behaviour of juvenile trout. *In Symposium on Salmon and Trout in Streams. Edited by T.G. Northcote. Institute of Fisheries, The University of British Columbia, Vancouver, B.C.* pp. 183–204.
- Northcote, T.G., and Larkin, P.A. 1956. Indices of productivity in British Columbia Lakes. *J. Fish. Res. Board Can.* **13**: 515–540.
- Parkinson, E.A., Berkowitz, J., and Bull, C.J. 1988. Sample size requirements for detecting changes in some fisheries statistics from small trout lakes. *N. Am. J. Fish. Manag.* **8**: 181–190.
- Paulik, G.J., Hourston, A.S., and Larkin, P.A. 1967. Exploitation of multiple stocks by a common fishery. *J. Fish. Res. Board Can.* **24**: 2527–2537.
- Pauly, D., Christensen, V., Guenette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., and Zeller, D. 2002. Towards sustainability in world fisheries. *Nature (Lond.)*, **418**: 689–695.
- Peterson, J.T., and Evans, J.W. 2003. Quantitative decision analysis for sport fisheries management. *Fisheries*, **28**: 10–21.
- Post, J.R., Parkinson, E.A., and Johnston, N.T. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. *Ecol. Monogr.* **69**: 155–175.
- Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada’s recreational fisheries: the invisible collapse. *Fisheries*, **27**: 6–17.
- Post, J.R., Mushens, C.J., Paul, A.J., and Sullivan, M. 2003. Assessment of alternative management strategies for sustaining recreational fisheries: model development and application to bull trout, *Salvelinus confluentus*. *N. Am. J. Fish. Manag.* **23**: 22–34.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* No. 191.
- Shuter, B.J., Jones, M.L., Korver, R.M., and Lester, N.P. 1998. A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Can. J. Fish. Aquat. Sci.* **55**: 2161–2177.

- Stone, M. 1988. British Columbia freshwater results of the 1985 National Survey of Sport Fishing. Prov. BC Fish. Tech. Circ. 79.
- Stringer, G.E., Tautz, A.F., Halsey, T.G., and Houston, C. 1980. Further development and testing of a lake stocking formula for rainbow trout in British Columbia. Prov. BC Fish. Manag. Rep. 75.
- Swain, D.P., and Wade, E.J. 2003. Spatial distribution of catch and effort in a fishery for snow crab (*Chionoecetes opilio*): tests of predictions of the ideal free distribution. Can. J. Fish. Aquat. Sci. **60**: 897–909.
- Walters, C.J., and Post, J.R. 1993. Density-dependent growth and competitive asymmetries in size-structured fish populations: a theoretical model and recommendations for field experiments. Trans. Am. Fish. Soc. **122**: 34–45.