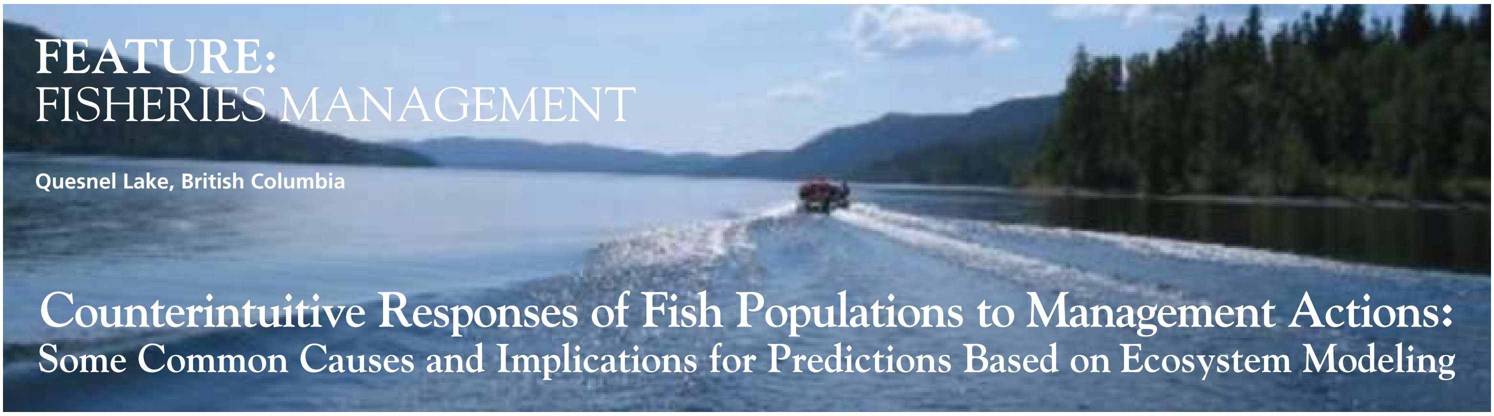

FEATURE:
FISHERIES MANAGEMENT

Quesnel Lake, British Columbia

H. J. FLOWERS

Counterintuitive Responses of Fish Populations to Management Actions:
Some Common Causes and Implications for Predictions Based on Ecosystem Modeling

ABSTRACT: Observed ecosystem responses to fisheries management experiments have often been either much smaller or in the opposite direction of the expected responses based on experience or population models. Examples of these responses can be found even for some very simple experimental management manipulations such as predator and prey manipulations in small lakes and ponds to fish population responses to harvest closures. Such counterintuitive prediction failures offer opportunities to identify key processes and variables that are not widely considered in models used to evaluate ecosystem-based fisheries management policies. A common denominator in the case histories presented are unexpected behavioral responses and strong changes in juvenile survival rates of fish driven by changes in competition, predation, and behavioral responses to predation risk. These factors restructured many of the ecosystems in our simple examples, yet are not widely included in models currently used to evaluate ecosystem-based fisheries management policies. This represents a critical need in the development of modeling tools to evaluate ecosystem-based policies based on an iterative process of model building and model testing, using fisheries management actions as probing tools to learn more about the ecosystems being managed.

Respuestas inesperadas de poblaciones de peces ante acciones de manejo: algunas causas comunes e implicaciones para la predicción basada en modelación de ecosistemas

La respuesta de los ecosistemas ante experimentos de manejo pesquero en ocasiones ha sido limitada e incluso opuesta a aquella que se espera de la experiencia o de acuerdo a modelos poblacionales. Pueden encontrarse ejemplos de esto en manipulaciones experimentales sencillas como en los sistemas depredador-presa en pequeños lagos y estanques, así como la respuesta de las poblaciones de peces a vedas de captura. Estas predicciones fallidas y contra-intuitivas ofrecen una oportunidad para identificar variables y procesos clave que comúnmente no son considerados en los modelos que se usan para evaluar las políticas de manejo pesquero basado en el ecosistema. El común denominador en los casos que aquí se presentan es el comportamiento inesperado y los cambios drásticos en las tasas de supervivencia de individuos juveniles de peces, determinados a su vez por cambios en la intensidad de la competencia, depredación y la conducta al riesgo de depredación. Si bien estos factores reestructuraron muchos de los ecosistemas en nuestros ejemplos, no se incluyen en los modelos que actualmente se emplean para evaluar políticas de manejo de pesquerías con consideraciones a nivel ecosistema. Esto representa una necesidad crítica de desarrollar herramientas de modelación para evaluar políticas pesqueras basadas en el ecosistema. Dicho desarrollo implica un proceso iterativo de creación y falsar de modelos utilizando acciones de manejo pesquero como herramientas para probar y aprender más acerca de los ecosistemas en cuestión.

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INTRODUCTION

Most fisheries management actions are motivated by predictions of how a single species will respond to the implemented policy, with little consideration given to the ecosystem as a whole. These predictions are developed in numerous ways, ranging from a single manager making predictions based on their experience and intuition to large international committees considering the latest in complex oceanographic and ecosystem-linked fish-

Redear sunfish were commonly used in stocking experiments to assess farm pond "balance" throughout the southeastern US.

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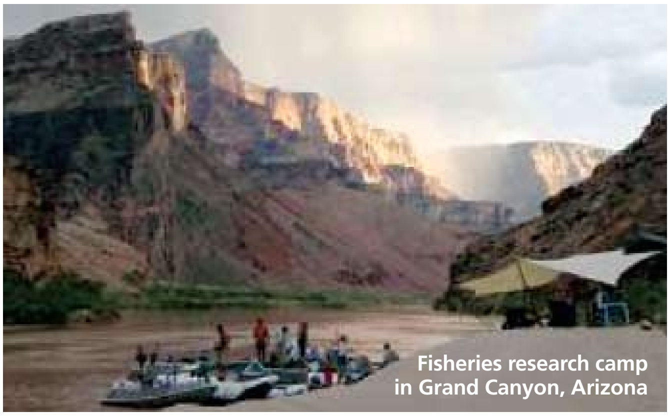
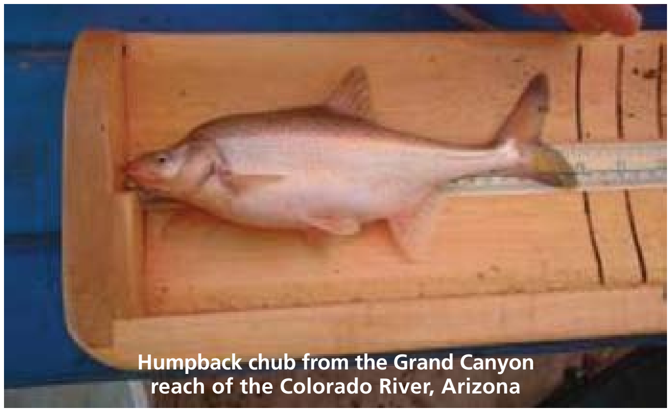


Fisheries research camp in Grand Canyon, Arizona

The mouth of the Little Colorado River in Grand Canyon, Arizona.

A Safe Run of Lava Falls, Colorado River, Grand Canyon, Arizona



Humpback chub from the Grand Canyon reach of the Colorado River, Arizona

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ery models with hundreds of parameters. It is widely expected that in a simple freshwater example the former approach would be most appropriate, while the latter would be adept at providing insight into effective management for complex oceanic fisheries, but how realistic are these expectations? Our ability to make predictions about how an ecosystem would respond to a management action is often not as good as we would hope, regardless of the system or model complexity.

Many fisheries management agencies are currently developing or expanding ecosystem-based management programs, motivated by concerns that fishing has impacts on ecosystems beyond localized depletions of targeted species (Link et al. 2002; Pauly et al. 2002; Christensen et al. 2003; Dulvy et al. 2003; Link 2005; NRC 2006; Murawski 2007). This emphasis on ecosystem-based approaches has been partially set in motion by increased public interest in fisheries impacts on marine systems, fueled by high profile scientific publications (Pikitch et al. 2004; Smith 2007) and major ocean policy reviews by national (U.S. Oceans Commission 2004), international (ICES 2000), and non-governmental organizations (Pew 2003). Concerns over the broader impact to ecosystems from fishing are not new (May 1984), and the issue has not been whether marine fisheries management should consider ecosystem-level effects, but instead how can management actions capture these interactions and develop effective policies to allow sustainable harvest while minimizing indirect effects to the ecosystem (Pauly et al. 2002; NRC 2006)? Freshwater fisheries policies also consider ecosystem-level interactions, with recent emphasis placed on developing a better understanding of the role of habitat manipulations (Minns 1996), water level management (Richter et al. 2003), or changes in stocking policy in enhancing fishery performance (Cowx and Gerdeaux 2004).

Recently the U.S. National Research Council (NRC 2006) synthesized the contemporary scientific debates and policy concerns related to ecosystem-based fisheries management. NRC (2006) defined ecosystem-based fisheries management as "developing ecosystem-level goals that are multispecies focused and that consider multiple kinds of human activities that are tied to healthy marine ecosystems." This definition suggests a process of developing management policies that integrate both consumptive and nonconsumptive uses of marine ecosystems with value judgments on what mix of uses people deem most desirable (NRC 2006).

Management policies, including ecosystem-based fisheries management, can be thought of as a mix of science and judgment and these policies represent a description of how the world works. Each of these descriptions serve as testable hypotheses from which we can construct diagnostic management experiments (e.g., adaptive management) and then compare these experiments to data to reveal the best policy (Holling 1978; Hilborn and Mangel 1997). When these management experiments are absent, we have a long history in fisheries management of constructing mathematical simulation models to evaluate various policy scenarios related to the harvest of single or multiple species, with mixed results in fishery and model performance (Pauly et al. 2002; Walters and Martell 2004; Lotze et al. 2006).

The development of ecosystem-based management policies clearly requires the development of models to test and screen proposed policy scenarios (Walters and Martell 2004) and there is growing debate about what quantitative models should be used to support decision making (Link 2005; NRC 2006; Smith et al. 2007). A range of modeling approaches to examine these policies are currently being tested, including expanded single species assessment models, whole ecosystem biomass or energy flow models (e.g., Ecopath, Atlantis), and very complex system models representing both bottom-up and top-down forces (e.g., SEAPODYM; see Whipple et al. 2000; Lehodey et al. 2003; Christensen and Walters 2004; Link 2005; NRC 2006). The range of choices can make it difficult for public agencies to invest wisely in data collection and model development to meet ecosystem-based fishery mandates (NRC 2006).

One way to develop a better sense of priorities for research investment is to look at past experience to examine why various predictions about the efficacy of particular policy choices turned out to be incorrect and to learn from our mistakes. This article offers a step in that direction by reviewing a set of case examples, where a model was proposed, an experiment carried out, and the results show that the model made incorrect predictions as to how an ecosystem would respond to a management action for various reasons. A surprising feature of these cases is that some of the most extreme failures of our expectations are in very simple systems (i.e., high mountain lakes or small ponds) where we would generally expect our ability to correctly predict ecosystem response would be high—yet the results were contrary to our expectations. Such cases are examples of highly counterintuitive dynamic responses. As governmental fisheries agencies work to meet ecosystem-based fishery mandates, the role of computer models in helping to meet these mandates has also grown. The examples we present serve as cautionary reminders by asking whether these models could have helped us foresee the counterintuitive responses observed in the examples. Our intent is not to dissuade the use of models, but instead to highlight these instances where model predictions and ecosystem responses diverged to promote improvements in model building, our understanding of basic fish ecology, and ultimately our ability to manage aquatic ecosystems.

The following section presents a wide range of case examples from freshwater and marine systems (summarized in Table 1), mainly involving direct manipulation of fish abundances or habitat factors thought to limit abundances of one or more species. We selected these examples because either we were involved in the original experiment or have experience working in very similar ecosystems. We summarize common factors that have caused simple or intuitive models to give incorrect predictions, and the implications of these factors for future development of ecosystem models as the basis for design and test of fisheries policies. We anticipate that there are many examples of these types of counterintuitive responses that are commonly viewed as management "failures," instead of as opportunities to learn from the unanticipated outcome. We hope that this article will serve as motivation to reconsider some of these unexpected outcomes in a variety of ecosystems.

EXAMPLES OF COUNTERINTUITIVE RESPONSE

The examples presented are from systems where we have close knowledge of scientific "experiments" to compare contrasting treatments (before-after or among spatial experimental units), preferably repeated (replicated) enough times to provide evidence that the apparent response was not due to factors other than treatment. These experiments cover a range or marine and freshwater lentic and lotic systems throughout North America. There are few examples in the published literature where both contrast (level of effect) and replication allow unambiguous interpretation of the data. These experiments generally break down into three cases: efforts to improve fishery performance (i.e., abundance or yield), recovering fisheries (i.e., population responses to fishery closures, gear restrictions), or habitat "improvements" (i.e., flow modifications).

CASE GROUP 1: LESSONS FROM TRYING TO IMPROVE FISHERY PERFORMANCE

Reducing brook trout density to improve growth

Study motivation

Brook trout (*Salvelinus fontinalis*) are widely introduced in alpine lakes of the Sierra Nevada Mountains, California, and can spawn successfully in most of the lakes of that region. Typically, in these and similar systems, brook trout overpopulate and deplete available prey resources, which leads to cascading effects throughout the lake foodweb on both predator and prey species (Donald and Alger 1989). If brook trout spawning is habitat limited this can lead to reduced recruitment, lower brook trout densities, higher prey availability, better growth for remaining brook trout, and improved fishing opportunities for anglers (Donald and Alger 1989).

Management action

In keeping with the evidence at hand and conventional wisdom of the time, we reasoned that lower brook trout densities would mean more food available per remaining adult brook trout (Donald and Alger 1989). During the 1980s and early 1990s, two of C.J.W.'s graduate students (Hall 1991; DeGisi 1994) did gillnet depletion experiments to reduce brook trout densities and estimate brook trout abundances in Sierra mountain lakes.

Prediction

These brook trout removal experiments were designed to test a management policy of whether regularly reducing adult brook trout densities could be used to improve brook trout growth and quality of fish for angling.

Counterintuitive response

To our surprise, there was either no growth improvement or even reduced trout growth in the years following 50%–80% density reduction in most of the lakes. Instead, there was dramatic improvement in age 0–1 survival rates, apparently due to reduced cannibalism (data available in the R. A. Myers worldwide stock-recruitment database, www.mscs.dal.ca/~myers/welcome.html). The resulting large juvenile cohorts spread widely over the lake surfaces rather than restricting their activity to littoral areas. It is highly likely these juveniles observed by DeGisi (1994) competed with adults for food resources, and that this competition resulted in much lower food availability to remain-

Table 1. Examples of case histories from a variety of freshwater and marine ecosystems demonstrating counterintuitive responses to expected management actions.

System	Management goal	Predicted response	Treatment	Counterintuitive observed response	Possible cause
Brook trout, Sierra Nevada Mountains	Increase trout growth	Reduce density, increase growth of adult brook trout	Intensive harvest	Reduced growth of adult brook trout	Increased juvenile abundance, competition with adults for available food
Rainbow trout, Bonaparte Plateau	Increase trout growth	Reduce competition	Intensive harvest	Reduced rainbow trout survival	Increased recruitment leading to density dependent mortality in early juveniles
Largemouth bass, southeastern US ponds	Maintain balance of predators and prey for sustained harvest	Increase bass yield	Increase prey abundance	Decreased yield of largemouth bass	Bass recruitment reductions due to competition with adult prey species for zooplankton
Coho salmon, Pacific Northwest	Stocking programs to increase coho salmon harvest	Increase coho salmon landings	Large-scale stocking programs	Declines in coho salmon landings	Enhanced predator abundances, declines in juvenile coho salmon survival
Sockeye salmon, Fraser River and Bristol Bay	Increased sockeye salmon harvest	Increase sockeye salmon recruitment	Increase escapement levels	Decreased sockeye salmon recruitment	Increased predator abundances, declines in juvenile sockeye salmon survival
Northern cod, Newfoundland	Restore northern cod stocks	Eliminate *F*, fishery recovers 6-60 years	16 years of fishery closure	Cod stock has continued to decline, no signs of recovery	Ecosystem now in alternative stable state that does not allow cod recovery
Red snapper, Gulf of Mexico	Decrease juvenile snapper mortality due to by-catch	Increase adult snapper landings	Restrict shrimp fisheries to decrease bycatch	Shrimp fishery may be enhancing red snapper recruitment	Reduced juvenile snapper *M* due to reductions in predators or juvenile habitat
Menhaden, Gulf of Mexico	Protect menhaden from overfishing	Clupeids highly vulnerable to overfishing	Reduce fishing mortality rate	Menhaden populations have increased over the history of the fishery	Reduced adult *M* due to high fishing mortality on menhaden predators
Coho salmon, British Columbia	Protect coho salmon spawning streams	Logging practices negatively impact coho salmon smolts	Experimental forest harvest coupled with intensive fish monitoring	Initial increase in coho smolt production following logging	Increase in coho survival from fry to smolt
Humpback chub, Colorado River, Arizona	Modify dam operations to enhance chub survival	Increases in humpback chub survival and abundance	Water flow schedules modified to stabilize mainstem flows	Declines in humpback chub survival and abundance	Declines in humpback chub survival and abundance along with concurrent increases in nonnative species (parasites, ongoing drought)
Wisconsin ponds and lakes	Prey respond to perceived predators	Behavioral response of prey different when predators are or are not present	Variety of experimental manipulations of predators-prey and access to each other	Prey demonstrate behaviors that would be expected when predators present, even when predators can not feed on prey species	Perceived risk of predation triggers overarching behavioral responses similar to predation effects

ing older fish thus negating the expected improvement in adult fish growth (Myers 2002).

Reducing a potential competitor to improve rainbow trout recruitment

Study motivation

In the Bonaparte Plateau, British Columbia, the only fish species present in some small lakes are rainbow trout (*Oncorhynchus mykiss*) and a predatory, but pygmy race (asymptotic body length around 220 mm) of the northern pikeminnow (*Ptychocheilus oregonensis*). We expected to find complex interactions between these species, such as predation on juveniles of one species by the other, which could possibly create multiple population equilibria (Carpenter 2000) of alternating adult biomass dominance between rainbow trout and pikeminnows. The key assumption for this to occur is that juvenile survival rate should increase in one species when the biomass of the other is greatly reduced, because pikeminnow and rainbow trout are possible competitors and predators based on diet observations from these lakes (N. Taylor and D. O'Brien, University of British Columbia, pers. comm.).

Prediction

Given the results from the brook trout experiments described in the first example (DeGisi 1994), we did not know whether an increase in the juvenile survival rate in one species would lead to an increase in the growth rate of the other because of uncertainty over the level of piscivory in adult rainbow trout or pikeminnow (N. Taylor and D. O'Brien, University of British Columbia, pers.comm.).

Management action

Two recent studies (Taylor 2006; D. O'Brien, University of British Columbia, pers.comm.) tested the assumption that reducing a potential competitor would increase rainbow trout biomass by massively reducing densities of pikeminnow via intensive gillnetting in four lakes and similarly reducing rainbow trout densities in another three lakes. One additional lake served as untreated "controls" for the experiment (eight lakes total).

Counterintuitive response

Mark-recapture data for years following the pikeminnow reduction indicated that juvenile rainbow trout survival rates have been lower in the pikeminnow removal lakes than in the control and rainbow trout removal lakes—exactly the opposite of our expectation. There are several possible explanations for this curious result. The simplest is that pikeminnow mainly prey on rainbow eggs and fry so that improvements (which we could not measure directly) in early life rainbow trout survival ultimately led to higher trout fry densities. These higher rainbow trout densities then led to higher density-dependent mortality rates of juvenile rainbow trout over the size-age range that the authors were able to study with tagging (Taylor 2006; D. O'Brien, University of British Columbia, pers.comm.).

Achieving "balance" in southeastern US farm ponds

Study motivation

A widely studied and difficult challenge in fisheries management, and a great example for research in basic population ecology, has been the search for "balance" in pond and reservoir ecosystems containing Centrarchid fishes from both a management (Swingle 1950; Swingle and Swingle 1967; Anderson 1973; Noble 1986) and ecosystem synthesis perspective (Werner and Gilliam 1984). In general, the objective is to understand the densities, predatory interactions, and behaviors involved that lead to producing populations of predatory basses (mostly *Micropterus salmoides*) capable of sustaining high harvest rates, while preventing overpopulation (of predators or prey) or depletion of prey resources (primarily *Lepomis*, *Dorosoma*, and *Notropis* spp.; Swingle 1950). This objective provided the basis for the construction of literally thousands of small farm ponds throughout the southeastern United States which served as replicate experiments for many early fisheries researchers interested initially interested in managing these ponds for food production and later for recreation (Swingle 1950; Noble 1986). This balancing act involves not only the fishes, but also the interaction between benthic and pelagic primary production (macrophytes and phytoplankton), with macrophytes providing needed cover for juvenile fish (Werner and Gilliam 1984) and phytoplankton providing primary production that fuels the food web components needed by those juveniles (Swingle 1950). These complexities are now interpreted using concepts like trophic cascades (Carpenter and Kitchell 1993a; Stein et al. 1996), strong impacts of behavioral response to predation risk ("indirect trait mediated effects," e.g., Peacor and Werner 2001; Werner and Peacor 2003; Schmitz et al. 2004), changes in behavior and reproductive strategies (Beard and Essington 2000), and multiple stable states where the desired "balanced" state may represent an unstable cusp between undesirable (stunted predator populations with low body condition), but persistent states (Holling 1973; Scheffer 1990; Holling and Meffe 1996; Scheffer et al. 2001).

Prediction

A "balanced" (Swingle 1950) fish community of predator and prey populations to maximize harvest is possible through top-down (regulated and experimental harvest of predators and prey) and bottom-up (fertilization, macrophyte control, forage fish stocking) control.

Management action

Efforts to teeter between two undesirable steady states, overpopulation of predators with low predator body condition vs. overpopulation of prey with low predator recruitment, have included diverse actions ranging from top-down effects related to stocking large predators (to reduce planktivores, increase zooplankton, and enhance water clarity) to large scale bottom-up treatments such as artificial fertilization to increase phytoplankton production and ultimately planktivore abundance for predatory fish. In pond systems, virtually every factor that can be beneficial can also be deleterious in high quantity. For example, extensive macrophyte development can lead to high recruitment of sunfish, which in turn leads to stunting and reproductive failure of basses through predation on their eggs and fry by the sunfish. The stocking of planktivores (e.g., *Dorosoma* spp.) to provide supplemental forage for predators such as largemouth bass can actually reduce bass populations via juvenile planktivores crashing zooplankton populations prior to juvenile bass's ontogenetic switch to zooplankton (DeVries and Stein 1990). This demonstrates that many of the intuitive steps to enhance production has the potential to cause just the opposite effect.

Counterintuitive response

After 50 plus years of experimentation, fisheries management policy in the U.S. southeast is changing from the search for long-term balance through stocking and harvest level manipulations in favor of other policy tools (Noble 2002), like habitat improvement, periodic ecosystem resets (draining or poisoning all or part of the ecosystem; Kim and Devries 2000), deliberate fluctuation of reservoir levels (Keith 1975; Ploskey 1986), and use of very different fish species combinations (e.g., minnows and bass). Yet even with these new approaches, including whole lake forage community manipulations, results counterintuitive to expectations continue to appear (Kim and DeVries 2000; Irwin et al. 2003), highlighting the difficulty of persisting between two alternative stable states (Gunderson and Holling 2002).

Predation effects without predation: impacts of predation risk on pond communities and lake ecosystems

Study motivation

All three of the previous case histories from small ponds and lakes share a common prediction and management action associated with manipulating direct effects of predation. In this case history, we examine results from small lakes where non-lethal effects of predators caused prey-populations to respond behaviorally in the same manner as if predation was occurring (Peacor and Werner 2001; Werner and Peacor 2003; Schmitz et al. 2004). These responses are nearly as high as would be expected if predation were actually occurring.

Prediction

Manipulations of fish communities such as additions or removals of a fish species can be done in experimental lakes to examine predator-prey interactions through traditional approaches, such as diet and prey selection studies and also non-traditional ways such as examining changes in predator or prey behavior. Simple predictions such as reductions in zooplankton in a small pond following high stocking densities of zooplanktivorous fishes or differing prey behavior when predators are included or excluded from prey species are often correct, but the mechanisms for these responses may be different than what was originally expected (Carpenter and Kitchell 1993b).

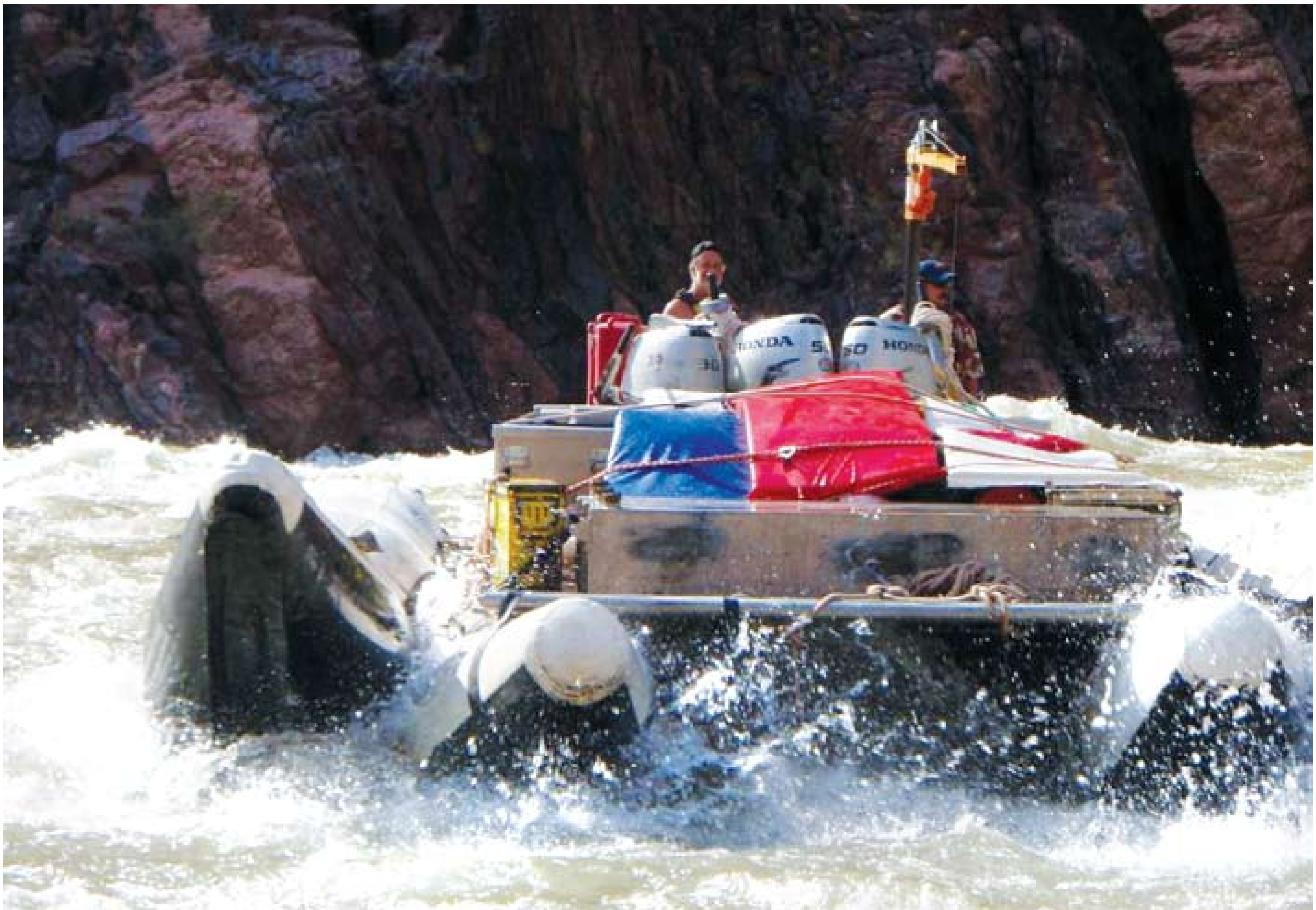
Management action

Carpenter and Kitchell (1993b) assembled a list of 32 specific predictions as part of hypothesis development for experimental lake food web manipulations (Carpenter and Kitchell 1993b). Predictions covered the full range of food web and ecosystem variables from nutrients to apex predator effects. Manipulations involved large-scale changes in food web structure through removal, manipulation, or restoration of fish populations.

Counterintuitive result

Of the 32 predictions documented by Carpenter and Kitchell (1993b), 16 were confirmed, one was equivocal, and 15 proved to be wrong, i.e., were not corroborated by the results. Most of the latter owed to unexpected behavioral responses, most often in the prey species. For example, in a small experimental lake in northern Wisconsin (Peter Lake, see Carpenter and Kitchell 1993a for description), when 90% of the largemouth bass were removed and 49,601 zooplanktivorous minnows added shortly thereafter, the minnows behaved as expected and immediately began exploiting large zooplankton as prey. That lasted about two weeks. Perception of predation risk owing to the remaining bass population rose (as measured by increased emigration rate) and by the end of the first month nearly all of the minnows were densely aggregated in refugia (beaver channels) where they gradually starved or were eaten by birds (He et al. 1993). Neither the models nor the conventional wisdom of the time were successful in anticipating these rapid and dramatic changes owing to the role of behavioral responses in food web interactions.

As a follow-up to observations of fish behavioral responses during previous experiments, He and Kitchell (1990) conducted a whole lake manipulation to measure the relative effects of behavioral responses vs. direct predation effects in a system that contained one species of potential prey fishes, but no piscivores. The lake was divided in half by installing a metal fence from surface to bottom and shore to shore. The fence allowed small fishes to pass through but not pike. Adult northern pike *Essox lucius* were added to one side of the fence in a planned "titration" of geometric increase over the course of a summer. We monitored both sides of the fence using a pre-post manipulation monitoring program to assess the prediction that potential prey would aggregate in littoral refugia and/or leave the side where pike had been added. The response was both more rapid and greater than expected. Emigration began immediately after a few pike were added and was led by those species whose size and morphology made them most vulnerable. Fish not only left the side with pike, but many left the lake through an outlet stream at the pike-free side. Pike did prey on some fishes, but over the course of the summer, emigration accounted for 50–90% of the total change in biomass for individual species when compared to direct predation effects (He et al. 1993). In these examples, neither the models nor the conventional wisdom of the time were successful in anticipating these rapid and dramatic changes owing to the role of behavioral responses in food web interactions.



Even after 20+ years of fisheries research, the highly managed Colorado River in Grand Canyon continues to offer many challenges to resource managers.

Stocking coho salmon smolts to increase harvestable abundance

Study motivation

Coho salmon (*Oncorhynchus kisutch*) have been the target of hatchery stocking programs to increase their abundance in the Pacific Northwest for over 100 years (Anderson 1997; Nichelson 2003). However, results of these stocking programs (as measured by increases in coho salmon catch) are generally poor and research efforts continue to try and understand the cause of these poor returns (Beamish et al. 1997).

Prediction

Food resources were thought to be available in ocean ecosystems to support increased coho salmon populations via intensive stocking efforts. These increased populations could then allow for increased harvest of coho salmon in West Coast fisheries (Walters et al. 1978).

Management action

The numbers of hatchery smolts released yearly in three "replicate" jurisdictions (coastal Oregon, Washington, and British Columbia) could at least double total coho salmon abundance in the ocean, absent any density-dependent survival effects (Walters et al. 1978). Early models for possible trophic impacts or limits of such high stocking rates (e.g., Walters et al. 1978) suggested that there was ample ocean food production to support the increases, even if coho feeding were limited to coastal areas near natal rivers. To take advantage of this perceived abundant ocean food supply, coho salmon hatchery releases increased in the late 1960s and 1970s.

Counterintuitive result

As these releases of coho salmon increased, total ocean coho salmon abundance (as indicated by catches) did initially increase. However, coho salmon catches soon stopped increasing and have declined dramatically in recent years (Bradford and Irvine 1999). The increases in hatchery production were also likely at the expense of both hatchery and wild adult coho salmon as measured by changes in their survival and wild coho escapement rates. If abundant food sources existed, why were there declining survival rates in adult coho salmon? The likely cause is a marine carrying capacity or limit on total adult abundance (Peterman 1991; Levin and Williams 2002). The remaining catches are now dominated by hatchery-produced fish and we now seem to be producing less coho than the natural system did, at substantial public cost. In particular, declines in coho ocean survival rate have continued well after hatchery releases stopped increasing, suggesting that progressive change in some other marine survival factor has been at least partly responsible for the decline of wild stock escapement and total ocean abundance.

Increasing escapement goals for cyclic populations of sockeye salmon to increase harvest levels

Study motivation

Analyses of stock-recruitment data for cyclic sockeye salmon (*Oncorhynchus nerka*) populations of the Fraser River and Bristol Bay led to the conclusion that the cycles might be due in part to depensatory fishing effects that prevent low cycle (abundance) lines from recovering from historical disturbances (Walters and Staley 1987; Eggers and Rogers 1987; Levy and Wood 1992; Myers et al. 1997). Later analyses supported this conclusion and led to recommendations for experimental increases in sockeye salmon escapement (reviewed in Martell et al. 2008).

Prediction

Increasing escapement rates (i.e., number of adults allowed to "escape" past the fishery and spawn) of the low-cycle lines would allow these lines to recover to historical abundances and allow for higher harvest in low-cycle years (Myers et al. 1997).

Management action

Based on the suggestions cited above, sockeye salmon escapement has increased in the largest Bristol Bay stock (Kvichak or Lake Iliamna) since the late 1980s and has also been occurring progressively for several Fraser River stocks, particularly the Horsefly (Quesnel Lake) stock. The goal of the increased escapement rates is to allow the low-cycle lines to recover to historical abundances to allow for higher harvest in low-cycle years (Myers et al. 1997).

Counterintuitive result

Initial responses to increased spawning escapement were as expected—recruitment rates increased and total sockeye salmon production was higher over each 4 or 5 year cycle. But over the last decade, there have been progressive declines in life-cycle survival rates (as measured by log[recruits/spawner]), even for spawning cycle lines that still have quite low spawner numbers. In addition, freshwater juvenile sockeye salmon body growth for the Quesnel stock is very low even in years when juvenile densities are low (when growth is expected to be high). This low growth and survival has occurred concurrently with measured increases in cladoceran copepod abundances (a key juvenile sockeye salmon food source) in Quesnel Lake, apparently associated with increases in marine-derived nutrients due to higher spawner abundances in peak years (C. Walters, personal observation). It appears that higher average abundances of juvenile sockeye (averaged over cycle lines of high and low abundance) is causing a numerical response of predators in the nursery lakes. We speculate juveniles are responding to these predators by reducing feeding and growth rates even in years when intraspecific competition is weak.

The counterintuitive response in this case is particularly worrisome since it implies not only that increased spawning abundance may fail to produce higher recruitments on a sustained basis, but also that higher stock sizes may not be attainable. It may be that the cyclic sockeye salmon populations can cause strong variation among cycle lines so as to allow nursery lake "fallow periods" analogous to crop rotation policies in agriculture (Walters and Kitchell 2001). In addition, a sequence of low sockeye years might reduce the likelihood of predator populations increasing in response to the higher abundance of juvenile sockeye as prey—thus lessening the depensatory effects of increased predation on juvenile sockeye salmon within the nursery lake.

CASE GROUP 2:
LESSONS FROM DEVELOPING AND RECOVERING FISHERIES

Restoring the Newfoundland northern cod stock through fishery closures

Study motivation

The collapse of the Newfoundland northern (2J3KL) cod (*Gadus morhuda*) stock is one of the best documented examples of fisheries assessment and management failure. Just before the fishery was closed in 1991, the remaining stock was highly concentrated and was subject to extremely high fishing mortality (Walters and Maguire 1996). Although this stock sustained intensive harvest for hundreds of years, since the closure it has shown no signs of recovery (Lily 2004).

Management action

Despite this high fishing mortality rate, virtually every assessment model for the stock predicted that it would eventually recover (Walters and Maguire 1996; Walters and Martell 2004). The key assessment models used to evaluate this recovery differed only in how fast recovery might occur. Estimates of recovery ranged from 6–8 years, based on the "millions of eggs" assumption that cod recruitment is independent of spawning stock, to 40–60 years, based on assumptions of severe recruitment overfishing and slow rebuilding of spatial stock structure (Walters and Maguire 1996).

Counterintuitive result

To date the stock has not started to recover and has even declined further since the closure (Walters and Martell 2004) which suggests the potential for multiple population equilibria (Holling 1973) and the population being trapped at low abundance. Recruitment rates remain very low, there has been a large increase in natural mortality rate of older cod, and there are few signs of reappearance of the offshore, migratory component of the stock (Anderson and Rose 2001; Lilly 2004; Olsen et al.

Research on juvenile native and nonnative fish in Grand Canyon may help researchers better predict fish population response to management actions.

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2004). Thus, in this case, there is no evidence in support of the simple and common assumption that removal or reduction in fishery mortality will cause stock recovery.

Restricting shrimp fisheries to reduce bycatch mortality of red snapper

Study motivation

Fisheries for red snapper (*Lutjanus campechanus*) and shrimp (*Penaeus* spp.) are among the most important recreational and commercial fisheries in the U.S. Gulf of Mexico (Gallaway and Cole 1999; Coleman et al. 2004). Analysis of shrimp trawl bycatch data has shown that the shrimp fishery kills large numbers of age 0–1 red snapper, on the order of 20–25 million juvenile fish per year (Gallaway and Cole 1999); in contrast, the commercial and recreational fisheries now take a total of around 2 million older snappers (NOAA SEDAR 7 2005).

Prediction

Declines in juvenile red snapper mortality through reductions in bycatch of juvenile red snapper in the shrimp fishery, will expedite red snapper stock recovery.

Management action

Recent management policy proposed by various U.S. federal fisheries management councils and agencies has been to encourage and eventually require use of bycatch reduction devices (BRDs), which are designed to substantially reduce unwanted bycatch, maintain shrimp catch rates, and greatly simplify onboard shrimp handling (Gallaway and Cole 1999). Age-structured stock assessment models for red snapper predict that these bycatch reductions will help to make the overall red snapper fishery sustainable at current catch levels, and even increase modestly. There has been some debate about whether the bycatch reduction "benefits" might be partly lost through density-dependent juvenile mortality of red snapper after the age of highest discarding, but that risk has been considered small enough to still make the BRD policy worthwhile (NOAA SEDAR 7 2005).

Counterintuitive result

Recent NMFS stock assessments for this species (NOAA SEDAR 7 2005) present a range of trends in historical recruitment patterns depending on data sources and assessment approac. Models using stock-reduction analysis techniques (Walters et al. 2006), and the full red snapper catch history from the late 1800s to the present, suggest that red snapper recruitment was possibly lower before the development of the shrimp fishery-positive recruitment "anomalies" began in the 1960s when the shrimp fishery became fully developed (NOAA SEDAR 7; Walters et al. 2006). These positive recruitment anomalies suggest that over this time period red snapper recruitment has actually been increasing rather than decreasing. How could this happen? One simple possibility could be increasing survival rates of juveniles due to declines in predators of juvenile red snapper (through direct and indirect effects of fishing). In this way, fisheries may be "cultivating" juvenile red snapper in ways that improve red snapper production through removal of predators or competitors (Walters and Kitchell 2001). Large-scale experiments including spatially closures of some areas to trawling to test these effects are currently being considered by governmental management agencies to better determine the impacts of trawl fishing on juvenile red snapper.

The curious response of menhaden in the Gulf of Mexico to fishery development

Study motivation

Beginning in the late 1940s, a large reduction fishery for menhaden (*Brevoortia patronus*) developed in the Gulf of Mexico, with peak landings approaching a million metric tons during the 1980s and peak fishing mortality rates (*F*) possibly exceeding 1.0 / y (Vaughn et al. 2000, 2007). During the 1990s, menhaden catches in the Gulf of Mexico declined, raising concerns that the stock may be overfished. Menhaden (and other clupeids) show the sort of schooling behavior that can produce strong density dependence in catchability coefficients and rapid, steep increases in *F* during stock size declines, similar to the cod example (Hilborn and Walters 1992).

Prediction

Through a combination of an intense fishery and schooling behavior of menhaden, Gulf of Mexico menhaden fisheries are likely to be overfished.

Management action

Based on experience with other clupeid stocks (i.e., British Columbia herring *Clupea pallasii pallasii* and Peruvian anchovies *Engraulis ringens;* Hilborn and Walters 1992), conventional fisheries experience would typically assume that this stock had likely already been overfished and had declined substantially in recent years.

Counterintuitive result

In a bizarre reversal of typical population responses to harvesting, the Gulf menhaden stock has apparently increased through much of the history of the fishery. Juvenile survey data and catch-at-age models indicate a general upward trend in recruitment since the fishery started (Vaughn et al. 2007). Analysis of the catch-at-age data in Vaughan et al. (2000) indicate that the total mortality rate Z of age 1+ menhaden has actually declined over time, causing a negative regression relationship between Z and fishing effort. One simple explanation for these patterns is that the natural mortality rate M decreased while the fishery was developing; the apparent decrease in M is roughly correlated with decreases in stocks of some major predatory fish, particularly red snapper and groupers (family Serranidae), which were likely caused by fishing—again a cultivation effect (Walters and Kitchell 2001) where fishers are removing natural menhaden predators, causing a decline in menhaden natural mortality.

CASE GROUP 3: LESSONS FROM HABITAT "IMPROVEMENT"

Protecting coho salmon Oncorhynchus kisutch *from impacts of logging*

Study motivation

Throughout the Pacific Northwest, intense debate over the impacts of stream habitat changes caused by logging (siltation, loss of bank cover, channel destabilization, increased nutrients and temperature) has led to the creation of a variety of experimental treatments where logging practices have been prescribed and carried out, and then salmon populations within the watershed closely monitored to discern possible impacts (Holtby 1988; Brown 1994).

Prediction

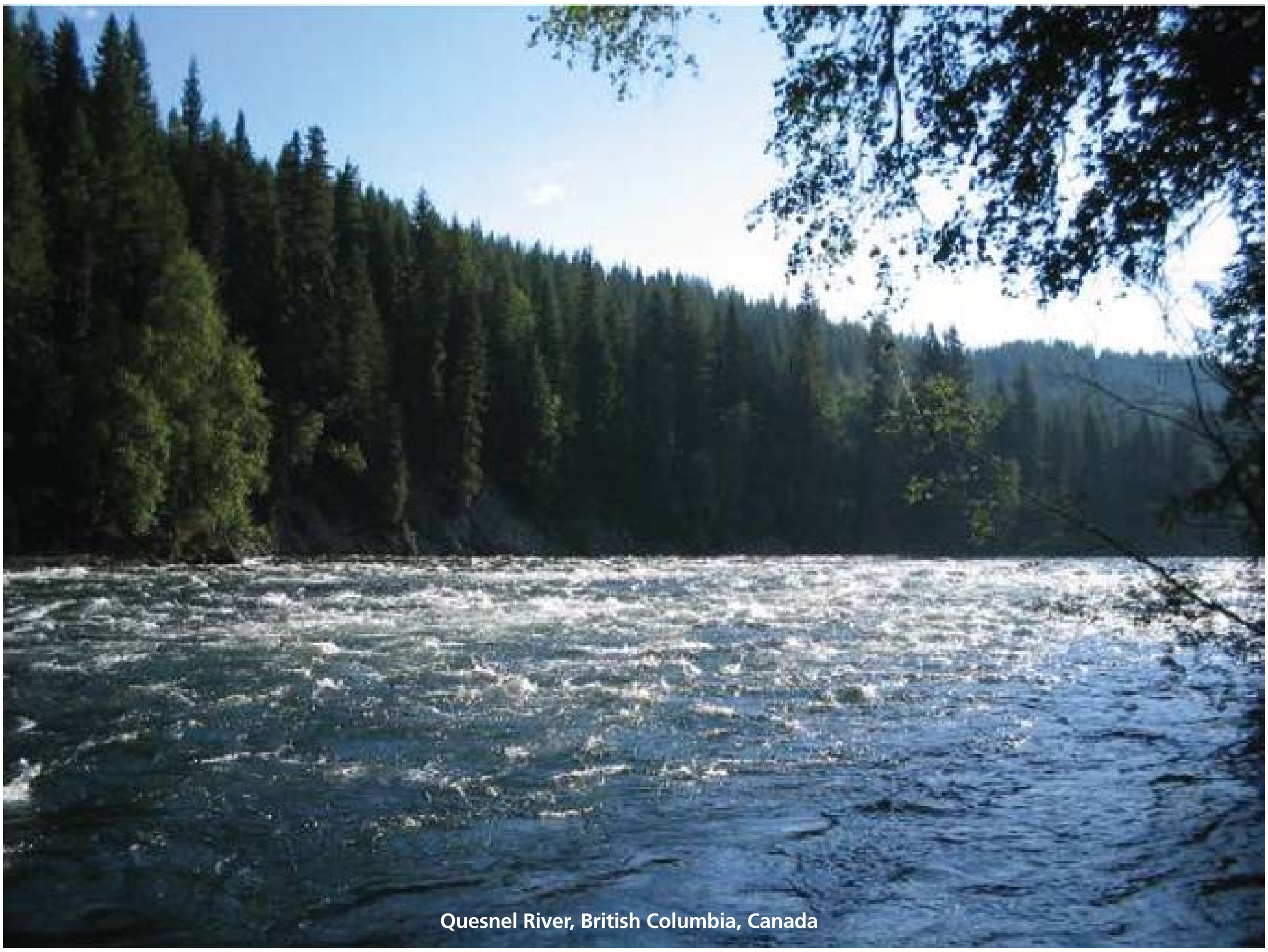
Governmental management agencies and researchers have expressed concern that that deleterious habitat changes caused by logging such as changes in temperature and sedimentation could result in negative effects to fish populations within the logged watershed (Holtby 1988).

Management action

In the early 1970s, an experimental program was initiated on Carnation Creek, British Columbia, to demonstrate impacts of logging on coastal watersheds and salmon (Hartman and Scrivener 1990; Hartman et al. 1996). The watershed was logged in a careful sequence, while closely monitoring stream habitat variables and anadromous fish abundances.

Counterintuitive result

The expected changes in egg-fry survival were observed, but surprisingly there were responses by different salmonid species. For example, out-migrant chum fry (*Oncorhynchus keta*) and steelhead smolts declined after longing, but coho salmon smolt output increased, rather than the expected decrease (Hartman and Scrivener 1990). This meant there must have been a very substantial increase in juvenile coho survival from the fry to smolt stage, and/or increased proportion of juveniles smolting at age 1 rather than 2 (Holtby 1988). These positive effects have been attributed to increased growth caused by warmer water (Holtby 1988). Similar responses have been observed in other experimental watershed studies (Thedinga et al. 1989), indicating that this may be an important area for additional cooperative



Quesnel River, British Columbia, Canada

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research between forest and fisheries management interests—at least with regard to coho salmon—to develop management practices that allow for sustained use of forest and coho salmon resources.

Managing Colorado River flows to restore the endangered humpback chub

Study motivation

The construction and operation of Glen Canyon Dam on the Colorado River turned the river in Grand Canyon from a warm, turbid, strong seasonally fluctuating ecosystem into a cold water ecosystem with large diurnal variations in water flow (Gloss et al. 2005). At least one population of the endangered humpback chub (*Gila cypha*) managed to survive the initial impacts of the dam, likely because it had potadromous behavioral specialization to spawn in a major tributary (Little Colorado River, LCR) with at least some of its juveniles rearing entirely in the LCR (Gloss et al. 2005). Humpback chub population viability has also become one of the centerpieces of a large management program designed to protect the ecological, cultural, and recreational resources of Grand Canyon (Gloss et al. 2005). A key component of the ecological research has been efforts to determine how physical (e.g., cold water, modified flows) and biological (e.g., introduced species) changes in the mainstem Colorado River impact or limit humpback chub populations. In an effort to track humpback chub population responses to management actions such as flow modifications or non-native species removal, an intensive fish tagging and monitoring program was initiated in 1989 to monitor trends in recruitment, adult survival, growth, movement, and abundance of humpback chubs in Grand Canyon (Gloss et al. 2005; Coggins et al. 2006; Coggins 2008a,b).

Prediction

The Glen Canyon Dam Adaptive Management Program was initiated to work with stakeholder groups to develop management plans for the operation of Glen Canyon dam to maximize benefits to resource users and aid in the recovery of the endangered humpback chub. Because of the wide range of cultural, ecological, and recreational values of stakeholders affected by Glen Canyon dam, much research has gone into developing dam operations policies that minimize the conflict between objective functions for each user group (Gloss et al. 2005).

An example policy was carried out in 1991 when modified low-fluctuating flows policy (MLFF) was tested to improve habitat for native fishes and create better recreational conditions for camping beaches in Grand Canyon. This flow policy severely restricted diurnal flow variations in hopes of reducing the impact of flow variation on native fishes by “improving” habitat for juveniles (by creating and stabilizing backwater areas which are warmer than the mainstem river) and adults (by stabilizing mainstem flows; Gloss et al. 2005; Follstad Shah 2007). The expectation was that by improving habitat for native fish, humpback chub populations would begin to increase and eventually be downlisted from the endangered species list.

Counterintuitive result

Humpback chub recruitment estimates from the tagging program, along with catch rate indices from long-term monitoring based on netting, indicate that humpback chub recruitment did not increase following implementation of MLFF, and may have declined (Coggins et al. 2006). Within a few years after implementation of MLFF, exotic salmonids (rainbow trout and brown trout *Salmo trutta*) increased in the Colorado River mainstem around the mouth of the LCR, possibly due to improved nearshore habitat conditions for non-natives coupled with downstream dispersal of rainbow trout from a large tailwater population just below Glen Canyon Dam (Gloss et al. 2005). In 2003, an experimental "mechanical removal" program (intensive electrofishing) was initiated as part of a 16-year experimental plan to test humpback chub population responses to flow experiments, non-native fish removals, and experimental increases in diurnal flow variations. The first of these tests was to remove nonnative fish as a test to see if these exotics were preventing the use of the mainstem Colorado River as a humpback chub juvenile rearing area (Gloss et al. 2005; Melis et al. 2006; Coggins 2008a,b). This program was designed to separate the effects of modified flow regimes from that of exotic trout or changes in water temperature (either experimentally or naturally via drought) on humpback chub populations (Melis et al. 2006; Coggins 2008b).

The sudden, unexpected decline in humpback chub recruitment immediately following the habitat "improvement" (MLFF) may have been purely accidental or a result of a range of factors including hydrology (Valdez and Ryel 1995), temperature (Coggins 2008a), or parasites (Hoffnagle et al. 2006). But there is little doubt that the predator increase has made the mainstem reach near the LCR a much more hostile environment for juvenile chub despite more favorable water flow conditions which helped to motivate the mechanical removal experiment. Index netting and early tag recapture data for chub cohorts produced after mechanical removal have started to show promising signs of recruitment increase (Melis et al. 2006; Coggins 2008b).

IMPLICATIONS FOR ECOSYSTEM MODELING AND MANAGEMENT

Modeling approaches for assessing policies for ecosystem-based management reviewed by NRC (2006) included linking trophic interactions of a few key species within an ecosystem (Punt and Butterworth 1995), simple biomass dynamics models parameterized using methods like Ecopath with Ecosim (EwE; Walters et al. 1997; Whipple et al. 2000; Koen-Alonso and Yodzis 2005), and complex size-age structured models like MSVPA/MSFOR (Anderson and Ursin 1977; Gislason 1991; Sparre 1991; Magnusson 1995; Collie and Gislason 2001). These kinds of ecosystem models have huge data requirements which do not necessarily reduce the uncertainty in their predictions, but could they have helped us foresee the counterintuitive responses observed in the case-histories we reviewed? Are these ecosystems we reviewed much more complex than we thought or do we need to develop a better understanding of how these ecosystems work before they can be effectively managed in a desired state?

There are several common denominators in the case histories we reviewed. Most counterintuitive responses involved unexpected changes in juvenile survival rates, primarily through changes in predation, recruitment (brook trout case history from the Sierras), or behavior (small lake fish communities in Wisconsin). Most case histories also involve changes in trophic interactions, predominantly changes in predation mortality (or threat of predation) on small fishes. None of the case histories we reviewed, except perhaps the initial recruitment decline of humpback chub, appear to involve subtle details of population genetics, bioenergetics, ecophysiology, or habitat modification. The common thread of changes in behavior, recruitment, and changes in survival patterns of juveniles are all intraspecific processes that were not anticipated and are not explicitly considered in single-species assessment models widely used by fisheries managers (Hilborn and Walters 1992).

Unexpected changes in juvenile mortality rates are particularly worrisome from the standpoint of developing more useful ecosystem models to screen policy options. The assumptions about early life survival and recruitment in many multispecies virtual population analysis models (VPA) are either not explicitly described (Jurado-Molina and Livingston 2002), or these models use simple stock-recruitment relationships to describe patterns in the multi-species virtual population analysis (MSVPA) recruitment estimates (Sparholt 1995; Vinther et al. 2001), which may not be able to adequately capture changes in juvenile survival. Other approaches like Ecosim, a component of the Ecopath software (www.ecopath.org; Christensen and Walters 2004), do allow for the use of multi-stanza size-age dynamics that permits the examination of juvenile mortality patterns. Ecosim can also be used to examine and make predictions about specific life history stages that may be particularly sensitive to changes in predation regimes or habitat factors (Walters and Martell 2004; NRC 2006), although the ability of the program to predict a complex ecosystem response to management policies continues to be evaluated (Walters et al. 2005; NRC 2006).

How well would the modeling approaches discussed above and those reviewed by NRC (2006) have done in making the correct predictions in the case histories we reviewed? While it is simple to incorporate different mortality rates for different fish life stages in the model, it is extremely difficult to partition these rates among the factors (i.e., predation, cannibalism, etc.) that we suspect typically cause them. The reason for this difficulty is simple but discouraging: juvenile fish biomasses are typically very small compared to the biomasses of the larger organisms that eat them, so juveniles typically contribute only a very tiny proportion of total predator diets. Such low diet proportions are typically ignored by ecosystem model developers since they may not appear "important" for the predator. Even rigorous diet studies have a low likelihood of capturing such low proportions in situations where predation is known to be a strong regulator of recruitment success (Post et al. 1998). This point has been understood for many years in relation to detecting impacts of cannibalism

(Sheperd and Cushing 1990), but it applies equally well to all predators that may cause changes in juvenile mortality rates.

If an ecosystem model were able to correctly make the predictions observed in these case histories, would a fishery manager or management council have taken those predictions seriously? How would the model predictions have fared in debates about whether to proceed with the experiments? Would having the "right" models as part of the decision making process of whether to conduct the experiment—or in the case of ecosystem based fisheries management, whether to implement a certain policy—change the decisions that were made? Would (or should) decision makers have abandoned Occam's razor in favor of the predictions from complex models? The idea of developing a hypothesis (a conceptual model), designing an experiment around the hypothesis, and then verifying the hypothesis through analysis, testing, and formal model development is certainly not new (Walters 1986; Hilborn and Mangel 1997). It has long been argued that the main value of modeling exercises is to help in designing better "research" programs aimed specifically at documenting possible causes of policy failure (Holling 1978; Walters 1986; Walters and Martell 2004).

There is no simple solution to the question of whether to trust mathematical models we build, or our intuition as to which management policies will be best to meet the stated objectives. Models can be made more elaborate, and data collection can be intensified, but doing only one or the other has both risks and costs. We suggest that the iterative process of conjecture (model building) and testing (experimental data collection) could have helped managers to recognize the two common features in the case histories we reviewed. First, it appears that behavioral responses accelerate and intensify interaction rates that might be too simply represented in biomass or population modeling efforts and would be difficult (if not impossible) to derive from controlled laboratory or mesocosm studies. Testing for behavioral and multi-trophic level ("mini-ecosystems") responses is readily conducted in the laboratory or in mesocosms, but estimation of its role in nature is most appropriate if evaluated at the ecosystem scale (Carpenter 1996). An understanding and representation of behavioral responses such as vulnerability exchange parameters in foraging arena theory is critical in the development of ecosystem models (Walters and Martell 2004). These behavioral responses are clearly demonstrated in the responses of prey to predator risk in the examples we provide (e.g., bass and minnows in northern Wisconsin). Capturing these dynamics with ecosystem models will likely reduce the predator-prey instability common in some ecosystem models, and make appropriate corrections for model predictions that produce higher potential population sizes based on crude, large-scale estimates of prey abundance and production (Walters and Martell 2004).

Second, it appears that both field studies and modeling efforts should focus more on the causes of mortality in juvenile fishes, suggesting a need for researchers to consider a broader range of alternative hypotheses about juvenile recruitment mechanisms. Several of our case histories (brook trout examples from the Sierras, red snapper and menhaden from the Gulf of Mexico) identified unexpected changes in survival patterns of juveniles as a likely reason for the counterintuitive response that was observed. This is not to say that less attention should be focused on other research concerns (e.g., factors regulating larval fish abundance). Instead, we see a need for research on juvenile life stages, simply because while larval fish are subjected to a myriad of uncontrollable and stochastic effects on their survival, selection has favored behavioral responses in juvenile fishes that foster their survival even though they are highly vulnerable to piscivory because of their small size (Walters and Juanes 1993).

We feel that the most instructive outcomes for improving learning and policy development have derived from combinations of two activities. The first are critical evaluations of expected vs. observed outcomes, where we examine the ecosystem response to our management action and compare this response to our prediction. The common thread in our case histories of changes in juvenile survival rates and behaviors could be tested in this framework as alternative hypotheses when management actions do not follow predictions. This approach could lead further research into changes in juvenile fish survival rates or lead to the discovery of other ecosystem interactions which we are not aware of and/or are not including in our current models. This simple exercise is rarely reported in the literature but offers important insight regardless of the management outcome. Second, whole system manipulations often have the potential to produce outcomes at ecosystem scales similar to the scale natural selection has operated on in the past. Whole system manipulations that can include mortality or selective removal caused by fishing (Law 2000) or whole system management actions (e.g., large ecosystem restoration, Florida Everglades) are a force unlike that experienced in the evolutionary history of fishes. Clearly, the most instructive manipulations are those that create the strong contrast required for maximum learning opportunities at the scale pertinent to fishery policy development. In short, fisheries management actions, and the counterintuitive responses that sometimes occur following these actions, should be viewed as a tool that can teach us about both fish population dynamics and the ecosystem context that supports them.

ACKNOWLEDGEMENTS

Financial support for this work was from a Natural Sciences and Engineering Discovery grant to C. J. W., and National Science Foundation and Wisconsin Sea Grant grants to J. F. K. We are especially indebted to N. Taylor and D. O'Brien for directing us to surprising findings in the Bonaparte Plateau study, L. Coggins and M. Allen for thoughtful discussion on these examples, Jared Flowers for the photographs, and to V. Christensen for help with modeling.

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