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DIVISION OF ENVIRONMENTAL STUDIES DAVIS, CALIFORNIA 95616

Aug. 14, 1995

Professor R.J. Behnke
Department of Fisheries and Wildlife Biology
Colorado State University
FT. Collins, CO 80523

Dear Dr. Behnke

My name is Michael Brett and I am a Lecturer and Research Scientist in the Division of Environmental Studies at the University of California Davis. I recently wrote a letter to John Randolph, Editor of Fly Fisherman Magazine, discussing the question of whether angling mortality is compensatory or additive for most special regulation streams (see enclosed). John Randolph indicated my letter needed clarification in order to be appropriate for the general readers of Fly Fisherman Magazine and he suggested you act as a "reviewer".

I approached the topic of angling mortality from the perspective of density-dependent and density-independent mortality and the theoretical relationship between density-dependent individual growth rates and density-dependent mortality. I argued that in general the trout populations of most special regulation streams have high individual growth rates and density-independent mortality and therefore in general angling mortality will be additive for most blue ribbon trout streams. In these cases relaxation of no-kill rules will probably result in a notable reduction in the number of older (and larger sized) fish in the population. Clearly there are many cases where one would theoretically expect mortality to be density-dependent and angling mortality to be compensatory. For example, stunted brook trout populations in alpine lakes. However, these cases are rarely managed with no kill regulations.

It was obvious from John Randolph's initial and subsequent reply to my letter, that there was a serious risk that I might end up confusing more than informing the readers. This is due to my difficulty conveying scientific concepts in a manner comprehensible to a general audience [I noticed you used very similar wording in your comment in *Fisheries*, Sept. 1994 page 30]. I have published extensively in aquatic ecology journals, but writing in layman's terms is a challenge. However, the question of whether angling mortality is additive or compensatory has vital management implications and sportfishers need to be correctly informed.

I fear that my approach may be too technical and confusing for most readers of a fly fishing publication. A possibly preferable approach would be to discuss the maximum sustainable yield model and its implications for angling mortality. In fact, I suspect that a simple misunderstanding of the MSY model may be the root case of the obvious confusion over angling's impact on trout population mortality rates. According to the MSY model some harvest will increase the production of a fish population. This has obvious implications for commercial fishermen who only want to harvest the production of a population so that in the long run the fishery is sustainable. [However, in almost all cases where the MSY has been used to manage commercial fisheries the fisheries have been driven to economic extinction]. In contrast, fly fishers do not harvest the production of a population they fish to its standing stock. The MSY predicts that as you drive down the population you will increase production (and individual growth rates) and decrease standing stock. By increasing the population's overall mortality rate you will also have a dramatic impact on the age structure of the population and will increase the proportion younger individuals in the population. This may be good for commercial fisheries because smaller fish have higher production to biomass ratio's, but this is certainly bad for flyfishers who want to catch older and LARGER fish. It should also be noted that a MSY model only applies if the population's mortality is primarily density dependent. I have already argued in my letter to John Randolph that I believe mortality in most blue ribbon trout streams is density-independent.

Unfortunately, when reviewing the relevant literature for the letter to Randolph I found few conclusive studies. Several papers simply assumed angling mortality was additive and interpreted or conducted their studies accordingly, for example Clark (1983) or Gigliotti and Taylor (1990). Another article (Wiley and Dufek 1980) presented results which very clearly suggested angling mortality for trout in the Fontelle tailwater of the Green River was additive and that the average size of fish caught decreased as angling effort increased. I am however, a little suspicious of their study because their regression coefficients between angling effort and total mortality were nearly perfect ($r^2 \approx 1.00$).

I think an article which discusses angling impacts on trout population mortality rates should cover several additional topics. For example, as you mentioned in some of your scientific articles, no kill regulations will in general return a stream to its pre-angling state. If the stream was mainly comprised of 8 to 12 inch fish before significant angling, then no kill rules will not result in a population comprised of larger fish. No kill regulations will, however, probably increase the number of 8 to 12 inch fish over that seen with heavy angling.

No kill regulations will in general have a dramatic impact on the age and size distribution of a trout population under one or two circumstances. The first is cases where the fish are long lived, such as many cutthroat trout populations. Because these fish have the potential to reach relatively old age, even small angling mortality rates have the potential to seriously impact the age distribution of the population. The other circumstance is in particularly productive systems where the trout have the potential to grow fast. In this case the fact that the average age of a catchable fish may increase by only one year may have a dramatic impact on the numbers of larger fish in the population.

I feel it is very important to communicate good science to both the scientific community and to the general public. I still have alot to learn when it comes to effective scientific writing for a non-technical audience. I would appreciate your input on several specific items:

1) Do you believe the density-dependent mortality or MSY approach is the easiest to understand for a general audience?

2) In my first letter to John Randolph I mentioned there was some controversy in the scientific literature regarding whether angling mortality was compensatory or additive. As a scientist I feel it is important to present all perspectives on an issue even if some are less well grounded. However, as a lecturer I have noted that many students have a very difficult time dealing with controversy in the scientific literature. This may also be true for readers of a general publication like Fly Fisherman Magazine. What is your opinion on this matter?

3) In your opinion, what are the 3 or 4 most important issues to be addressed when discussing the relevance of angling mortality?

4) I believe I have already read most of your papers on catch and release angling, but just in case I missed any I would appreciate copies of them. If you are aware of other scientific articles on this topic please indicate their citations. Have you seen a preprint of Frank Rahel's article on special regulations?

I realize I am asking for quite a bit of assistance. Thanks for any time you are able to devote to this. I hope that once the rough edges are worked out this project will turn into an informative presentation of a very important management question.

Sincerely,

Mike

Michael T. Brett

Gigliotti, L.M., and W.W. Taylor. 1990. The effect of illegal harvest on recreational fisheries. N. Am. J. Fish. Manage. 10: 106-110.

Clark, R.D. 1983. Potential effects of voluntary catch and release of fish on recreational fisheries. N. Am. J. Fish. Manage. 3: 306-314.

Wiley, R.W., and D.J. Dufek. 1980. Standing crop of trout in the Fontenelle tailwater of the Green River. Trans. Am. Fish. Soc. 109: 168-175.

CC: John Randolph

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Compensatory / Additive

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Sturgeon 20 yrs.
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Life span
- catchable size (hit fish) ...
1 ... - ... yrs
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II + 3rd yr. ... IV ... VI - VII
yolk ... sac

Is Hooking Mortality Compensatory or Additive to Natural Mortality?

In a recent review of the technical hooking mortality literature, Patrick Trotter presented several hypotheses as if they were ***axioms*** of fisheries biology. Specifically, Trotter argued that any hooking mortality that occurs will be compensatory if it is lower than the population's natural mortality rate. According to Trotter "It turns out that [if angling mortality is below the population's natural mortality rate], angling mortality is compensatory. In other words, . . . the catchable-sized fish lost to angling are offset by fewer fish succumbing to natural causes . . and the population will maintain itself." As a person who also holds a Ph.D. in the field of Aquatic Ecology and is very active in research and education, I can attest that Trotter views on angling mortality impacts on trout population size and age structure are definitely ***not supported*** by a careful or even a cursory reading of the relevant scientific literature.

The crux of the issue is this: is hooking mortality compensatory or additive to the trout population's natural mortality rate? Trotter believes it is compensatory as long as the aggregate angling mortality rate (the percentage of all trout in the population which die each year due to being hooked) is significantly below the population's natural mortality rate (that is all mortality which is unrelated to fishing). I believe this is a fancy way of phrasing the oft repeated fishing myth that the population needs a certain amount harvest to keep it healthy. Trotter's premise is also demonstrably false. If it is true that some fishing organizations are lobbying to allow bait fishing on special regulation trout streams, then it is essential that this matter be clarified immediately.

First off, it must be emphasized that this issue is not mere esoterica. Whether hooking mortality is compensatory or additive will have profound impacts on trout population size, age structure, and appropriate management strategies. As Trotter correctly pointed out this issue is worth an article in and of itself. If you accept Trotter's premise that hooking mortality is simply compensatory, then you would also accept fairly high aggregate hooking mortality rates.

Lets start by assuming that we do not know whether hooking mortality is compensatory or additive (I will later show we have strong evidence suggesting it is additive). Lets consider a hypothetical population of catchable trout with a natural mortality rate of 50% (Trotter's hypothetical rate). Recruitment to this population of catchable fish is in the form of approximately 1000 two-year old fish per year. If a population's size is stable its age structure is determined by its mortality rate. The fish in our hypothetical population obtain the following sizes at each age: two years - 12 inches, three years - 15 inches, four years - 17 inches, and five years - 18 inches. If the population is stable and hooking mortality is compensatory our population will have 500 15 inch fish, 250 17 inch fish, and 125 18 inch fish. If however, annual hooking mortality is 50% and additive to the population's natural mortality rate, then total annual mortality will be 75%. [This is because 50% of the fish in the population will die of natural causes each year, and half of those fish which survive natural mortality will succumb to angling mortality]. Under additive mortality the population will only have 250 15 inch fish, 63 17 inch fish, and 16 18 inch fish (see Figure 1).

If hooking mortality was really compensatory the population would have 375 17-18 inch fish, if however, mortality was additive the population would only have 79 17-18 inch fish, or an 80% reduction in "Big Fish". If a trout stream was managed as if hooking mortality was compensatory, but it was in fact additive, a whole lotta big fish would be missing and many fisherman would be very angry. Clearly it is imperative that we determine whether hooking mortality is in general compensatory or additive. For this we can rely on a wealth of scientific studies and theoretical population ecology.

As a matter of policy we should always adopt the most conservative assumptions when managing a natural resource. A conservative assumption is that assumption which will least likely result in harm to or over exploitation of a resource if subsequently found to be incorrect. In this particular case, additive angling mortality is the most conservative assumption. This philosophy is the equivalent of the physicians rule of "first do no harm to the patient".

Compensatory mechanisms occur when a population's mortality rate is primarily ***density-dependent***. That is the population's mortality rate increases as the population's abundance increases. The most common form of density-dependent mortality is starvation or indirect responses to starvation such as increased susceptibility to disease. Quite often, however, a population's mortality rate is found to be ***density-independent***. For example, a period of high water temperature might cause a trout die-off. The percentage of trout which die would have no relationship to the number of trout in the population. A certain percentage of trout would be more sensitive to high temperatures and these would be the first to die. If the population was 10 fish 5 might die, if the population was 1000 fish 500 might die. Predators (such as Osprey of River Otters) are often found to have density-independent or ***inversely density-dependent*** affects on prey. That is they consume a fixed proportion of the prey population (density-independence) or they consume a higher proportion of the prey population as its abundance decreases (inverse density-dependence). Schooling occurs in small fish because in general their predators do not have density-dependent impacts on their numbers.

Compensation will occur only when mortality is density-dependent. For example if an alpine lake has a large population of stunted brook trout, harvesting half the population would in the long run act to release the other fish from competition and increase their survival and growth rates. In this particular case there would be fewer but larger fish one year latter. However, ***compensation will not occur*** when mortality is density-independent or inversely density-dependent. This ***is an axiom*** of population ecology.

In reality every animal population is influenced to a certain extent by all three types of mortality (i.e. density-dependence, density-independence, and inversely density-dependence). However, in general populations are usually primarily density-dependent ***or*** primarily density-independent. Obviously the challenge is to determine which of these mechanisms are the main determinant of a population's mortality rate. This is in practice quite difficult. Most deaths are never witnessed and when a dead fish is found it can be very difficult to determine what actually lead to its demise. This again is where the scientific literature comes to the rescue.

Although it is in practice quite difficult to directly determine whether a specific population's natural mortality rate is density-dependent or alternatively density-independent, we do know that other parameters are directly correlated with density-dependent mortality. If we can directly measure these parameters we can ***infer*** whether density-dependent mortality is the main form of natural mortality. For trout it is theoretically well established that density-dependent population mortality should be strongly inversely correlated with density-dependent ***individual growth rates*** (see Figure 2). [It is equally well established that individual growth rates can also be influenced by density-independent factors such as average water temperature]. For example, if a population is on the brink of starvation it will have high density-dependent mortality and low density-dependent individual growth rates. Likewise, if a population is small and food is abundant it will have low density-dependent mortality and high average individual growth rates.

Now we have something we can sink our teeth into because it is relatively easy to determine the average individual growth rate for any particular trout population. One need merely collect a sample of 20 or so fish, count annual rings on their otolithes, and calculate their average age specific weight. The relationship depicted in Figure 2, predicts that when individual growth is high density-dependent mortality should be low. If we knew that a given trout population had high individual growth rates we could infer that density-dependent mortality is likely to be weak.

By now most readers of this article should see where I am headed. In general the trout fisheries where special regulations are in effect are those fisheries where average individual growth rates are ***high.*** It is not unusual for a 3 to 4 year old trout to be 16-18 inches in length. In some cases growth is even better than this. Thus, we have strong reason to believe that natural mortality in most blue-ribbon trout streams is density-independent and compensation does not occur or is very weak. Therefore, theoretically we have every reason to also believe that hooking mortality is additive to the population's natural mortality rate.

In a computer search of the germane literature, I found four scientific investigations relevant to the present discussion. The first by Donald and Alger was a study of a stunted brook trout population in Olive Lake British Columbia. These researchers found that by imposing a 20% angling mortality rate on the brook trout population for 3 years, they were able to increase the mean age adjusted size of individual fish without affecting the total population biomass. <u>This is a very clear case of compensation.</u> It is also entirely consistent with the predictions afforded by Figure 2, that is when individual growth rates are low we expect high density-dependent mortality and compensation.

The most relevant studies of trout population mortality were of the blue ribbon fisheries on the Au Sable River in Michigan, the Green River in Wyoming, and the Madison River in Montana. In Alexander's investigation of fishing and natural mortality in the Au Sable River, it was concluded that because predators generally killed more trout than anglers compensation probably occurred and there was probably little angling impact on total trout mortality. It is difficult to understand how Alexander's data, which found higher predator than angling mortality, justifies his conclusion that compensation actually occurred. If you start out by hypothesizing that compensation will occur when natural mortality exceeds angling mortality, simply observing that natural mortality was greater than angling mortality in no way proves the hypothesis of compensation. It simply restates the original premise.

In a comparison of two sections of the Madison, one open to catch and release fishing for three years and one closed to all fishing for same period, Vincent and Clancey found a major impact of catch and release fishing on the trout

1000
500 – 250 – 125
– 250 – 125 – 50
500 – 250
500 – 50% – 500
out

population. Three years after fishing was terminated on the one section, the total abundance of wild trout increased by 400%. In addition, the catch and release section had higher trout mortality than the closed section of the Madison River. The authors did not report whether the mean size of trout was affected by the fishing closure. These results clearly show that even a catch and release fishery can have a substantial impact on the population characteristics of blue ribbon trout stream. These results are inconsistent with the notion that angling mortality is merely compensatory.

In the most detailed of these studies, Wiley and Dufek compared total annual catchable trout mortality to angling effort in the Fontenelle tailwater of the Green River (see Figure 3). Total annual mortality was calculated by analyzing change in the age structure of the trout population from one year to another. Theoretical natural mortality was calculated by simply back-calculating to a theoretical point with no fishing effort (zero on the horizontal axis) and determining the value were the curve intersected the vertical axis. In Figure 3 this procedure gives a natural mortality rate estimate of 0.31 for brown trout and 0.92 for rainbow trout. If mortality in these trout populations was truly compensatory the total mortality curve would have intersected the hypothetical "zero effort" point at the mean of all the mortality estimates. In these calculations, angling mortality was calculated by subtracting the theoretical natural mortality from the total annual mortality.

According to these calculations, Wiley and Dufek found a nearly perfect relationship between angling effort and total mortality for both rainbow and brown trout. These results provide unequivocal support for the hypothesis that <u>angling mortality is additive.</u> Quite simply the more fishing the higher the population's mortality rate. In addition, the authors found, in the case of rainbow trout, that <u>angling mortality was additive even when it was substantially lower than natural mortality.</u> This study also found the average size of the fish caught decreased markedly as angling effort increased.

In conclusion, of four scientific investigations, one found compensation did occur in a stunted population of brook trout. This result is according to theoretical expectations but of little relevance to management strategies for blue ribbon trout streams. Another study used circular logic to argue compensation may have occurred. Two studies, on the Madison and Green Rivers, clearly showed angling mortality does have substantial impacts on the trout population characteristics in blue ribbon streams. In sum, these results suggest very strongly that angling mortality is additive in blue ribbon trout streams. The obvious management implication is we should strive to keep angling mortality rates as low as is practical given the range of management options available.

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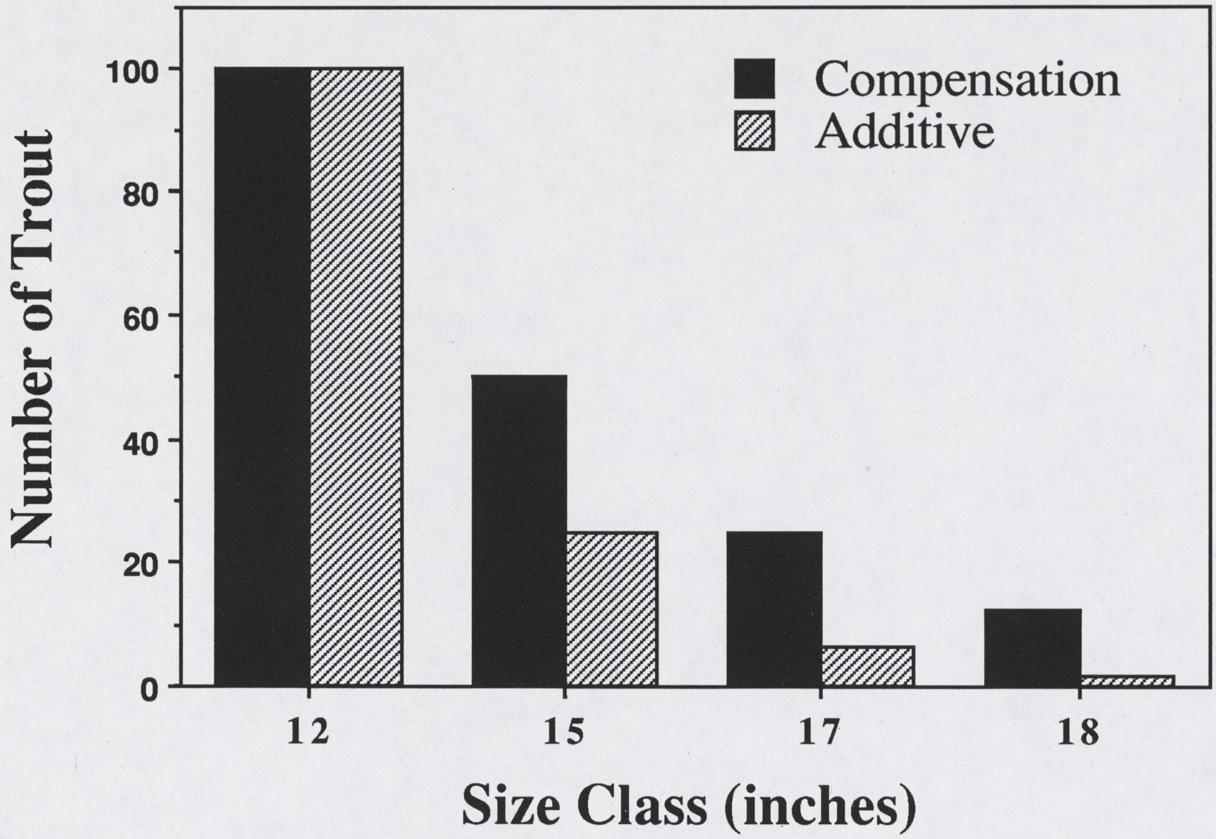
University of California, Davis


Compensation
Additive
Number of Trout
100
80
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20
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15
17
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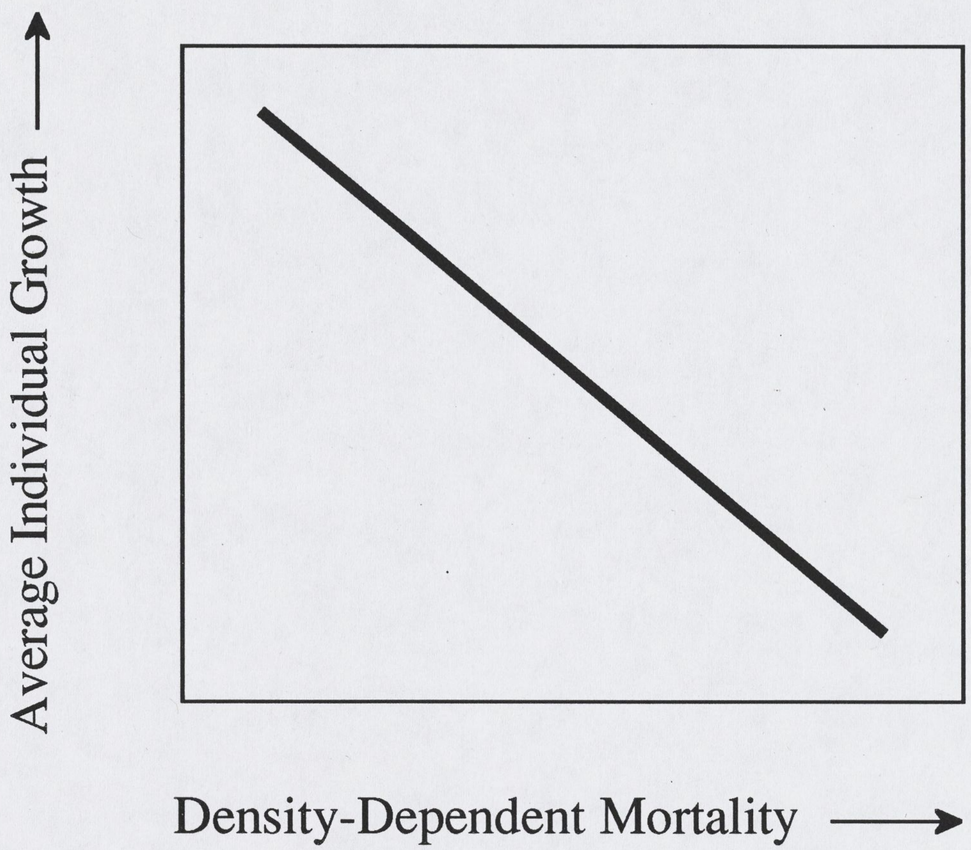
Size Class (inches)


Average Individual Growth
Density-Dependent Mortality

Compensatory mortality will only occur when competition for food is strong. The best measure of the strength of competitive interactions is the average growth rate per age class in the population. If biologists determine that the trout population has poor growth, they must then determine whether the poor growth is due to competition for food or other factors like poor habitat quality, inoptimal temperatures, etc. If it is determined that the poor growth is in fact due to competition then angler induced mortality can be used as a tool to reduce competition. However, angler induced mortality will only improve the fishery if it is selectively applied to the non-preferred sized fish (i.e. fish below 12 inches), otherwise known as a slot limit. If angling mortality is applied to the largest fish in the population it will only result in more and better growing small trout!

Some argue slot limits are ineffective management tools because fly fisherman refuse to kill fish. I would argue that this is more a matter of ineffective communication on the part of management biologists, than of intransigence on the part of fly fisherman. In general, fishermen are not told whether slot limits are intended to appease the fishermen who want to kill trout (in which case most fly fisherman would logically release all fish) or to release the larger fish from competition with smaller fish (in which case it would be beneficial to keep a few smaller fish). If properly informed more (but by no means all) fly fisherman would comply with slot limits.

Killing trout will only improve a fishery if angling mortality is compensatory to the trout population's natural mortality. If angling mortality is primarily additive to the populations natural mortality, it will only act to decrease the abundance of the size classes of fish which are most commonly caught. Compensatory mortality will only occur when the growth of individual trout is limited due to competition. The best indicator of competition is poor growth, but poor growth is not always due to competition. Slot limits allowing the killing of smaller trout can be an effective management tool in cases where high recruitment of smaller fish results in competition for food with larger fish. However, to be an effective management tool, the rationale behind specific slot limits must be explained to the fishermen. Most fly fishermen will, and should, continue to limit their kill of trout unless provided with clear evidence that taking a few smaller fish could be beneficial to the overall population.

Instead of dubiously arguing that our blue ribbon trout fisheries need more kills, we should be asking what impact the extremely high fishing pressure on streams is having on their fisheries. It is not uncommon for streams like Silver Creek, Henry's Fork, and Hot Creek to have elbow to elbow fishing during extended periods of the season. [I won't even comment on the esthetic implications of this]. We can debate what effects angling mortality is having, but virtually nothing whatsoever is known about sub-lethal angling effects. What affect do repeated captures have on the growth rates of fish in these streams? We all know that it is all too easy to put fish down (or to halt their feeding). What effect do continued feeding interuptions have on overall growth rates? Similarly, it is obvious that the more fish are fished to the more selective they become. This greater selectivity also means they will also forgo a greater portion of natural drift, again one wonders what affect this has on growth rates. My suspicion is that with additive mortality, and sub-lethal affects on behavior and growth we are probably having a pronounced impact on the population abundance and size structure. Instead of not killing enough fish, I suspect that we are fishing many of the most popular trout fisheries into the ground.

Appendix II. Compensatory Mortality Model.

Model of the relationship between fishing mortality and natural mortality.

INTRODUCTION

The relationship between fishing mortality and natural mortality is complex and poorly understood. The result of this confusion is that simplistic and unrealistic assumptions are made regarding the effect of fishing mortality on natural mortality. This section presents a model of this relationship and relates this model to a commonly used approach in fisheries.

Compensatory mortality refers to a change in natural mortality induced by fluctuation in fishing mortality. Stated differently, natural mortality is a function of fishing mortality. Additive mortality occurs when fishing mortality adds directly to total mortality with no compensatory decrease in natural mortality. The idea of purely additive mortality in fish populations probably started with the work of Baranov (1918). However, it became firmly entrenched with the works of Beverton and Holt (1957) and Ricker (1958). The relatively simple mathematical properties possible under the additive hypotheses probably account for its initial use. This hypothesis has become so ingrained in fishery science that alternative explanations for the relationship between fishing and natural mortality are seldom considered. Anderson and Burnham (1975) presented a detailed mathematical model of the effect of exploitation on the survival of mallard ducks (Anas platyrhynchos) where they address the issue of compensatory mortality. They model the relationship between hunting and non-hunting (natural) mortality, considering the additive and compensatory hypotheses as well as intermediate cases. Their ideas are presented here in a simple geometric framework omitting the complex estimation procedures they presented.

MODEL DEVELOPMENT

Mortality rates are often modeled using the equation of Ricker (1958), where $A = m + n - mn$ (A = total mortality, n = natural mortality, m = fishing mortality). One problem with this approach is that m and n are potential mortality rates assuming only one source of mortality is operating (Anderson and Burnham 1976:47). It is useful to denote these parameters as m_a and n_a, where m_a is fishing mortality measured in the absence of natural mortality and n_a is natural mortality measured in the absence of fishing mortality. The model then becomes $A_a = m_a + n_a - m_a n_a$ (Anderson and Burnham 1981). Caughley (1977:98) referred to these parameters as "isolated rates" of mortality and pointed out that this relationship does not hold for actual (observed) mortality rates. Anderson and Burnham (1981:1053) referred to m_a

and n_a as "..'potential' or 'a priori' rates useful, at best, in a hypothetical sense." The term $m_a n_a$ in Ricker's equation is often confused as representing some sort of compensatory mortality. Anderson and Burnham (1976:47) pointed out that this term actually represents the degree to which the two forces of mortality compete with one another (e.g., a fish that is killed by a fisherman is no longer available for natural mortality).

Observed finite mortality rates are estimable, because they are measured when both forms of mortality are operating. It is possible to estimate n_a if a population is available where no fishing is allowed. However, it is essentially impossible to estimate m_a, because one could not find a population where natural mortality does not occur. Biologists deal with observed rates on a regular basis and it is intuitively difficult to conceptualize isolated mortality rates.

Using observed rates of n and m in Ricker's equation generally results in an underestimate of total mortality, because one would expect observed values of $n \leq n_a$ and $m \leq m_a$. However, the rates usually observed are A and m, so that n is often overestimated. For example, given an observed total mortality rate of A = 0.6 and an estimate of fishing mortality m = 0.3, one would expect that n = 0.3 (n = A - m = 0.6 - 0.3). Using Ricker's equation, n = (A - m)/(1 - m) = 0.43, which is a significant overestimate. Alternatively, one could estimate A based on n = 0.3 and m = 0.3, yielding an estimate of A = 0.51. While this example is rather simplistic, it points out potential for error when using observed rates in an equation that was developed in a probabilistic framework intended for isolated rates.

Some definitions are necessary for the discussion that follows. All mortality rates are finite annual rates, that is, they are the observed mortality rates for a given year. For example, fishing mortality (m) is any mortality which is the result of angling and includes such things as hooking mortality of fish caught and released as well as legal and illegal harvest. Fishing mortality is calculated as the proportion of the fish alive at the start of year i that die due to fishing in year i.

$$m = \frac{\text{Number of fishing mortalities during year } i}{\text{Number of fish alive at start of year } i}$$

Natural mortality (n) is defined as any mortality not attributable to fishing and is calculated similarly. The compensation point (C) is the point at which the relationship between n and m changes. Natural mortality is denoted as n_0 at the point when fishing mortality is zero and as n_c at the compensation point. The shaded areas in Figure 13 represent values which are not possible for a given relationship. The lines $n + m = 1$ and $S + m = 1$ are given as points of reference. These lines are of little practical value because it seldom makes sense to discuss a total mortality rate of 1, but it is useful because it represents the upper bound for the given relationships. The unshaded portions represent all possible values for the mortality and survival relationships. The slope

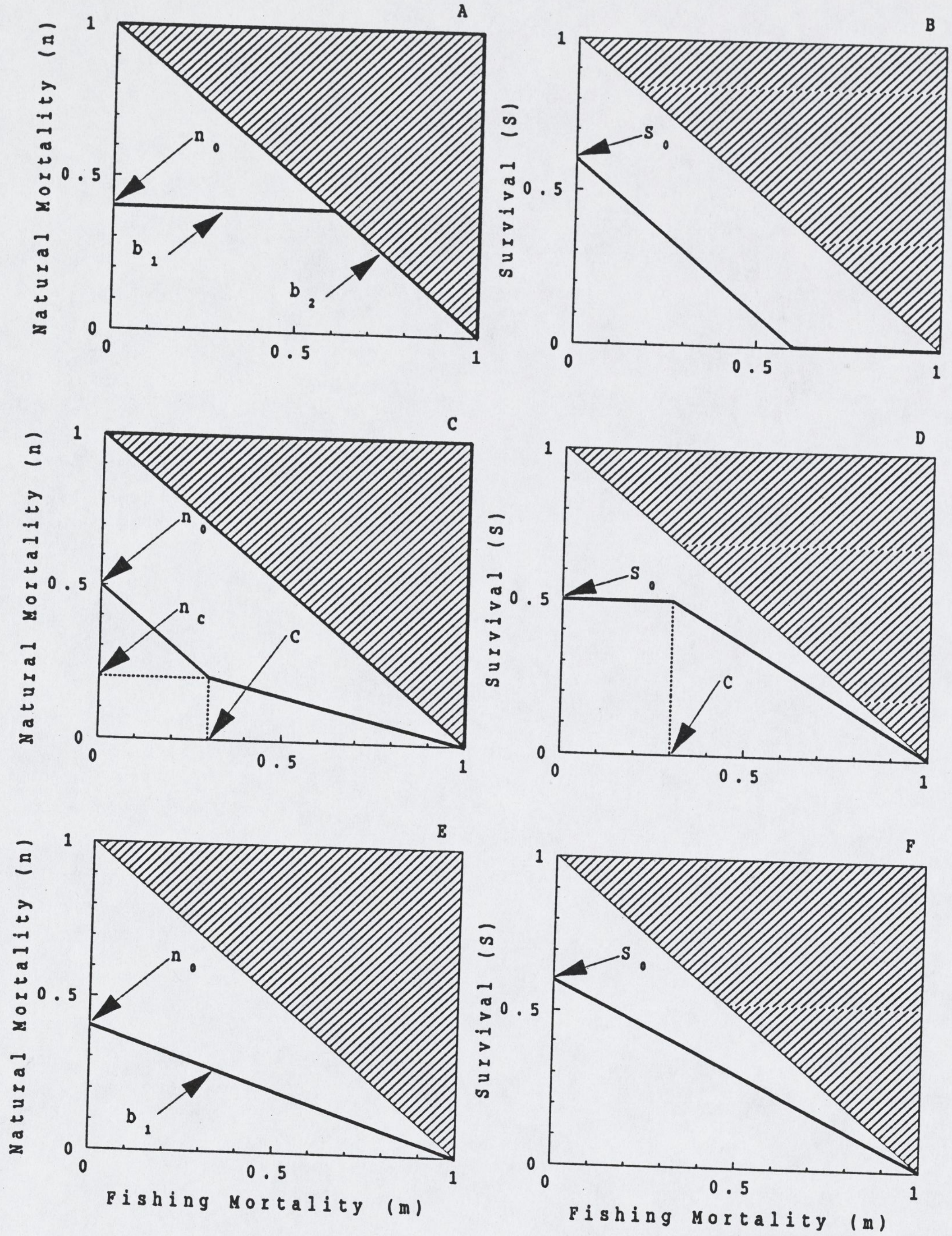


Figure 13. Examples of the relationship between fishing mortality and natural mortality.

of the line in the region where $m \leq C$ is defined as b1 and the slope of the line in the region where $m > C$ is defined as b2 (Figure 13a). Total mortality (A) is equal to the sum of fishing mortality (m) and natural mortality (n), thus $A = n + m$. Survival is defined as the complement of the total mortality (1 - A) and S_0 is defined as the survival rate which corresponds to n_0 (Figure 13b). All the graphs in Figures 13 and 14 are paired with the fishing mortality/natural mortality relationship on the left and the corresponding fishing mortality/survival relationship on the right.

The simplest relationship between natural mortality and fishing mortality is a straight line (Figures 13e,13f). Natural mortality is defined by the line $n = n_0 + b_1 m$, where n is the estimated natural mortality for a given slope (b_1) and fishing mortality (m). In the case where the line runs from $(0,n_0)$ to (1,0) the slope reduces to $b_1 = -n_0$. Possible values for the slope of this line range from $-n_0$ to 0, with compensation increasing as the slope approaches $-n_0$. Therefore, mortality will be most compensatory for lines with large values of n_0 and steep negative slopes. Conversely, fishing mortality will be more additive when the value of n_0 is low or when the slope approaches zero (Figure 13a).

Under the additive hypothesis, increasing fishing mortality simply adds to the total mortality without affecting natural mortality (Figure 13a). As total mortality increases there is a linear decrease in survival (slope = -1) until survival is 0

(Figure 13b). Changing fishing mortality has no affect on natural mortality, up to the point where all fish are dead.

A more complex representation of the mortality relationship is possible using two separate line segments. Under the completely compensatory hypothesis there is a 1:1 reduction in natural mortality as fishing mortality increases, up to some compensation point (C) (Figures 13c,13d). In this example, fishing mortality above the compensation point is intermediate between compensatory and additive up to the intersection with the line where total mortality equals 1 and all fish are dead. Increasing fishing mortality, in the region where $m \leq C$, will result in a compensatory decrease in natural mortality, thus keeping total mortality constant. A slope of -1 is the maximum degree of compensation because a steeper slope would result in natural mortality decreasing faster than fishing mortality increases (a condition considered to be unlikely).

The case which represents the maximum compensation from a 2 segment line allows complete compensation in the range where $m \leq C$ and partial compensation where $m > C$ (Figures 13c, 13d). The maximum compensation in the range $m > C$ is expressed by a line from the point (C,n_c) to (1,0) and has slope b_2 ($b_2 = ((n_0 + (b_1 C)) / (C - 1))$), any smaller slope would result in a line which intersects the x-axis somewhere to the left of the point (1,0). This case with $b_1 = -1$ and $b_2 = ((n_0 + b_1 C))/(C - 1))$ represents the extreme case of compensatory mortality for the two segment line model. The range of possible values which fall between the extreme cases of compensatory and additive mortality is represented by the shaded area (Figure 14). In this example C was arbitrarily set at 0.3 and could actually take any value from 0 to C_{max}, where $C_{max}<(n_0/-b_1)$. Refer to Natural Mortality section in Appendix I for a description of all the parameter constraints.

An interesting point to consider is how these relationships change with different levels of n_0 under the compensatory hypothesis (Figures 14a, 14b represent the baseline). It is conceivable that n_0 would change in response to changes in habitat or population density. Two hypotheses address extremes in the effect of changes in n_0 on the compensation point C. One hypothesis is that C will remain constant and that n_c changes as n_0 changes (Figures 14c,14d). The alternative is that n_c remains constant and that C changes as n_0 changes (Figures 14e,14f). The latter hypothesis is more realistic because it implies that there is a base level of natural mortality which is independent of fishing mortality and population density. The most realistic situation likely involves an intermediate case.

DISCUSSION

Conditions which favor compensatory mortality include: (1) limited food supply, (2) limited habitat, (3) severe winter conditions, and (4) intense predation (including harvest). Mortality should be most compensatory for young and old fish and more additive for 'middle-aged fish.' If young fish are

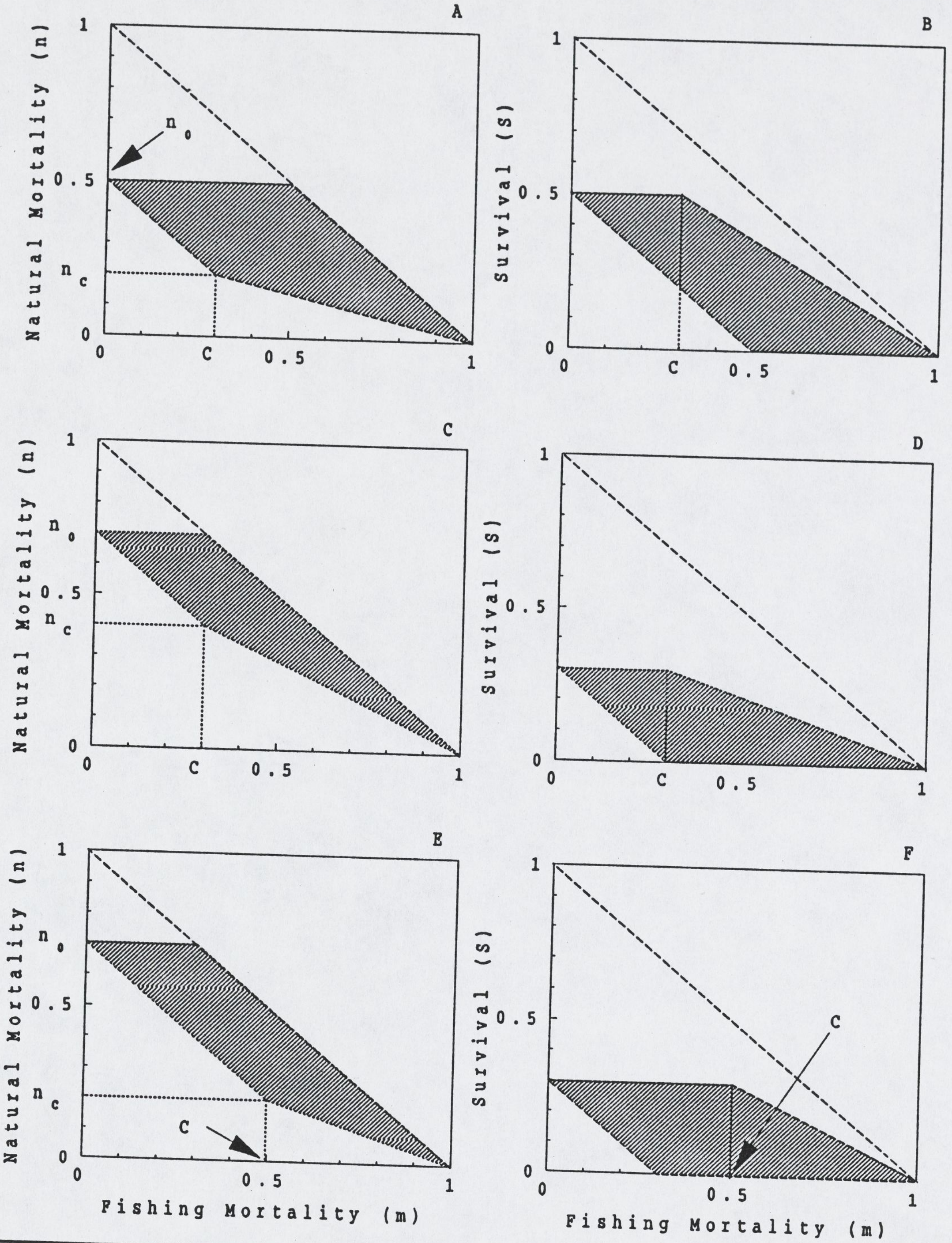


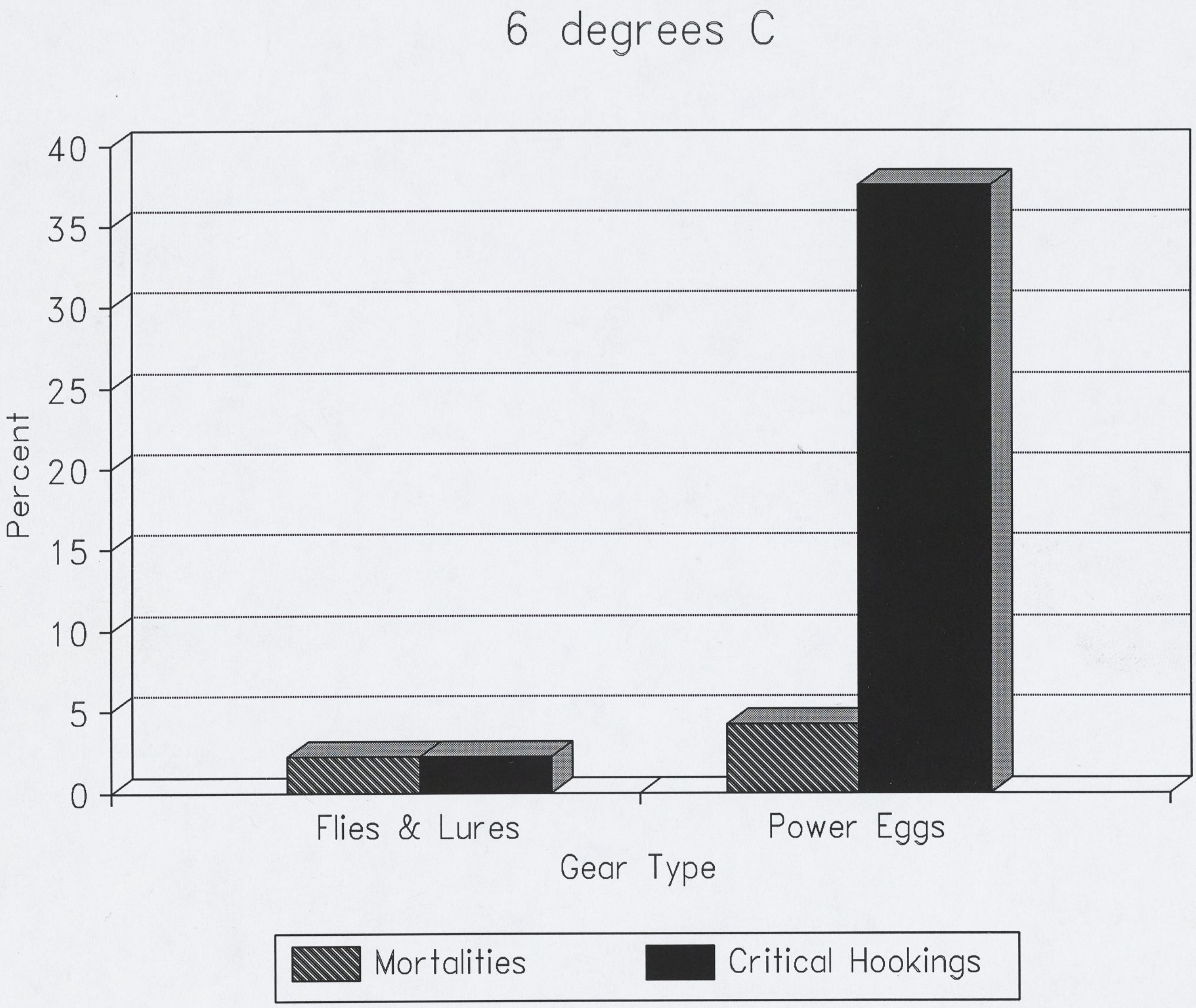
Figure 14. Range of possible values which lie between the additive and compensatory hypotheses.

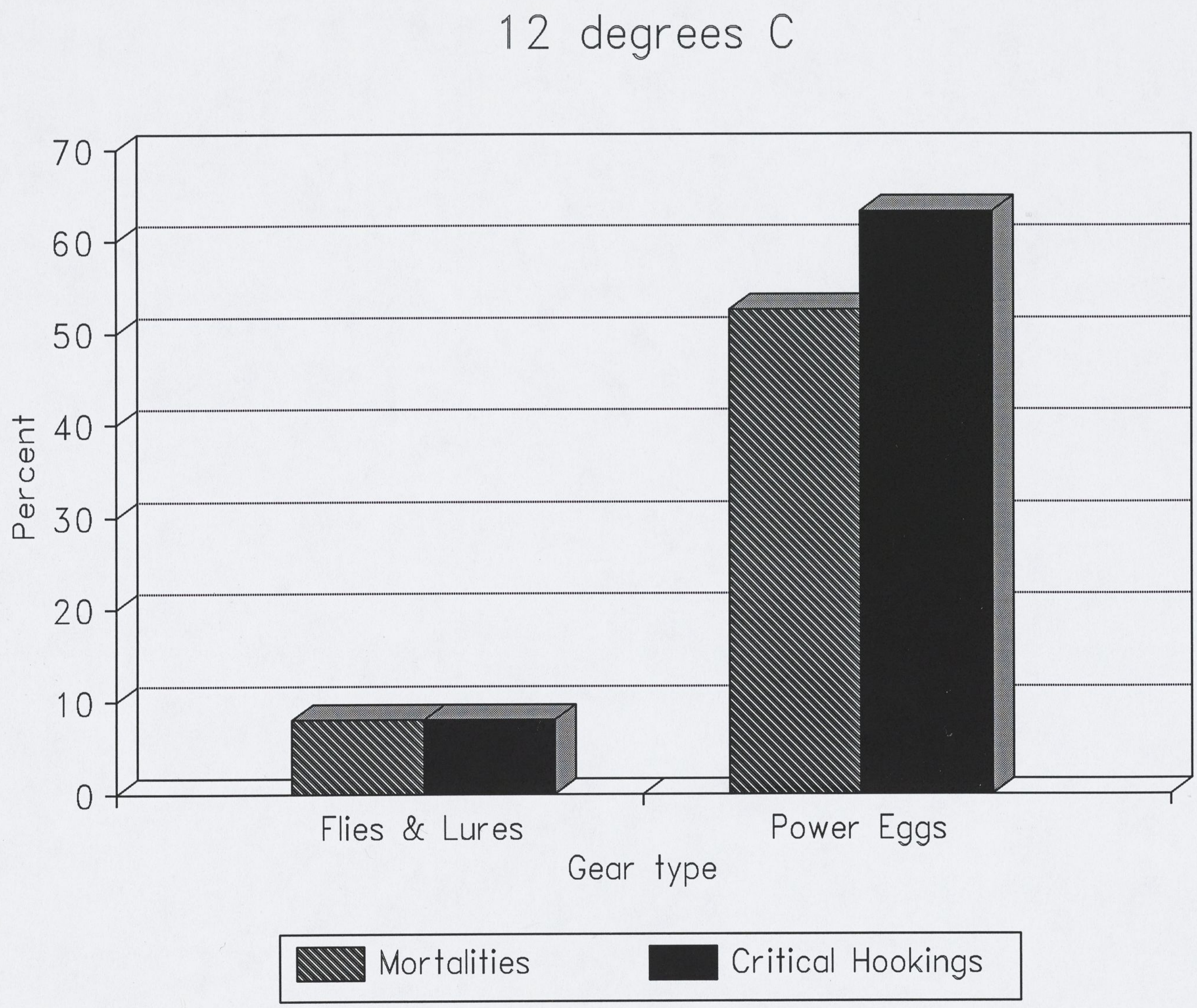
experiencing density-dependent mortality any removal by angling would reduce the density in a manner similar to the ongoing density-dependent process. Behnke (1988) discussed the fact that each population has a terminal age, which has a very high value of n_0. The terminal cohort is 'about to die' and angling mortality will simply allow the harvest of fish which would otherwise have died of 'natural causes.' In both cases natural mortality is decreased by increased fishing mortality, while total mortality is changed very little, if at all.

In a finite sense, fishing mortality is 100% additive on an instantaneous basis; i.e., the fish was alive when it was caught. Fishing mortality is additive in the short term and becomes more compensatory with time. Thus the importance of defining a time frame when modeling mortality. Fishing mortality may compensate for overwinter mortality such that any fishing mortality is 100% compensatory after 1 year, but could be 100% additive after six months. This case has management implications because an angling regulation might be considered a failure when no more fish are carried to the next year. However, it is likely that this regulation would increase catch rate by recycling these fish during the season. Thus, the 'success' of the regulation depends on management objectives.

There are other functions which may better portray the relationship between natural and fishing mortality (curvilinear, sigmoid, etc.). However, the linear model presented offers a significant improvement over the purely additive assumption commonly used. This model also has an intuitive appeal in that it offers an explanation for the success or failure of various angling regulations to increase the number of older and larger fish. Protective angling regulations will have the greatest opportunity for success in populations which have lower values of n_0, because mortality is most compensatory at high levels of n_0 and most additive at low levels of n_0. In populations which have high levels of n_0, any fish 'saved' by the regulation are likely to succumb to other sources of mortality. Conversely, streams where angling regulations have been successful probably had populations where the 'middle-aged fish' experience relatively low levels of n_0. Any fish 'saved' from death by angling would grow; ultimately caught many times and possibly harvested at a larger size.

Dr. Behnke - FYI





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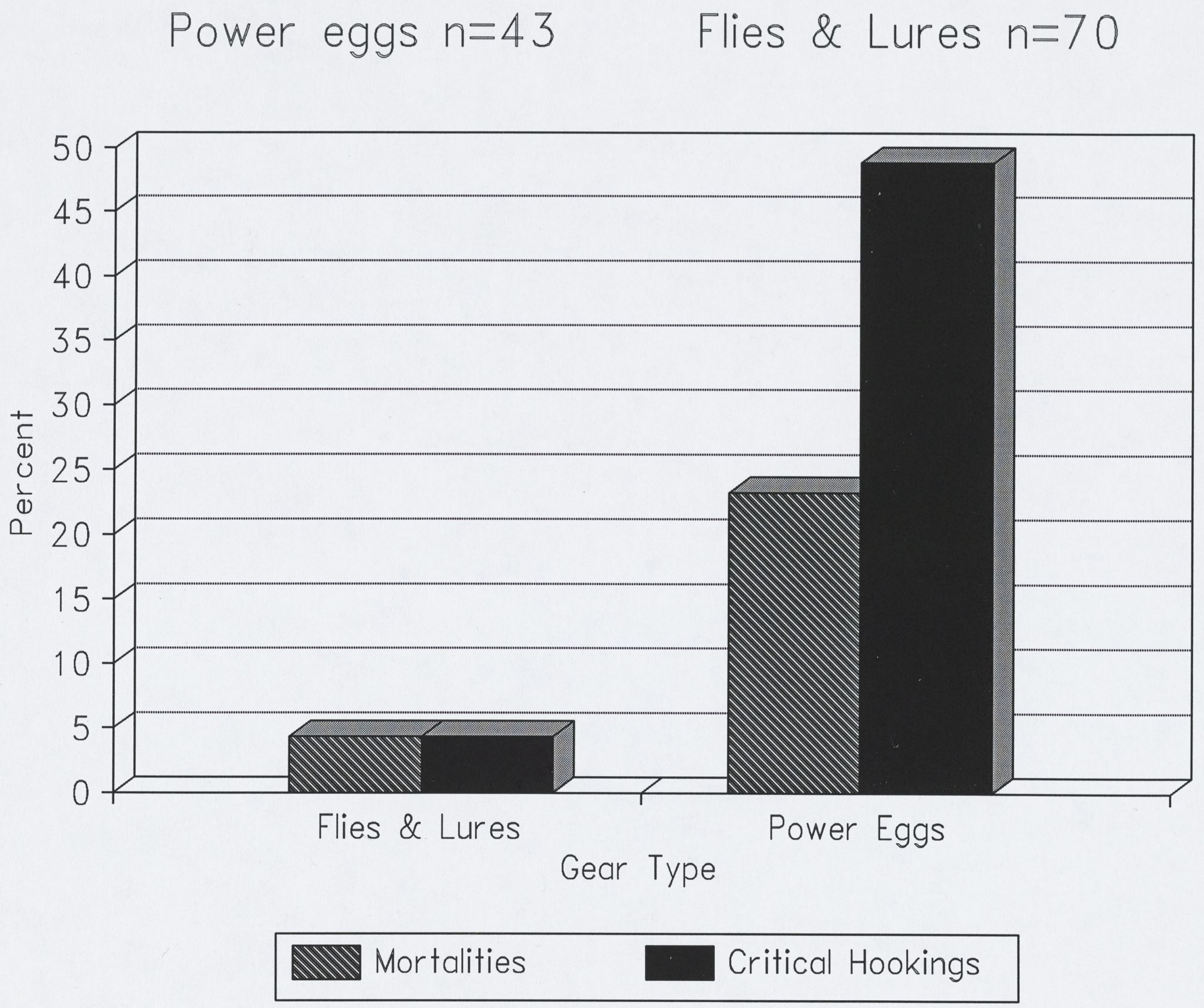
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Percent
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Gear Type
Mortalities
Critical Hookings

Michael T. Brett
(updated July, 1995)

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Education:
Ph.D. - Limnology, received December 1990, Institute of Limnology, Uppsala University, Uppsala Sweden.
M.Sc. - Zoology, received December 1985, Department of Zoology, University of Maine, Orono, Maine, USA.
B.Sc. - Fisheries Biology, received March 1983, Department of Fisheries, Humboldt State University, Arcata, California, USA.

Awards:
Fulbright Graduate Student Fellowship, carried out at the Institute of Limnology, Uppsala University, from September 1985 to December 1986.

First Authored Publications:
Brett, M.T., C.R. Goldman, F.S. Lubnow, A. Bracher, D. Brandt, O. Brandt, A. Müller-Solger (in press). Effects of a major soil fumigant spill on the planktonic ecosystem of Shasta Lake, California. Canadian Journal Fisheries and Aquatic Sciences.
Brett, M.T., K. Wiackowski, F.S. Lubnow, A. Müller-Solger, J.J. Elser and C.R. Goldman 1994. Species-dependent effects of zooplankton on planktonic ecosystem processes in Castle Lake, California. Ecology **75:** 2243-2254.
Wiackowski, K., M.T. Brett, and C.R. Goldman. 1994. Differential effects of zooplankton species on ciliate community structure. Limnology and Oceanography **39:** 486-492.
Brett, M.T. 1993. Comment on "Possibility of N or P limitation for planktonic cladocerans: An experimental test" (Urabe and Watanabe) and "Nutrient element limitation of zooplankton production" (Hessen). Limnology and Oceanography **38:** 1333-1337.
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Brett, M.T., L. Martin, and T.J. Kawecki. 1992. An experimental test of the egg-ratio method: estimated versus observed death rates. Freshwater Biology **28:** 237-248.
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Brett, M.T. 1989. The rotifer communities of acid-stressed lakes of Maine. Hydrobiologia **186/187:** 181-190.

Brett, M.T. 1985. Zooplankton and nekton community structure in lakes of varying pH in Maine. MSc. Thesis, Department of Zoology, University of Maine, Orono, Maine, USA.

Brett, M.T. 1984. The littoral zooplankton communities of an acid and a nonacid lake in Maine. p. 385-388 *in* Proceedings of the Third Annual Conference: North American Lake Management Society. EPA 440/5/84-001.

Junior Authored Publications:

Elser, J.J., F.S. Lubnow, E.R. Marzolf, M.T. Brett, G. Dion, and C.R. Goldman. 1995. Factors associated with interannual and intraannual variation in nutrient limitation of phytoplankton growth in Castle Lake, California. Canadian Journal of Fisheries and Aquatic Sciences **52**: 93-104.

Elser, J.J., C.J. Luecke, M.T. Brett, and C.R. Goldman. 1995. Effects of food-web compensation after manipulation of rainbow trout in an oligotrophic lake. Ecology **76:** 52-69.

Ahlgren, G., L. Lundstedt, M. Brett, and C. Forsborg. 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. Journal of Plankton Research **12:** 809-818.

Submitted Manuscripts:

Brett, M.T., and C.R. Goldman. A quantitative test of the freshwater trophic cascade. Submitted Manuscript.

Brett, M.T., Lubnow, F.S., M. Villar-Argaiz, and C.R. Goldman. Strong evidence for decoupling of bacteria and phytoplankton growth in a mesotrophic lake. Submitted manuscript.

Reports:

Brett, M.T., C.R. Goldman, and S. Ayers. 1994. A limnological investigation of Whiskeytown Reservoir: potential impacts of temperature control curtains. Report to the US Bureau of Reclamation.

Brett, M.T., and C.R. Goldman. 1994. Crayfish population size and recolonization potential in the upper Sacramento River following the Cantara Vapam® spill, Report of 1993 field sampling. Report to the California Department of Fish and Game.

Brett, M.T., and C.R. Goldman. 1993. Crayfish population size and recolonization potential in the upper Sacramento River following the Cantara Vapam® spill. Report to the California Department of Fish and Game.

Brett, M.T., C.R. Goldman, and F.S. Lubnow. 1992. Effects of the Cantara Vapam® spill on the planktonic ecosystem of Shasta Lake. Report to the California Department of Fish and Game.

Scientific Writing for the General Public:

Brett, M.T., et al. 1994. Welcome to Castle Lake. Interpretive brochure describing the natural history, aquatic ecology, and ongoing limnological research at Castle Lake, site of the University of California, Davis Limnological Research Station.

Brett, M.T., et al. 1994. Cui-ui and ignorance. California Flyfisher July-August: 48-50. An article on the interests of conserving an endangered nongame fish versus a sport fishery.

Brett, M.T. 1994. Ongoing study keeps track of health of Castle Lake. The Dunsmuir News. page 2, Nov. 9, 1994. Newspaper article based on a press release I prepared.

Brett, M.T. 1995. Castle Lake has record clarity. Mt. Shasta Herald. July 19, 1995. Newspaper article based on a press release I prepared.

Successful Proposals:

I have prepared a total of seven successful grant proposals. These include three proposals to the National Science Foundation (two at 90% and one at 40% effort), two proposals at 90% effort to the California Department of Fish and Game, and individual proposals at 90% effort to the US Bureau of Reclamation and the private McConnell Foundation. The total amount of these proposals was over **$650,000**, with the majority coming from NSF. I also helped prepare (20% effort) a successful proposal to the University of California Water Resources Center and I played a pivotal role in bringing a $300,000 contract from the US Bureau of Reclamation.

Invited Reviews:

I have been invited to review manuscripts submitted to several prominent journals including *Science, Nature, Limnology and Oceanography, Ecology, Canadian Journal of Aquatic Sciences and Fisheries*, *Archiv für Hydrobiologie*, and *California Fish and Game*. I have also been asked to review several proposals submitted to the *National Science Foundation*.

Teaching Experience:

I taught the Principles of Environmental Science (EST 110) at the University of California, Davis. This is an upper division class with approximately 100 students. I independently developed the entire curriculum for this course on very short notice. The Department asked that I teach the principles of environmental sciences using current topical issues as examples. Because I am focusing on topical issues I was unable to find a textbook which fit the needs of the course. I therefore developed an extensive set of reading materials based exclusively on current primary and secondary literature. The topics covered have included the Philosophy of Science (Plato, Popper, Platt), The Tragedy of the Commons, The Collapse of Georges Bank, The Decline of Pacific Salmon, Coral Bleaching, The Endangered Species Act, Evolutionary Significant Units, The Spotted Owl Issue, Wetlands Delineation, Eutrophication, Desertification, Global Climate Change, Acidification, and Pending Land Reform Legislation. I have attempted to emphasize critical and independent thinking, as well as develop research and writing skills. I have found teaching this course to be one of the most challenging and rewarding endeavors I have undertaken during my entire career in academia.

While working towards my Ph.D. in Sweden, I taught the equivalent of several semesters of Scientific Writing. In graduate school and particularly while a PostDoc at UCD, I have given extensive guest lectures to Limnology courses. I also TA'd Introduction to Biology and Fisheries Biology courses at the University of Maine. I have also been very active in helping a local public school district incorporate environmental sciences into its science and mathematics curricula. This has included leading a teacher training seminar, hosting eight field trips, offering seminars to several High School classes, and developing an extensive interpretive display and brochure. During review of a recently funded NSF proposal the panel commented on "the excellent efforts at community outreach" which primarily relates to work I did as the supervisor of the Castle Lake Project. I have also worked as a research advisor to several undergraduate and graduate students, with several of these joint efforts resulting in publications.

Recent Responsibilities:

During my postdoctoral fellowship, I have been the supervisor of the Castle Lake Field Research Station and associated National Science Foundation grants. During the time I have managed the project, it has had approximately $150,000 yearly support from the National Science Foundation, with five to ten graduate students and undergraduate assistants in residence at the field station each summer. During this time, I also designed and supervised a limnological investigation of a pesticide spill's impact on a large reservoir, an investigation of the same spill's impact on the crayfish population of a river, as well an investigation of temperature-control curtain impacts on the limnology of a reservoir.

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Aug. 30, 1995

Professor R.J. Behnke
Department of Fisheries and Wildlife Biology
Colorado State University
FT. Collins, CO 80523

Dear Dr. R.J. Behnke

Thank you very much for your extremely detailed response to my letter. Your input will be of tremendous assistance when preparing my article for Fly Fisherman Magazine, which John Randolph has now requested. I am very interested in the your student's thesis on hooking mortality. It is obvious that this study will be an important contribution to the topic. When reading your letter describing the student's research I immediately thought of a hooking mortality study conducted by a colleague of mine (Titus and Vanicek 1988). Because this study was published in an obscure journal it has received very little attention. However, Titus concluded temperature was the most important factor influencing hooking mortality rates at his study site. He also included a figure which plotted hooking mortality versus temperature for a large number of studies. This figure showed quite clearly that hooking mortality is approximately 5% between the temperatures of 45 to 64 °F and rises very rapidly at temperatures above 64 °F. I would suggest your student update Titus' temperature versus hooking mortality by including his data as well as any additional data from studies published after Titus'.

Sincerely,

Mike

Michael T. Brett

Titus, R.G., and C.D. Vanicek. 1988. Comparative hooking mortality of lure-caught Lahontan cutthroat trout at Heenan Lake, California. *California Fish and Game*, volume 74, pp. 218-225.

Brett

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– "Death by warming"
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DIVISION OF ENVIRONMENTAL STUDIES DAVIS, CALIFORNIA 95616

Sept. 6, 1995

Professor R.J. Behnke
Department of Fisheries and Wildlife Biology
Colorado State University
FT. Collins, CO 80523

Dear Dr. R.J. Behnke:

Enclosed is a "rough draft" of an article on angling mortality for Fly Fisherman Magazine. As you will notice it benefited tremendously from your input. My wife told me the article is still way too technical for a non-academic audience. I am going to let this draft sit a couple of weeks before I make another attempt at reducing the scientific jargon and redundancy. I would also like to take another opportunity to thank you very much for the extensive material you sent me. Now that I have read all the enclosures several times and have begun to digest their contents, I fully appreciate the wealth of material you provided me. Unfortunately, the UC Davis library does not subscribe to Trout so I was unable to obtain a copy of your 1989 article on special regs.

In my first letter to you I mentioned to a paper on special regs by Frank Rahel, which was referred to in one of the flyfishing articles. I have not seen this paper in print, I have only seen it referred to in the above mentioned articles. I checked the Current Contents computer data base of publications, and Rahel's paper was not listed yet.

I have passed your letter to Cal Fish and Game concerning their hatchery program on to other Davis flyfishers. You raised some very good points. Your comments are especially apropos because today in California most trout fisherman are flyfishers. And the vast majority would rather see their license money spent on wild trout programs that on wasteful hatchery programs. I thought it was interesting how you pointed out that CDFG was cooking its numbers to make it look like their hatchery program is cost effective. In my opinion, their should be a few hatchery programs which are designed for those that would like to take their lawn chairs to a lake or river, pop open a Coors lite and listen to a baseball game with one of those little bells on their line to tell them when a fish is swallowing their bait. This should however be a very small portion of CDFG's expenditures. On a positive note CDFG has been developing some wonderful programs to introduce urban children to fishing. They have been stocking city parks with hatchery trout during the winter and with catfish during the summer. Their should be more heavily stocked streams and ponds set aside for kids only. License sales are going down in California because we are becoming a very urban and suburban population with very few opportunities for children to learn the sport. Their parents would rather shop or watch TV, so kids need easy access to fishing opportunities. CDFG should learn from the cigarette industry that the key to selling fishing licenses (and unfortunately tobacco) down the road is recruiting children to the habit. However, if CDFG were to spend less money on their hatchery program this money could be spent on habitat acquisition and protection. I am currently working on a proposal with CDFG to study sedimentation problems in the Fall River (which is arguably California's most famous trout stream). The problem is nobody has the money to control the severe erosion problems in the watershed.

I fully agree with you that the distinction between scientific and precise is one of the greatest misunderstandings that the public has about the scientific process. I did not however include any comments on this topic in my article to John Randolph on angling mortality because I was unable to find a logical place for this in the article. As the article is currently written, a comment on the general lack of precision in science would end up dangling. However, I feel this is such an important issue that it is the first lecture I give in my Principles of Environmental Science course at UC Davis. I approach this issue from Plato's Allegory of the Cave. Basically I tell the students that we as scientists are only able to observe shadows of the real variables we are interested in. And when they read a scientific paper they are only reading somebody else's interpretation of the shadows on the wall of a cave. Most of my research is in limnology and the most common parameter we measure is chlorophyll concentrations in lake water. However, there are important measurement uncertainties associated with how we collect and measure Chl in our samples. Far more importantly Chl is actually a poor descriptor of phytoplankton biomass, phytoplankton species composition and primary production which is what we are really interested in. I think this can be explained to students and to the lay public and is probably worth an article in a flyfishing magazine all by itself.

I must say I was very impressed by the section of George Schisler's MS thesis dealing with compensatory mortality. I thought the paragraph which explained how angling mortality could be entirely additive or entirely compensatory for the same population depending on whether you are considering the impact on numbers of fish available for that season or whether you are considering survival to the next season to be particularly insightful. I tried to think of a way I could incorporate this idea into my article without co-opting George Schisler. I decided that since George's work was not presently published that I should be very careful not to steal his thunder. If I was writing a scientific paper this would not have been a problem at all because I could simply paraphrase George and cite his MS thesis profusely in the relevant paragraph. I guess I could get around this problem by writing something like "According to George Schisler, a fisheries biologist at Colorado State University, angling mortality can be entirely additive or entirely compensatory for the same population depending on whether you are considering the impact on numbers of fish available for that season or whether you are considering survival to the next season." However, George may prefer that his ideas first see the day of light in a scientific venue as opposed to a flyfishing magazine article written by another person. If I do not hear back from you I WILL NOT include George's ideas in my article. However, if you have the chance you might ask George if it is okay if I use his idea provided I clearly indicate its origin.

Sincerely,

Mike

Michael T. Brett

ANGLING MORTALITY AND SPECIAL REGULATIONS

Many flyfishers have such a reverence for special regulations that they actually believe that all one needs to do to create a blue ribbon fishery is implement no kill regulations. In fact, the quality of a trout fishery and in particular the age and size structure of the population is determined by a myriad of environmental and demographic variables. The most important of these is the population's mortality rate.

In a sport fishery there are two components to mortality. The first is natural mortality. This is the mortality a population would have in the absence of any angling mortality. Factors which contribute to a population's natural mortality rate include competition for food and habitat, predation, disease and extreme environmental conditions like flooding, anchor ice, etc.

The second component to a trout population's mortality rate is angling mortality. This is a function of the likelihood that a fish will die when caught multiplied by the average number of times a fish is caught during a season. The probability of dying is about 30% for bait caught fish and approximately 3 to 5% for fly or lure caught fish. However, hooking death rates can be much higher at water temperatures above 64 °F. Depending on how heavily a stream is fished and the species of trout in a stream the typical fish may be caught very rarely or up to 10 times per year. Cutthroat trout are particularly susceptible to angling, while browns can withstand heavy angling with only a small proportion of the population being caught.

Natural and angling mortality interact to determine a trout population's total mortality rate. It is a population's overall mortality which determines its age and size structure and the abundance or scarcity of large fish. Natural and angling mortality interact to determine total mortality differently depending on whether angling mortality is *additive* or *compensatory*.

Additive mortality means each trout killed by angling will directly add to the population's overall mortality rate. According to Ricker, a famous fishery biologist, when angling mortality is completely additive total mortality is equal to natural mortality plus angling mortality minus the product of natural and angling mortality. The later part of Ricker's equation simply accounts for the fact that a fish can only die once. For example if a population's natural annual mortality rate is 50% and its angling mortality rate is 50% then the population's total mortality rate will be 75%. That is half of the fish will die due to natural causes and half the remaining fish will die due to angling.

Compensatory mortality means each fish killed due to angling simply replaces fish which would have died due to natural causes. For example, due to the stresses associated with competing for limited food or habitat. When angling mortality is compensatory, angling will have little impact on a trout population's age and size structure until the angling mortality rate exceeds the population's natural mortality rate. As an example, if the natural mortality rate is 50%, and angling mortality is completely compensatory angling will have virtually no impact on the population until it exceeds the natural mortality rate of 50%.

The first thing every flyfisher needs to know about additive and compensatory angling mortality is <u>every sport fishery is influenced by both processes</u>. However, the relative importance of these processes may vary considerably from one fishery to another. The balance between additive and compensatory mortality also varies considerably during the life cycle of a trout. Mortality in young trout (age 0 to 1 year) is generally strongly compensatory, while mortality in older catchable sized, trout is relatively speaking additive. That is, within any trout population the incidence of compensatory mortality will decrease when going from younger to older age classes.

Whether angling mortality is additive or compensatory depends in large part on the average growth rates and life spans of the fish in the population. Trout populations dominated by short lived and slow growing fish tend to have compensatory angling mortality. A classic example of this is the stunted brook trout populations of many alpine lakes. Research has shown that angling mortality will not have a detrimental impact on the numbers and size of fish in these populations. This is because every trout removed through angling will act to lessen the severe competition for limited resources amongst the remaining fish. This is the reason why many state fishing regulations allow, and even encourage, anglers to take between 10 and 20 small brookies per day in alpine lakes.

Angling mortality tends to be additive when trout growth rates are high and when life spans are long. Probably the best known example of special regulations restoring a trout fishery is the cutthroat fishery in the Yellowstone River below Yellowstone Lake. Cutthroats often live to be 6 to 8 years old and they are extremely vulnerable to anglers. Biologists have calculated that the average fish in this area is caught 10 times per year. No kill regulations have also been dramatic successes on some very productive trout fisheries.

The single most important management decision which can be made is deciding whether to manage as if angling mortality is additive or compensatory. If biologists assume mortality is compensatory when in fact it is primarily additive, a dramatic reduction in the numbers of older and larger sized fish will result. If on the other hand, a stream is regulated as if angling mortality is additive when in fact it is primarily compensatory, some anglers will be denied the opportunity to harvest fish with little benefit to the population.

It should also be pointed out that special regulations, which assume angling mortality is additive and limit harvest, can in most cases only help to restore a fishery to its pre-angling state. In other words, you cannot make a silk purse out of a sow's ear. If a fishery was dominated by small sized fish before significant angling occurred, which is probably true for many if not most trout streams, then special regulations will in all likelihood result in a fishery dominated by small sized fish. However, there will probably be a few more of them.

The Au Sable River in Michigan is a classic example of where special regulations failed to restore a fishery and in fact coincided with its decline. This is because non-angling processes had a much greater impact on the trout population than did angling mortality. The trout fishery deteriorated because a fish hatchery and a sewage treatment plant both quit discharging effluent into the river. This greatly reduced the supply of nutrients to stimulate plant growth in the river, which in turn greatly reduced the availability insects and habitat for trout. In essence the change in trout growth rates and survival had a far greater impact on the abundance of larger sized fish than did the reduction in their harvest rates.

The improvement realized with special regulations is also related to the relationship between natural mortality and that angling mortality which is additive. In cases where natural mortality is high and angling mortality is minimal, through light fishing pressure or de facto no kill management, special regulations will lead to virtually no improvement in the fishery. In fact, I suspect that in fisheries where few fishers presently keep fish, which is common on many rivers today, special regulations may actually do some harm by drawing attention and more anglers to these fisheries.

In some cases trout fisheries may have good survival but poor growth. For example there may be many fish between 12 and 16 inches which are skinny. In this case one can use slot limits to reduce competition between smaller and larger sized fish. This will allow the larger fish to obtain greater growth rates without reducing their numbers.

However, a slot limit will only reduce competition between large and small trout if it is practiced. To be an effective management technique, fisheries biologists need to clearly communicate their objectives. In cases where slot limits are merely intended to appease fishers who want to keep fish, many flyfishers would and should continue to limit their take of fish. However, in cases where the intent of the slot limit is to reduce competition, many flyfishers would probably be willing to help the cause by taking a few small fish provided they were sufficiently informed of the rational behind the regulations. The effectiveness of slot limits as a management tool, is I believe dependent on the effectiveness of fishery agency education programs.

Special regulations have been wholly accepted by virtually the entire community of flyfishers. However, it is important that fishers understand the conditions under which these regulations are likely to lead to substantial improvements in fisheries. It is equally important that flyfishers realize that in many cases special regulations will not result in greatly improved fisheries. In cases where natural mortality is high compared to angling mortality, and growth and survival rates are low, angling mortality will primarily be compensatory and special regulations will not improve the fishery notably. Special regulations have been shown to dramatically improve the quality of trout fisheries when the trout have the potential for high growth rates, long life spans, and angler use is heavy. Fisheries which fit these criteria should be managed to limit harvest. Better educated anglers will result in more well thought out sport fishing regulations.

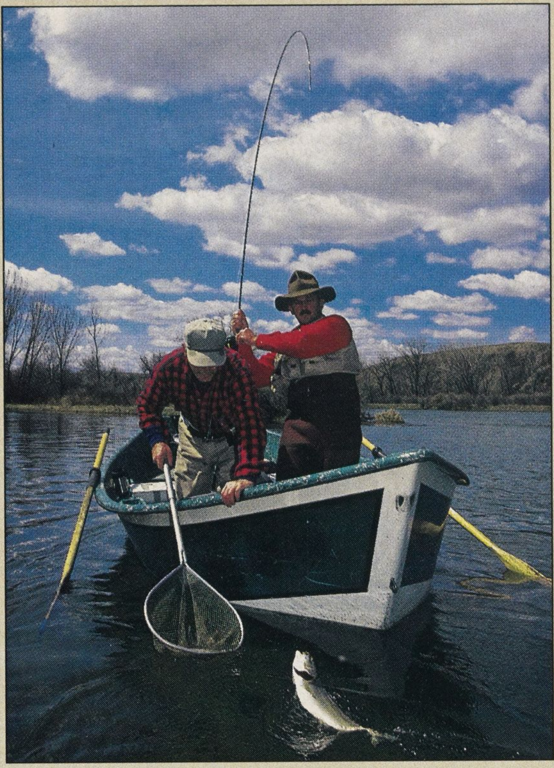
Michael T. Brett, Ph.D.
Davis, California

[No Date]

ANGLING MORTALITY

MICHAEL T. BRETT PH.D.

Sometimes killing a few fish can improve a fishery.



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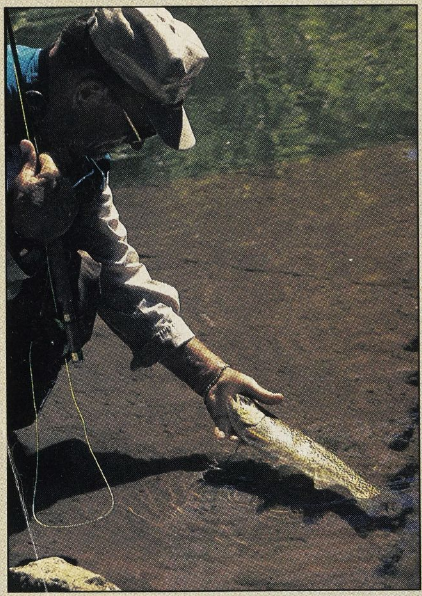

JOHN RANDOLPH PHOTO

Natural mortality and angling mortality (angler harvest and hooking mortality) combine to determine a trout population's mortality rate. Whether angling mortality adds to the fish's mortality rate depends largely on the average growth rates and life spans of the fish in the population.

MANY FLY FISHERS have such a strong reverence for special regulations that they believe that all that is needed to create a blue-ribbon fishery is to implement no-kill regulations. In fact, the quality of a trout fishery—in particular, the age and size structure of the fish population—is determined by myriad environmental and demographic variables. The most important is the population's mortality rate.

There are two components to mortality in a sport fishery: natural mortality and angling mortality. Natural mortality is the mortality a fish population has in the absence of any angling mortality. Factors that contribute to a fish population's natural mortality rate include competition for limited food and habitat, predation, disease, and extreme environmental conditions such as flooding, erosion, anchor ice, etc.

Angling mortality can be further divided into two parts: angler harvest and hooking mortality. Angler harvest is the number of fish kept by anglers. It is of greatest concern, and also the subject of greatest dispute. With heavy angling pressure, angler harvest can have marked impacts on some trout fisheries. The challenge to fisheries biologists is to determine which trout fisheries will be negatively impacted by angler harvest and which will not.

Hooking mortality is a function of the likelihood that a fish will die when caught, multiplied by the average number of times a fish is caught during a season. The probability of a fish dying is about 35 percent if it is caught on bait, and three to five percent if it is caught on a fly or lure. However, hooking mortality rates can be much higher when water temperatures are above 64 degrees Fahrenheit because fish in warm water do not recover as quickly.

Depending on how heavily a stream is fished and the species of trout in a stream, the typical fish may be caught very rarely or up to ten times per year. Cutthroat trout, for example, are particularly susceptible to angling, while browns can withstand heavy angling with only a small proportion of the population being caught. Although hooking mortality is considered important in some cases, it is generally assumed to be sufficiently low and of little practical concern when only flies or lures are used and when water

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temperatures are not much higher than 64 degrees Fahrenheit.

Natural and angling mortality combine to determine a trout population's total mortality rate. This overall mortality determines its age and size structure and the abundance or scarcity of large fish. Natural and angling mortality interact to determine total mortality differently, depending on whether angling mortality is additive or compensatory.

With additive mortality, each trout killed by angling adds directly to the population's overall mortality rate. According to fisheries biologist William Ricker, when angling mortality is completely additive, total mortality is equal to natural mortality plus angling mortality minus the product of natural and angling mortality $\{T = N + A - (N \times A)\}$. The latter part of Ricker's equation simply accounts for the fact that a fish can only die once. For example, if a population's annual natural mortality rate is 50 percent and its angling mortality rate is 50 percent, then the population's total mortality rate will be 75 percent—half of the fish will die due to natural causes and half of the remaining fish will die due to angling.

Compensatory mortality means each fish killed due to angling will simply replace a fish that would have died due to natural causes; for example, kills due to the stresses associated with competing for limited food or habitat. When angling mortality is compensatory, angling will have little impact on a trout population's age and size structure until the angling mortality rate exceeds the population's natural mortality rate. As an example, if the natural mortality rate is 50 percent and angling mortality is completely compensatory, angling will have virtually no impact on the population until it exceeds the natural mortality rate of 50 percent.


BEN ARDITO PHOTO

Cutthroat trout are extremely vulnerable to anglers.

Every sport fishery is influenced by both additive and compensatory angling mortality processes. However, the relative importance of these processes may vary considerably from one fishery to another. The balance between additive and compensatory mortality also varies considerably during the life cycle of a trout. Mortality in young trout (age 0 to 1 year) is generally strongly compensatory, while mortality in larger, older trout is relatively additive. That is, within any trout population, the incidence of compensatory mortality will decrease when going from younger to older age classes. For this reason, the majority of trout fisheries can withstand harvest of smaller fish (say, 8 to 12 inches, depending on the fishery) with very little negative impact on the numbers of larger fish.

Whether angling mortality is additive or compensatory depends in large part on the average growth rates and life spans of the fish in the population. Trout populations dominated by short-lived and slow-growing fish tend to have compensatory angling mortality. A classic example of this is the stunted brook-trout populations of many alpine lakes. Research has shown that angling mortality will not have a detrimental impact on the numbers and size of fish in these populations, because every trout removed through angling will act to lessen the severe competition for limited

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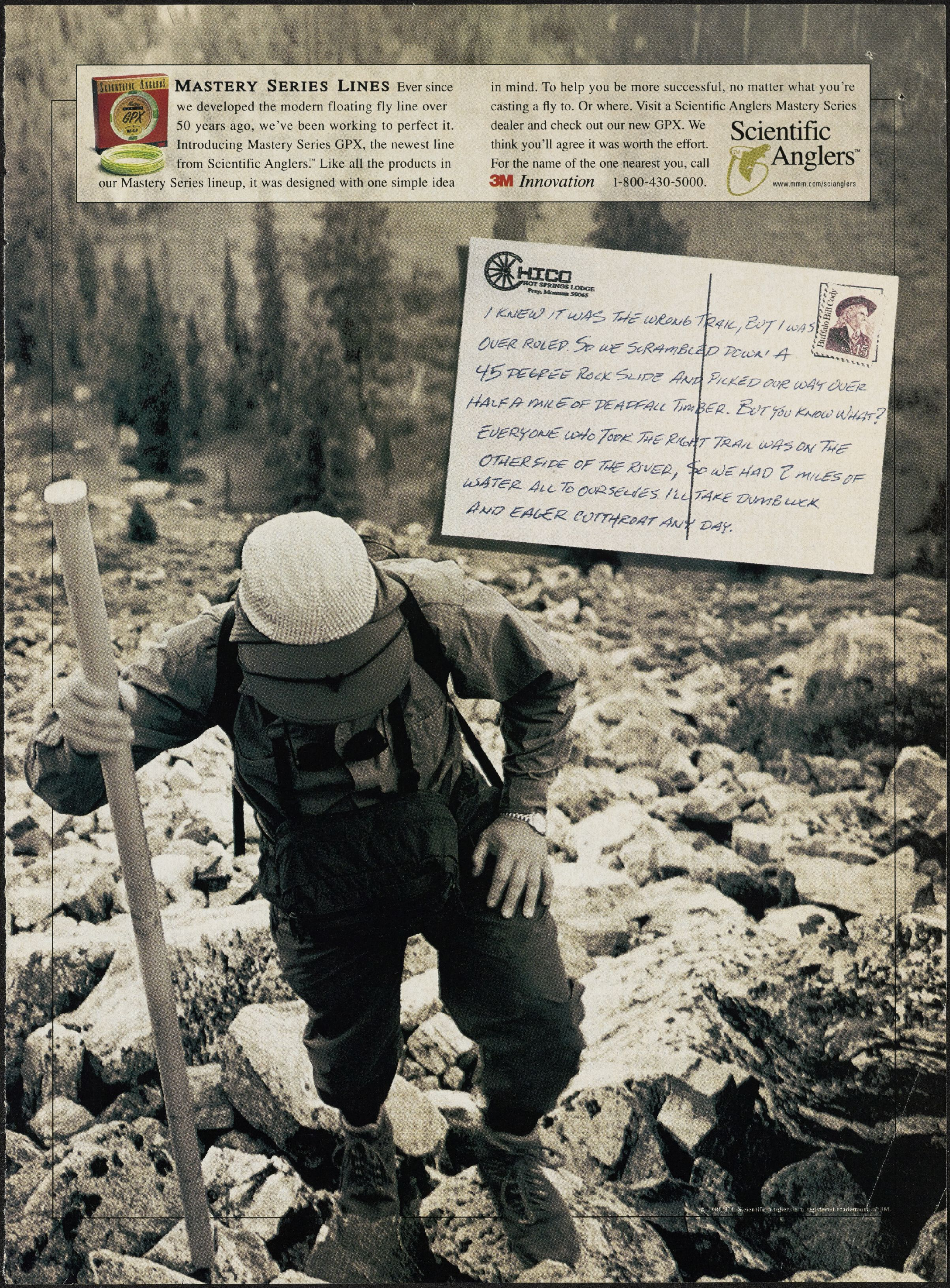

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Continued from page 20

resources amongst the remaining fish. This is the reason why many state fishing regulations allow, and even encourage, anglers to take between 10 and 20 small brookies per day in alpine lakes.

Angling mortality tends to be additive when trout growth rates are high and when life spans are long. Probably the best known example of special regulations (no-kill) restoring a trout fishery is the cutthroat trout fishery in the Yellowstone River below Yellowstone Lake. Cutthroats often live to be six to eight years old, and they are extremely vulnerable to anglers. Biologists have calculated that the average fish in this area is caught approximately ten times per year. No-kill regulations have also been dramatic successes on other very productive trout fisheries.

Interestingly, angling mortality can be additive or compensatory, simply dependent on what time frame is considered. Consider a hypothetical blue-ribbon trout stream where each fish is caught, on average, three times during each fishing season. In many trout streams, natural mortality is concentrated during the winter when environmental conditions are the most severe and resources the most limited. In our hypothetical trout stream, natural winter mortality is about 50 percent and natural summer mortality below 10 percent. Any trout that is killed through angling during the summer will not be available for subsequent recapture during the remainder of the summer. This means that any angling mortality will be virtually 100 percent additive for the summer.

However, since winter mortality is high and largely determined by the availability of suitable habitat and food, any fish killed during the summer may only act to lessen the severe competition during the winter. Fish killed during the summer may have little impact on the total number of fish that survive the winter and the numer of fish available to anglers during the next fishing season. This would mean angling mortality was virtually 100 percent compensatory on an annual basis. Therefore, in this hypothetical fishery, angling would be 100 percent additive on the short term by reducing recycling of catchable fish during the season and 100 percent compensatory on the long term because it has little impact on the numbers of fish that survive from one season to the next.

Management Decisions

THE SINGLE MOST IMPORTANT management decision that can be made is whether to manage a sport fishery as if angling mortality is additive or compensatory. If biologists assume mortality is compen-

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satory when in fact it is primarily additive, a dramatic reduction in the numbers of older and larger fish will result. On the other hand, if a stream is regulated as if angling mortality is additive when in fact it is primarily compensatory, some anglers will be denied the opportunity to harvest fish with little benefit to the trout population.

It should also be pointed out that special regulations, which assume angling mortality is additive and which limit harvest, can in most cases only help to restore a fishery to its pre-angling state. In other words, you cannot make a silk purse out of a sow's ear. If a fishery was dominated by small fish before significant angling occurred, which is probably true for many trout streams, then special regulations will in all likelihood result in a fishery dominated by small fish. However, there will probably be a few more of them.

> *". . . special regulations may actually do some harm by drawing attention and more anglers to these fisheries."*

The Au Sable River in Michigan is a classic example of special regulations failing to restore a fishery and, in fact, coinciding with its decline. This is because nonangling processes had a much greater impact on the trout population than did angling mortality. The trout fishery deteriorated because the town of Grayling and a fish hatchery quit discharging effluent (or in the case of Grayling, marginally treated sewage) into the river. This greatly reduced the supply of nutrients to stimulate plant growth in the river, which in turn greatly reduced the availability of insects and habitat for trout. In essence, the change in trout growth rates and survival had a far greater impact on the abundance of larger fish than did the reduction in their harvest rates.

The likelihood that special regulations will improve a fishery is also related to the relationship between natural and angling mortality. In cases where natural mortality is high and angling mortality is minimal, through light fishing pressure or de facto no-kill management, special regulations will lead to virtually no improvement in the fishery. In fact, it is conceivable that in fisheries

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where few fishers presently keep fish (common on many rivers today), special regulations may actually do some harm by drawing attention, and more anglers, to these fisheries.

In some cases, trout fisheries may have good survival, but poor growth. For example, there may be many skinny fish between 12 and 16 inches long. In this case, fisheries can use slot limits to reduce competition between smaller and larger fish. This will allow the larger fish to obtain greater growth rates without reducing their numbers. However, a slot limit will only reduce competition between large and small trout if it is practiced. To be an effective management technique, fisheries biologists need to communicate their objectives clearly.

In cases where slot limits are merely intended to appease those who want to keep fish, many fly fishers would and should continue to limit their takes. However, in cases where the intent of the slot limit is to reduce competition, many would probably be willing to help the cause by taking a few small fish, provided those fishers were sufficiently informed of the rationale behind the regulations. The effectiveness of slot limits as a management tool is dependent on the effectiveness of fishery agency education programs.

Special regulations have been accepted by virtually the entire fly-fishing community. For this reason, it is imperative that fishers understand the conditions under which these regulations are likely to lead to substantial improvements in fisheries. It is equally important for fly fishers to realize that in many cases, special regulations will not result in greatly improved fisheries. In cases where natural mortality is high compared to angling mortality and growth and survival rates are low, angling mortality will primarily be compensatory and special regulations will have little impact on the numbers of larger fish. Special regulations have been shown to dramatically improve the quality of trout fisheries when the trout have the potential for high growth rates and long life spans, and angler use is heavy. Fisheries that fit these criteria should be managed to limit harvest. Better educated anglers will result in more planned sportfishing regulations.

Author's note: Thanks to Professor Robert J. Behnke for his help in preparing this article and George Schisler for the insights contained in his thesis on angling mortality.

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LIMIT YOUR KILL, DON'T KILL YOUR LIMIT

This phrase has been Trout Unlimited's most enduring slogan. It really wasn't a new idea 40 years ago as Dame Juliana Berners (or her ghost writers) had given similar advice to anglers about 500 years earlier by urging them not to be greedy . . . "as in taking too much at one time."

During the early years, TU leaders faced a dilemma. They intuitively believed that limiting the kill would result in increased abundance of older and larger trout in a population exploited by anglers. They also believed in science and research, as a basis for fisheries management and angling regulations. What TU people heard from scientists about the results of research on restrictive angling regulations that greatly reduced or eliminated the kill was discouraging.

Several studies on small stream populations of brook trout in Wisconsin and Michigan in the 1950's and '60's showed that population abundance and size-age structure was unaffected by any type of regulation that limited or even eliminated the kill. Reducing mortality due to angling during the fishing season only resulted in a proportionate increase in natural mortality, especially during the winter period, so that total annual mortality remained unchanged. A classic example was Lawrence Creek, Wisconsin, where a one-mile section of stream was closed to angling for five years and the trout population was closely monitored. At the end of five years with no angler kill of trout, there were fewer trout than before the experiment when this section was open to statewide fishing regulations.

Forty years ago the fisheries profession followed the now rejected paradigm of "maximum sustained yield" (MSY). MSY sought to keep "surplus" fish from going to "waste" by designing regulations so that fishing mortality largely replaced natural mortality.

Thus, what scientists were telling the early TU leaders was not good news. According to their research, if you catch a trout and release it, it will only die a natural death before the next year, and it goes to "waste."

The first TU policy statement (in the fall 1960 TU quarterly) reads as follows:

1. To promote and support continuing research programs to determine the basic biology and ecology of trout populations.

   a. The causes of the high annual winter mortality of all trout in streams are a primary concern of Trout Unlimited and we encourage investigations and research in this regard.

No doubt the Michigan and Wisconsin brook trout populations under study did exhibit very high mortality from one year to the next, mainly during winter. Typically, there is high mortality within a few weeks after young trout hatch and emerge from redds. If they survive to the end of their first growing season (age 0), there can be relatively good (ca. 40-50%) overwinter survival to the next year (age 1). Most brook trout populations in small streams attain sexual maturity and spawn in the fall of second growing season (still age 1, but two years after their parents spawned). Overwinter mortality can be very high after spawning. In these Michigan and Wisconsin populations, mortality between age 1 and 2 (after spawning) often ranged from 80% to 95%. From age 2 to age 3, mortality ranged from 95% to 98% despite any angling regulations to limit the kill. There were very few fish living to age 3 (fourth year of life).

The first well-documented examples of highly successful special regulations that "limited the kill" and greatly increased abundance came in the 1970's and concerned cutthroat trout in Idaho (St. Joe River, Kelly Creek) and in Yellowstone National Park (Yellowstone Lake and River).

The autumn 1989 issue of Trout contains my article: "We're putting them back alive." In that article I review the history of special angling regulations and the conditions that favor success, as with cutthroat trout, and those that cause failure, as with the small stream, short-lived, Wisconsin and Michigan brook trout populations. For details see the autumn 1989 issue of Trout, but the important determinants of success for any regulation designed to limit or eliminate angling mortality are: rates of recruitment (success of natural reproduction), production (the percent of biomass increase of population in one year), age-growth dynamics (annual survival rates and increase in size — how many years to attain 12", 16", 20" etc.) Also an accurate predictor of success is the species of trout; how vulnerable are they to being caught by angling? For example, how many hours of angling per surface acre of water, to catch (and release) each catchable-size trout, on average, once per year. For a brown trout population, it may take 500 to 1,000 hours or more of angling per acre to catch, on average, each fish once. For a cutthroat trout population, this level of exploitation can be achieved in 10-12 hours of angling per acre. In the 1960's, the cutthroat trout of Yellowstone Lake were managed for "maximum sustained yield." The population was severely overexploited at no more than 5-6 hours of angling per acre per year. After a 13-inch maximum size limit went into effect (all trout larger than 13" must be released), the numbers of adult trout of five, six, seven, and eight years of age on spawning runs increased by several fold. The no-kill regulation protecting the cutthroat trout in the Yellowstone River now supports much greater angler use than in the old days and maintains a much more abundant population of older, larger fish than before the no-kill regulations. It has been calculated that, on average, each cutthroat trout in the Yellowstone River population is caught and released 9.7 times during the fishing season.

This vulnerability to being caught and caught again and again has been a boon for the popularity of several rare subspecies of cutthroat trout. They are stocked in lakes for restoration (after all non-native trout removed) and provide a high catch rate as they are recycled over and over. No other species of trout can sustain such a high catch rate as cutthroat trout.

To illustrate the significance to anglers and the economic importance of catching the same fish several times, data from the "Miracle Mile" (a six-mile segment of the North Platte River, Wyoming) can be cited. Electrofishing sampling in the Miracle Mile in 1996 estimated that there were a total of 20,795 catchable-size brown trout (all from natural reproduction) and 5,777 rainbow trout (4,197 hatchery trout stocked a year or two before and 1,580 wild, naturally reproduced rainbows). The ratio of brown trout to rainbow trout was 78:22. About 115,000 hours of angling occurred during the year (about 700 h/acre) to catch an estimated 70,138 trout (catch rate of 0.62/hr). The catch consisted of 24,519 brown trout, averaging about 16 inches and 45,303 rainbow trout averaging about 17 inches. On average, each of the 20,795 brown trout was caught 1.2 times during the year to give a total catch of 24,519. Rainbow trout which made up only 22% of the total trout numbers (brown trout 78%) made up 65% of the angler catch. To do this, each of the 5,777 rainbows available to be caught had to be caught (and released) several times to provide a catch of 45,303. On average, each wild rainbow was caught 6.3 times and each hatchery rainbow (which appear to be "wild" after a year or two in the wild) was caught 8.3 times. The new paradigm of fisheries management should be "maximum sustained catch (and release)." There's no other alternative for maintaining an acceptable catch rate of older, larger fish under intense fishing pressure.

I think the famous fishery of the Miracle Mile is what the early TU people had in mind in regard to what could be accomplished by limiting your kill, and not killing your limit. Surprisingly, there are no gear restrictions on the Miracle Mile — flies, lures, bait, single, double, treble, barbed or barbless hooks can be used, and two trout per day can be harvested. About 90% of all trout caught are released. For each pound of hatchery rainbow trout stocked, about 15 pounds are caught, of which, 1.7 pounds are harvested. There are reservoirs, well stocked with trout (and walleye), above and below the Miracle Mile where anglers can harvest fish to eat. Thus, most anglers seeking fish to catch, kill, and eat, go to the reservoirs. The Miracle Mile is much preferred by anglers practicing catch-and-release.

Although limited kill (typically one or two trout per day), wild trout management programs have been expanded in recent years, it is common to face strong opposition when a new wild trout regulation is proposed. Most opposition focuses on the theme of "elitist" angler vs. the "common" angler who wants to keep and eat fish. You can bet that state legislators will take up the cause of protecting the "common" angler from the "elitists" if an intense controversy develops. The less restrictive the regulations in regard to gear and methods, the more likely new wild trout management waters will find acceptance. Also, the availability of fish for catching and eating in near-by waters, enhances the chances of gaining more limited-kill fisheries for wild trout.

A more philosophically-based opposition to catch-and-release angling is based on the European tradition of hunting and fishing as "blood sports," whereby the hunter stalks and kills the prey. This is what makes hunting a "sport." The line of reasoning of this philosophy concludes that catching and releasing a fish demeans the sport, reducing angling to a trivial, cruel game whereby humans obtain pleasure by inflicting unnecessary pain on animals. There is strong circumstantial evidence that "pain" in fishes is not comparable to that of higher vertebrates, nor is catching a fish a very traumatic experience for the fish (otherwise catch-and-release regulations wouldn't work).

A new philosophy of American sport fishing should argue that fishing is not a "blood sport" comparable to hunting. From the earliest literature of the mysterious Dame Juliana, followed by Izaak Walton, the descriptive words associated with fishing are gentle, contemplative, therapeutic, etc. Fishing is more spiritual, hunting more worldly.

Considering Yellowstone Park as an example, the hundreds of thousands of trout that are caught and released to meet a natural death, are not "wasted," but provide a large food supply to fish-eating birds and bears and recycle nutrients — the trout's natural role in the processes of ecosystem functioning. As such, catch-and-release angling is environmentally correct, a "nontrivial" pursuit.