

ANGLER NUMERICAL RESPONSE ACROSS LANDSCAPES AND THE COLLAPSE OF FRESHWATER FISHERIES

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Abstract. Recreational angling opportunities in lakes are distributed across landscapes and attract anglers based on the combination of angling quality, travel distance, and availability of facilities. The relationship between angler density and fishing quality, as measured by catch rate, represents a numerical response that is analogous to a predator numerical response to variability in prey abundance. We quantified this numerical response of anglers to rainbow trout, *Oncorhynchus mykiss*, populations distributed over a large lake district in south-central British Columbia, Canada. We developed a harvest dynamics model by linking this empirical description of the spatial numerical response of anglers to a logistic population growth rate model. The model was parameterized for rainbow trout and simulated spatial patterns of angler density and catch rates over a landscape. At locations distant from urban centers, angler density is low and catch rate high, suggesting near pristine conditions; at intermediate distances angler density is higher while catch rates are lower and approximate maximum sustainable levels; and at short distances angler density is sufficiently high to harvest to local extirpation. We extrapolated the model to other lake districts varying in human population size using an empirically derived angling participation rate relationship. Extrapolation to lake districts with one-tenth the human population maintained viable fisheries close to the urban area, and districts with 10 times the human populations could not maintain viable fisheries across much of their lake district. Landscape-scale spatial patterns differed quantitatively for species varying in rates of intrinsic population growth and carrying capacity, but the qualitative spatial patterns were consistent among species, demonstrating the pervasive impacts of the angler numerical response. To achieve a management goal of sustaining fisheries across landscapes, a change in management perspective is necessary, from that of individual lakes to one of dynamic harvest processes across landscapes. This new approach makes it clear that a one-size-fits-all management approach must be replaced with a mosaic of approaches cognizant of landscape-scale processes.

Key words: *British Columbia, Canada; harvest dynamics; landscapes; numerical response; Oncorhynchus mykiss; rainbow trout; recreational fisheries; sustainable harvest.*

INTRODUCTION

We have witnessed the collapse of many of the world's largest and most productive commercial fisheries over the last several decades (Hilborn et al. 2003, Pauly et al. 2003, Worm et al. 2006). Evidence is also mounting that similar pressures and collapses are occurring in freshwater recreational fisheries (Arlinghaus et al. 2002, Post et al. 2002, Lester et al. 2003, Cooke and Cowx 2004, Allan et al. 2005). Yet these observations in freshwater recreational fisheries rarely attract much scientific or public attention and have been referred to as "invisible" collapses (Post et al. 2002). This is despite the observation that the gross economic value of the aggregate of recreational fisheries can exceed the value of commercial fisheries (Post et al. 2002, Cooke and Cowx 2004). In reference to commercial fisheries,

Hilborn suggested that the "sad litany of fishery disasters can be ascribed to a poor understanding of the dynamics of fishermen" (Hilborn 1985). This appears to be particularly true in recreational fisheries in North America that are essentially open access, and managed on the basis of, at best, a poor understanding of the dynamics of anglers (Johnston and Carpenter 1994, Smith 1999, Beard et al. 2003, Cox et al. 2003, Carpenter and Brock 2004).

Recreational fisheries in lake districts can be considered as multi-stock systems connected by a highly mobile angler population (Carpenter and Brock 2004, Parkinson et al. 2004). This system is analogous to a predator-prey system in which predators forage among patches of prey. Simplifying assumptions such as ideal free distribution theory (IFD) suggest that predators will behave in such a way as to homogenize the marginal value across prey patches (Fretwell 1972). In the context of multi-stock fisheries in a lake district, IFD theory predicts that fisheries of equivalent access costs (i.e., travel distance, time, or financial costs) should have

Manuscript received 19 March 2007; revised 30 October 2007; accepted 29 November 2007. Corresponding Editor: P. S. Levin.

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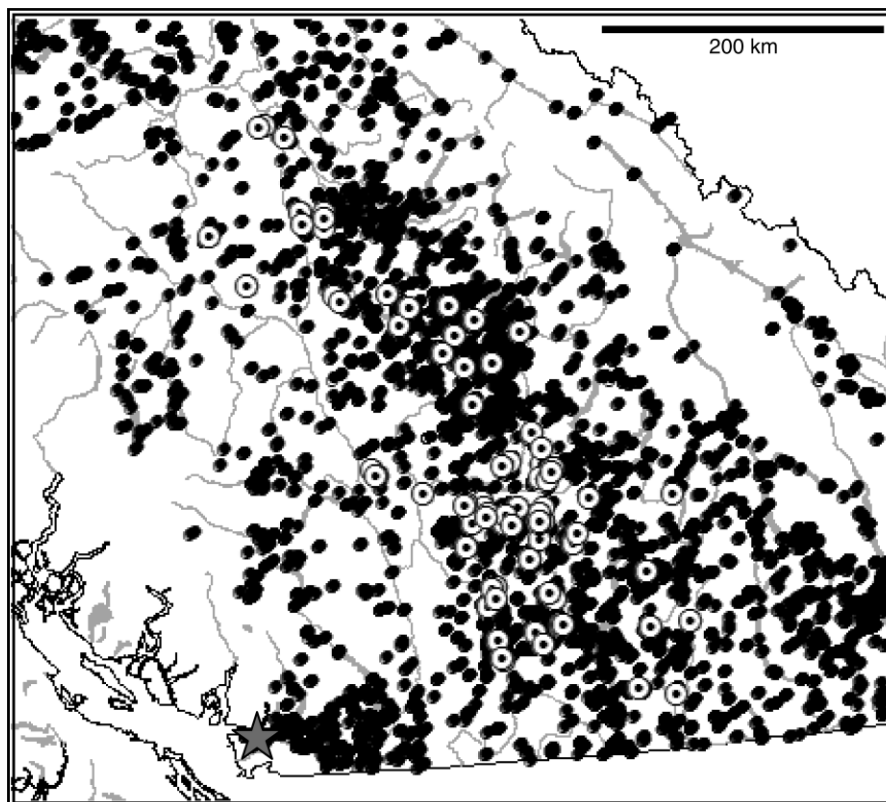


FIG. 1. Map of the southern interior plateau of British Columbia, Canada. Lakes containing rainbow trout are shown as solid dots, and our 76 study lakes are indicated with open circles surrounding a dot. The city of Vancouver is indicated with a star.

catch rates that would tend toward the same level. Attrition of fishing effort over increasing distances would result in a pattern of catch rates inversely related to distance (Parkinson et al. 2004). These general patterns have been observed within and among lake districts of recreational fisheries. Variance in catch rates was low within regions and mean catch rates among regions were inversely related to distance from the population centers of anglers (Cox 2000, Post et al. 2002, Lester et al. 2003).

There has been a general perception in recreational fisheries that they tend toward self-regulation, that is, effort and therefore fishing mortality rates decline to zero as fish populations decline (Post et al. 2002, Beard et al. 2003, Radomski 2003), but this is in conflict with the evidence of collapse cited previously. Assessment of this apparent contradiction requires an understanding of angler behavior in open-access multi-stock fisheries. We need to include angler dynamics into approaches and models aimed at determining sustainable management strategies of recreational fisheries (Cox et al. 2003, Post et al. 2003, Carpenter and Brock 2004, Salas and Gaertner 2004). The spatial dynamics of angler behavior is an important feature of recreational fisheries as we move toward a more active management of fisheries distributed over landscapes (Cox et al. 2003, Lester et al. 2003, Sullivan 2003).

In this paper we develop an empirical model of angler numerical response to fish population abundance from a data set in which angler density is decoupled from natural production dynamics through fish stocking. The model includes distance-dependent attrition of effort term and population size-dependent fishing participation rates. These three functions (angler numerical response to fish density, distance, human population size) are concatenated to a simple fish production function providing a model from which we extrapolate to landscape-scale spatial patterns in fishing effort, catch rates, and yield for naturally reproducing populations. We also use this harvest model to assess landscape patterns for species that are more and less productive than that which forms the empirical basis for this model.

DESIGN AND FIELD DATA

The southern interior of the province of British Columbia in Canada is a lake district with ~17,000 lakes of >1 ha in surface area. This district provides ~2.8 million angler-days of recreational fishing annually (Cox 2000). The primary focus of the recreational fishery is rainbow trout, *Oncorhynchus mykiss*, which occur in ~3,550 lakes of which ~24% are maintained through hatchery stocking (Fig. 1). The occurrence of multiple stocked populations ranging substantially in stocking density provides an opportunity to examine the numer-

TABLE 1. Characteristics of the study lakes in the southern interior plateau of British Columbia, Canada.

Lake characteristics	N^\dagger	Mean	Minimum	Maximum
Area (ha)	76	84.1	3.1	538.2
Maximum depth (m)	69	19.6	4.0	73.0
Mean depth (m)	58	8.1	1.5	30.4
Elevation (m above sea level)	45	1028	598	1550
Total dissolved solids (mg/L)	48	255	29	610
pH	32	8.2	6.9	9.0
Fish density (no. fish/ha)	76	108.6	4.2	409.7
Angler density (angler-days/ha)	76	54.6	2.1	241.5
Distance from Vancouver (km)	76	378.6	225.6	639.0
Distance from asphalt road (km)	76	3.1	0.1	13.7
No. lakes with/without lodges	17/59			

† Data unavailable for some study lakes ($N < 76$).

ical response of angler density to the quality of individual fisheries across regions. This is only viable because the fish population dynamics has been decoupled from the angler density dynamics through stocking. The pattern emerging from this “management experiment” can be interpreted as the numerical response of anglers to variation in catch rate across lakes that vary in travel distance.

We have assembled data from 76 stocked rainbow trout fisheries from this lake district. The city of Vancouver and surrounding urban areas are the primary source of the angling pressure in this lake district, and average angler density declines across fisheries management districts sequentially more distant from Vancouver (Cox 2000, Post et al. 2002). Our study lakes vary in road distance from Vancouver and in several physical and chemical characteristics (Table 1). In addition, 17 of these fisheries have fishing lodges on the lakes (Table 1).

The primary data that we collected for these 76 fisheries are rainbow trout density and angler density. Fish density available to anglers was estimated from at least five years of stocking data for each lake in the 1980s and 1990s. Rainbow trout are stocked either in the fall at age 0 or spring at age 1. They became vulnerable to the fishery at age 2. We calculated the density of catchable sized age-2 rainbow trout as follows:

$$N = \frac{\sum_{\text{year}=1}^i (\alpha_1 N_{0i} + N_{1i}) \times \alpha_2}{i \times A} \quad (1)$$

where i is the number of years of stocking data available; N_{0i} and N_{1i} are numbers stocked at age 0 and age 1 in year i , α_1 is the average survival from the fall as age 0 to spring as age 1, α_2 is the average survival from spring at age 1 to catchable size at age 2; and A is the lake surface area. Reasonable estimates of α_1 and α_2 for rainbow trout in this region are 0.5 and 0.75 (Stringer et al. 1980, Post et al. 1999, Parkinson et al. 2004). Angling effort was estimated using aerial boat counts made during the open water season during the same time period as the stocking rate data (Tredger 1992, Cox and Walters 2002, Post et al. 2002). Angler density is presented as angler-

days/ha using an average angler-day of four hours (Tredger 1992, Cox and Walters 2002) divided by the surface area of the lakes.

MODEL DEVELOPMENT

The development of the full model involves a series of sequential steps. The first is the development of an empirical numerical response of angler density to fish density and other lake-specific characteristics. Building this numerical response depends on the decoupling of angler density from fish production through the use of data from stocked lakes, and is directly applicable to the particular landscape over which the data were gathered. The second step is to develop an empirical scalar of human population size so that the numerical response developed from a single landscape can be extrapolated to others with smaller or larger human populations. The third step is to develop a fish production and harvest model (based on the Gordon-Schaefer model; Clark 2006) parameterized for the fish species for which the numerical response was developed, and in which the normally fixed effort term is replaced by our dynamic numerical response function. This then allows application of the full model to explore harvest dynamics of naturally reproducing fish populations over landscapes. The last step is to develop generic production parameters for species that are less and more productive than that for which we have empirical data, to explore the influence of life history characteristics on landscape patterns in harvest dynamics for other species.

Empirical prediction of effort from lake characteristics

We developed a series of logical and sequentially more complex numerical response models and used log-likelihoods calculated with log-normal error structure to calculate AIC and Δ AIC to differentiate among models, using the information-theoretic approach (Hilborn and Mangel 1997, Haddon 2001, Burnham and Anderson 2002). Data were available on fish density (N), distance of the fish population from Vancouver by road (D_0), distance of the lake from the road (D_1), and the presence or absence of a fishing lodge (L) on the lake. The simplest model was an intercept alone

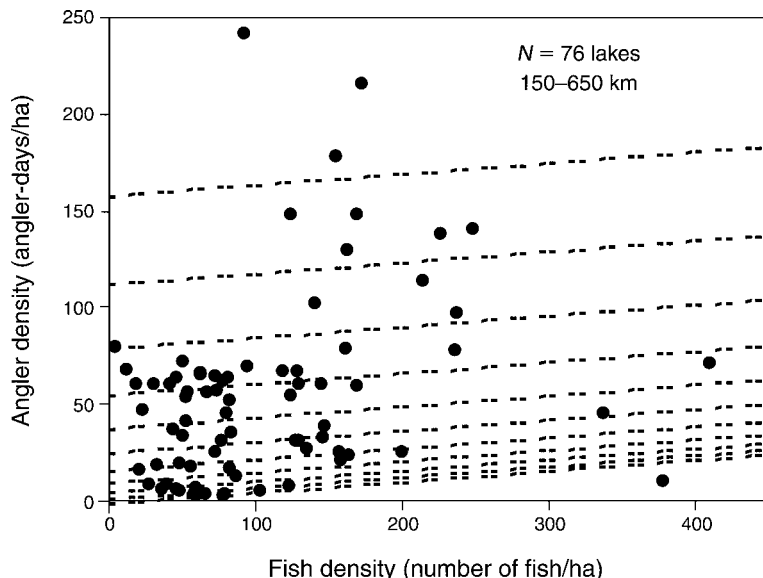


FIG. 2. Numerical response of anglers to variation in the density of rainbow trout in lakes in the southern interior of British Columbia, Canada. The dashed lines are predicted angler densities at distances of 150 to 650 km (top to bottom with an increment of 50 km) from Vancouver. The contours shown are for rainbow trout lakes without lodges.

representing a constant angler density across lakes, and we then built sequential one-, two-, and three-factor models representing the interactions of numerical response with distance and presence of a lodge (L). We also assessed an interaction between N and D_0 . The core of a predator-prey numerical response model is the density of each. In this case it is angler density and fish density, assessed as linear (Type I), asymptotic (Type II), and exponential functions. The travel distance terms, either from Vancouver (D_0) or from the nearest road (D_1), were modeled as negative-exponential functions, which is the standard approach to characterize the dissipation of participation in an activity as a function of increasing distance, travel time, or costs (Sanchirico and Wilen 1999). The presence or absence of a lodge on the study lakes was coded as 0 or 1 leading to the interpretation that the slope for this term is the mean additional angling effort resulting from the presence of a fishing lodge on the lake. The best model was identified as the lowest AIC and all other models are assessed as deviations from the best model (ΔAIC). Models with $\Delta\text{AIC} \leq 2.0$ were assessed as equivalent fits to the data.

The best approximating model was one of intermediate complexity with a linear (Type I) numerical response, a negative exponential travel distance term, and a lodge presence term (Model 7; Fig. 2, Table 3, Eq. 2):

$$E = -8.37 + 0.0567N + 438e^{(-0.00647 * D_0)} + 13.81L \quad (2)$$

where E is angler-days/ha; N is rainbow trout density in fish/ha; D_0 is distance of the trout population from Vancouver in kilometers; and L is coded as absence = 0 and presence = 1 of a lodge on the lake.

The goodness of fit of the chosen model was examined further with a residual analysis, assessment of structural uncertainty, and parameter uncertainty (see Appendix). The best approximating model was substantially better than the intercept-alone model, and any of the single- or two-factor models. Inclusion of distance of the lake from the nearest road did not improve the model fit. The model with the Type I linear numerical response had a lower AIC than the Type II asymptotic model but was not a significantly better fit to the data ($\Delta\text{AIC} = 1.63$) (see the Appendix for further assessment of the implications of Type I and Type II responses). The model that included an interaction term between fish density and the exponential distance term fit less well, implying that the fish density effect is the same at all distances. This suggests a numerical response with a series of parallel lines with intercepts that decline exponentially with distance (Fig. 2). An exponential fish density term fit the data less well than did the linear model ($\Delta\text{AIC} = 5.04$). The best approximating model is therefore model 7 (Tables 2 and 3). The sum of the intercept (β_0) and the coefficient of the negative exponential distance from Vancouver term (β_1) is interpreted as the effort density that would be attracted to a lake adjacent to Vancouver (i.e., $D_0 = 0$) with no fish ($N = 0$), and no lodge ($L = 0$).

Extrapolation of model results to other landscapes

Extrapolation of this numerical response function to regions with smaller or larger cities requires scaling of the expected per capita angling density as measured empirically for the landscape surrounding Vancouver. There are two challenges associated with this extrapolation, one of which we can not address and one which

TABLE 2. Alternative numerical response models posed to explain the relationship between angler density (y) and the independent variables of rainbow trout density (N), distance from the primary source of anglers (D_0), distance of lakes from roads (D_1), and the presence or absence of lodges on the lakes (L).

Model no.	Model structure	Log-likelihood	No. parameters	AIC	Δ AIC
1	β_0	-85.59	1	173.2	56.95
2	$\beta_0 + \beta_1 N$	-81.75	2	167.5	51.28
3	$\beta_0 + \beta_1 \exp(\beta_3 D_0)$	-57.57	3	121.1	4.91
4	$\beta_0 + \beta_4 L$	-83.50	2	171.0	54.78
5	$\beta_0 + \beta_5 \exp(\beta_5 D_1)$	-85.59	3	177.2	60.95
6	$\beta_0 + \beta_1 N + \beta_2 \exp(\beta_3 D_0)$	-55.87	4	119.7	3.52
7	$\beta_0 + \beta_1 N + \beta_2 \exp(\beta_3 D_0) + \beta_4 L$	-53.11	5	116.2	0.00
8	$\beta_0 + \beta_1 N + \beta_2 \exp(\beta_3 D_0) + \beta_6 N \exp(\beta_3 D_0) + \beta_4 L$	-55.83	6	121.7	5.44
9	$\beta_0 + \beta_1 N + \beta_2 \exp(\beta_3 D_0) + \beta_4 L + \beta_7 \exp(\beta_5 D_1)$	-52.24	7	118.5	2.25
10	$\beta_0 + \beta_1 N / (\beta_8 + N) + \beta_2 \exp(\beta_3 D_0) + \beta_4 L$	-52.93	6	117.9	1.63
11	$\beta_0 + \beta_1 \exp(N/\beta_9) + \beta_2 \exp(\beta_3 D_0) + \beta_4 L$	-54.63	6	121.3	5.04

Notes: Estimated log-likelihood, AIC, Δ AIC, and the number of parameters in the models are reported. The model that was the best fit to the empirical data (lowest AIC) is identified in boldface, and all other models are contrasted to this best model, with Δ AIC = AIC_{*i*} - AIC_{BEST}.

we make a reasonable attempt to address. The first problem is that the per capita participation rate that we measure for Vancouver and its surrounding landscape is a function of the demand:supply ratio of angling opportunities across that particular landscape. Because we have data only from that single landscape, and no measure of total supply, extrapolations that we make to other landscapes will assume that equivalent densities of fishing opportunities are available as in the landscape from which we derived our empirical numerical response model.

We attempted to solve the second problem by developing an empirical scalar to population size. Increasingly populated urban centers are likely to have smaller proportions of anglers. We have no direct empirical estimate of this function or parameters from our data. In fact, even if it existed, a time series of the population of Vancouver and fishing effort densities in the surrounding lake district would be confounded by the changing supply:demand ratio as a function of this dynamic interaction between angler density and fish population dynamics. We therefore develop a participation rate function from independent data available in the 2000 Canadian Recreational Fishing Survey (Fisheries and Oceans Canada 2000) and the 2001 Canadian Census (Statistics Canada 2001) data aggregated by province. Data from the provinces of Newfoundland and Prince Edward Island and the Territory of Nunavut were excluded because of the dominance of either marine or aboriginal food fisheries, respectively. The resulting relationship between population size and participation rate is

$$PR = 8.86POP^{-0.108} \tag{3}$$

where PR is the percentage participation rate of anglers from a region of human population size POP ($R^2 = 0.335$, $N = 10$, $P < 0.05$; Table 3). The interpretation of this relationship is that increases of population sizes from 0.1 to 10 million will reduce participation rate by

~60%. We recognize that there is uncertainty in this rate due to differential supply of fishing opportunities among provinces and territories, but aggregation at this large scale should average over variation due to the heterogeneity of lake districts. We can therefore use this relationship to extrapolate to regions with larger and smaller populations using this participation rate and region population size relationship.

Fish production and harvest model

Fish population dynamics with harvest was modeled using a Gordon-Schaefer model, which has at its core a logistic population growth function and a harvest term (Hilborn and Walters 1992, Clark 2006):

$$\frac{dN}{dt} = P - H \tag{4}$$

where

$$P = rN(1 - N/K) \tag{5}$$

and

$$H = qEN. \tag{6}$$

The simple harvest dynamics model (Eqs. 4-6) integrates the density dependence of birth and death rates into a single parameter, r , which is assumed to decline linearly with increasing density. Populations will then tend toward carrying capacity, K , at a rate that is density dependent. We have no direct estimates of r for rainbow trout in south-central British Columbia lakes. We do have estimates of typical catch rates and angler density and an estimate of carrying capacity (K) of 500 fish/ha (Table 3; Post et al. 1999, 2002, Parkinson et al. 2004). We then used our combined production and harvest model to estimate r . A creel census on a subset of 15 lakes averaging 380 km from Vancouver yielded an average daily catch of 1.9 fish/angler-day. We therefore used simulations of the dynamic harvest model to calculate the r that produced this catch rate, given the

TABLE 3. Estimates of parameters for the angler numerical response and harvest models, confidence limits, and parameter ranges over which simulations were conducted.

Parameter	Description	Value
Numerical response of anglers		
β_0	intercept	-8.37 (-11.8, -4.20)†
β_1	fish density effect	0.0567 (0.0215, 0.101)†
β_2	effort density when $D_0 = 0$	438 (381, 503)†
β_3	exponential rate of decline in effort density with distance	-0.00647 (-0.00686, -0.00610)†
β_4	presence of lodge effect	13.8 (3.07, 28.6)†
POP	population size of centers in millions	0.1, 1, 10
Participation rate		
	intercept	8.86 (7.00, 11.22)‡
	exponential slope	-0.108 (-0.231, -0.016)‡
Fish production and harvest		
r	intrinsic rate of increase	0.7 (0.35, 1.4)§
K	carrying capacity	500 (250, 750)§
q	catchability	0.0134

† Values in parentheses are approximate 95% confidence limits using the log-likelihood profile method with lognormal errors (Haddon 2001).

‡ The values in parentheses are 95% confidence limits fit using regression with normal errors.

§ Values in parentheses indicate the range of parameters used for simulation.

observed effort densities at this distance from Vancouver (Table 3). Harvest is modeled with a constant catchability, q , which has been estimated for rainbow trout populations (Cox and Walters 2002, Parkinson et al. 2004).

Linking angler dynamics to fish population dynamics

The combination of the numerical response of angler density, the negative exponential effort–distance function, the population size and participation rate function, and the lodge presence or absence coefficient provides a complete model of the distribution of angling effort across this landscape. We now link this representation to fish production in naturally reproducing populations across the landscape. Because angler density is modeled as functions of N and D_0 (Eq. 2) plus H , $E = f\{N, D_0, \text{POP}\}$, behavior of the full model can be explored by

$$0 = rN(1 - [N/K]) - 9EN \tag{7}$$

and solving for N . We then calculate fish population size, effort, and catch rate over a range of population center sizes (POP) and distance from the population center (D_0). The full model is then equivalent to the Gordon-Schaefer harvest model (Clark 2006) with the constant effort term (E in Eq. 6) replaced with dynamic angler density that responds numerically to changes in fish abundance (Eq. 2).

Extrapolation to other species

We also explore the importance of life history variation as it impacts the dynamic balance between P and H by developing parameters for generic species that are more and less productive species than are rainbow trout, the empirical subject of this data set. We modeled

more productive and less productive species by varying r and K (Table 3). We then recalculated the spatial pattern in harvest, effort, harvest per effort, and proportion that harvest is of maximum sustainable yield (MSY) over a range of D_0 for a single population center size (POP = 1.0×10^6 million).

LANDSCAPE-SCALE MODEL PREDICTIONS

Catch, effort, and yield

We simulated this harvest model to estimate population size, catch, effort, catch rate, and percentage of MSY over distance (0–1000 km) from population center sizes of 0.1×10^6 , 1×10^6 , and 10×10^6 people (Fig. 3). Angling effort and catch rate vary substantially across distance from the population centers, due to the dynamic interactions between angler catch rate (proportional to fish population abundance), angler density, and rainbow trout intrinsic growth rate and carrying capacity. Near small cities of 0.1×10^6 people, catch rates and effort are intermediate between severely overexploited and unexploited conditions (Fig. 3a). MSY occurs at ~100 km from the city (Fig. 3d), with minor overexploitation closer to the city and under-exploitation at greater distances. Adjacent to intermediate size cities (1×10^6 people), potential effort is high, resulting in extirpation of populations within ~250 km of the city. Populations can persist at greater distances but only provide high catch rates once effort declines below ~20 angler-days/ha. MSY occurs at ~440 km from the city whereas populations at greater distances are under-fished (Fig. 3d). Adjacent to large cities (10×10^6 people), potential effort is high and acts to extirpate populations within a 500 km radius (Fig. 3c). Populations and catch rates recover to about one-half of those

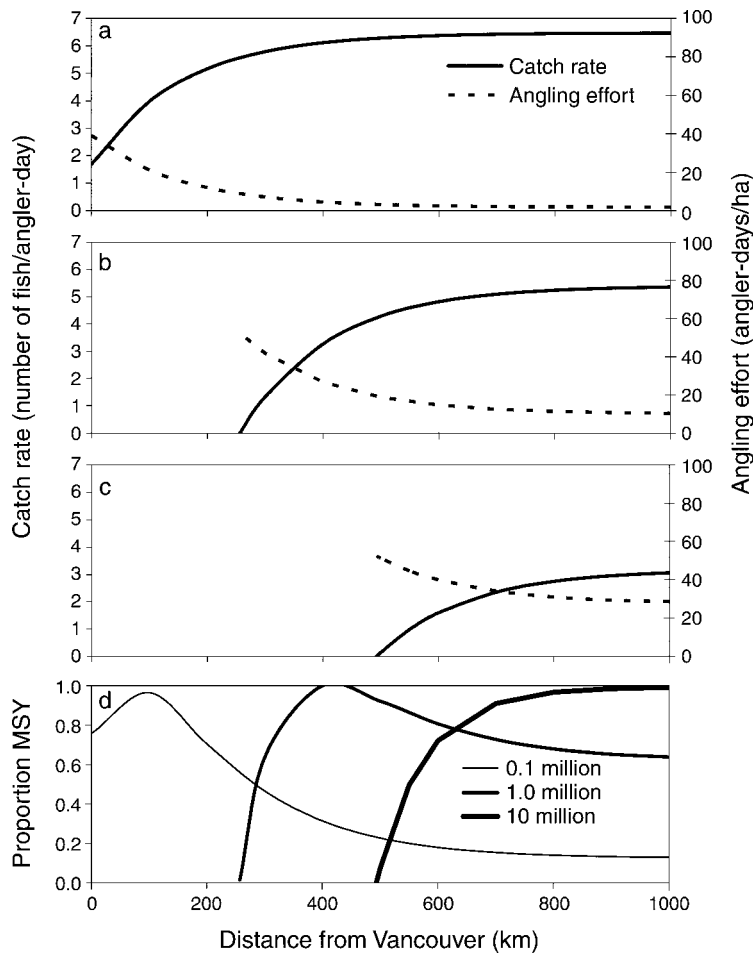


FIG. 3. Spatial patterns in catch rate and angler density (effort) for cities with population sizes of (a) 0.1×10^6 , (b) 1×10^6 , and (c) 10×10^6 people, and (d) the proportion of maximum sustainable yield (MSY).

expected from unexploited populations, but not until a distance of 1000 km from the largest cities. As a result fish populations are severely overfished near large cities and do not approach MSY until >1000 km from the city (Fig. 3d).

Variation in life history traits

The shape and magnitude of the response of catch rate, effort, and the distances at which MSY occurs are also functions of the fish production component of the differential equation population model. Species of recreational fish can differ from rainbow trout in both r and K . We therefore varied these parameters to explore the importance of life history characteristics of recreationally important fish species to spatial patterns in catch rate.

The harvest dynamics model parameterized for a more productive species predicts maintenance of populations at sites closer to cities than does the species with intermediate life history characteristics, rainbow trout (Fig. 4). Maximum sustainable yield also occurs in fish populations closer to cities, and overall catch rates are

maintained at higher levels than for the intermediate productivity species. The less productive species demonstrates the opposite pattern, with lower sustainable catch rates at all distances from population centers with MSY occurring at the most distant sites (Fig. 4). Even the most productive species is extirpated near popula-

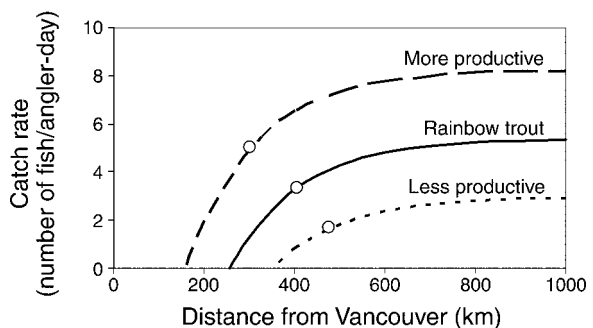


FIG. 4. Spatial pattern of catch rate for rainbow trout in comparison to a single more productive species and a single less productive species. The distance and catch rate at which maximum sustainable yield is attained is indicated by a circle.

tion centers. This suggests that the effort response near large population centers is sufficiently strong to depress even highly productive species. It is not until effort dissipates with increasing distance from population centers that fish populations can maintain abundance and catch rates approaching those provided by MSY. The shapes of these responses, that are qualitatively consistent across species that vary in their production parameters, are functions of the exponential angler density dissipation, the numerical effort response to fish abundance, and fish density-dependent production. The structure of the logistic population model leads to compensation in per capita production with harvesting. If a Type II numerical response had provided the best fit to empirical data, it would have provided an additional source of compensation (see the Appendix for additional discussion of this source of structural uncertainty). The addition of compensatory processes would lower the effort threshold for fish population viability forcing fish populations to extirpation at greater distances. Therefore, angling quality can not be maintained near large population centers in the presence of numerical angler responses, even in productive species.

DISCUSSION

Anglers allocate effort based on the quality of the fishery and the travel time and costs to access the fishing opportunity. Fish population abundance is a function of the dynamic interaction between fishing effort and fish production because: (1) harvest is the product of effort and catch rate, (2) catch rate is proportional to fish abundance, (3) abundance is the outcome of the production-harvest dynamic, and (4) effort is a function of fish abundance. Because effort has a spatial component, this dynamic interaction results in a spatial pattern in fish population abundance and fishing quality over landscapes of lake districts. Fishing quality, as measured by catch rate, is inversely related to the distance that individual fisheries are from the human population centers. This inverse relationship is nonlinear because of the dynamic interactions between the effort response and the nonlinear density-dependent fish production function. This landscape-scale perspective differs from an individual fish population perspective where the paradigm has been that recreational fisheries tend toward self-sustaining (Post et al. 2002, Radomski 2003). The mechanism inferred in discussion of self-sustaining recreational fisheries is that fisheries would not be driven to collapse because anglers would stop fishing depressed populations or shift their effort to other populations with higher catch rates. This presumption is qualitatively correct, but suffers from several omissions at the population, landscape, and temporal scales. At the population scale, several compensatory processes can accelerate rates of population decline as overfishing proceeds (Post et al. 2002, de Roos and Persson 2003). At the landscape scale, the magnitude of the effort response as fishing quality declines is

related to distance from human population centers. Although reduced fishing quality elicits a decline in fishing effort across the landscape, resources near large population centers still illicit sufficient angling effort to result in persistent overexploitation. Fisheries remote from large population centers, or closer to small population centers, maintain higher quality resources. Therefore, the self-sustaining nature of recreational fisheries is context specific within the landscape. At the temporal scale, it might be that the attrition of effort in response to declining fishing quality would be ameliorated due to the intergenerational declines in expectations of quality (i.e., shifting baselines; Pauly 1995, Post et al. 2002). It is likely that some combination of these processes occurring at the population, landscape, and temporal scales led Lester et al. (2003) to conclude that "the elasticity of demand for fishing is not sufficient to prevent overexploitation."

The landscape pattern of regions of overexploitation, optimal exploitation, and under-exploitation poses challenges to fishery managers with the mandate to maximize fishing opportunities while at the same time conserving wild stocks. Traditional recreational fishing regulations that control harvest by individual anglers such as daily bag limits, size limits for harvest, and catch and release with associated release and noncompliance mortality have failed to optimize total harvest and conserve stocks leading to calls for direct effort limitation (Post et al. 2002, Cox et al. 2003, Lester et al. 2003, Sullivan 2003). Cox and Walters (2002) argue that the two key issues involve choosing optimum fishing mortality rate and setting total allowable harvest (or effort). This approach, which has been called "active management" (Radomski 2003, Sullivan 2003), is the approach used in many commercial fisheries that directly control harvest or effort (Clark 2006). A number of sophisticated simulation models have been built to calculate optimum fishing mortality, harvest, and effort for recreational fisheries (examples include Shuter et al. 1998, Cox et al. 2003, Post et al. 2003). Radomski (2003) argues that these bio-economic objectives be broadened to include societal goals, but the general approach involves using a precautionary approach that manages for long-term maintenance of the value of the recreational fisheries resource. There is no question that we can manage for the quality of fishery that we strive to provide given the regulatory tools to control harvest or effort. The problem is that North Americans typically view recreational fisheries as common property resources and are loathe to surrendering unrestricted access and associated property rights (Sullivan 2003).

When considered as a multi-stock, spatially structured fishery, it becomes clear that one-size-fits-all management approaches cannot maintain quality fisheries across landscapes. Fisheries near large cities will be severely overfished if managed as open access. The only viable approach in these regions is active management in which effort (or harvest) is appropriately scaled back to

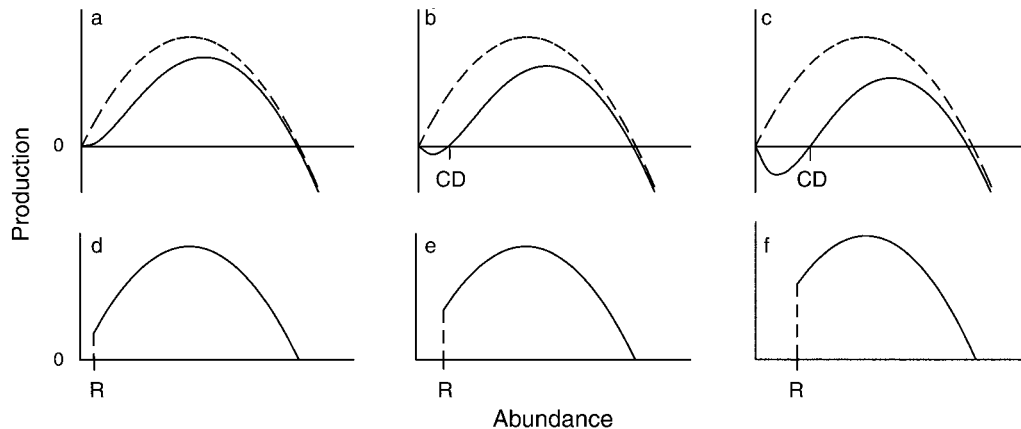


FIG. 5. Two counteracting processes that may occur at low fish density are depensation and a giving-up catch-per-unit-effort density. Increasing levels of depensation are depicted with solid lines in panels a, b, and c with the abundance that leads to critical depensation (CD) below which per capita production declines below zero. The upper dashed line indicates the pure compensation processes, as in the Schaeffer harvest model with no depensation. If anglers abandon harvesting once catch-per-unit-effort declines below increasing thresholds indicated in panels d, e, and f, a refuge abundance (R) will prevent the stock from declining to extirpation.

match the biological productivity of the fishery rather than allowing an unrestricted numerical response. At more distant locations, where potential fishing effort has dissipated due to travel time or cost constraints, less restricted or unrestricted effort dynamics would be sustainable.

A complex ecological-social system such as recreational fisheries cannot be reduced to a simple empirical and simulation model such as ours without omissions and uncertainties. The numerical response model that we built depends on a rather unique data set, which is both a strength and weakness. Our data come from an open-access lake district where the fishery is focused on ~3500 populations of rainbow trout. Within this fishery, about one-quarter of the lakes are managed by stocking. Our effort and fish abundance data come from a subsample of these lakes. The advantage is that by stocking, the natural production-harvest dynamic is decoupled, and therefore the effort allocation behavior we observe is in response to angling quality and not vice versa. We then use this function in the dynamic harvest-production model to interpolate and extrapolate over the landscape of fish populations with natural production. The disadvantage of this empirically parameterized model is that predictions are particular to the lake district from which the data and model are derived, with characteristic angling participation rates and the supply:demand ratio of potential angling opportunities and anglers. The shapes of the numerical response and the landscape pattern should be robust, but the location specific quantitative predictions will vary among lakes and lake districts. We suggest that the processes and patterns, but not the quantitative predictions, are general for other multi-stock spatially structured recreational fisheries.

A structural uncertainty involves the choice of a Type I numerical response model. The best set of parameters did indicate a linear relationship, but it was not significantly better than a Type II asymptotic model. The primary difference between these two model options is that effort is reduced more at low fish density in a Type II response, providing a refuge, or partial refuge, as populations are overharvested. Examination of predictions from the best model (Type I) and the Type II, that fit the data almost as well, suggests only minor curvilinearity (see Appendix). Unfortunately, we have little data at the lowest range of fish density (only three observations at <20 fish/ha). We therefore have no signal in the data consistent with the hypothesis that anglers abandon fishing at very low catch rates, leading to a refuge from angler driven extirpation. This is equivalent, in terms of the density consequences to prey patches, to giving up times by predators (McNair 1982). On the other hand, there is likely another set of low density behaviors at play in recreational fisheries that led to one or more of several depensatory processes occurring in these systems (Post et al. 2002). Although we have no direct evidence of depensatory processes occurring in these rainbow trout fisheries, or of the density threshold below which critical depensation (sensu Post et al. 2002) would occur, the best numerical response fits to our data have nonzero intercepts. This implies higher per capita fishing pressure at low density, indicating angler induced depensation. Interestingly, these two low density phenomena, as characterized in Fig. 5, a refuge from extirpation if anglers abandon low catch rate fisheries, and an increase in per capita mortality rate through one or more depensatory processes, are in opposition to one another (Clark 2006). A refuge from harvest at low abundance ensures that net production remains positive whereas a depen-

satory process results in negative net production at low abundance (Fig. 5).

Our data set on angler density specific to a region and fish supply rate has substantial variance. More data and analysis are necessary to assess if this variance can be explained by variability in the suite of lake specific characteristics of the fisheries for which we have no estimates. Access is not equivalent among lakes that vary in distance by paved or gravel roads, or trails of various lengths, although a model that incorporated such a variable fit the data less well. The presence of fishing lodges did significantly increase the effort density beyond that which would be expected based simply on fishing quality and distance. Other features of fisheries may lead to variable effort including proximity to campgrounds, outfitters, or other amenities that will attract effort. Despite this variance, the general numerical response is the best fit to the data, and the model predictions are not particularly sensitive to uncertainty in these particular coefficients.

A parameter to which model predictions is quite sensitive is the exponential decline in potential effort with distance from population centers. This parameter and formulation is analogous to the rate at which economic rents decline due to increasing travel costs across space (Anderson 1993, Sanchirico and Wilen 1999). The magnitude of the decline in effort across the spatial gradient should be directly proportional to the sharpness in the gradient of catch rate (and population abundance). Our results are qualitatively similar to simulations of angling quality across a landscape dominated by tourists rather than local residents (Carpenter and Brock 2004). Improved quantitative understanding of how anglers trade off travel costs against fishing opportunities and implications to entry and exit dynamics would be a useful topic for further study in fishery resource economics.

Our analysis implicitly assumes that anglers are a homogenous group in terms of their allocation of effort across fisheries that vary in distance and quality. This is certainly not the case. The angler population is made up of tourists and locals, experienced and inexperienced members, and frequent and infrequent anglers, all of which have variable expectations and responsiveness to the quality of their fishing opportunities. These variable expectations likely lead to a diversity of entry and exit dynamics. Unfortunately we have no data on the travel time, origin, or effort of individual anglers, so our approach here is to model the extant population of anglers within our empirical sample of revealed behaviors. Any extrapolations we make over the landscape, city size, or ecological productivity presumes that the mix of anglers and their response to quality remains fixed. There is substantial opportunity to improve our understanding of this source of heterogeneity and their dynamics by collecting data on the behavior of these subpopulations of anglers with additional revealed and stated preference studies. It is likely that such studies

would lead to more precise predictions for individual systems, and a more complete landscape pattern in response to the spatial origin of the heterogeneous population of anglers.

So what is the prognosis for multi-stock, spatially structured recreational fisheries of the sort we studied? We can use contemporary landscape patterns and extrapolations of human population growth to characterize temporal patterns in fishing quality. These extrapolations suggest that over the last 100 years we have seen fisheries such as rainbow trout, within a few hundred kilometers of what are now large urban areas, decline from near pristine to collapse. Extending these projections into the future suggests a further erosion of fishing quality as human populations continue to grow. Clearly a one-size-fits-all management regime is inadequate to reverse these spatial and temporal trends. Highly restrictive harvest or effort limitation is necessary to prevent collapses in fisheries close to medium to large urban areas. The proliferation of hatchery production and stocking in lakes near urban areas may be the only recourse to provide angling opportunities in these areas (Evans and Willox 1991, Post et al. 2002). Because hatchery production decouples the dynamics of harvest from natural production, it is conceivable that high quality fisheries could be maintained within the shadow of large cities where wild populations could not be sustained, given sufficient hatchery capacity. Because spatial angler density dynamics tend to homogenize angling quality within regions, a mixture of management policies will be the only recourse to provide a mosaic of opportunities within regions. This leads to the caution raised by Cox et al. (2003) and Carpenter and Brock (2004) that we need to know more about how effort redistributes over the landscape to assess if there is any net benefit of lake-specific regulations within lake districts.

Each of the components of a model like ours is not complex, but when assembled into a simulation model provides a dynamic context within which to interpret spatial and temporal patterns. Over the last several decades we have witnessed the collapse of many of the world's largest marine commercial fisheries (Hilborn et al. 2003, Pauly et al. 2003). Over the last several years evidence is mounting that freshwater recreational fisheries are following the same path (Post et al. 2002, Lester et al. 2003, Cooke and Cowx 2004, Allan et al. 2005). The most common response is to deny the problem (Radomski 2003). Resort owners, and others with a commercial vested interest, perceive they will lose business and therefore deny the problem. Resource agency managers perceive that admitting to declining fisheries within their jurisdiction reflects badly on their professional abilities to manage so they deny the problem. Anglers may not perceive declines in angling quality because they have been subjected to declining baselines and expectations.

For these, and other reasons, the status of recreational fisheries has been referred to as the “invisible collapse” (Post et al. 2002). In the substantial media and public attention that followed the publication of Post et al. (2002), criticism came from individuals and institutions that clearly demonstrated a lack of understanding of the dynamic nature of the interactions between effort and fish production over spatial and temporal scales. Several anecdotes make this clear. The work was accused as being alarmist by a senior manager from a resource agency. This agency happened to reside in a jurisdiction in which there was a high density of fishery resources and low density of anglers. From that perspective, where the supply:demand ratio is high, there should be no issue of overharvesting leading to collapse hence the manager’s rejection that overharvest in recreational fisheries was an issue. Our simulations quantify this scenario where either population centers are small or resources are remote resulting in high quality fisheries. A second criticism emanated from a resource manager who criticized managers of northern slow-growing fish populations for allowing overexploitation and collapse to occur. This criticism came from a manager who very successfully managed southern, highly productive, fast-growing, and short-lived species. Again, a focus on the dynamic rates of the processes involved in the balance between harvest and production, rather than simply the outcome, would better inform the debate. We need to enhance our understanding of the spatial and temporal processes involved in both the harvest and production sides of this dynamic interaction as we attempt to design more effective management regimes to rehabilitate depleted fisheries and maintain quality fisheries.

ACKNOWLEDGMENTS

The initial ideas for this research developed through formative discussions with Carl Walters and Sean Cox, who were collaborators on a Natural Sciences and Engineering Research Council Strategic Grant. Further funding was provided by an NSERC Discovery Grant to J. R. Post and funding from the British Columbia Ministry of Environment to E. A. Parkinson. We thank Barry Smith and Nigel Lester for excellent peer reviews that substantially improved the manuscript.

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APPENDIX

Model diagnostics (*Ecological Archives* A018-034-A1).

J. R. Post, L. Persson, E. A. Parkinson, and T. van Kooten. 2008. Angler numerical response across landscapes and the collapse of freshwater fisheries. *Ecological Applications* 18:1038–1049.

Appendix A. Model diagnostics.

Residual Analysis

Graphical analysis of the residuals from the best approximating model (Model 7) suggests that the model was best at predicting angler density when it was low, but less accurate at higher predicted densities (Fig. A1a). The largest residuals are observed at high predicted angler density, occur at sites relatively close to Vancouver, and tend to be those with intermediate fish density (Fig. A1). This residual pattern suggests that the range of models that we assessed were unable to predict processes that lead to exceptionally high angler density at a small number of rainbow trout populations closest to Vancouver. It could be that amenities for which we have no data attract more anglers than are predicted based on simply fish density, distance and lodge presence. This small number of large positive residuals is not of much concern to our predictions from the dynamic angler numerical response and fish production model because the underestimated angler densities close to large cities are higher than necessary to collapse populations. Therefore, these underestimates will have little impact on predicted spatial patterns in fish density or catch rates.

Structural Uncertainty

The data set could not differentiate between Type I and II numerical responses (Fig. A2a). Although the Type I gave the lowest LL estimate, the Type II had a $\Delta AIC < 2$. We used the Type I numerical response in further analyses involving spatial harvest dynamics, but the implications of the two numerical response models could be important. A linear Type I numerical response that does not go through the origin implies depensation, with higher per capita fishing pressure at low fish density than at high fish density (Fig. A2a). A Type II numerical response that has reduced angler density at low fish density could provide compensation at low fish density. But both the Type I and II model fits differ little quantitatively and are almost identical in per capita fishing pressure (Fig. A2b). Therefore, the selected model with a linear numerical response would yield the same qualitative pattern as the best fit asymptotic numerical response. Improved resolution of the functional form of the numerical response at low fish density would require more data at low fish density.

Parameter Uncertainty

We used an individual parameter perturbation experiment to assess the sensitivity of model predictions to uncertainty in numerical response and harvest parameters by varying parameters $\pm 5\%$ and $\pm 20\%$ from nominal values and calculating the percent change in catch-per-unit effort. This sensitivity analysis was done at the D_0 that produced the maximum sustainable yield for the rainbow trout biological parameters in a region with a human population of 1×10^6 . There appears to be sufficient compensation in the interactive dynamics of the effort response and logistic population growth that perturbations of β_1 , β_2 , β_3 and q have minor impacts on catch rates (Table A1). The parameter to which predictions are most sensitive is β_3 , the exponential rate of decline in angler density with distance. Analysis done for a distance closer to the population centre, or further from the location of MSY, may yield different quantitative results, but biologically are not as important because these represent fisheries that are either close to extirpation or near carrying capacity. But clearly this is an important rate to estimate with precision and accuracy in order to extrapolate broadly over landscapes. Unfortunately, this is very difficult to measure in natural populations since changes in observed effort are a function of both distance and fish abundance. Our estimate is based on a system in which angling effort is decoupled spatially through stocking efforts allowing independent estimation of the effort dissipation with distance term.

TABLE A1.

Sensitivity of predicted catch-per-unit effort to variation in the numerical response and catchability parameters. The simulations were done using biological parameters for rainbow trout at the distance from a city of 1 million people that produced the maximum sustainable yield. Values are percentage change from nominal values. Bold entries are those that resulted in deviations greater than the percent change of input parameter values.

Percentage change	Parameters				
	β_0	β_1	β_2	β_3	q
+5%	0.8	-1.4	-3.1	7.5	1.3
-5%	-0.8	1.4	3.1	-8.6	-1.5
+20%	3.2	-5.2	-12.2	25.0	3.5
-20%	-3.2	5.8	12.2	-42.3	-7.7

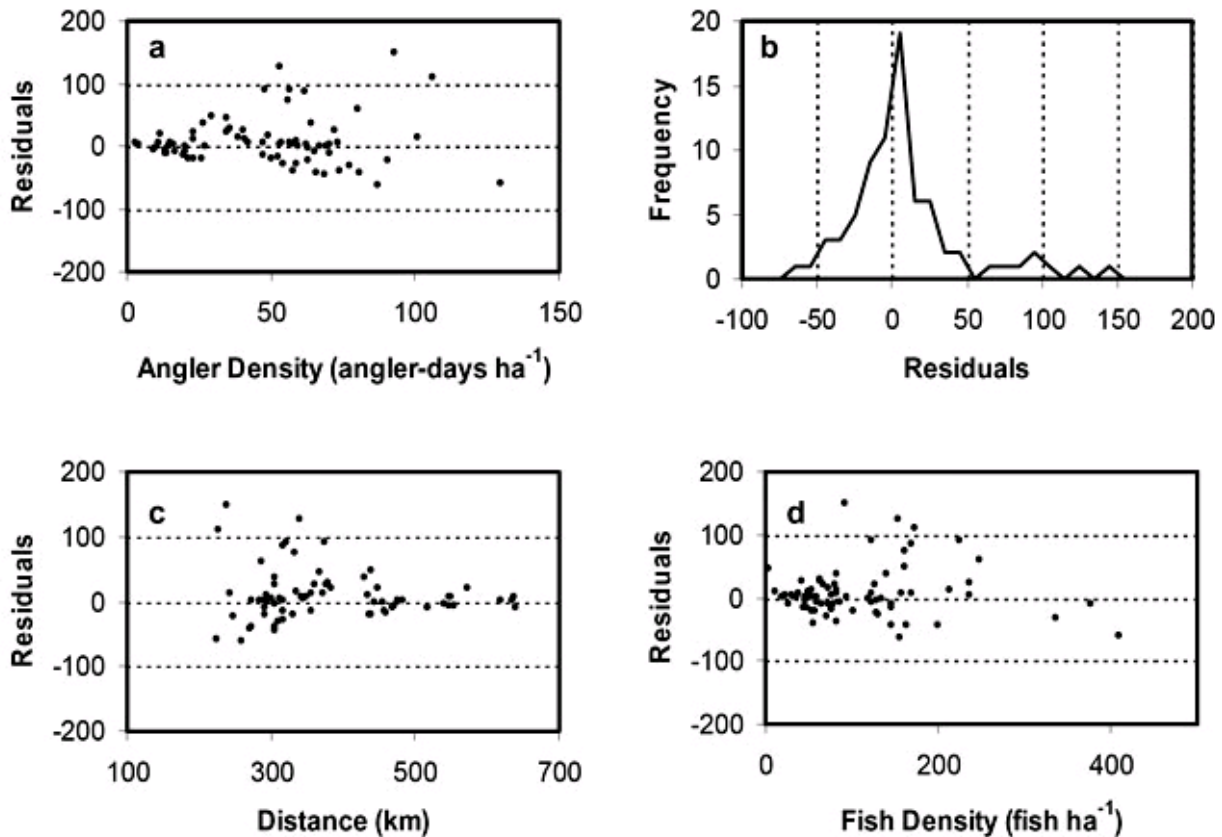


FIG. A1. Analysis of residuals from the best approximating model (Model 7). (a) residuals and predicted angler density, (b) frequency distribution of residuals, (c) residuals and observed distance from Vancouver, and (d) residuals and observed fish density.

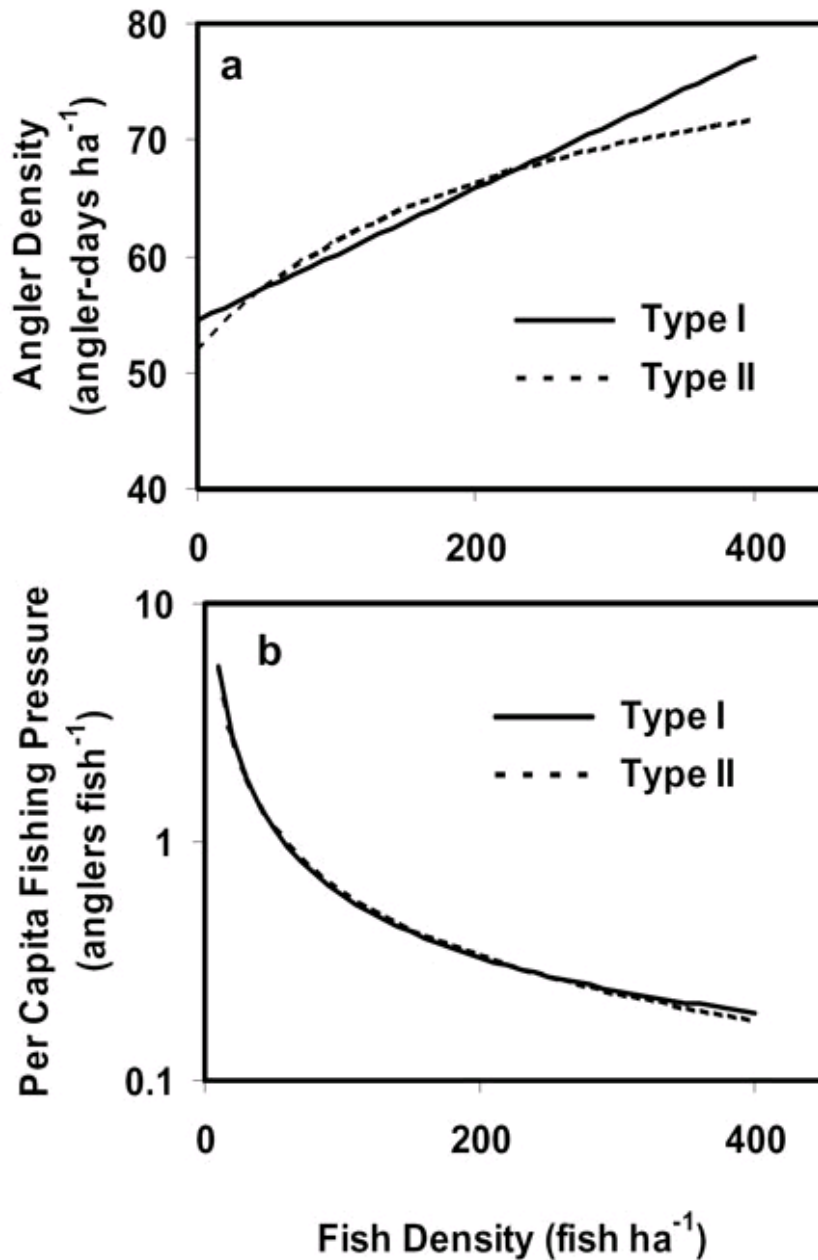


FIG. A2. (a) Predicted angler density across a range of fish density for the best approximating model with a Type 1 linear numerical response (Model 7) and with a Type II asymptotic numerical response (Model 10). The predictions are for a distance from Vancouver of 300 km with no lodge on the lake. (b) Per capita fishing pressure calculated for the Type I and II numerical responses shown in panel a.