

APPENDIX D



Promoting the Science of Ecology

Why are Quantitative Relationships between Environmental Quality and Fish Populations so Elusive?

Author(s): Kenneth A. Rose

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WHY ARE QUANTITATIVE RELATIONSHIPS BETWEEN ENVIRONMENTAL QUALITY AND FISH POPULATIONS SO ELUSIVE?

KENNETH A. ROSE

Coastal Fisheries Institute and Department of Oceanography and Coastal Sciences, Wetlands Resources Building, Louisiana State University, Baton Rouge, Louisiana 70803-7503 USA

Abstract. Despite the ecological and economic importance of fish, fisheries management has generally failed to achieve its principal goal of sustainability. Management is hindered because most exploited fish are long-lived species that utilize a variety of habitats and exhibit high interannual fluctuations in abundance. Effective management requires that we understand how natural and anthropogenic sources of variability in abiotic variables (termed environmental quality [EQ]) affect fish population dynamics. Quantifying the effects of anthropogenic changes in EQ on fish populations has remained elusive and controversial. I illustrate, with examples, six issues related to quantifying EQ effects on fish populations. These examples also serve as demonstrations of how modeling can be used to address these issues. The six issues are: (1) detectability—high interannual variation and interaction effects among climatic variables that affect population dynamics make isolating effects of individual stressors difficult; (2) complex habitat and nonintuitive responses—spatial heterogeneity in habitat can result in population responses that are disproportionate to the changes in EQ; (3) regional predictions—biological realism is often sacrificed unnecessarily when broad spatial scale predictions are needed; (4) community interactions—too little attention is paid to how community-level interactions can affect population-based analyses; (5) sublethal effects—sublethal effects are often ignored but can have large effects on population dynamics; and (6) cumulative effects—the combined effect of multiple stressors can be much different than expected from the sum of their individual effects. Examples include a variety of freshwater and marine species. Quantifying EQ effects on fish populations can be improved by considering these issues in analyses, and by taking a true multidisciplinary approach that combines individual-based modeling and life history theory.

Key words: *environmental quality; fish; fisheries; habitat, and pollution; individual-based models; life-history theory; multidisciplinary studies; population dynamics.*

INTRODUCTION

Fish are important ecologically, economically, and as a source of animal protein. Despite the importance of fish and the enormous efforts devoted to the monitoring and analysis of their populations, fisheries management has failed to achieve one of its principal goals: sustainability (Botsford et al. 1997). More than 66% of commercially harvested fish stocks worldwide are considered exploited to a heavy or greater extent; 22% of these are considered either overexploited or depleted (Garcia and Newton 1997). Recreational fishing in freshwaters may also be close to exceeding sustainable levels, as evidenced by the widespread use of management practices to limit harvest (e.g., Shramm et al. 1995) and of stocking to augment natural populations (e.g., Fenton et al. 1996).

Aspects of fish life histories create management problems. Most exploited fish are long lived, utilize a

variety of habitats over their lifetimes, and exhibit large interannual fluctuations in abundance. Long-lived species tend to have delayed maturation (Winemiller and Rose 1992), and thus are unable to rebound quickly from overharvest or other dramatic increases in mortality. Many years are required before newly produced young mature and contribute to the spawning stock. Complete manifestation of the long-term effects of increased mortality during early life stages, or decreased fecundity of adults, requires multiple generations, which can span decades.

Many fish species use a variety of habitats and can migrate over long distances. Many coastal species use estuaries for spawning or nursery areas. Anadromous species migrate from the open ocean through estuaries to spawn in the freshwater portion of tributaries. Although their migrations are not as extensive, many freshwater species use tributaries or the littoral zone for spawning and nursery areas. The variety of habitats used makes it difficult to identify and protect critical habitats, and these habitats can involve multiple management jurisdictions.

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Marine and estuarine fish populations are notorious for exhibiting wide interannual fluctuations in recruitment and abundance (Rothschild 1986, Fogarty et al. 1991). Often, much of the variation in abundance results from variability in hydrographic and climate-related variables that affect the very sensitive prerecruit life stages (Shepard et al. 1984, Rose and Summers 1992, Laevastu 1993). Freshwater fish populations also exhibit large variations in recruitment and abundance, with biological interactions probably playing more of a role in the postlarval life stages that are less sensitive to environmental conditions (Houde 1994). High "natural" variability, which is often unpredictable beyond the next year, creates havoc for managers trying to balance a healthy population with the constant, dependable harvest desired by anglers.

Effective management requires that we understand how abiotic conditions (which I refer to collectively as environmental quality [EQ]) affect fish populations. Much of the interannual variation in fish populations arises during the first year of life because of variation in abiotic variables. Early life history stages, especially the first year of life, are often considered to be the time when recruitment is at least coarsely established for many marine species (Sissenwine 1984, Rothschild 1986, Houde 1987, Fogarty et al. 1991; but see Bradford 1992). Abundances of early young-of-the-year (YOY) life stages (e.g., eggs and larvae) tend to be both highly variable from year to year and uncorrelated with their abundances as adults some years later. In contrast, abundances of post-YOY life stages tend to be correlated with their subsequent adult abundances. For freshwater species, the idea that recruitment may be set during YOY life stages is not as widely embraced. However, the literature is full of examples of the strong influence of abiotic variables on first-year survival of freshwater species: for example, water-level fluctuation effects on centrarchids (e.g., Milzner 1991) and temperature effects on percids (Koonce et al. 1977). Early life stages of most fish species exhibit high growth and mortality rates (Houde 1987, Pepin 1991), and are very sensitive to changes in environmental conditions (e.g., McKim 1985). Thus, understanding how EQ affects YOY survival is critical for predicting population dynamics and effective management. Knowing how populations respond to variation in EQ would allow for early detection of unhealthy populations, for identification of the causes, and for the targeting of remediation actions.

In this paper, I highlight six issues that confound efforts to quantify the effects of anthropogenic changes in EQ on fish populations. These issues are: detectability, complex habitat and nonintuitive responses, regional predictions, community interactions, sublethal effects, and cumulative effects. Many of these issues have been discussed by others in general terms. My aim is to emphasize their importance by illustrating

each with specific examples from personal experience. I intend these quantitative illustrations to define the problems clearly, and also to show how modeling, carefully performed, can be used to address these issues. It seems appropriate to illustrate difficulties in quantitative estimation with quantitative examples. I conclude with a discussion of how better to quantify EQ effects by taking a multidisciplinary approach that combines individual-based modeling and life history theory.

Several caveats are necessary. To demonstrate the general applicability of the issues, I selected examples from a variety of fish species from estuaries, reservoirs, streams, and lakes. While the examples all involve fish, I suspect the issues are also relevant to other organisms. I warn the model-wary reader that I focus on selective aspects of model results, rather than on the rationale or validation of each model. I refer the reader to the original publications for detailed model descriptions and validation results.

Almost all of the examples presented use individual-based modeling. Individual-based modeling offers a promising approach for modeling population and community dynamics (DeAngelis et al. 1994), and has features that should help in quantifying EQ effects on fish. Representing local interactions in space, size-based interactions, episodic effects, movement, and stochasticity is relatively easy in individual-based models (DeAngelis and Rose 1992, Tyler and Rose 1994). EQ effects are often expressed as individual responses. These effects can be imposed directly in individual-based models, and the model can then scale these effects to the population and community levels.

ENVIRONMENTAL QUALITY

I define EQ for the purposes of this paper to be the suite of abiotic variables that either exert a direct effect on individuals of the population of interest, or cause an indirect effect via directly affecting the population's competitors, predators, or prey. Abiotic variables considered here include water temperature, water velocity, water depth, contaminants, substrate type and size, and dissolved oxygen (DO) concentrations, all of which can influence the many processes affecting the growth, mortality, and reproductive rates of individuals. Direct effects of abiotic variables can include limitation of spawning, reduced growth, increased mortality, and altered movement patterns. An example of an indirect effect included as part of EQ would be increased temperature increasing the foraging activity of a predator, resulting in higher mortality on individuals of the population of interest.

Although many abiotic variables can vary as a result of both natural and anthropogenic causes, my focus is on anthropogenic changes in EQ. Contaminant exposure, altered flow regimes, and thermal discharges are obvious examples of anthropogenic changes in EQ.

However, not all anthropogenic effects are seen through changes in EQ. For example, harvest can directly remove adults without changing EQ. Also, the introduction of an exotic species that alters the food base of the population of interest technically would not affect EQ because no abiotic variables were altered.

Quantifying environmental quality

The goal of quantifying EQ effects on fish populations has been elusive and controversial. It has been elusive because of the high degree of interannual variation in abundance resulting from complex interactions among the many factors that affect fish reproduction, growth, and survival. This variability often appears as "noise" to investigators and resource managers, making the measurement and detection of the effects of individual factors difficult. Rose and Summers (1992) showed how interactive effects among environmental factors were important contributors to interannual variation in the abundances of estuarine fish stocks. Thus, for example, the effects on population size of changes in temperature during months of spawning differed depending on the magnitude of freshwater flow. Interactions confound simple one-factor-at-a-time analyses; they imply that partitioning variation to a single factor requires long data records, including observations under the many different possible combinations of conditions.

While the general need to quantify EQ effects on fish populations is undisputed, controversy often plagues case-specific analyses. The high uncertainty associated with many quantitative analyses puts resource managers in a difficult position. Managers must decide among various options, each vehemently favored by different stake-holder groups, but with low confidence of how the different options will affect future population trajectories. Analyses performed by the various interested parties that are based on alternative, but equally valid assumptions, often yield very different predictions of population consequences. Even when population-level effects can be demonstrated and agreed upon, remediation actions are not typically forthcoming. Often the nonquantifiable ecological, economic, or societal importance of the fish population is weighed against the easily expressed and typically high monetary costs of remediation actions (e.g., construction of cooling towers on power plants) or lost revenues due to changed operations (e.g., foregone hydropower generation due to minimum flow requirements).

Striped bass as an example

Striped bass (*Morone saxatilis*) serves as the archetypical example. Striped bass are long-lived (maximum age of ~17 yr), use estuaries for spawning, and are heavily exploited both by commercial and recreational fisheries. Their population dynamics are dominated by density-independent environmental factors (Cooper

and Polgar 1981, Uphoff 1989). Striped bass populations declined dramatically during the 1970s and 1980s in Chesapeake Bay and the Sacramento-San Joaquin river system. Much effort and debate were associated with the relative contributions to these population declines of water quality (acid rain or eutrophication) and fishing in Chesapeake Bay (Goodyear 1985, Coutant and Benson 1990), and of changes in prey composition, reduced adult survival, and increased mortality related to water diversions for agricultural usage in the Sacramento-San Joaquin river system (Stevens et al. 1985). An enormous amount of research and monitoring was performed to isolate the cause of the striped bass population declines (e.g., see CDFG 1987 Hall 1991). Yet there has never been a complete resolution of the causes of the declines. Both harvest and water quality were strongly regulated in the Chesapeake Bay, resulting in a recovery of striped bass. The debate continues for the Sacramento-San Joaquin population (e.g., W. J. Kimmerer, J. H. Cowan, L. W. Miller, and K. A. Rose, *unpublished manuscript*; K. A. Rose, J. H. Cowan, L. W. Miller, D. E. Stevens, W. J. Kimmerer, and R. Brown, *unpublished manuscript*), which remains depressed.

Striped bass in the Hudson River were also the center of controversy during the 1980s. The population-level effects of early life stage mortality from power plant entrainment and impingement were hotly debated (Barnthouse et al. 1984). Millions of fish were killed at the power plants, and electrical utilities were faced with the expensive prospect of having to convert power plants to closed-cycle cooling to minimize entrainment. Utilities and regulatory agencies both funded the development of models to express entrainment and impingement losses on striped bass populations. Barnthouse et al. (1984) concluded that "After more than a decade of study and tens of millions of dollars, it was still not possible to draw definitive conclusions about the long-term effects of entrainment and impingement on fish populations in the Hudson River . . . We believe that it (lack of success) occurred because of insufficient understanding of the underlying biological processes (affecting population dynamics)."

ISSUE 1: DETECTABILITY

High interannual variation in fish populations makes isolating EQ effects difficult. Much of the variation in population abundances arises from variable survival during YOY life stages. YOY fish exhibit high mortality rates and are extremely sensitive to abiotic conditions. Interaction effects among variables are often important, greatly reducing the statistical power of straightforward correlation-based analyses.

I use a time-series analysis of estuarine fishery landings and a model analysis of the effects of polychlorinated biphenyls (PCBs) on largemouth bass (*Micropterus salmoides*) recruitment as two illustrations of the

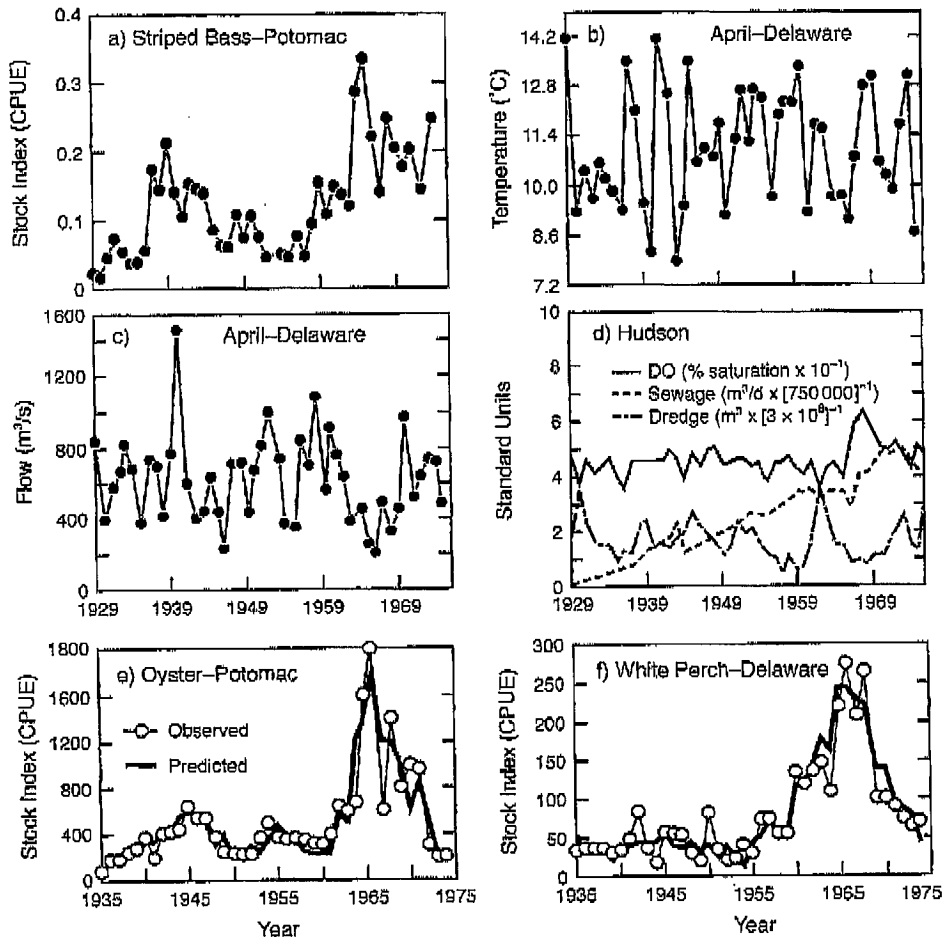


FIG. 1. Examples of typical catch-per-unit-effort (CPUE), temperature, freshwater inflow, pollution-related variables, and predicted and observed CPUE of well-modeled species from the time-series regression analysis (Rose et al. 1992): (a) striped bass CPUE in the Potomac River, (b) April inflow in the Delaware River, (c) April temperature in the Delaware River, (d) annual dissolved oxygen, sewage loading, and volume dredged in the Hudson River, (e) predicted and observed CPUE of oyster (*Crassostrea virginica*) in the Potomac River, and (f) predicted and observed CPUE of white perch (*Morone americana*) in the Delaware River.

difficulties in detecting EQ effects. The time-series analysis shows the importance of interactive effects among abiotic variables in affecting population dynamics. Both the time-series analysis and the PCBs-effects model demonstrate the difficulties in detecting EQ effects under conditions of high natural variability.

Example 1: multispecies CPUE

Rose and Summers (1992) used categorical time-series regression to partition variation in catch-per-unit-effort (CPUE) of a variety of exploited estuarine species between hydrographic and pollution-related variables. CPUE was assumed to be an index of population abundance. Annual CPUE data from 1929 to

1974 for 53 stocks (19 species in five estuaries) were formulated from available catch and effort records. Monthly water temperatures and freshwater inflows for each of the estuaries, and a monthly index of wind direction and speed at offshore stations near each estuary, were estimated from available data. Annual pollution indices were determined for each estuary: sewage loading (adjusted by sewage treatment level), dissolved oxygen (DO) concentrations, and volume of material dredged. Examples of typical CPUE, temperature, freshwater inflow, and pollution-related variables are shown in Fig. 1a-d. Examples of well-modeled CPUE time series are shown in Fig. 1e and f.

Interactions were important in affecting annual

April 2000

FISHERIES, HABITAT, AND POLLUTION

371

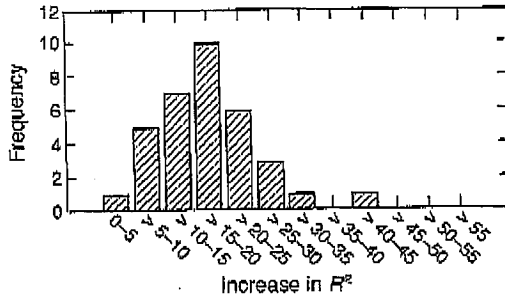


FIG. 2. Frequency histogram of the 30 values of the increase in R^2 attributable to pollution-related variables for the 30 stocks whose annual CPUE was well modeled (total model $R^2 > 0.55$) by time-series regression. The increase in R^2 attributable to pollution is after the variation in CPUE attributable to hydrographic and stock variables has been statistically removed (Rose et al. 1992).

CPUE, and the incremental variability in CPUE explained by pollution-related variables was relatively small. Of the 30 well-modeled stocks ($R^2 > 0.55$), interactions were important in 26 stocks, 20 stocks had significant interactive effects involving variables that were not important as main effects, and 5 of the 30 stocks had final models that involved interaction effects only. Once the variation attributable to hydrographic and stock effects was removed, pollution-related variables accounted for significant but small (typically 15%) additional variations in CPUE (Fig. 2).

Example 2: largemouth bass and PCBs

Jaworska et al. (1997a) predicted the effects of PCBs on first-year growth and survival of largemouth bass using coupled PCB effects and individual-based models configured for southeastern U.S. reservoirs. The model followed the daily spawning, development, growth, and survival of YOY largemouth bass until October (end of the growing season) in a length of littoral zone. Mating was size based, with the largest males pairing with the largest females. Eggs, yolk-sac larvae, and swim-up fry were associated with their natal nest; upon reaching 20 mm (end of swim-up stage), individuals became juveniles and dispersed from the nest, mixing with other juveniles from other nests. Growth was based on daily bioenergetics, with the realized daily consumption rate dependent on random encounters with an array of size classes of zooplankton and benthos prey. Mortality rate was fixed for eggs and yolk-sac larvae and decreased with increasing length for later life stages. Temperature-induced desertion of the nest by the guarding male resulted in loss of individuals associated with the nest.

Monte Carlo simulation was used to simulate realistic interannual variations in the number of survivors until October. A variety of model inputs, including the initial number of spawners, water temperature, prey

densities and timing, and predation-related mortality, were varied based on empirical data for reservoirs. The frequency distribution of predicted October abundances was similar to that observed for Chickamauga Reservoir (Fig. 3a), a well-studied reservoir in the Tennessee River system. The lognormal-like shape of the recruitment frequency histogram (thick-tailed to the right) is common to many fish species (Hennemuth 1979, Myers et al. 1995). PCB effects were imposed as increased mortality and decreased growth, which were dependent on specified tissue concentrations of PCBs. Although median predicted October abundances decreased with increasing concentrations of PCBs, predicted distributions overlapped substantially (Fig. 3b). According to this model, samples sizes needed to statistically detect significant differences in mean October

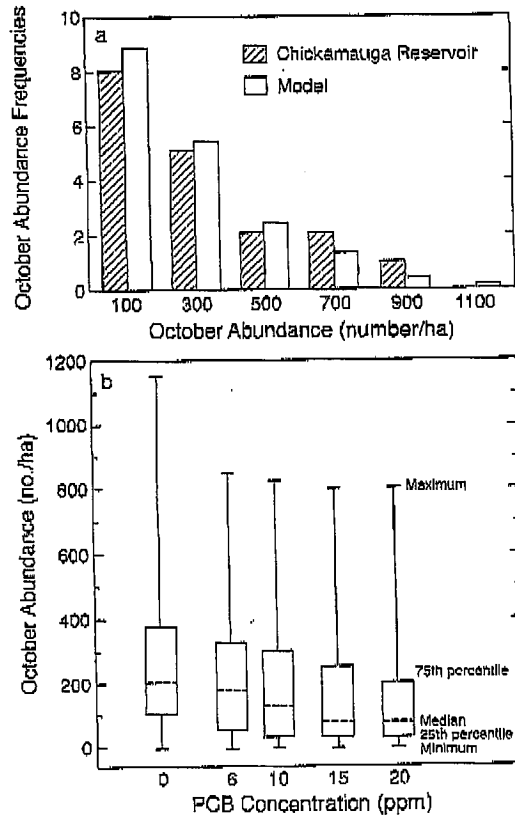


FIG. 3. Predicted effects of PCBs on October abundances of largemouth bass based on an individual-based YOY model (Jaworska et al. 1997a). Monte Carlo simulation was used to vary model inputs to mimic realistic interannual variation. (a) Frequency histogram of model-predicted and observed (from Chickamauga Reservoir) October abundances. (b) Predicted percentiles, minimum, and maximum October abundances under baseline (0 ppm), 6, 10, 15, and 20 ppm of PCBs.

abundances (t test, $\alpha = 0.05$, $\beta = 0.2$) between baseline (0 ppm; parts of PCB per million parts of fish biomass) and PCBs simulations were 300 samples for 6 ppm, 92 samples for 10 ppm, 47 samples for 15 ppm, and 32 samples for 20 ppm. These sample sizes represent the number of years over which October abundances would need to be measured, under both baseline and PCB-effects conditions, to detect a statistically significant difference in mean abundance values.

Results of detectability examples

The time-series analysis and PCBs examples demonstrate alternative ways of dealing with the low-detectability problem. The time-series analysis showed the value of cross-species comparisons and of the tailoring of statistical methods to the specifics of the available data. The problems with CPUE data are notorious, but detecting pollution effects on long-lived species requires long data records that exceed the duration of most monitoring programs. We developed our own version of time-series regression that treated the highly uncertain data as categorical (high or low) and dealt with multiple lags that arise from multiple age-structured populations. Although it requires more work, statistical methods should be adapted to the available data, rather than the data being forced to fit into standard statistical methods. Our confidence in the results was increased by the consistency of results with life history differences among the species. Such reality checks on the statistical results are only possible in comparative analyses that involve many species. The PCB-effects example demonstrated that Monte Carlo methods can be used to portray realistic natural variation in models. One can then impose known stresses and determine the detectability of their effects. Such information can be used to distinguish between a true lack of effects and a lack of power to detect effects.

ISSUE 2: COMPLEX HABITAT

Complex spatial heterogeneity in habitat can result in nonintuitive population responses. We often are tempted to extrapolate population responses under the belief that improved EQ is always beneficial. However, the relationship between population response and EQ can be dome-shaped rather than increasing monotonically. Also, population responses are not necessarily proportional to the changes in EQ. Small changes in EQ can result in large population responses, and large changes in EQ can lead to small population responses.

The first example uses effects of dissolved oxygen (DO) on predator-prey interactions in a vertically stratified water column to illustrate that increasing EQ (DO) does not always lead to increased larval survival. The second example uses survival of spiny lobster (*Panulirus argus*) from settlement to emigration to illustrate that large EQ effects (massive algal blooms) can result in unexpectedly small population-level responses. Ex-

amples that will be presented under Issue 5 (Sublethal Effects) below illustrate the converse: small EQ effects can sometimes lead to large population-level responses.

Example 1: low DO and larval fish survival

Breitburg et al. (1999) simulated the interaction between low DO concentrations and predation on larval fish survival in a vertically stratified water column. The model water column was configured based on extensive experimental and field data from the Chesapeake Bay. The prey fish was based on naked goby (*Gobiosoma bosc*). Three types of predators were simulated: sea nettle (*Chrysaora quinquecirrha*), fish sensitive to DO, and DO-tolerant fish. The water column was divided into three layers: surface, pycnocline, and bottom. The daily growth, survival, and movement of individual goby larvae were followed in the model for 30 days from hatching. Larval survival was determined based on encounters and successful captures by individual predators. Encounter rates and capture success depended on the swim speeds and lengths of the prey and predators. Movement among the surface, pycnocline, and bottom layers was updated daily by randomly assigning individual prey and predators to layers based on specified proportional densities.

The model was formulated so that DO concentrations affected larval growth rates, predator capture success, and the vertical distributions of prey and predators. All baseline parameter values were based on high (no-effects) DO levels. Larval growth rates were specified to decrease with decreasing DO concentrations. Sea nettle capture success was specified to increase, while fish predator capture success decreased (more so for the sensitive fish predator), with decreasing DO concentrations. Proportional densities by layer were specified to shift individuals from a distribution proportional to the water volume in each layer (corresponding to high DO concentrations) to distributions reflecting individuals progressively avoiding the bottom layer with decreasing DO concentrations (Fig. 4). DO concentrations in the surface layer were always set to no-effects levels. DO concentration in the pycnocline layer depended on the concentrations specified for the bottom layer (3 mg/L when bottom layer was 0 mg/L, and 4 mg/L when bottom layer was 0 or 1 mg/L). Thirty-day simulations were performed for four bottom-layer DO concentrations, three water-column configurations (shallow, intermediate, and deep) that had increasing proportions of the water column assigned to the bottom layer, and four predator combinations.

One unexpected result of the model predictions was that the highest survival generally occurred at intermediate DO concentrations (Fig. 5). Highest DO did not usually lead to highest larval survival. The 3 to more than 10-fold variations in larval survival predicted across bottom DO concentrations resulted from DO effects on the spatial overlap of prey and predators.

April 2000

FISHERIES, HABITAT, AND POLLUTION

373

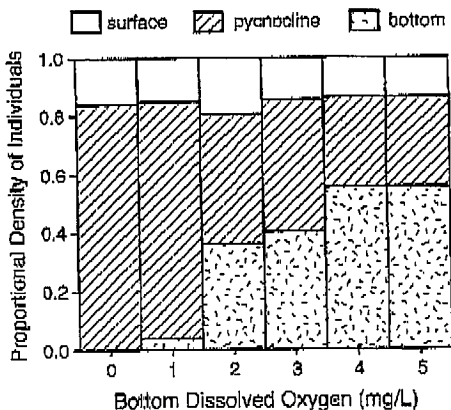


FIG. 4. Proportional densities in each of the surface, pycnocline, and bottom layers of the water column based on bottom DO concentration (from Breitburg et al. [1999]). The values shown were used for larvae (the prey) and the tolerant fish predator.

These results were obtained without the usual phenomenon of increased production of the lower trophic levels caused by eutrophication, and without any hypoxia-induced mortality.

Example 2: spiny lobster

M. J. Butler, J. H. Hunt, W. F. Hernkind, and K. A. Rose (unpublished manuscript) simulated spiny lobster

survival in Florida Bay from the time of settlement to emigration ~18 mo later. Lobster postlarvae settle in sea grass (*Thalassia testudinum*) beds and then move to crevices. Sponges are the major source of crevices; recently, algal blooms have caused massive die-offs of sponges (Butler et al. 1995).

The daily growth (molting), survival, and movement of individuals was simulated in a 7 × 35 grid of cells configured for the strip of Florida Bay bordering the Florida Keys. Each cell was characterized by specified percentages of different habitats (sponges, solution holes, other shelters, and open space). Incoming post-larval lobsters arrived with each new moon, and each lobster was assigned an initial cell based on known settlement and water movement patterns in Florida Bay. Daily growth was based on temperature. On each day, lobsters left their shelters to forage and then competed for preferred shelters upon their return. Mortality was dependent on shelter type. A suite of size-based rules was used to simulate the complex behaviors of developing lobsters. Empirical estimates of total annual influxes of postlarvae from 1988 to 1996 were used to drive the model. Algal blooms were simulated by reducing abundances of loggerhead and other sponges in selected grid cells based on their exposure duration. The 1991 bloom lasted ~3 mo and involved ~10% of the grid cells; the 1992 bloom lasted ~7 mo and involved ~20% of the grid cells. No regrowth of sponges was permitted.

Predicted population abundances showed surprising-

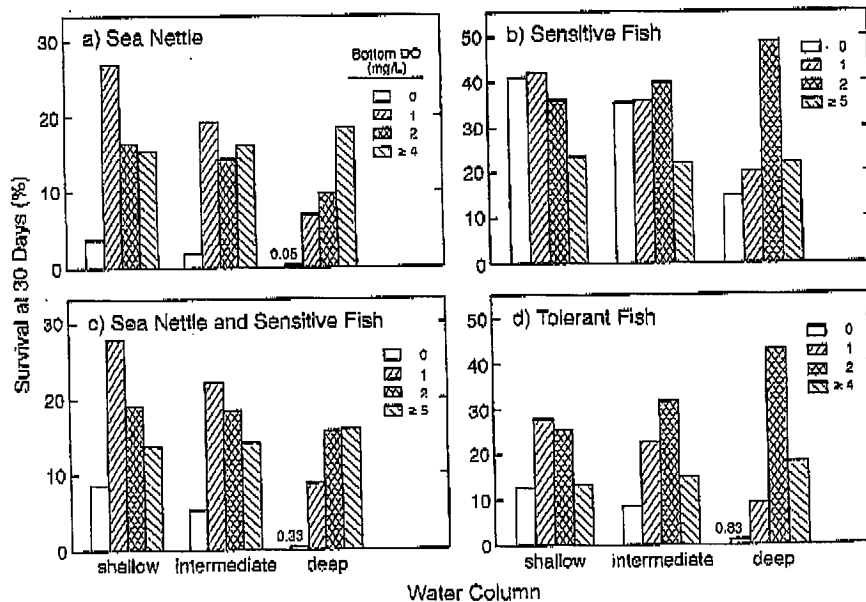


FIG. 5. Predicted larval cohort survival to 30 d for four predator combinations (a-d), three water column configurations (shallow, intermediate, and deep), and four levels of bottom DO based on an individual-based predator-prey model (Breitburg et al. 1999): (a) sea nettle, (b) sensitive fish, (c) sea nettle and sensitive fish, and (d) tolerant fish.

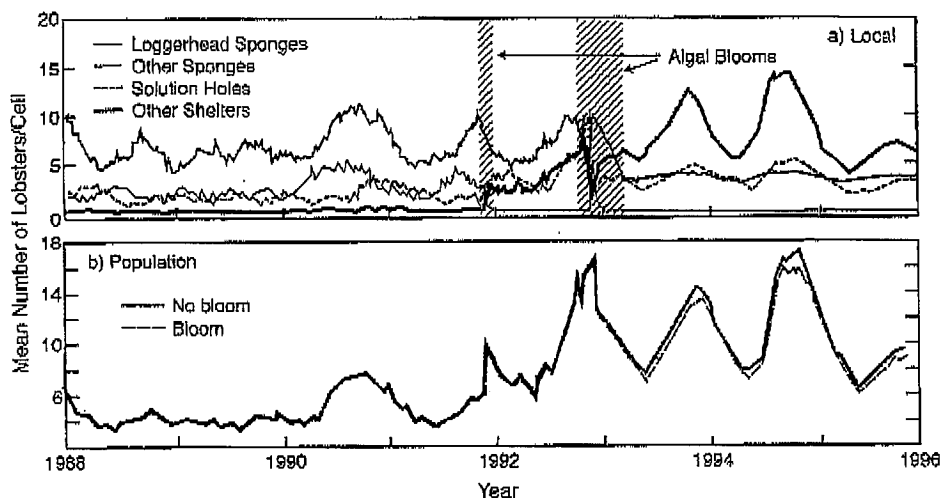


FIG. 6. Predicted spiny lobster densities from postlarval influx (settlement) to emigration in Florida Bay from 1988 to 1996 based on an individual-based lobster recruitment model (M. J. Butler et al., unpublished manuscript). The shaded periods show when algal blooms that removed sponges in selected cells of the model grid were simulated. (a) Lobster densities in each of the habitat types in cells in the vicinity of the algal blooms. (b) Population densities (i.e., sum over all habitats and cells) for simulations with and without algal blooms.

ly remarkable resilience in response to massive losses of sponges (Fig. 6). Simulated algal blooms caused dramatic shifts in the shelter types used by lobsters in cells in the vicinity of the algal blooms (Fig. 6a). However, when summed across all cells, population densities were similar in simulations with and without algal blooms (Fig. 6b). The observed influx of postlarval lobsters based on field data was unusually high for the years just after the algal blooms. A similar small population response was also predicted by the model when postlarval influxes were set to their historical average value for the years during and after the blooms.

Results of complex habitat examples

The examples provided by the DO effects on larval fish survival and the spiny lobster generated believable counterintuitive results. Both models benefited from extensive laboratory experiments and field monitoring that predated the modeling effort. In both cases, the empirical scientists accumulated a wealth of data that addressed many of their specific questions, but they also recognized the limits to empirical monitoring. To their credit, they realized that addressing some of the larger questions required a modeling approach that would complement and synthesize their extensive laboratory and field data. The resulting modeling efforts benefited from close collaboration between the empirical and modeling researchers: the empiricists learned some things about their data and system not obvious from field monitoring, and the modelers had access to natural history information (not available in published

papers) that enabled the development of more realistic models.

ISSUE 3: REGIONAL PREDICTIONS

Many analyses of fish focus on the population level for pragmatic reasons. With a population-level focus comes the tendency toward single-site analysis. For some EQ effects, however, a single-site analysis is not always appropriate. For example, studying how global climate change will affect species distributions requires regional- or landscape-level analyses involving multiple, site-specific populations. The tendency has been to sacrifice biological realism within populations in order to predict effects on multiple populations spread over broad geographic areas. Simple habitat models, rather than population dynamics models, generally have been used to predict global climate change effects on fish distributions (e.g., Meisner 1990, Kelcher and Rahel 1996). I argue that with the computing capabilities available, one does not need to sacrifice realism in order to make regional predictions. The growing use of geographic information systems (GIS) and geo-referencing of data will enable regional predictions with realistic population dynamics models.

Example: trout and watersheds

M. E. Clark, K. A. Rose, D. A. Levine, and W. Hargrove, (unpublished manuscript) coupled a detailed, individual-based model of brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) population dynamics with a GIS database to predict effects

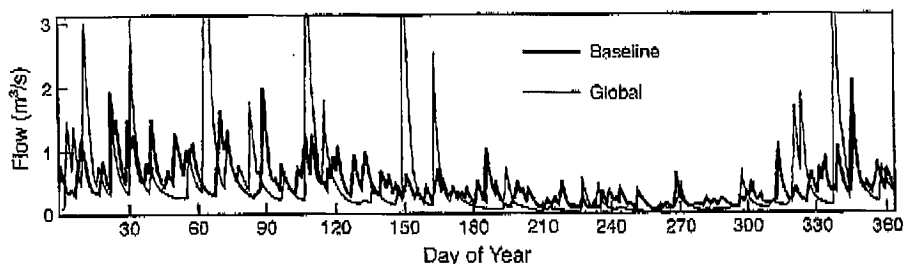


FIG. 7. Daily water flows for a typical year under baseline and global-climate-change conditions used in the individual-based model of brook and rainbow trout population dynamics (M. E. Clark et al., unpublished manuscript).

of global climate change on trout abundances for all streams in the Southern Appalachian plateau. Brook and rainbow trout compete for space and prey in Southern Appalachian streams. The model followed individuals of both species through their lifetimes on a daily time step (Clark and Rose 1997). A baseline stream representative of typical fourth order streams in the Southern Appalachian plateau under today's climate conditions was configured from available data. The baseline streams consisted of a series of connected pools, runs, and riffles. Daily flow was specified; velocity and depth were computed from flow for each cell for each day. Redd site selection, feeding rates, movement, and mortality depended on trout life stage, length, and growth rate. Feeding rate was determined by location in the stream (larger individuals were assigned better feeding sites) and by flow effects on rates of downstream drift of insect prey.

The Southern Appalachian plateau was divided into 34 watersheds, and each watershed was split into three elevation bands. Every stream was not modeled. Instead, simulations were performed for representative streams in each watershed using modified versions of the baseline stream, and predicted trout abundances were scaled up to the watershed level. The baseline stream was adapted to representative streams by adjusting daily temperatures, daily flows, and slope based on stream order and watershed characteristics. Seasonal adjustments to the daily water temperatures used to adapt the baseline stream to representative streams in each watershed-elevation band were derived from an extensive air temperature database in the GIS. The task of deriving seasonal multipliers of flow to adjust daily flows in model simulations was more complex. Each stream was first assigned a stream order number (1-6) based on the branching patterns of streams in the watershed using GIS-based software; the total lengths of each stream order were then computed with the GIS. The effective watershed area draining the average stream of each stream order in each watershed-elevation band was then computed using a complex hydrological routing algorithm. The algorithm had to account for some streams originating or terminating within an elevation band, and for the contribution of streams

that originated in higher elevation bands of the same watershed.

The trout model was used to predict the 30-yr average rainbow and brook trout densities (number per meter of stream) for each stream order for each watershed-elevation band combination. Total trout abundances were then obtained by multiplying densities by the total lengths of each stream order. Global climate change was simulated as increased temperatures and altered daily flows. Daily temperatures were increased by 1.5°C in summer, by 2°C in spring and fall, and by 2.5°C in winter. Daily flows were modified to simulate more temporally clumped and higher extreme values of both high-rainfall events and drought periods (Fig. 7).

Trout example results

Predicted changes in abundances between baseline and the global climate change scenario were complex. I show the results for brook trout only (Fig. 8); an analogous map of changes in abundance was obtained for rainbow trout. There was considerable variation in the direction and magnitude of predicted changes both among elevation bands within watersheds and among watersheds. One pattern we observed was that most of the decreased brook trout abundance was predicted for low-elevation streams, while increased brook trout abundance was generally predicted for high-elevation streams (Fig. 9).

M. E. Clark, K. A. Rose, D. A. Levine, and W. Hargrove, (unpublished manuscript) examined these results in more detail, and added a more realistic relationship between redd loss and water velocity to better account for the effect of higher flows under the global change scenario. They showed that forecasts based on the population model differed from those based on simple static changes in potential habitat. Simulated changes that included a water-velocity based mortality on redds resulted in a 10% reduction in region-wide brook trout abundance and a 24% reduction in rainbow trout abundance. In contrast, a static measure of trout habitat, defined as the total length of streams with average summer water temperature $\leq 19^{\circ}\text{C}$, exhibited an 80% reduction under climate change. While many simplifying

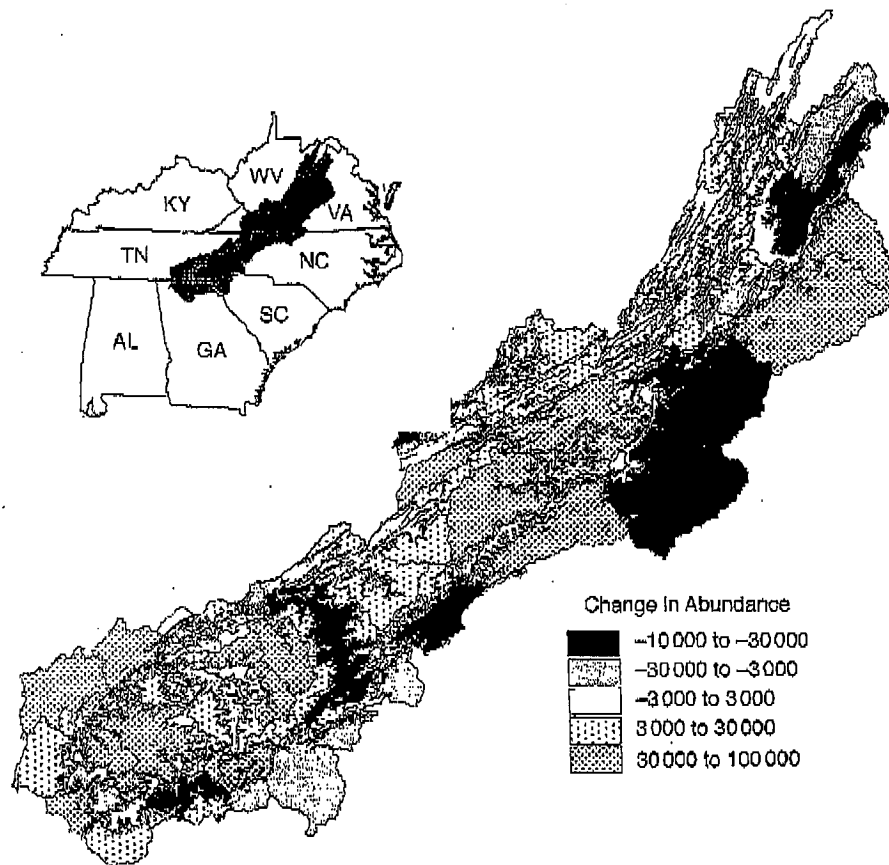


FIG. 8. Predicted changes in brook trout abundances between global-climate-change and baseline (present-day) conditions for each watershed-elevation band of the Southern Appalachian plateau (M. E. Clark et al., unpublished manuscript). Abundance was computed as the total number of trout in each watershed-elevation band. The GIS was used to define temperature, water flows, and stream geometry of representative order 1–6 streams as input to a daily time-step, individual-based model of brook and rainbow trout. Mean predicted abundances from 30-yr simulations of the representative streams were then extrapolated to the watershed scale using total stream lengths computed by the GIS.

assumptions were made, the analysis demonstrates that realistic population dynamics models can and should be used to generate regional-scale predictions.

ISSUE 4: COMMUNITY INTERACTIONS

Most analyses are conducted on populations, even though populations rarely exist in isolation. Uncertainty in interspecific interactions usually deters the performance of analyses on communities. There has been the belief that we have enough difficulty modeling population dynamics without also attempting to represent interspecific competition and predation. Yet population responses can be greatly influenced by community-level interactions (see review in Rose et al. 1996).

I use a predator–prey model to illustrate how community interactions can affect population responses to an increase in metabolic rate typical of the sublethal

effects of many contaminants. The daily spawning, growth, and mortality of individuals of yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) were followed throughout their lifetimes (Rose et al. 1999). Adult walleye predation is the major source of mortality on YOY juvenile and yearling yellow perch. Although the model contained only two species, the predator–prey interactions represented were complex (Table 1). The model was developed and corroborated using an extensive 35-yr database collected on Oneida Lake, New York (Mills and Forney 1988).

The model was run in population and community modes (Jaworska et al. 1997b). The community mode corresponded to a two-species model in which predation on yellow perch was dependent on walleye dynamics. The population version removed walleye from the model; mortality rates of YOY juvenile and year-

April 2000

FISHERIES, HABITAT, AND POLLUTION

377

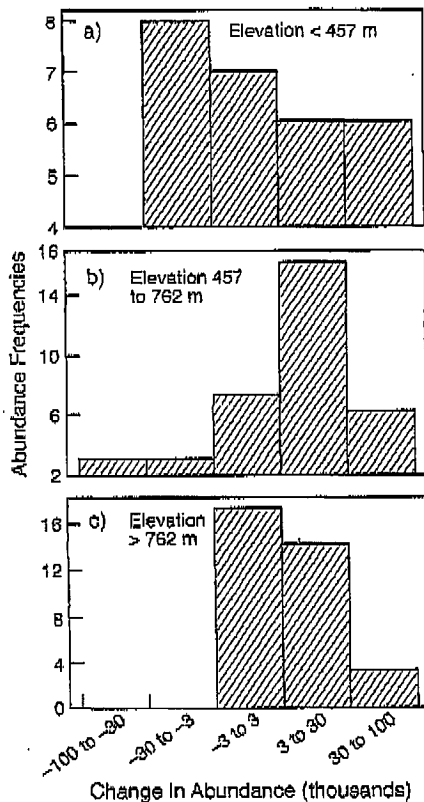


FIG. 9. Frequency histograms of predicted changes in brook trout abundances between global-climate-change and baseline (present-day) conditions by elevation band: (a) elevation < 457 m; (b) elevation 457–762 m; (c) elevation > 762 m. The frequency histograms were constructed by aggregating the predicted changes in brook trout abundances specific to each watershed–elevation band shown in Fig. 8.

ling life stages of yellow perch (usually eaten by walleye) were set to average values from the baseline simulation of the community version. In both modes, the metabolic rate of juvenile yellow perch was increased by 20% to mimic sublethal effects of a contaminant. Four 100-yr simulations were analyzed: baseline and 20% increase in metabolism for each of the population and community versions. The percentage change in average values (computed over the 100 yr) of a variety of prediction variables between the 20% increase in metabolic rate simulation (Y) and the baseline simulation (Y_B) was computed as $100 \times (Y - Y_B)/Y_B$. Percent changes were compared between the population and community versions.

Inclusion of a dynamic predator (walleye) in simulations reversed the effects of increased metabolism on yellow perch population abundances. Increased metabolism caused a 10% decrease in adult yellow perch abundance in the population model, but a 55% increase in the community model (Fig. 10). In the population model, increased metabolism caused the expected decrease in mean length of age-1 yellow perch, reduced survival to recruitment age (due to increased overwinter mortality), and resulted in fewer recruits, adults, and spawners. Shorter age-1 mean lengths were also predicted in the community model, but juvenile-to-recruitment survival (juvenile = 20 mm) increased greatly, resulting in higher yellow perch recruitment. Density-dependent responses of reduced adult (age-5) growth, and of associated delayed maturation and reduced fecundity (eggs per spawner), were not sufficient to offset increased recruitment, and adult yellow perch abundances increased. The higher juvenile-to-recruitment survival of yellow perch resulted because shorter age-1 yellow perch provided less biomass of prey for walleye. Less prey biomass led to increased cannibalism, and reduced walleye growth led to delayed maturation, lowered fecundity, and reduced egg produc-

TABLE 1. Predator–prey interactions defined in the individual-based yellow perch–walleye population dynamics model by nonzero vulnerability factors (Jaworska et al. 1997b; Rose et al. 1999).

Prey	Predator						
	Yellow perch			Walleye			
	Larval	YOY and yearling	Adult	Larval	YOY	Yearling	Adult
Zooplankton	+	+	+	+	‡		
Benthos		†	+	+	+	+	+
Forage fish					+	+	†
Larval perch				+	+	+	
Larval walleye				+	+	+	
YOY perch			+		+	+	+
YOY walleye					‡	+	+
Yearling perch						+	+
Yearling walleye						+	+

Note: YOY are juvenile young-of-year exclusive of larvae (i.e., YOY > 20 mm in length).

† Yellow perch > 30 mm.

‡ Walleye < 100 mm.

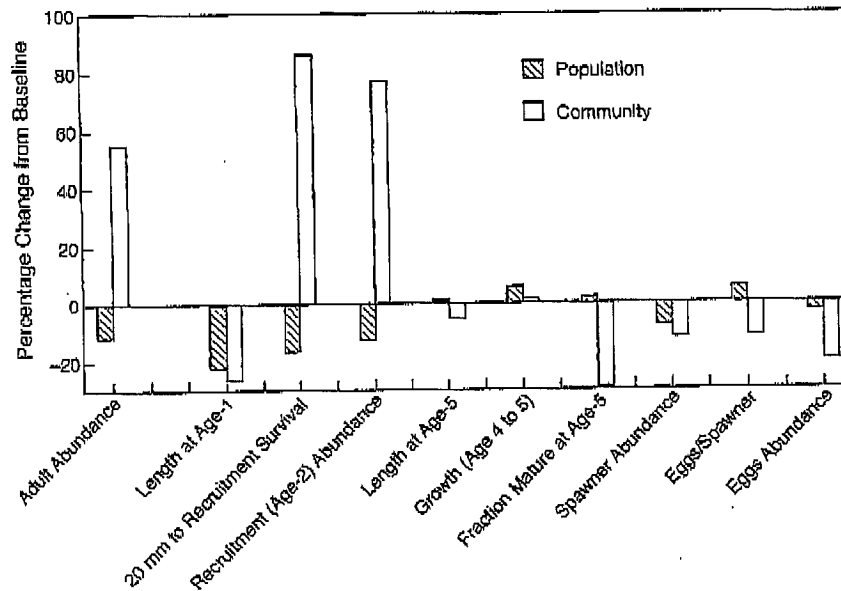


FIG. 10. Predicted changes in a variety of yellow perch variables between the baseline simulation and a simulation with a 20% increase in juvenile yellow perch metabolism for the population and community versions of the individual-based model of Oneida Lake (Jaworska et al. 1997b). The population version uses fixed mortality rates of YOY juvenile and yearling yellow perch, while the community version simulates mortality based on the dynamics of walleye. Adults are defined as age-2 and older individuals. Length and fraction mature of age-5, and growth from age-4 to age-5, are shown as representative of adult dynamics.

tion. Increased mortality of YOY walleye and reduced egg production resulted in lower walleye abundances and lower predation mortality of YOY and yearling yellow perch.

The predator-prey model enabled direct comparison of a yellow perch response to increased metabolism under population vs. community conditions. While such manipulation is of obvious theoretical interest, the results also have practical implications. The extensive database on Oneida Lake permitted us the luxury of developing a complex and dynamic predator-prey model, and predictions for Oneida Lake would certainly be based on the community version of the model. But many other systems are data limited, resulting in the development of population models, with predators (or prey and competitors) treated as nondynamic, static entities. The Oneida Lake example demonstrated that, while population models are often pragmatic, populations are embedded in food webs and predictions from population models should be viewed with some caution.

ISSUE 5: SUBLETHAL EFFECTS

Sublethal effects of changes in EQ can be important. Sublethal effects are often ignored, or discussed but not included, in analyses. While the possible population effects of mortality are obvious, population-level

consequences of many sublethal effects are less clear. Resource managers and regulators usually can be convinced that some sublethal effects, such as reduced growth, are important. However, the vast majority of other sublethal effects, such as developmental deformities, altered biochemical composition, or behavioral responses (Atchison et al. 1987, von Westernhagen 1988, Little et al. 1993) are difficult to directly link to changes in growth, survival, or reproductive success.

Two previous examples already presented also illustrate the potential importance of sublethal effects of changes in EQ. Behavioral effects of DO on predator-prey interactions caused 3- to more than 10-fold differences in predicted larval fish survival (Fig. 5). Increasing yellow perch metabolism by 20% led to a 55% increase in their long-term average abundance in a community model (Fig. 10).

A third example is a simulation of how changes in larval striped bass growth rate and prey-capture success can affect striped bass recruitment. Rose et al. (1993) imposed a variety of EQ-related effects on a YOY model of striped bass in the Potomac River. Daily spawning, development, growth, and mortality were simulated. Growth depended on random encounters of striped bass with various zooplankton types and size classes of benthos prey. Once encountered, probability of successful capture determined the number encountered that were

April 2000

FISHERIES, HABITAT, AND POLLUTION

379

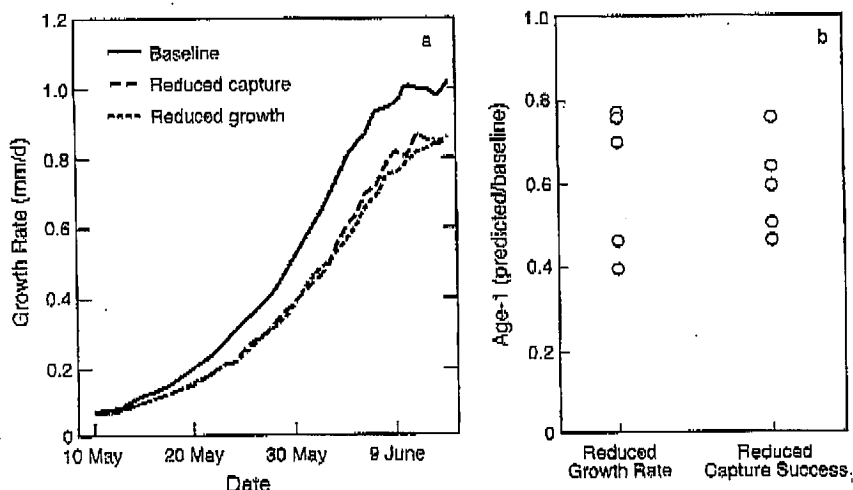


FIG. 11. Predicted growth and survival to age-1 of striped bass under baseline, reduced growth rate, and reduced prey-capture success scenarios based on the Potomac River version of an individual-based model (Rose et al. 1993): (a) daily growth rate of the 10 May day-cohort, and (b) predicted number of survivors to age-1 divided by the baseline number of survivors for five replicate simulations that used different random number sequences.

eaten. Encounter rate and capture success increased with striped bass length.

In addition to baseline conditions, one-year simulations were performed with reduced larval growth rate and reduced capture success. Reduced growth is an obvious sublethal effect of many stressors; reduced capture success has been reported for a variety of species exposed to contaminants in the laboratory (Mathers et al. 1985, Morgan and Kiceniuk 1990). Predicted number of survivors to age 1 (recruitment) under reduced growth or capture success was divided by predicted number under baseline conditions. Simulations were repeated five times using different random number sequences.

As illustrated by the 10 May cohort for one of the simulations (Fig. 11a), realized reductions in growth rates were relatively small (0.5 mm/d under baseline, compared to 0.45 mm/d for reduced growth and 0.47 mm/d for reduced capture success). Yet the effects of reduced growth rate and capture success on predicted recruitment varied greatly among simulations (Fig. 11b); predicted recruitment varied from ~80% to almost 40% of baseline.

These three examples demonstrate that sublethal effects can have potentially large effects on population-level variables. Predicting the population consequences of such sublethal effects requires models that can be linked to the processes and subprocesses associated with the sublethal effects. For example, scaling from reduced prey-capture success of an individual to recruitment and population dynamics requires a way to translate changes in capture success into changes of model inputs that relate to growth and survival. An

individual-based approach provides a straightforward way to link changes in individual characteristics and rates to population and community responses. While the three examples used here included sufficient detail to allow sublethal effects to be imposed as direct changes of model inputs, this may not be the case in other situations. One could envision an individual-based model of a particular life stage or process that would act as a bridge model between the sublethal effect and the model inputs of a matrix projection or other population dynamics model. The bridge model would convert sublethal effects into changes in the values of inputs to the population dynamics model.

ISSUE 6: CUMULATIVE EFFECTS

EQ and other factors are often analyzed singly, ignoring their cumulative effects. Populations are often faced with multiple stressors that cause simultaneous changes in EQ. The cumulative effects of multiple stressors can differ greatly from the sum of their independent effects. Multiple stressors can result in larger or smaller cumulative effects than expected, depending on how they interact with each other. Stressors that act synergistically would increase effects, while those that act antagonistically would diminish cumulative effects.

Example 1: Sacramento and San Joaquin river system striped bass

Striped bass population dynamics in the Sacramento River-San Joaquin river system were simulated using an individual-based YOY model coupled to an age-structured adult model (K. A. Rose, J. H. Cowan, L.

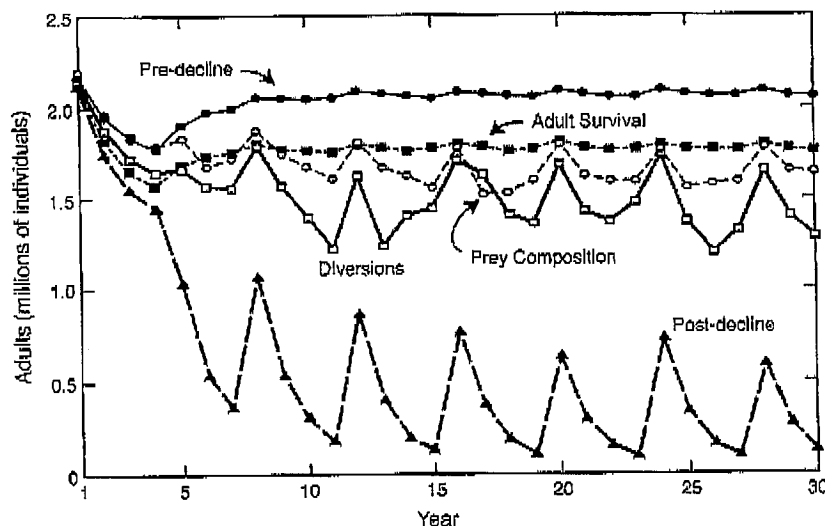


FIG. 12. Annual adult (age-3 and older) abundances from 30-yr simulations of the Sacramento-San Joaquin river system striped bass population model with prey composition, diversion mortality, and adult survival all at pre-decline values, each changed singly to its post-decline value, and all changed to their post-decline values (K. A. Rose, J. H. Cowan, L. W. Miller, D. E. Stevens, W. J. Kimmerer, and R. Brown, unpublished manuscript).

W. Miller, D. E. Stevens, W. J. Kimmerer, and R. Brown, unpublished manuscript). The model was developed to evaluate the likely causes of striped bass population decline. The striped bass population has been declining over the past several decades, and a variety of causes (including reduced food, increased diversion of water for agricultural use, and reduced adult survival rates) have been blamed for the decline (Stevens et al. 1985).

The adult model tracked the number and mean length of age-1 and older fish on an annual time step. Survival from age 1 to age 3 was specified to be density dependent based on long-term monitoring data. Age-based maturation determined the number and size distribution of female spawners each year, and these distributions were used to initiate the individual-based YOY model. The YOY model computed the number of age-1 survivors from each year's spawners, based on their daily spawning, and the subsequent development, growth, mortality, and movement of their progeny. Four spatial boxes were simulated for the YOY life stages: the upper Sacramento River box leads to the lower Sacramento River box; the lower Sacramento River box joins with the San Joaquin River (Delta) box to form the most downstream box, Suisun Bay. Movement of YOY individuals among the four spatial boxes was based on predictions of passive particle movement from a two-dimensional hydrodynamics model. Two flow conditions were simulated: 141.6 m³/s (5000 cubic feet/s) Delta outflow, which is considered a critically low flow condition, and 566.4 m³/s (20 000 cubic feet/s), which is considered an above-normal flow condition.

Prey composition (zooplankton and *Neomysis*), YOY mortality due to diversions of water for agriculture, and adult survival rates were specified at values reflective of pre- and post-decline periods. Thirty-year simulations were performed with prey composition, diversion mortality, and adult survival all at pre-decline values, each changed singly to its post-decline value, and all changed together to their post-decline values. All simulations started with pre-decline numbers of spawners, and the low Delta outflow condition was used except every fourth year, when the high Delta outflow condition was imposed. (Similar results were obtained when the high Delta outflow condition was randomly assigned with probability 0.25 to individual years.) Systematically imposing the high Delta outflow conditions every four years permits easier interpretation of results because single simulations can be compared.

Striped bass example results

Predicted population abundances remained stable when prey composition, diversion mortality, and adult survival were all at their pre-decline values, and exhibited a dramatic decline (similar to the observed decline) when all three were set to their post-decline values (Fig. 12). However, whenever each was set to post-decline values singly, only small reductions in population abundances were predicted. The combined effects of all three factors at their post-decline values resulted in reductions in survival that could not be compensated for by density-dependent processes. The ratio of mean adult abundances (for years 16 to 30)

April 2000

FISHERIES, HABITAT, AND POLLUTION

381

was computed for each factor as: mean abundance with that factor only at its post-decline value divided by mean abundance with all factors at their pre-decline values. The value of this ratio was 0.80 for reduced adult survival, 0.79 for prey composition, and 0.71 for diversions.

If these factors were operating independently, then their combined effect would be approximated by the product of their ratios. Evidence for the synergistic effects of the three factors in the model was provided by calculating the ratio of mean abundances with all three factors at their post-decline values. This ratio of 0.15 is much less than the product of the three ratios based on each factor changed singly ($0.80 \times 0.79 \times 0.71 = 0.43$). Examination of each of these factors alone would have implied that the combined effects of all three factors would be a mean population abundance that was 45% of the pre-decline abundance, whereas the simulated combined effect of all three factors showed a mean abundance that was 15% of the pre-decline abundance. The usual approach of examining factors individually can result in inaccurate predictions of the cumulative effects of multiple factors.

DISCUSSION

Understanding the effects of anthropogenic changes in EQ on fish populations is critical for effective resource management. Yet isolating and quantifying these effects has been elusive in many situations. Six issues associated with quantifying EQ effects on fish population were illustrated with examples: detectability, complex habitat and nonintuitive responses, regional predictions, community interactions, sublethal effects, and cumulative effects. Examples included time-series analysis of long-term historical catch records, as well as individual-based models ranging from 30-d simulations of larval cohort survival to multiyear simulations of two-species competition and predator-prey models. These examples serve both to illustrate the issues quantitatively and to demonstrate that these issues can be dealt with using modeling.

Detectability, community interactions, and regional predictions

Separating the effects of specific EQ variables from the noise and variation introduced by other sources of variability is difficult. High variation causes many analyses of EQ effects to suffer from low statistical power (i.e., inability to detect effects when they are present) and large Type II errors (failure to reject the false null hypothesis of no effects). The low statistical power of many analyses must be considered before a no-effects conclusion is reached. Without modeling approaches, isolating EQ effects on long-lived species, such as fish, requires years of monitoring that span a range of natural conditions. Often, sufficient data to detect effects are not obtained until it is too late and the population has

dramatically declined or easy recovery is hindered. This is not to imply that data collection is not needed. The accuracy and precision of model predictions depends on the quality and quantity of the empirical data used to develop and corroborate the model. But maintaining funding for sufficient long-term monitoring and waiting decades for definitive signals in the data is not possible in many situations.

Many analyses of fish focus on populations. While population-level analyses tend to require fewer data that are more readily available, they also imply several simplifying assumptions that are often briefly stated and then ignored. Populations rarely exist in isolation, and community interactions can greatly alter the response of the population of interest. For example, the inclusion of a dynamic predator (walleye) in a model resulted in a reversal (increase) in the response of yellow perch population abundance to a chemically induced increase in yellow perch metabolic rate. Population-level analyses are often necessary, however, for pragmatic reasons. Indeed, many of the examples used in this paper were population oriented. However, the effects of community-level interactions are too often dismissed early in analyses without consideration of how they would affect predicted population responses. I encourage those performing population-level analyses to consider community interactions more carefully. I think that keeping the broader community context in mind will help our understanding of population responses to EQ effects, and perhaps explain some of the responses in nature that we consider surprises.

The focus on population-level analyses also has resulted in many analyses being site specific. When problems have required regional predictions involving multiple populations of a species of interest, the tendency has been to sacrifice biological realism. I used the example of an analysis of global climate change effects on trout, which coupled a biologically detailed, individual-based model with a GIS database, to illustrate that realism can be maintained for regional predictions. Regional predictions of EQ effects would benefit by using realistic population dynamics models.

Magnitudes of responses relative to effects

The remaining three issues all relate to the magnitudes of responses relative to effects. Analyses focus on mortality effects because of their direct connection to population models and their obvious relevance to population dynamics. I used three examples to illustrate that sublethal effects can also lead to large population responses. The drawback to many sublethal effects is that they do not directly relate to standard inputs of most population models. One alternative approach would be the development of separate "bridge" models that would convert sublethal endpoints into changes in the inputs of population dynamics models. For example, one could develop an individual-based model of

mating success of nesting fish in which a contaminant that alters the searching behavior for mates would cause an effective reduction in fecundity. Reduced fecundity could then be used in an age- or stage-based matrix population model to forecast the long-term consequences. The scenario of sublethal effects interfering with mating was recently illustrated by Sechausen et al. (1997). They described how increasing turbidity caused by eutrophication in the Great Lakes of Africa has interfered with mate selection among cichlid species, resulting in the loss of populations and species diversity.

Responses by populations are not necessarily proportional to the magnitude of changes in EQ. Large changes in EQ can lead to small responses, and small changes can lead to large responses. Spatial heterogeneity in habitat can dampen large changes or amplify small changes. Despite the visual impact of the algal blooms and associated massive sponge die-offs observed in Florida Bay, the simulation model of spiny lobster population abundance predicted little response to the algal blooms. I suspect that it would be difficult to convince many people who have seen Florida Bay before and after algal blooms that the algal blooms probably had little effect on spiny lobster. In contrast, I used a predator-prey model to show that a 20% change in juvenile yellow perch metabolism led to a 55% increase in their predicted population abundance. Response and EQ are not always monotonically related. In the example of the three-layer water column simulations of larval fish and their predators, highest DO rarely led to highest predicted larval survival. Too much reliance on intuition can lead to erroneous extrapolations and predictions.

The emphasis in many EQ studies on determining the effects of a particular stressor can result in misestimation of population responses. Many, if not all, populations are subjected to multiple stressors. The cumulative effects of multiple stressors can be much greater or much less than expected from the sum of their individual effects. In the Sacramento-San Joaquin river system striped bass example, the cumulative effect of multiple stressors in the model was much greater than predicted by their individual effects. Changes in prey composition and increased mortality from water diversions affected simulated growth and survival of YOY life stages; reduced adult survival caused lowered egg production. Imposition of each of these changes individually caused only small reductions in long-term predicted striped bass population abundances, but that when applied all together, resulted in dramatically lower model populations.

Misinterpretation of the effects of a particular stressor can also arise when multiple stressors affect different life stages. I argue that we must study the major factors affecting a population throughout its life cycle in order to quantify the effects of individual stressors that often

affect specific life stages. Too much focus on a specific stressor alone (and often the affected specific life stage alone) can result in misleading predictions of responses because of inadequate information on how other factors affect the response by the population. For example, considerable publicity and effort have been devoted to nurturing sea turtle eggs on southeastern U.S. beaches, whereas a full life cycle model analysis showed that juvenile mortality at sea (partially as a result of trawl bycatch) was more important to population dynamics than egg survival (Crowder et al. 1994).

Individual-based models, life history theory, and multidisciplinary studies

Prediction of EQ effects on fish populations would benefit by increased consideration of three areas: individual-based modeling, life history theory, and multidisciplinary studies. Individual-based models are ideal for simulating EQ effects and avoiding intuition traps. While one cannot prove that an individual-based approach is necessary (other approaches might also work), the examples presented in this paper show that the individual-based approach is sufficient in many situations. An individual-based approach is obviously useful when there are few individuals in the population of interest. But the utility of the individual-based approach is not limited to small-number populations. All of the examples presented herein involved large-number populations. An individual-based approach was useful in these examples because variation in characteristics among individuals was important to growth, survival, or reproduction; because all models were spatially explicit, requiring movement of individuals among locations; and because many of the predatory and competitive interactions between individuals were size based. Many EQ effects are measured with individuals as the unit. Individual-based models allow effects to be directly imposed on individuals and then scaled up to population or community responses. It is not necessary for the entire model to track individuals. Individual-based bridge models can be used to link EQ effects on individuals to changes in inputs of more aggregated population-dynamics models.

Life history theory provides a framework for putting the stressor and species of interest into a broader context. Life cycle diagrams that show the many abiotic and biotic factors affecting individuals as they progress through successive life stages are a valuable first step in population analyses. Life cycle diagrams enable each effect of a specific stressor acting on a specific life stage to be viewed as one of many factors affecting population dynamics. I disagree with Walters and Collic (1988), who argued that, from a management perspective, more can be gained by investing in better monitoring programs than in research aimed at uncovering the causes of variability. They argued that the predictive power obtainable by field studies would nev-

er be adequate for management purposes. However, it is simply not feasible to monitor all of the important populations adequately. Development of realistic models requires some understanding of the major factors affecting population dynamics.

Comparison of life cycles across species enables responses of the population of interest to be viewed relative to other species in the same system and to ecologically similar species in other systems. Winemiller and Rose (1992) offered a general framework for portraying the life history strategies of North American fishes. Species can be viewed as some mix of three extreme strategies based on age of maturity, juvenile survivorship, and fecundity. Understanding the life cycle of particular species in a broad context increases the generality and robustness of population analyses.

Finally, the idea of multidisciplinary studies is more frequently discussed than truly implemented. Researchers tend to want to perform their science using their usual protocols. True multidisciplinary efforts, in which ecologists, toxicologists, economists, hydrologists, and others work together from the initiation to the completion of a project, and adjust their methods to accommodate linkages with the methods of others, would greatly advance our quantitative understanding of EQ effects on fish populations. Successful collaboration requires the empirically inclined to be willing to acknowledge the gaps in their data, to make guesses in lieu of exact information, and to be amenable to modifying their data collection methods. The modeling inclined must recognize the large effort involved with data collection, must listen carefully to people who know the data and the system being studied, and must take the time to explain how the model works and to update everyone involved frequently on decisions and progress. A critical first step for successful collaboration is the clear formulation of the questions to be addressed, including the degree of site-specificity to be expected in predictions. In short, successful collaboration requires the empiricists to loosen up a bit (data are not truth, data cannot answer all questions, and types of data other than their own can be useful), and the modelers to listen and explain better (so that models are not black holes for data and effort, or black boxes of understanding).

Fish populations are under ever-increasing pressures from an expanding human population. Short-term economic considerations, and the resulting resistance to implementing high-cost remediation actions, forces us as scientists to formulate quantitative relationships between EQ and fish populations. Examples of overfishing causing population declines are numerous. However, despite extensive efforts, definitive quantitative demonstrations of dramatic fish population declines (especially for coastal species) caused by anthropogenic changes in EQ are embarrassingly lacking (Sindermann 1996). Increased consideration of the six is-

ssues discussed in this paper, coupled with a true multidisciplinary approach that uses individual-based modeling and life-history theory, can help in documenting these elusive relationships. The modeling and measurement methods are available to accomplish true multidisciplinary science. The greatest obstacle is overcoming communication and personality barriers. The benefits would be worth the effort. As the stakes continue to rise, either we must show the importance of anthropogenic changes in EQ to fish population dynamics, or we must conclude that these changes are insignificant relative to other sources of variation.

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April 2000

FISHERIES, HABITAT, AND POLLUTION

385

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APPENDIX E



Council for Endangered Species Act Reliability

February 17, 2009

CESAR

Via Certified Mail and Facsimile: 703-358-2251 and 503-231-6259

Johnny Hunt, FWS FOIA Officer
Division of Information Resources and Technology Management
4401 N. Fairfax Drive, Suite 380
Arlington, Virginia 22203

Patti Carroll, FOIA Coordinator
Budget and Administration
Eastside Federal Complex
911 NE 11th Avenue
Portland, Oregon 97232-4181

Re: Freedom of Information Act Request for Materials on the Biological Opinion
Addressing Formal and Early Section 7 Endangered Species Consultation on the
Coordinated Operations of the Central Valley Project and State Water Project
and the Operations Criteria and Plan to Address Potential Critical Habitat Issues

Dear Mr. Hunt and Ms. Carroll:

The Council for Endangered Species Act Reliability (CESAR) is a non-profit, public interest conservation organization whose mission is to ensure the efficient and effective enforcement of the Endangered Species Act (ESA), fulfill the educational goals of our members and provide educational information on the ESA and its application to the general public in the process.

REQUEST FOR MATERIALS

Consistent with our mission, and consistent with the Freedom of Information Act (FOIA), 5 U.S.C. § 552, we respectfully request a copy of the following information within the next twenty days:

1. Grimaldo, L.F., Sommer, T., Van Ark, N., Jones, G., Holland, E., Moyle, P., Smith, P., Herbold, B. *Factors Affecting Fish Entrainment into Massive Water Diversions in a Freshwater Tidal Estuary: Can Fish Losses be Managed?* North American Journal of Fisheries Management (accepted manuscript)
2. Grimaldo, L.F., A. R. Stewart, and W. Kimmerer. *Dietary Segregation of Pelagic and Littoral Fish Assemblages in a Highly Modified Tidal Freshwater Estuary.* Marine and Coastal Fisheries (in review)

REQUEST FOR FEE WAIVER

CESAR requests that you waive all fees in connection with this matter. As shown below, we meet the two-pronged test under FOIA for a fee waiver, 5 U.S.C. § 552 (a)(4)(A)(iii), as implemented by the Department of the Interior's (DOI) fee waiver regulations at 43 C.F.R. § 2.21.

1. **Disclosure of this information is in the public interest because it will significantly contribute to public understanding of the operations of activities of government.**

This requested information will significantly contribute to public understanding of the issues involved, as defined by DOI's three factors at 43 C.F.R. § 2.22 (each factor is addressed below). In considering whether CESAR meets these fee waiver criteria, it is imperative that the DOI remember that FOIA, in general, carries a presumption of disclosure and that fee waiver amendments of 1986 were designed specifically to allow non-profit, public interest groups such as CESAR access to government documents without the payment of fees. As stated by one Senator, "[A]gencies should not be allowed to use fees as an offensive weapon against requesters seeking access to Government information..." 132 Cong Rec S 14298 (daily ed. Sep. 24, 1986) (statement of Sen. Leahy). In interpreting this amendment, the 9th Circuit has stated that:

The amended statute "is to be liberally construed in favor of waivers for noncommercial requesters." The amendment's main purpose was "to remove the roadblocks and technicalities which have been used by various Federal agencies to deny waivers or reductions of fees under the FOIA. (citing Sen. Leahy).

McClellan Ecological Seepage Situation v. Carlucci, 835 F.2d 1282, 1284 (9th Cir. 1987).

Thus, both Congress and the courts are clear in their interpretation that the main legislative purpose of the amendments is to facilitate access to agency records by "watchdog" organizations which use FOIA to monitor and challenge government activities. As the influential District of Columbia Circuit Court has stated:

This waiver provision was added to FOIA, "in an attempt to prevent government agencies from using high fees to discourage certain types of requesters and requests," in clear reference to requests from journalists, scholars, and most importantly for our purposes, nonprofit public interest groups.

Better Gov't Ass'n v. Department of State, 780 F.2d 86, 93-94 (D.C. Cir 1986), quoting *Ettlinger v. FBI*, 596 F. Supp. 867 (D. Mass. 1984).

Further, in his February 10, 2009 Memorandum to Heads of Executive Departments and Agencies, President Obama explicitly reiterated that, 'All agencies should adopt a presumption in favor of disclosure, in order to renew their commitment to the principles embodied in FOIA, and to usher in a new era of open Government. The presumption of disclosure should be applied to all decisions involving FOIA.'

http://www.whitehouse.gov/the_press_office/FreedomofInformationAct/

A. The subject of the request concerns 'the operations and activities of the government'.

The referenced papers were included as supporting documentation for the Effects Analysis contained in the U. S. Fish and Wildlife Service's (FWS) Final Biological Opinion for the Operations Criteria and Plan for the Central Valley Project and the State Water Project completed on December 15, 2008.

B. The disclosure is 'likely to contribute' to a public understanding of government operations or activities (the informative value of the information to be disclosed and ability to disseminate).

The information requested will help provide insight into the policies and decision-making processes of the DOI. People and species in multiple states are affected or can be affected by DOI decisions regarding permitting, activities, budgets, and decisions related to the biological opinions prepared by the FWS as required by the ESA. DOI staff interactions with outside groups, including document leaks and other non-public forms of information sharing are controversial, and given that many of the documents used for decision making are not more generally available to the public, a review of the requested records should offer very valuable insight. In this case, a highly influential scientific assessment in the form of a biological opinion prepared under the requirements of Section 7 of the ESA relied on the studies requested, which to date have not been released.

Without this information, we cannot fully understand the decisions of the agency and how they relate to public natural resources. Therefore, it is clear that having this requested information will contribute to a greater understanding of government operations or activities.

C. The disclosure is likely to contribute to public understanding of government operations or activities (ability to disseminate).

CESAR is a non-profit organization that is dedicated to ensuring the efficient application of the ESA. CESAR will disseminate to members and the public information regarding the interaction between science and policy and the application of the ESA. It is our intent to disseminate the information provided to our members and the general public through our web page at <http://www.bestscience.org>.

In consistently granting waivers to non-profit organizations such as the Center for Biological Diversity, Western Watersheds Project, and the National Resources Defense Council, the Department recognizes non-profit organizations enhance their membership's and the public's understanding of the Department's activities under the ESA. In addition, recent substantive FOIA responses consistently conforming with the spirit of the FOIA and with the FOIA fee waiver have been provided to the above mentioned organizations and others by DOI.

D. The disclosure is likely to contribute significantly to public understanding of government operations or activities.

Public oversight and enhanced understanding of DOI's highly controversial regulatory actions is absolutely necessary. In determining whether the disclosure of requested information will contribute significantly to public understanding, the guiding test is whether the requester will disseminate the disclosed records to a reasonably broad audience of persons interested in the subject (*Carney v. U.S. Dept. of Justice*, 19F. 3d 807 (2nd Cir. 1994).

The information requested in this FOIA request will be used to contribute to one of more of the following: production or defense of listing petitions; production or defense of court documents; public interest litigation; production of local, national or international newsletters; public educational presentations; local, national, or international news stories on TV; radio and newspapers; all contributed or written by CESAR and its members.

In addition to the above channels of dissemination, our informational publications supply information not only to our membership and individuals accessing our web page, but also to the members of other conservation, business, and non-profit organizations. Information concerning DOI's activities and the basis for those activities, including budgets and dealings with non-federal entities, will be disseminated through as many widely publicly available means as possible.

2. Obtaining the information is of no commercial interest to CESAR.

Access to government documents, disclosure forms, and similar materials through FOIA requests is essential to CESAR's role of educating the general public. CESAR is a non-profit organization, has no commercial interests and will realize no commercial benefit from the release of the requested information.

Should you decide not to waive fees, we request that you contact us prior to incurring any costs in excess of \$25.00. Please feel free to request additional information concerning our fee waiver request if you believe it is needed to make a final decision.

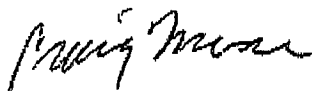
If you elect to withhold any documents responsive to this request under Exemption 5 of FOIA, please explain:

- 1) Why is each document predecisional?
 - a. To what decision is each of the documents leading?

- b. Has this decision been finalized?
- 2) Why is each document deliberative?
- a. To what extent does each make a recommendation on a legal or policy matter?
 - b. What policy recommendation qualifies this document for exemption?

Please reply within twenty working days as required by FOIA. (5 U.S.C. § 552(a) (6)(A)(i).)
Please call me at (916) 341-7407 if you have questions or concerns.

Sincerely,



Craig Manson
Executive Director
Council for Endangered Species Act Reliability

cc: Office of Management and Budget

ACTIVITY REPORT

TIME : 04/02/2009 02:00
 NAME : DIRECTOR US FWS
 FAX : 2022086817
 TEL : 2022084545
 SER.# : BROJ7J701746

NO.	DATE	TIME	FAX NO./NAME	DURATION	PAGE(S)	RESULT	COMMENT
	04/01	20:50	4	31:06	99	OK	RX ECM

BUSY: BUSY/NO RESPONSE
 NG : POOR LINE CONDITION / OUT OF MEMORY
 CV : COVERPAGE
 POL : POLLING
 RET : RETRIEVAL
 PC : PC-FAX