

An Overview of Methods for Developing Bioenergetic and Life History Models for Rare and Endangered Species

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Abstract.—Many fish species are at risk to some degree, and conservation efforts are planned or underway to preserve sensitive populations. For many imperiled species, models could serve as useful tools for researchers and managers as they seek to understand individual growth, quantify predator–prey dynamics, and identify critical sources of mortality. Development and application of models for rare species however, has been constrained by small population sizes, difficulty in obtaining sampling permits, limited opportunities for funding, and regulations on how endangered species can be used in laboratory studies. Bioenergetic and life history models should help with endangered species-recovery planning since these types of models have been used successfully in the last 25 years to address management problems for many commercially and recreationally important fish species. In this paper we discuss five approaches to developing models and parameters for rare species. Borrowing model functions and parameters from related species is simple, but uncorroborated results can be misleading. Directly estimating parameters with laboratory studies may be possible for rare species that have locally abundant populations. Monte Carlo filtering can be used to estimate several parameters by means of performing simple laboratory growth experiments to first determine test criteria. Pattern-oriented modeling (POM) is a new and developing field of research that uses field-observed patterns to build, test, and parameterize models. Models developed using the POM approach are closely linked to field data, produce testable hypotheses, and require a close working relationship between modelers and empiricists. Artificial evolution in individual-based models can be used to gain insight into adaptive behaviors for poorly understood species and thus can fill in knowledge gaps.

Over one-third of the freshwater fishes in the United States (37%; 296 of 799 species) are at some degree of risk: possibly extinct, critically imperiled, imperiled, or vulnerable (Stein et al. 2000; Postel and Richter 2003), and 137 species are listed as threatened or endangered under the U.S. Endangered Species Act (ESA; USFWS 2006). Wild Atlantic salmon *Salmo salar* have disappeared from over 300 river systems in North America and Europe and are threatened with extinction in many other rivers (WWF 2001). In the Pacific Northwest over 300 stocks of Pacific salmon *Oncorhynchus* spp., steelhead (anadromous rainbow trout) *O. mykiss*, and coastal cutthroat trout *O. clarkii* are at risk of extinction (Allendorf et al. 1997). Similar losses

have occurred for a variety of other species. Fish populations are also in decline throughout Asia, Africa, Europe, South America, and Australia (Postel and Richter 2003).

The total economic cost of recovering threatened and endangered fish populations is difficult to estimate, but it can be very high. In fiscal year 2000, direct federal and state spending in the United States on all species listed under the ESA was US\$610 million (USFWS 2000). Considering lost property values and other indirect costs, recovery of endangered fish could cost \$2.4 billion (Simmons and Frost 2004). In the Pacific Northwest, over \$3.3 billion dollars has been spent during the last 20 years on projects to recover Pacific salmonids (GAO 2002), and large-scale efforts continue. State and federal agencies are spending about \$12 million per year on recovery in the Colorado River basin, largely for endangered humpback chub *Gila cypha*, Colorado pikeminnow *Ptychocheilus lucius*, razorback sucker *Xyrauchen texanus*, and bonytail *G.*

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elegans (USFWS 2000). In the fiscal year 2000 alone, over \$2.2 million was spent by state and federal agencies to recover sturgeon species in the central and eastern U.S. (USFWS 2000).

Imperiled fish populations are often regulated by federal, state, and tribal entities that are responsible for making decisions about river flows, water quality, and fish habitat in a variety of waterways. Decisions are often made with incomplete information, and the needs of fish may differ from those of various stakeholders who have conflicting interests. Recent clashes in the Klamath River basin (USA) over two endangered sucker species (family Catostomidae) demonstrate the intensity and animosity that can develop when water is needed by both fish and irrigators (NRC 2004).

Models and decision-support tools are often helpful in assisting managers and scientists to synthesize disparate data and to narrow the range of options available for recovering endangered fish. In many situations, the alternatives for population recovery that need to be compared are complex mixtures of habitat, flow, dam passage, temperature, water quality, invasive species, and other factors. Bioenergetic and life history models for fish are tools that have been used in many analyses of commercial and recreational fishes (e.g., Stewart et al. 1981; Railsback and Rose 1999; Mullon et al. 2003), but have rarely been used for endangered species recovery. These models are especially useful in considering the positive or negative effects of temperature manipulation, the importance of specific diet components, or to estimate whether sufficient food resources are available to support recovering populations of fish. Bioenergetic models have also been used to examine historical changes in fish communities (Stewart and Ibarra 1991; Rutherford et al. 1999), study the effect of climatic regime shifts on predation (Petersen and Kitchell 2001), consider the potential future impacts of climate change on fish abundance and distribution (Shuter and Post 1990; Clark et al. 2001), and explore seasonal variation in prey abundance (Beauchamp and Van Tassell 2001).

Models for rare species are often difficult to develop because of logistical or funding constraints. Rare populations obviously have fewer individuals that can be sampled than abundant populations, often making it a challenge to collect a sufficient number of individuals. Species listed under some regulation as rare or threatened will require state, federal, or tribal sampling permits, and there are other considerations when fish are returned to the laboratory for study. Although large amounts of money are often spent on species recovery, funding for the development of models is often limited, with much of the recovery costs going toward a few species, on-the-ground habitat improvements, exper-

sive dam modifications, and alterations to water quality.

We present a range of options for developing bioenergetics or life history models for rare species. The approaches range from commonly used methods (e.g., parameter borrowing) to emerging techniques (pattern-oriented modeling and artificial evolution). We take a broad view of "bioenergetic modeling" and discuss models that include physiological, life history, and behavioral components. Our intention is to suggest a range of approaches for consideration by researchers, rather than to advocate a specific modeling methodology or parameterization solution.

Approaches to Developing Bioenergetic and Life History Models

Overview

Five alternatives for model building and parameter estimation, both direct and indirect approaches, are discussed below. Parameter borrowing (alternative 1) from related species, is simple and may be the only alternative in some cases. The next two methods require collection of the rare species and some laboratory experimentation. Direct measurement of parameters (alternative 2) has been used for many abundant species and is, in some ways, considered the best approach, while Monte Carlo filtering (alternative 3) is a relatively new method (Rose et al. 1991; Petersen and Paukert 2005). In addition, at least two new important approaches have been developed over the last several years for developing life history and behavioral models when direct estimates of key parameters are difficult to obtain. These are termed, pattern-oriented modeling (alternative 4) and artificial-evolution modeling (alternative 5). Both employ individual-based modeling (IBM); that is, models of populations in which each individual is simulated. Pattern-oriented modeling (POM) has been used to improve or test estimates of parameters of individual energetics or life history, using observed patterns at the population level (Grimm et al. 1996; Wiegand et al. 2003, 2004). The artificial-evolution modeling approach (AE) begins with estimates of basic physiological parameters and attempts to estimate the behavioral strategies, such as time and energy budgets, of the organism (Strand et al. 2002).

Parameter Borrowing

Perhaps the most commonly used and easiest approach to building bioenergetics models for a fish species is to borrow parameters and model equations from related species or species with similar life histories (e.g., Beauchamp and Van Tassell 2001). Perhaps all bioenergetics models have been developed

TABLE 1.—Freshwater fishes listed as threatened or endangered under the Endangered Species Act for which a bioenergetics model has been developed and published.

Species	Source
Bull trout <i>Salvelinus confluentus</i>	Beauchamp and Van Tassell (2001)
Sockeye salmon <i>Oncorhynchus nerka</i>	Beauchamp et al. (1989)
Pink salmon <i>O. gorbuscha</i>	Beauchamp et al. (1989)
Chinook salmon <i>O. tshawytscha</i>	Stewart and Ibarra (1991)
Atlantic salmon	Nislow et al. (2000)
Steelhead or rainbow trout	Rand et al. (1993); Railsback and Rose (1999)
Cutthroat trout <i>O. clarkii</i>	Beauchamp et al. (1995); Cartwright et al. (1998)
Humpback chub	Petersen and Paukert (2005)

with some degree of parameter borrowing, with a few possible exceptions such as yellow perch *Perca flavescens*, walleye *Sander vitreus*, largemouth bass *Micropterus salmoides* and lake trout *Salvelinus namaycush* (Kitchell et al. 1977; Rice et al. 1983; Stewart et al. 1983). Authors generally review the available parameter sets in the literature (e.g., Hanson et al. 1997) and select parameters based on their understanding of a fish's behavior, taxonomic relationship, physiology, and range of habitats occupied, particularly its temperature range and tolerance. Model output is often very sensitive to respiration and consumption parameters (Bartell et al. 1986; Petersen and Ward 1999), so borrowing these parameters requires caution. Excretion and egestion parameters rarely have major impacts on model output (Bartell et al. 1986), so they are often borrowed from species with similar life histories or physiology. Borrowing parameters may be the only alternative for extremely rare or poorly studied fishes, but we believe that one or more of the following approaches will often result in a better and more useful model.

Direct Parameter Estimation

Although rare species present many specific problems for building bioenergetic, habitat, or life history models, there are cases where direct parameter estimation is feasible. A variety of models have been developed for ESA-listed species, and parameters have been estimated directly by using animals collected from abundant subpopulations, fish from closely-related stocks, or fish reared in hatcheries (Table 1). For example, numerous steelhead stocks are listed as threatened or endangered, but a model has been developed using wild and hatchery stocks (Rand et al. 1993; Railsback and Rose 1999). Similar approaches have been available for salmon that have endangered stocks (Table 1). In all cases, model development assumed close physiological relationships between rare and abundant stocks of a species.

Bull trout is another salmonid that is listed as threatened in the northwestern United States, but some

relatively strong local stocks can be sampled for laboratory experiments. Consumption, thermal tolerance, and preliminary respiration experiments have been completed for bull trout collected in Montana and Oregon where these fish are locally abundant (Selong et al. 2001; J. Petersen and M. Mesa, USGS, unpublished data), and these data will be used to develop species-specific parameters. This model should be an improvement over the model used by Beauchamp and Van Tassell (2001), which borrowed parameters from lake trout, another char species. Other rare or imperiled species may have relatively abundant local populations that can be sampled and used in the laboratory to develop parameter sets or model equations. If possible, samples should be collected throughout the species range to avoid biases that might arise from local geographic adaptations.

Parameter Estimation Using Monte Carlo Filtering

Parameters for bioenergetic models can also be estimated indirectly using various assumptions and simulation techniques. Monte Carlo filtering is a procedure for randomly sampling within a range of parameter values in a model, running the model with these parameter values to produce output, and statistically comparing the output with a test criterion, which may be from field or laboratory studies (Rose et al. 1991). If the model output is not different from the test criteria, then the particular parameter value or set of parameter values are assumed to be acceptable. Numerous iterations of the simulation model can be conducted, each with a different random set of parameter values, eventually generating many sets of parameter values. Central tendency, ranking, or other techniques can be applied to decide on the final parameter values among the acceptable sets (Figure 1).

Using Monte Carlo filtering, Petersen and Paukert (2005) developed a set of bioenergetic model parameters for humpback chub in the lower Colorado River. They first assumed that taxonomic relationships, especially fish in the same genus as humpback chub, could be used to set the upper and lower bounds on

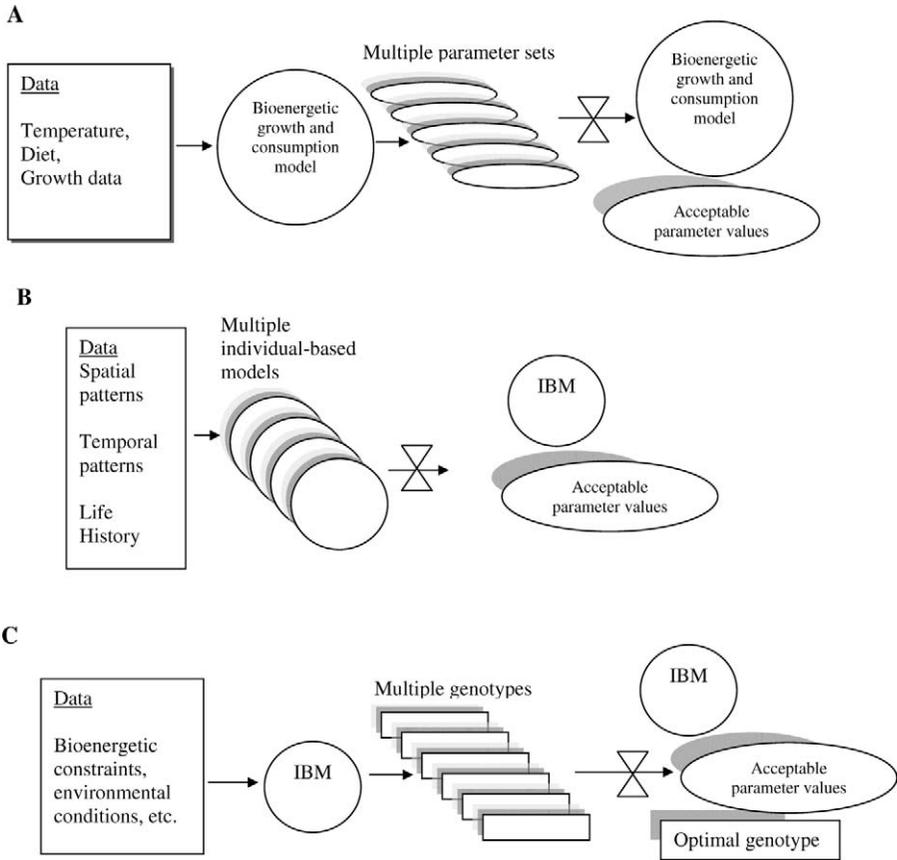


FIGURE 1.—Schematic comparison of three modeling approaches described in the text, namely, (A) Monte Carlo sampling to estimate parameters, (B) pattern-oriented model development, and (C) artificial evolution. The three approaches use different input data and have somewhat different objectives. Comparison of parameter sets, models, or model output is indicated by the hourglasses.

parameters for consumption and respiration in a bioenergetics model. Once the bounds for critical parameters were determined through a literature review, a Monte Carlo simulation was constructed to sample parameters from a uniform distribution within the bounds and grow simulated fish at different temperatures. Simulated fish started at a specific size and were grown for a period of days at a constant temperature. Starting size and temperature for simulated fish matched fish grown in a laboratory experiment (Gorman and Van Hoosen 2000). The final size of the simulated fish was compared with the observed size of fish grown in the laboratory (the test criterion) to determine whether a particular set of parameters were acceptable or unacceptable. To establish the test criteria, laboratory growth experiments were conducted at 13, 15, 18, and 24°C (Gorman and Van Hoosen 2000). Through many iterations of the Monte Carlo simulation, a set of “fitted” parameter values were

selected that could sufficiently match fish growth in the laboratory.

This specific example depended on the ability of the researchers to obtain a small number of fish from the field and conduct growth experiments across a temperature range in the laboratory. Developing test criteria in this manner has two advantages over direct estimation procedures when working with imperiled fish. First, simple growth experiments are generally less stressful and may have lower rates of mortality than respiration experiments using respirometers. Second, parameters can be fit to both consumption and respiration processes with this one laboratory experiment, reducing the total number of fish necessary. Petersen and Paukert (2005) fitted six consumption parameters and five respiration parameters with just one laboratory experiment. The direct approach to fitting these parameters would have required at least four separate laboratory studies – a maximum con-

sumption experiment to determine optimal feeding temperature, examination of consumption by fish of different size to obtain allometric parameters, a respiration experiment across fish size for respiratory allometric parameters, and a study to determine the temperature-dependence of respiration. With the Monte Carlo procedure, fish growth acts as the integrator of several physiological processes, and researchers make some informed assumptions about parameter ranges (e.g., parameter bounds can be derived from similar species) and model equations to begin the parameter search.

Pattern-Oriented Modeling

The pattern-oriented modeling (POM) approach was first described formally by Grimm (1994) and Grimm et al. (1996), although they acknowledged that this approach has long been used informally by ecologists. This encompasses a set of techniques to make use of a variety of observable population-level patterns to both identify the main mechanisms that need to be included in a model and to refine the parameter estimates. It can be applied to bioenergetics modeling. A fundamental idea of the POM approach is that a single strong pattern in nature (for example, very good data on changes through time of the size distribution of a population) may not be sufficient to specify a model attempting to explain these dynamics, because several alternative models (based on, for example, varying types and levels of resources, changes in activity patterns, size-selective predation on the population, or weather fluctuations) may be able to produce the same pattern. However, if there are several additional patterns in the population data (for example, differences in the size distribution in different spatial areas, seasonal variations in size distribution, information on size-selective mortality), even if each of these is a fairly weak signal in the data, the testing of these patterns against various model structures may be sufficient to eliminate many competing models and leave one clear model (Figure 1). Usually, individual-based modeling (IBM), and, especially, spatially explicit individual-based modeling (SEIBM), are used in this process, as they can incorporate a level of detail at the individual level to produce many patterns. Grimm and Railsback (2005) and Grimm et al. (2005) provide descriptions and examples of this approach.

In addition to helping determine the general design of an IBM, the POM approach is also used to refine estimates of parameters that are only roughly known initially. This is done using techniques such as the Monte Carlo filtering described above. But the POM approach uses a broader range of empirical patterns to estimate or improve the estimates of parameters and

filters out ranges of parameters that do not produce agreement to some reasonable extent with all of the observed patterns (Wiegand et al. 2003). Therefore, it is essential to pattern-oriented modeling that, in addition to the direct information on bioenergetics, there be a great deal of indirect information that can also be used to parameterize a model.

The technical details of the application of the POM approach can vary. One variation, used in a model of bears existing at low population levels in northern Spain (Wiegand et al. 2004), could be adapted to fish as follows. Suppose that a model of fish bioenergetics and life history can be partially parameterized but that a number of parameters are known only within fairly broad ranges. These parameters may involve basic bioenergetics and behaviors of individuals. To narrow down the range of the unknown parameters, many simulations, usually at least tens of thousands, are performed. For each of these, the unknown parameters are chosen randomly from the known ranges. The outputs of each of the simulations are compared with a variety of patterns at the population level. These patterns may include age or size distributions, ages of spawning, timing of spawning, foraging patterns, population distributions in space, temporal patterns, or any other observation that can be quantified. The comparisons are used as a 'filter' to remove all combinations of parameters that do not produce good agreement with patterns, based on certain criteria.

Railsback and Harvey (2002) applied the POM approach to determine habitat selection in a model of stream trout production. Specifically, the authors used the approach to test among the following three alternative theories of trout habitat selection: (1) fish are assumed to make a simple prediction of habitat conditions over a future time horizon and then select the habitat that maximizes their expected probability of surviving (and their growth to reproductive size, for juveniles) over the time horizon; (2) fish maximize their immediate growth rate; and (3) fish maximize their immediate probability of survival. The authors incorporated these hypotheses for individual strategies in different versions of their model and then tested the model output against several population-level patterns that could be observed. The six patterns are as follows:

- (1) Hierarchical feeding: trout of similar size exhibit a preference for a single best feeding site, which is occupied by the most dominant individual. When this dominant individual is removed, the preferred site is then occupied by the next most dominant individual.
- (2) Response to high flow: when extremely high stream flows occur, trout move to slower water along

the stream margin and return to their previous location as flow recedes.

(3) Response to interspecific competition: in the presence of another trout species with larger individuals, trout shift their habitat, usually to higher velocities.

(4) Response to predatory fish: in the presence of large, predatory fish, juvenile trout use faster, shallower habitat.

(5) Seasonal velocity preference: the average velocity used by trout increases with temperature among seasons.

(6) Response to reduced food availability: when food availability is reduced, trout shift habitat to obtain higher food intake, and this shift happens before starvation is imminent.

The complete set of six patterns could only be generated by the version of the model that incorporated theory (1). The authors then refined their model by including rules for activities (daytime feeding and night feeding, daytime feeding and night hiding, etc.) in each potential habitat patch. By using additional observed patterns, they were able to derive a set of both habitat choice and activity rules that worked well.

A second example of the use of POM is the model of the growth of roach *Rutilus rutilus* in a heterogeneous lake environment (Hölker and Breckling 2002). The authors' particular objective was to estimate the energy cost of swimming. The movement patterns of fish are difficult to observe, but they can have a large effect on energy costs, so it is important to have a reasonable estimate of activity. Hölker and Breckling (2002) developed a SEIBM for roach in a lake, which included bioenergetics and rules for activity and habitat choice. The activity rules included a model of correlated random walk and three modes of swimming: high-cost swimming pattern, low-cost swimming pattern, and spawning. The mode of swimming depended on physiological status, light conditions, and habitat choice (pelagic or littoral). These behavioral rules were tested and modified by comparing the movement patterns produced in the model with observed patterns of individual fish obtained by telemetry, as well as the density patterns of roach in the lake averaged over time. Van Nes et al. (2002) also used the POM approach to unravel the bioenergetic mechanisms driving the dynamics of a multispecies lake fish community.

Other examples of the use of patterns at a large scale to infer parameters at the individual level (although not related to bioenergetics) include a modeling study of herring migration (Huse et al. 2002). Herring schools usually overwinter in the same location year after year,

but in occasional years the location was observed to suddenly change. This led to the investigation of how the direction of migration is influenced by the fraction of experienced adult migrants in the migrating school. Mechanisms at the individual level were identified in the model that could cause changes in the migration direction and overwintering location in years when the experienced adult migrants made up an exceptionally low fraction of the whole school (Huse et al. 2002). As a tool, POM is just beginning to be used in modeling populations. Other fish modeling papers that use the POM approach, although not including bioenergetics models, include Mullon et al. (2003) and Parada et al. (2003).

Artificial Evolution

Artificial evolution (AE) is an emerging method that can be used to estimate parameters for bioenergetics and life-cycle models. In this approach, models are used to infer unknown behaviors and life-history strategies of the organism by assuming that the species will be optimally suited for the conditions of the environment in which it lives. Therefore, the relevant environmental conditions, such as resource availability, temperature, spatial heterogeneity of suitable habitat, and temporal variability of conditions, are modeled. Whatever information is available relative to a species' bioenergetics and life history is used to set constraints. Other aspects of energetics and life history, such as an individual's behaviors, which may not be well-known, are included as variables in an AE simulation. An individual-based model of the species' population is developed using environmental conditions, bioenergetic constraints, and behaviors. Simulations start with an initial set of individuals with a wide range of genotypes. Computer simulation is performed over many generations, in which these genotypes can undergo mutation, natural selection, and recombination through time (Figure 1).

Strand et al. (2002) describe a sophisticated version of this process in detail. Their method rests on the genetic algorithm (GA), which allows a species to evolve so as to better adapt to its environment under the constraints of its own physiology. For example, assume there are some unknown traits or behaviors such as energy allocation, time spent foraging, choice of microhabitat. These can all be built as traits into an IBM with no initial specification, but instead many different strategies are represented as the equivalent of a gene pool of a population. Each trait is expressed by a genetic code. The genetic analog of a chromosome is a string, the analog of a gene is a character, and alternative characters are alleles. This pool of codes evolves over time as the result of mutation, recombina-

TABLE 2.—Primary assumptions, advantages, and disadvantages of the model parameterization approaches discussed in this paper.

Approach	Assumptions	Advantages	Disadvantages
Parameter borrowing	Borrowed parameters similar to needed parameters	No need to acquire fish for experiments	Need some field or experimental corroboration
Direct parameterization	Experimental conditions mimic field conditions	Directly estimates parameters	Need to acquire fish for experiments
Monte Carlo filtering	Parameters of interest are bounded by range of parameters used	Few fish needed for experiments	Need some field or experimental data (e.g., growth)
Pattern oriented modeling	Population-level patterns determine individual model parameters	No need for laboratory experimentation	Empirical patterns may be too vague or not relate to the model parameters being estimated
Artificial evolution	Individuals are optimally suited for the conditions where they live	No need for laboratory experimentation	Biologically unreasonable or suboptimal life history traits could emerge from the modeling

nation, and selection. Simulations do not attempt to model actual evolution, but AE is a way of gradually sifting out poorer strategies through the computer analog of natural selection. Individuals are allowed to compete with each other and reproduce. Better strategies survive and leave more offspring behind. In the version of this approach used by Strand et al. (2002), an artificial neural network (ANN) is used as the intermediate between genetics and behavior. Sensory observations (temperature, zooplankton density, stomach fullness) constitute inputs, which may be linked to behaviors through a hidden layer in the ANN structure. The pattern of behavioral response is governed by the GA.

Strand et al. (2002) applied their method to a fish whose life history is well-known, Mueller's pearlside *Maurollicus muelleri*. Using the model, they were able to determine the energy allocation, fat reserve, age and month of spawning, diurnal pattern, and vertical distribution of juveniles and adults. They started out with a set of bioenergetic equations and an initial population of the fish that contained a broad range of genotypes. The genetic strings, used in the model as analogs of chromosomes, were haploid and the chance of recombination of a spawner's and partner's strings was 0.6 (i.e., 40% of all offspring were clones of the spawner except for mutations). The chance of mutation occurring on a single character in the energy allocation and spawning string of the offspring was set at 0.001. Seasonal environmental conditions in the model included temperature and zooplankton distribution. Natural selection was allowed to occur in the model for hundreds of generations until a set of characters of the fish stabilized. The authors validated their model against data on the fish species.

The AE approach may be useful in filling in gaps in the strategies of species when limited information is available, a common situation with rare species. A certain amount of physiological information is neces-

sary and information on key aspects of the environment must be supplied. Using this to start AE is able to determine the probable behavioral and life history strategies based on optimization through natural selection. This approach works in cases where density-dependence is a factor, so an evolutionarily stable strategy should evolve, rather than just an optimal strategy.

The AE approach is relatively new, and as far as we know it has not been applied to problems in which a species has to adapt to drastically modified conditions that might result from changes in available habitat, water temperature, salinity, and other factors. There may be constraints due to evolutionary history on the ability of a species to evolve quickly enough to survive under such circumstances. This is an area that needs investigation.

Discussion

The approaches listed represent a range of options, from simple borrowing to fairly complex modeling with pattern-oriented or artificial evolution approaches. Each approach requires different assumptions that must be weighed during the model building, testing, and application process (Table 2). Parameter borrowing is simple, but without some degree of laboratory or field testing there can be little confidence that model output is useful. Direct parameter estimation in the laboratory assumes that laboratory responses are applicable in natural situations, which may or may not be correct (Boisclair and Sirois 1993). Monte Carlo filtering assumes that reasonable ranges can be developed for parameters, requires some assumptions about the underlying consumption or respiration equations, and data are needed on the upper and lower bounds of parameters. The POM approach has perhaps the greatest potential to build models that are tested at each step to assure that output matches the field data patterns. The approach must be used with caution,

TABLE 3.—Major fish taxa listed as threatened or endangered under the Endangered Species Act.

General common name	Genus or taxa	Family	Number of species
Sturgeon	<i>Scaphirhynchus</i> and <i>Acipenser</i>	Acipenseridae	5
Trout and salmon	<i>Oncorhynchus</i>	Salmonidae	6
Chubs	<i>Gila</i>	Cyprinidae	11
Daces	<i>Rhinichthys</i>	Cyprinidae	5
Pupfish	<i>Cyprinodon</i>	Cyprinidae	7
Shiners	<i>Notropis</i>	Cyprinidae	6
Suckers	Four genera	Catostomidae	7
Madtom	<i>Noturus</i>	Ictaluridae	5
Darters	<i>Etheostoma</i> and <i>Percina</i>	Percidae	18

however. In particular, when the empirical patterns used for parameter estimation are vague, or the number of parameters to be estimated is large, several sets of parameters may produce similar agreement with data (Wiegand et al. 2003). In such cases other methods may be needed to sort out the best parameter set. Artificial evolution also has limitations as a method for making estimates of life cycle processes. It is always possible for such methods to produce population behaviors that are not biologically plausible. Technical problems, such as the evolutionary model getting stuck on local optima, are also possible (Strand et al. 2002). Thus, both verification of the efficiency of the model and careful checking of the biological reasonableness of model results are essential. The advantages and disadvantages of these various approaches will vary considerably with species, available data, the time available to develop a model, management objectives, funding, and other conditions.

The choice of a modeling approach or parameter estimation method will depend in part on the accuracy needed for the questions asked. There has been recent concern on the accuracy of bioenergetics models, particularly those developed by direct parameter estimation and parameter borrowing (e.g., Slaughter et al. 2004; Madenjian et al. 2006; Whitley et al. 2006). Although a high degree of accuracy and precision should be the ultimate goal, this may not be realistic without further evaluation and possible experimentation with imperiled species. A higher degree of accuracy may be needed to estimate consumption of specific organisms or the testing of hypotheses (Madenjian et al. 2006) and therefore the analyst should consider models that have been evaluated or have model outputs based on field data patterns like POM. Although the parameter borrowing or Monte Carlo filtering approaches may have lower accuracy because the parameter estimation is based on mere speculation, these models may be useful to determine relative outcomes (e.g., how much more did a fish grow after an increase in temperature of 5°C?).

The modeling approach must be carefully selected to assure it will adequately answer the specified question within the accuracy needed (Madenjian et al. 2000).

Some of the methods we have described might be used to develop parameter sets that are applicable to groups of species that are taxonomically or physiologically related. Of the species currently listed under the ESA, we have identified nine groups within single genera or with unique common names that might be evaluated for parameter development (Table 3). These nine groups account for 70 species, or about half of the total number currently listed under the ESA. We recognize that there are certainly differences among many of the species in these groups that would not allow common use of some bioenergetic parameters. Close inspection of such groups, however, should lead to suites or guilds of species that have similar physiological responses or life histories. With rapid declines in many species and limited resources to conduct studies, researchers may not be able to study in detail every species on the list, but may need to pool similar species and build models that apply to these guilds. These generic models could be a useful starting point for developing more rigorous models to answer specific questions about species conservation and recovery.

Finally, model selection, development, and application must be strongly driven by the overall objectives and usually by the management need. Not all species at risk need a bioenergetics or life history model to assist in their recovery. For many species, recovery and conservation issues may be the destruction of suitable spawning or rearing habitat, or insufficient flows through streams or rivers. Bioenergetic models that predict individual growth or consumption are not designed to explore these types of limiting factors, although individual-based or other models may often be useful (Petersen and DeAngelis 1992; Jager et al. 1997; Railsback and Rose 1999). Density-dependence and habitat selection, often critical elements in fish population recovery, can be explored more effectively

in individual-based and spatially-explicit models than with simple size-structured bioenergetics models that disregard density and assume random mixing of individuals. The methods we have described should be useful tools in developing both simple bioenergetics and complex life history or population models.

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