

Using a bioenergetic model to assess growth reduction from catch-and-release fishing and hooking injury in rainbow trout, *Oncorhynchus mykiss*

J. M. MEKA

United States Geological Survey, Alaska Science Center, Anchorage, AK, USA

F. J. MARGRAF

United States Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK, USA

Abstract A bioenergetic model was used to predict the potential effects of feeding cessation caused by catch-and-release capture and a reduction in feeding efficiency from hooking injuries on rainbow trout, *Oncorhynchus mykiss* (Walbaum), growth in southwest Alaska, USA. Simulations indicated that a 1-day feeding cessation for a rainbow trout captured one to two times during summer months resulted in deviations from expected growth of –3% to –15%. To represent debilitating hooking injuries, the proportion of the maximum feeding potential was decreased by 5–50% resulting in deviations from expected growth of –9% to –164%. Simulated growth effects were most prominent from captures during months when salmon eggs and flesh constituted the majority of the trout diet. Simulated growth effects from reduced foraging efficiency were most prominent when hooking injuries occurred early in the fishing season. These simulations suggest that rainbow trout are most vulnerable to decreases in growth when salmon are abundant and spawning and, coincidentally, during the months when most fishing occurs.

KEYWORDS: bioenergetics, catch-and-release fishing, growth, hooking injury, rainbow trout.

Introduction

Catch-and-release fishing has become an increasingly frequent management strategy and voluntary choice by anglers for fish populations that are heavily fished or otherwise vulnerable to exploitation (Cooke, Schreer, Dunmall & Philipp 2002). The Alagnak National Wild River in southwest Alaska, USA, is one of the areas most popular fly in fishing destinations and home to a world-renowned rainbow trout, *Oncorhynchus mykiss* (Walbaum), sport fishery as well as Pacific salmon, *Oncorhynchus* spp., Arctic grayling, *Thymallus arcticus* (Pallas), Arctic char, *Salvelinus alpinus* (Linnaeus), and lake trout, *Salvelinus namaycush* (Walbaum), sport fisheries. Reports of a decrease in trout size and abundance and an increase in fishing pressure during

the 1990s introduced concerns for the sport fishery, and permanent catch-and-release fishing regulations were eventually adopted (Meka, Knudsen, Douglas & Benter 2003). A recent study of Alagnak River rainbow trout suggested that injuries from catch-and-release fishing may be substantial enough to result in cessation of foraging for a period of time or even a permanent reduction in foraging efficiency from a debilitating hooking injury (Meka 2004).

The cessation of feeding for hours to days after exposure to stress events such as handling, electrofishing, tagging or angling has been demonstrated for rainbow trout, cutthroat trout, *Oncorhynchus clarki* (Richardson), brown trout, *Salmo trutta* Linnaeus, Atlantic salmon, *Salmo salar* Linnaeus, Arctic grayling and largemouth bass, *Micropterus salmoides*

Correspondence: Julie Meka, Nongame Branch, Arizona Game and Fish Department, 2221 W. Greenway Rd, Phoenix, AZ 85023, USA (e-mail: jmeka@azgfd.gov)

(Lacepède), sometimes resulting in a reduction in growth (Pickering, Pottinger & Christie 1982; Mesa & Schreck 1989; Schreck, Olla & Davis 1997; Hughes 1998; McCormick, Shrimpton, Cary, O'Dea, Sloan, Moriyama & Bjornsson 1998; Siepker 2005). The energetic demand during the capture process at variable seasonal temperatures results in changes in the physiological status, such as increased plasma cortisol, glucose and lactate levels (Pankhurst & Dedual 1994; Meka & McCormick 2005). Pacific salmon subjected to these types of stressors generally exhibit normal feeding behaviour when baseline physiological levels resume (Schreck *et al.* 1997). Fish subjected to a catch-and-release fishery may be exposed to additional stressors during the capture process, such as air exposure and angler handling, which cause the physiological changes to increase above baseline levels with the amount of time fish are played, handled and exposed to air (see Ferguson & Tufts 1992). Therefore, it is reasonable to assume that fish subjected to a catch-and-release fishery may refrain from feeding for a period of time after capture, but little research has been devoted to this topic for wild fish. Further, fish captured by angling may lose their place in a foraging hierarchy, which may also contribute to a temporary feeding cessation (Lewynsky & Bjornn 1987) and ultimately influence growth.

The anatomical hooking site affects initial mortality of angler-caught fish (Warner 1979; Muoneke & Childress 1994). Fish hooked in the eye, tongue, gill region or oesophagus suffer the highest initial mortality rates (Stringer 1967; Hunsacker, Marnell & Sharpe 1970; Dubois & Dubielzig 2004). There are many studies on how the severity of hooking injuries influences mortality in rainbow trout (see Taylor & White 1992), but few address the sublethal impacts of hooking injuries to trout, including the potential effects on growth resulting from non-lethal injuries (Dubois & Dubielzig 2004; Dubois & Kuklinski 2004; Meka 2004; Meka & McCormick 2005). A foraging disadvantage due to an eye or jaw injury resulting from hooking can potentially affect growth (Dubois & Dubielzig 2004; Dubois & Kuklinski 2004; Meka 2004). The most common recently inflicted hooking injuries of Alagnak River rainbow trout caught in the sport fishery using conventional 'J' style hooks were to the jaws (61%) and eye (17%) (Meka 2004). A recent study of trout captured by angling reported that 10% had sustained severe eye injuries, most likely resulting in long-term visual impairment (Dubois & Dubielzig 2004). They observed some minor eye injuries healed to functionality; however, feeding efficiency during and after

this healing period for wild fish released into their natural environment is unknown.

Bioenergetic modelling can be used as an initial step to assess the potential effects of different types of stress on growth of wild fish (Beyers & Rice 2002). In this study a bioenergetic model was used to estimate the potential effects of a cessation of feeding and a reduction in foraging efficiency caused by catch-and-release angling on rainbow trout growth in southwest Alaska. Rice's (1990) application of a null model hypothesis of a 'healthy fish' was used to simulate expected growth of rainbow trout feeding normally and trout subjected to one of the following conditions: (1) cessation of feeding for 1 day during one summer month; (2) cessation of feeding for 1 day during two summer months to mimic two captures; or (3) decreased proportion of maximum food consumption (*P*-value) to simulate hooking injury from capture. Results from the simulations were compared with the 'healthy-fish' model to determine whether changes in growth occurred.

Materials and methods

Bioenergetic model for rainbow trout

The revised Wisconsin model with programmed physiological parameters configured for steelhead trout (anadromous *O. mykiss*) was used for this investigation (Hanson, Johnson, Schindler & Kitchell 1997). The input values entered into the model included daily surface temperatures, daily diet proportions, prey energy density, predator energy density, digestible proportion of prey and start and end weights of rainbow trout for the simulated time interval. Water temperatures were measured during rainbow trout captures on the Alagnak River in June (9.5–13.6 °C), July (10.3–15.5 °C) and August 2001 (12–16.9 °C) (J.M. Meka, unpublished data). Diet proportion data were taken from a study in which stomach contents of rainbow trout were evacuated and measured in June, July and August in the Wood River lake system in southwest Alaska to determine the importance of sockeye salmon carcasses and eggs to trout growth during the summer (Eastman 1996). Eastman (1996) observed an average trout weighing 596 g before peak sockeye salmon spawning to reach 697 g at peak spawning (over a 3-week period in August). The 'healthy-fish' null hypothesis model used in this study simulated growth of a 525-g rainbow trout growing to 700 g in June (525–550 g), July (550–600 g) and August (600–700 g). Insects and juvenile fish dominated the trout diet in June and most of July, with salmon

Table 1. Diet proportions during June, July and August for Alagnak River rainbow trout

Prey category	Prey composition in simulated trout diet					
	June (days 1–30)	July (days 31–49)	July (days 50–58)	July (days 59–60)	August (days 61–74)	August (days 75–90)
Invertebrates	0.75	0.75	0.5	0.09	0.09	0.02
Fish	0.25	0.25	0.5	0	0	0
Salmon eggs	0	0	0	0.89	0.89	0.5
Salmon flesh	0	0	0	0.02	0.02	0.48

Table 2. Input parameters used to simulate Alagnak River rainbow trout growth

Prey category	Prey caloric density (J g^{-1})	Proportion digestible
Invertebrates	2000	0.90
Fish	4900	0.91
Salmon eggs	18 694	0.95
Salmon flesh	2700	0.90

eggs and flesh becoming the primary food source in late July and August and contributing to most of the weight gain (Table 1; Eastman 1996; Hendry & Berg 1999; J.M. Meka, unpublished data).

Caloric values of rainbow trout prey and the prey digestibility were taken from a combination of three field studies (Table 2; Eastman 1996; Davis, Myers & Ishida 1998; Hendry & Berg 1999). The predator energy density of rainbow trout (6000 J g^{-1} wet weight) was estimated from similar values used in studies for rainbow trout, steelhead and other salmonids (Davis *et al.* 1998; Railsback & Rose 1999; Connolly & Peterson 2003). The *P*-value (proportion of maximum consumption) was considered to represent an individual fish's foraging efficiency. There were different diet proportions each month (Table 1); thus, the *P*-value fluctuated during the simulation period to reflect diet differences (prey availability and prey caloric value) for the healthy-fish model based on the start and end weights. For example, in the healthy-fish model, the *P*-value represents the proportion of consumption necessary for a fish to reach the assigned end weight for that month. For June, the bioenergetic model was calibrated to fit to the start and end weight of 525–550 g, resulting in a *P*-value of 0.413. For July, the model was fit to the start and end weight of 550–600 g, giving a *P*-value of 0.218; and for August, the model was fit to the start and end weight of 600–700 g, resulting in a *P*-value of 0.131. Using the Wisconsin model's standard calibrated *P*-value approach assumes that the only varying parameter in the model is the *P*-value.

Simulation 1: Effect of feeding cessation on growth

The first set of model simulations estimated any effect on rainbow trout growth after cessation of feeding (0 caloric intake) for 1 day in June (day 12; see Table 1) when diets were dominated by invertebrates. One-day feeding cessations in July (days 50 and 59) and August (days 74 and 75) were simulated using two different days during each month to account for varying proportions of salmon eggs, salmon flesh and invertebrates in the diets during those months. The feeding cessation period of 1 day was based on studies that found the physiological response (e.g. cortisol) of fish to acute stress events generally returned to pre-stress levels in 24 h (Barton, Schreck & Sigismondi 1986; Pickering, Pottinger, Sumpter, Garragher & Le Bail 1991; Schreck *et al.* 1997). Models simulated one and two captures during the study period to mimic true angling conditions on the Alagnak River; approximately 30% of Alagnak River rainbow trout have previously been captured in the sport fishery (Meka 2004). The simulations used the healthy-fish *P*-value during all months, including when the cessation of feeding occurred. This resulted in an end weight less than the healthy-fish model end weight because of the zero caloric values for the number of days of no feeding. The resulting end weight from loss of food was then used as the new start weight for the next 30-day period. The same modelling procedures were used to mimic expected fish growth after being caught and released twice in one season, except caloric intake was 0 for 1 day in each of 2 months.

Simulation 2: Effect of reduced foraging efficiency

The second set of simulations involved the reduction of the *P*-value from the healthy-fish model by 5% and 10% to mimic a decrease in foraging efficiency resulting from a hooking injury to the jaw, such as a torn maxillary or one that interferes with anatomical function, and by 50% to mimic permanent injury to one eye with loss of functionality. Reductions in *P*-values were simulated to mimic an injury from a

capture at the beginning of the fishing season on June 1 and later in the fishing season on the first day of both July and August.

Healing from hooking injuries, so that normal feeding resumed, was not taken into account; thus, trout sustained a reduction in the *P*-value from the time they were injured until the end of the simulation period. Little research has been conducted on the healing of eye injuries or hooking injuries in general. Aalbers, Stutzer & Drawbridge (2004) found shallow hook wounds in white seabass, *Atractoscion nobilis* (Ayres), healed during a 90-day period after capture. Dubois & Dubielzig (2004) observed some minor eye injuries (e.g. choroidal and extraorbital haemorrhage) healed to functionality within their study period, but suggested that severe eye injuries (e.g. corneal opacity, lens rupture and traumatic enucleation) could cause long-term visual impairment, potentially influencing feeding efficiency and survival rates. McLaughlin, Grizzle & Whiteley (1997) suggested eye injuries that include cornea perforation and anterior chamber collapse would form scar tissue during the healing process that would inhibit functionality. Based on the limited information available on the healing of injuries

in fish, using a wide range of reductions in foraging efficiency for rainbow trout with hooking injuries was considered to yield reasonable approximations of effects of hooking injuries. The appropriate input parameters for diet proportions were used for feeding cessation and reduced foraging efficiency models and trout were simulated to feed every day.

Results

Effect of feeding cessation on growth

Model predictions for expected growth varied depending on the month of feeding cessation and when in the month the capture occurred. The simulations for 1 day of missed feeding revealed that the predicted growth of angled fish deviated from expected growth by -3% to -13% (Table 3). Deviations from expected growth were greatest when fish were captured at the end of July (-13%) and mid-August (-8%), when salmon eggs accounted for 89% of trout diets (Table 1). Deviations from expected growth were -11% to -15% with two simulated captures. The greatest predicted growth deviation was for trout captured in

Table 3. Weight gains and deviations predicted by bioenergetic models for healthy rainbow trout and rainbow trout that: (1) did not feed for 1 day during one summer month following capture by angling; (2) did not feed for 1 day during two summer months to mimic two captures in one fishing season; and (3) had reduced foraging efficiency resulting from hooking injury. Healing from hooking injuries was not factored into the simulations; thus, trout sustained a reduction in foraging efficiency from the time they were injured until the end of the simulation period. The healthy fish model predicted a trout feeding at a normal rate without injury to gain 175 g over the 90-day summer simulation period

Model simulation	Healthy fish weight gain (g)	Angled fish weight gain (g)	Deviation (g)	Per cent deviation
No feeding 1 day in 1 month				
No feeding day 12 in June	175	169	-7	-3
No feeding day 50 in July	175	161	-14	-8
No feeding day 59 in July	175	153	-22	-13
No feeding day 74 in August	175	162	-13	-8
No feeding day 75 in August	175	166	-9	-5
No feeding 1 day during 2 months				
No feeding day 12 in June, day 50 in July	175	155	-20	-11
No feeding day 12 in June, day 74 in August	175	155	-20	-11
No feeding day 50 in July, day 74 in August	175	148	-27	-15
Injured in June; foraging efficiency reduced in June, July, August by				
5%	175	141	-34	-20
10%	175	109	-66	-38
50%	175	-112	-287	-164
Injured in July; foraging efficiency reduced in July and August by				
5%	175	148	-27	-15
10%	175	123	-52	-30
50%	175	-55	-230	-132
Injured in August; foraging efficiency reduced in August by				
5%	175	159	-17	-9
10%	175	143	-32	-18
50%	175	30	-145	-83

July and August, when salmon eggs dominated trout diets. Although dates in the month when fish were captured were not varied for two captures, the results from simulations with one capture suggest growth decreases would likely be smaller when salmon eggs were not the primary food source in trout diets.

Effect of reduced foraging efficiency

Deviations from expected growth varied with the reduction in foraging efficiency (P -value) and the date when the hooking injury occurred (Table 3; Fig. 1). Deviations in expected growth during the simulation period ranged from -9% to -20% when foraging efficiency was reduced by 5% , and from -83% to -164% when foraging efficiency was reduced by 50% . Simulations with the 50% reduction of foraging efficiency resulted in end weights less than initial weights for some fish. Effects on growth were greater when foraging efficiency was impaired during all

summer months, mimicking injury occurring at the beginning of the fishing season.

Discussion

Effect of feeding cessation on growth

Predicted reductions in growth were greatest when time of capture occurred when trout were feeding on salmon carcasses and eggs, with the strongest reductions occurring when trout were feeding predominantly on salmon eggs. In watersheds such as the Alagnak River, the eggs and flesh of five species of Pacific salmon are predominant sources of food to rainbow trout during late July and August and largely influence the migratory activity of trout from spawning to feeding habitats and from feeding to overwintering habitats (Meka *et al.* 2003). The high calorific value of salmon eggs and flesh in the trout diet is necessary to meet the energetic demand required for such extensive seasonal movement.

In general, the rainbow trout sport fishery occurs in June, August and September, with the most fishing pressure in June (Jaenicke 1998; J.M. Meka unpublished data). Approximately 30% of Alagnak River rainbow trout have been previously hooked at least one time, 38% of which had greater than one hooking scar indicating multiple captures (Meka 2004). Trout subjected to multiple captures per season may be more vulnerable to reduced growth as suggested by the model simulations, particularly if the effects of each capture are cumulative (Barton *et al.* 1986; Stockwell, Diodati & Armstrong 2002) or captures occur during months when salmon are most influential in trout diets. It is unknown if deviations in expected growth of -3% to -15% as observed in feeding cessation model simulations could result in individual long-term growth loss or population-level effects for Alagnak River rainbow trout.

There is a general lack of information on growth effects caused by catch-and-release fishing with heavy angling pressure. The physiological changes from different stressors may increase with the duration and intensity of the stress event (Pickering & Pottinger 1989; Pankhurst & Dedual 1994; Meka & McCormick 2005) and delays in feeding may also vary with exercise duration and intensity, and water temperatures (Siepkner 2005). However, it is not known whether fish subjected to multiple captures in a catch-and-release fishery with heavy angling pressure will exhibit greater delays in feeding or growth effects than fish subjected to single captures (Pope & Wilde 2004). It is likely that the duration of feeding cessation and growth effects would vary by species because of differences in feeding

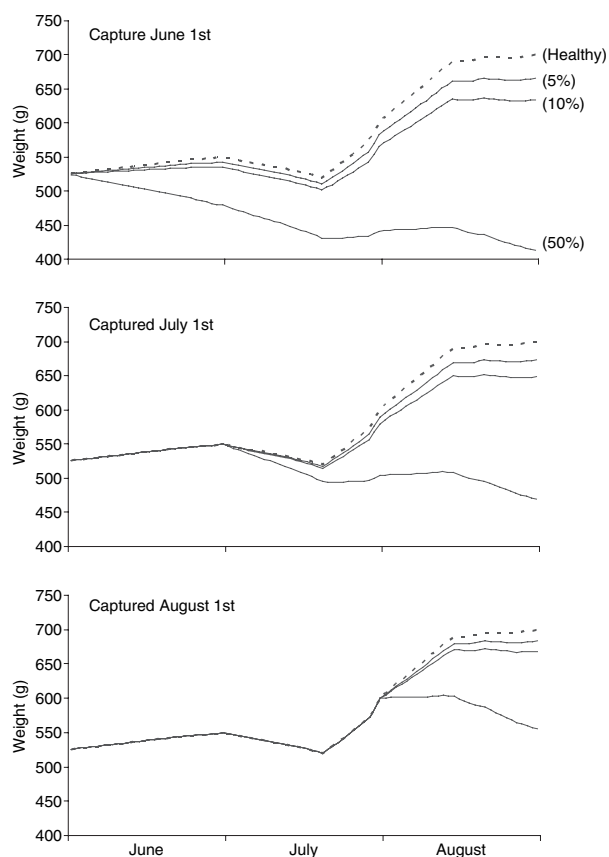


Figure 1. Simulated growth of healthy (no foraging impairment, dashed line) rainbow trout and rainbow trout with foraging efficiency impaired by 5% , 10% and 50% to mimic a hooking injury sustained during angler capture and release.

behaviour and be different in natural environments where food is limited. It is also possible that feeding cessations were greater or less than the 24-h cessation period simulated in this study. Thus, the results of model simulations in this study warrant field studies for model verification and investigation into feeding cessation and the long-term viability of the population under present angling pressure and recapture rates.

Effect of reduced foraging efficiency

The influence of reducing the P -value to mimic reduced foraging efficiency resulting from hooking injury produced a notable decrease in rainbow trout growth. The most prominent deviation from expected growth occurred when foraging efficiency was reduced during all summer months to mimic trout captured in June, the month with the most angling effort for rainbow trout. When the feeding efficiency of trout was reduced to indicate a severe eye injury occurring in June or July, the deviation in expected growth was so extreme that the predicted end weights were actually less than the initial weights. Fish injured in sensitive locations such as the eye, oesophagus, gills and tongue suffer the highest mortality rates (Hunsacker *et al.* 1970; Warner 1979; Siewert & Cave 1990; Meka 2004), and fish that survive injuries in these locations may be subject to sublethal effects. For example, Aalbers *et al.* (2004) found white seabass surviving deep hooking wounds had significantly lower growth rates than fish with shallow hooking wounds and hypothesised that lower growth rates could have resulted from longer recovery periods for deeply hooked fish that may have experienced delayed initial feeding or poor feeding efficiency. Studies that have observed eye injuries in fish have suggested that severe eye injuries likely inhibit functionality, resulting in visual impairment that could influence survival rates (McLaughlin *et al.* 1997; Dubois & Kuklinski 2004). The commonality of eye injuries sustained by Alagnak River rainbow trout (17%, Meka 2004) and the degree of growth loss predicted for a simulated severe eye injury may be significant enough to influence survival, further warranting field verification of the simulated results and investigation into the potential growth effects in fish surviving severe hooking injuries.

Problems and assumptions in the model

The version of the Wisconsin model used in this investigation incorporated physiological estimates for steelhead. Although Alagnak River rainbow trout are

a purely riverine population, their life history characteristics such as highly migratory behaviour, fast growth and dependence on salmon as a food resource (Meka *et al.* 2003) warrant the use of a bioenergetic model for steelhead rather than models based on the life history of non-migratory rainbow trout.

According to Ney (1993), the most common types of error associated with the use of bioenergetic models include unknown activity metabolism costs, unjustified data extrapolation, incorporating data into models specific to other species and insufficient estimation of external variables. Potential errors associated with application of the model most likely resulted from measurement error and variability in the data taken from various field studies that were incorporated as input data into the model. For example, constant predator (rainbow trout) and prey energy densities were assumed throughout the model simulations, yet it has been demonstrated that these densities can vary throughout the season and be influenced by size and sex (Ney 1993). Because of the lack of daily feeding rate data for wild rainbow trout in southwest Alaska, trout were assumed to feed daily on the prey available. Rainbow trout feeding rates observed by Eastman (1996) in the Woods Lake watershed were assumed to be applicable for simulations of Alagnak River rainbow trout growth.

Compensatory growth by trout was not included in the model. The ability of fish to exhibit an accelerated growth rate to compensate for food deprivation or shortage has been noted widely in captive fish from controlled studies (Abbott & Dill 1989; Whitley, Hayward, Noltie & Wang 1998; Ali, Nieceza & Wootton 2003; Whitley, Bajer & Hayward 2006), but information is lacking for wild fish inhabiting streams with limited and seasonal food resources. In addition to the duration of food deprivation influencing weight gain of rainbow trout, past nutritional history, energy content of the diet and whether fish are fed at or below satiation has also been found to influence weight gain and feeding intensity (Jobling & Koskela 1996; Boujard, Burel, Médale, Haylor & Moisan 2000; Ali *et al.* 2003). Because many experiments on compensatory growth restrict food from days to weeks to mimic natural starvation periods (Weatherley & Gill 1981; Boujard *et al.* 2000), it is difficult to predict whether compensatory growth exists in fish with very short food deprivations such as in this experiment. In addition, because growth in rainbow trout may be influenced by dominance status (Abbott & Dill 1989), factoring compensatory growth into our bioenergetic models at this stage would be premature. The 1-day duration of food deprivation used in this

modelling application is considered conservative compared to most studies on compensatory growth, one of which used fish with a 1-day food deprivation period as the control group (Boujard *et al.* 2000).

Summary

This investigation was based on the application of a bioenergetic model to estimate potential changes in growth of rainbow trout subjected to catch-and-release fishing. The results of the model simulations indicated substantial effects on cumulative seasonal growth experienced by rainbow trout that feed on salmon eggs and flesh and were subjected to one or two captures per season. While the significance of these results warrants further study and field verification, fishery managers should be cognizant of the potential growth effects associated with catch-and-release fishing in some populations, particularly those subjected to multiple recaptures and subsequent hooking injuries. Future research should focus on quantifying feeding rates of free-swimming fish before and after angling, monitoring the healing process of hooking injuries, identifying changes in feeding efficiency from varying degrees of hooking injury and identifying compensatory growth in wild populations. The results of this study and the precautionary principle suggest that anglers should adopt gear types (e.g. barbless hooks) and strategies (e.g. reduce stress and feeding cessation through shorter handling times) that minimise injury and stress to minimise growth penalties.

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