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| Species at Risk: Habitat Literature Review | Quantification | Espèces en péril : Quantification de l'habitat et examen de la documentation |

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#### Abstract

As the jurisdiction responsible for aquatic species, provisions of the Species at Risk Act (SARA) require that the Department of Fisheries and Oceans (DFO) must identify critical habitat for threatened and endangered aquatic species and protect such habitat from destruction. Workshops and projects over the last five years have provided the scientific foundations for identifying critical habitat for species at risk, and guidelines are likely to be developed in 2007/08.

This project conducted a review of the scientific literature on methods for the quantification of the amount of critical habitat available to populations of animals, with a focus on aquatic species, particularly fish (marine and freshwater) and marine mammals. In total, four approaches were identified that have been used to identify critical habitat; each with its own set of possible models, assumptions and limitations. The approaches have been described as Optimal Reserve Size, Area per Individual, Meta-analysis and Matrix Models.

Most of the papers that describe the approaches suggest that the lack of data for a particular species should not be a deterrent to starting the assessments described. In fact, the lack of data and the need for a framework that incorporates the uncertainties associated with many population parameters appears to be the impetus for most approaches. Many advocate using data from similar species or species that have similar life histories. Many see the assessment process, whatever the process, as an initial step in structuring the available data and a means to identify the gaps and focus research.

Many of the methods described are based on species population vitals such as fecundity, survival and recruitment and habitat quantity and/or quality. It has been noted that while habitat quantity may limit a population by acting on a single life-cycle stage, habitat quality may act on several life-cycle stages and hence improvements in habitat quality may benefit populations on numerous levels without the identification of the actual population limiting factor. This may be important in Species-at-Risk as identified habitat quality issues could be addressed without, or prior to, the determination of critical habitat.


## RÉSUMÉ

En tant qu'autorité responsable des espèces aquatiques, le ministère des Pêches et des Océans (MPO), en vertu de la Loi sur les espèces en péril (LEP), doit désigner l'habitat essentiel des espèces aquatiques menacées et en danger de disparition et protéger cet habitat contre la destruction. Au cours des cinq dernières années, des ateliers et des projets ont jeté les bases scientifiques de la désignation de l'habitat essentiel des espèces en péril et des lignes directrices devraient être élaborées en 2007-2008.

Le présent projet consistait à passer en revue la documentation scientifique sur les méthodes utilisées pour quantifier l'étendue d'habitat essentiel dont disposent des populations de différentes espèces, en particulier aquatiques, notamment le poisson (de mer et d'eau douce) et les mammifères marins. Au total, quatre méthodes ont été utilisées pour désigner l'habitat essentiel; chacune dispose d'un ensemble de modèles, d'hypothèses et de contraintes possibles. Les méthodes sont décrites comme la taille optimale de la réserve, la superficie par individu, la méta-analyse et les modèles matriciels.

La plupart des documents qui décrivent ces méthodes semblent indiquer que le manque de données pour une espèce particulière ne devrait pas nuire à la mise en œuvre des évaluations. De fait, le manque de données et la nécessité d'avoir un cadre qui englobe les incertitudes associées à de nombreux paramètres de la population semblent être le facteur incitatif de la plupart des démarches. Beaucoup préconisent l'utilisation de données relatives à une ou des espèces semblables ayant des cycles biologiques similaires. Par ailleurs beaucoup voient le processus d'évaluation, quel qu'il soit, comme une étape initiale de la structuration des données disponibles et un moyen de cerner les lacunes et de cibler les recherches.

Un bon nombre des méthodes décrites sont basées sur les caractéristiques essentielles de la population, tels que la fécondité, la survie et le recrutement, ainsi que la quantité ou la qualité de l'habitat. On a constaté que même si la quantité d'habitat pouvait limiter une population en agissant sur un stade unique du cycle biologique, la qualité de l'habitat peut influer sur plusieurs stades du cycle biologique et, par conséquent, l'amélioration de la qualité de l'habitat peut bénéficier à des populations sur plusieurs plans, sans que puisse être déterminé le facteur limitatif réel de la population. Cet aspect pourrait être important pour les espèces en péril, puisque les problèmes de qualité de l'habitat définis pourraient être réglés avant ou même sans que soit désigné l'habitat essentiel.

## INTRODUCTION

As the jurisdiction responsible for aquatic species, provisions of the Species at Risk Act (SARA) require that the Department of Fisheries and Oceans (DFO) must identify critical habitat for threatened and endangered aquatic species and protect such habitat from destruction. Workshops and projects over the last five years have provided the scientific foundations for identifying critical habitat for species at risk, and guidelines are likely to be developed in 2007/08.

Moreover, SARA requires the jurisdiction to evaluate the feasibility of recovery of species assessed by COSEWIC as threatened, endangered, or extirpated; and mandatory consultations require estimation of the social and economic costs of recovery, if undertaken for such species. To make these evaluations or estimates for any species where habitat pressures are one of the threats to the species' survival or recovery, it is necessary to quantify the amount of critical habitat that would be available at the commencement of the recovery plan as well as the quantity necessary for achievement of recovery goals in population size and range.

In many cases the "critical habitat" description is likely to be categorical; either simply a list of features whose presence or absence (for example, substrate of "rock", "gravel", sand, or mud) determines suitability or else a range of a feature (for example, water temperature between 5 and $15^{\circ} \mathrm{C}$ ) with no basis for assessing differential quality within the range. In some data rich cases, however, the "critical habitat" description might specify how habitat quality for the species varies with a habitat feature (for example, there could be a functional equation from directed research describing how fish density or productivity varies with density of aquatic plants).

## OBJECTIVES / METHODS

The project conducted a review of the scientific literature on methods for the quantification of the amount of critical habitat available to populations of animals, with a focus on aquatic species, particularly fish (marine and freshwater) and marine mammals. It has been assumed that the features which characterize critical habitat have been identified by other processes. Likewise the review did not address how habitat data should be collected or archived.

The review addressed:

0 when the information on features of critical habitat is qualitative (categorical or an acceptable range), what methods are available to take habitat inventory data and estimate a) the amount of critical habitat that exists and/or b) the total size ${ }^{1}$ that can be supported by the available habitat.
o When quantitative information exists on both population abundance and features of critical habitat, what methods are available to:
o Quantify how abundance varies systematically with the habitat feature(s)

[^1]o Take habitat inventory data and estimate the amount of critical habitat that exists, and/or the total size (or productivity) that could be supported by the habitat known to be available.

It was likely that many publications were variants on common basic methods. In such cases it is the basic methods which were reviewed. The variants on a common theme were identified in 6 and 7 below, but only discussed in 1-5 where they differ in important ways.

For each method reviewed, the following were highlighted wherever possible:

1. List the general mathematical (or bio-mathematical) assumptions of the method (detailed mathematical derivations were not required; only a summary of assumptions made);
2. Discuss the type and amount of data required to apply the method legitimately;
3. Discuss the biological circumstances where the method might be particularly favoured, or might be inappropriate;
4. Summarize how uncertainty is addressed with the method;
5. Highlight any particular risks or dangers in using the method or interpreting results;

In addition for each method the review lists references to:
6. Some key publications (primary or "grey" literature) where the method (and variants) was presented and described fully
7. Some publications (if any) applying the method to quantify habitat for a species.
8. If specific software was available / required for applying the method, sources for such software, and license requirement to use the method, if any.


#### Abstract

RESULTS A literature review was conducted on available resources through all sources. Sources included the Memorial University of Newfoundland QEII library (and its inter-library loan network), the North Atlantic Fisheries Centre (DFO) library and any reliable references available online. Reports and information were focused on critical habitat, species at risk and quantification of habitat. Outlined below are the models which best fit the needs for habitat quantification, in particular to Species-at-risk where datasets may be limited. Other methods were reviewed and not included (eg. IFIM and PHABSIM, Newfoundland and Labrador DFO Habitat Quantification and inSTREAM) as they were felt to be less applicable; however most references reviewed are listed in Section 6.0 so that other reviewers may assess these options if desired.


## Species at Risk and Critical Habitat

Section 2 of the Species at Risk Act (SARA) defines Critical Habitat as the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in a recovery strategy or in an action plan for the species (Species at Risk Act 2002). Defining critical habitat can be illustrated as a three-step process:

1. Determination of a recovery target for a population;
2. Development of a relationship between habitat and population; and
3. Determination of the quantity of habitat required to meet the recovery target (Rosenfeld and Hatfield 2006).

It should be kept in mind that while recovery targets are generally determined for adult (i.e. mature individuals) stages of a species, the critical habitat may be associated with another life-cycle stage and therefore multiple iterations of the above process may be required to ensure that the "target" for each life-cycle stage is met. This can be more challenging when various life-cycle stages utilize different habitat types or utilize existing habitat types to varying degrees.

Besides the relatively vague description of critical habitat outlined in the SARA, Rosenfeld and Hatfield (2006) provide more practical working definitions of critical habitat that assist in defining what is needed for delineation and its quantification:

1. Habitat that is disproportionately important whose singular or cumulative loss will result in significant population-level effects;
2. The minimum subset of habitats required for a species or population to persist (or achieve a recovery target); and
3. Habitats necessary to maintain ecosystem integrity and function.

The core assumptions of critical habitat designation are a positive relationship between habitat and population size and that a minimum area is required to achieve a recovery target. For some species, habitat may play a minor role in population limitation compared with other factors such as predators, invasive species and disease. In these latter cases, other limiting factors may modify the designation of critical habitat such as refuge from predation (Rosenfeld and Hatfield 2006). While most factors limiting a population can ultimately be linked in some way to habitat, all potential aspects that are more non-habitat should be assessed in the initial stages of a recovery plan (eg. invasive species).

Critical habitat, or habitat that limits a population, can be described and quantified within two general categories; habitat quantity and habitat quality. Increases in the number of individuals in a limiting life stage can be achieved either through increasing the quantity or quality of available habitat or through a combination of both. That is, populations may be limited by habitat quality at multiple life stages even though limited by habitat quantity at a single life-cycle stage. In this way, if existing habitat quality could be increased, it could provide increased population production without implicit identification of the overall limiting habitat or life-cycle stage relationship. It is important not to lose sight of this when determining critical habitat and that a broader assessment of habitat and its quality may yield equivalent results with respect to meeting adult targets (perhaps while still trying to identify the actual critical habitat). This assessment would relate to the second critical habitat definition above as it does not specifically identify the critical habitat but the subset of habitats that may be limiting production. Ultimately, the population that is supported by a given critical habitat will be the product of habitat quantity (i.e. the aerial extent) and habitat quality (i.e. animal density). Credible metrics of habitat quality are densityindependent (eg. individual/population growth, survival and fecundity at low population density). These are often difficult to measure in the field as they may have density effects.

The key information for identification of critical habitats are:

1. A solid understanding of the life history and basic habitat associations of the species of interest;
2. Inferences of habitat limitation require accurate information on the quantity and distribution of different habitats available to a species;
3. An established population recovery target; and
4. Habitat abundance relationships at a scale that allows the limiting factors with respect to habitat to be identified (Rosenfeld and Hatfield 2006).

## Critical Habitat Modelling and Quantification

Habitat-explicit population models can be a practical alternative for identifying limiting habitat, potential impacts of habitat change and leverage points for recovery actions (Rosenfeld and Hatfield 2006). In this respect, they can test hypotheses regarding population limitations without actual manipulations or validation of assumptions through further reduction in the population of a Species-at-Risk (SAR).

Habitat models can range from simple models that generate population estimates by extrapolating densities of animals in different habitat types to larger habitat-explicit, sizestructured population models. Habitat-explicit models are the most realistic for exploring the potential of different habitat configurations to meet population recovery targets.

In practice, essential habitat can be described by matrices of environmental variables by life-cycle stages (Cross et al. 1998). Its designation will involve the identification and description of habitat requirements and the characterization and mapping of habitat for the critical life stages of each species (Brown 1998). This is similar to those methods employed for fish habitat quantification in Newfoundland and Labrador (Bradbury et al. 1999; Bradbury et al. 2001; Grant and Lee 2004; McCarthy et al. 2006; 2007). In any quantification of critical habitat, it is important to keep in mind that the methods must be transparent, scientifically credible and legally defensible (Gerrodette and DeMaster 1990; Bean 1983).

Provided below are descriptions of various methods and models to determine critical habitat. A general description of the model is given as well as the assessment points outlined in Section 2.0 where possible. The models below are listed in no particular order.

## Optimal Reserve Size

Gerrodette and Demaster (1990) describe two methods for determining the optimum sustainable populations for marine mammals. In their discussion, they state that the U.S. Marine Mammal Protection Act recognizes that all organisms live in necessary interdependence with each other but that this new perspective has been difficult to implement, not only because of insufficient knowledge of the biology and ecology of marine mammal species, but also an insufficient theoretical foundation. The ecological perspective was relatively new compared to management based on single species.

However, recent modelling and Geographic Information System (GIS) tools have allowed multi-species assessments to occur. While the use of the "optimal reserve" model was not specifically developed for Species-at-Risk, there is no reason why the method could not be used for any species or species assemblage as it is an "ecosystem" approach and habitat based rather than a species-specific method (Parnell et al. 2005). It is a habitat-
based scheme for designing marine reserves that prioritizes certainty in design by focussing on habitats, the importance of habitats and its resilience. The algorithm, however, could be applied across different ecosystems, spatial scales and any number of species.

A description of the model-type theory and development is recorded in papers such as Ward et al. (1999), Possingham et al. (2000), Jones (2002), Leslie et al. (2003), Airame et al. (2003), Meester et al. (2004) and Parnell et al. (2005). The specific model described here is based on Parnell et al. (2005) as it is different from other reserve siting methods in that it doesn't set a priori goals based on area, diversity or biomass but allows the model to generate its own. This paper also describes the algorithm and describes a case study to determine optimal reserve size to provide adequate protection of the species associated with the habitat.

The model relies heavily on statistical methods but the premise is that in order for reserves to be successful they need to be large enough to include and sustain the important populations that spend most of their time within the immediate area. This is not unlike the description of critical habitat for a Species-at-Risk. It should be noted that the optimal reserve model is primarily based on adult individuals as the model is used to protect habitat of exploited species which may be an initial limitation in its use for Species-at-Risk.

By necessity, the design of a reserve must be based on site-specific information including habitat as well as the biological and physical factors that might affect the resilience and stability of these habitats. The method has three Phases of implementation:

Phase I: Discrimination and mapping of sub-habitats and estimating the affinity of each species to the sub-habitats.

The discrimination of sub-habitats and species affinities was conducted using fine-scale measures of habitat and species presence. In this case for example, measurements were conducted within 250 m habitat blocks. The habitat and the affinity of adults were surveyed at the same time and didn't rely on summaries of literature-based suitabilities. This may be more of a challenge with Species-at-Risk with limited individuals. It should also be noted that since the species of interest were exploited, their recorded distribution/affinity to the habitats present may have been affected by harvesting activities. This could lead to an underestimation of habitat affinity in habitats most important to a particular species as harvesters may concentrate their efforts within habitats of greatest animal densities. Landings data at a similar scale to that of the habitat measures would be needed to address this (which would be very unlikely using existing catch records).

Major habitat types were determined using hierarchical divisive clustering analysis of substrate, bottom features, vertical relief and algal data. Utilization of the resulting habitats by identified species was calculated as a measure of habitat specificity using the BIO-ENV procedure (Clark and Ainsworth 1993). The spatial distribution of species diversity throughout the habitat was estimated for each survey location using Hill's N1 diversity (Parnell et al. 2005). Values were then spatially interpolated to a raster map using ordinary kriging in ArcView GIS software.

Phase II: Determine optimal size and location for a reserve to protect identified species using a simple and generally applicable algorithm.

The reserve design algorithm uses random mapping of contiguous habitat blocks within the habitat boundary to generate a "reserve value" in bootstrap or Monte Carlo simulations. The reserve values generated produce an asymptotic value, above which additional reserve size (or additional blocks added to the reserve) did not provide added significant value.

The algorithm calculates an index of reserve value that was defined as the relative value of protecting a particular area based on its size, the habitats located within it, the affinities of exploited species to these habitats and individual species mobility. The approach used in the algorithm was to build a hypothetical reserve beginning at a randomly chosen box, calculate a reserve value for that box and then add to the reserve box by box in a random but contiguous fashion until the reserve encompassed the entire habitat. At each increase in reserve size, the reserve value is recalculated. The optimal reserve size can then be determined from a plot of reserve value as a function of reserve size. The optimal reserve size is the size where average reserve value approaches an asymptote.

Phase III: Determine the stability of the habitat over time using historical data of spatial distribution and existing physical data that would be involved in mechanisms during habitat structure and stability (in this case water temperature, currents and wave energy).

The total number of blocks required to generate the optimum reserve size were then placed in the location which would provide the best overall diversity and habitat resilience. Historical and recent air photos of the habitat area (over approximately 50 years) were used to determine the resilience of the habitat and whether the final location could be adjusted to areas of greater resilience. Additional historic data on large current patterns such as El Nino were also used. In addition, data on temperature, currents and wave energy were measured to determine if habitat types/resilience and affinity could be explained and used to modify the final reserve location.

Bottom temperature was sampled at six locations to determine the spatial distribution of temperature. Bottom temperatures were sampled at 10-minute intervals between two time periods; June 2002 to February 2003 and April 2004 to January 2005. Thermistor strings with sensors were also deployed at two sites with sensors at 0.5 and 2 m above the bottom as well as 8 and 1 m below the surface. Strings recorded temperatures at 4 -minute intervals between September 2003 and December 2004.

Currents were measured simultaneously at two locations near the habitat using bottommounted acoustic doppler current profilers (ACDP). The units were place at 25 m depth and recorded in 1 m bins between October 27 and November 14, 2003 and May 14 to May $30,2004)$.

Wave exposure was determined from output from a coastal model of wave refractiondiffraction off San Diego which was used to develop spatial maps of significant swell heights along the 10 m contour off the habitat. Wave energy was then calculated from significant wave heights to generate spatial maps of mean and maxim daily wave energy along 100 m long segments along the 10 m contour to produce a time-averaged map of wave energy.

The specific habitat information was used to allow the ultimate determination of the location of the reserve. It was interesting to note that the entire habitat area was not included in the reserve, only the area that was determined to be necessary to maintain the
species within the habitat area, in this case an eelgrass ecosystem. This method would be considered useful for Species-at-Risk in areas where extensive habitat affinity data exists or where population numbers would allow the data to be collected. The process is transparent and based on standard methods.

## Area per Individual (API) Model

Animal density per unit area decreases in a predictable manner with increases in animal size (Randell and Minns 2003). The hypothesis that the density body-size model is sufficiently accurate to calculate the area requirements of Species at Risk was tested by Randell and Minns (2003). The relationship between animal abundance and adult size is used to estimate an average habitat area per individual (API). Animal abundance (D) decreases inversely with adult size as determined by the allometric relationship:

$$
D=a W^{-b} \quad\left(\text { or }^{\log _{e} D}=\log _{\mathrm{e}} a-\log _{\mathrm{e}} \mathrm{~W}\right)
$$

Where $\mathrm{W}=$ the size of adult fish (grams);
$\mathrm{a}=\mathrm{a}$ scaling constant (value will depend on the taxa, population and region); and
${ }^{-b}=$ the allometric coefficient (typically approximates -0.75 to -1.00 ).
For freshwater fish, Randell et al. (1995) found ${ }^{-b}$ to be -0.96 and the scaling constant to depend on the habitat.

This equation was used to estimate fish abundance in various habitat types. Equations were established for fish assemblages as well as for individual species. Results were tested using Ancova analysis of covariance to determine whether the density:body-size models were similar in different habitats. Fish assemblage density and individual species density were both used as dependant variables, habitat type was the categorical predictor and average fish size was the covariate.

In the current example, the model was tested using boat electrofishing data (transects) collected from fish assemblages in the lower Great Lakes. Data was collected at six locations with three habitat types over three dates (May to October). The mean weight of the total assemblage or individual species per transect was calculated as total biomass of the three combined samples divided by total captures. Catch-per-unit-effort was converted to fish density by estimating catch efficiency and area sampled. It should be noted that transects with an average fish size less than 20 grams were excluded from calculations of the density fish-size relationship due to inefficient capture rates of smaller individuals.

The Ancova analysis was run and the interaction term (habitatsize) was checked to see if there was interaction between habitats. If it was not significant, the term was dropped. Comparisons were completed between each habitat as well as the general fish densitysize regression for the Great Lakes.

Area-per-fish was estimated by inverting the density-size relationship with a correction factor for the re-transformation bias. The results indicated a negative relationship between fish catch and fish size in different habitat areas. The slope of the fish-size relationship for pooled data was not significant among habitats but the intercepts or "elevations" were habitat dependant (that is, they were significantly different). The results suggest that the density fish-size models can be used to estimate the average area per fish with sufficient
precision for the management of Species-at-Risk (Randell and Minns 2003). The model could be used two-fold: it could estimate the minimum habitat area to sustain a viable population size if that size is known, or it could conversely estimate the number of individuals an existing habitat area could support. Based on differences observed among different habitat types, it may also be used to compare different habitat types and/or qualities with respect to enhancement or rehabilitation scenarios.

The first assumption of the method outlined is the estimation of fish density. Capture efficiency was used to generate a density from boat electrofishing data. Any uncertainty associated with capture efficiency or changes in efficiency between different habitat types would need to be incorporated if required. In addition, the model only used fish greater than 20 grams in weight due to low capture efficiency of smaller fish. This may be overcome by alternate methods to estimate abundance or smaller lifecycle stages, however these life-cycle stages would need to be further incorporated into the model as the current version only assesses adults (see below).

The calculated densities showed an overall high degree of variance and this caused a large correction factor for estimates of area-per-fish. This could be compensated to some degree by using the upper 95\% confidence interval of the area-per-fish to ensure a cautious estimate of area required, especially for Species-at-Risk.

With respect to Species-at-Risk, or any species for that matter, the model does not predict or provide an estimate of viable population levels. The model as presented above also only gives the area-per-individual of mature adults of a population and does not address any other life-cycle stage, however the equation appears to be similar for different species and literature values can be used for parameter inputs such as size at maturity and habitat preferences (particularly COSEWIC documentation). The equations could be used as a first-order and tentative estimate of area requirements if specific data for the target species were not available.

## Life-cycle Stage Incorporation

The area-per-individual model was extended to include various life-cycle stages. Minns (2003) uses baseline data for species life-cycle stages to predict the number of individuals at the end of each life-cycle stage. This result is then used as the starting point of the next life-cycle stage. The number of individuals is again based on species vitals and habitat availability/suitability for each life-cycle stage. The model again uses the assumption that population numbers generally decrease through life-cycle stages and that the API will increase through life-cycle stage as a result of increasing body size. Therefore the population as a whole is generally regulated by the habitat that is most limiting. Critical habitat is that which limits a particular life-cycle stage to a maximum population number as a result of API for the habitat supply. Suitable habitat supply is the quantity (eg. aerial extent) and quality (eg. suitability) of habitat available to a particular life-cycle stage. The suitability of habitat for each life-cycle stage is standardized similar to the weighted suitable area (WSA) approach outlined in Terrell et al. (1995).

The life-cycle based API model uses several population parameters to estimate the population number at the end of each life-cycle stage. The survival rates, and hence population number for each life-cycle stage were generated using literature values. While literature values can be quite will known for some species, less known and indeed some Species-at-Risk populations may be very limited. The approach addresses this potential
issue by using surrogate values from similar species or data from species which share a similar life history and/or habitat preference. The current example in Minns (2003) used lake trout (Salvelinus namaycush), a freshwater species whereupon much research has been conducted, and deepwater Sculpin (Myoxocephalus thompsoni), a Species-at-Risk which is poorly studied. Habitat suitabilities for available habitats were also generated from literature values.

Upon generating the potential API for each species based on habitat supply, the model can be interrogated by adjusting habitat supply at various life-cycle stages to estimate the outcome on the adult population. In this way, the critical life-cycle stage and habitat can be identified for the population.

The life-cycle based API model as outlined was initially developed for lake fish, particularly northern pike (Randell et al. 1995; Minns et al. 1995) and modified for the presented study. The use of the API model does ignore a number of areas known to play a role in fish populations:

1. Growth patterns are typically indeterminate and growth rates at different life stages may be density dependant. The growth patterns are fixed in the model.
2. While the current life-cycle based API model addresses life-cycle stages, as presented in Minns (2003) it only considers three stages. It should be noted that some species may have more complex life histories where the model would require modification.
3. The model ignores male-female differences. It does however use the proportion of females in a mature population to generate areas needed for spawning.
4. Fecundity was not estimated based on age or size parameters. This could be incorporated to provide further estimation accuracy.

The case studies presented in Minns (2003) show that development and implementation of API models are feasible as many parameters needed could be obtained from literature. Even with species less well known, surrogate parameters could be used as a starting point until more information becomes available on the species in question. The API model is considered a prototype and the author emphasized that a much more thorough synthesis of available information for parameter estimates will be required, especially for species with varied life histories. However, the approach can provide insight into the role of habitat supply on a species population. It can also provide reasonable identification of the lifecycle stage which may be most limiting by the available habitat supply and how changes to habitat quality may affect a species popultion.

## Meta-Analysis of Habitat Carrying Capacity

Meta-analysis uses data from many populations of the same species, or closely related species that share similar life histories to generate estimates of a species population growth rate. In this way, parameter estimates such as maximum reproductive rate and habitat carrying capacity can be combined from multiple populations. The inclusion and analysis of multiple populations allows for parameter estimates to be generated from a probability distribution. The resulting probability distributions can be combined with comparatively limited population-specific data to make inferences at the level of the specific population in question (see Myers et al. 1999; Myers et al. 2001; Prevost et al. 2001; Gibson and Myers 2003; Barrowman et al. 2003; Gibson 2006).

Meta-analysis uses spawner-recruit models (either the Beverton-Holt or Ricker models) that express recruitment as a density-dependant function of spawner biomass, and the replacement line, the slope being the inverse of the rate at which recruits produce replacement spawners.

The method has been applied to many species, if only in a cursory fashion, in Myers et al. (1999, 2001) and Gibson and Myers (2003). As stated in Gibson and Myers (2003), the two parameter estimates from meta-analysis (carrying capacity and maximum reproduction rate) can provide a basis for evaluating the status of a population and assessing the change to a population resulting from habitat alterations or other human activities.

The datasets used in Gibson and Myers (2003) were spawner-recruit time series for eight populations of alewife (Alosa pseudoharengus) in eastern North America. For this assessment, the Beverton-Holt model was used to represent the spawner-recruit relationship between the spawning biomass in year $t\left(S_{t}\right)$ and recruitment $\left(R_{t}\right)$ as

$$
\mathrm{R}_{\mathrm{t}}=\alpha \mathrm{S}_{\mathrm{t}} / 1+\left(\alpha \mathrm{S}_{\mathrm{t}} / \mathrm{R}_{\mathrm{o}}\right)
$$

where $\alpha$ is the slope at the origin of the spawner-recruit relationship and $R_{0}$ is the asymptotic recruitment level, which is the carrying capacity expressed as the number of fish that survive to maturity (age three in this specific example). The recruit-spawner relationship (the inverse of the replacement line) was also modelled using a spawning biomass per recruit ( $\mathrm{SPR}_{\mathrm{F}=0}$ ) calculation to standardize the rate at which recruits produce spawners among populations. The spawner biomass per unit area of nursery habitat, produced by members of year-class ( $t$ ) throughout their lives in the absence of anthropogenic mortality, was standardized among populations. Once standardized, all differences in the population dynamics are in the spawner-recruit portion of the model and hence data and parameter estimates are directly comparable among populations (Gibson and Myers 2003).

The model is applied to multiple populations by assuming the $\alpha$ and R values are normally distributed random variables of the median maximum lifetime reproductive rates and median carrying capacity. Estimates are obtained using the approximate maximum likelihood algorithm of Lindstrom and Bates (1990) and the S-Plus nonlinear mixed-effects library of Pinheiro and Bates (1999).

The main assumptions with respect to compensatory spawner-recruit models is that the per capita survival from egg to the age of recruitment is a decreasing monotonic function of the number of eggs and that the maximum reproductive rate occurs at the origin (Gibson and Myers 2003). The specific alewife example in Gibson and Myers (2003) also lists assumptions regarding population regulation for that species. It was assumed that year-class strength of anadromous alewife is regulated primarily through intra-specific competition occurring during the pre-migratory larval and juvenile life-cycle stages. As such, the carrying capacity of freshwater nursery habitat is the factor that ultimately limits the size of an alewife population. An assumption is also made that all density-dependant processes occur between spawning and recruitment (i.e. age of maturity).

This method is interesting and could be used for Species-at-Risk as it is possible to combine data from several populations of the same species or a species with a similar life
history. However, based on the assumptions outlined for the alewife calculations, the species combined would have to share a similar limiting factor which may be difficult to acquire or assume with a Species-at-Risk population with limited data available.

## Life History Stage-based Matrix Models

The idea that all habitat utilized by a species is equally important to the species has been shown by many approaches to be flawed in that some habitats may be more important to fish than others (Levin and Stunz 2005). This would also hold true for life-cycle stages within a single species. As mentioned previously, habitat quantity can limit a population by acting on a single life-cycle stage where as habitat quality can act on numerous life-cycle stages simultaneously.

A life-cycle stage-based matrix model has been suggested by Levin and Stunz (2005) to identify essential fish habitat (EFH). They propose that essential fish habitat is habitat that has significant impacts on vital rates (eg. fecundity and survival) of sensitive life-cycle stages. Defined in this manner, small changes in the quantity or quality of EFH will have large impacts on population dynamics. This approach could be useful with respect to Species-at-Risk in that it could quickly identify critical habitat needed for slowing and potentially reversing a population's growth rate.

The paper emphasizes the importance of carefully using sensitivity analysis to identify life history stages as potential management targets. The matrix model-based methodology is considered common, however the technique uses sensitivity analysis to identify sensitive life-cycle stages. This, with the identification/quantification of habitat for each life-cycle stage can determine critical/essential habitat that can limit a species population growth rate.

The stage-based matrix model is described as a three-step process:

1. Development of a stage-structured matrix model that can represent vital parameters (eg. survival or growth) of a population;
2. Use of the model to identify sensitive life-cycle stages; and
3. Determinations of what habitats, if any, are important to these stages.

The stage-based matrix model is the standard technique. It uses common vitals to model a population's growth rate. Vitals include fecundity, survival rates for each stage and species-specific data relating to habitats utilized such as density of life-cycle stages, the aerial extent of these habitats for the population in question and habitat-specific survival rates. It is the proportions of these habitat types present and the habitat-specific survival rates for each life-cycle stage which are used to determine how the population growth rate would respond to alterations of habitat types present and possibly to modifications of existing habitat.

The matrix generates an average long-term population growth rate ( $\lambda$ ). A sensitivity analysis is then performed on the survival rates of each life-cycle stage to determine the relative variability explained within $\lambda$. Variance in survival rates were drawn from a normal distribution with a mean equal to the rate specified in the matrix models and specified by:

$$
\sigma^{2}=(\mu)=\exp [2.231 \ln (\mu)-1.893] \text { (see Bradford 1992). }
$$

The life-cycle stage with the greatest relative variability explained (i.e. the highest) is considered the most sensitive life-cycle stage. The habitat-specific information can now be used to estimate how the population growth rate can be affected by changes in habitat quantity and/or quality.

Much of the data required (fecundity and survival for life-cycle stages identified) for the matrix model is typically available from the literature, particularly for exploited species. Model limitations relate to various considerations:

1. The life-cycle stages for the species in question need to be properly identified prior to model implementation;
2. The data needs may be limited or lacking for habitat-specific survival (most likely for juvenile life-cycle stages);
3. The model does not include density-dependence;
4. The model assumes a closed population (may be more valid for a Species-atRisk); and
5. The model itself is considered conceptual rather than an actual application tool.

Similar to other models, Species-at-Risk data may be limited to start with a complete dataset for a species in question.

## DISCUSSION

Most of the papers that describe approaches suggest that the lack of data for a particular species should not be a deterrent to starting the assessments described. In fact, the lack of data and the need for a framework that incorporates the uncertainties associated with many population parameters appears to be the impetus for most approaches. Many advocate using data from similar species or species that have similar life histories. Many see the assessment process, whatever the process, as an initial step in structuring the available data and a means to identify the gaps and focus research.

Many of the methods are based on species population vitals such as fecundity, survival and recruitment and habitat quantity and/or quality. It has been noted that while habitat quantity may limit a population by acting on a single life-cycle stage, habitat quality may act on several life-cycle stages and hence improvements in habitat quality may benefit populations on numerous levels without the identification of the actual population limiting factor. This may be important in Species-at-Risk as identified habitat quality issues could be addressed without, or prior to, the determination of critical habitat.

Many species models are based on information regarding the adult life-cycle stage as many come from exploited populations. However, it has been indicated that the limiting factor for many species occurs during the pre-adult life-cycle stage such as egg-to-age 1 or juvenile. These life-cycle stages typically are less studied and hence have more limited data. Approaches need to include juvenile life-cycle stages and therefore must accommodate limited data, at least initially, at least in the form of surrogate values of needed parameters.

It is also important to keep in mind that critical habitat alone will not protect a species, they are linked to their surrounding landscapes and hence quality of habitat could be greatly affected by larger landscape changes that may not be directly within critical habitat. For example, changes in agriculture or forestry operations within a landscape could have the potential to severely alter stream temperature regimes such that what appears to be critical (and high quality) spawning habitat becomes unsuitable (Rosenfeld and Hatfield (2006).

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[^1]:    ${ }^{1}$ In some cases population productivity or other indicator of population status may be used instead of abundance in all cases where "abundance" is referenced in this project description.

