Fisheries and Oceans Canada
Science

Pêches et Océans Canada
Sciences

C S A S
Canadian Science Advisory Secretariat

S C C S
Secrétariat canadien de consultation scientifique

Research Document 2003/061

Document de recherche 2003/061

Not to be cited without
permission of the authors *

Ne pas citer sans
autorisation des auteurs *

Fish productivity and habitat productive capacity: definitions, indices, units of field measurement, and a need for standardized terminology.

Productivité du poisson et capacité de production de l'habitat : définitions, indices, unités de mesure sur le terrain et besoin de normaliser la terminologie.

R. G. Randall

Fisheries and Oceans Canada
Central and Arctic Region
Great Lakes Laboratory for Fisheries and Aquatic Sciences
P.O. Box 5050
Burlington, Ontario, L7R 4A6

Pêches et Océans Canada
Région du centre et de l'Arctique
Laboratoire des Grands Lacs pour les pêches et les sciences aquatiques
C.P. 5050
Burlington, Ontario, L7R 4A6

* This series documents the scientific basis for the evaluation of fisheries resources in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

* La présente série documente les bases scientifiques des évaluations des ressources halieutiques du Canada. Elle traite des problèmes courants selon les échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

Research documents are produced in the official language in which they are provided to the Secretariat.

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

This document is available on the Internet at:

Ce document est disponible sur l'Internet à:

http://www.dfo-mpo.gc.ca/csas/

ISSN 1499-3848 (Printed)

Canada

Abstract

Effective aquatic resource conservation involves the management of fish populations and their habitat. Differences between habitat and fisheries science in the use of terms like productivity and productive capacity are highlighted to emphasize that a common terminology should be adopted. Habitat evaluation should occur, implicitly or explicitly, at a spatial scale that encompasses entire fish populations. Knowledge of the population level spatial scale is poorly known in most instances but the spatial scale of many habitat projects is likely smaller than the population scale. This mismatch is a challenge for science. Productive capacity is a characteristic of fish habitat, while productivity is a characteristic of populations. The concepts and measurement units of fish production (kg ha^{-1} yr^{-1}), productivity (survival, e.g., recruits per spawner) and habitat productive capacity (kg ha^{-1}) are defined and explained in a manner that bridges both habitat and fisheries science. Fish production is measured for fisheries assessment of individual populations, but it is usually not measured for habitat management. Rather, biological indices of production (density, biomass, richness, IBI, HPI) and physical habitat surrogates (area, cover, substrate, depth, pools, riffles, Defensible Methods) of productive capacity are used. The indices and surrogates can apply to species, assemblages or whole communities; the latter is paramount for resource management as maintaining natural biodiversity is a primary mandate of Fisheries and Oceans Canada. Habitat biologists must be mindful of the limitations and implied assumptions when indices or surrogates are used to assess the productive capacity of fish habitat. Research to provide science support for habitat and fisheries management is mutually beneficial, and the objectives often overlap. The Canadian Science Advisory Secretariat (CSAS) publication series provides a national forum for reporting both science and management advisories, and highlights the parallels between habitat and fisheries science.

Résumé

La conservation efficace des ressources aquatiques repose sur la gestion des populations de poisson et de leur habitat. Nous mettons en évidence les emplois différents que font les scientifiques de l'habitat et les halieutistes de termes comme productivité et capacité de production afin d'insister sur le besoin d'uniformiser la terminologie. On devrait évaluer les habitats, de façon implicite ou explicite, à une échelle spatiale qui englobe les populations entières de poissons. Dans la plupart des cas, l'étendue spatiale des populations est méconnue, mais elle est sans doute plus grande que l'échelle spatiale de la plupart des évaluations de projets visant les habitats. Cet écart constitue un défi pour les scientifiques. La capacité de production est une caractéristique de l'habitat du poisson, tandis que la productivité est une caractéristique des populations. Nous définissons et expliquons les notions et unités de mesure de production du poisson (kg ha^{-1} an^{-1}), de productivité (survie, p. ex. recrues par géniteur) et de capacité de production de l'habitat (kg ha^{-1}) de façon à concilier la science de l'habitat et la science halieutique. On mesure la production du poisson pour l'évaluation halieutique de populations individuelles, mais habituellement pas pour la gestion de l'habitat. On se sert plutôt d'indices biologiques de la production (densité, biomasse, richesse, indice d'intégrité biologique et indice de productivité de l'habitat) ainsi que de mesures de l'habitat physique (superficie, couvert, substrat, profondeur, fosses, radiers et méthodes défendables) comme variables substitutives de la capacité de production. Les indices et les variables substitutives peuvent s'appliquer à des espèces, à des assemblages d'espèces ou à des communautés entières. Les mesures caractérisant des communautés entières sont primordiales pour la gestion des ressources étant donné que le maintien de la biodiversité naturelle constitue une responsabilité fondamentale de Pêches et Océans Canada. Les biologistes de l'habitat doivent être conscients des limites et des postulats implicites lorsqu'ils utilisent des indices ou des variables substitutives pour évaluer la capacité de production de l'habitat du poisson. La recherche scientifique soutenant la gestion de l'habitat et celle soutenant la gestion des pêches sont mutuellement avantageuses et leurs objectifs se recoupent souvent. La série de publications du Secrétariat canadien de consultation scientifique (SCCS) constitue une tribune nationale pour la communication d'avis scientifiques et d'avis sur la gestion et fait ressortir les liens entre la science de l'habitat et la science halieutique.

Introduction

The objectives of fisheries and habitat management are closely tied but the association is not always explicit and the terminology may be different. The objective of fisheries management is to achieve sustainable fisheries by regulating fishing effort. The objective of habitat management is to conserve and protect the fish habitat that sustains fish production by preventing habitat loss or by mitigating the effects of potentially harmful alterations. Assuring long-term sustainability of aquatic resources is the common goal for both management groups. Both fisheries and habitat conservation involves the management of human activities, but the intervention mechanisms are directed at fish populations (fishing effort) and at physical habitat, respectively. For this reason, there is a spatial-scale mismatch between the management activities, with the area being managed by harvest regulations often being larger than the area affected by habitat alteration. Another significant difference is that fisheries management targets exploited species and their prey, while habitat management is concerned with all co-habiting species and biodiversity, regardless of whether the species are exploited by fishers or not. These differences lead to different use of terms of productivity and productive capacity by fisheries and habitat managers.

The objective of this report is to compare the terminology used by fisheries and habitat biologists to descibe capacity and productivity, to call for the adoption of a standardized terminology, and to emphasize that the meaurement units should always be identified. Definitions are provided of productivity and productive capacity as they apply to populations and their habitat, and biological indices and habitat surrogates for field evaluation of capacity are described, along with an acknowledgement and implication of the scale mismatch between fisheries and habitat management. The role of science is to provide the tools for evaluating habitat productive capacity. The role of habitat management is to provide detailed spatially explicit descriptions of habitat before and after proposed alteration and to use the science-based tools for evaluating net change in capacity. Standardized terminology will lead to a closer association between fisheries and habitat science, and make the link between habitat and fish population conservation explicit.

Fish Productivity and Production

In recent publications that explicitly link population dynamics to habitat capacity (Moussalli and Hilborn 1986, Musick 1999), **productivity** is defined and measured as a population trait such as the maximum survival rate. Historically, however, productivity was used to describe ecosystems, sometimes vaguely and inconsistently, and consequently there is a difference and potential confusion between fisheries and habitat ecologists in the use of the term productivity.

In describing ecosystems, Wetzel (2001), citing earlier publications from a number of well-known ecologists, described productivity as the maximum growth of organisms under optimal conditions, or the maximum ‘potential’ production of organisms. Reference to ‘optimal conditions’ meant that productivity was an adjective describing the habitat or ecosystem. Wetzel correctly noted that ‘optimal’ conditions for an organism, population, community or ecosystem can only be approximated after extensive investigation. Therefore, although maximum potential production is a valuable concept, it is difficult to measure in the field. Realized production of a species of interest is easier to measure and conceptualize than potential production (Wetzel 2001). To be useful and applicable, the species, units and time frame used for field measurement of productivity must be clearly defined.

Fish stock assessment biologists define productivity as the maximum survival rate of a population of fish. The management of fish stocks is based on the premise that recruitment is dependent on the numbers of spawners. Fishing effort is managed by quota or restrictions on fishing season to ensure that a known target abundance of spawners is conserved each year to maintain population viability. Biological reference points, such as the required spawning stock size, is based on a stock (S) and recruitment (R) relationship for the population being managed (Fig. 1). Recruitment increases as spawning stock increases, and then reaches an asymptote (Beverton and Holt 1957) or declines (Ricker 1954) at higher spawning densities. The shape of the stock-recruitment relationship is non-linear because at low densities survival is density-independent, but at high fish abundance survival is density-dependent because of resource limitations (intraspecific competition). If long term data on stock size and resulting recruitment are available, the productivity for the population can be calculated. Productivity is the maximum survival (number of recruits per spawner) at low density (i.e., when survival is density-independent), calculated as the initial slope of the S-R relationship (R/S; see Moussalli and Hilborn 1986; Myers et al. 1997; Bradford and Irvine 2000; Sharma and Hilborn 2001). Maximum population growth rates, expressed as an annual instantaneous intrinsic rate of natural increase (r_m), are calculated using this slope parameter as well (Myers et al. 1997) and can be used to estimate the recovery times for depleted populations (Musick 1999). If recruits (R) and parents (S) are measured in the same units, the replacement level can be plotted as the 1:1 line on the SR curve (Fig. 1).The difference between the replacement line and the recruitment line represents surplus production and potential yield to a fishery.

Productivity of a fish species is inherently related to its life history strategy (Musick 1999), but productivity can also vary within populations over time because of changes in environmental conditions (e.g., Bradford and Irving 2000). In addition to survival, other parameters are also used as measures of population productivity, such as fecundity and size-at-maturity. FAO (www.fao.org/fi/glossary) provided a generic definition of productivity as a population trait that 'relates to the birth, growth and death rates of a stock'. Individual population traits that determine productivity are interrelated and population-specific (Musick 1999; but also see caveats of Hutchings 2001).

Recruitment, survival and growth rates are determinants of fish production. **Production rate** is a key population parameter of interest to habitat and fisheries managers, as it is a measure of habitat capacity, and it determines the maximum sustainable catch or yield. Fish production is the 'total elaboration of new body substance in a stock in a unit of time, irrespective of whether or not it survives to the end of that time' (Ricker 1975). Production rate is the product of specific growth rate (G) and average biomass (B) for a specified duration, usually one year. Average biomass in turn is determined by recruitment of young fish, survival and somatic growth through time. Habitat alteration that impacts on any of these process rates will influence production. When expresssed on an unit area basis, the units of production (e.g., grams per unit area per unit time) make the link to habitat capacity explicit. Formulae for estimating production are given by Mertz and Myers (1998), whereby fish production through growth is balanced with losses from natural mortality (and fishing mortality if the stock is exploited). Mertz and Myers (1998) also provide a simple formula for the production over biomass ratio (P/B), and for a yield over production ratio (Y/P); both ratios have been used as biological indices of production. The observation that maximum P/B is equal to the maximum intrinsic rate of population increase (r_m; Peters 1983), provides a conceptual link between the stock and recruitment relationships described above and fish production. The product of r_m and adult weight is an estimate of the maximum production rate (Peters 1983). For a target population, the calculation of production requires much quantitative field data on time-dependent numbers-at-age and growth-at- age. A recent example of a fish production study is provided by Clarke and Scruton (1999) who illustrate how the production of brook trout (*Salvelinus fontinalis)* in Newfoundland is linked to nutrients and habitat.

Habitat Capacity and Productive Capacity

For individual fish populations, **capacity** (= carrying capacity) is the equilibrium density (numbers of fish) that a particular habitat can support indefinitely by the resources available (Shuter 1990). For unfished populations, capacity can be conceptualized and calculated as the point in the Beverton-Holt recruitment curve that intersects with the replacement line (Hayes et al. 1996; Fig. 1). In contrast to productivity, capacity is the density-dependent component of the recruitment curve (Moussalli and Hilborn 1986). Capacity is dependent on the quantity and quality of the habitat where the population resides. Increasing the habitat area will affect capacity, whereas changes to habitat such as reducing cover or predator removal may affect both productivity and capacity.

For communities, **productive capacity** can be defined as the sum of the maximum production of all co-habiting species (Minns 1995). Capacity and productive capacity both describe habitat; for this report, I differentiate between capacity, the capability of a habitat area to support a single population of interest, and productive capacity - the capability of habitat to support a fish community. In the policy for the management of fish habitat, the Department of Fisheries and Oceans (1986) defined Productive Capacity 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' (DFO 1986). To make this concept operational for habitat managers, field measures of productive capacity were needed (Jones et al. 1996; Minns et al. 1996; Minns 1997). Minns (1997) emphasized that the definition of productive capacity includes three important concepts: production, maximum [production] and natural [diversity]. At a population level, techniques for measuring fish production rate are well known as described above, and production is routinely calculated for fisheries management (assessment of exploited stocks). The production component of productive capacity is measurable in the field, although the time and effort required to collect the necessary population data are considerable. Stock assessment models also include an estimation of maximum production (the second key term) or some other measure of stock performance, for a defined time period. For the entire fish community, productive capacity was defined for an arbitrary area of habitat as 'the sum of all production accrued by all stock during the time they spend any part of their life history in that area' (Minns 1997). Productive capacity is a habitat characteristic that denotes the capability of habitat to support not just individual populations but all cohabiting species that reside in that habitat. Productive capacity is determined by whole-system attributes like thermal characteristics (seasonal water temperatures) and nutrient availability, and by smaller spatial scale habitat attributes that potentially act as life-history bottlenecks to production (Shuter 1990). Habitat bottlenecks affecting production are poorly understood, and conventional wisdom is unreliable. For example, the amount of spawning habitat is often suggested as being a limiting factor, but the quantitative evidence to support this contention is lacking (Minns et al. 1996).

The third key word in the definition of productive capacity is natural, which denotes the qualitative or diversity aspect of community production. That is, the fish species being produced in a specific area are considered in the context of an historical reference point or benchmark of the natural fish community and natural habitat for that area (Minns 1997). Habitat alteration is more likely to impact on fish distribution and species composition than on production *per se* (Minns et al. 1996). Changes is species composition caused by habitat changes are often detrimental. The comprehensive measurement of productive capacity requires information on both the production and the diversity aspect of the fish community (Randall and Minns 2002).

Biological Indices of Production and Biodiversity

Fish production rate is not usually measured by habitat biologists because of the time and cost; rather, biological indices of production such as fish density or biomass are used to measure habitat quality. Also, the measurement of surrogate habitat variables is frequently used to measure habitat capacity. The use of both the indices and habitat surrogates are based on the often untested assumption that there is a possitive correlation between these indicators and population production.

From the perspective of population dynamics, short term estimates of numeric or biomass density (e.g. grams m^{-2}) have only limited value for assessing different habitats. It is challenging to estimate the dynamic process rates (growth, survival, production) from static data, and it is even more difficult to attribute these functional processes to the specific habitat area where the fish were captured. Habitat evaluation for a species must involve some measure of population fitness (Van Horne 1983). Average seasonal estimates of biomass density are more meaningful, but knowledge of the functional linkage to localized habitat is still often lacking.

Randall and Minns (2002) recommended a two-axis approach for assessing habitat productive capacity (Fig. 2). A Habitat Productivity Index (HPI) and an Index of Biotic Integrity (IBI) were used together as field indices of fish community composition and fish community production, respectively. The HPI is the product of average seasonal biomass (kg ha^{-1}) and P/B ratio (y^{-1}), summed for all species, to provide an index of production rate (kg ha^{-1} yr^{-1}; Randall and Minns 2000). The P/B ratio was calculated using an allometric equation that linked P/B to average fish weight in the sample. The IBI was a measure of the diversity and trophic composition of the fish community. IBI integrates several fish community metrics, based on species richness, trophic-group composition, and fish abundance, into one index (Minns et al. 1994). IBI scores are positively correlated with habitat diversity and ecosystem health. Habitat with high scores of both HPI and IBI would rank high for productive capacity. This two-axis approach for assessing habitat productive capacity includes both production and biodiversity as measures of water and habitat quality (Randall and Minns 2002).

HPI was validated by comparison with literature estimates of fish production in whole lakes (Randall and Minns 2000). However, the utility of this index when based on average fish biomass from localized areas within lakes (e.g., different littoral habitats) has yet to be tested. Although the unit of HPI is production rate (kg ha y^{-1}), it is considered to be an index of production because the growth component is inferred from body size rather than from fish growth studies in the field, and because of the uncertainty of the link between localized biomass and fish production.

Both traditional (density, biomass) and recent multi-parameter indices of production (HPI, IBI) are based on an implied assumption of a positive correlation between the index and population production. Fish catches that are used to estimate seasonal biomass may be from areas that are small relative to the larger area utilized by the population. If this is the case, there is a scale mis-match between habitat evaluation and fish population production, and the expected covariance between biomass and production remains untested. Evaluation of habitat productive capacity using static indices is based on the assumption that the habitat provides a good area for growth, survival and hence production, but often this assumption is untested and therefore unfounded.

Habitat Surrogates of Productive Capacity

Obviously wetted area is the primary determinate of total fish production in a system. For lakes, there is a strong correlation between lake size and total fish production (expressed as kg per lake; Fig. 3), and similar relationships between smolt production and river length or wetted area are shown by Bradford et al. (1997) and Prévost et al. (2001). Coefficients of determination for these regressions are often high (e.g., R^2=0.67 in Fig. 3). Loss of wetted area because of habitat alteration (infilling, stream water extraction) will invariably result in the loss of productive capacity. Area is a strong predictor of productive capacity.

Residuals of the regression in Fig. 3 divided by lake area indicate the difference in productive capacity (kg ha^{-1}) of the individual systems, in comparison to the average capacity for all lakes in the data set. Production per unit area depends on the capacity of the ecosystem or habitat. Differences in habitat capacity can be easily conceptualized for whole systems (lakes or rivers) because of the obvious differences in large scale determinants of production such as the thermal properties (geographic latitude). Differences in capacity also occur within systems, but it is more challenging to conceptualize and validate these differences at the smaller spatial-scales. Typical habitat surrogates of productive capacity in coldwater streams are mesoscale classes of stream type based on water depth and substrate such as runs, rapids, flats and pools (Caron and Talbot 1993). Typical habitat surrogates in the near shore areas of lakes are areas with or without macrophytes or other types of cover (Weaver et al. 1997; Pratt and Smokorowski 2003). For both lakes and rivers, spatial scale resolution for validating the different classes may be low. For littoral habitats in the Great Lakes, Randall et al. (1998) was able to discriminate between 2 or 3 fish-abundance classes based on habitat predictors. After comparing densities of juvenile salmon at a large number of rivers in Quebec, Caron and Talbot (1993) concluded that only two categories of habitat could be distinquished. Habitat surrogates of capacity are useful, but the spatial resolution (number of habitat classes) may be limited.

The average area used per fish increases with fish size and it is habitat-dependent. Density fish-size relationships of two ubiquitous species (*Perca flavescens and Lepomis gibbosus*) in littoral habitats of the Great Lakes illustrate the inverse relationship between fish size and density (Fig. 4, upper). The area per fish (inverse of density) for both species is about two times greater in moderate than in good habitat. Grant et al. (1998) used the predicted the area per fish to calculate a percent habitat saturation (PHS) index as the sum of areas of all cohabiting cohorts of *Salmo salar* in a stream. PHS is a useful measure for managers because it indicates the likelihood that a population is at the carrying capacity of the habitat (Grant et al. 1998). Grant et al. emphasized that a goal is to 'calibrate the PHS that is equivalent to the carrying capacity of populations'. Used in this way, area per fish would be a useful surrogate of habitat capacity for different populations in different regions.

Building on earlier quantitative models for evaluating habitat suitability, Minns et al. (2001) developed a Habitat Suitability Matrix (HSM) method for quantifying productive capacity. The method is based on the 'idea that the habitat preferences of individual fish species and life stages can be quantified and aggregated into habitat suitability indices that in turn can be used as surrogate measures of fish habitat productivity' (Minns et al. 2001). The general assessment framework is known as Defensible Methods of Assessing Fish Habitat (Minns 1995), and HSM is the software product used to implement the method. Habitat preferences (depth, substrate and cover) by species and life stage were obtained from the literature and were peer reviewed. Defensible Methods and HSM provide a standardized method for assessing habitat productive capacity based on habitat surrogates. Minns and Moore (2003) empasized that although fish-habitat associations are often uncertain, robust management decisions can be made with simple habitat classifications (i.e., three or four levels of productive capacity).

Validation is a prerequisite to the use of habitat surrogates for determining habitat productive capacity. Randall (2001) differentiated between two levels of validation. Level 1 validation is the traditional testing of significant differences in fish density (or some other fish measure) among habitat classes, followed by cross validation using new data sets. The Randall et al. (1998) and Caron and Talbot (1993) studies cited above are examples of level 1 validation. In contrast, level 2 testing of habitat classes involves validation at a larger spatial scale, that is at a scale that encompases whole populations. This has rarely been done in habitat science (Smokorowski et al. 1998), but it is becoming increasingly important for stock assessment. Randall cited one study that provided data that could be used for level 2 validation (Baglinière et al. 1993). Salmon (*Salmo salar*) abundance was compared using a habitat method (density times area of habitat class, summed for all habitat classes) and independent trap counts of emigrating smolts. The quantitative importance of habitat classes on coho salmon (*Oncorhynchus kisutch*) production has been demonstrated by Sharma and Hilborn (2001) using stock and recruitment data from a number of watersheds; they demonstrated a significant correlation between pool density and stream capacity (smolts per unit area). Bradford and Irving (2000) showed a signficant correlation between temporal changes in coho productivity (recruitment) and land use. Level 2 validation demonstrates an explicit link between habitat and population production. Validation of habitat classes at a population or system scale is a current goal for both habitat and fisheries (stock assessment) science.

Population Geography

When assessing habitat alterations, knowledge of the population level spatial scale is poorly known in many instances but the spatial scale of many activities that impact on physical habitat is likely smaller than the population scale (Minns et al. 1996). This mismatch is a challenge for science, but it is not insurmountable. For determining the extinction risk of fish populations, an estimate of the minimum viable population size is often sought (Musick 1999). The product of minimum size and average area per fish described earlier provides an estimate of the minimum area required to support the population (Minns, pers. comm.). Using the density fish-size relationships from the Great Lakes (Fig. 4), and assuming a minimum population size of 3000 fish (adult spawners, even sex ratio), Randall and Minns (2003) estimated that an area of about 100 hectares was needed to sustain a species that resides in littoral areas with macrophyte cover. This is a first-order estimate yet to be confirmed, but it demonstrates that the area requirements for populations can at least be roughly estimated. Evaluation of habitat within the spatial context of whole populations is tractable and a desirable goal, not only for managing species-at-risk, but also for managing fish and fish habitat in general. Quantitive estimates of population abundance, total area and habitat capacity are needed for the effective management of habitat and the fish populations that are sustained by the habitat.

Role of Science

Fisheries science in support of fish stock assessment and fisheries management has a long history because of the food and economic value of the fishing catch. Recently, the interest in fish habitat science has been increasing exponentially for a number of reasons, the first of which is directly related to stock assessment as well; that is, the influence of habitat on fish recruitment. In addition, habitat research provides science support for Fish Habitat Management, the impact of climate change on biodiversity, and aquatic species-at-risk. To provide advice to fisheries managers on a timely basis, stock assessment and science in support of these assessments are reported in the Canadian Science Advisory Secretariat (CSAS) publication series as research and advisory documents and workshop proceedings. Science support for habitat managers could be provided increasingly in this forum as well (see for example, Levings and Jamieson 2001). The goals of fisheries and habitat management are complementary and overlapping. Focusing on a population scale, using similar terminology with clearly defined measurement units, will facilitate improved interaction between fisheries and habitat science that will be mutually beneficial.

Summary and Recommendations

Habitat assessment should be linked to fish populations so that the impact of habitat alteration is explicity evaluated at the appropriate geographic scale. Terminology related to habitat capacity may be vague or possibly contradictory unless the units of measurement are identified. Production and productivity refer to fish population traits, while capacity and productive capacity are habitat traits. Both capacity and productivity are obviously interrelated, as both depend on environmental conditions. The measurement of productive capacity using biological indices or habitat surrogates is based on the sometimes untested assumption that these static indices are indicators of the dynamic population processes of recruitment, survival and growth, that together determine production. Validation of the habitat surrogates should be done at the population level. The role of both fisheries and habitat science is to link stock and recruitment processes to environmental conditions and habitat at different life-history stages, and to provide validated tools that link indices and habitat surrogates of productive capacity to population and community fish production. Adoption of a common terminology between fisheries and environmental science is a prerequisite to reporting the results of habitat research in the publication series of the Canadian Science Advisory Secretariat.

Acknowledgement

Drs. C.K. Minns and T. Pratt provided helpful comments on an early draft. This work was supported by the Environmental Sciences Strategic Research Fund (ESSRF), Fisheries and Oceans Canada.

References

Baglinière, J.L., G. Maisse, and A. Nihouarn. 1993. Comparison of two methods of estimating Atlantic slamon (*Salmo salar*) wild smolt production, p. 189-201. In R.J. Gibson and R.E. Cutting [ed.] Production of juvenile Atlantic salmon, Salmo salar, in natural waters. Can. J. Fish. Aquat. Sci. 118.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. U.K. Minist. Agric. Fish. Invest. Ser. 2, 19:533 p.

Bradford, M.J. and J.R. Irvine. 2000. Land use, fishing, climate change, and the decline of Thompson River, British Columbia, coho salmon. Can. J. Fish. Aquat. Sci. 57:13-16.

Bradford, M.J., G.C. Taylor and J.A. Allan. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Trans. Amer. Fish. Soc. 126:49-64.

Caron, F. and A. Talbot. 1993. Re-evaluation of habitat classification criteria for juvenile salmon, p. 139-148. *In* R.J. Gibson and R.E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

Clarke, K.D. and D.A. Scruton. 1999. Brook trout production dynamics in the streams of a low fertility Newfoundland watershed. Trans. Amer. Fish. Soc. 128:1222-1229.

Downing, J.A. and C. Plante. 1993. Production of fish populations in lakes. Can. J. Fish. Aquat. Sci. 50:110-120.

Downing, J.A., C. Plante and S. Lalonde. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Can. J. Fish. Aquat. Sci. 47:1929-1936.

Department of Fisheries and Oceans (DFO). 1986. The Department of Fisheries and Oceans Policy for the Management of Fish Habitat. Department of Fisheries and Oceans, Ottawa, Ontario.

Grant, J.W.A., S.O. Steingrimsson, E.R. Keeley and R.A. Cunjak. 1998. Implications of territorial size for the measurement and prediction of salmonid abundance in streams. Can. J. Fish. Aquat. Sci. 55(Suppl. 1)181-190.

Hayes, D.B., Ferreri, C.P. and W.W. Talor. 1996. Linking fish habitat to their population dynamics. Can. J. Fish. Aquat. Sci. 53 (Suppl. 1):383-390.

Hutchings, J.A. 2001. Conservation biology of marine fishes:perceptions and caveats regarding assignment of extinction risk. Can. J. Fish. Aquat. Sci. 58:108-121.

Jones, M.L., Randall, R.G., Hayes, D., Dunlop, W., Imhof, J., Lacroix, G. and Ward, N.J.R. 1996. Assessing the ecological effects of habitat change: moving beyond productive capacity. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 446-457.

Levings, C. and G. Jamieson. 2001. Marine and estuarine riparian habitats and their role in coastal ecosystems, Pacific Region. Canadian Science Advisory Secretariat Research Document 2001/109.

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

Minns, C.K. 1995. Calculating net change of productivity of fish habitats. Can. Manus. Rep. Fish. Aquat. Sci. Number 2282.

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

Minns, C.K. and J.E. Moore. 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.

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’ Areas of Concern. Can. J. Fish. Aquat. Sci. 51:1804-1822.

Minns, C.K., Kelso, J.R.M. and Randall, R.G. 1996. Detecting the response of fish to habitat alterations in freshwater ecosystems. Can. J. Fish. Aquat. Sci. 53 (Suppl. 1):403-414.

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

Moussalli, E. and R. Hilborn. 1986. Optimal stock size and harvest rate in multistage life history models. Can. J. Fish. Aquat. Sci. 43:135-141.

Musick, J.A. 1999. Criteria to define extinction risk in marine fishes. Fisheries 24:6-12.

Myers, R.A., G. Mertz and P.S. Fowlow. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. Fishery Bulletin 95:762-772.

Peters, R.H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, U.K.

Pratt, T.C. and K.E. Smokorowski. 2003. Fish habitat management implications of the summer habitat use by littoral fishes in a north temperate, mesotrophic lake. Can. J. Fish. Aquat. Sci. 60:286-300.

Prévost, É., G. Chaput and E.M.P. Chadwick. 2001. Transport of stock-recruitment reference points for Atlantic salmon, pg. 95-135. In: É. Prévost and G. Chaput. Stock, recruitment and reference points: assessment and management of Atlantic salmon. INRA Paris, 223 p.

Randall. R.G. 2001. Productive capacity of nearshore habitat in the lower Great Lakes: habitat classes, power of resolution and validation, p. 18-27. In Randall, R.G. (ed). Field measurement of the productive capacity of fish habitat – proceedings of the second project workshop, November

2000. Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Burlington, Ontario. 103 p.
Randall, R.G. and Minns, C.K. 2000. Use of fish production to biomass ratios for measuring the productive capacity of fish habitats. Can. J. Fish. Aquat. Sci. 57:1657-1667.
Randall, R.G. and C.K. Minns. 2002. Comparison of a Habitat Productivity Index (HPI) and an Index of Biotic Integrity (IBI) for measuring the productive capacity of fish habitat in nearshore areas of the Great Lakes. J. Great Lakes Res. 28:240-255.
Randall, R.G. and C.K. Minns. 2003. Using density fish-size relationships to predict the habitat area of species-at-risk in the Great Lakes. Canadian Science Advisory Secretariat Research Document (*in revision*).
Randall, R.G., C.K. Minns, V.W. Cairns, J.E. Moore, and B. Valere. 1998. Habitat predictors of fish species occurrence and abundance in nearshore areas of Severn Sound. Can. Manuscr. Rep. Fish. Aquat. Sci. 2440:vii+30 p.
Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.
Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada No. 191.
Sharma, R. and R. Hilborn. 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.
Shuter, B.J. 1990. Population-level indicators of stress. American Fisheries Society Symposium 8:145-166.
Smokorowski, K.E., K.J. Withers and J.R.M. Kelso. 1998. Does habitat creation contribute to management goals? An evaluation of literature documenting freshwater habitat rehabilitation or enhancement projects. Can. Tech. Rept. Fish. Aquat. Sci. No. 2249.
Van Horn, B. 1983. Density as a misleading indicator of habitat quality. J. Wildlife Management 47:893-901.
Weaver, M.J., J.J. Magnuson, and M.K. Clayton. 1997. Distribution of littoral fishes in structurally complex macrophytes. Can. J. Fish. Aquat. Sci. 54:2277-2289.
Wetzel, R.G. 2001. Limnology. Lake and River Ecosystems. Academic Press, New York.

Terminology

To be useful and operational, the terms below include units of measurement for field studies.

Biomass: weight of all living fish in a unit area at a given instant in time, calculated as the product of mean individual weight and density. Sometimes specified as an average for the period for which production is calculated. Units: kg ha^{-1}.

Production: total elaboration of fish tissue during a unit of time (often 1 yr), regardless of whether or not fish survive during the time interval (Ricker 1975). Units: weight per unit area per unit time (e.g., kg ha^{-1} yr^{-1}), or less commonly absolute production for a specified area (kg per river or lake per yr).

Productivity [population]: 1) survival parameter of a population. Productivity is sometimes defined as the maximum survival rate at low density, i.e., when survival is density-independent. Units: the number of recruits per spawner, e.g., for salmon, smolts per female spawner. Example calculation for *Oncorhynchus kisutch* (most return to spawn at a total age of 3 yrs): $r_m = \ln(R/S)$, where r_m is the productivity index, R is recruits (yr i + 3) and S is spawners (year i) (Bradford and Irving 2000); 2) 'relates to the birth, growth, and death rates of a stock. A highly productive stock is characterized by high birth, growth and mortality rates, and as a consequence, a high turn-other or production to biomass ratios (P/B)' (www.fao.org\fi\glossary). In addition to survival rate, productivity parameters include fecundity, age-at-maturity, maximum age (Musick 1999; but also see Hutchings 2001); 3) production rate (see below).

Productivity [ecosystem]: Maximum potential production under optimum growth conditions (Wetzel 2001). Or, productivity is synomous with production rate (Wetzel 2001). That is, production rate is a measure of ecosystem productivity. Reference to ecosystem productivity should include the biota, measurement units, and time frame that were used to measure productivity (e.g., phytoplankton production in g carbon m^{-2}, as measured for a specified time period and date).

Production to biomass ratio (P/B): ratio of annual production (P) to mean biomass (B); also called population production or average specific production (Peters 1983). Mean value of specific production rates of all individuals in a population, weighted for their temporal duration (Peters 1983). P/B is a rate and can be used to determine the turnover time of a population (turnover = inverse of P/B ratio). Units: inverse time (1/yr).

Capacity: equilibrium population size or the number of fish that can be indefinitely supported by the resources available in a defined habitat area (Shuter 1990; Hayes et al. 1996). E.g. for andromous salmonids, the maximum sustainable number of smolts that can be produced, as determined by density-dependent survival. Capacity and carrying capacity are synonymous. Units, number unit $area^{-1}$; smolts km^{-1}.

Productive Capacity: 1) The natural maximum capability of habitats to produce healthy fish, safe for human consumption, or to support or produce aquatic organisms upon which fish depend (DFO 1986). 2) Sum of production of all co-habiting fish species for a defined time period (Minns 1995).

Habitat Production Index (HPI): indicator of community fish production and habitat productive capacity, calculated for each species as the product of average fish biomass and the P/B ratio, summed for all co-habiting species in the area (Randall and Minns 2000). Units: kg ha^{-1} yr^{-1}.

Habitat Suitability Matrix (HSM): quantitative model for assessing net change of productive capacity of fish habitats(Minns et al. 2001).

Index of Biotic Integrity (IBI): integration of several fish community metrics (species richness and composition, trophic composition, and fish abundance and condition) into a single index of ecosystem health (Minns et al. 1994). Metrics are extracted from fish community catch data obtained using standardized field survey methods. Units: individual metrics are standardized and summed; final IBI scores vary from 0 to 100.

Biological indices: indices of fish production or productive capacity, such as fish biomass, fishing catch (yield), IBI and HPI. Units: index specific.

Habitat surrogates of productive capacity: physical habitat classes within a lake or river system, with varying capacities to support fish production. Examples in rivers are pools, riffles and runs, and in lakes, cover versus non-cover near shore habitats. Surrogates are validated by quantitative science-based verification of the habitat-capacity factors. Measurement units for verification can be relative (differences in fish density or biomass by habitat class; Type I validation), or absolute (differences in population production by habitat type; Type II validation).

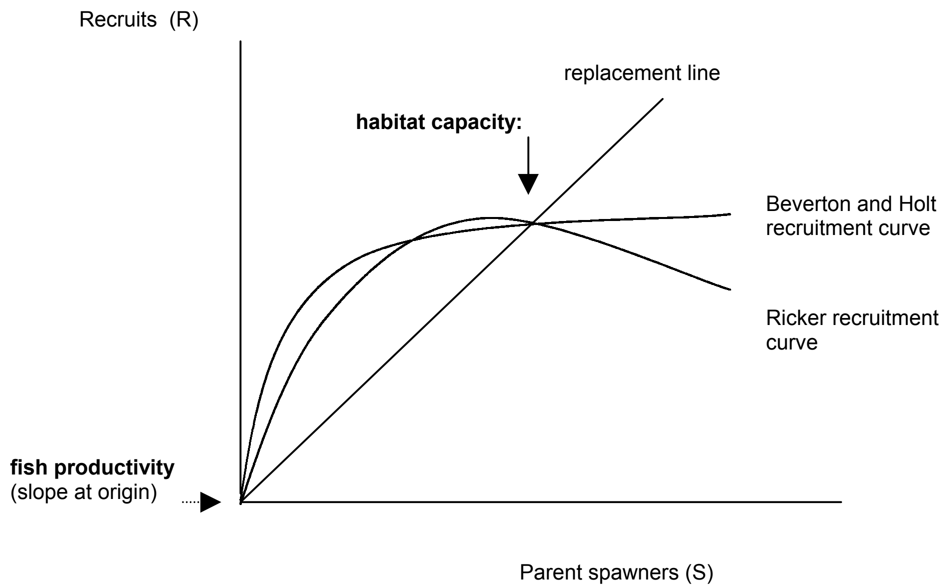


Figure 1. Generalized stock-recruitment relationships for fish populations. Beverton and Holt and Ricker recruitment curves are shown, along with the replacement line. Biological reference points of habitat capacity (equilibrium density, determined by density-dependent processes) and productivity (maximum density-independent survival rate) are indicated with arrows.

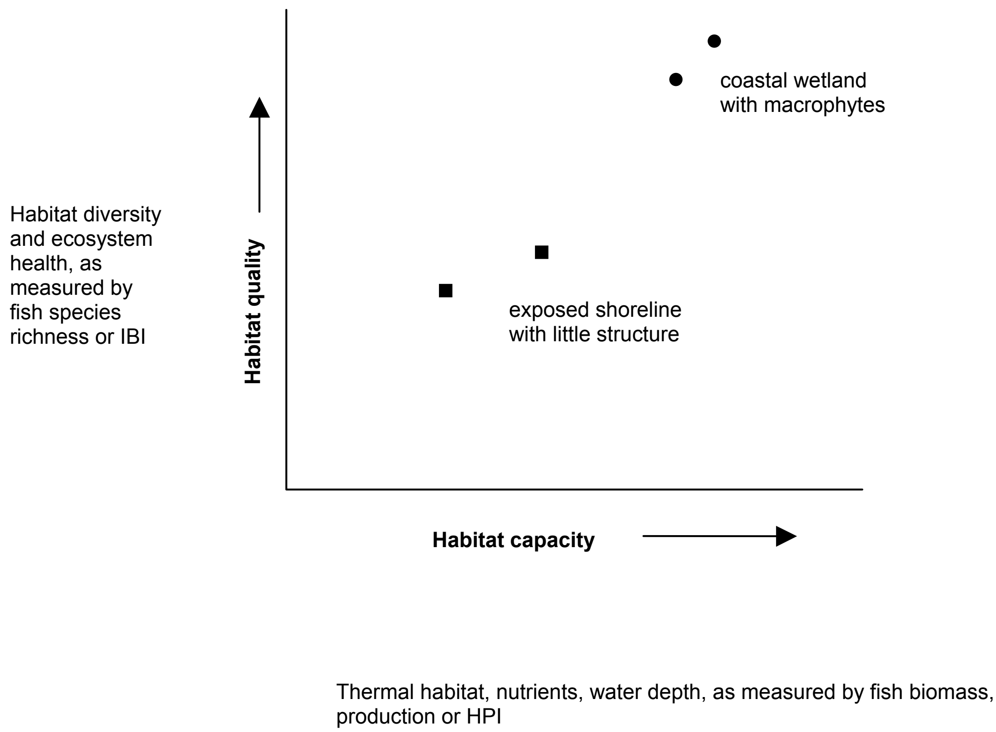


Figure 2. Conceptual diagram to illustrate a two-axis approach for evaluating habitat productive capacity in species rich areas. Habitat capacity and fish production increases to the right on the x axis, and habitat diversity and species richness increases on the y axis. Habitats with high productive capacity and high natural biodiversity would be in the upper right quadrant of the diagram (circles). IBI is the Index of Biotic Integrity and HPI is the Habitat Productivity Index (see text). Diagram modified from Randall and Minns (2002).

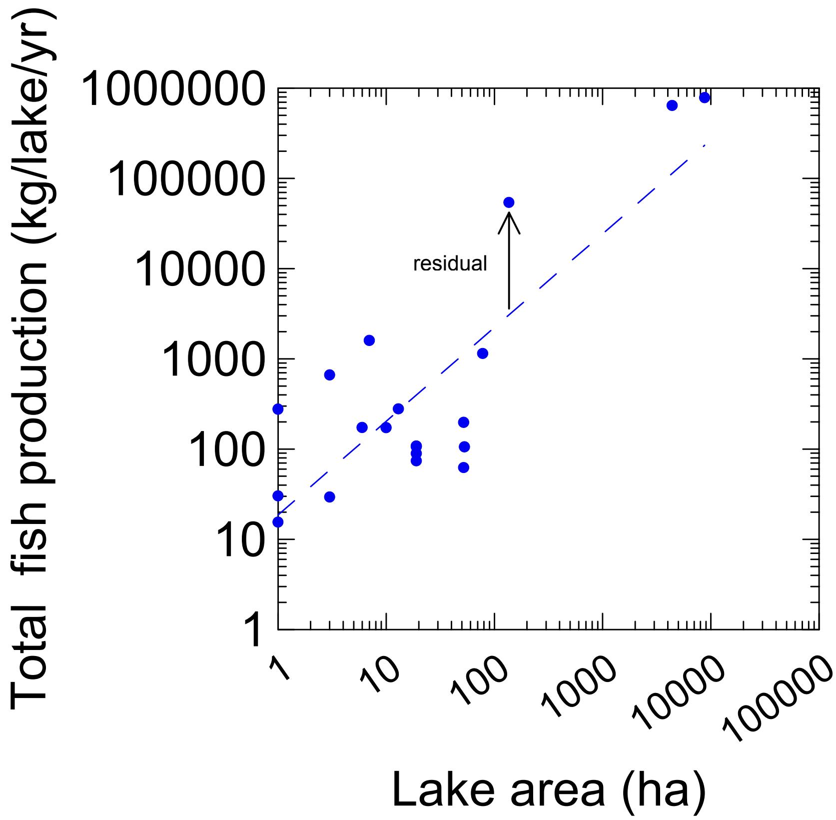
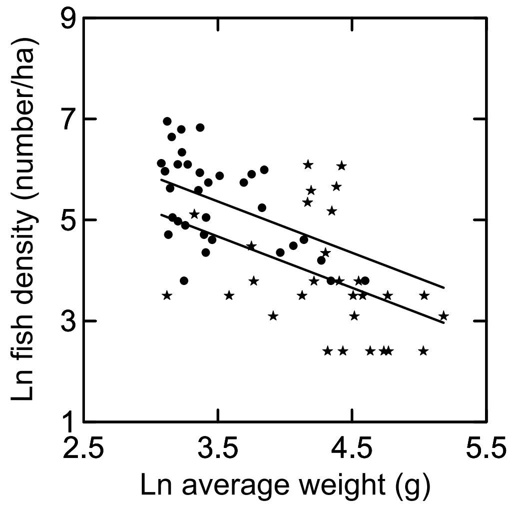


Figure 3. Relationship between lake area and total fish production (kg $lake^{-1}$ yr^{-1}). Data for community fish production (re-calculated as total production per lake) and lake area are from Downing et al. (1990) and Downing and Plante (1993), respectively. Each point represents an individual lake. Residuals from this regression divided by lake area indicate differences in the productive capacity of individual lakes from the average (kg ha^{-1} yr^{-1}).



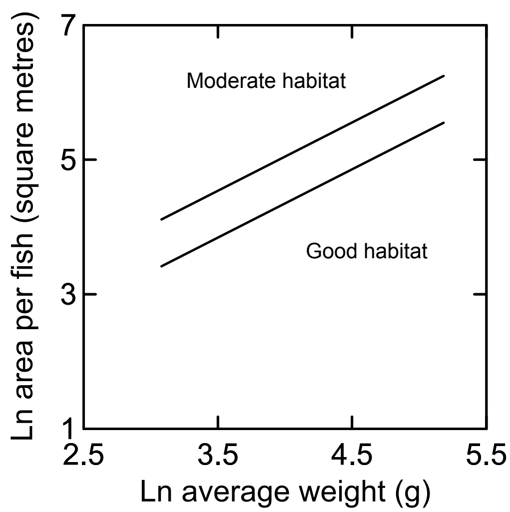


Figure 4. Upper: Density fish-size relationship of *Perca flavescens* and *Lepomis gibbosus* in littoral habitat of the Great Lakes. Circles indicate good habitat (coastal wetlands, upper regression line) and stars are moderate habitat (harbour areas with some cover, lower line). Lower: Area per fish in areas of moderate habitat is about 2 times greater than in areas of good habitat. Figure modified from Randall and Minns (2003).