A Primer on Fish Habitat Models

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ABSTRACT

De Kerckhove, D.T., Smokorowski, K.E. and Randall, R.G. 2008. A primer on fish habitat models. Can. Tech. Rep. Fish. Aquat. Sci. 2817: iv + 65 p.

Mathematical and simulation models of fish and fish habitat are becoming increasingly used as tools for providing science advice for management programs, Environmental Impact Assessments and for guiding further research. Therefore the understanding of these models is a great benefit for fish habitat managers and a necessity for evaluating applications under the *Fisheries Act* which employ modeling techniques. Models allow for both the representation of complex ecological systems in quantifiable terms and for predictions of the consequences of management actions. This primer introduces nine categories of modeling that are currently used, or have the potential for use, in the management of fish habitat in Canada. In each case an overview of the model is given, followed by a case study to demonstrate its application, and ending with a list of the model's main strengths and weaknesses. The primer is intended for DFO fish habitat managers and biologists.

RÉSUMÉ

On utilise de plus en plus les modèles mathématiques et de simulation des poissons et de leur habitat pour fournir des conseils scientifiques pour les programmes de gestion, les évaluations des impacts environnementaux et pour guider des recherches complémentaires. Par conséquent, la compréhension de ces modèles est très avantageuse pour les gestionnaires de l'habitat du poisson, et elle est nécessaire pour évaluer les applications en vertu de la *Loi sur les pêches* qui font appel aux techniques de modélisation. Les modèles permettent, d'une part, de représenter des systèmes écologiques complexes en termes quantifiables et, d'autre part, de prédire les conséquences des interventions de gestion. Le présent guide dévoile neuf catégories de modélisation actuellement utilisées, ou qui recèlent un potentiel d'utilisation, dans la gestion de l'habitat du poisson au Canada. Dans chaque cas, on donne d'abord un aperçu du modèle, puis une étude de cas pour démontrer son application et enfin, une liste des principaux points forts et points faibles du modèle. Le guide est destiné aux biologistes et gestionnaires de l'habitat du poisson du MPO.

1 Introduction

The management of fish habitat in Canada is regulated federally by the *Fisheries Act* (1985) which is implemented following the guidelines in the *Policy for the Management of Fish Habitat* (1986). The guiding principal of the 1986 policy is to ensure no-net-loss of the productive capacity of fish habitat in Canada. While trying to achieve the goals of this policy a wide range of tools have been used to assess, monitor and model the productive capacity of fish habitat in aquatic environments. This primer examines how mathematical modelling techniques can be used to simulate fish and/or fish habitats to evaluate the quality of habitat for different fish species under different anthropogenic impacts. These techniques are increasingly being used to assess the potential impacts of development or the success of habitat remediation projects.

The use of mathematical models is found throughout fisheries biology in a range of applications, from statistical analyses of observed field sampling results to simulating complex aquatic ecosystems interactions. Modelling is increasingly being used in fisheries biology because many standardized methods of habitat assessment require components of mathematical modelling or statistical analyses. In 2001, the use of mathematical models (excluding statistical analyses) accounted for 35% and 60% of the articles from the scientific journals *Ecology* and *American Naturalist*, respectively (Otto and Day 2007). As these models are also increasingly found in Environmental Impact Assessments (EIA, a requirement of the *Canadian Environmental Assessment Act*) of proposed developments affecting fish habitat in Canada, it is important that they are familiar to habitat biologists. This document outlines the general properties of common categories of fish and fish habitat modelling.

Models can be thought of in two ways: 1) as a "black box" in which information is inputted and a result is generated (e.g. Instream Flow Needs models), or 2) as a representation of a system in which the interaction of the parts is the result of interest (e.g. food web models). Both of these examples represent the power of models to present knowledge of a biological system in a form that can be manipulated. Mathematical models can be classified in many different ways however a general classification defines models as either *static* or *dynamic*, and *deterministic* or *stochastic*. Static models are simply those that do not account for changes in the system over time. Therefore static models are independent of time and generate the same result regardless when or for how long the interactions take place. For example the conversion efficiency of food to growth in fish is a static model in which the input of energy in Joules can be used to determine the resulting growth in grams of wet weight (VanWinkle *et al.* 1996). Dynamic models examine how a system might change over time and often use differential equations to determine the state of a system at a given moment in time. A classic dynamic model is that of logistic growth in a population over

time (Otto and Day 2007). Deterministic models are those that consistently generate the same result as long as the same information is inputted into it (i.e., no variation or probabilities). Stochastic models contain elements of randomness in some or all components, therefore repeatedly running the same model will create outputs within a range of potential results. These model classifications are found throughout fisheries biology and are a useful way of delineating the types of results one would expect from a model.

Models are created using relationships between known and unknown values. The relationships are represented by mathematical equations, or *functions*, and the known and unknown values are called *parameters* and *variables,* respectively. "Variables" is a broad term that can represent many different types of values, however they generally refer to components of the model that have either unknown values or a range of known values. Parameters generally refer to constant values that are known and are incorporated into the mathematical equations to provide the proper context or calibration of the model. For example, a simple fish growth model may involve one equation that can estimate the growth rate of fish depending on the variable of ambient water temperature. Parameters such as the standard metabolic rate can be used to calibrate the equation for different fish species.

This document will describe different types of fish habitat models that can be used to estimate or simulate the productive capacity, quality or type of fish habitat within Canada. The assessment of fish habitat can be conducted from many different perspectives (i.e., water quality, a single species, a single trophic level, and the productivity of the ecosystem) which allows for the same essential question, "how good is a specific habitat for a fish species in Canada" to be posed and answered multiple ways. Relatively recently, biologists and proponents under the *Fisheries Act* have used mathematical modelling to quantify proposed or actual losses or gains in fish habitat in response to alterations of the aquatic ecosystems. The quantification of fish habitat is useful for addressing the no-net-loss principle of the Policy for the Management of Fish Habitat (Fisheries and Oceans Canada 1986). Nine specific categories for the types of models commonly used will be examined including:

1. Habitat Suitability Index
2. Population Productivity and Habitat Capacity
3. Defensible Methods
4. Habitat Productivity Index
5. Index of Biotic Integrity
6. Bioenergetic Models
7. Trophic Models
8. Stage-Structured Population Models
9. Individual Based Models

This document is intended for fish habitat biologists to provide a primer on fish habitat modelling. It is the goal of this primer to provide Fisheries and Oceans Canada with an introduction to nine categories of fish habitat models with critiques of their strengths and weaknesses. Not all of the nine categories of models are used to directly estimate the types of changes to fish habitat (or productive capacity) found in many management issues. Although some of the models in this primer are commonly used, or were designed specifically, to assess losses or changes to fish habitat (Habitat Suitability Indices, Defensible Methods and Habitat Productivity Index), other models introduced here are rarely used in a spatial context or as a tool for quantifying lost or gained habitats (Bioenergetic Models, Trophic Models and Individual Based Models). However, all the models in this primer are presented within the context of habitat management such that their usefulness for those types of assessments is demonstrated. These mathematical models have been reviewed, described in detail, critiqued and improved upon in journal articles and academic textbooks. The references cited in this primer will provide additional detail if required. When possible, available modelling software for specific modelling categories is introduced.

2 Habitat Suitability Index

2.1 Overview

Habitat Suitability Indices (HSI) were developed as a tool to objectively assess the range of environmental conditions that fully, marginally or do not meet the requirements of a species (Wakeley 1988). The goal of a Habitat Suitability Index is to quantify how appropriate a habitat variable is for a given species within a study area. The suitability of a habitat variable is measured between 0 (does not meet the species' requirements) to 1 (meets the species' requirements fully). A Habitat Suitability Index is plotted as the relationship between the suitability index and a range of values for the habitat variable (Figure 2.1).
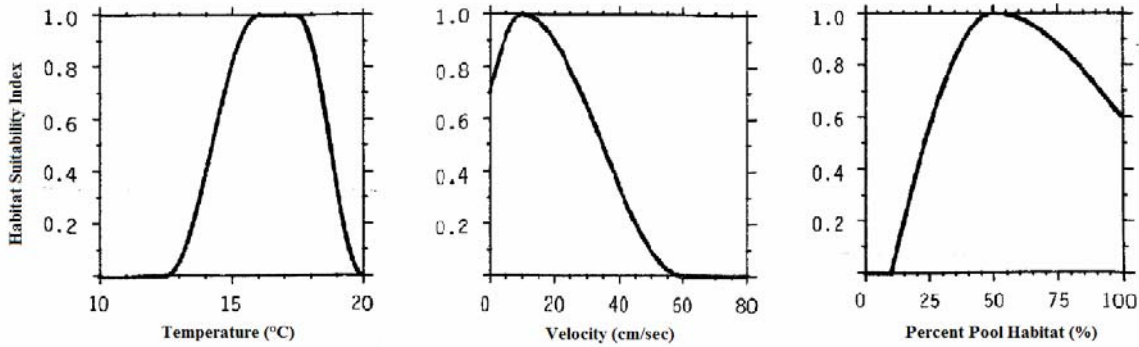
Figure 2.1. Habitat Suitability Index curves developed for the common shiner in the United States showing habitat variables (from left to right) for summer water temperature, stream velocity in pools and percent pool habitat in the reach (from Trial and Nelson 1983)

The HSI curves presented in Figure 2.1 indicate the common shiner's suitability range for summer water temperatures (>13°C and <20°C), stream velocity (<50 cm/sec, optimum of about 15 cm/sec) and percent pool habitat (>10%, optimum about 50-55%). It is also useful to note from the curves the quantification of marginal habitat values (for example, a water temperature of 15°C provides only 60% of the ideal habitat requirement). Habitat Suitability Indices are therefore a useful tool for ecosystem simulations and spatial modelling because they associate a biological value with a physical feature. They also allow biologists to assess the environmental risk of the loss or alteration of a habitat feature to a population or individual (Stalnaker *et al.* 1995). In the common shiner example, if a stream development was to increase the average water velocity from 20 cm/sec to 40 cm/sec one could expect a 30% decrease in suitability. Government agencies (including Fisheries and Oceans Canada), private research groups and academic institutions have developed Habitat Suitability Indices for many species of fish within small and large spatial scales (Wakeley 1988). These published indices have been mostly used as components in the development of other environmental tools and models; the most notable in aquatic assessments being the Instream Flow Incremental Methodology (IFIM) and its associated habitat models such as the Physical Habitat Simulation Model (PHABSIM). These tools allow managers and biologist to assess the value of different habitats in the maintenance of a healthy ecosystem.

The development and use of Habitat Suitability Indices can be described as a three-part process involving: 1) the collection of data, 2) the derivation of the suitability index and 3) the incorporation of indices into further studies (Figure 2.2).

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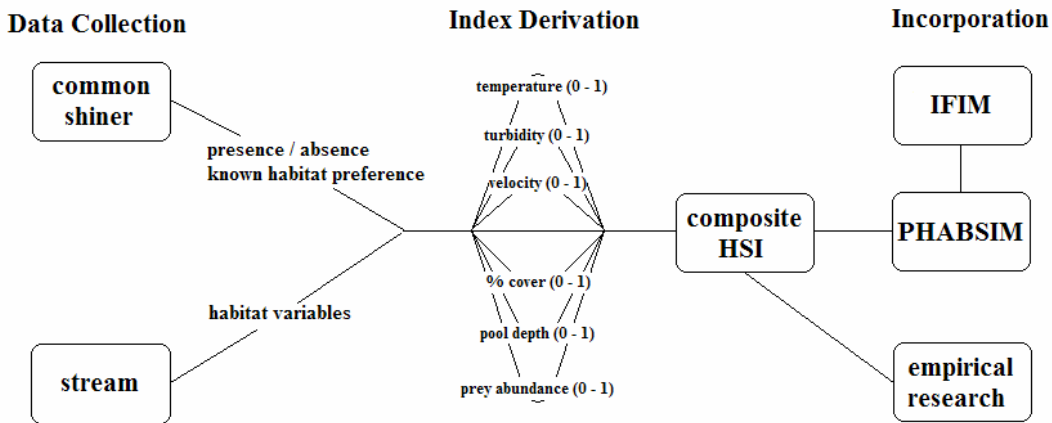
Figure 2.2. A generalized process for developing and using Habitat Suitability Indices and incorporating them into other environmental assessment tools.

To develop HSI curves the associations of different habitat variables with the relative presence and abundance of a focal species needs to be collected (Ahmadi-Nedushan *et al.* 2006). Often the distribution of fish over a range of habitat variables is taken to represent their range of preferences for those habitat variables. Many habitat variables can be chosen and it is not uncommon for more than 20 variables to be selected to characterize a species' overall habitat requirements (Wakeley 1988). Local habitat variables are most often used however as the spatial scale of the study increases, stream order and geology should also be included. In addition, the preference of an individual fish species must be known for the entire range of substrates that are expected to be found in the system being studied.

HSI models generally use variables that can be quantified on a continuous scale (i.e., particle size of substrate) and plotted against the continuous scale of suitability (i.e., 0 to 1). There are three categories of HSI depending on how the suitability of the habitat variables are determined (Ahmadi-Nedushan *et al.* 2006). Category I HSI derives the suitability of habitat variables from published life history studies or from the professional judgement of an expert. These indices are often general in scope and large in geographic scale. They are also the most common and found in many Environmental Impact Assessments. Category II HSI use population abundance and distribution data collected at a specific study location to derive habitat suitability. The suitability index can be derived by using the frequency of individuals occupying a particular habitat variable. Category III HSI also use the data from specific habitat studies, however, it also includes additional information on the other habitat combinations in a study location which allows suitability to be defined as a ratio of percent utilization (% of the individuals associated with the habitat variable) with percent availability (% of the habitat variable

available in the study location) (Vadas and Orth 2001). Both Category II and III HSI can be used at very small scales such as within or between pool, riffle and run habitats. Once the suitability index is generated the Habitat Suitability Index can be plotted in a graph (Figure 2.1). There are many available statistical methods used to generate the equation for the Habitat Suitability Index curve (Ahmadi-Nedushan *et al.* 2006).

The suitability indices have to be combined to create one measure of overall suitability, which is called the Composite Habitat Suitability Index. The method which is chosen to combine the Habitat Suitability Indices must be supported by assumptions on how the habitat variables interact in aquatic ecosystems. In most cases two assumptions are implicit: 1) all variables are equally important (i.e., water temperature is as important as substrate composition), and 2) there are no interactions between environmental variables (i.e., substrate composition does not influence water temperature). Using these assumptions the most common method to generate the composite HSI involves multiplying each of suitability indices (SI) together (Wakeley *et al.* 1988). Some variables can be weighted if they are known to be more important to the focal species than others (Vadas and Orth 2001).

The best known usage of HSI is within the Instream Flow Incremental Methodology (IFIM) developed by the US Fish and Wildlife Service in the early 1980s (Stalnaker *et al.* 1995). The IFIM is a problem-solving methodology that was developed to assist with the environmental assessments of developments that had the potential to lower water levels or alter flows in watercourses. The methodology is based on determining the critical flows in rivers to maintain a desired level of habitat to support aquatic resources. The IFIM uses a spatial modelling tool called the Physical Habitat Simulation Model (PHABSIM) to calculate the amount of aquatic habitat available at incremental changes in stream discharges. This is achieved by combining site-specific habitat data with hydraulic simulations and HSI curves. The output of the PHABSIM is the weighted usable area (WUA) which is the amount of available suitable habitat at different flow regimes for the target species (Figure 2.3).

The IFIM provides a study design with key phases for assessing a project which may impact aquatic resources. The PHABSIM model is developed during the *Study Implementation Phase* in which the field work, data analysis, model creation and the acquisition of results are completed. In any modelling exercise it is critical at this stage to identify and verify the model assumptions, determining the geographic and temporal scales of the project (Scruton *et al.* 1998) and select the habitat variables. Site-specific HSI will require the collection of site specific information (water quality, stream morphology, and fish abundances), creation of the model equations (multiple-regressions), the calibration of the model, and generation of the model output. Because HSI curves are usually based on correlations (i.e., the number of fish observed at a range of water temperatures) they are vulnerable to missing important or subtle habitat

associations. Manipulative experiments may be needed to expose underlying mechanisms and evaluate potential biases in the HSI models. HSI can also be derived by examining the association of habitat variables with true fitness (i.e., growth, survival and forage success) which gives an alternate method for testing existing indices (Baker 1997). If the HSI is instead obtained from standard models it is important to screen the indices to determine which ones are transferable to the site conditions. Screening can be achieved by first ensuring that the habitat characteristics used in the standard models are found in the site of interest. Second, since fish species demonstrate a great variety of physiological and behavioural across their distributions it is important to verify that the suitability ratings for each habitat variable in the standard model match the expected fish habitat preferences in the study site. If they don't, the variable should be modified or removed from the model.
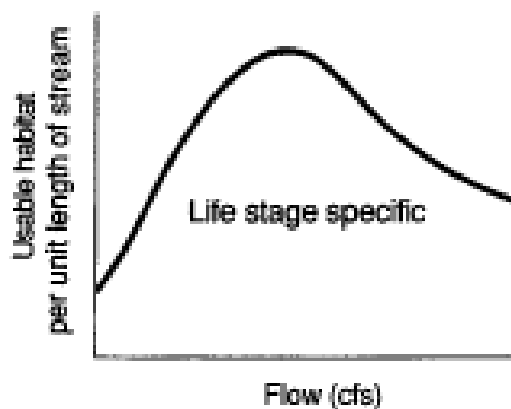
Figure 2.3. The output of the PHABSIM model showing the relationship between the Weighted Usable Area and the stream discharge for a non-specified species (from Stalnaker *et al.* 1995).

It is important to validate the PHABSIM once it has been developed. The IFIM provides an overview on how to use observations on natural systems to calibrate and validate the model (Figure 2.4). The IFIM indicates that calibration and validation are similar processes for PHABSIM and rely upon the collection of site specific data. Baker (1997) also recommends that models are run on different parts of the system or similar watersheds to verify the model outputs. The IFIM also indicates that statistical error can be associated with observed values in natural systems and therefore within the model. Confidence intervals for the WUA can be generated and should be included with the PHABSIM output (Williams 1996).
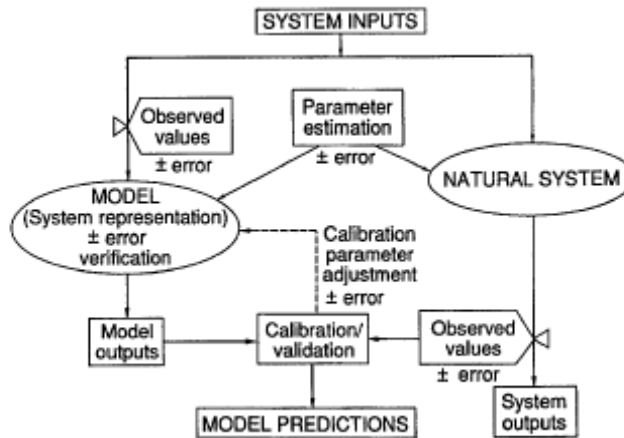
Figure 2.4. The model calibration process for the Instream Flow Incremental Methodology. Note that from the System Inputs the calibration process is based around finding the error value for the parameters of the Model through comparisons between the model outputs and observed values found in the Natural System. (from Stalnaker *et al.* 1995).

2.2 Case Study

A Habitat Suitability Model for walleye was developed by McMahon, Terrell and Nelson (1984) for the United States Geological Survey. The objective of the model was to be able to provide a series of HSI curves that could be adopted across the United States to evaluate the quality of walleye habitat. Separate curves were developed for lacustrine and riverine populations. In addition, separate habitat variables were considered for different age classes of walleye. It is the stated hope of the project that there is a positive relationship between HSI curves and the carrying capacity of the environment. However it is acknowledged that it is difficult to validate the link between the two.

Fifteen selected habitat variables were grouped under four categories that were considered "life requisites": food, cover, water quality and reproduction (Table 2.1). It was acknowledged early in the study that the model was likely to give the most accurate predictions of suitability only at the extremes of the curves (100% or 0% suitable). Habitat variables not included in the model included ones that were highly correlated with existing variables or were too difficult to measure or estimate. All of the habitat variables in this study were applied to a habitat suitability framework using multiple published reports and expert opinion. Therefore the models are not tailored to any particular region and remain general. Suitability curves were developed for each parameter similar to the ones presented in Figure 2.1. The study was able to suggest how some of the indices related to each other when calculating an overall HSI. For example, for water quality the most important HSI was determined to be the lowest of the five categories. The lowest HSI of consumption, cover, reproduction and water

quality was determined to be the overall HSI (which is different than the typical method of multiplying the indices together).

Table 2.1. Habitat variables used for the development of Habitat Suitability Indices for walleye in North America (McMahon *et al.* 1984).

Life Requisite	Habitat Variable
Food	Transparency
	Forage Fish Abundance
Cover	Transparency
	Percent Cover
Water Quality	pH
	Dissolved Oxygen (adult and juveniles)
	Dissolved Oxygen (fry)
	Temperature (adult, juvenile)
	Temperature (fry)
Reproduction	Dissolved Oxygen (embryo)
	Temperature (embryo)
	Temperature (gonad maturation)
	Spawning Habitat Index
	Water Levels
Other	Trophic Class (lacustrine only)

Another interesting result of the Habitat Suitability Indices development for the walleye case study was that the authors stated which curves could be used for IFIM studies. Not all the curves were used due to a lack of existing information, large assumptions or an inappropriate habitat measure.

Additional information and case studies on the PHABSIM and IFIM can be found in the US Fish and Wildlife IFIM Primer (Stalnaker *et al.* 1995) as well as an Instream Flow Needs Primer developed for Fisheries and Oceans Canada (Kilgour *et al.* 2005).

2.3 Strengths and Weaknesses

The use of HSI, and particularly its use within the PHABSIM method to predict optimal habitat requirements and WUA, has been the source of a great deal of debate over the last thirty years. Both techniques remain widely used throughout the world primarily because:

1. Many HSI are available for commercially important and environmental sensitive fish species;
2. Both the development of HSI curves and the use of the PHABSIM methodology is simple and easy to use (Stalnaker *et al.* 1995);
3. Advances in statistics and technology are improving the accuracy and resolution of both techniques (Ahmadi-Nedushan *et al.* 2006);
4. The techniques have proven useful for designing and restoring aquatic habitat (Gore 1998);
5. Confidence intervals for the WUA improve the validity of the PHABSIM output; and,
6. A large number of studies empirically evaluating PHABSIM assessments find that the method can be a robust predictor of fish habitat requirements (Lamoureux and Capra 2002).

There are strengths in the many specific applications of HSI to fisheries science and management including:
1. Conducting aquatic environmental assessments and long term fish habitat monitoring studies (Ahmadi-Nedushan *et al.* 2006);
2. Predicting environmental risk and loss of fish habitat (Stalnaker *et al.* 1995);
3. Predicting invasion potential of exotic species;
4. Designing and restoring aquatic habitat; and,
5. Analyzing and predicting fish species distributions.

On the other hand, there are many criticisms of the methods. Because the validity of the HSI is critical to the accuracy of the PHABSIM many of the criticisms are directed towards how the HSI was created. The assumptions needed to generate the composite HSI restrict the ability to include common ecological phenomena such as competition which therefore limit the reality of the results. In addition, with the development of two-dimensional habitat simulation models, such as River-2D (Steffler and Blackburn 2002), many of the identified hydraulic modelling problems with PHABSIM can now be significantly improved upon. Empirical evaluations of both techniques have found that:

1. PHABSIM and HSI models demonstrate large biases in their results and low correlations with empirical studies completed on the same or similar watercourses (Bourgeois *et al.* 1996);

2. PHABSIM does not function well on low-order, high gradient streams (Azzellino and Vismara 2001);
3. Results vary greatly based on the combination of habitat variables chosen and how data were collected, such that even the time of day that field assessments were carried out can bias the results (Vilizzi *et al.* 2004);
4. The transferability of HSI models across watersheds is uncertain and has often found to give false results for forage fish (Glozier *et al.* 1997) and well known sport fish species (Hedger 2004);
5. PHABSIM is not able to model species interactions, dynamic feedback among system components, high degree of spatial and temporal variability and connectivity between habitats (Anderson *et al.* 2006); and,
6. The output of PHABSIM does not incorporate the productive capacity of the environment (Shirvell 1986).

Because of the many weaknesses associated with the use of HSI and PHABSIM modelling techniques, it becomes critical to evaluate the selection of the habitat suitability variables, the calibration of the hydraulic model, and type of ecological interactions expected to occur in the system before accepting the model.

3 Population Productivity and Habitat Capacity

3.1 Overview

For the purpose of this chapter, and to be consistent with fish science literature, we differentiate between habitat productive capacity and population productivity (Randall 2003). Productive and habitat capacity are characteristic of an area (of habitat), while productivity is a characteristic of a population. Both terms can be illustrated with a generalized stock-recruitment (S-R) curve (Figure 3.1). Recruitment in a fish population increases as the number of spawners increases which causes the population to grow. At high densities the S-R curve can either reach an asymptote (Beverton and Holt curve) or decline (Ricker curve), depending on the species. The shape of the S-R curve is not linear because at low fish abundance survival is independent of population density, but at high fish abundance survival is density-dependent because of resource limitations (e.g., competition for food resources). If long term data on spawning stock size and resulting recruitment are available, the productivity of the population can be determined. Productivity is calculated as the maximum survival rate at low population densities (i.e., when survival is independent of density), and it can be measured by the initial slope of a stock-recruitment curve (Figure 3.1). Habitat capacity can be determined on recruitment curves as the intersection with the replacement line, where

spawners are replaced equally by new recruits (Figure 3.1). Habitat capacity is also known as the carrying capacity and refers to the total density of fish that can be supported by the resources found within a habitat. Randall (2003) describes two levels of capacity: one at the population level (habitat or carrying capacity as described above) and one at the community level (the true productive capacity of the ecosystem).
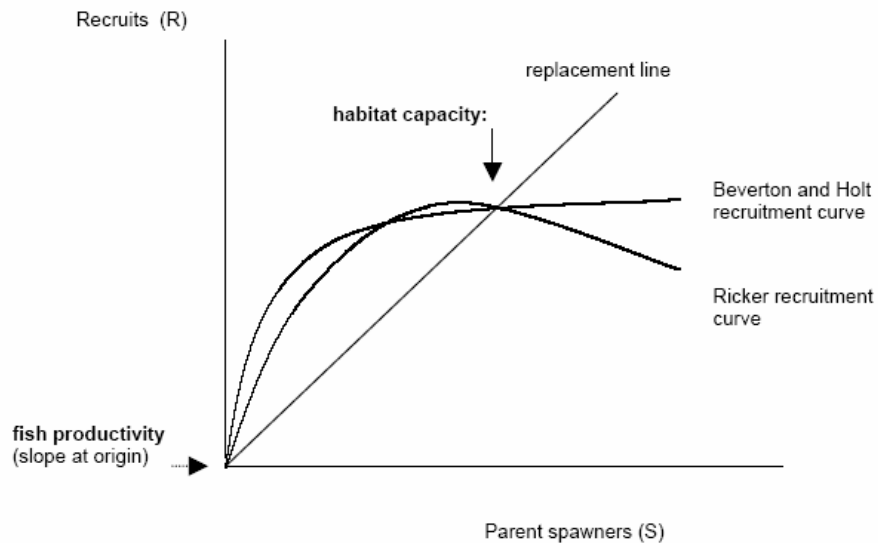
Figure 3.1. A generalized stock recruitment relationship for a fish population. Both Beverton and Holt and Ricker curves are shown, along with the replacement line. The biological reference points of fish population productivity (maximum density-independent survival rate) and habitat 'carrying' capacity (equilibrium density of recruits determined by density-dependent processes) are shown with arrows. (from Randall 2003)

Productive capacity is defined in the DFO policy for the management of fish habitat as "the maximum natural capability of habitats to produce healthy fish, safe for human consumption, or to support or produce aquatic organisms upon which fish depend" (Fisheries and Oceans Canada 1986). From a modeling perspective the productive capacity would therefore be the sum of the maximum production for each population in a community (Minns 1995). The biodiversity of the fish community is also an important component of the DFO definition because the composition of fish assemblages is often more sensitive to habitat alterations than the total production within the habitat. This typically occurs because the loss of one species is compensated for by an increase in productivity of a competing species. Productive capacity is influenced by a wide range of attributes including ones at the scale of ecosystems such as seasonal thermal

gradients and nutrient availability as well as at small spatial scales such as the amount of spawning substrates.

Fish production (P) can be modelled as the sum of the rates of net increase in fish tissue (dw_i) of all the fish in a population (or community) within a time period (dt):

$$P = \Sigma \, dw_i \, / \, dt$$

However to measure this value in the field would require long term data sets for multiple species within the community which is often not feasible from an economic or project scheduling perspective. This model can be expanded (Mertz and Myer 1998) to include characteristics that are somewhat easier to measure (or estimate) such as the fish age classes (a), mass of each age classes per unit of area ($W_c(a)$), age specific mortality rates ($M(a)$), age specific harvesting rates ($F(a)$), and age specific somatic growth rates ($G(a)$):

$$P = \int [G(a) - (M(a) + F(a))] \, W_c(a) da$$

This model is integrated over the possible ages of the fish (i.e. from hatching to death). The age specific somatic growth rates would need to take into account the loss of energy due to investments into reproductive growth once the fish have reached sexual maturity.

A direct measure of productive capacity is difficult to obtain and takes a large amount of data from experimental manipulations of habitat quality with associated measures of fish biomass (Hunt 1974). Productive capacity can instead be estimated by some habitat characteristics. For example, habitat area and fish production are strongly correlated (Figure 3.2) such that a loss of habitat will result in a decrease in fish production. Therefore habitat surrogates are often used for estimating the productive capacity of ecosystems. However it is difficult to validate the use of one surrogate over the other, especially at small spatial scales. Examples of well used surrogates include coolwater stream habitat units (runs, riffles and pools) or near shore macrophyte cover in lakes. The use of habitat surrogates can be validated at either a small spatial scale by comparing fish densities on different types of habitat (such as in pools, riffles and runs) or at larger spatial scales that include the health or location of entire populations.
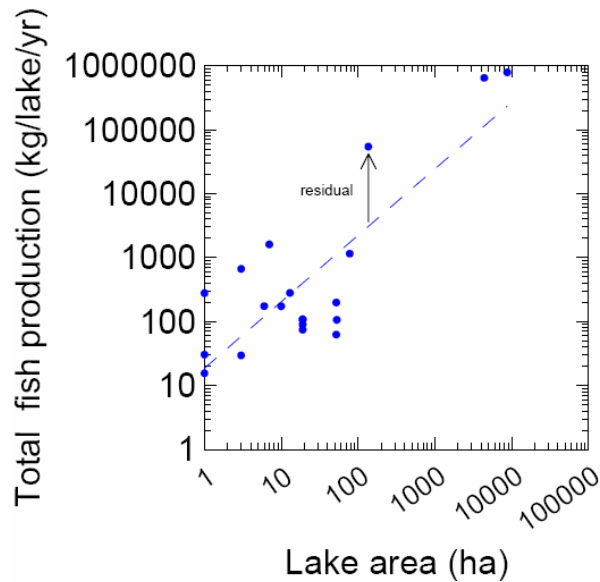
Figure 3.2. The relationship between habitat area and fish production (from Randall 2003).

3.2 Case Study

Sharma and Hilborn (2001) employed estimates of productivity and habitat capacity to examine the relationships between watershed characteristics and coho salmon smolt abundance. Although a large number of empirical studies had been conducted on the impact of habitat degradation on salmonid species, little was known about the relationships between habitat variables and their ability to produce coho salmon in the watershed. The objective of the study was to find relationships between coho salmon smolt abundance and habitat / watershed variables such that predictions for stream capacity could be made on a regional scale.

Smolt counts, female escapement counts and peak index counts were available for 14 rivers in Washington State, of which 14 stream specific habitat and watershed attributes were collected from each watercourse. Spawner – recruitment analyses were conducted where data were available for both spawner and smolt counts. The equation for the analyses included the need for estimates of productivity and habitat capacity which were found in existing data using the number of smolts per female at low density and the maximum number of smolts that could be produced by the stream, respectively. Enough data were only available at four streams to estimate productivity, and nine streams for capacity (Table 3.1). The relationship between habitat / watershed variables and smolt abundance was achieved by using linear regression on the relationship between capacity estimates on each stream with the habitat variables.

Table 3.1. Table listing the estimated productivity of female coho salmon populations and the habitat capacity of 9 watercourses in Washington, USA (from Sharma and Hilborn 2001).

Locations	Productivity, smolts·female^{-1} (95% CI)	Capacity, smolts·km^{-1} (95% CI)
Big Beef Creek	146 (100–600)	2156 (1340–3659)
Snow Creek	71 (52–106)	910 (739–1818)
Bingham Creek	na (na)	1236 (112–1351)
Deschutes River	51 (35–83)	2745 (1852–5926)
S.F. Skykomish River	247 (130–850)	3352 (2706–4058)
Bear Creek	na (na)	218 (165–297)
Mission Creek	na (na)	915 (766–1109)
Little Tahuya Creek	na (na)	4145 (3022–6259)
Courtney Creek	na (na)	323 (258–499)

As shown in Table 3.1, estimates of productivity and capacity varied across watersheds. Correlations between the habitat capacity (measured as smolt abundance / km) and habitat per watershed variables were found for pool density, stream gradient, valley slope, pool and pond densities, and large woody debris abundance (Figure 3.3). Maximum likelihood profiles of the relationships allowed for more detail on the impact of changes to habitat quality on habitat capacity. For example, smolt abundances were negatively correlated with stream gradient such that a 1% decrease in gradient resulted in an estimated increase of 400 smolts / km. The results of the study were able to illuminate other relationships between habitat capacity and smolt abundance. Habitat capacities in pool and pond areas were estimated as 0.4 smolt / m^2 of pool area and 0.07 smolt / m^2 of pond area. The relationships uncovered in this study allowed the researchers to make conclusions on the state of the watershed. Previously the decline of the coho salmon had been attributed to limited spawning habitat, however this study suggested that habitat capacity for smolts was generally high in the watersheds and that fish abundance must be limited by something else. This study was able to complete a watershed scale validation by examining the habitat capacities among watersheds and at greater spatial scales than discrete habitat units.
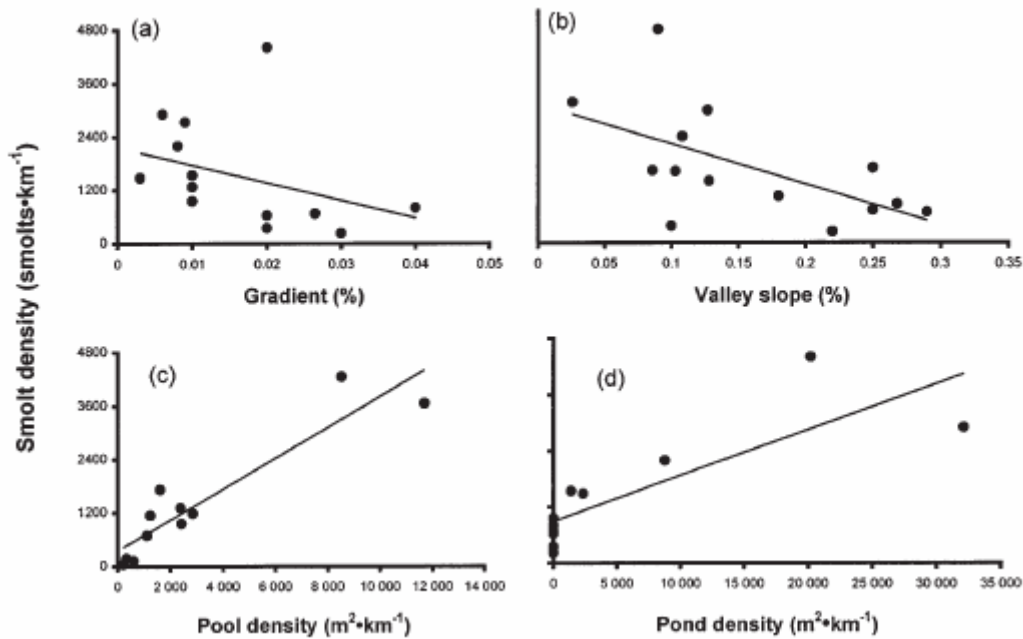
Figure 3.3. Relationships between habitat capacity and habitat variables for coho salmon productivity in Washington State watercourses (from Sharma and Hilborn 2001).

Note that a large database was required for the direct estimates of habitat capacity. The authors were able to show the regressions because the diversity of the gradients, valley slopes, and pool and pond densities were found in the system. If this had not been the case, a series of experimental removals and additions would have been required to generate similar data (at an even greater cost). Another example of the use of stock-recruitment models to assess habitat carrying capacity was provided for Atlantic salmon by Gibson (2006). Habitat carrying capacity was shown to vary by a factor of 16 among the rivers of eastern Canada.

3.3 Strengths and Weaknesses

The main strength of these direct estimates of fish production and habitat capacity is that they allow managers to assess the relative contribution different types or amounts of habitat have on the viability of fish populations. As in the case study, it allows for direct estimates of gains or losses to fish production from proposed gains or losses of habitat. It provides for an excellent monitoring tool for harvested or threatened populations. The model presented by Mertz and Myers (1998) facilitates the estimate of fish production using variables that can be obtained from field studies on the focal population or from known values in similar populations or species.

The main weakness of these methods is that they cannot be used for a wide range of populations or habitats. Identification of the habitat capacity at a population scale can best be achieved using long term data sets on stock and recruitment. However, these data sets are available for a few species and regions only, usually involving only species that are harvested. Because of the cost, timeframe, and spatial scale, S-R models will only occasionally be used by habitat management for large scale (e.g., watershed) habitat projects and rarely for smaller projects or remote systems where less in known about the populations. In addition, correlations found in studies such as Sharma and Hilborn (2001) may only give rough approximations of habitat relationships and cannot necessarily be used to evaluate site specific productivity measures.

In response to the inconsistency in defining the terms of production and productive capacity, a terminology of the key terms as they related to fisheries and fish habitat management has been included following the definitions in Randall (2003).

Production: the total amount of fish tissue produced in a specified area over a specified time period (units = biomass / area / time).

Productivity: in populations it is 'the maximum survival rate of individuals at a low population density (units = number of recruits / spawner); in ecosystems and communities it is the maximum potential production under optimal growth conditions (same units as production – biomass / area / time).

Habitat Capacity: equilibrium population or community size that can be indefinitely supported by available resources in a defined area (units – biomass or population size / area).

Productive Capacity: sum of production (maximum and current) of all co-habitating fish species over a defined time period within a defined area (same units as production – biomass / area / time). This term relates to the maximum capacity of an environment to support fish and aquatic life.

4 Defensible Methods

4.1 Overview

Defensible Methods was created to specifically address the Fisheries and Oceans Canada no-net-loss policy and provide a tool to measure change in the productive capacity of aquatic environments. It is useful to note that this is one of the only approaches in this primer that was specifically designed to demonstrate net changes to productive capacity. Minns (1997) created a framework to measure losses to the

productive capacity of habitat due to losses in habitat area. He defined productive capacity (P) as the product of a unit-area rate of production (*p*) with the habitat area (*A*). Using this simple model, losses and modifications to the productive capacity of habitats (from overall state 1 to 2) can be estimated for a habitat type as:

$$P_{NOW} - P_{AFTER} = (p_{AFTER} - p_{NOW}) * A_{AFTER} - (p_{MAX} * A_{LOST})$$

The model presented here shows that the difference in productive capacity will be due to a potentially altered unit-area rate of production ($p_{AFTER} - p_{NOW}$) at the modified habitat (A_{AFTER}) as well as the permanent loss of any potential maximum production (p_{MAX}) within the lost habitat (A_{LOST}). The final term of the equation is important and distinguishes this framework from other habitat models as it states the assumption that there is an unrealized potential productivity which is lost when habitat is destroyed (Minns 1997). Therefore existing habitat quality cannot be judged only on how good it is at the time of the assessment but how good it could have been at its maximum productivity. This framework is useful for conceptualizing how productive capacity is reduced during fish habitat losses and alterations. For example, the productive capacity of a river is potentially altered by the use of riprap armouring which contributes to A_{LOST} through the loss of the wetted channel width, $p_{MAX} * A_{LOST}$ if the productive capacity had a potentially higher value, and p_{AFTER} by the introduction of instream boulder substrate in existing habitat.

In 2001 Minns, Moore, Stoneman and Cudmore-Vokey presented a methodology to assess losses and gains to productive capacity in lakes within the Great Lakes basin using a Habitat Suitability Matrix combined with the conceptual framework identified in 1997. The process was called Defensible Methods as it provides a quantification of not only the pre-development fish habitat but also the predicted losses due to a disturbance as well as the predicted mitigative effect of habitat compensation. This method allows both Fisheries and Oceans Canada and proponents to defend a decision on a proposed development under the terms of the Fish Habitat Policy and no-net-loss using quantifiable data. The predicted effect of a compensation project (both on and off-site) is included in the above equation by adding

$$A_{COM} * (p_{COM} - p_{NOW})$$

to the right hand side of the equation, where A_{COM} and p_{COM} represents the area and productive capacity, respectively, of the compensation project. This term doesn't have to be explicit if the compensation is on-site because it may be found in the p_{AFTER} term.

A variety of measurements or estimates may be used to quantify the productive capacity of the fish habitat, including fish biomass, fish productivity, habitat suitability or indices of biotic integrity (Minns *et al.* 2001). Whichever method is chosen, the maximum productive capacity of the habitat should be set to the value of 1 such that all

other measurements of existing and predicted productive capacity represent a proportion of that value. The fish habitat area should be defined to include habitat units (or patches) that contain different habitat characteristics or physical qualities (i.e. water temperature, depth).

The framework requires that a few principles are accepted:

1. The entire assemblage should be used rather than one or two key fish species.

2. Surrogate physical and chemical indicators of fish productivity may be used.

3. The fisheries science concerning the site is likely incomplete and therefore existing knowledge must be accepted in the decision making process.

4. Where uncertainty is high in the result of the process the Precautionary Principle should be applied in which no development is approved until further studies can reduce the uncertainty surrounding the assessment.

5. The quantitative approach is integral to keeping the assessment of loss or gains to fish habitat productivity explicit and transparent.

6. Only habitat areas affected directly or indirectly by the development should be included in the analysis. If the assessment is at too large a scale, the impacts to fish habitat will appear minimized or trivial.

Pre- and post-development scenarios should be treated with the same criteria (i.e. habitat features, fish assemblages, etc.).

In 2001, a web-based software application developed by BioSoftware.com of Hamilton Ontario was created specifically for the use of Fisheries and Oceans Canada for fish habitat management. The software uses a standard habitat suitability model and is based on the analysis of habitat feature preferences by species and life stage in the Ontario-Great Lakes Area. Fisheries and Oceans Canada used this tool to implement a scheme, known as HAAT (Habitat Alteration Assessment Tool) to guide the use of the software by Fish Habitat Management biologists for a defined range of referrals involving near-shore lake habitats. Additional features were added to the software after 2001:

1. The ability to modify the form of the standard model that estimates suitabilities from the habitat feature preferences of species by life stage.

2. The ability to build new groups of fish species based on a range of life history criteria. The habitat preferences of species in those groups are then used to compute a standard suitability model.

3. The ability to define as many different habitat types based on combinations of

habitat features (depth, substrate, cover in lakes, plus flow type in streams).

4. Beside standard suitability models for lake habitats in the Ontario Great Lakes region, the software includes habitat preference databases for a number of other parts of Canada (Newfoundland and Labrador (Lakes, Streams), Ontario (L,S), Prairies (L), British Columbia and Yukon (L,S), and NWT and Nunavut (L,S)) based on fish species lists for those areas. The habitat preference databases were published in a series of Canadian Fisheries and Aquatic Sciences Manuscript Reports which are available on-line from Fisheries and Oceans Canada on the WAVES on-line library.

5. Besides the standard suitability models which are computed within the software, the package provides for the use of user-specified simple suitability models which consist of a rectangular matrix of species groups by habitat types. Minns and Moore (2003) showed that it is hard to justify detailed habitat classification schemes with many classes and recommended limiting the number of classes based on evidence of their utility to fish. Use of simple models requires that the user provide supporting evidence to justify their use in assessing net change of productive capacity. Simple models have been developed for Great Lakes lacustrine habitats and Ontario stream habitats.

6. The software package also has extensions which incorporate consideration of uncertainty and time-lags when gauging net change as described by Minns (2006) and Minns and Moore (2003).

7. The software is currently being revised by BioSoftware.com with a view to creating a version that will be freely available to any users in 2009.

4.2 Case Study

Minns *et al.* (2001) and Frezza and Minns (2002) both present case studies which evaluate and demonstrate the use of the Defensible Methods technique to predicting losses and gains to fish habitat productive capacity. However, in 1997 Minns presented a sample application of the method which will be summarized here. A proponent proposes to infill 46 hectares of a 100 hectare coastal wetland on the Great Lakes (Figure 4.1). The existing wetland is highly degraded due to the presence of common carp and a stream outlet which both contribute to high turbidity and a loss of rooted vegetation. The wetland contains few top predators (bass and northern pike) and little fish cover in the form of submerged vegetation or logs, stumps, rocks or boulders. In compensation for the lost wetland habitat the proponent proposes to improve the quality of the remaining 56 hectare by controlling the carp population, reducing the stream's

sediment load, replanting cattails and greatly increasing the amount of submerged cover.
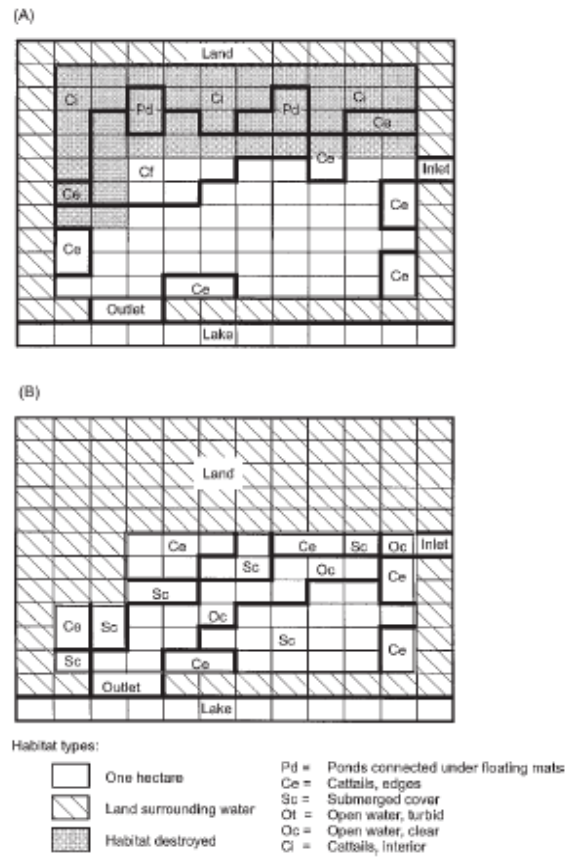
Figure 4.1 The pre- (A) and post- (B) development schematic of the coastal wetland infilling project including the destroyed and modified habitat. Note that the habitat units are separated by type (Pd, Ce, Sc, etc.) and standardized by size as they are made up of numbers of the same basic unit (from Minns 1997).

The p and p_{MAX} values for each habitat type are determined by a group of experts familiar with the local ecosystem (this could also be determined following targeted field assessments). The vegetation, substrates and water quality features are taken into consideration in regards to the requirements of the fish known to occupy coastal areas in the lower Great Lakes. In particular the spawning habitat is given the greatest priority (and rating) as it is considered a limiting resource in the Great Lakes and the existing size of the wetland is believed to be too small to support adult feeding requirements. Therefore the highest p_{MAX} values are assigned to the floating and edge cattails with lesser values for other habitats. In addition, the existing poor water quality contributes to low p_{NOW} values and would lead to higher p_{AFTER} values if the proposed compensation is

successful (Table 4.1). The generalized equation used to evaluate the changes in the wetland is

$$\Delta P_{NOW} = P_{AFTER} - P_{NOW} - P_{LOSSES}$$

where the P_{NOW} and P_{AFTER} refer respectively to the productive capacity of the wetland before and after project completion, including the infilling and habitat compensation. However, it is important not to exclude from the model the maximum potential fish habitat productive capacity that has been lost from wetland area that was filled in. This has been defined in this general equation as P_{LOSSES}. Also it is important to remember that each habitat criteria (such as open water, edge cattails…) must be included in the total productive capacity of the wetland. The expanded equation is therefore

$$\Delta P_{NOW} = \Sigma[(p_{AFTER-X} - p_{NOW-X})^*A_{AFTER-X}] - \Sigma[(p_{MAX-X} - p_{NOW-X})^*A_{LOSSES-X}]$$

where the subscript X refers to the different habitat criteria. In Table 4.1 each criteria is indicated by a line with the type identified. The totals at the bottom of the table indicate the sums of the individual habitat criteria and therefore the overall P_{NOW}, P_{AFTER} and P_{LOSSES}. In this example the framework equation results in

$$\Delta P_{NOW} = P_{AFTER} - P_{NOW} - P_{LOSSES} = 42.9 - 33.4 - 12.6 = -3.1$$

which indicates that following the development a deficit of 3.1 units of habitat productivity remain. To achieve a no-net-loss the 3.1 units will require additional compensation.

This example illustrates both the usefulness of the framework to provide a quantifiable measurement of the predicted habitat productivity following development but also of the importance of taking into account the additional losses in overall productive capacity from the maximum habitat productivity of lost habitat. If the difference between the potential maximum and the existing productivity had not been included in the losses, the compensation would have appeared adequate at an overall gain of 9.5 units.

Table 4.1 The parameter values used in the application of the Defensible Methods techniques on a wetland infilling project. Note that the 'Habitat after' reflects different productive capacity values for each habitat type than those for the 'Habitat now' and the 'Habitat losses'. (from Minns 1997)

Line	Habitat now				Habitat losses				Habitat after				ΔP
	Type	A_{NOW}	p_{NOW}	P_{NOW}	A_{LOSS}	p_{MAX}	P_{LOSS}	Δ_{LOSS}	Type	A_{MOD}	p_{MOD}	P_{MOD}	
1	Ci	23	0.3	6.9	23	0.5	11.5	−4.6					−11.5
2	Cf	15	0.7	10.5	10	1.0	10.0	−3.0					−10.0
3									Ce	5	0.8	4.0	0.5
4	Ce	13	0.4	5.2	4	0.9	3.6	−2.0					−3.6
5									Ce	9	0.8	7.2	3.6
6	Ot	44	0.2	8.8	4	0.7	2.8	−2.0					−2.8
7									Oc	14	0.6	8.4	5.6
8									Sc	25	0.9	22.5	17.5
9									Ce	1	0.8	0.8	0.6
10	Pd	5	0.4	2.0	5	0.6	3.0	−1.0					−3.0
Total		100		33.4	46		30.9	−12.6		54		42.9	−3.1

4.3 Strengths and Weaknesses

In the framework presented, Minns (1997) indicated the danger of relying on the traditional approach of anecdotal, non-quantitative evidence to evaluate losses to the productive capacity of fish habitat. His framework presented a method in which developments that modified or destroyed fish habitat could be quantified on the basis of lost productive capacity. This same method was able to also evaluate compensation plans to ensure that the productive capacity of the new habitats adequately off-set the losses due to development. This demonstrates the main strengths of the defensible methods and productivity models in general. They allow fish habitat managers to make decisions on issues such as habitat conservation and watershed management with a quantifiable measure of what is being lost or gained from the fish populations.

A weakness associated with habitat productivity models is the large amount of information required to validate them, however this is true of many types of models. To mitigate this weakness redundancy among measures can allow for the reduction of the number of species and life stages used to define the overall habitat capacity (Minns and Moore 2003). Since habitat suitability models drive the estimates of productive capacity, the defensible methods share the HSI weaknesses particularly in respects to the use of habitat surrogates or expert panels to determine the values of habitat. There are typically high levels of uncertainty associated with productive capacity estimates, however, as Minns and Moore (2003) indicate uncertainty should be incorporated in management decisions and is included in more recent versions of the HAAT. Last, the assumption of a fixed optimal habitat value for each species leads to the conclusion that existing species will not adapt to habitat changes and therefore may underestimate the altered habitat productivity.

Habitat Suitability Indices rely on knowing the local habitat preferences of the fish species of interest. To disseminate local habitat preferences of Canadian fish species the citations for the habitat preference manuscripts published for different regions in Canada are listed below.

Canada

Coker, G.A., C.B. Portt, and C.K. Minns. 2001. Morphological and ecological characteristics of Canadian freshwater fishes. Can. MS Rpt. Fish. Aquat. Sci. 2554:iv+86p.

Arctic

Richardson, E.S., J.D. Reist, and C.K. Minns. 2001. Life history characteristics of freshwater fishes occurring in the Northwest Territories and Nunavut, with major emphasis on lake habitat requirements. Can. MS Rpt. Fish. Aquat. Sci. 2569:149p.

Evans, C.E., J.D. Reist, and C.K. Minns. 2002. Life history characteristics of freshwater fishes occurring in the Northwest Territories and Nunavut, with major emphasis on riverine habitat requirements. Can. MS Rpt. Fish. Aquat. Sci. 2614: xiii+169p.

Newfoundland and Labrador

Grant, C.G.J. and E.M. Lee. 2004. Life History Characteristics of Freshwater Fishes Occurring in Newfoundland and Labrador, with Major Emphasis on Riverine Habitat Requirements. Can. Manuscr. Rep. Fish. Aquat. Sci. 2672: xii + 262p.

Bradbury, C., M.M. Roberge, and C.K. Minns. 1999. Life history characteristics of freshwater fishes occurring in Newfoundland and Labrador, with emphasis on lake habitat requirements. Can. MS Rep. Fish Aquat. Sci. 2485:vii+150p.

British Columbia

Roberge, M., T. Slaney, and C.K. Minns. 2001. Life history characteristics of freshwater fishes occurring in British Columbia with major emphasis on lake habitat characteristics. Can. MS Rpt. Fish. Aquat. Sci. 2574:189p.

Prairies

Langhorne, A.L., M. Neufeld, G. Hoar, V. Bourhis, D.A. Fernet, and C.K. Minns. 2001. Life history characteristics of freshwater fishes occurring in Manitoba, Saskatchewan, and Alberta, with major emphasis on lake habitat requirements. Can. MS Rpt. Fish. Aquat. Sci. 2579:170p.

Great Lakes

Portt, C.B., G. Coker, and C.K. Minns. 1999. Riverine habitat characteristics of fishes of the Great Lakes watershed. Can. MS Rep. Fish Aquat. Sci. 2481:vii+62p.

Lane, J.A., C.B. Portt, and C.K. Minns. 1996. Nursery habitat characteristics of Great Lakes fishes. Can MS Rep Fish Aquat Sci. 2338:42p.

Lane, J.A., C.B. Portt, and C.K. Minns. 1996. Adult habitat characteristics of Great Lakes fishes. Can MS Rep Fish Aquat Sci. 2358:43p.

Lane, J.A., C.B. Portt, and C.K. Minns. 1996. Spawning habitat characteristics of Great Lakes fishes. Can MS Rep Fish Aquat Sci. 2368:48p.

5 Habitat Productivity Index

5.1 Overview

The goal of the Habitat Productivity Index (HPI) is to provide a measure of the productive capacity of aquatic environments (Randall and Minns 2000). As previously shown, habitat capacity is difficult to measure directly and often requires subjective estimates from experts. Using HPI reduces the need for the productivity value to represent the exact value found in the ecosystem, as well as offers a simpler way to measure productive capacity. Fish production rate is a key measure of the carrying capacity of the habitat (Randall 2002). Production rate (P) is estimated as the product of the instantaneous growth rate ($G_{\Delta t}$) of the population and average biomass (B), for a defined time period (Δt, usually one year):

$$P = G_{\Delta t}\, B, \text{ and therefore } P/B = G_{\Delta t}$$

Measuring fish production rate to estimate the productive capacity of fish habitat can be expensive and time consuming however an alternative is to estimate habitat quality by calculating biological indices of production. The Habitat Productivity Index (HPI) was developed to allow biologists to quantify the quality of fish habitat by using the average fish biomass of all species at a location. The HPI is defined as the product of the average seasonal biomass of species i (B_i) with the ratio of fish production over biomass for species i $(P/B)_i$ summed for each species in the assemblage (number of species = n). The HPI provides an index of production capacity (kg / ha / yr) for the habitat area:

$$HPI = \Sigma\, B_i\, (P / B)_i$$

The P/B ratio is the annual production rate per unit of biomass and is used as an estimate of population growth (above equations). The maximum P/B ratio for a fish species is the same measure as the intrinsic growth rate of a species (r_{max}) which is used in population studies to investigate the ability of a species to rebound from population declines, colonize new habitats or withstand exploitation. For freshwater fish populations, the specific production rates do not vary systematically with biomass (i.e., the slope of production to biomass is not significantly different from 1; Figure 4.1A). However, P/B ratios vary depending on the size of fish (Figure 4.1B). Therefore the P/B ratio can be estimated by allometry with fish size. An example of such an estimate was used by Randall et al (1995) to determine the community P/B ratio in both lakes and rivers:

$$\log P/B = 0.12 - 0.35 \log W + 0.18 X$$

The W coefficient stood for average fish weight in the community and the X is an indicator variable that is 0 for lakes and 1 for rivers. In a subsequent study (Randall and Minns 2000) showed that for individual species, P/B could be estimated from weight-at-maturity (W_{mat}) as

$$P/B = 2.64 W_{mat}^{-0.35}$$

P/B ratios have been estimated for many freshwater fish species in Canada and can be obtained from the literature or government databases (Randall and Minns 2000).
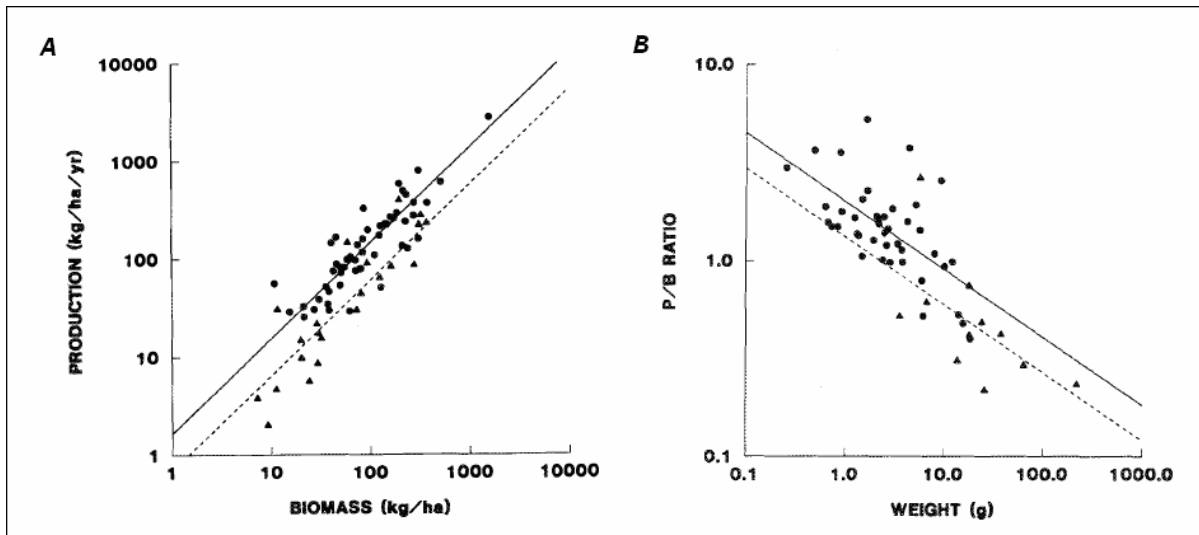
Figure 5.1. Scatter plots of data from rivers and lakes showing in A) the positive relationship between fish production and biomass and in B) the negative relationship between the unit production over biomass ratio and average fish weight (from Randall *et al.* 1995).

The assumptions associated with the HPI are:

1. Fish production is correlated with average fish biomass
2. Fish biomass density (kg/ha) is linked to habitat capacity
3. The P/B coefficient adjusts for the effects of fish size on the population production, (i.e., it is a proxy for population growth rate)

The HPI is useful for habitat management as it provides an estimate of the productive capacity of a habitat. However, it is important to remember that HPI values, although expressed as a rate, are best used as an index because of the reliance of estimates of growth from body size rather than field studies on actual fish growth.

Note that the term 'productivity' in the Habitat Productivity Index is a misnomer, in view of the definitions presented in Chapter 3. To achieve standardization in terminology between fisheries and habitat science, a definitions document (Randall 2003) was published after the HPI document (Randall and Minns 2000). The Habitat Productivity Index is an index of habitat productive capacity, and in this context, capacity is a more appropriate term than productivity.

5.2 Case Study

Randall and Minns (2002) compared two indices, HPI and the Index of Biological Integrity (IBI), in three habitat types in southern Ontario. Coastal wetlands, harbours and exposed shorelines were assessed in both Lake Erie and Lake Ontario. Fish were sampled by boat electrofishing along 100 m transects within the three habitat areas. Fish data from the sites were used to calculate the HPI. An average biomass (kg/ha) was calculated for each species that was sampled. The production index was then derived by multiplying the average biomass by the species P/B ratio (calculated from Randall and Minns 2000 by $P/B = 2.64W^{-0.35}$, where W is the average weight of each species captured). A final HPI was calculated as the sum of all the production indices in one location. Macrophyte abundance, substrate particle size, temperature and fetch (site exposure) were the main habitat characteristics and measured during the fall at each location.
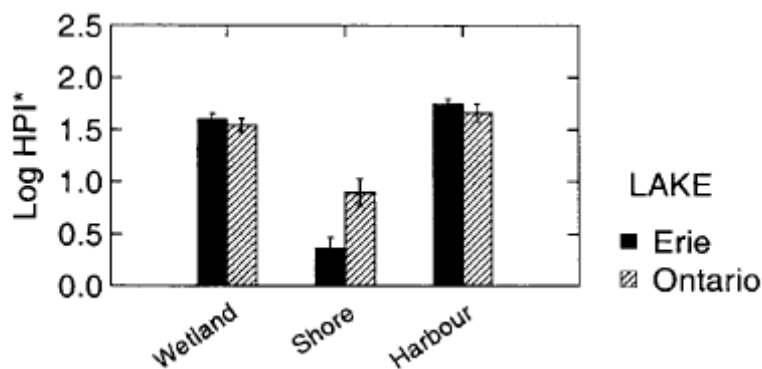
Figure 5.2 Habitat Productivity Index (HPI, log scale) for wetland, exposed shoreline and harbour habitat in Lake Erie and Lake Ontario (from Randall and Minns 2002).

The Habitat Productivity Index was shown to be statistically different at the habitat types in the lower Great Lakes (Figure 5.2). The HPI was higher at coastal wetlands and harbour breakwalls than at exposed shoreline habitat, and the difference was consistent between the Lake Ontario and Lake Erie survey sites. The average fish size was smaller at the coastal wetlands than at the harbours, and the HPI reflected this

difference. Although highly correlated with fish biomass (Figure 5.3), the HPI accounted for the size structure of the fish assemblages at the different habitats. HPI was significantly different among habitats only after adjusting for biomass. Sites with similar biomass but smaller fish had a higher HPI value than sites with larger fish. The HPI did not reflect the species richness found in the different habitats because it is a measure of biomass and not the fish assemblage.
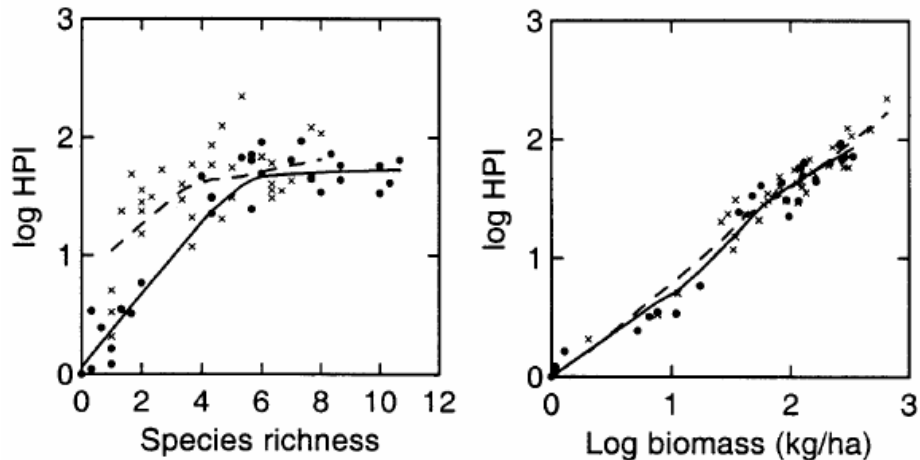
Figure 5.3 Scatterplots of logHPI data from Lake Erie (circles) and Lake Ontario (crosses) related to species richness and biomass. Note that the HPI increases linearly with species richness until it reaches an asymptote in both lakes, whereas it increases linearly with log biomass throughout the range of values (from Randall and Minns 2002).

Randall and Minns (2002) contended that to effectively measure the habitat productive capacity of species-rich habitats in the Great Lakes, a two axis-approach was needed, combining both HPI and IBI. HPI and IBI were measures of the fish production and species diversity characteristics of the fish community, respectively. IBI is discussed in the next section.

Other studies showing the potential utility of P/B ratio/fish biomass models to measure habitat capacity and production dynamics were Randall (2002) and Cote (2007) for salmonids in rivers and Roth *et al.* (2007) for fish species in lakes.

5.3 Strengths and Weaknesses

The main strength of the HPI method is that it provides a measure of productive capacity that is intuitive to the kind of questions that are routinely asked to achieve no-net-loss in an aquatic community or evaluate potential developments. The process is

also straightforward and has shown to be adaptable across multiple environments. The method is likely to be used more in the future because:

1. P/B ratios can be obtained from the literature or from existing allometric models;

2. Biological indices of habitat capacity are easy to interpret by both biologists and habitat managers; and,

3. Habitat conservation goals are explicitly linked to fish population goals.

As shown in the example however, the main weakness of HPI models is that they capture the value but not the nature of the productive capacity that is found in the system. In the example given the HPI was influenced strongly by the size of the fish and therefore could remain the same in a site in which a development was influencing the average fish size if the number of fish compensated for the change. As shown, HPI also does not account for changes in biodiversity. Therefore it is recommended that an additional index or measure is used to complement the HPI. Other weaknesses include:

1. Quantification of fish biomass density (kg/ha) in different habitats is challenging particularly in deep (non-wadeable) areas of rivers and near shore habitats of lakes; and,

2. Factors other than habitat may limit fish biomass (e.g., exploitation).

6 Index of Biotic Integrity

6.1 Overview

The Index of Biotic Integrity (IBI) was developed in the early eighties as a tool to classify and rank the environmental quality of aquatic habitats using the presence of biological indicator species (Karr 1981). Before the development of the IBI method the quality of aquatic habitats was assessed based on chemical indicators through toxicological and water quality studies. However, it was found that assessment methods that did not include the biological components of the ecosystem lacked predictive power and a proper ecological context. The IBI methodology was designed to use biological components (metrics) to determine the relative health of the aquatic environment (Table 6.1). The metrics could be tailored to a specific environment however they usually included measures of taxonomic richness, habitat and trophic guild composition, species health and species abundance. The main criteria for a metric are that it demonstrates a range of values across a gradient of environmental quality and is expected to be found in most aquatic ecosystems. Fish assemblages provide good indicator species because they vary in their tolerance to degraded habitat conditions,

are well distributed throughout many watersheds, are economically important, and rely on both primary and secondary production.

Table 6.1. List of metrics and their scores of the first IBI developed (from Roset *et al.* 2007).

Category	Metrics	Scoring criteria 5	Scoring criteria 3	Scoring criteria 1
Species richness	Total number of fish species		Varies with stream order	
Species composition	Number of darter species		Varies with stream order	
	Number of sunfish species		Varies with stream order	
	Number of sucker species		Varies with stream order	
Tolerance guilds	Number of intolerant species		Varies with stream order	
	% Individuals as green sunfish	<5	5–20	>20
Trophic guilds	% Individuals as omnivores	<20	20–45	>45
	% Individuals as insectivorous cyprinids	>45	20–45	<20
	% Individuals as piscivores	>5	1–5	<1
Abundance	Number of individuals		Varies with stream order	
Reproduction and condition	% Individuals as hybrids	0	>0–1	>1
	% Individuals with anomalies	0–2	>2–5	>5

Scoring: 5, near reference; 3, significant deviation from reference; 1, strong deviation from reference.

The IBI is developed by first choosing appropriate indicators (or metrics) to evaluate the habitat quality. The metrics presented in Table 6.1 are often used as a guide to tailor more site specific metrics. For example, an IBI developed in Europe would likely use different species (in the Species Composition category) and different criteria (in the Tolerance Guilds, Trophic Guilds, and Reproduction and Condition categories) to assess degraded habitat. In addition, the scale of the study must be considered when choosing metrics. Those tailored only for headwater environments will likely not translate well if the IBI is going to be used across the watershed. Once the metrics are chosen, scoring criteria for the value of the site specific indicators must be chosen. There are many types of scoring criteria developed for IBI methodologies however the most common is the 1 / 3 / 5 criteria. Poor habitat quality is scored as 1, moderate habitat quality is scored as 3 and good habitat quality is scored as 5. Expert knowledge is often used to determine which values for each metric correspond with poor, moderate or good habitat quality. For example in the original IBI model (Table 6.1) poor habitat quality for the '% Individuals with Anomalies' metric is defined as 'greater than 5% of the population'. Once the scoring criteria are established, reference and study sites within the watershed are sampled for the identified metrics. Each site specific metric is scored individually and then summed together to create an overall IBI site score. This IBI score can be used to determine the relative health of the site within the watershed or as compared to reference sites.

It is important to distinguish between natural variation and habitat degradation in the IBI methodology. Natural variation between sites could result in altered IBI scores that could wrongly be attributed to habitat degradation. The scale of the study will determine

what types of variation between sites should be expected and accounted for. The study site sampling methodology must be robust enough to ensure that an equal amount of effort is expended for each site. Many of the metrics proposed rely on population estimates therefore it is important that the catch-per-unit effort is the same for each site. Site sampling must be conducted over a range of conditions to ensure that variation due to seasonal influences (such as migrations) is accounted for. Typically reference and impact (or study) sites are chosen within the watershed. Reference sites are ideally pristine sites that will result in high IBI scores against which the impact site scores can be compared. However, pristine sites are not found in many watersheds in southern Canada therefore reference sites may consist of sites that demonstrate a range of habitat qualities found in the watershed. Some authors suggest testing the correlation between metrics because many published IBI models have a high amount of redundancy. Others have suggested that the redundancy is necessary to prevent a high value in only one metric from artificially raising the overall IBI score.

6.2 Case Study

Long and Walker (2005) developed and tested an Index of Biotic Integrity on a large boreal river to assess the impact of riprap on habitat quality. A hydroelectric impoundment on the Winnipeg River had raised average water levels by 2 m causing concerns for downstream bank erosion. Riprap armouring was installed along multiple stretches of the river to protect the banks. An IBI study was initiated because little information was available on the impact of riprap to fish habitat in large boreal rivers. In addition, the study offered novel approaches to the IBI method as there were few pristine sites to create a reference index and the IBI method is rarely used for point-sources of potential habitat degradation.

The original 12 metrics recommended by Karr 1981 were modified to suit the conditions of the northern boreal river (Table 6.2). Appropriate representative fish species were chosen over the ones proposed for American rivers (where the IBI was developed) and the use of the 'proportion of hybrids' metric was removed. Twelve sampling locations were randomly chosen over armoured and unarmoured banks. All sampling locations were sampled on a weekly basis for two seasons (late spring to early fall). Fish sampling was conducted using beach seines (4 mm mesh) and was designed to target juvenile and small fish. At each sampling location an identical area and number of passes was sampled to ensure that the catch per unit effort was equivalent across sites. Data for each site were pooled across seasons and years to minimize variation in the data. Due to the lack of pristine sites to make the reference index, the IBI scores were generated by comparing each site to the variability found within the study area. Each site was judged on the basis of what can be realistically expected in the river rather than

in an ideal scenario. The raw data for each metric was sorted into quartiles. Quartiles are simply the ordering of values from lowest to highest and the division of the values into four groups from lowest (first quartile) to highest (fourth quartile). For each metric IBI scores were assigned based on the following criteria:

1. A score of 1 was given to site metric values that were within the 25% lowest values for the entire system (first quartile);

2. A score of 3 was given to site metric values that were between 25% and 75% of the ordered values for the entire system (second and third quartiles); and,

3. A score of 5 was given to site metric values that were within the 25% highest values for the entire system (fourth quartile).

The site scores were summed to generate the overall IBI score for each site. The IBI scores were tested for statistical difference from each other using the Mann-Whitney *U*-test. Further statistical tests were used to determine the contribution of each metric to determining the different IBI scores across the sites on the Winnipeg River.

Using the habitat quality ratings proposed by Karr (1981) the fish habitat ranged across the sampling locations from "very poor" to "good". The IBI scores for armoured and unarmoured sites were found to be significantly different from each other (Table 6.3). Sites with riprap were found to score higher IBI scores than unarmoured sites suggesting the riprap has a positive impact on habitat quality in the Winnipeg River. The authors concluded that the armouring contributed to higher biotic integrity because the riprap created local environments similar to the rocky outcroppings found throughout the river. It was also found that many of the metrics were redundant, which is consistent with early findings on the IBI methodology. The study demonstrated that the IBI methodology can be robust but must be tailored to the local study area. In this study, the use of johnny darters as indicators of habitat degradation and sticklebacks as indicators of intolerance to turbidity were well suited to conditions found in the Winnipeg River. Minns *et al.* (1994) also modified the IBI for use in littoral habitats of the Great Lakes. In their study IBI values were shown to be correlated with physical habitat, water quality and biotic features.

Table 6.2. List of metrics developed for an IBI model on a northern boreal river (from Long and Walker 2005).

	Metric	Karr's 1981 metric	Modified metric	Source	Study context
Number of	1	Fish species	Unmodified		
	2	Darter species	Benthic species (darters, sculpins & Longnose dace)	Karr et al. (1986)	Theoretical model
				Steedman (1988)	Urban drainage basin
				Ganasan & Hughes (1998)	Chemical contamination
				Schleiger (2000)	Land use effects
	3	Sunfish species	Centrarchidae species	Simon & Emery (1995)	Water quality great rivers
	4	Sucker species	Unmodified		
	5	Intolerant species	Stickleback species	*sensu* Goldstein & Simon (1999)	Guild structure assessment
	6	Individuals	Unmodified		
Proportion of	7	Green sunfish[1]	Johnny darters[1]	Karr (1981)	Warm water streams
	8	Omnivores[1]	unmodified[1]		
	9	Insectivorous cyprinids	Unmodified		
	10	Top carnivores[2]	Unmodified[2]		
	11	Hybrids	Removed		
	12	Disease, etc.[1]	DELTS[1]	Yoder & Smith (1999)	Ohio USEPA

For all metrics except [1] higher raw data values produced higher IBI scores. Exceptions work in reverse, where lower values yield higher IBI scores. YOY smallmouth bass were not assigned to metric ten [2], since most specimens captured were < 50 mm TL. Where appropriate, source citations for modifications are given. Species allocation to metric nine (insectivorous cyprinids) according to Goldstein & Simon (1999) and to metric 10 (top carnivores) according to Scott & Crossman (1998).

Table 6.3. List of metrics and site scores calculated for an IBI model on a northern boreal river (from Long and Walker 2005).

	1	2	3	4	5	6	7	8	9	10	11	
	Number of						Proportion of					Total IBI Site Score
	Species	Benthic species	Centrarchid species	Sucker species	Stickleback species	Individuals in sample	Johnny darter	Omnivores	Insectivorous Cyprinids	Top Carnivores	DELTS	
IBI Metric Data and Site Scores												
Site 1	19(5)	6(5)	1(3)	1(3)	1(3)	1515(3)	0.326(1)	5.94(1)	17.0(3)	14.719(3)	0.660(5)	35
Site 2	17(3)	5(3)	1(3)	1(3)	1(3)	978(1)	0.308(1)	20.04(1)	16.2(1)	12.986(3)	7.157(1)	25
Site 3	18(3)	4(3)	1(3)	1(3)	1(3)	1071(3)	0.565(1)	2.33(3)	6.5(1)	8.217(1)	2.801(3)	27
Site 4	14(1)	4(3)	1(3)	1(3)	0(1)	953(1)	0.773(1)	0.84(3)	4.7(1)	5.352(1)	6.296(1)	19
Site 5*	16(3)	5(3)	1(3)	1(3)	1(3)	1305(3)	0.255(3)	3.83(1)	19.4(3)	18.238(5)	1.533(3)	33
Site 6*	19(5)	5(3)	1(3)	1(3)	1(3)	2027(3)	0.038(5)	0.20(5)	39.6(3)	18.106(3)	1.480(3)	39
Site 7*	18(3)	6(5)	1(3)	1(3)	2(5)	1293(3)	0.087(3)	1.24(3)	40.6(3)	27.920(5)	5.414(1)	37
Site 8	18(3)	3(1)	1(3)	1(3)	1(3)	1423(3)	0.203(3)	0.91(3)	23.3(3)	8.152(1)	4.919(3)	29
Site 9	14(1)	3(1)	1(3)	1(3)	0(1)	750(1)	0.240(3)	0.27(3)	35.1(3)	18.133(5)	0.000(5)	29
Site 10*	19(5)	5(5)	1(3)	1(3)	1(3)	10500(5)	0.005(5)	0.01(5)	64.0(5)	10.610(3)	0.667(3)	45
Site 11*	15(1)	3(1)	1(3)	1(3)	1(3)	4707(5)	0.031(5)	0.23(5)	56.6(5)	12.195(3)	0.000(5)	39
Site 12*	20(5)	4(3)	2(5)	1(3)	2(5)	3465(5)	0.051(5)	0.40(3)	57.6(5)	14.315(3)	1.154(3)	43
1st quartile	15.75	3.75	1	1	1	1048	0.047	0.26	16.8	10.011	0.665	
3rd quartile	18	5	1	1	1	2387	0.312	2.71	44.6	18.113	5.043	

For metrics 7, 8 & 11, lower values receive higher scores. *Denotes sites armoured with rip rap armouring.

6.3 Strengths and Weaknesses

Biological Indices of Diversity share many strengths and weaknesses with the HPI and P methods. The strengths of the IBI models include:

1. Allows for excellent long term monitoring programs;
2. Provides a standard assessment tool that uses assemblages that have immediate social, economic and conservation value;
3. Allows for standardization of fish sampling methods such that IBI studies can be compared and data from equivalent reference sites can be used for large scale analyses; and,
4. Wide application across the world resulting in refinement of methods and demonstration of versatility of method.

Criticisms of the use of IBI models for habitat studies include:

1. Difficulties accounting for natural and temporal variation rather than human induced impacts if sampling design cannot explicitly test these different sources of variation;
2. Not as accurate for large rivers or species poor areas;
3. IBI values are gear dependent (Jackson and Harvey 1997);
4. Need for rigorous testing of candidate indices for redundancy and sensitivity as well as a more rigorous testing of hypotheses associated with the index; and,
5. No method for the objective determination of the number of metrics to be used in final analyses. The method leaves room for subjective judgement on which indices described the best situation.
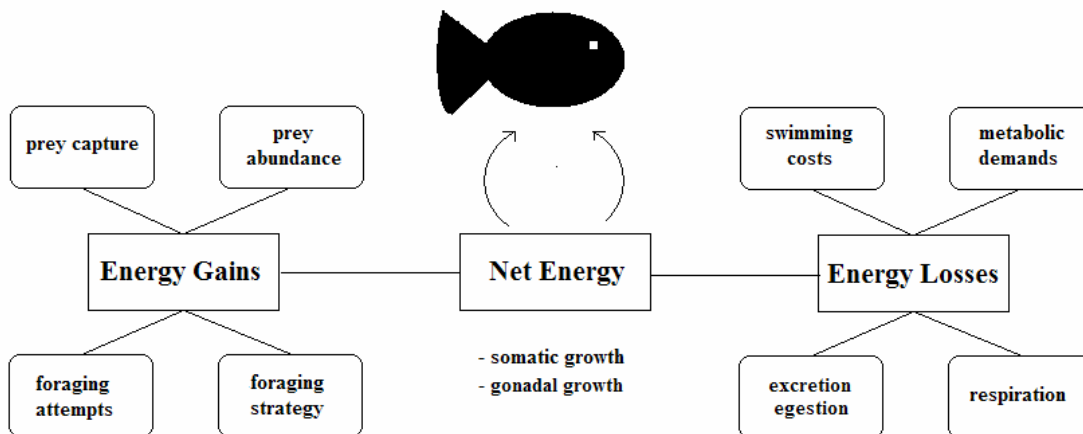
7 Bioenergetic Models

7.1 Overview

The goal of bioenergetic modelling in habitat models is to use the physiology of the species to determine how changes in the environment might impact its population's productivity. These models can be related to estimates of productivity rather easily as they often lead to direct estimates of fish tissue growth. Bioenergetic modelling involves the use of known physiological and metabolic relationships to create a net energy budget for an individual fish. The models are all based on a simple equation (Figure 7.1):

Net Energy = Energy Ingested – (Energy Expenditures and Losses)

In this equation the use of the Net Energy is not specified but it is usually used for one or a combination of growth in body size (somatic) and reproduction (gonadal). The model output of energy is usually measured in Joules and can then be converted into a growth rate.   Energy in fish is assumed to only come from eating prey items. This makes the first half of the equation easy to conceptualize and often easy to measure or predict. The second half of the equation involves variables that result in a loss of net energy. Expenditures refer to metabolic demands including the energy costs of swimming, digestion and respiration. Losses refer to the energy contained in unused or unassimilated food items that are released during excretion and egestion. Bioenergetic models can either be designed as discrete or continuous. Discrete models offer a snapshot of an energy budget over a time period, for example the daily net energy of a foraging fish in a stream. Continuous models are used to examine cumulative energy budgets and how the net gain changes as the fish grows or enters reproductive maturity. Because energy losses are most often related to the fish's body size and behaviour, the energy budgets are expected to change over the life span of an individual. However, although some of parameters of the model may change as a fish reaches maturity or alters its behaviour, many of the key elements of a bioenergetic model can be used from the moment the fry begins exogenously feeding through to its adult form.

Figure 7.1. A generalized process for developing bioenergetic models.

The parameters for bioenergetic models vary between models and are typically species or family specific; however, there are some general categories that are found in all models. The Energy Ingested in its simplest form can be estimated as the satiation level for the fish. This is only possible if the fish has an unlimited source of food and no restrictions on obtaining or capturing the food, a situation commonly found in aquaculture facilities and therefore can be realistically incorporated into a model. However, wild fish rarely feed to satiation and are restricted by the abundance of prey,

the ease of capture of the prey and the amount of time they can devote to foraging each day. The abundance of prey can be estimated from field studies or other known relationships in the target habitat. The ease of capture for a prey type is usually represented by a rate of capture, or a probability of success per attempt. The foraging time for many fish species is known or can be estimated. An important component of the model is to know the energy value of each prey type. Some prey types are more nutritionally valuable and easier to digest than others.

The Energy Expended is often derived by estimating the activity of the fish during the day. Metabolic demands can be estimated by applying a resting or active metabolic rate to the fish's daily activities. A resting metabolic rate represents the energy expended by the fish when it is holding its place in still water. The active metabolic rate represents the energy expended by the fish when it is moving through the water column or holding a position in a current. Published relationships for these metabolic rates are available for many fish species in Canada. Additional energy expenditures include swimming (active and passive), respiration and digestion. The energy required for swimming is estimated based on the type of swimming (steady or unsteady), the speed and the duration. The energy required for respiration and digestion involves relationships that take into account how much food was eaten as well the temperature of the ambient water. Temperature has a great influence on many physiological processes in aquatic environments and is often a component of relationships found in bioenergetic models. This is similar to the Energy Losses which are often derived from laboratory experiments on the fish species. If published relationships are not available for the target species they can either be created from physiology experiments or estimated using a similar fish species' known relationships. As the number of parameters required for bioenergetic models is high, many assumptions are typically made to be able to borrow known relationships from other species.

Bioenergetic models can be integrated with spatial information to determine how the quality of fish habitat impacts the net growth or fitness of the fish. The relationship between the environment and the individual fish can be complex and involve many of the variables in the model. A few examples to illustrate the point include 1) a standard metabolic rate is often related to the ambient temperature, 2) stream current velocities influence how much energy will be expended from swimming, and 3) prey abundance influences the available energy ingested. Variables such as these can be used to compare the overall energetic costs and benefits of using different habitats. In addition, alterations to fish habitat can be modeled to determine the potential impact to fish. For example, if a hydroelectric facility releases cooler water into a reach the impact to the average growth of the fish solely due to temperature can be relatively easy to predict. Jones, Tonn, Scrimgeour and Katopodis (2003) also used temperature to determine the effectiveness of a compensation stream in NWT for Arctic grayling growth. More

complex relationships between available habitat and habitat complexity can also be used to integrate a higher degree of spatial detail however they usually require additional assumptions or known relationships.

Due to the high information needs to develop bioenergetic models, their integration with spatial models has mostly been used at microhabitat scales. However, a few bioenergetic modelling studies involving the whole stream (Hughes 1998), multiple habitats (Rosenfeld and Boss 2001) and long time periods (Hayes *et al.* 2000) have shown the potential to increase the scales of the spatial and temporal integration.

Bioenergetic models are often field verified or tested through a sensitivity analysis. Field verification involves inputting parameter values measured in field studies and comparing the output of the model with the field observations. It is sometimes not possible to find or measure the proper parameters for a model in the field. In these situations a sensitivity (or elasticity) analysis can be used to determine the relative importance of the parameters to the model output. A sensitivity analysis is usually conducted by selecting a suite of parameters and artificially changing each of their values while keeping the rest at normal levels. These analyses are useful because they tease out the relative importance of each parameter which can allow the researcher to ask whether the level of importance seems justified given what is known about the natural system.

A commonly used commercially available software is Fish Bioenergetics 3.0 which is also known as the Wisconsin Model (Hartman and Kitchell 2008). This software offers a modelling platform as well as physiological information for over 75 species of freshwater fish. The software is derived from some of the early bioenergetic models designed in the 1970s (Kitchell et al. 1977).

7.2 Case Study

Nislow, Folt and Parrish (2000) created a bioenergetic model of young-of-the-year Atlantic salmon to determine the quality of rearing habitat in the Connecticut River. The aim of the model was to predict the growth rate potential (GRP) for the Atlantic salmon in different areas of the river to assist with a stocking program on the river. It had been hypothesized that some of the candidate habitats were not suitable for rearing due to low foraging success, low water temperatures and high spring discharges. The researchers also wanted to know if 1) the salmon densities were highest at the rearing sites with corresponding model outputs of predicted high GRP, and 2) habitat preferences changed over the course of the summer in response to changing GRP at the rearing sites. The overall objective of the study was therefore to allow researchers

to input fish habitat values found in a potential rearing site in the model and find out if it was suitable for young-of-the-year Atlantic salmon.

The researchers developed a spatially explicit bioenergetics model which took into account the potential energy gains and losses of the Atlantic salmon along with their spatial distribution, their prey's distribution and the physical conditions that affected their growth and foraging success. Tables 7.1 and 7.2 demonstrate the parameters used in the foraging and growth components, respectively, of the model. Note that not all the parameters were derived for this particular study and were instead borrowed from others. The foraging component of the model converted the prey abundance into a value of potential consumption (i.e., Energy Gained) and the growth component of the model converted the consumption into the potential growth rate (i.e., Net Energy). Prey abundance, stream habitat characteristics (depth and velocity), fish territory sizes, time spent foraging and fish body size were some of the parameters that determined the predicted consumption for each individual. These parameters were dependent on the season as prey abundances and stream characteristics typically change in rivers from spring to the end of the summer. Therefore the model was made to account for the different conditions in spring, mid summer and late summer. The growth component of the model included the parameters discussed in this primer to predict the energy losses and expenditures of each Atlantic salmon. The only parameter that changed in the growth model over the course of the summer was metabolism which is dependent on the ambient water temperatures. The model output was the Atlantic salmon growth potential for the target rearing site.

Table 7.1 Table of equations and parameters for the foraging component of a spatially explicit young-of-the-year Atlantic salmon bioenergetics model (from Nislow *et al.* 2000)

Parameter	Units	Equation or value	Derivation
Consumption (C)	Prey·d^{-1}	$= P \cdot S \cdot T$	
Prey supply rate (P)	Prey·d^{-1}	$= D \cdot A \cdot V$	
Prey density (D)	Prey·(m^3)$^{-1}$	Early $= 7.85$	Folt and Parrish (1994)
		Mid $= 23.33$	
		Late $= 15.17$	
Proportion of appropriate-sized prey (A)		Early $= 0.8$	Folt and Parrish (1994)
		Mid $= 0.5$	
		Late $= 0.4$	
Volume flux (V)	m^3·d^{-1}	$= \text{TW} \cdot Z \cdot \text{CV}$	
Territory width (TW)	m	Early $= 0.1$	Kalleberg (1958); Grant and
		Mid $= 0.25$	Kramer (1990)
		Late $= 0.3$	
Water depth (Z)	m	Individual measurements	Nislow et al. (1999)
Current velocity (CV)	m·s^{-1}	Individual measurements	Nislow et al. (1999)
Capture success (S)		$= \text{SI} + \text{SC(CV)}$	
Capture success coefficient (SC)		Early $= -3.2$	Nislow et al. (1999)
		Mid $= -2.17$	
		Late $= -1.12$	
Capture success intercept (SI)		Early $= 0.83$	Nislow et al. (1999)
		Mid $= 0.93$	
		Late $= 1.0$	
Time spent at feeding station (T)	h	12 h/d	Nislow et al. (1998)

Table 7.2. Table of equations and parameters for the growth component of a spatially explicit young-of-the-year Atlantic salmon bioenergetics model (from Nislow *et al* 2000).

Parameter	Units	Equation or values	Derivation
Growth (G)	$g^{-1} \cdot g^{-1} \cdot d$	$= EAG \cdot SED^{-1} \cdot SWT$	
Energy available for growth (EAG)	J	$= EI - (W + R)$	
Energy intake (EI)	$J \cdot d^{-1}$	$= C \cdot PWT \cdot PED$	
Prey dry weight (PWT)	g	$1.35 \cdot 10^{-4}$	Folt and Parrish (1994)
Prey energy density (PED)	$J \cdot g^{-1}$	4,800	Cummins and Wuychek (1971)
Salmon energy density (SED)	$J \cdot g^{-1}$	9,800	Gardiner and Geddes (1980)
Salmon dry weight (SWT)	g	Early $= 0.4$	
		Mid $= 1.2$	
		Late $= 3.0$	
Waste losses (W)	$J \cdot d^{-1}$	$= EG + EXC$	
Egestion (EG)	$J \cdot d^{-1}$	$= 0.15 \cdot EI$	Hill and Grossman (1993)
Excretion (EXC)	$J \cdot d^{-1}$	$= 0.10 \cdot EI$	Hill and Grossman (1993)
Respiration (R)	$J \cdot d^{-1}$	$= M + SDA$	
Metabolism (M)	$J \cdot d^{-1}$	$= M_r + M_a$	
Activity metabolism (M_a)	$J \cdot d^{-1}$	$= (T \cdot 24^{-1}) \cdot M_r$	
Resting metabolism (M_r)	$J \cdot d^{-1}$	Early $= 24$	Hill and Grossman (1993)
		Mid $= 65$	
		Late $= 80$	
Specific dynamic action	$J \cdot d^{-1}$	$0.15 \cdot EI$	Hewett and Johnson (1992)

To test the model the researchers employed both a field verification study and a sensitivity analysis. Field studies were conducted on six study streams within the Connecticut River basin. The stream habitat characteristics and the abundance of prey and Atlantic salmon at the study sites were collected over the course of the spring and summer. Fish distribution data was also obtained from yearly inventory records from the Vermont Department of Fish and Wildlife. The model was verified by comparing the predicted GRP with the observed proportional Atlantic salmon densities at each site. In addition the fish gut contents were analyzed to test the foraging rates predicted by the model. The sensitivity analysis involved altering the capture success, appropriate prey abundance, resting metabolism and salmon energy density to determine the impact on the GRP. The value of the parameter would be changed by 60% while holding the other parameters at the same value. The sensitivity analysis was run at each season to determine how the relative importance of the parameters changed over the course of the summer.

The results of the modelling exercise indicated that areas with a predicted higher growth rate potential did in fact demonstrate higher densities of Atlantic salmon in the field (Figure 7.2). The model was therefore a good predictor of suitable rearing habitat. As suggested by the model, the rearing habitat increased in value over the course of the summer such that the GRP was low in the spring due to low prey abundances and high water currents. In addition the model was successful at predicting foraging rates of young-of-the-year Atlantic salmon (Figure 7.3).
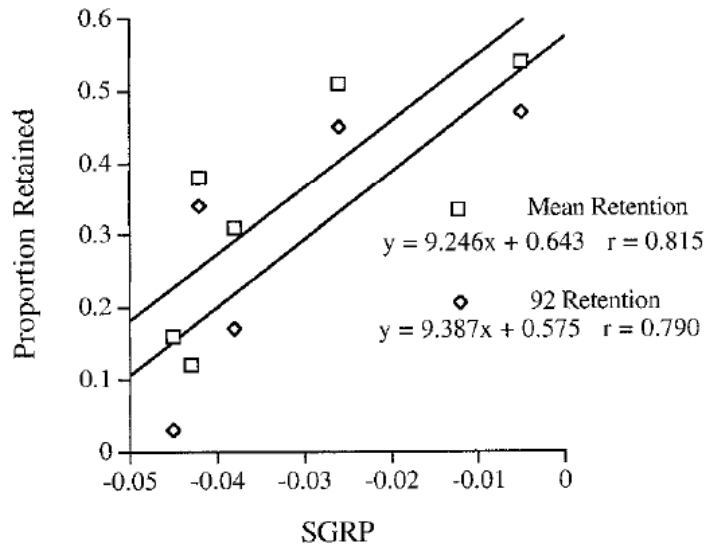
Figure 7.2. The correlation between the proportional retention of young-of-the-year Atlantic salmon and the predicted growth rate potential of a rearing site on the Connecticut River (from Nislow *et al.* 2000). One line is for 1992 data whereas the other is for a five year average.
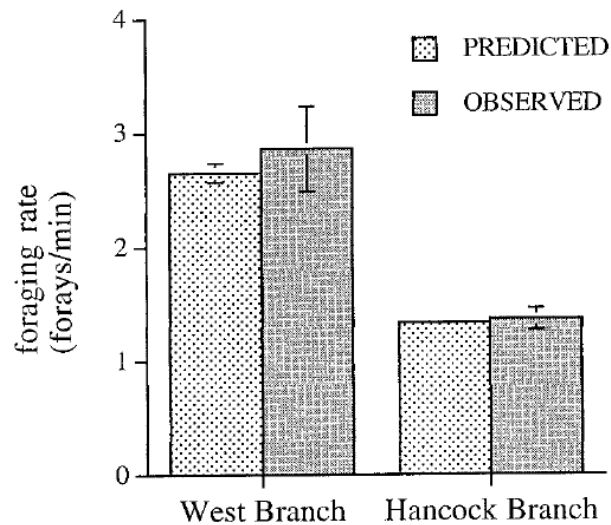
Figure 7.3. Predicted versus observed foraging rates in two different young-of-the-year Atlantic salmon rearing sites on the Connecticut River (from Nislow *et al.* 2000)

7.3 Strengths and Weaknesses

The use of bioenergetic modelling in fish habitat management is relatively low and correlative models such as Habitat Suitability Indices and Index of Biotic Integrity are much more common. However, bioenergetic models offer many strengths which will likely result in their increased use in the future:

1. As a mechanistic model with functional relationships between its parameters bioenergetic models allow for the exploration of causal relationships rather than only correlative relationships;
2. The bioenergetic models provide a realistic base for the relationship between the organism and its environment. Once the basic model is developed other ecological, evolutionary and behavioural models can be easily added to it to explore a wide variety of questions;
3. Outputs provide real behavioural or physiological data that can be verified in empirical research; and,
4. Foraging models integrate habitat structure with ecosystem productivity.

Criticisms of the use of bioenergetic models for habitat studies include:

1. Not as applicable to large spatial or temporal systems because the level of ecosystem complexity can limit the model;
2. Difficult to incorporate or estimate rates of mortality to scale the model from individuals to populations;
3. There is sometimes a high amount of error associated with its output due to the need for many assumptions for creating the metabolic relationships;
4. Large data needs (e.g., see Tables 7.1 and 7.2) make the model unfeasible for rare species for which little is known
5. Little data on larval and juveniles available to create lifetime energy budgets; and,
6. Large uncertainties are often associated with the modelling of the prey movements or abundances.

8 Trophic Models

8.1 Overview

Trophic models differ from the other models presented in the primer mainly due to their inclusion of multiple species within a food-web. Single species models, even bioenergetic and stage-structured, do not typically account for the energy being transferred through the food web and the inter-relationships among species within the community. Trophic interactions are however key parts of a functioning ecosystem and

contribute to the overall stability of the system. Modelling food webs has been conducted in ecological research for many decades, however, with a relatively recent interest in the role of biodiversity for ecosystem stability, many new trophic modelling approaches have been developed for both research and management purposes. The large benefit in using trophic models is that indirect and direct impacts of habitat alterations can be estimated. Indirect actions transferred through the food web may have unexpected impacts to top predators which may be recreationally important or protected for conservation purposes. For example, changes in near shore habitat availability may not directly impact the spawning or rearing habitat of lake trout, however, if it significantly decreases the productivity of its prey, or that of the primary consumers, the lake trout population could also decline.

An important question in trophic modelling is how to define the position of an organism within a food web. Ecosystem structure is complex and in most cases not as simple as a linear food chain. Some modelling techniques group species based on similar functions to create a food chain with discrete trophic levels. However, many fish species contribute to multiple trophic levels (for example through omnivory) which makes it difficult to group them. If the concept of discrete trophic levels is put aside and instead replaced with that of continuous trophic positions, the modelling of the ecosystem becomes more realistic.

Trophic models are often based on the flow of energy through a system. The flow of energy from one species to another can be approximated to define the trophic path from one species to another. For example, in Figure 8.1, a simplified food web is presented with primary producers (phytoplankton), primary consumers (zooplankton), other consumers (insects and forage fish) and a top predator (large fish). A modelling schematic accompanies the figure which demonstrates the direction of the flow of energy (up the food web) as well as the relative proportion of energy each trophic position provides to next one. In the simplified diagram, small fish mostly feed on insects (80%) yet also feed on zooplankton (20%). All of their energy is transferred to the top predators however this only accounts for 60% of their energy source as they also feed on insects. Note that the energy flow does not suggest that the total energy is equally transferred from one position to another. As noticed in nature a large amount of energy is lost between each trophic position (as heat or by-products of metabolism). Also note that consumers (especially those at higher trophic positions) can receive their energy through multiple paths. In Figure 8.1 the top predator can receive its energy through three main pathways: 1) S1 to S2 to S3, 2) S1 to S2 to S4, or 3) S1 to S2 to S3 to S4. The trophic position of the top predator is determined by the average of the lengths of each pathway which in this case is 3.33. To determine the probability of each pathway, one must multiply the energy flow estimates together, thus in our example

large fish are most likely to gain their energy from small fish that eat insects: 1) 0.4, 2) 0.12 and 3) 0.48.
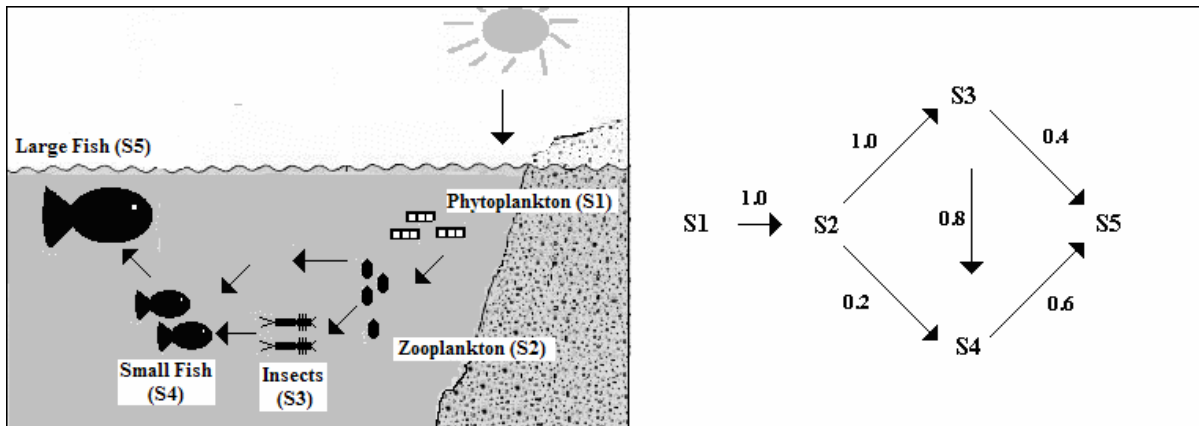
Figure 8.1. Generalized aquatic food web with an associated modelling schematic to represent the proportion of energy received at a trophic position from its prey.

These types of schematics can be modeled using matrices which allow for the application of a great deal of statistical models and experimental manipulation of the relationships. A model equation used to represents this schematic relationship is (Saito *et al.* 2001):

$$TP'_i = \Sigma (a_{ij}TP_j + 1)$$

where TP'_i is the estimated trophic position of consumer i, a_{ij} is the proportion of diet of consumer i due to prey j, and TP_j is the trophic position (i.e., path length) of prey j. This base model can be incorporated in other larger models to explore questions requiring a community or ecosystem scale. For example, the model used for ECOSIM, a popular commercial modelling program used primarily for "risk management", employs the following equation (Walters *et al.* 1999):

$$dB_i / dt = g_i \Sigma C_{ji} - \Sigma C_{ij} + I_j - (M_i + F_i + e_i) B_i$$

in which C_{ij} represents the flow of energy from group i to group j over a specific period of time. This model therefore incorporates elements of mortality (M and F), emigration (e), and growth (g) with a trophic model to determine the production of biomass (B) over time.

The use of trophic models within a spatial and temporal context was achieved by the suite of Ecopath modelling software designed for fisheries research (the development of the modelling software was centered around the University of British Columbia Fishery Center). The suite of Ecopath modelling software incorporates three main models:

Ecopath, Ecosim and Ecospace. The Ecopath model is the foundation of the suite and is a static, mass balanced snapshot of an ecosystem represented by trophically linked groups (Christensen and Pauly 1992). Ecosim allows for the model to be run over time to look for changes within and among the groups. Ecospace is designed primarily for the assessment of protected areas and also uses a temporal and dynamic model. The modelling software can be downloaded from www.ecopath.org.

Trophic models have been used abundantly in marine biology to explain the cycling of nutrients and energy. The NPZD biogeochemical model is used to model the cycling of energy at the lower trophic levels including nutrients (N), phytoplankton (P), zooplankton (Z) and detritus (D) (Fennel 1999). These types of models create good foundations for whole ecosystem modelling and can be coupled with hydrodynamic models to incorporate environmental variables such as temperature, irradiance, salinity and currents (Travers *et al.* 2007). Trophic models are useful for ocean fisheries management and include such modelling programs as the MultiSpecies Virtual Population Analysis (MSVPA) (Kempf *et. al.* 2006). These models take into account the predatory interactions of exploited species and how fishing mortality and growth may impact related species (Magnusson 1995). Marine habitat models have also been linked to trophic models such as the Spatial Ecosystem and Population Dynamics Model (SEAPODYM). This model was used to characterize the physical – biological relationships between tuna populations and the pelagic ecosystem in the Pacific Ocean (Lehodey *et al.* 2003). It represents a good example of how models can be combined to link habitat characteristics with changes to fish populations. Three sub-models are found in SEAPODYM including a biogeochemical model (like NPZD) providing impacts of habitat variables on primary production, a forage fish trophic model which defines the energy flow in the system and a detailed age-specific growth, foraging and fitness model for tuna which defines their population dynamics based on the available resources as well as their impact on the lower trophic levels.

8.2 Case Study

Saito, Johnson, Bartholow and Hanna (2001) used a trophic modelling procedure in tandem with a water quality model to assess the impact of dam operating regimes on Shasta Lake, a reservoir in northern California within the Sacramento River system. A temperature control device (TCD) was proposed to be installed on the dam to allow water to be released at pre-determined temperatures with the aim of improving downstream chinook salmon habitat. This study used a modelling approach to determine how the potential changes in the operating regimes would impact the fish in Shasta Lake, including rainbow trout and multiple species of bass. The TCD operation had the potential to change thermal and temperature regimes deep in the hypolimnion

which would have very little direct impact to fish populations as few lived in that area. However, these changes could impact nutrient availability and phytoplankton productivity which could contribute to indirect impacts to fish populations.

The objective of the model was to determine how changes to plankton productivity due to different dam operating regimes could impact the Shasta Lake fish assemblages. A water quality model (CE-QUAL-W2) was used to estimate phytoplankton productivity in the reservoir from physical characteristics and phytoplankton bioenergetics. The water quality model reported net algal production in grams of dry weight in response to simulations from three yearly conditions (with and without the operation of the TCD): 1) a wet year, 2) a dry year and 3) an average year (1995). The food web was mapped for Shasta Lake using stable isotope analyses. Eighteen species / groups were examined in the food web including fish species, crustaceans, terrestrial and aquatic insects, phytoplankton, zooplankton, periphyton and detritus (Table 8.1). The isotope analysis resulted in a food web diagram (Figure 7.2) with the same components as presented in Figure 8.1. The biomass of each fish and invertebrate species was estimated using the following equation:

$$\text{Biomass for species 'i'} = \Delta E_{phyto} (ET_i / ED_i)$$

where ΔE_{phyto} is the change in net phytoplankton production, ET_i is the energy transfer from phytoplankton to species 'i' and ED_i is the energy density of species 'i' (known for all species in the study). The general trophic position model presented in this primer was used to derive the energy transfer value with the assumption that only 10% of available energy at one trophic level can be transferred to the next. Therefore the amount of energy available for each trophic position could be calculated. The energy transfer value assumption is well supported by empirical research.

Table 8.1. Fish, invertebrate and plant taxa used in the food web analysis on Shasta Lake (from Saito *et al.* 2001).

Taxon	Scientific Name	Code	Size Class
Chinook salmon	*Oncorhynchus tshawytscha*	CHS	320–538 mm TL
Brown trout	*Salmo trutta*	BRT	510 mm TL
Big bass	*Micropterus salmoides and M. punctulatus*	BBS	>290 mm TL
Medium smallmouth bass	*M. dolomieu*	MSMB	114–290 mm TL
Medium bass	*M. salmoides and M. punctulatus*	MBS	114–290 mm TL
Rainbow trout	*O. mykiss*	RBT	290–410 mm TL
Threadfin shad	*Dorosoma petenense*	TFS	All sizes
Small bass	*M. salmoides and M. punctulatus*	YC1BS	0–113 mm TL
Green sunfish	*Lepomis cyanellus*	GSF	83–125 mm TL
Sacramento pikeminnow	*Ptychocheilus grandis*	SQF	75–122 mm TL
Bluegill	*Lepomis macrochirus*	BLG	All sizes
Crayfish	Order *Decapoda*	CRA	All sizes
Zooplankton	Class *Branchiopoda*	ZOO	>64 μm
Terrestrial insects	—	TINS	All sizes
Aquatic insects	—	AINS	All sizes
Phytoplankton	—	PHY	—
Periphyton	—	PER	—
Detritus	—	DET	—

Fish size classes were chosen based on trophic ecology and sizes represented in our samples.
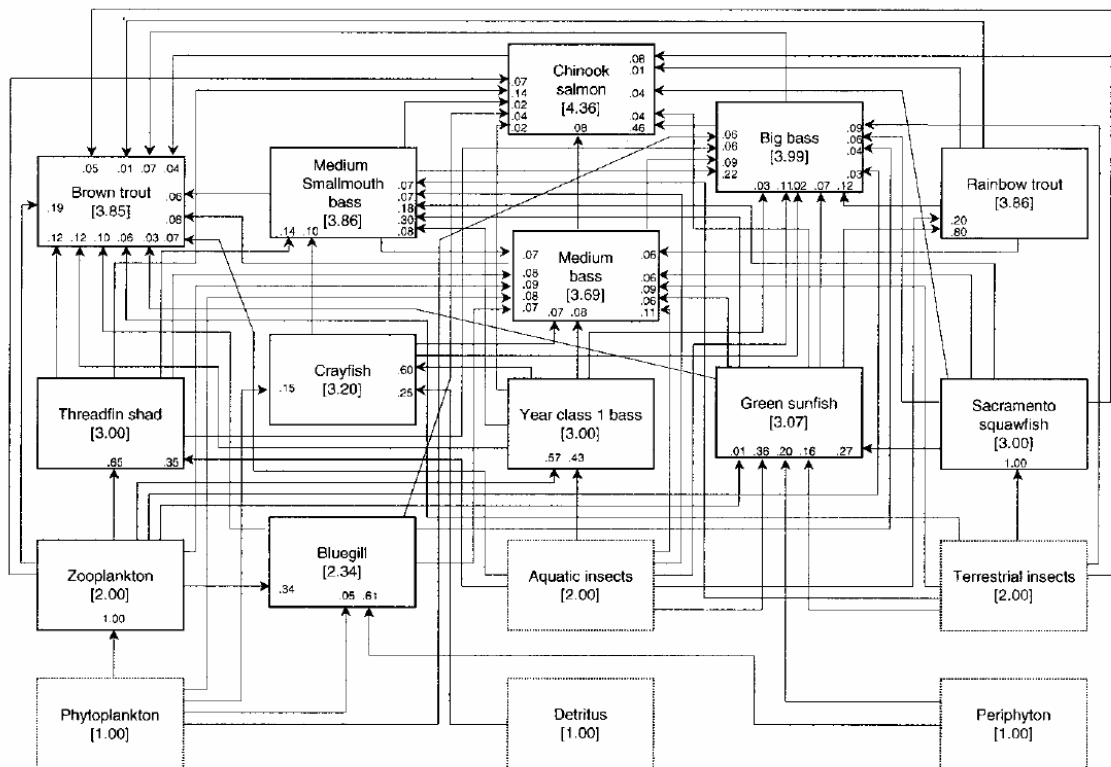
Figure 8.2. Food web structure in the Shasta Lake reservoir. Note the trophic position indicated in brackets beneath the species / group's name and the proportional energy flow indicated where the arrows meet the boxes (from Saito *et al.* 2001).

The study demonstrated results for three environmental conditions with and without the operation of the TCD. The operation of the TCD was found to have only a slight impact to phytoplankton biomass in average years, a positive impact in wet years and a negative impact in dry years (Figure 8.3). The study demonstrated which fish species within Shasta Lake were energetically linked to phytoplankton through trophic interactions and thus sensitive to changes in phytoplankton biomass. Rainbow trout and Sacramento pikeminnow were found not to be linked to phytoplankton as their diets consisted of aquatic and terrestrial insects which both feed primarily on energy from terrestrial inputs. Therefore any changes to the dam operations would not impact those species. The most sensitive fish species to changes in phytoplankton biomass were the bass species and the threadfin shad (Table 8.2). The top predator, chinook salmon, was not significantly impacted by changes in the phytoplankton biomass. Given that the predicted changes to phytoplankton biomass due to the TCP operations were considered slight the authors tentatively concluded that fish biomass in Shasta Lake was generally unaffected by dam operations.
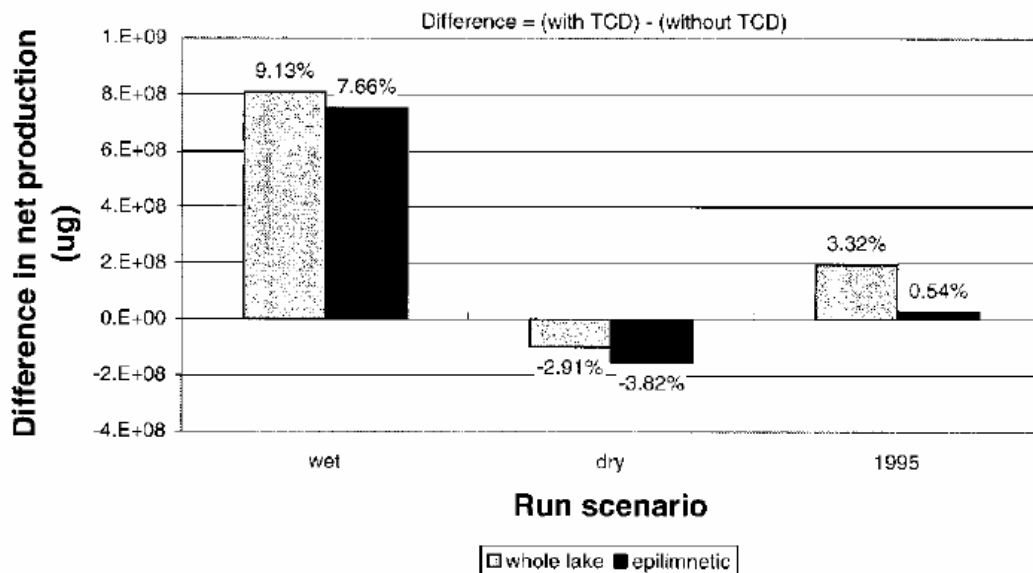
Figure 8.3. Differences in net phytoplankton production due to TCD operations in Shasta Lake over three yearly conditions (wet, dry and average). Note that the values are from estimates with the TCD operations minus the estimates without the TCD operations. Both whole lake (shaded) and epilimnetic (black) value of net production are reported (from Saito *et al.* 2001)

Table 8.2. Changes in consumer biomass due to changes in net phytoplankton productivity. Note that the energy transfer coefficient has been estimated in this table however a 10% transfer efficiency was used for modelling purposes (from Saito *et al.* 2001)

Consumers	Trophic Position	Energy Transfer Coefficient, ET_i^a	Primary Organic Source Fraction Derived from Phytoplankton[b]	ED_i $(J\,g^{-1})$	Change in Consumer Biomass (g [g phytoplankton]$^{-1}$)
Zooplankton	2.0	0.1000	1.00	2514[c]	0.8460
Bluegill	2.3	0.0084	0.39	4186[c]	0.0427
Sacramento pikeminnow	3.0	—[d]	0.01	—[d]	—[d]
Year class 1 bass	3.0	0.0057	0.49	4186[c]	0.0290
Threadfin shad	3.0	0.0065	0.58	6200[e]	0.0223
Green sunfish	3.1	0.0001	0.00	4186[f]	0.0005
Crayfish	3.2	0.0153	0.54	4512[g]	0.0721
Medium bass	3.7	0.0092	0.32	4186[c]	0.0467
Rainbow trout	3.9	—[d]	0.00	—[d]	—[d]
Medium smallmouth bass	3.9	0.0003	0.17	4186[c]	0.0015
Brown trout	3.9	0.0023	0.40	6059[h]	0.0063
Big bass	4.0	0.0065	0.18	4186[c]	0.0330
Chinook salmon	4.4	0.0012	0.28	7736[i]	0.0042

[a]Calculated by applying Eq. (1) along food web pathways.
[b]Calculated using the approach of Harrigan and others (1989).
[c]Energy density values from Hanson and others (1997).
[d]Sacramento pikeminnow and rainbow trout were not energetically connected to the phytoplankton.
[e]Pierce and others (1980).
[f]Energy density for green sunfish assumed to be same as for bluegill.
[g]Energy density value from Cummins and Wuycheck (1971).
[h]Energy density calculated as in Hanson and others (1997) for 299-g fish.
[i]Energy density calculated as in Hanson and others (1997) for 2000-g fish.

8.3 Strengths and Weaknesses

The strengths of the trophic models include:

1. The trophic model shares a mechanistic approach using functional relationships between its parameters with bioenergetic and individual based models (see Section 10) which allow for the exploration of causal relationships rather than only correlative relationships;
2. Similarly trophic models provide a realistic base for the relationship between the community and its environment. Once the basic model is developed other ecological, evolutionary and behavioural models can be easily used to explore a wide variety of questions as shown in the example case study;
3. Trophic models offer a large amount of control over the modelled system as the structure of the primary producers and the subsequent flow of energy determines the level of detail that will follow in other analyses; and,
4. Allows for community wide analyses that do not pool species together. Also allows for the simultaneous modelling of species with very different population dynamics.

Criticisms of the use of trophic models for habitat studies include:

1. Not as applicable to temporal systems because the level of site specific detail required can limit the use of the model over long time series;
2. Definition of trophic levels is subjective and can lead to biased results; and,
3. Trophic models are often difficult to test using experimental data. One limitation of the transferability of trophic models to natural systems is whether the populations being modelled or studied are in a steady state.
4. Requires much data to populate the model (e.g., stable isotope analysis of the entire food web for the case study, Table 8.1).

9 Stage Structured Population Models

9.1 Overview

Many population modelling techniques are not able to incorporate multiple stage or age classes into one model. For example, the Habitat Suitability Models must be run separately for eggs, fry, juveniles and mature fish because many of the habitat preferences are not equal for each life stage. Stage structured population modelling is able to include and incorporate changes in life history requirements, survivorship and recruitment that come with different life stages into a fish or fish habitat model. The main benefit of including this method is that the relative importance of each stage to the survival of the population can be assessed. In addition, the suitability of stage-specific habitat such as rearing habitat can be assessed not only for the juvenile fish but also indirectly for the rest of the population. Therefore the use of a stage structured approach allows for a more inclusive picture of the habitat requirements of the fish population.

A general stage structure model is based on the probability that one life stage will contribute individuals to another through reproduction, survival and maturation. Figure 9.1 demonstrates a generalized stage structured model. Each circle represents a year-class of a fish species from year 1 to 3+. The arrows represent the addition of individuals to each age class. The "s" variables represent the proportion of individuals that survive to the next year (and corresponding age class) and the "F" variables represent the probability of individuals within each age class successfully reproducing and therefore contributing fish to the first age class. These parameters are not always known but they would be available for fish species and populations that are well studied for fisheries stock assessments or other reasons.
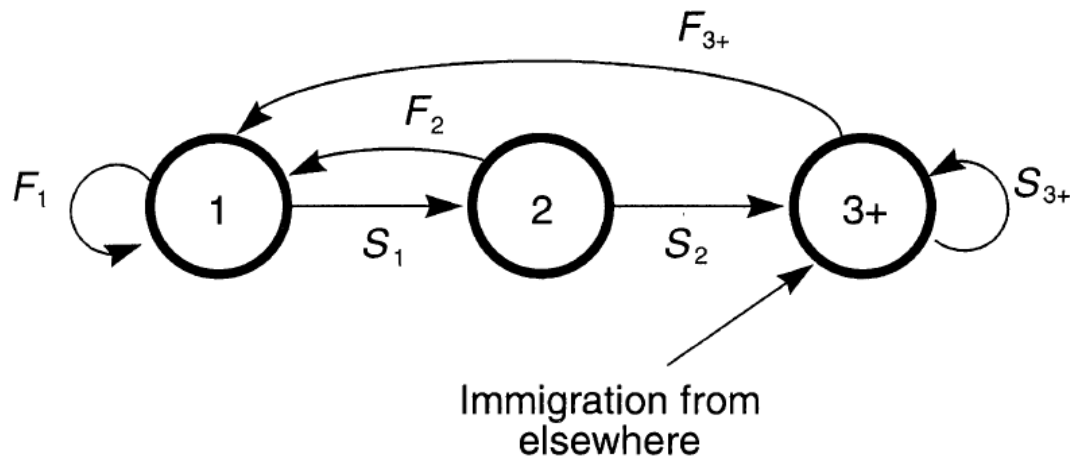
Figure 9.1. A general stage-structured population model which demonstrates survivorship (S) and recruitment (F) between age classes (from Hitchcock and Gratto-Trevor 1997).

An example of a stage structured model is the Area-Per-Individual (API) model (Minns 2003). The API model is based on a common allometric relationship between population density and body mass found in most fish species' natural populations. This is the same relationship that forms the basis of P, P/B and HPI models. What the relationship tells us is that regardless of the population there is an optimal balance between the number of individuals and the growth of each individual. The optimal balance can be thought of as the necessary area of habitat that an individual requires for optimal growth. For example, the hatching success of eggs declines as eggs begin to crowd each other in even high quality spawning habitat. The optimal API is found in every life stage and is generally smaller for eggs and juveniles than for adults. In consequence the API value for a fish is often only dependent on the fish size (here indicated as length, L):

$$API \ (m^2) = e^a \ L^b$$

The constants 'a' and 'b' are derived from empirical studies. The API model combines a stage structured model with an area suitability model so that each of a fish population's life stage is accounted for in the assessment of the overall suitability of the fish habitat for the population. The stage structured model is dynamic and its output is the population sizes (N) at each age class (A, B, C …) following one year (t). For example, the B year class after one year is made up of the proportion of survivors (s) from the previous year class (A):

$$N_B(t+1) = N_A(t) {}^* s_A$$

Minns (2003) incorporated habitat into the stage structured model by estimating the minimum required area of suitable habitat (a) and the total ecosystem area (A) and using the proportion of the two to estimate the relative survivorship from one age class to the next. API models require a large amount of known parameter values which can be acquired either through field estimates or literature review. As the habitat parameters of the model are altered, the output demonstrates the resulting impact to the overall and stage specific population sizes. This allows for sensitivity analyses as well as the identification of critical stages in the fish's development that requires suitable habitat.

9.2 Case Study

In 2003, Minns prepared a technical document on the use of API models to evaluate habitat quality in stage structured populations. To test the application of the model, Minns chose to run it on two freshwater fish species: lake trout and deepwater sculpin. The lake trout was chosen for the large amount of existing knowledge on the biology of the species and conversely, the deepwater sculpin was chosen for the lack of available information on the species. In addition, the deepwater sculpin is a species at risk.

The model was built for a small population with a running period of 100 years and three life stages: 0 (eggs/hatched), 1- (young of the year) and 1+ (juvenile / mature). After 100 years the state of the populations was considered the model output. The API was estimated using the body size relationship previously identified in this section. However two values were calculated for both the 1- (emergence and juvenile) and the 1+ life stages (at maturity and maximum sizes). Hatching successes, spawning areas, survival estimates and fish fecundity were all taken from published literature for the species or closely related species. From the model, four population size indicators were outputted: number of eggs hatched, number of young of year reaching 1, number of 1+ individuals and number of mature individuals. The suitability of the habitat was assessed by running the model once with an unlimited supply of suitable habitats for all life stages, followed by realistic estimates of limited available habitat. A sensitivity analysis was run by reducing by 50% or increasing by 100% the estimates of available habitat. An analysis was also completed to determine how sensitive each life stage was to loss in the habitat.

The results of the analysis were similar for lake trout and deepwater sculpin despite their differences in life history and availability of information. To maintain 95% of their populations the minimum percentage of suitable habitat from total habitat per life stages was:

Species	Spawning Habitat	Rearing Habitat (young of year)	Adult Habitat (1+)
Lake Trout	0.019	7.047	95.00
Deepwater Sculpin	0.006	6.650	36.72

Note the higher habitat requirements for young of year rearing and adult habitats. It is of considerable interest that spawning habitat was not considered limiting as it is often placed at a higher conservation value than other habitat. In both sensitivity analyses the spawning habitat was robust to changes and did not significantly impact population sizes. However, it was noted that uncertainties in parameters involving survival from hatching to year 1 would impact these results.

9.3 Strengths and Weaknesses

Strengths of stage structured models and the API methodology include:

1. Allows for the analysis of stage structured interactions and population dynamics which give a more realistic ecological model;
2. Associated with well supported allometric and population growth relationships;
3. Applicable to studies involving movements between sub-populations in response to resources or source / sink interactions including meta-population models, migration models and patchy resource dynamics;
4. Applicable to fisheries management models if an exploitation rate is incorporated with the survival of age classes; and,
5. The impact of habitat quality on population viability and growth can be examined by altering life processes performance.

Criticisms of the use of stage structured models and the API method for habitat studies include:

1. Stage structured growth rates may be density dependent which is not taken into account in API models;
2. Many species have complex life histories which may not be well represented by following a staged approached;
3. Male / female differences are often ignored in stage structured models; and,
4. An age / size dependent fecundity should be incorporated in the models and therefore has to be available for the species of study.
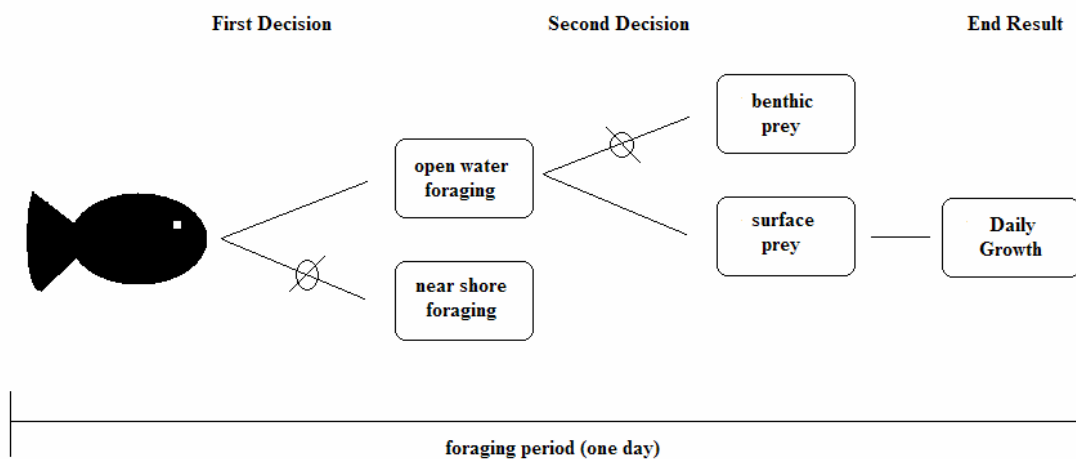
10 Individual Based Models

10.1 Overview

An individual based model (IBM) differs mechanistically from the other models presented in this primer because it is more often based on creating a computer simulation rather than working through equations. The use of IBMs is also more restricted to research into ecological theory rather than as a management tool. However, IBMs can be used to effectively evaluate fish habitat quality and fish habitat preferences. The basis of the IBM is that each individual fish is modeled and tracked through a simulated experiment. This allows each fish to be given a specific set of behavioural and morphological traits which is more realistic than a uniform population of identical individuals. An important feature of IBM is that it also allows those traits to change over its life cycle in response to the simulated environment or its own behaviour. Often the simulated environment is modeled to include a heterogeneous landscape over which the fish must complete an activity (such as foraging, spawning or migrating). Because IBM models often attempt to simulate realistic field conditions and fish biology, they require a high number of parameters as well as some of the other models we have examined in this primer. Bioenergetic models are often needed to determine the growth of each individual based on its activities. Hydraulic, Productivity and Habitat Suitability models are often required to simulate the fish's virtual habitat. Trophic models may also be needed to simulate the energy flow through the community.

The process of the IBM is to design a set of conditions or a spatial habitat that a fish must move through over a certain time period (Figure 10.1). This could be as simple as the movement of a fish through a culvert over one day, or a more complex simulation of fish distribution in a patchy environment over a month. Although IBMs may occur over long time periods they are often discrete and involve a distinct sequence of actions (such as spawn, feed, migrate, feed, overwinter, etc.) by the fish over equal time steps. IBMs are also usually stochastic models which are made to mimic random events found in nature.

The first component of an IBM model which must be created is the environment or set of conditions that the fish will encounter and interact with. These can be created either as a physical two or three dimension environment that the fish can navigate through, or as a predetermined and ordered set of choices and activities that are presented to the fish. The environment can be created as a hierarchy of scales (individual, home range, population and watershed) which allows for the examination of small scale questions concurrently with big picture questions. The simulation of the environment and how the fish interacts with its habitat is a key component of IBM.

The second component is that of the fish itself. The individual being simulated will likely require a bioenergetic submodel to link its metabolic interactions with the environment. The individual may also require a behavioural model to allow it to make decisions based on external and internal stimuli. IBMs attempt to recreate an organism and include enough traits to allow it to react in a realistic way to the simulated spatial habitat. The benefit of this approach is that it allows the individual to change its behaviour during the simulation if there is a need. Many IBMs incorporate a learning model to allow for the individual to optimize its choices. The simulation must also keep a record of the movements or activities of the fish in the virtual environment such that the traits of the fish can be modified.


Figure 10.1. A generalized process for developing Individual Based Models. Note that the fish has decisions to make over a time period which will result in its end of day growth.

IBMs are typically validated using similar methods described for bioenergetic modelling. Because the basis of IBMs is a bioenergetic model, field verification of growth rates as well as sensitivity analyses can be used to calibrate and test the model.

10.2 Case Study

Maes, Limburg, Van de Putte and Ollevier (2005) created an Individual Based Model to examine the habitat choices of juvenile North Sea herring in estuarine nurseries. Estuaries provide nursery habitat for a wide variety of fish species. Within the estuaries some habitats are better suited to fish rearing than others and it is generally believed that the estuaries provide poorer foraging opportunities but lower predation risk than the open sea. Although a great deal of empirical work has been useful for identifying important nursery habitat for management purposes, it has not been helpful in

explaining why the fish choose certain habitats over others or what is the habitat-specific growth and mortality ratio. A spatially explicit, IBM was created to clarify the role of the nursery in the herring's life cycle and to examine what makes them shift their habitat use (Figure 10.2).
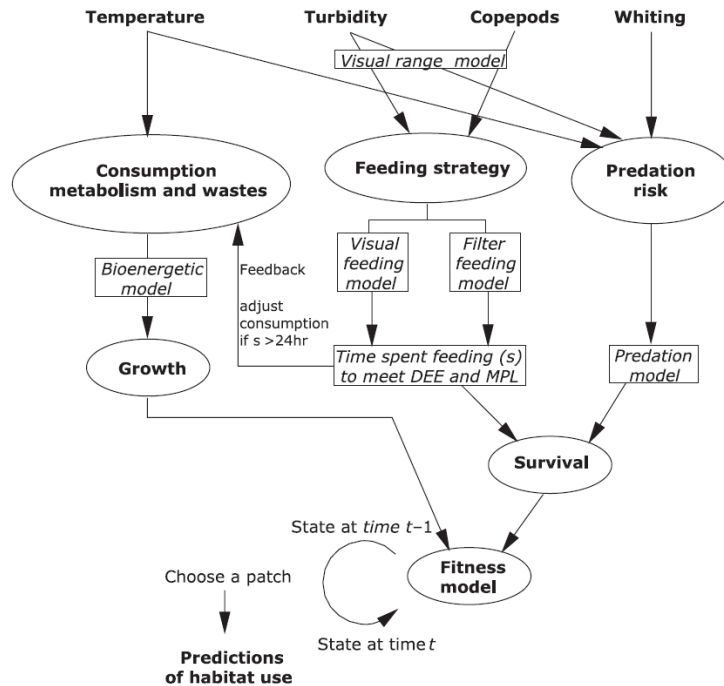
Figure 10.2. The flow diagram for the North Sea herring IBM. Note the many other models incorporated into the overall IBM. DEE stands for Diel Energy Expenditures and MPL for Maximum Prey Loading. (Maes *et al.* 2005)


The spatial environment simulated in the model included five locations that the herrings were able to migrate between over the course of two years. The locations included 1) open sea, 2) coast, 3) lower estuary, 4) middle estuary and 5) upper estuary. Each of the locations was given a set of environmental conditions that changed seasonally and differed from each other in temperature, turbidity, copepod density (prey) and whiting density (predator). These values were not estimated but instead obtained from field studies. A bioenergetic model was used to simulate the growth of the herring and mortality and foraging rates were estimated using density relationships between the simulated herring populations and the field prey and predator populations. In addition, known empirical relationships were incorporated such that extreme temperatures and turbidity could cause increased herring mortality rates. The mechanism of the IBM is determined by the decision making model for the herring within the spatial environment. The herring is assumed to maximize its growth and survival. Therefore at each time

step (t) the herring makes its decision of where to feed based on the optimal conditions for the next time step (t-1). This decision is based not only on the spatial environment but on the fish's current body condition, foraging strategy and predation risk. A parameter sensitivity analysis was run by randomizing the value of each environmental parameter separately and rerunning the model 100 times. The model was initiated with a 3 cm and 0.25 g herring in the open North Sea in April 1989.
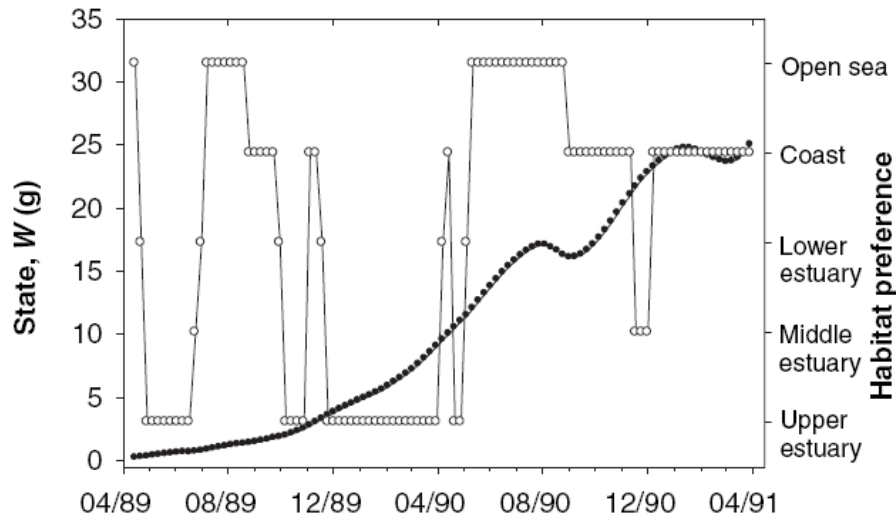
Figure 10.3. The output of the model showing the habitat preferences of the North Sea herring for optimal growth over a period of two years. "State, W" is the dark line and refers to the weight of the herring (Maes et al 2005)

The model results suggested that the herrings make three main habitat shifts over the course of the two years to optimize growth (Figure 10.3). The first year is spent in the Upper Estuary where the higher turbidity offers protection from predation and the copepod densities offer growth opportunities. During the summer in the first year the herring move back to the open sea to escape high temperatures that limit growth and gradually move back after a period of feeding on the coast. By the second summer the herring remain in the open sea and during the third winter they remain on the coast. When the predation parameter was minimized in the sensitivity analyses, the herring were found to stay in the open sea and rarely enter the estuaries. The model successfully demonstrated the trade-offs the herring are forced to make due to the risk of predation and fluctuating temperatures. The growth opportunities are better in the open sea however the estuaries offer better protection until they attain a larger size. The model also demonstrated which habitats within the estuary offered better rearing opportunities. The model was verified with field data from herring inventories in the upper estuary (Figure 10.4).
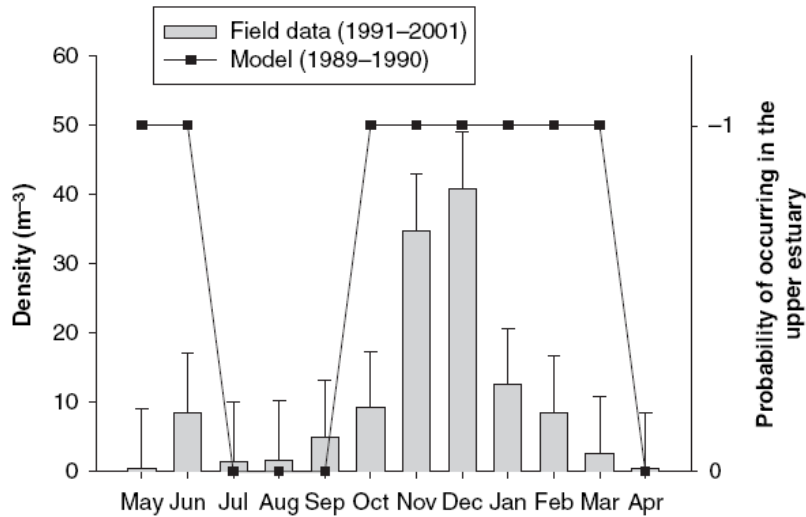
Figure 10.4. Verification of the North Sea herring habitat preference IBM in the upper esturary (Maes *et al.* 2005)

10.3 Strengths and Weaknesses

The use of IBMs in fish habitat management is relatively new because it requires a great deal of computational power which was not readily available twenty years ago. Like bioenergetic models, IBMs offer many strengths which will likely result in their increased use in the future:

1. The models typically include variables that are often overlooked by mathematical models including individual variability, local interactions, complete life cycles, adaptation to external and internal environments, and advanced learning and behavioural traits;
2. IBMs allow the incorporation of many other models which opens up the range of what they can accomplish;
3. Outputs provide real population, behavioural or physiological data that can be verified in empirical research; and,
4. Integrates multiple spatial and temporal scales in single simulations.

Criticisms of the use of IBMs for habitat studies include:

1. The model structures are hard to communicate and therefore make it hard to identify the inherent biases or develop reproducible results;
2. Much more complex in structure than analytical models;
3. No standard protocol for building or describing them;
4. There is sometimes a high amount of error associated with its output due to the need for many assumptions;

5. Large data needs make the model unfeasible for rare species for which little is known; and,
6. Susceptible to the same weaknesses inherent to its sub-models.

11 Summary

The primer introduced nine categories of ecological models, some commonly used to evaluate fish habitat management issues in Canada, others used more often in ecological research but with the potential to be used to evaluate losses and gains in fish habitat. The models each have their particular strengths and weaknesses, and work best to answer some types of questions over others. In this summary we will discuss the models' strengths and weaknesses as well as group them based on their type of utility in fish habitat management.

The models presented in this primer can be loosely grouped between those that estimate fish habitat via an index or relative scale, and those that estimate a specific parameter or response. The former of these two groups includes the Habitat Suitability Indices, Defensible Methods, Habitat Productivity Indices and Index of Biotic Integrity. These types of models all provide indices which in some way interprets existing and estimated fish habitat and are most useful as a comparative tool rather than an exact representation of the natural environment. The latter of the two groups include mechanistic models such as Bioenergetic Models, Trophic Models and Individual-Based Models. These models each present specific outputs often related to fish growth or population viability. These outputs can be related to fish production and therefore have a great potential to evaluate changes in fish habitat, particularly if environmental variables are included in the structure of the models and can be manipulated. Of the nine categories presented in the primer, the Productivity Models and Stage Structured Models (API) were not included in any of these two groupings because they often belong to both. Estimates of productivity or habitat capacity can be either used as a direct measure (as shown in Sharma and Hilborn 2001 in Section 3) or incorporated into suitability indices. Similarly stage structured population models can be developed to estimate some direct measure (such as juvenile foraging rates), or can be combined with area suitability models (as in the API models introduced in Section 9).

The main strength of the index models is that they have in the most part been designed specifically to assess changes in fish habitat. The HSI and PHABSIM models were developed in the United States in the mid-1970s to standardize the impact assessment of large industrial developments on rivers such as hydroelectric facilities. In Canada,

the Defensible Methods were also developed specifically for the use of Fisheries and Oceans Canada to evaluate the losses and gains of fish habitat in terms of productive capacity following the implementation of a proposed development. Last, the IBI was developed in the United States to complement chemical indicators of water quality and provide a biological context to changes in aquatic environments. The HSI and IBI provide a standard method that can be used for comparisons over space and time. The strength of these index models lies in the abundance of prior models and suitability curves that have been developed specifically for fish species. As listed in Section 4 there are regional Habitat Suitability Curves developed for many aquatic environments across Canada. From these HSI curves the species of interest can be found and easily modeled. In addition, existing modeling software exists (also presented in Section 4) to complete the assessments of proposed developments. Other specific strengths of this group of models are presented in Sections 2, 3, 4, 5 and 9.

The index models all share a weakness that they may not accurately represent natural systems and would require a very large data set to validate them. However, these are criticism of all types of ecological models as models can only be a simplified representation of real systems. Our concern should only be that the simplification did not compromise our ability to evaluate the variable of interest (in our case a measure of productive capacity, or habitat suitability). Within most HSI and IBI studies the critical question to evaluate is, "How were the multiple indices (i.e., for different species, indicators or habitat variables) combined to create an overall measure of habitat quality?" In some cases the limiting variable is considered to be the overall measure whereas in other cases the indices are combined as a sum, product or weighted product (see Section 2). It is always important to verify the assumptions that were made when selecting the overall measure of suitability. Similarly it is important to ensure that the variables included in the model were appropriate and that no important habitat measures were left out of the analysis. Other specific weaknesses of this group of models are presented in Sections 2, 3, 4, 5, 6 and 9.

It is more difficult to generalize the mechanistic models as they have a wide range of uses and are in structure very distinct from each other. However, all of these models incorporate known elements from the biology of the species or the characteristics of their environments to derive a result that should be found in the real world. In many cases these models are verified by ensuring that the output is similar to observations from natural populations. A main strength of this group of models is that they offer a mechanistic approach to ecosystem modelling that can present a causal relationship between a change in habitat and a gain or loss in fish production. Many suitability

models can only show correlations between habitat quality and fish abundance which does not necessarily explain why we expect a particular result. Therefore, mechanistic models have the potential to be very useful in mitigating potential impacts from development and tailoring compensation and habitat restoration initiatives to maximize work on the habitat variables that create the greatest gain in fish production. In addition, many of these models have the ability to incorporate environmental variation and the ability for species to adapt to new environments. This is a great strength as we often expect a species to alter aspects of its life history in response to changes in its environment. Last, modelling software is available for many of these groups including some designed specifically around fisheries including Fish Bioenergetics (Section 7) and the Ecopath suite (Section 8). Other specific strengths of this group of models are presented in Sections 3, 7, 8, 9 and 10.

The main weakness of the mechanistic models is that they do not lead directly to the evaluation of gains or losses in fish habitat. Many of these models are designed to measure an aspect of individual fish behaviour or growth, or population growth. They rarely incorporate community dynamics (with the exception of trophic models) and often will require additional modeling or analysis to convert their results to a useful measure of fish productivity or fish habitat productivity. This is likely the main reason why the index models are used more often in fish habitat management. Although the HSI and IBI may not provide causal relationships, they provide a more intuitive and accessible measure of fish habitat quality. However, once enough mechanistic models are developed specifically for fish habitat and are available to fish habitat managers, they could become much more common (as seen with the Ecopath suite). A second main weakness of these models is that most of the parameters used to create the model will carry with them some level of uncertainty and consequently the output of the model can be very biased and inaccurate. It is therefore very important to verify causal models with the study system to demonstrate that their outputs are realistic. Other specific weaknesses of this group of models are presented in Sections 3, 7, 8, 9 and 10.

In many ways, habitat modeling is still a relatively recent research area in ecology. Many of the models presented in this primer were only developed in the last few decades with the increased use of computers by biologists. The ongoing development of computing power is leading to new methods of ecological modeling including neural networks (Olden et al. 2008) and Geographical Information Systems (GIS) spatial modeling (LePichon et al. 2006). In addition, as more information on fish species becomes available through continued ecological, behavioural and physiological studies, the existing models become more and more refined (Giske et al. 1998). Finally, fisheries

science can also borrow tools from other disciplines which become useful in risk management and decision frameworks such as the Expert Systems from medical sciences (McKindsey et al. 2006). In the light of the continued development and refinement of modelling techniques it is very likely that their increased use in fisheries and fish habitat management will continue in the years ahead.

12 Literature cited

Ahmadi-Nedushan, B., St-Hilaire, A., Bérubé, A., Robichaud, É., Thiémonge N., and Bobée B. 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. Rivers Res. Appl. 22:503-523. doi: 10.1002/rra.918

Anderson, K.E., Paul, A.J., McCauley, E., Jackson, L.J., Post, J.R., and Nisbet, R.M. 2006. Instream flow needs in streams and rivers: the importance of understanding ecological dynamics. Front. Ecol. Environ. 4: 309-318.

Azzellino, A., and Vismara, R., 2001. Pool quality index: new method to define minimum flow requirements of high-gradient, low-order streams. J. Environ. Eng. – ASCE 127: 1003-1013. doi:10.1061/(ASCE)0733-9372(2001)127:11(1003)

Baker, E.A., and Coon, T.G. 1997. Development and evaluation of alternative habitat suitability criteria for brook trout. Trans. Am. Fish. Soc. 126: 65-76. doi: 10.1577/1548-8659(1997)126<0065:DAEOAH>2.3.CO;2

Bourgeois, G., Cunjak, R.A., Caissie, D., and El-Jabi, N. 1996. A spatial and temporal evaluation of PHABSIM in relation to measured density of juvenile Atlantic salmon in a small stream. N. Am. J. Fish. Manage. 16: 154-166.

Christensen, V., and Pauly, D. 1992. ECOPATH II - A software for balancing steady state ecosystem models and calculating network characteristics. Ecol. Model. 77: 3-32.

Cote, D. 2007. Measurements of salmonid population performance in relation to habitat in eastern Newfoundland streams. J. Fish Biol. 70:1134-1147. doi: 10.1111/j.1095-8649.2007.01384.x

Fennel, K. 1999. Interannual and regional variability of biological variables in a coupled 3-D model of the western Baltic. Hydrobiologia 393: 25-33. doi: 10.1023/A:1003552723929

Fisheries and Oceans Canada. 1986. Policy for the management of fish habitat. Communications Directorate, Fisheries and Oceans Canada, Ottawa, ON.

Frezza, T. and Minns, C.K. 2002. Assessing fish habitat supply and potential responses to habitat manipulation in small Canadian Shield lakes. Can. Manuscr. Rep. Fish. Aquat. Sci. 2599: vi + 27p.

Gibson, A.J.F. 2006. Population regulation in eastern Canadian Atlantic salmon (*Salmo salar*) populations. Can. Sci. Advis. Sec. Res. Doc. 2006/016.

Giske, J., Huse, G., and Fiksen, O. 1998. Modelling spatial dynamics of fish. Rev. Fish Biol. Fish. 8: 57-91.

Glozier, N.E., Culp,J.M., and Scrimgeour. G.J. 1997. Transferability of habitat suitability curves for a benthic minnow, *Rhinichthys cataractae*. J. Freshw. Ecol. 12: 379-393. doi: 10.1111/j.1600-0633.2004.00069.x

Gore, J.A., Crawford, D.J., and. Addison, D.S. 1998. An analysis of artificial riffles and enhancement of benthic community diversity by Physical Habitat Simulation (PHABSIM) and direct observation. Regul. Rivers: Res. Manage. 14: 69-77. doi: 10.1002/(SICI)1099-1646(199801/02)14:1<69::AID-RRR477>3.0.CO;2-D

Hartman, K.J., and Kitchell, J.F. 2008. Bioenergetics modelling: progress since the 1992 symposium. Trans. Am. Fish. Soc. 137: 216-223. doi: 10.1577/T07-040.1

Hayes, J.W., Stark, J.D., and Shearer, K.A. 2000. Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. Trans. Am. Fish. Soc. 129: 315-332. doi: 10.1577/1548-8659(2000)129<0315:DATOAW>2.0.CO;2

Hedger, R.D. 2004. Quantifying the effectiveness of regional habitat quality models for predicting densities of juvenile Atlantic salmon (*Salmo salar* L.). Ecol. Freshw. Fish 13: 266-275. doi: 10.1111/j.1600-0633.2004.00069.x

Hitchcock, C.L. and Gratto-Trevor, C. 1997. Diagnosing a shorebird local population decline with a stage structured population model. Ecology: 78: 522-534.

Hughes, N.F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology 79: 281-294.

Jones, N.E., Tonn, W.M., Scrimgeour G.J., and Katopodis, C. 2003. Productive capacity of an artificial stream in the Canadian Arctic: assessing the effectiveness of fish habitat compensation. Can. J. Fish. Aquat. Sci. 60: 849-863. doi: 10.1139/F03-074

Karr, J.R. 1981. Biological integrity: a long-neglected aspect of water resource management. Ecol. Appl. 1: 66-84.

Kempf, A., Floeter, J., and Temming, A. 2006. Decadal changes in the North Sea food web between 1981 and 1991 – implications for fish stock assessment. Can. J. Fish. Aquat. Sci. 63: 2586-2602.

Kilgour, B.W., Neary J., Ming D., and Beach, D. 2005. Preliminary investigations of the use and status of Instream-Flow-Needs methods in Ontario with specific references to application with hydroelectric developments. Can. MS Rpt. Fish. Aquat. Sci. 2723: v + 30p.

Lamoureux, N., and Capra, H. 2002. Simple predictions of instream habitat model outputs for target fish populations. Freshw. Biol. 47: 1543-1556. doi: 10.1046/j.1365-2427.2002.00879

Lehodey, P., Chai, F., and Hampton, J. 2003. Modelling climate-related variability of tuna populations from a coupled ocean-biogeochemical-population dynamics model. Fish. Oceanogr. 12: 483-494.

Le Pichon, C., Gorges, G., Boet, P., Baudry, J., and Goreaud, F. 2006. A spatially explicit resource-based approach for managing stream fishes in riverscapes. Env. Mgmt. 37: 322-335.

Long, J.M. and Walker, D.J. 2005. Small scale application and assessment of a Index of Biotic Integrity for a large boreal river. Hydrobiologia 544: 177-187. doi: 10.1007/s10750-005-0543-4

Maes, J., Limburg, K.E., Van de Putte, A., and Ollevier. F. 2005. A spatially explicit, individual-based model to assess the role of estuarine nurseries in the early life history of North Sea herring, *Clupea harengus*. Fish. Oceanogr. 14: 17-31. doi: 10.1111/j.1365-2419.2004.00300.x

Magnusson, K.G. 1995. An overview of the multispecies VPA – theory and applications. Rev. Fish Biol. Fish. 5: 195-212. doi: 10.1007/BF00179756

McKindsey, C.W., Thetmeyer, H., Landry, T., and Silvert, W. 2006. Review of recent carrying capacity models for bivalve culture and recommendations for research and management. Aquaculture 261: 451-462.

Mertz, G. and Myers, R.A. 1998. A simplified formula for fish production. Can. J. Fish. Aquat. Sci. 55: 478-484.

McMahon, T.E., Terell, J.W. and Nelson, P.C. 1984. Habitat Suitability Information: walleye. Fish and Wildlife Service – U.S. Department of the Interior. FWS/OBS-82/10 43p.

Minns, C.K. 1997. Quantifying "no-net-loss" of productivity of fish habitats. Can. J. Fish. Aquat. Sci. 54: 2463-2473.

Minns, C.K. 2003. An Area-Per-Individual (API) model for estimating critical habitat requirements in aquatic species-at-risk. Can. Sci. Advis. Sec. Res. Doc. 2003/074. 21p.

Minns, C.K., Cairns, V.W. Randall, R.G. and Moore, J.E. 1994. An Index of Biotic Integrity (IBI) for fish assemblages in the littoral zone of Great Lakes' area of concern. Can. J. Fish. Aquat. Sci. 51: 1804-1822.

Minns, C.K., Moore, J.E., Stoneman, M., and Cudmore-Vokey, B. 2001. Defensible methods of assessing fish habitat: lacustrine habitats in the Great Lakes Basin – conceptual basis and approach using a Habitat Suitability Matrix (HSM) method. Can. Manuscr. Rep. Fish. Aquat. Sci. 2559: viii + 70 p.

Minns, C.K. and Moore, J.E. 2003. Assessment of net change of productive capacity of fish habitats: the role of uncertainty and complexity in decision making. Can. J. Fish. Aquat. Sci. 60: 100-116. doi: 10.1139/F02-168

Nislow, K.H., Folt, C.L. and Parrish, D.L. 2000. Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. Trans. Am. Fish. Soc. 129: 1067-1081. doi: 10.1577/1548-8659(2000)129<1067:SEBAOH>2.0.CO;2

Olden, J., Lawler, J.J. and LeRoy Poff, N. 2008. Machine learning methods without tears: a primer for ecologists. Quart. Rev. Biol. 83: 171-193.

Otto, S.P. and Day, T. 2007. A Biologist's Guide to Mathematical Modeling in Ecology and Evolution. Princeton University Press. New Jersey, USA. 732p.

Randall, R.G. 2002. Using allometry with fish size to estimate production to biomass (P/B) ratios of salmonid populations. Ecol. Freshw. Fish. 11:196-202. doi:10.1034/j.1600-0633.2002.00012.x

Randall, R.G. 2003. Fish productivity and habitat productive capacity: definitions, indices, units of field measurement and a need for standardized terminology. Can. Sci. Advis. Sec. Res. Doc. 2003/061. 14 pg.

Randall, R.G., Kelso, J.R.M., and Minns, C.K. 1995. Fish production in fresh-waters – are rivers more productive than lakes. Can. J. Fish. Aquat. Sci. 52: 631-643.

Randall, R.G., and Minns, C.K. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Can. J. Fish. Aquat. Sci. 57: 1657-1667.

Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Trans. Am. Fish. Soc. 132: 953-968.

Rosenfeld, J.S., and Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Can. J. Fish. Aquat. Sci. 58: 585-593. doi:10.1139/cjfas-58-3-585

Roset, N., Grenouillet, G., Goffaux, D., Pont, D., and Kestermont, P. 2007. A review of existing fish assemblage indicators and methodologies. Fish. Manage. Ecol.14: 393-405. doi: 10.1111/j.1365-2400.2007.00589.

Roth, B.M., Kaplan, I.C., Sass, G.G., Johnson, P.T., Marburg, A.E., Yannarell, A.C. Havlicek, T.D., Willis, T.V., Turner, M.G., and Carpenter. S.R. 2007. Linking terrestrial and aquatic ecosystems: the role of woody habitat in lake food webs. Ecol. Model. 203:439-452.

Saito, L., Johnson, B.M, Bartholow, J., and Hanna, R.B. 2001. Assessing ecosystem effects of reservoir operations using food web-energy transfer and water quality models. Ecosystems 4: 105-125. doi: 10.1007/s100210000062

Scruton, D.A., and Heggenes, J., Valentin, S., Harby, A., and Bakken, T.H. 1998. Field sampling design and spatial scale in habitat-hydraulic modelling: comparison of three models. Fish. Manage. Ecol. 5: 225-240. doi: 10.1046/j.1365-2400.1998.00098.x

Sharma, R. and Hilborn, R. 2001. Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. Can. J. Fish. Aquat. Sci. 58: 1453-1463. doi: 10.1139/cjfas-58-7-1453

Shirvell, C.S. 1986. Pitfalls of Physical Habitat Simulation in the Instream Flow Incremental Methodology. Can. Tech. Rep. Fish. Aquat. Sci. 1460: 68p.

Stalnaker, C., Lamb, B.L., Henriksen, J., Bovee K., and Bartholow, J. 1995. The Instream Flow Incremental Methodology – A Primer for IFIM. National Biological Service. U.S. Department of the Interior, Biological Report 29. 44 pg.

Steffler, P., and Blackburn, J. 2002. Two-dimensional depth averaged model of river hydrodynamics and fish habitat. Introduction to depth average modeling and user's manual. University of Alberta. 120p.

Travers, M., Shin, Y-J., Jennings, S., and Cury, P. 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. Prog. Oceanogr. 75: 751-770.

Trial, J.G. and Nelson, P.C. 1983. Habitat Suitability Information: Common Shiner. Fish and Wildlife Service – U.S. Department of the Interior. FWS/OBS-82/10.40. 22p.

Vadas Jr., R.L., and Orth, D.J. 2001. Formulation of Habitat Suitability Models for stream fish guilds: do standard methods work? Trans. Am. Fish. Soc. 130: 217-235. doi: 10.1577/1548-8659(2001)130<0217:FOHSMF>2.0.CO;2

Van Winkle, W., Jager, H.I. & Holcomb, B.D. (1996) *An individual based instream flow model for coexisting populations of brown and rainbow trout.* Electric Power Research Institute, Interim Report. EPRI TR-106258.

Vilizzi, L., Copp, G.H., and Roussel, J-M. 2004. Assessing variation in suitability curves and electivity profiles in temporal studies of fish habitat use. Rivers Res. Appl. 20: 605-618. doi: 10.1002/rra.767

Walters, C., Pauly, D., and Christensen, V. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on impacts of marine protected areas. Ecosystems 2: 539-554.

Wakeley, J.S. 1988. A method to create simplified versions of existing Habitat Suitability Index (HSI) models. Environ. Manage. 12:79-83. doi: 10.1007/BF01867379

Williams, J.G. 1996. Lost in space: minimum confidence intervals for idealized PHABSIM studies. Trans. Am. Fish. Soc. 125: 458-465. doi:10.1577/1548-8659(1996)125<0458:LISMCI>2.3.CO;2