Canada's Recreational Fisheries:
The Invisible Collapse?

ABSTRACT

Fishing for recreation is a popular activity in many parts of the world and this activity has led to the development of a sector of substantial social and economic value worldwide. The maintenance of this sector depends on the ability of aquatic ecosystems to provide fishery harvest. We are currently witnessing the collapse of many commercial marine fisheries due to over-exploitation. Recreational fisheries are typically viewed as different from commercial fisheries in that they are self-sustaining and not controlled by the social and economic forces of the open market that have driven many commercial fisheries to collapse. Here we reject the view that recreational and commercial fisheries are inherently different and demonstrate several mechanisms that can lead to the collapse of recreational fisheries. Data from four high profile Canadian recreational fisheries show dramatic declines over the last several decades yet these declines have gone largely unnoticed by fishery scientists, managers, and the public. Empirical evidence demonstrates that the predatory behavior of anglers reduces angling quality to levels proportional to distance from population centers. In addition, the behavior of many fish species and the anglers who pursue them, the common management responses to depleted populations, and the ecological responses of disrupted food webs all lead to potential instability in this predator-prey interaction. To prevent widespread collapse of recreational fisheries, fishery scientists and managers must recognize the impact of these processes of collapse and incorporate them into strategies and models of sustainable harvest.

Introduction

By the end of the 20th century, many of the world's largest commercial fisheries have collapsed (Roughgarden and Smith 1996; Cook et al. 1997; Lauck et al. 1998). Reasons vary, but typically include economic or social incentives that drive fishers to over-exploit fish stocks (Steele 1996; Myers et al. 1997; Hutchings et al. 1997; Masood 1997). Furthermore, technologies have increased the efficiency of modern fishing such that we can search for, find, and exploit fish populations even when their abundance is low. Combined with incentives to maximize profits and employment, this technological ability leads to depensatory mortality (i.e., increases in per capita fishing mortality as populations decline in abundance) that acts to drive fish populations into commercial, if not biological, extinction.

In contrast, without the economic incentives of fishers to over-exploit, or social systems that demand employment, recreational anglers might be expected to abandon fishing opportunities that do not satisfy their expectation of quality angling and instead choose other recreational opportunities as fisheries decline (Johnson and Carpenter 1994; Hansen et al. 2000). Quantifying such a numerical response for recreational fisheries remains elusive because it appears to depend on complex angler behaviors and decisions and not a tightly coupled interaction as in typical predator-prey interactions (Johnson and Carpenter 1994; Smith 1999). Despite these uncertainties, such a numerical response should lead to compensation in the fish

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population (i.e., reductions in per capita mortality as populations decline in abundance) and stability in the angler-fish population interaction. If recreational fisheries behave in this self-regulating fashion, the dramatic collapses observed in many of the world's commercial fisheries should not occur in recreational fisheries.

Consistent with that expectation, the leading North American fisheries journals, *Canadian Journal of Fisheries and Aquatic Sciences*, *Transactions of the American Fisheries Society*, and *North American Journal of Fisheries Management*, published only 13 papers that refer to declines or collapses of recreational fisheries out of a total of 4,904 papers published in the 1990s. Yet, when you ask recreational fishers with several decades of experience for their assessment of the quality of fisheries resources, they invariably say "It ain't as good as it used to be!" Critical examination of the scientific and popular literature does reveal some evidence of declines in some recreational fisheries, although much of the evidence is anecdotal (Pearse 1988; Ryerson and Sullivan 1998; Schindler 1998; Brewin 1999; Sullivan 1999; Walters and Cox 1999; Cook et al. 2001; Radomski 2001; Schindler 2001). In addition to the uncertainty in the value of anecdotal information, and in contrast to commercial fisheries where a collapse simply means the elimination of the economic incentives to fish, a definition of collapse in recreational fisheries remains elusive. How low does the fish population abundance and angler catch-per-unit-effort have to be driven by overfishing until we call it a collapse? The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the International Union for the Conservation of Nature (IUCN) risk categories and criteria of a 50% and 80% decline in 10 years, or 3 generations, which are used to define endangered or critically endangered respectively, provide us with some guidelines (Hutchings 2001). But these guidelines are not really sufficient because it is likely that it is the total magnitude of the decline from pristine conditions to the present, not the short-term rate of decline, that should be used to define a collapse. Certainly a decline in fish abundance or angler catch rates by 80% from some earlier benchmark, equivalent to the IUCN critically endangered criteria, must be acceptable as a conservative definition of a recreational fishery collapse in this era of precautionary management.

In this article we examine data for several high profile Canadian recreational fisheries and conclude that at least some recreational fisheries fit this definition of collapse. We present empirical evidence of several mechanisms inherent in recreational fisheries that are depensatory and should lead to declining fish populations and ultimately to collapse. We conclude that recreational fisheries are not necessarily self-regulating, and can operate in a manner similar to commercial fisheries and will likely suffer the same fate unless there is rapid and substantial intervention.

Evidence of Collapse

The quantitative data required for a definitive assessment of the overall state of Canada's recreational fisheries do not exist. A qualitative survey of Canadian freshwater fisheries, based largely on expert opinion, identified substantial areas showing general declines in a number of recreational fish species (Pearse 1988). These areas of decline tend to be adjacent to urban areas and the Canada-United States southern border. An assessment of trends in abundance of 14 recreational fish species in the 4 continental-scale drainage basins of Canada identify declines due to overfishing and habitat deterioration as common in salmonids, percids, and esocids (Table 1). A number of these fisheries are maintained, at least partly, by stocking (Table 1). In addition, a more quantitative assessment of temporal trends in several high profile fisheries, including 2 salmonid species, 1 percid species, and 1 esocid species (Figure 1) demonstrates that at least some Canadian recreational fisheries are collapsing. Because these 3 families make up approximately 70% of the total harvest of recreational fishes in Canada (DFO 1998), we believe these cases are representative of many recreational fisheries.

The rainbow trout (*Oncorhynchus mykiss*) fishery in south-central British Columbia includes approximately 800 trout populations (Figure 1).

Table 1. Trends in the abundance of recreational fish species by continental scale drainage basins in Canada (adapted from Pearse 1988). Symbols: declining due to overfishing ↓; declining due to habitat deterioration ⇓; stable →; increasing ↑; maintained at least partially by stocking **S**. The trends depicted in this table were extracted from tables in Pearse (1988) for all species but bull trout which was described by Post and Johnston (2001).

	Drainage Basin			
Species	**Pacific**	**Arctic**	**Hudson Bay**	**Atlantic**
Salmonids				
Rainbow trout	↓ **S**		↓ **S**	
Steelhead trout	↑ **S**			
Pacific salmon	↓ **S**			
Bull trout	↓⇓	→	↓⇓	
Arctic grayling	→	↓		
Lake trout	↓	⇓	⇓**S**	↓⇓**S**
Brook trout			**S**	↓⇓
Arctic char		→	↓	
Atlantic salmon				↓⇓
Whitefish		↓	↓	↑ **S**
Percids				
Yellow perch			↓	→
Walleye		↓⇓	↓⇓**S**	↓⇓**S**
Esocids				
Northern pike		↓	↓	↓⇓
Centrarchids				
Bass				→

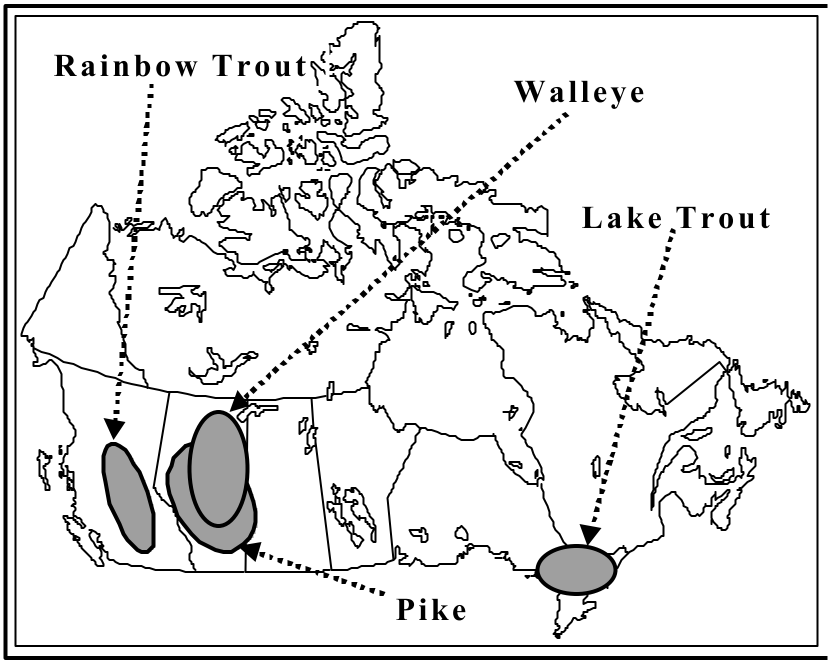


Figure 1. Canadian recreational fisheries for which there is evidence of collapse include the rainbow trout of south central British Columbia, walleye and pike of Alberta, and lake trout of southeastern Ontario.

Two populations for which time series are available show that over the last 3-4 decades, substantial increases in total angler effort are coupled with >6-fold reductions in catch rates. For example, Puntzi Lake angling effort has more than doubled from the 1960s to 1980s while catch-per-unit-effort (CPUE) has declined from 5.6 to 0.25 fish/h. Carp Lake has also seen a doubling of angler effort from the 1970s to 1980s coupled with a decline in CPUE from 2.8 to 0.5 fish/h (Eric Parkinson, B.C. Fisheries, unpublished data). Although there may be a habitat deterioration component, high angling effort is almost certainly a large factor leading to the decline.

In Alberta, 21 of 27 walleye (*Stizostedion vitreum*) populations for which we have data have collapsed because of overfishing (Sullivan in press a) (Figure 1). In Wolfe Lake, Alberta, for example, 2,000 anglers per year enjoyed a CPUE of 0.25 fish/h in the early 1980s but by the 1990s, 10,000 anglers/year experienced a catch rate of only 0.02 fish/h.

Pike (*Esox lucius*) populations in Alberta also show strong evidence of over-exploitation leading to collapse; catch rates in the 1990s were only 15% of what they were two decades earlier in 9 pike populations for which we have data (Michael Sullivan, Alberta Fish and Wildlife Service, unpublished data). For example, an angler at Kehiwin Lake would have fished approximately 2.5 hours to catch a pike in 1969 whereas in 1995 it would have taken an average of 25 hours. Associated reductions in average age, size, number of age-classes in the catch, and failed year-classes all indicate severe overfishing of Alberta pike populations.

In the Ontario lake trout (*Salvelinus namycush*) fishery of the southeast region (Figure 1), nearest the largest human population centers of the province, 60% of formerly naturally sustained lake trout populations are now maintained through stocking (Evans and Wilcox 1991). This is in sharp contrast to <1 % of lake trout lakes that are stocked in northwest Ontario, far from large urban centers.

None of these fisheries are considered collapsed by their respective management agencies, in spite of the large decline in fishing quality that has occurred. Yet these data lead one to question the hypothesis that recreational angling cannot collapse fisheries. It may be no coincidence that two of the examples come from the province of Alberta. This should not be interpreted as an indictment of Albertans or of their fishery management, but is probably a result of geography and human distribution and density. Of the four inland provinces in Canada, Alberta has ~375 licensed recreational anglers per lake, whereas Saskatchewan, Manitoba, and Ontario have <3 licensed anglers per lake (Sullivan in press a). If angling pressure is a factor responsible for Alberta's collapsed fisheries, the state of Alberta's fisheries may be a precursor of what to expect in other jurisdictions as human populations continue to grow and the pressure on fish populations increase.

Why Invisible?

Why are such collapses largely invisible in the scientific literature, public perception, and management action? Why are disgruntled anglers, outfitters, bait dealers, and fishing lodge owners not up in arms? It cannot be because recreational fisheries have a trivial economic impact at home and abroad. The recreational fishing "industry" in Canada has been evaluated at CAN$ 4.4–7 billion annually (DFO 1998). Non-Canadians contributed

26% of the expenditures directly attributed to recreational fishing in Canada, through the participation of 750,000 American, 10,000 British and European, and 1,600 other anglers (DFO 1998). These non-Canadian anglers spent 5.3 million angler-days taking advantage of the perceived unlimited recreational fishing opportunities in Canada. Direct expenditures by anglers on recreational fishing in 1995 exceeded the cumulative value of the landings of all Canadian commercial fisheries in that year by 1.4 times (DFO 1998, 2000).

We propose several reasons for the invisibility of collapses. First, recreational fisheries in Canada number in the hundreds of thousands and tend to be small and diffuse across the landscape. Each one impacts only a relatively small number of anglers and localized economies and therefore receives little regional or national exposure as it collapses. Second, fish populations display considerable spatial and temporal variability and it is difficult for individual anglers or management agencies to develop an accurate picture of processes occurring at scales longer and larger than their own experience. Declines in populations of long-lived species can be slow, and poor intergenerational memory may lead to declining angler expectations as fish populations decline (coined the “shifting baseline” syndrome by Pauly 1995). Photographs of anglers and their catch from the first half of the 20th century provide a sobering perspective of the decline of recreational fisheries over the century (see photo). Third, the declining quality of fisheries can be temporarily masked by fish stocking, fertilization of water bodies, or other management initiatives intended to artificially maintain angling opportunities in the face of increasing demand coupled with dwindling natural stocks. And finally, managers of recreational fisheries have literally thousands of discrete populations to manage with woefully inadequate resources (in proportion to the economic and social value of the resource) to do the assessments necessary to inventory and characterize the status of the recreational fisheries within their jurisdiction.

Fisheries as Predator-Prey Systems

Recreational fisheries can be considered as a series of resources distributed spatially across a landscape and subject to exploitation by human predators with substantial capacity for mobility and communication. Therefore, the system is analogous to the ideas of functional and numerical responses from predator-prey theory (Hilborn and Walters 1992; Smith 1999). Human predator behavior interacts with fish populations at two spatial scales. At the larger regional scale, anglers respond numerically by allocating effort in response to quantitative measures of fishing quality such as fish density (Figure 2a). This numerical response is stronger if the travel time to a prey patch is short. For example, rainbow trout lakes close to the main population center in British Columbia, the greater Vancouver area, attract approximately 2.5 times more anglers-per-unit fish density than do more distant lakes (Figure 2a). This effort response, which depends on resource quality, has a direct consequence on fish populations through exploitation rate (Cox 2000) and therefore mortality and population growth. As a consequence, measures of the functional response, such as angler catch rate, are low in patches characterized by short travel time and high in patches characterized by longer travel time (Figure 2b). These processes result in a reduction in fish abundance as an inverse function of travel distance. Further, homogenization of angling quality within strata of similar travel time may occur based on low variance in catch rate within travel distance strata (Figure 2b). Nevertheless, there is no evidence that the angler effort response at this regional scale would lead to collapse of recreational fisheries. In fact, the numerical response relationships would suggest that as fish abundance declines, angler effort should dissipate in a compensatory manner, allowing stabilization of the predator-prey dynamics, albeit in a low quality state. It is this general observation that leads to the supposition that recreational fisheries tend towards self-regulation (Johnson and Carpenter 1994; Hansen et al. 2000).

At a smaller spatial scale, that of individual fish populations, angler behavior interacts with fish populations in a manner that results in density-dependent catchability. Catchability is the proportion of the fish stock removed per-unit-effort. For fish species that aggregate, catchability should increase as fish population abundance declines if fishers are capable of successfully locating aggregations and exploiting them. Aggregation can be behavioral or habitat-mediated. Behavioral aggregation (shoaling or schooling) is common in pelagic fishes whereas many other species aggregate in association with preferred and spatially limited habitat. A reduction in overall abundance would result in a reduced number of aggregations or an overall range contraction as fish abandon less preferred habitat; however, the density of fish within localized aggregations would remain unchanged or even increase as abundance decreases (Rose and Kulka 1999). This interaction between anglers and fish populations can be predicted by ideal free distribution theory, which assumes the predators have knowledge of prey aggregation behavior (Rosenzweig 1991). Information on fish location and effective communication among anglers provides this knowledge (Smith 1999). Aggregation behavior is common in freshwater fish species targeted by recreational fishers and should result in inverse density-dependent catchability. Data from

12 Ontario lake trout populations that range approximately 25-fold in density, provides strong evidence of inverse density-dependent catchability (Shuter et al. 1998) (Figure 3). This same process, based on the spatial behavior of individual fishers and fish, has led to the dramatic collapse of many commercial fisheries (Rose and Kulka 1999) and likely functions no differently in recreational fisheries.

The occurrence of density-dependent catchability is key to our understanding of the dynamics of recreational fisheries. First, it can lead to population collapse since the proportion of the fish population caught per-unit-effort increases as densities decline causing an increased rate of decline as populations are fished down. Second, angler catch-per-unit-effort, a commonly used measure of population abundance, will initially be invariant as populations decline. Ontario lake trout populations show density-invariant CPUE over broad ranges of density (Figure 3). Therefore, invariant CPUE is not evidence of population stability in fisheries with density-dependent catchability. Density-invariant CPUE has the pathological effect of lulling managers into the belief that everything is fine until the system is well down

Changes in the catches of species of fish at one family's fishing lodge at a large (20,000 ha) northern Saskatchewan lake illustrate the hidden decline in recreational fisheries. The young girl in this 1942 photograph is second author M. Sullivan's mother, balancing a stringer of large walleye. At that time, the highly-desired lake trout fishery of her grandfather's time had collapsed through overfishing, and the family's guiding business had shifted to the large, abundant, and popular walleye. During the mid-1970s, lake trout were extirpated, walleye of the size and abundance in this photograph were unheard-of, and guiding was exclusively for large, but least-desired, northern pike. In recent years (1990s), pike remain abundant but small, a clear sign of growth overfishing. In spite of these spectacular collapses, sport fishermen have continued to travel to the lake (sustaining the guiding business), but with expectations that mirror the decline and change in species availability throughout lakes in this popular Canadian fishing area. In this manner, the collapse of highly-desired prey items such as trout and walleye is masked by the human predators' shift to other less-preferred species such as pike. If the pike fishery collapses (as has happened at lakes in nearby Alberta), the guiding business will also then collapse, because no sportfish species remain to be exploited. This will appear to be a "sudden" economic loss, but in reality it has been in progress for many decades and is only clearly understood when considering the changes spanning five generations of this family. This long-term and critical perspective is seldom available to fisheries managers.

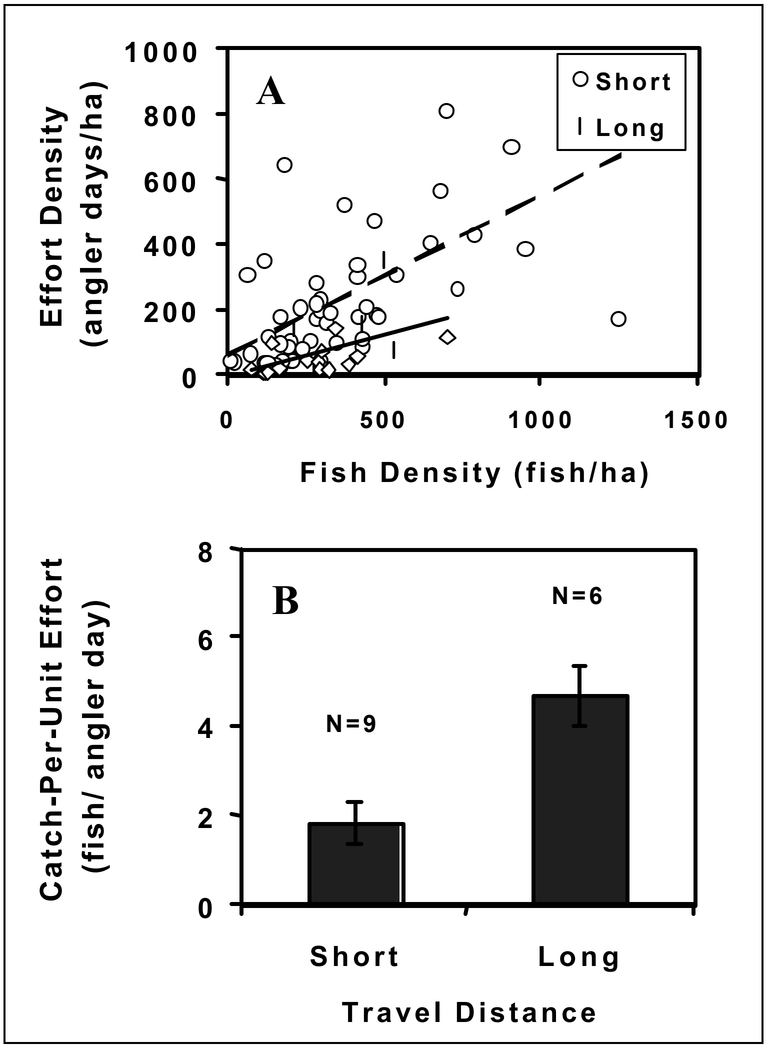


Figure 2. (a) Numerical response of anglers (angler days/ha) to fish density (fish/ha) of rainbow trout in two regions of south central British Columbia that differ in distance from Vancouver (52 lakes in the Kamloops and Okanagan regions with a short travel distance of 3–5 hours indicated by circles and dashed line and 20 lakes in the Williams Lake region with a long travel distance of 5–8 hours indicated by diamonds and solid line). The two numerical responses have the same slopes (F-ratio 0.776, df=1, p=0.382) but different intercepts (F-ratio 9.033, df=1, p=0.004). (b) Catch-per-unit-effort (fish/angler/day) in short and long travel distance regions differed significantly (F=47.88, df=1, p<0.001). Fish density was estimated from mean annual stocking rate of rainbow trout; angling effort density was estimated from aerial boat counts; catch-per-unit-effort was estimated from a creel census on a subset of 15 lake-years (Cox 2000).

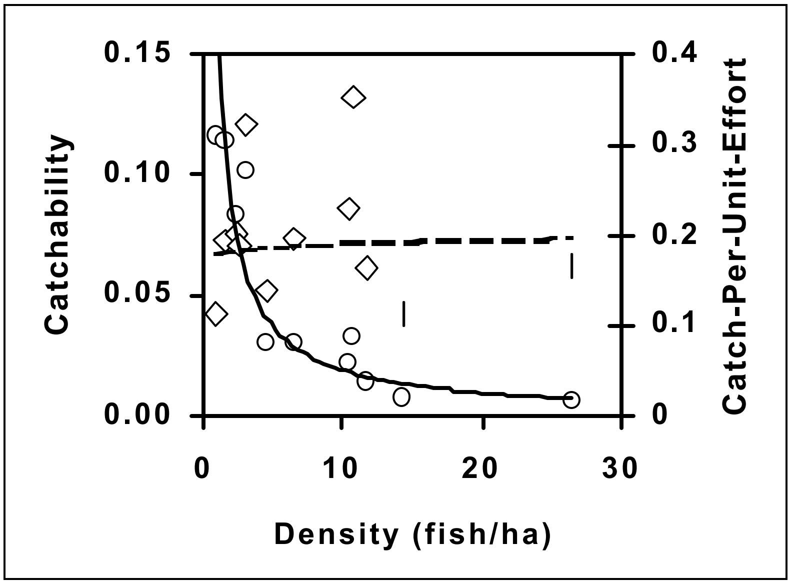
the slippery slope towards collapse. The reductions in CPUE over two to three decades for the several fisheries presented above are likely indicative of dramatic population collapses, not merely subtle changes in population abundance.

Management Actions and Human Behavior

A common management response to declines in angling catch rates is the imposition of regulations to reduce harvest (Radomski et al. 2001). Regulations limiting fish size for harvest or maximum per-angler daily harvest limits provide only a blunt instrument to control total harvest because they only limit the harvest by individual anglers and not the total number of anglers using the resource. Imposition of minimum-size limits for harvest is a common regulation intended to reduce total harvest by protecting juvenile fish. Unfortunately, these regulations are not always successful. In Alberta walleye fisheries, noncompliance with regulations increased with declining catch rates (Figure 4) leading to greater per capita mortality at lower fish abundance (Sullivan in press b). If general, this human behavior will also contribute to depensatory mortality as fish populations decline.

Another common management response to declines in recreational fisheries is artificial propagation in hatcheries and stocking into natural waters (Hilborn 1992; Radomski et al. 2001). Indeed, the development of the huge hatchery infrastructure in North America in the second half of the last century may itself be credible evidence of the decline of native stocks (Pearse 1988; Hilborn 1992) and also one reason for the apparent invisibility of collapses. We stock a diversity of native and non-native species in waters containing native species despite a large literature on the negative ecological and genetic impacts of these stocking programs (Hilborn 1992). Ontario lake trout are prized recreational fish, yet 60% of formerly viable natural lake trout populations in southeastern Ontario are now maintained partially or exclusively by hatchery propagation (Evans and Wilcox 1991). Stocking on top of depleted wild stocks of lake trout leads to the loss of wild

Figure 3. Catch-per-unit-effort (fish/day) did not vary significantly with fish density (fish/ha) for 12 Ontario lake trout fisheries (F=0.072, df=11, p=0.794) (diamonds and dashed and line). Catchability (proportion caught/effort) varied significantly as a negative exponential with fish density (F=44.52, df=1, p<0.001) (circles and solid line) (data from Shuter et al. 1998).

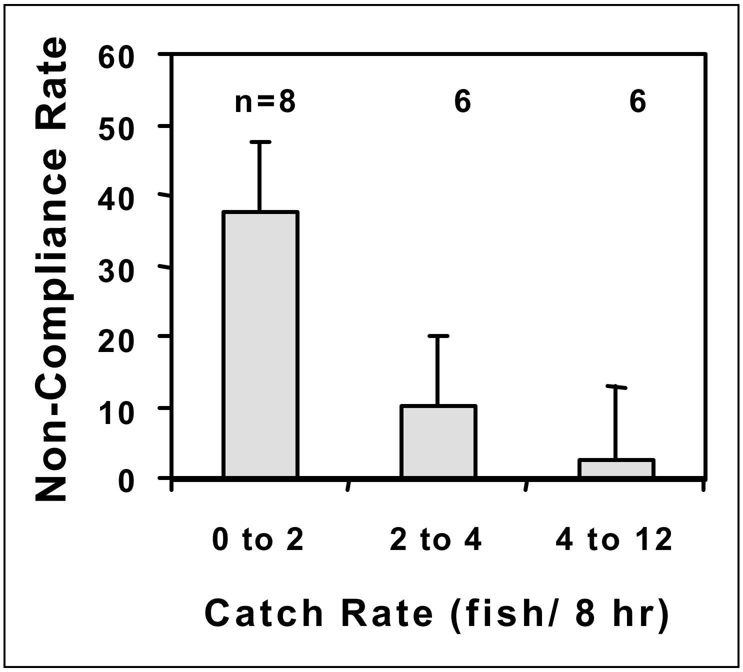


stocks because: (1) the number of artificially produced recruits can easily exceed the number of natural recruits at low natural stock densities, particularly in small lakes, (2) high angling exploitation rates differentially reduces the reproductive potential of the wild stocks, and (3) juvenile hatchery-produced lake trout will cannibalize the smaller-bodied naturally produced juveniles (Evans and Wilcox 1991). Stocking is capable of maintaining exploitation rates well above that which is sustainable by wild stocks, thereby compounding the angling effort imposed on natural stocks. From the standpoint of maintaining natural gene pools, stocking depleted populations is a management response that also acts in a depensatory manner and can hasten the collapse of native stocks.

Altered Food Web Structure

Recreational fish species are often imbedded in complex food webs. The large-bodied freshwater fish species that are the primary targets of many recreational fisheries are successful, in part, due to "cultivation effects," where they crop down forage species that are competitors and/or predators on the juveniles of their own species (Walters and Kitchell 2001). When the abundance of adults of a recreational species is depressed due to exploitation, compensatory increases in the forage species may limit the ability of recreational species to rebound due to suppression of juveniles through predation and competition. We have evidence from food webs in which walleye populations have been reduced in abundance by exploitation that there has been a predatory release on small-bodied fishes (of the family Cyprinidae) (Figure 5a) and that these small-bodied fishes both eat and compete with larval and juvenile walleye. Since fisheries tend to reduce the abundance of the larger and more fecund individuals in a population, total population fecundity declines more quickly than numerical abundance (Figure 5a). As a consequence of this decline in population fecundity, there is a substantially higher potential for predation by small-bodied fishes on eggs or juveniles of the targeted species (Figure 5b). If these depensatory food web processes are as common in aquatic systems as has been recently suggested (Walters and

Figure 4. Non-compliance rate (percent of sub-legal sized fish caught that are not returned) as a function of angler catch rate (fish/8 hr) from Alberta walleye fisheries. The sample size in lake-years and standard errors are indicated for each catch rate class. Angler non-compliance with size-limits was determined for 20 walleye fisheries in Alberta that varied widely in walleye abundance, between 1992 and 1998, by contrasting size ratios of illegal-legal size ratios in a test fishery with ratios reported by anglers during creel surveys (data from Sullivan in press b).



Kitchell 2001), they produce another depensatory mechanism that will exacerbate rates of collapse and would likely foil attempts to rehabilitate collapsed fish stocks through simple reductions in harvest.

Uncertainties, Dynamics and the Future

Dynamics of angler effort alone should not lead to collapse of recreational fisheries but instead force the quality of fisheries to lower levels that are inversely proportional to anglers' travel distance. However, the combination of an angler effort response and several processes capable of producing depensatory fish mortality should lead to a dynamic predator-prey system for which instability and collapse are likely. The presence of depensatory dynamics in commercial fisheries has been assessed rigorously with the benefit of hundreds of data time series, although the occurrence, strength, and mechanisms of depensation are under debate (Myers et al. 1995; Liermann and Hilborn 1997; Myers et al. 1999; Shelton and Healey 1999; Frank and Brickman 2000). What is clear, is that most overexploited commercial stocks showed only limited or no recovery within three generations (Hutchings 2000). It is unclear to what degree depensatory mechanisms are responsible for this lack of recovery, but depensation may be more prevalent than formerly thought (Liermann and Hilborn 1997). We don't yet know how prevalent depensatory dynamics are in recreational fisheries because of the paucity of time series from these systems. But, by demonstrating here the potential of four mechanisms of depensation in recreational fisheries, we suggest that depensatory dynamics are likely a general feature of these fisheries.

Many models of fishery dynamics used by managers assume logistic population growth (Hilborn and Walters 1992):

$$\frac{dN_t}{N_t dt} = r\left(1 - \frac{N_t}{K_U}\right)$$

This representation of population growth assumes linear negative density-dependence with the maximum per capita rate of population growth (r) as the population size (N) approaches zero with a carrying capacity (K_U) at which per capita growth rate is zero. Population densities above K_U are characterized by a negative per capita growth rate that has the effect of returning N to K_U. This implies a stable unfished equilibrium at the environmental carrying capacity and compensation in birth and death rates that result in negative density-dependence in the per capita growth rate (Figure 6a). This form represents pure compensation with the highest positive per capita growth at the lowest population size, zero per capita growth at the carrying capacity and negative per capita growth at population sizes exceeding carrying capacity. To this model of compensation we add a negative exponential depensation term, similar in form to that which we observed for density-dependent catchability and human cheating behavior:

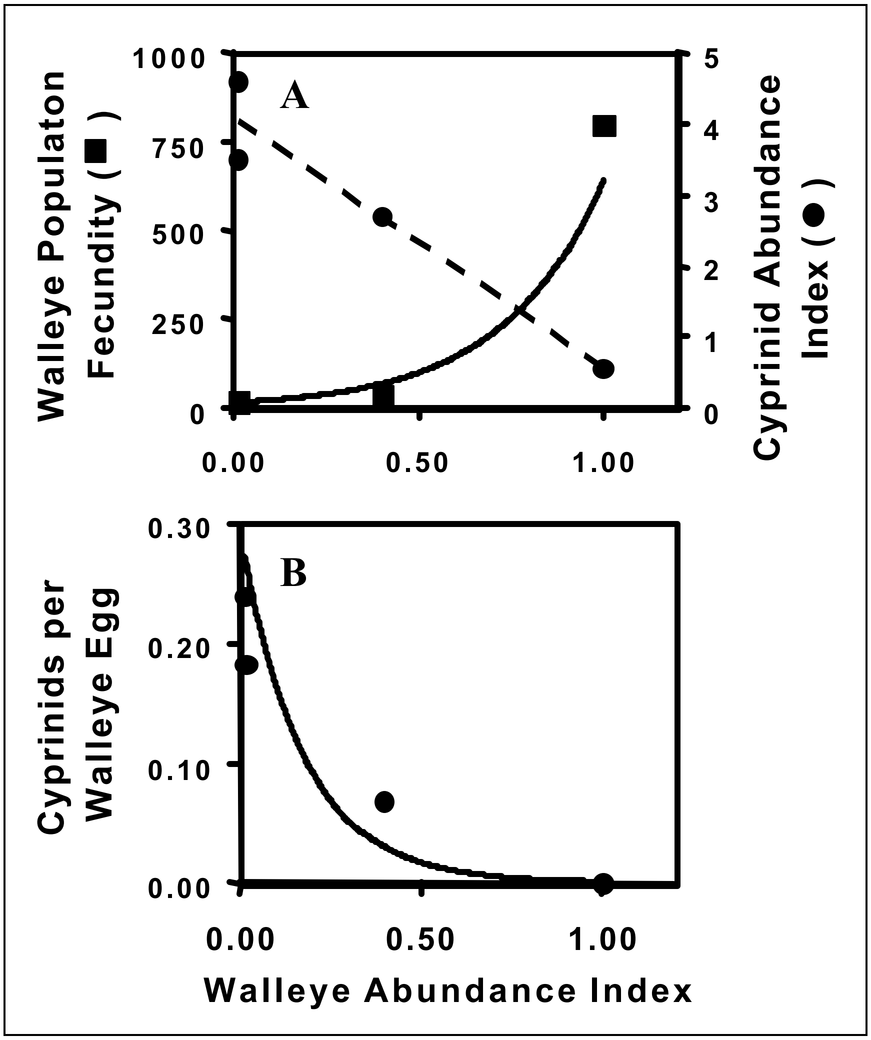


Figure 5. (a) The relationship between an index of Cyprinid abundance and an index of walleye abundance (r^2=0.90, p=0.034) and an index of walleye population fecundity versus an index of walleye abundance (r^2=0.98, p<0.004) in 4 Alberta walleye lakes that have been differentially overexploited by angling. (b) The relationship between an index of the number of Cyprinid predators per walleye egg and an index of walleye abundance (r^2=0.97, p<0.011). Catches of Cyprinids in beach seine hauls near the mouths of walleye spawning rivers in the spring provided estimates of relative abundance among lakes. Laboratory feeding trials demonstrated that Cyprinids would consume larval walleye. Walleye population fecundity was estimated from direct counts of eggs of females of a range of sizes, size structure of mature female walleye and an index of walleye abundance across lakes (unpublished data from M. Sullivan, Alberta Fish and Wildlife Service, Edmonton, Alberta).

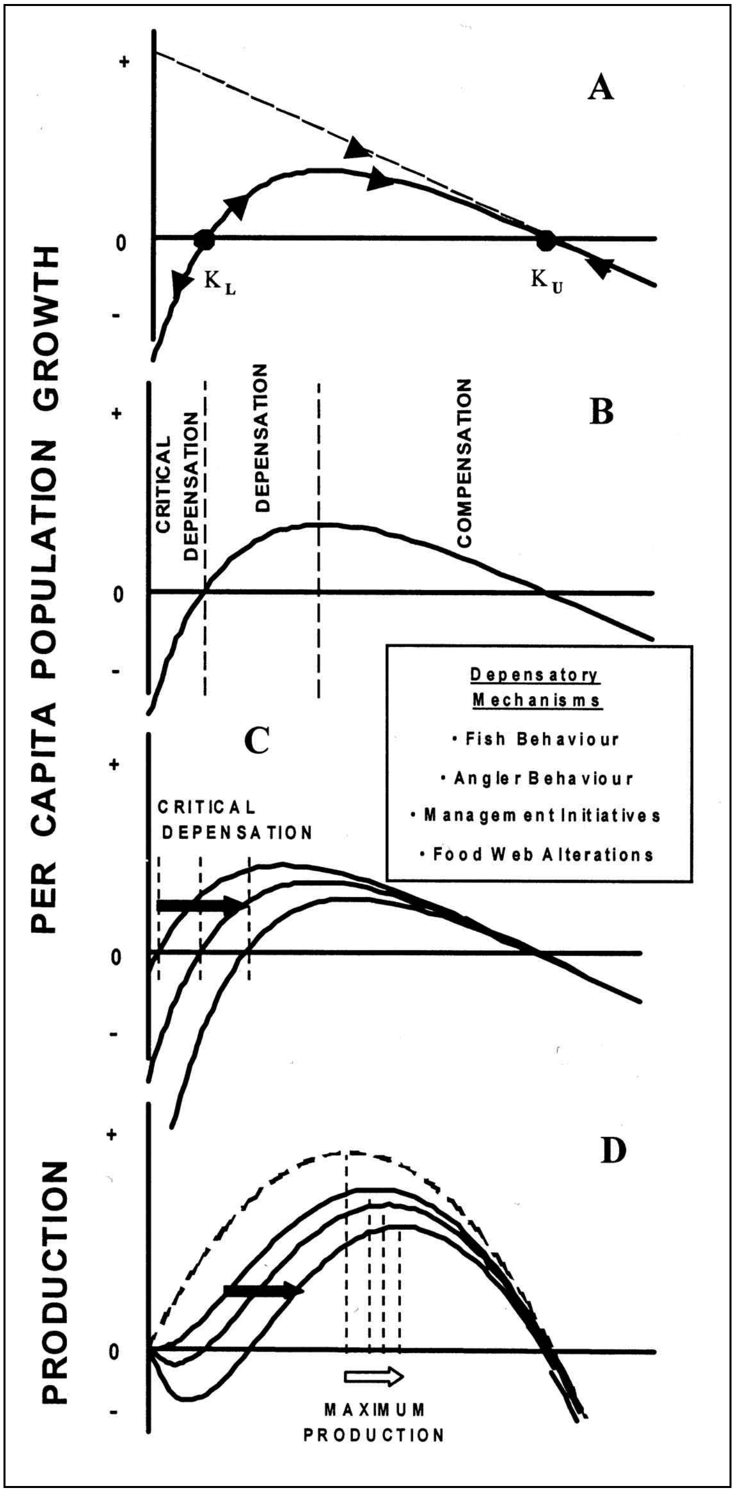


Figure 6. (A) Predicted per capita population growth rates as a function of population size for populations with logistic growth (dashed line) and logistic growth plus exponential depensatory mortality (solid line). The arrows indicate the predicted direction of population change across ranges of population size. Both models predict an upper stable equilibrium (upper carrying capacity K_U). The depensatory model also has a lower unstable equilibrium (K_L). (B) The combined compensatory and depensatory model has three phases noted by net compensatory growth, depensatory growth, and critical depensatory negative growth. (C) The occurrence of multiple additive depensatory mechanisms increases the population size at the lower unstable equilibrium (from weak to strong depensation indicated by the arrow). (D) The population size that maximizes production increases from logistic population growth (dashed line) to increasing strengths of depensatory mechanisms (solid lines) and the maximum production decreases. The black arrow indicates declines in production as the strength of depensatory processes increases and the open arrow indicates the resultant change in the population size that maximizes production.

$$\frac{dN_t}{N_t dt} = r\left(1 - \frac{N_t}{K_U}\right) - \alpha e^{\beta N_t}$$

where α represents the mortality rate as $N \rightarrow 0$ and β is the rate at which mortality declines as N increases. The presence of depensatory processes alters the simple dynamics observed in their absence and has important implications for how we manage recreational fisheries. An upper unfished stable equilibrium still exists with depensation (K_U), but in addition, there is also a lower and unstable equilibrium (K_L), above which reductions in fishing will allow recovery (Figure 6a). If exploitation reduces population size below this lower equilibrium, the population will progress to extinction because the strength of depensation exceeds the compensatory abilities of the population. These alternate caricatures of dynamics thus appear qualitatively similar at intermediate-to-high population densities, where the net effect is compensation (i.e., per capita population growth declines with increasing population abundance). Above the lower unstable equilibrium, though, is a region of depensation where declines in density are exacerbated by reduced per capita population growth and increasing sensitivity to overexploitation (Figure 6b). Critical depensation occurs below the lower unstable equilibrium, where population growth becomes negative and populations are predicted to decline to extinction (Figure 6b).

The depensatory mechanisms that we characterize, involving fish behavior, angler behavior, management initiatives, and food web alterations should all be capable, when coupled with sufficient angler effort, of reducing fish populations to the lower unstable equilibrium and therefore to collapse. The occurrence of multiple depensatory mechanisms likely would be additive, increasing population sizes at which this critical depensation is reached and population collapse becomes inevitable (Figure 6c).

The presence of depensatory processes therefore has three important consequences for managers of recreational fisheries. As fisheries decline in response to exploitation, depensation will accelerate the decline towards collapse. A second, and more insidious implication, is that with depensation, there is no guarantee that if populations are reduced below this lower unstable equilibrium, the effects of overfishing can be reversed. Third, if depensatory processes occur in harvested systems, not only will production be lower than predicted in purely compensatory systems, but the population size required to support maximum production will increase with the strength of depensation (Figure 6d). Therefore, management models not incorporating depensatory processes will underestimate population size at maximum sustainable production, overestimate sustainable exploitation, and expose fisheries to risk of collapse.

To ignore the potential for depensation in recreational fisheries would be inconsistent with precautionary approaches to management and conservation. Identification of the threshold that delimits critical depensation provides a minimum population size target for conservation. The maximum net population growth rate that results from the difference between the intrinsic rate of population growth and depensatory mortality provides a higher minimum threshold for precautionary management target population size. Research aimed at determining the extent and strength of the depensatory processes that we identified in specific recreational fisheries is necessary to identify these population size thresholds for conservation and precautionary management.

All recreational fish species, and populations of species, are not likely to be equally vulnerable to depensatory processes and collapse. Species with age-dependent survival and fecundity schedules that lead to high net reproductive rate and short generation times have a higher capacity for compensation (Winemiller and Rose 1992), reducing the range of population sizes susceptible to critical depensation and collapse. Species with early maturity and high juvenile survivorship, such as many centrarchids, are less likely to be driven to collapse through depensatory processes. Latitudinal variation in life history traits within species, such as age-dependent growth and survival and age-at-maturity (Shuter and Post 1990), imply decreasing compensatory ability with latitude and therefore increasing susceptibility to depensation and collapse. As an example, age-at-maturity of walleye in North America varies markedly with latitude and climate (Baccante and Colby 1996). Southern populations (>5,000 growing degree days) mature at 2–3 years of age and northern populations (1,000 growing degree days) at >8 years of age. This broad variation in life history traits across latitude leads to decreasing compensatory abilities, greater impacts of depensatory processes, and to increased risk of collapse as latitude increases.

What is the prognosis for Canada's recreational fisheries? We argue that if the collapses that we observe in some high profile recreational fisheries are real and general, and remain largely invisible, that many recreational fisheries are headed in the same direction as are the world's commercial fisheries. Unfortunately, the quantitative data required to assess the general state of recreational fisheries are not available. The National Recreational Fisheries Survey of Canada (DFO 1998) supplies data describing the state of the resource from the perspective of the angler, but not of the fish populations. We have seen that data on angler catch rates are not necessarily reflective of fish abundance until populations are near collapse. This lag between observed angler catch rates and fishery declines ensures management inaction until it is too late. We therefore require: (1) fishery independent assessments of the status of fish populations, and (2) changes in the management of recreational fishing that increase the visibility of fish population declines to agency biologists, the public, and politicians. We must also recognize, quantify, and incorporate depensatory processes, where and when they exist, into dynamic management models to identify thresholds of population abundance that are necessary to sustain fish populations and the social and economic value that they provide. Only then can fisheries management, and society as a whole, hope to respond in a timely fashion to avoid the collapses and costly mistakes that have characterized the science and management of many of the world's commercial fisheries.

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