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Components of a Science-based Framework for Assessing the Impact of Development Activities under Section 73 of Canada's *Species at Risk Act*

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems 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.

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TABLE OF CONTENTS

ABSTRACT

Under Section 73(3) of Canada's *Species at Risk Act*, the competent minister may not authorize an activity that jeopardizes the survival or recovery of a SARA-listed species. Since 2004, the concept of jeopardizing survival and recovery has received considerable attention from DFO's Science Sector in the form of allowable harm advice; however, allowable harm is a species, not project-specific concept, and to date has not typically incorporated habitat effects, which are expected with development projects in and around aquatic ecosystems. Here, an overview of allowable harm advice is presented as it relates to interpreting Section 73(3). Components of a science-based framework to assess the impact of development activities under Section 73(3) are then presented. The three components are: 1) the ability to relate individual projects to changes in habitat condition; 2) relationships between habitat condition and species vital rates, including considerations for behavioural and sub-lethal effects; and, 3) the relationship between population growth rate and vital rates, explored through elasticity analysis for 143 COSEWIC-assessed species (fishes, freshwater mussels, marine mammals, marine turtles) across five population states (crashing, declining, stable, growing, booming). These components are combined to estimate changes to a species' population growth rate resulting from a single development activity, and thus also provide an accounting framework to evaluate harm from all activities in a permitting period. The components will require future work to inform taxa-specific functional responses, especially concerning relationships between habitat and vital rates, and sub-lethal effects. Further work is also required to determine the ability to achieve measurable gains in vital rates and populations through offsetting measures, if applied. If adopted into a decision support tool, this body of work would ensure that project decisions around Section 73(3) can be made in a rigorous, transparent, and nationally consistent manner.

DEFINITIONS

Definitions below are taken from DFO (2014b):

Jeopardize: to place a wildlife species or population in a situation where its survival or recovery is at risk

Recovery: a return to a state in which the population and distribution characteristics and the risk of extinction are all within the normal range of variability for the wildlife species

Survival: the achievement of a stable or increasing state where a wildlife species exists in the wild in Canada and is not facing imminent extirpation or extinction as a result of human activity

Threat: any human activity or process that has caused, is causing, or may cause harm, death, or behavioural changes to a wildlife species at risk, or the destruction, degradation, and/or impairment of its habitat, to the extent that population-level effects occur. A human activity may exacerbate a natural process

Limiting factor: a non-anthropogenic factor that, within a range of natural variation, limits the abundance and distribution of a wildlife species or a population (e.g., age at first reproduction, fecundity, age at senescence, prey abundance, mortality rate)

Harm: The adverse result of an activity where a single or multiple events reduce the fitness (e.g. survival, reproduction, growth, movement) of individuals

Stress: a wildlife species at risk is stressed when a key ecological or demographic attribute of a population, or behavioural attributes of individuals, are impaired or reduced resulting in a reduction of the species viability (Salafsky et al. 2003)

Allowable harm: harm to the wildlife species that will not jeopardize its recovery or survival

Pathway of effects: description of the mechanisms through which potential environmental effects of a threat may cause a stress on a wildlife species

INTRODUCTION

Fisheries and Oceans Canada (DFO) has the regulatory responsibility "to prevent wildlife species in Canada from being extirpated or becoming extinct, to provide for the recovery of wildlife species that are extirpated, endangered, or threatened as a result of human activity, and to manage species of special concern to prevent them from becoming threatened or endangered", as outlined in Canada's *Species at Risk Act* (s.6). For DFO these responsibilities are limited to fish as defined under the *Fisheries Act* (including fish, marine mammals, shellfish, crustaceans, marine reptiles). To help fulfill responsibilities under SARA, science advice is provided to DFO's Species at Risk Program on various aspects of the species listing and recovery planning process (e.g., DFO 2014b), which forms the scientific basis by which DFO undertakes recovery planning activities.

As a result of a growing number of SARA-listed species and ongoing human development in or near aquatic ecosystems in Canada, DFO is increasingly forced to make decisions on a case-by-case basis about the impact of human development activities on SARA-listed species. Management of activities that may impact a SARA-listed species is permitted and guided by Section 73 of the Act, which states that:

> "73 (1) The competent minister may enter into an agreement with a person, or issue a permit to a person, authorizing the person to engage in an activity affecting a listed wildlife species, any part of its critical habitat or the residences of its individuals.
>
> (2) The agreement may be entered into, or the permit issued, only if the competent minister is of the option that (a) the activity is scientific research relating to the conservation of the species and conducted by qualified persons; (b) the activity benefits the species or is required to enhance its chance of survival in the wild; or, (c) affecting the species is incidental to the carrying out of the activity.
>
> (3) The agreement may be entered into, or the permit issued, only if the competent minister is of the opinion that (a) all reasonable alternatives to the activity that would reduce the impact on the species have been considered and the best solution has been adopted; (b) all feasible measures will be taken to minimize the impact of the activity of the species or its critical habitat or the residence of its individuals; and, (c) ***the activity will not jeopardize the survival or recovery of the species***" (italics and bold added for emphasis).

Subsection (c) of Paragraph 73(3) requires that prior to authorizing a SARA permit, the competent minister must make a determination about whether development projects (hereafter referred to as individual works/undertakings/activities or w/u/a, sensu Koops et al. 2013) will jeopardize the survival or recovery of listed species.

The concept of jeopardizing survival or recovery has received considerable attention from DFO's Science Sector as the concept of 'allowable harm', which describes the aggregate harm a species can sustain without jeopardizing its survival or recovery (DFO 2004a,b,c; DFO 2006; Vélez-Espino and Koops 2007; DFO 2017a). The basis for this research document is to develop components of a scientific framework, building on past science advice concerning the concept of allowable harm (DFO 2004a,b,c) and other guidance about impacts to fisheries productivity (Koops et al. 2013, Bradford et al. 2014, Bradford et al. 2015), to assess whether w/u/a will jeopardize the survival or recovery of a SARA-listed species. Once operationalized into a decision support tool, the framework will provide a scientific, nationally consistent basis for the determination of Section 73(3) as it relates to SARA-listed species.

Therefore, this document has three objectives:

1. To provide a science-based interpretation of the wording of Section 73(3)(c) as it relates to DFO's recovery planning process.
2. Building on previous science advice (e.g., allowable harm; science advice to support implementation of the *Fisheries Act*), to assemble the components of a science-based framework to assess the impact of development activities (w/u/a) on SARA-listed aquatic species in Canada; and,
3. To identify the preliminary elements needed to operationalize the framework into a decision support tool.

This document is divided into six sections. Section 1 provides an interpretation of allowable harm and a review of approaches for allowable harm assessment. Sections 2, 3, and 4 provide the components of a framework for assessing the impact of development activities under SARA Section 73 (Section 2: The effect of individual w/u/a on habitat condition; Section 3: Relationship between habitat condition and vital rates; Section 4: population sensitivity of Canadian aquatic species at risk). Section 5 provides considerations around offsetting if used as a means to reduce the impact of development activities. Section 6 provides advice around operationalizing the framework.

SECTION 1: REVIEW OF APPROACHES FOR ALLOWABLE HARM ASSESSMENT

Before describing the components of a scientific framework to address permitting decisions, it is helpful to review past DFO science advice around the interpretation of Section 73. DFO first addressed subsection 73(3)(c) during a national CSAS meeting to assess the level of 'allowable harm' to several fish stocks (see DFO 2004a,b). The concept of allowable harm was defined as "harm to the wildlife species that will not jeopardize its recovery or survival" (DFO 2004a,b). With this definition in mind, DFO (2004a,b) established a scientific framework based on four guiding principles to assess allowable harm, hereafter referred to as allowable harm assessment (AHA). This initial allowable harm framework was designed to understand the total harm (i.e., aggregate mortality from all potential sources) that would not jeopardize survival or recovery, rather than harm for individual w/u/a. DFO (2004a,b) concluded that harm to SARA-listed species could be allowed (permitted under Section 73) if the following four criteria were satisfied:

- Criterion 1: "The current population is neither so small that random factors threaten population viability nor so concentrated in space that it is vulnerable to elimination by a catastrophic event."
- Criterion 2: "The recent trajectory of the stock is stable or likely to be increasing, so that survival or recovery is not in jeopardy in the period when the permit is in place."
- Criterion 3: "The known sources of human-induced mortality are unlikely to increase during the permitting period. This means that there is high confidence that the causes of human-induced mortality are under management control, monitored, and can be enforced effectively."
- Criterion 4: "There is a relatively high likelihood that recovery goals will be achieved in biologically reasonable time frames with the activity present."

An extension of these guiding principles was developed subsequently in 2004 with the "Moncton Protocol" (DFO 2004c), which provided additional detail around the four criteria and divided the allowable harm assessment into several phases (DFO 2004c):

“Phase I – Recovery Potential: Is survival or recovery of the species in jeopardy if human activities affecting the species continue? This involves questions 1 – 4 regarding species status:

1. What is present/recent species trajectory?
2. What is present/recent species status?
3. What is expected order of magnitude / target for recovery?
4. What is expected general time frame for recovery to the target?

Phase II – Sources of Harm: What are the important activities affecting the species and how does the aggregate harm compare to what is allowed? (Questions 5 – 8):

5. What is the maximum human-induced mortality which the species can sustain and not jeopardize survival or recovery of the species?

6. (a) What are the major potential sources of mortality/harm? More specifically: What are the activities that are permitted by DFO, or are permitted by someone else who looks to DFO for advice, or are permitted by another authority on behalf of DFO— and which may contribute to total mortality or harm to the species? Should consider, *inter alia*, and give reasons for dismissing (when appropriate) each of:

   a) Directed fishing (with or without a quota) for a listed species— international as well as domestic fisheries; b) bycatch in fisheries directed at other species; c) detrimental impacts on habitats by fishing activities; d) direct mortality by permitted habitat alterations (for example smolts killed in power turbines; e) oil & gas exploration, blasting); f) detrimental alteration of habitats by permitted activities (for example loss of lacustrine or riverine productive capacity due to water draw-downs; gear impacts, all the “foreign materials, forces, and noises”); g) ecotourism & recreation; h) shipping & transport & noise; i) fisheries on food supplies; j) aquaculture; introductions & transfers; k) scientific research; and, l) military activities.

   *Note— If an activity is just causing general harm and not directed mortality determined through reasonable cause-and-effect, then it doesn’t qualify for a permit (but its cumulative effect needs to be considered in determining the level of mortality/harm that we do allocate among sources). (b) Do Canadian activities alone impact the species? For transboundary species that migrate in and out of Canadian waters, list all International activities that may impact the species.

7. For those factors NOT dismissed, quantify to the extent possible the amount of mortality or harm caused by each activity.

8. Aggregate total mortality/harm attributable to all human causes and contrast with that determined in Question #5.

Phase III - If mitigation measures or alternative activities are required, what are the options for those activities? (Questions 9 – 12):

9. To support condition (a), science and management will have to: develop an inventory of all reasonable alternatives to the activities in #7, but with potential for less impact. (e.g. different gear, different mode of shipping); document expected mortality/harm rates of alternate activities; document nature and extent of major ecosystem effects caused by the alternate activities (e.g. habitat impacts,

> impacts on dependent predators, etc.); document expected costs and benefits of options which could be adopted, at least when options may look promising.
>
> 10. To support condition (b) science and management will have to: develop an inventory of all feasible measures to minimize the impacts of activities in #7; document the expected effectiveness of the mitigation measures for permitted activities; document the expected costs and benefit of options which could be applied, at least when options may look promising.
>
> 11. To support condition (c), science and management will have to document: the expected mortality or harm for various scenarios carried over from #9 and/or #10 are below that determined in #5 and; ***the projected population trajectory under the various scenarios indicates that survival or recovery is not in jeopardy***, considering cumulative sources of impact.
>
> 12. Prepare options and (where justified) recommendations regarding permits, including rationales, relevant conditions to ensure (a), (b), and (c) are covered, and performance measures. A document suitable for the Minster to enter on the SARA Public Registry should be prepared."

The Moncton Protocol (DFO 2004c) was revisited in 2006 through the National Science – Habitat Management Workshop on Allowable Harm Assessments for Aquatic Species with Habitat-Related Threats (DFO 2006). Rationale for the workshop was that the Moncton Protocol had limited ability to link species with habitat-related threats to mortality or other reference points used in allowable harm assessment. Several modifications and alternative approaches were presented that allowed the linking of habitat threats with mortality, such as population viability analyses with habitat functions, and approaches involving DFO's Pathways of Effects to describe changes to habitat quality and function. Several outstanding issues were noted, including: 1) the selection of appropriate units by which harm to habitat could be measured and allocated; 2) the need to accommodate both quantitative and qualitative approaches for data-poor and data-rich species, including the determination of uncertainty, especially for freshwater species that are typically data-poor and with primarily habitat-based threats; 3) developing a template for the provision of allowable harm advice from Science to Habitat Management (now the Fish and Fish Habitat Protection Program) to inform decision making for SARA permitting; and, 4) encouraging further discussions between sectors on tracking SARA permits and authorizations and evaluating cumulative effects (DFO 2006). A key conclusion of the 2006 workshop was that "…national consistency in the implementation of SARA within the regions and across the regions is currently constrained by a need for guidance and the development of an approach for allowable harm assessment for aquatic species with habitat-related threats".

It is necessary to define the condition(s) of Section 73(3)(c) that the allowable harm framework should serve to assess. The wording of Section 73(3)(c) is sufficiently broad that several scientific interpretations could be made. First, the word "***or***" in "jeopardize survival ***or*** recovery" implies that a distinction needs to be made about when survival vs. recovery is the population condition to be assessed. A precautionary view is that the more restrictive clause should be relevant for a given species: the term "recovery" should hold as the population condition of interest where recovery of the species has been deemed feasible by DFO; if recovery is not feasible, survival should be the population condition of interest. This view is consistent with the 2016 Draft SARA Permitting Policy (Government of Canada 2016)

The guiding principles outlined in DFO 2004 (a,b), the Moncton Protocol (DFO 2004c), and the workshop on Allowable Harm Assessment for Aquatic Species with Habitat-Related Threats (DFO 2006) indicate that population size (criterion 1), population trajectory (criterion 2), the timeframe for recovery (criterion 3, established by considering the current and recovered population size and population trajectory), and an evaluation of all sources of harm during the permitting period (loosely, criterion 4) should form the basis for AHA, provided that guidance can be developed about linking habitat condition with mortality. However, differences exist in the way AHA has been conducted by DFO's Science sector owing to data availability, the suitability of analytical approaches for each species, the nature of recovery targets, and interpretation of DFO 2004 (a,b,c). Examples of AHA, which are included within Recovery Potential Assessments[1] (RPA) or as Science Response Reports, are provided below:

Spotted Wolfish RPA (DFO 2004d):

An early example of AHA, the authors noted the widespread distribution of the species and stable or slightly increasing population trajectories since the early 1990s, despite ongoing human-induced mortality. Based on the apparent building of the stock in the face of fishing mortality, the authors concluded that there was scope for harm, but that the level of human-induced mortality should be kept at or below current levels. The authors indicated that the AHA should be revisited if the species showed significant changes in abundance.

Nooksack Dace (Harvey 2007)

Due to the lack of life history parameters and poor knowledge about population trajectory, the authors used a subjective, qualitative process to suggest that "…there is little scope for human-induced mortality. Permitting….should consider the consequence(s) to achieving stated recovery goals".

Black Redhorse (Vélez-Espino and Koops 2007)

Due to limited empirical data and the lack of population size and trajectory estimates, the authors used an inferential approach to establish: 1) the presumed rate of population decline at time of species listing, based on COSEWIC criterion A; 2) population equilibrium, based on a population regulated by the carrying capacity of its occupied habitat; and, 3) the theoretical maximum intrinsic rate of population increase (r_{max}), based on the relationship between r_{max} and body size in freshwater fishes. These population trajectories were averaged to establish an assumed, baseline population trajectory in the absence of empirical time-series data. The level of population growth was assumed as that which is reasonable for a population below its maximum, and which could occur for several generations. AHA was conducted by developing a stage-structured matrix model and exploring the dependency of population growth rate (λ) to perturbations to stage-specific mortality and fertility, commonly referred to as elasticity analysis. The authors reported maximum allowable harm as the perturbations to stage-specific mortality or fertility that would still result in positive population growth, assuming the inferred baseline population trajectory was a reasonable approximation of actual population growth. The authors noted that while maximum allowable harm can be interpreted as the level of harm to vital rates that still allows for positive population growth (as any growing population is theoretically heading towards recovery), a target minimum population growth rate should be informed by management considerations.

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[1] 2015 Recovery Potential Assessment Guidelines, Element 22 (DFO 2015a) require authors to: "Estimate maximum human-induced mortality and habitat destruction that the species can sustain without jeopardizing its survival and recovery". In addition, in relation to Section 73, authors are required to: 1) Identify and quantify (to the extent possible), potential impacts on recovery goal(s) and recovery targets (e.g., whether allowable harm will result in a lower probability of and a longer time to recovery", 2) Report results in risk-based language, factoring in uncertainty, 3) Provide options and recommendations regarding the potential permitting for allowable harm under Section 73 or SARA, including rationales, relevant conditions and performance measures.

Bowhead Whale RPA (DFO 2008)

Population projection models, including a deterministic growth model, were used to evaluate the current status of the population, pre-exploitation population size, current population growth rate, and future harvest levels. These factors were used to examine potential population growth and "years to recovery" for Bowhead Whale, noting that all harvest scenarios would result in the recovery of the population (defined as the return of population size to 70% of pre-exploitation levels) if total annual harvest was kept under 15 animals per year.

The authors noted: "The time it takes for a population to reach a recovery target is directly related to its biology (growth rate, mortality rate, etc.). In a case where harm is allowed, without jeopardizing recovery of the population [i.e., while allowing positive population growth], the time to reach recovery increases as allowable harm increases." The authors also noted that "Ultimately the time allowed for a population to meet its recovery target is based on policy considerations" and "there is no biological basis for setting a maximum time to achieve recovery".

Silver Chub (Young and Koops 2013a)

Similar to Black Redhorse (Vélez-Espino and Koops 2007), AHA was conducted by developing a stage-based matrix model, which was used to calculate the elasticity of population growth rate to perturbations of stage-specific mortality and fecundity. In addition to estimating the effect of chronic harm (i.e., ongoing, year-after-year changes to mortality or fecundity, as would be expected due to constant removals or permanent habitat loss), the authors also explored the effect of transient harm, modeled as a one-time perturbation to stage-specific vital rates. Two baseline population trajectories were used to reflect uncertainty in empirical time-series data from Lake Erie. Estimates of maximum allowable harm were provided as the total harm that the population could sustain while still maintaining positive population growth under each baseline scenario.

Carmine Shiner (Young and Koops 2013b)

Similar to Black Redhorse (Vélez-Espino and Koops 2007), allowable harm was assessed through elasticity analysis with a population matrix model. In addition to estimating allowable harm, the authors predicted the change in time to recovery for a population subjected to increasing levels of harm. Results indicated that the delay to recovery can increase exponentially with harm.

Porbeagle (DFO 2015b)

The authors indicated that "there are no accepted recovery or fishing reference points for Porbeagle", but proposed a target that involved achieving 80% of female spawning stock numbers (SSN) at maximum sustainable yield (MSY) within three generations (approximately 54 years). A forward-projecting age- and sex-structured population model was fit to empirical data with four scenarios around population productivity. Allowable harm assessment was conducted by determining how different levels of total mortality would lead to changes in recovery timeframes, both for the assumed $SSN_{80\%}$, and SSN at MSY. A 4% harvest rate, corresponding to total allowable catch in Canadian waters, would result in slow population recovery; whereas, a 2% mortality rate from all sources would allow recovery under all scenarios. The final determination was that total mortality from all sources should not exceed a 4% morality rate, which would allow the population to experience a positive trajectory towards the assumed targets. Mortality greater than 4% would not provide positive population growth, and thus was deemed to jeopardize survival and recovery.

Salish Sucker (Pearson 2015)

Due to the lack of life history parameters and empirical data about population trajectory, the authors used a subjective, conservative process to recommend that allowable harm should be 2% of the lower confidence limit of the population estimate for each locality, up to a maximum of 10 individuals per year.

Southern Designatable Unit of Atlantic Cod (Clark et al. 2015)

Allowable Harm Assessment was determined by exploring the effect of different fishing mortality rates on: a) the probability of the stock experiencing no decline in abundance over 36 years; and, b) the number of years to reach B_{lim} with 50% and 95% certainty. In the assessment, B_{lim} was the precautionary approach reference point of spawning stock biomass limit.

Cumberland Sound Beluga (Marcoux and Hammill 2016)

This allowable harm assessment was conducted to address harvest considerations after a draft recovery plan for the species was developed. A recovery target (5,000 animals by 2091) was available on which to base the assessment. Based on an initial population estimate of 1,000 animals, the authors calculated that an average instantaneous rate of increase of approximately 0.021 would be required to reach the recovery target in 2091. When considered at shorter timescales, this translated to a target 10-year expansion to about 1,235 animals. Two approaches for assessing allowable harm were used, reflecting different endpoints (reaching the predetermined recovery timeframe vs. maintaining stability or growth of the population). The first approach involved calculating sustainable yield, defined as the removal of animals that would maintain a constant population. This was also reported as the probability of causing a decline in the population over a 10 year period.

A second analysis involved the Potential Biological Removals (PBR) method outlined in Wade (1998), which describes the removal levels that allow the population to continue towards the recovery target based on a recovery factor. The PBR threshold was calculated as:

$PBR = N_{min} * 0.5 * R_{max} * F_r$,

where R_{max} is the maximum rate of population increase (default value of 0.04 was assumed for cetaceans), F_r is the recovery factor (a value between 0.1 and 1), and N_{min} is the estimated population size. The authors also provided the probability that the population would reach the recovery target (1,235 animals in 10 years) at different harvest levels. Results indicated that at harvest levels of 25 animals per year, there was a 0% chance of reaching the 10-year recovery benchmark, and at 0 animals per year, there was a 32% chance in meeting the benchmark. The PBR approach was also incorporated in the RPA for Offshore Killer Whale (DFO 2014). See Taylor et al. 2003 for additional guidance on the PBR approach.

Scope for Harm for White Shark in Canadian Waters (DFO 2017a):

Estimating allowable harm for White Shark involved a detailed evaluation of each criterion outlined in DFO (2004a,b). Population size (Criterion 1) was evaluated by reviewing available abundance estimates from the North Atlantic. Although substantial variation existed in published estimates, available information indicated that population size was not so small (or spatially concentrated) as to be at high risk of environmental stochasticity. Population trajectory (Criterion 2) involved analyzing time-series log book data, and concluded that there was a likelihood of a positive population trajectory. The likelihood of increasing harm over the permitting period (Criterion 3) was explored by considering the potential for short-term increases in bycatch and bioaccumulation rates. Also based on log-book analysis, it was concluded that the Canadian population was experiencing extremely low bycatch rates, and stringent bycatch controls suggested these rates were unlikely to increase. The authors also noted that changes in vital rates have not been observed due to bioaccumulation. Finally, the likelihood of achieving recovery goals with harm applied (Criterion 4) was evaluated by determining the sensitivity of population growth to mortality. The recovery target for the species was to 'maintain or increase White Shark abundance in the North Atlantic'. Unlike other approaches reviewed here, a time- and abundance-based recovery target was not available for which to base the calculations, so the authors used an approach based on the ability to maintain positive population growth. The F_{crit} value was determined based on deterministic projections using the Euler-Lotka equation and assuming exponential growth. Ultimately, it was concluded that growing populations could endure mortality while allowing for positive population growth. The authors concluded that fishing mortality in Canadian waters was so low relative to F_{crit} that the population could support some mortality without going deterministically extinct. Based on back-calculations, mortality would have to be very high in Canadian waters for the population trajectory to be declining. Finally, the authors evaluated the probability of population decline under different mortality scenarios, noting that the majority of simulations led to positive population growth.

Redside Dace (van der Lee et al. 2020)

Similar to Black Redhorse and Silver Chub, AHA was conducted by developing an age-based meta-population matrix model based on best available population parameters. As with Black Redhorse, no empirical estimates of population trajectory or size were available; therefore, the authors used stage-specific perturbations of mortality and fertility to determine the response of population growth rate under different assumed population trajectories (see detail in van der Lee et al. 2020). COSEWIC's criterion A was used to infer the population trajectory at time of listing, while body-size allometric relationships (similar to Black Redhorse) were used to infer theoretical maximum population growth. Both chronic and transient harm were evaluated for the growing population as the maximum perturbations to stage-specific rates that would not reduce population trajectory below stability. Simulations were then used to estimate the probability of observing population decline over three time frames (1, 10, 100 years) under various levels of harm (mortality).

Sakinaw Lake Sockeye Salmon (DFO 2018)

Noting that the stock was currently suppressed by limiting factors and not human-mediated mortality, the authors emphasized the importance of the current enhancement program and fisheries management plans in reducing exploitation rates. Models were used to determine the average exploitation rate for Sakinaw Sockeye Salmon from 2011 to 2015. Model results indicated that reducing this rate from 5% to 0% would have very little effect on recovery due to small population size and low marine survival. The conclusions were that maintaining the 5% exploitation rate would not change the trajectory of recovery of Sakinaw Sockeye Salmon, though the rate should be kept to the lowest level possible. Conclusions were that minimal allowable harm should be permitted and reduced below current levels to the extent possible.

CONCEPTUAL DIFFERENCES IN ALLOWABLE HARM ASSESSMENTS

The review of selected approaches for allowable harm assessment is provided to illustrate the range of methods used by DFO's Science sector to address Section 73(3)(c). Several important differences among approaches are noted:

1. The extent to which quantitative advice has been provided

In some cases, the lack of empirical data concerning population size, trajectory, and life history parameters has resulted in qualitative approaches for allowable harm assessment. The lack of data is often used to suggest there is little or no scope for harm until additional information can be obtained (e.g., Harvey 2007). The lack of empirical data is relevant to Criterion 1, 2, and 4.

2. The extent to which current population trajectory is known or has been assumed

It is common for SARA-listed species to lack time-series data, or for available index data to have poor spatial or temporal coverage. In some cases, limited data have led authors to pursue qualitative approaches for assessing allowable harm.

However, in the absence of index data, assumed rates of population decline at time of species listing based on COSEWIC criterion A have been used (see Vélez-Espino and Koops 2007, 2009, van der Lee et al. 2020, and related RPAs for freshwater fishes). Alternatively, assumed rates of population growth, both in terms of maximum possible growth given the biological limitations of a species (see Young and Koops 2013a,b; Marcoux and Hammill 2016; DFO 2017a), as well as expected growth in the presence of harm, have been used in several assessments and are explored further within this document.

3. The extent to which allowable harm is conditional on population decline, stability, or growth

Although most authors indicate that there is no scope for harm when populations are declining (e.g., Vélez-Espino and Koops 2007), not all AHA's have 'stopping points' when populations are in decline. For example, the potential biological removals method (see Wade 1998; Taylor et al. 2003), determines the scale of allowable mortality based on 1) maximum population growth rate (e.g., with default values for cetaceans and pinnipeds), 2) allowances for uncertainty in population parameters, and 3) a scalar to determine the harm that still allows for population growth. The rationale behind PBR is that harvest levels can be low enough that stock rebuilding should occur, given the best-possible biological scenario. However, if the population is in a sustained period of decline, such as due to high rates of ship strikes or other unaccounted mortality that surpasses the built-in level of precaution, the PBR method would allow harm to occur while the stock is declining.

4. The extent to which changes to harm during the permitting period (Criterion 3) has been incorporated

In most cases, authors have stated that allowable harm advice is conditional on status quo sources of natural mortality or other parameters (e.g., growth, fecundity) during the permitting period. In other cases (e.g., DFO 2017a), authors have explicitly quantified the likelihood of additional pressures on a population.

5. The extent to which habitat-related threats have been incorporated

To date, most AHAs have not made quantitative linkages between harm to habitat (expressed as changes to habitat area, condition, and/or weighted suitable area) and harm to populations, though these linkages are becoming more common within RPAs, and generally in the primary literature (e.g., van der Lee and Koops 2016). Several approaches exist to make links between threats to habitat and population responses, and are explored further in the remainder of this document.

6. The extent to which current population size is known

Current population estimates are lacking for many SARA-listed species owing to data limitations. When population size is known, analyses to address Criterion 1 have been used to understand whether the population size is at risk of extinction due to environmental stochasticity (e.g., DFO 2017a). In the absence of population size estimates, allowable harm takes the form of percent change to mortality or other vital rates (e.g., Vélez-Espino and Koops 2007), rather than the number of individuals removed or killed. The lack of information about current population size also presents difficulties in estimating the time to reach a recovery target (see issue 7, below).

7. The inclusion and specificity of recovery targets

When allowable harm assessments are conducted, candidate recovery targets may be proposed within an RPA. However, recovery targets are not finalized with population and distribution objectives until the recovery strategy is completed. Thus, allowable harm advice may need to be revisited if final recovery targets differ from those proposed within an RPA.

Recovery targets, whether proposed or final, can be generic or prescriptive. Generic targets can be "to maintain or increase the current population", while prescriptive targets can be "rebuild the population to *x* animals in *y* years". Prescriptive targets are chosen when current population size can be estimated and sufficient information is available on growth potential of the species given biological constraints, coupled with the combined effects of threats and recovery actions (e.g., DFO 2014c; Marcoux and Hammill 2016; DFO 2017a).

When recovery targets are generic (i.e., lack defined timeframes) or unavailable, science advice on allowable harm is often provided as the maximum harm that a growing population can sustain while still resulting in growth (Fig. 1, harm H_{max} in box A). This interpretation results in potentially large harm to growing populations (H_{max}), with long times to recovery at or just below this value (T_1), and indefinite times to recovery beyond this value. However, applying harm to reduce population growth to just above stability is not consistent with the recovery goals or intent of SARA, and such advice should be interpreted as the absolute maximum estimate of harm that would not jeopardize survival or recovery.

When recovery targets describe the time to reach a given population size, allowable harm assessments are often conducted as the harm that would allow the population to reach the recovery target 'within a reasonable timeframe' as described in Criterion 1, DFO 2004a,b (Figure 1, box B, T_2,H_2). However, as outlined in several RPAs, the acceptable delay for recovery of growing populations is a risk tolerance decision (i.e., difference between T_2 and T_3,), where T_3 is the best achievable scenario in the absence of all human-induced mortality. There is a generally consistent interpretation by DFO's Science sector that there is no scope for chronic harm when populations are declining (Figure 2).

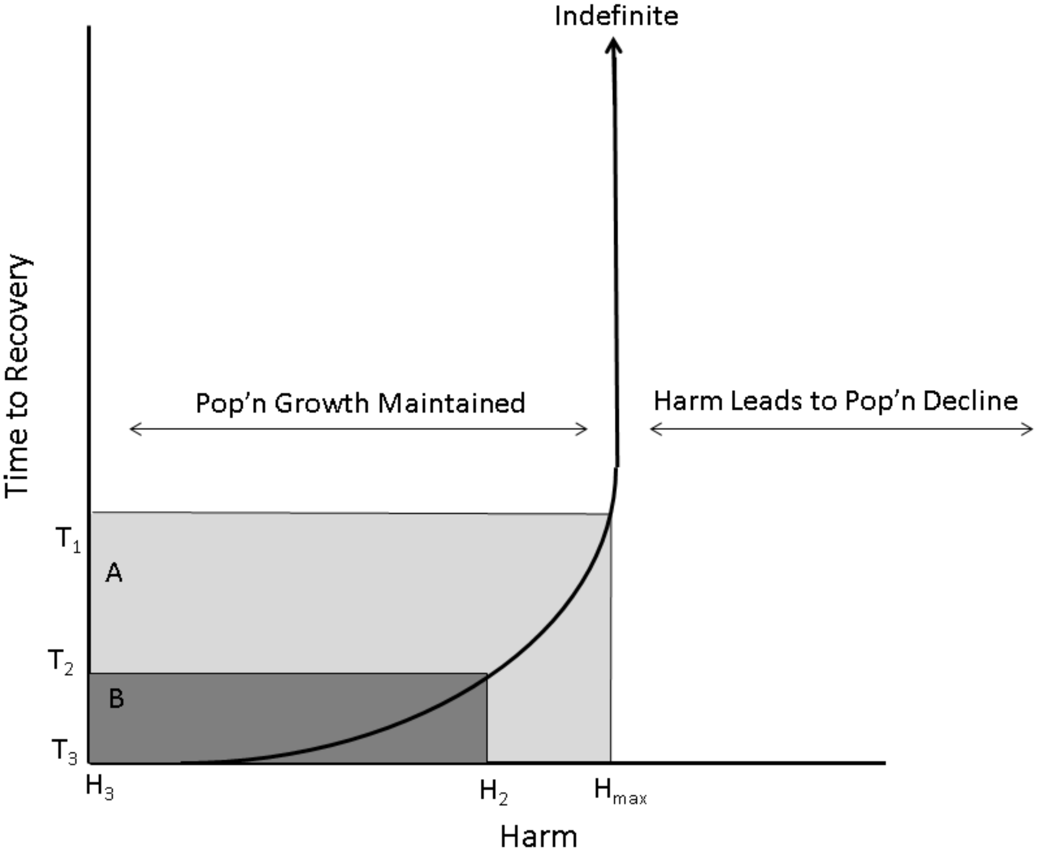


Figure 1. Relationship between harm and time to recovery for a growing population. Harm H_{max} describes the maximum allowable harm that allows for a positive population trajectory, but with potentially very long times to recovery (T_1). Time to recovery becomes indefinite as harm surpasses H_{max} because harm causes population decline. As harm moves to the left of H_{max}, the population maintains positive population growth and time to recovery is decreased accordingly (Box A; light grey). Box B (dark grey) describes harm (H_2,T_2) that provides a smaller deviation from the best achievable recovery scenario (T_3) defined by the absence of harm (H_3). The size of the allowable harm box (A,B) will vary depending on whether the policy endpoint is to maintain population growth rate > 1, or meet a predetermined recovery timeframe.

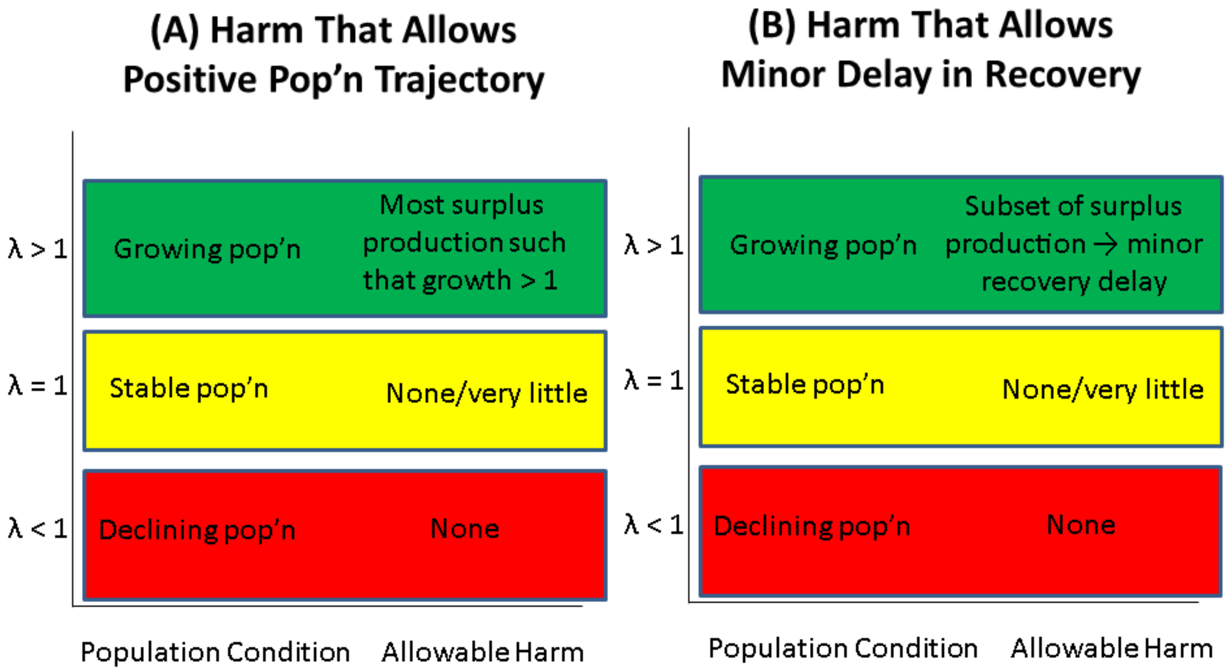


Figure 2. Two interpretations of reference points used in allowable harm assessment (population growth rate, λ, is presented on the Y-axis). Panel (A) describes allowable harm advice provided when specific recovery targets are not available for a species. Here, allowable harm is often provided as the maximum chronic harm that will maintain a positive population trajectory. Panel (B) describes allowable harm advice that is typically provide when time- and abundance-based recovery targets are available, with chronic harm as the deviation in the ability to meet the recovery target. The approach in (B) requires risk tolerance decisions about the acceptable delay in recovery imposed by the activity.

COMPONENTS OF A SCIENCE-BASED FRAMEWORK TO SUPPORT PERMITTING UNDER SECTION 73 OF THE SPECIES AT RISK ACT

Given the different allowable harm approaches applied for SARA-listed species, a single approach to inform permitting under Section 73 is likely unrealistic given widespread differences in data availability for individual species. Further, the decision points in allowable harm assessment need to be refined, especially around the acceptable delay for recovery. However, the primary building block upon which to estimate allowable harm is the relationship between harm and population growth or decline (Criterion 2 from DFO 2004a,b). Therefore, establishing components of a national framework to support permitting within Section 73 requires an understanding of a) the aquatic habitat changes (habitat condition, area) expected from an individual w/u/a; b) the relationship between changes to habitat and the resulting changes to vital rates; and, c) how populations responds to changes in vital rates (mortality, fecundity, growth, migration) (Figure 3).

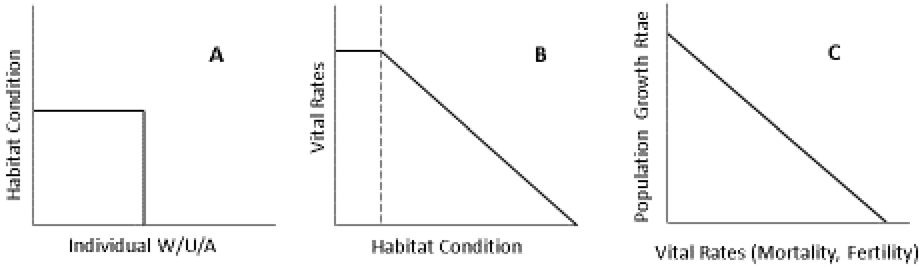


Figure 3. The primary components to connect an individual w/u/a to changes in population productivity are: a) the estimated changes to habitat condition from an individual w/u/a; b) the functional relationship between changes to habitat condition and changes to vital rates; and, c) the functional relationship between changes to vital rates (e.g., mortality, fertility) and changes to population growth rate. In some cases, it may be necessarily estimate direct changes to vital rates from an individual w/u/a, such as when species experience non-habitat shifts in mortality or fertility (e.g., construction-related mortality). Linear relationships are shown for simplicity and do not necessarily reflect expected changes.

These three components do not provide a stand-alone assessment framework for an individual w/u/a, but would be combined with additional information on the baseline condition of the population (e.g., current trajectory) and its habitat (e.g., habitat conditions in the vicinity of the w/u/a, as well as total habitat available to the species) so that the change to habitat and populations could be estimated. Finally, considerations around offsetting in a recovery framework may also be required to make a determination of the effect of an individual w/u/a on a population. In remaining sections, the three components (Section 2: the change in habitat from an individual w/u/a; Section 3: relationships between habitat condition and vital rates; Section 4: elasticities between vital rates and population growth) are described as the primary building blocks to assess an individual w/u/a. Considerations around offsetting are presented in Section 5, and Section 6 provides an overview of how the Sections could be combined in a decision support tool. Additional data needs to operationalize the framework are also described.

SECTION 2: EFFECTS OF WORKS/UNDERTAKINGS/ACTIVITIES ON AQUATIC HABITAT

The first component to estimate the effect of individual w/u/a on SARA-listed species is an estimate of residual project impacts on aquatic habitat (Figure 3, panel A). Bradford et al. (2014) indicated that habitat impacts from w/u/a can take the form of: 1) changes to habitat quality or condition; 2) changes to habitat area; or, 3) changes leading to broad ecosystem transformations. Bradford et al. (2014) also indicated the need to determine the duration of the impact as it relates to the generation time of the species. Changes to habitat across space in relation to the total habitat area required by that life stage must also be considered. Therefore, project impacts to aquatic habitat can be evaluated along three axes: the intensity of habitat change, the duration of habitat change, and the spatial extent of habitat change (Figure 4).

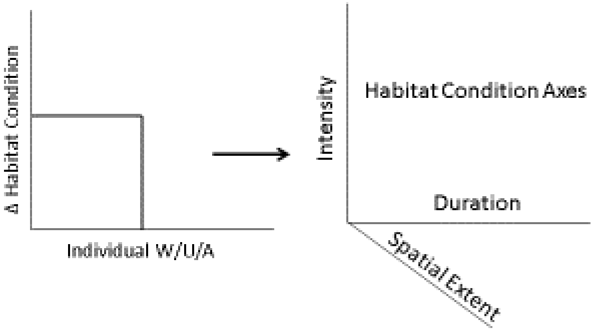


Figure 4. Estimating the effect of an individual w/u/a on aquatic habitat (left panel) requires assessing changes in the intensity, duration, and spatial extent of habitat variables influenced by the project (e.g., dissolved oxygen, nutrients; right panel).

DFO's Pathways of Effects (PoE) framework can be used to identify individual habitat variables that are likely to change following residual impacts (e.g., dissolved oxygen, nutrients). A detailed review of the PoE framework is outside the scope of this document (see Clarke et al. 2008 and Coker et al. 2010 for background information, and Koops et al. 2013 for applications), but the basic premise of PoE's is to identify common hypotheses about how a development activity can lead to the occurrence of habitat stressors. The PoE framework does not quantify the intensity or area of habitat stress from the w/u/a, but identifies the habitat variables (PoE endpoints) that are likely to change from common activities ranging from clearing of riparian vegetation, use of industrial equipment, explosives, wastewater management, and dredging (18 activities in total, see Coker et al. 2010). In a review of common project impacts, DFO (2014a) identified 12 frequently encountered PoE endpoints, which included changes to habitat area, sediments, structure/cover, nutrients, food supply, mortality, temperature, noise, electromagnetic field, access to habitat, dissolved oxygen, and flow. A single w/u/a can have multiple PoE's, each with multiple habitat stress endpoints.

The PoE framework should be used to determine the types of habitat stressors that are likely to occur from the w/u/a, which can be assessed along the intensity, duration, and spatial extent axes (Figure 4). This provides an n-dimensional characterization of expected habitat changes for an individual w/u/a, which will necessarily be species-specific as characteristics such as generation time (in relation to project duration) are incorporated (Figure 5).

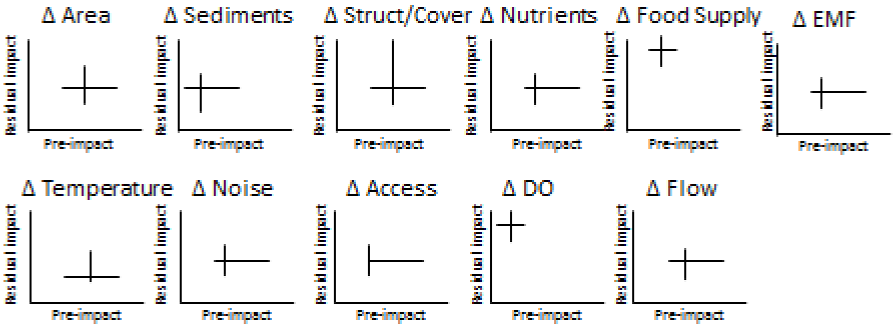


Figure 5. The DFO Pathway of Effects framework can be used to identify the PoE endpoints (habitat variables) expected to change from the w/u/a, thereby allowing the pre-impact and predicted residual impact state of habitat to be described. Habitat changes can be described along the intensity, duration, and spatial extent axes. Short form labels are Struct/Cover = Structure/Cover; EMF = Electromagnetic Field; Access = Access to Habitat; DO = Dissolved Oxygen.

In some cases, individual w/u/a may directly impact species in ways that are independent from habitat effects. Examples of such changes include physical strikes to aquatic species from construction activities, which may reduce survival or fertility. In these circumstances, the effect(s) of the activity on the species should be estimated by identifying the life stage and vital rate(s) (e.g., mortality, fertility) that are likely to be impacted. Here, intensity can be interpreted as the intensity of the vital rate change from the w/u/a, with duration and spatial extent also describing direct changes to vital rates (e.g., duration of vital rate changes; area or amount of population experiencing vital rate changes).

SECTION 3: RELATIONSHIPS BETWEEN AQUATIC HABITAT AND VITAL RATES

In most cases, considerations around whether an individual w/u/a will jeopardize the survival or recovery of SARA-listed species will involve estimating changes to vital rates imposed by the habitat alterations of the w/u/a. This section presents information used to connect changes in aquatic habitat with vital rates (Figure 3, panel B), thereby providing an intermediate link between the project and expected population responses. Information in this section draws heavily on science advice in relation to recent amendments to Canada's *Fisheries Act* (Koops et al. 2013; Bradford et al. 2014, 2015). For example, DFO (2014a) presents a series of productivity-state curves to illustrate how changes in common PoE endpoints (i.e., habitat stressors) may lead to changes in fisheries productivity (Figure 6).

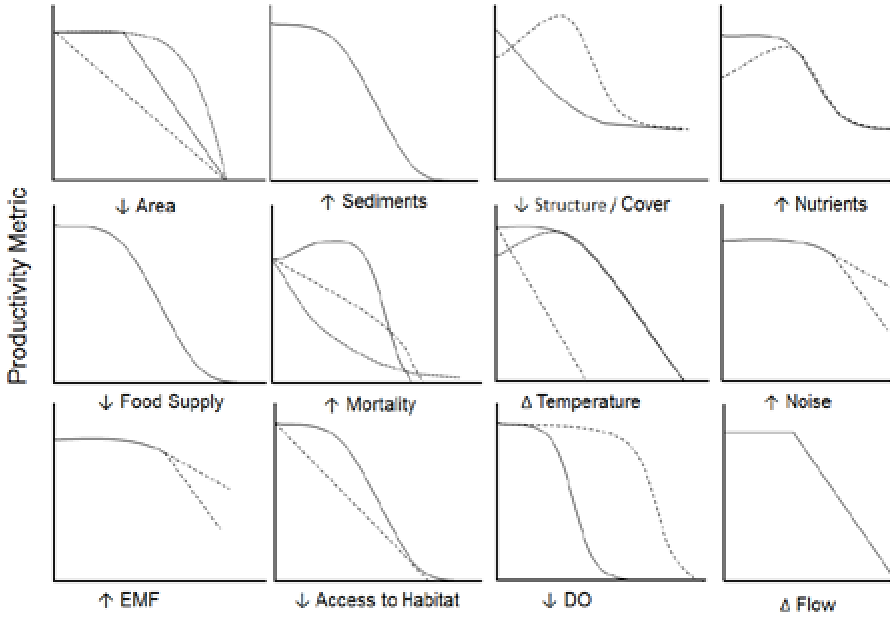


Figure 6. Productivity-state response curves, reproduced from DFO (2014a). Shown are 12 common types of habitat stress for projects recently reviewed by DFO.

Considerable research has been conducted on the habitat features that support aquatic species, from tagging studies to correlation analysis with field and experimental data. Assessing the relationship between habitat changes from the w/u/a and productivity of the population requires a detailed assessment of the contribution of each habitat feature (e.g., food supply) on each life stage (e.g., juveniles) and vital rate (e.g., survival). Although this information is difficult to obtain for many species, some generalities can be drawn and are explored later in this section, with examples for freshwater mussels and fishes. Estimating changes to vital rates from habitat impacts (or the direct impact of the w/u/a itself) is needed to estimate changes in the productivity (i.e. trajectory or abundance) of SARA-listed species.

To consider how vital rates are influenced by changes in habitat condition, consider the relationship between a single habitat variable on the x-axis (in this case, changes in the intensity of flow), and a component of species productivity on the y-axis (in this case, survival; Figure 7). The response of vital rates can be considered along an axis that begins with the greatest possible contribution of the habitat feature to performance of the vital rate (e.g., Figure 7, position A). As habitat condition declines, an inflection point is reached where changes in habitat condition reduce the performance of the vital rate. As the decline continues, benchmarks along the stress axis are reached describing, for example, the loss of 50% of maximum vital rate function (c), to the inability of the habitat feature to support vital rate function (d). For a given habitat feature, life stage, and life history process, these relationships can be scaled to describe the contribution of each habitat feature to the vital rate ranging from 1 (maximum performance of the vital rate) to 0 (no value). Bradford et al. (2014) referred to this as an impact factor, *I*.

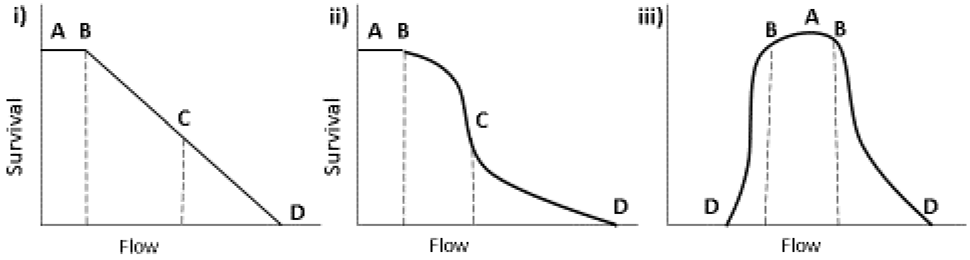


Figure 7. Examples of productivity state-response curves developed in Koops et al. (2013) and DFO (2014a). In panel i), there is a linear relationship between habitat stress and performance of the vital rate, with A representing the flow intensity where the vital rate is maximized, B as an inflection point where the performance of the vital rate declines beyond optimum, C a benchmark where 50% of vital rate performance is expected, and D, the point where the habitat no longer supports the function of the vital rate. In addition to linear responses (i), non-linear responses are possible (ii, iii).

As there are many possible shapes for these relationships, some of which will have important thresholds on vital rates and therefore species productivity, Braoudakis et al. (unpublished manuscript) conducted a meta-analysis of the relationship between habitat condition and survival (plus density and abundance as surrogates for survival) in freshwater mussels (3,686 papers and 667 univariate relationships), focusing on the prevalence of six functional forms (Figure 8). Key findings were 1) linear responses were relatively uncommon, and 2) although the parameters of each curve differed across species and ecosystems, dominant shapes could be generalized across the different classes of habitat stressors outlined in DFO (2014a) (Figure 9). A similar study was conducted for freshwater fishes (Figure 9; Braoudakis et al., unpublished manuscript), with similar findings. These results indicate that although the specific parameters of the relationship for the species in question may not be known, especially for SARA-listed species, some general response shapes exist across species and habitat stressors, which provides a starting point to generalize the shape of habitat-vital rate relationships in an assessment framework.

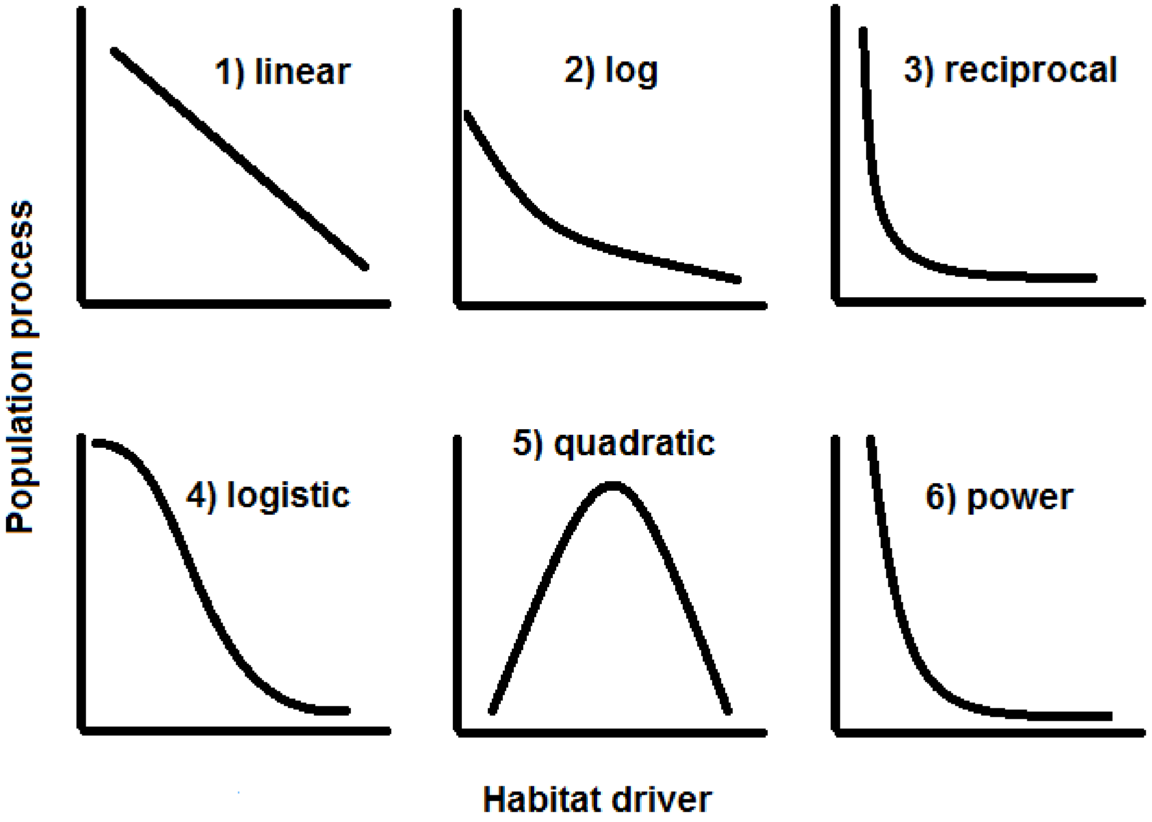
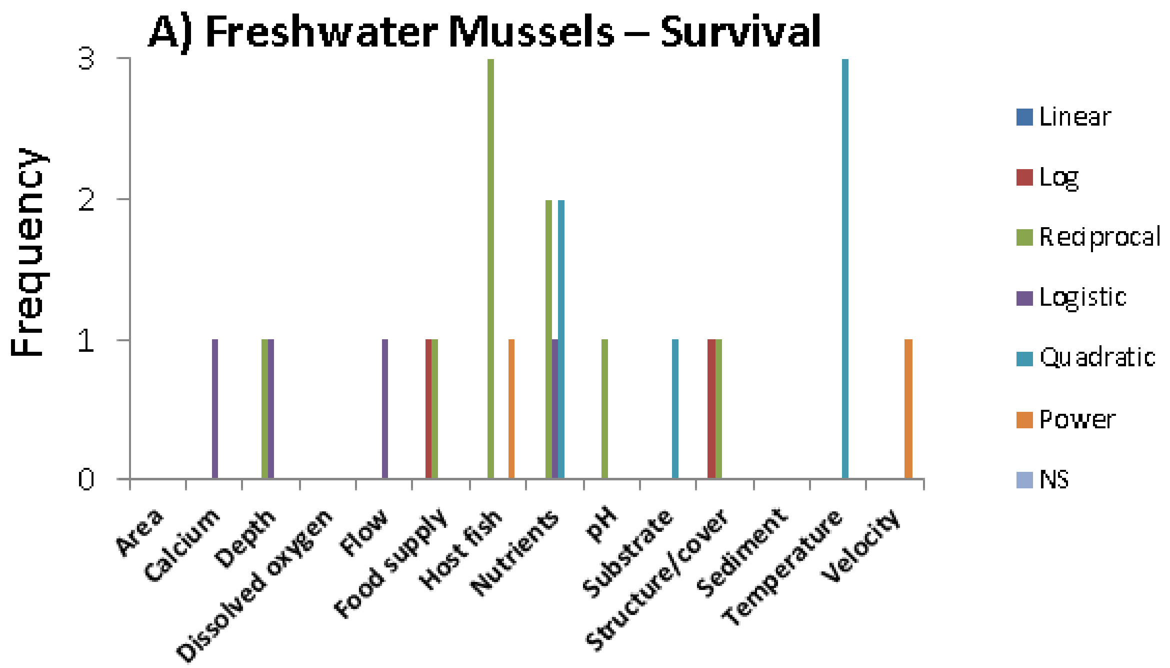
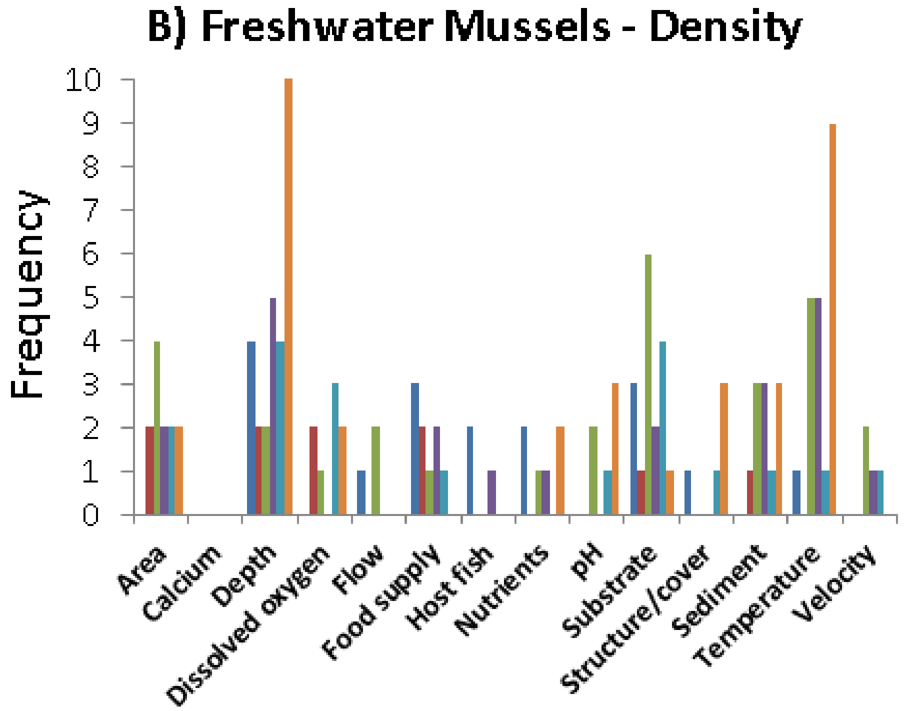


Figure 8. Six possible shapes describing the relationships between habitat drivers (condition) and population processes (vital rates). Reproduced from Braoudakis et al. (unpublished manuscript).


A) Freshwater Mussels – Survival
Frequency
0
1
2
3
Area
Calcium
Depth
Dissolved oxygen
Flow
Food supply
Host fish
Nutrients
pH
Substrate
Structure/cover
Sediment
Temperature
Velocity
Linear
Log
Reciprocal
Logistic
Quadratic
Power
NS


B) Freshwater Mussels - Density
Frequency
0
1
2
3
4
5
6
7
8
9
10
Area
Calcium
Depth
Dissolved oxygen
Flow
Food supply
Host fish
Nutrients
pH
Substrate
Structure/cover
Sediment
Temperature
Velocity

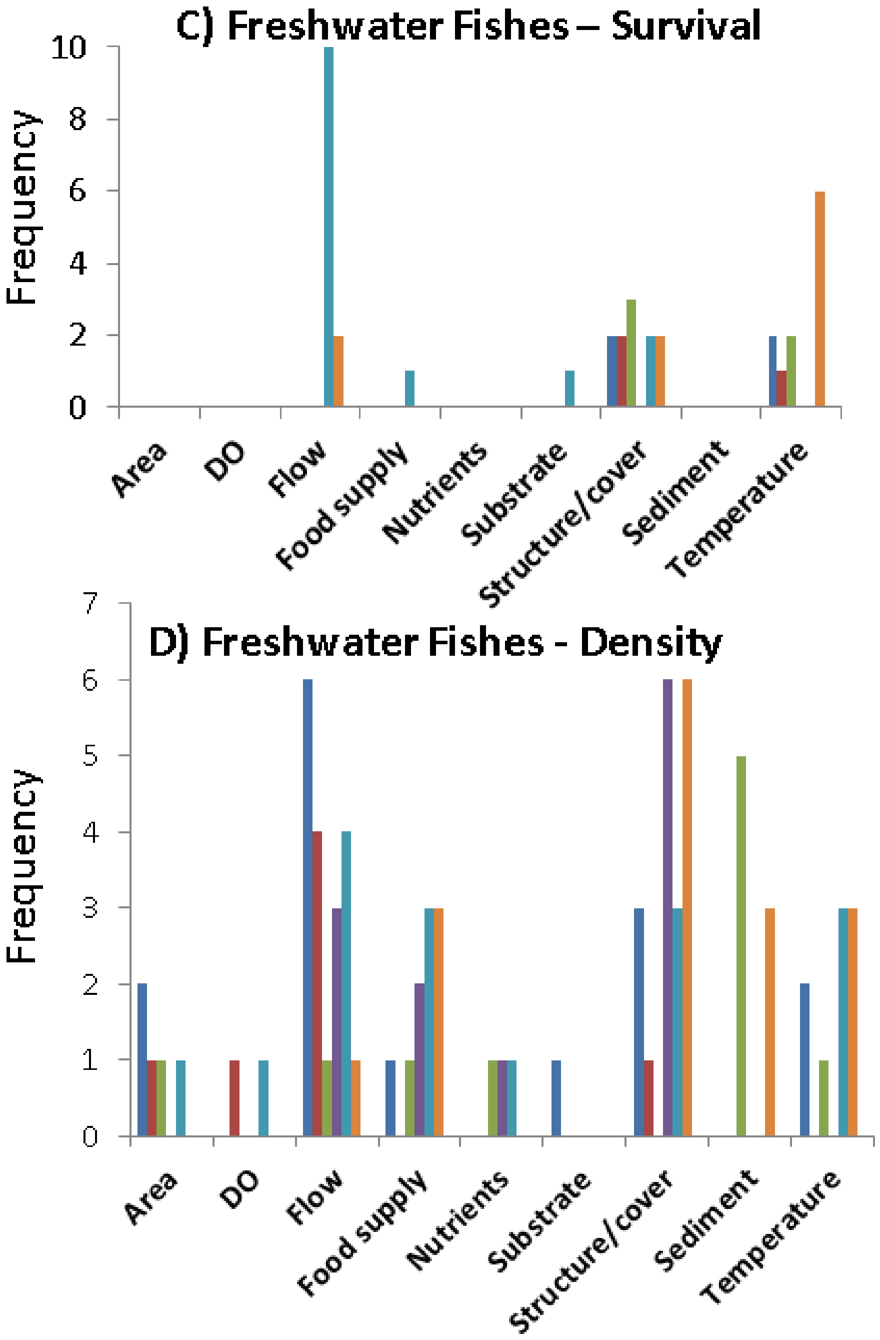


Figure 9. Frequency of different relationship shapes describing how changes in habitat condition lead to changes in freshwater mussels (survival, A; density, B) and freshwater fishes (survival, C; density, D) (reproduced from Braoudakis et al., unpublished manuscript).

Although the relationships reviewed in Braoudakis et al. (unpublished manuscript) and related studies provides an opportunity to connect changes in habitat condition to vital rates for a subset of species, in many cases, a w/u/a will produce habitat conditions that lead to behavioural or other sub-lethal effects on fishes, mussels, or mammals. These effects can be considered as a gradient of harm to individual performance, ranging from (least offensive) startle and alarm, through to abandonment, displacement, and growth effects (Figure 10; e.g., NRC 2005; King et al. 2015; Lacy et al. 2017; see DFO 2017c as it relates to cumulative effects assessments for marine mammals). For these effects to influence population productivity, there must be some underlying linkage with one or more vital rates (growth, fertility, mortality); otherwise, population trajectory will remain unchanged in the presence of sub-lethal or behavioural effects. Although the ability to link sub-lethal and behavioural effects to vital rates is challenging, there are examples of such linkages made quantitatively (Lacy et al. 2017) or with expert elicitation (King et al. 2015). For example, Lacy et al. (2017) determined the effect of prey limitation and PCB accumulation on population growth rate of Southern Resident Killer Whales, while King et al. (2015) developed an expert elicitation process to identify the relationship between the number of days of disturbance that an individual Southern Elephant Seal was exposed to and the corresponding effect on survival or fertility (see NRC 2005 for other examples).

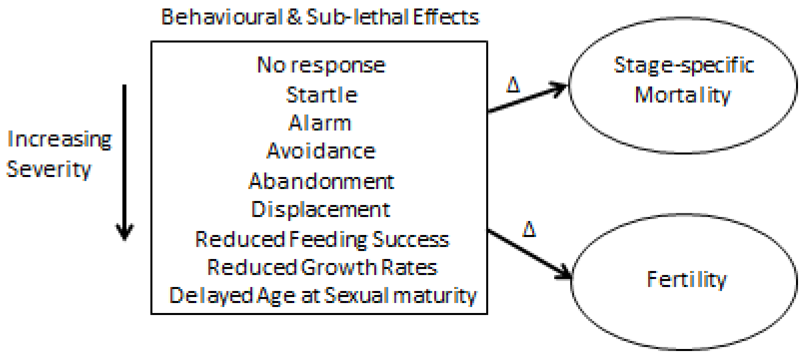


Figure 10. Examples of behavioural and sub-lethal effects, listed in increasing order of severity. Relationships between behavioural and sub-lethal effects and their effect on mortality and fertility have been demonstrated for some aquatic species at risk.

Results from Braoudakis et al. (unpublished manuscript) indicate that common response shapes can be derived for a given taxon and habitat stressor; however, it is typical for multiple habitat features to influence the performance of a single vital rate. Therefore, predicting the change in a vital rate must consider i) all relevant habitat features that can reasonably be expected to influence that vital rate, and, ii) the nature of interaction between the habitat features.

When considering the effect of multiple habitat stressors on a population, four main effects may occur (Figure 11). The first, simple additive effects (Figure 11, panel A), describes the scenario where the effect of two stressors on a vital rate is equal to the effect of the magnitude of the first stressor, plus the magnitude of the second stressor. In this context the stressors are functionally independent and their joint effects are predictable based on knowledge of each stressor in isolation. The second, dominant driver (Figure 11, panel B), describes the scenario where the effect of a single stressor overwhelmingly determines the response of a vital rate to the magnitude of habitat change (Figure 11, panel B). The third, multiplicative increasing (also known as synergistic), describes the scenario where the presence of two stressors leads to a greater rate of change in the vital rate than would be expected if the effects were simply additive, i.e., an interaction occurs, with the effect greater than the independent effect of S1 or S2 (Figure 11, panel C). Finally, the fourth scenario, multiplicative decreasing (also known as antagonistic), describes the scenario where the presence of two stressors leads to a lower rate of change than would be expected if the effects were simply additive, i.e., interaction occurs, with the effect lesser than if the effects were simply additive (Figure 11, panel D). Note that dominant stressor and multiplicative decreasing are similar, with the distinction based on the intensity of the single stressor on habitat change. For simplicity, these relationships are denoted as linear with similar origin points, but as with single stressors, multiple forms can exist (e.g., non-linearities and different origins).

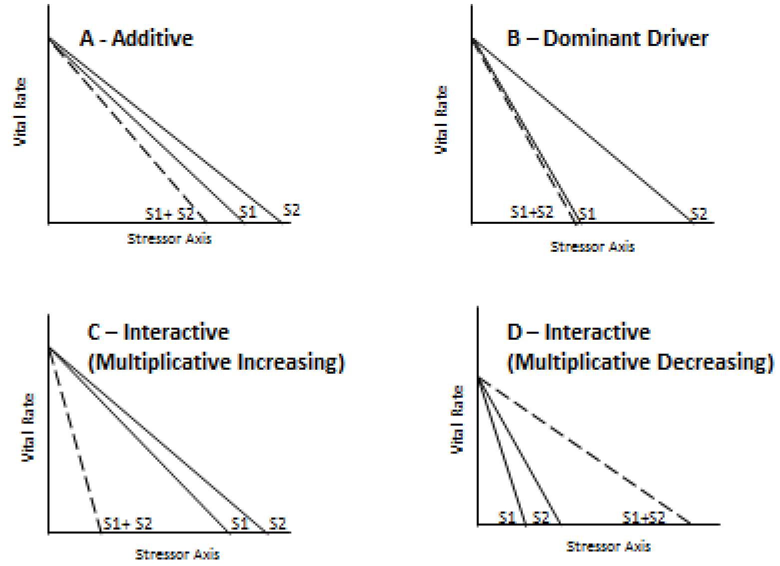


Figure 11. Four scenarios for the effect of multiple stressors. The stressor axis describes an increase in habitat stress (i.e., decrease in habitat suitability or condition). The labels S1 and S2 denote the effect of individual stressors, and the dashed line denotes the aggregate effect of both stressors under each scenario (A – Additive, B – Dominant Driver, C – Multiplicative Increasing, D – Multiplicative Decreasing).

Bradford et al. (2014) emphasized the importance of understanding changes to habitat condition by determining the duration of the impact factor, *I*, as it relates to the generation time of the species in the project area. Changes to habitat condition can also occur across space as it relates to the total habitat area required by that life stage. As the impact factor drops to 0, changes to habitat condition can be interpreted as changes in effective habitat area. The effect of changes in habitat area on vital rates will be a function of whether the habitat is currently limiting population productivity. Several approaches exist for understanding the effect of changes in suitable habitat area on vital rates and/or individual performance (e.g., see ‘Area per Recruit’, DFO 2015c).

Given the information summarized in Section 3, for a single w/u/a, the following information can be considered: 1) the types of habitat changes relevant for a species, life stage, and vital rate (including sub-lethal or behavioural effects), 2) their functional form(s), and 3) the nature of interactions, if any.

SECTION 4: PREDICTING POPULATION SENSITIVITY FOR CANADA’S SARA-LISTED AQUATIC SPECIES

Section 2 provides the basis to estimate the impact of a w/u/a on aquatic habitat. Section 3 provides an approach to relate the changes in aquatic habitat to changes in species vital rates. In Section 4, population models are presented to illustrate the sensitivity of Canada’s SARA-listed aquatic species to perturbations in their vital rates. Therefore, this section provides the third and final component of relating impacts of the w/u/a to population productivity (Figure 3, panel C). The approach is not intended to replace existing population models for SARA species; rather, it is intended to identify general patterns in how species respond to perturbations of their vital rates. In cases where population models are lacking, the models in Section 4 would allow interpretations of Section 73 to be made due to impacts from the w/u/a.

One method of quantifying impacts is through elasticity analysis of matrix population models. Elasticities measure the proportional change in population growth rate (λ) that results from proportional change in vital rates (e.g. survival, growth, and/or fertility; Caswell 2001). For example, an elasticity value (ε_a) of 0.2 for adult survival (σ_a) would indicate that a 10% change in σ_a (i.e. if a σ_a of 0.6 was increased to 0.66 ($0.6 \times (1 + 0.1) = 0.66$)) would result in a 2% ($10\% \times 0.2 = 2\%$) increase to λ (i.e. a λ of 1.1 would increase to 1.122 ($1.1 \times (1 + 0.02) = 1.122$)). Elasticities provide an indication of how a population is likely to react to stage-specific perturbation when other conditions remain the same; the larger the elasticity value the greater the expected impact. Lower elasticity values, however, do not indicate that a population is insensitive to a perturbation to that vital rate but rather less sensitive than other life stages. This suggests that recovery measures may be best applied to affect other life stages. Elasticities quantify impacts as permanent perturbations independent of density-dependence or stochasticity. As well, elasticities are additive, such that impacts of actions affecting two or more vital rates can be quantified by simply summing elasticities.

Here, elasticity analysis was used on 143 aquatic species that have been assessed as species of Special Concern, Threatened, or Endangered by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) to categorize sensitivities across species. A decision tree analysis was used to identify the life-history characteristics that best determine group membership. From this, when demographic data are lacking, managers can predict how a species might react to potential harm or what recover measure might be most effective in stimulating recovery.

METHODS

Stage-specific population models of species-at-risk were used to estimate vital rate elasticities. Distinct patterns in elasticity values across life stages were identified with use of cluster analysis. Data mining techniques (random forests and decision trees) were used to determine which life-history characteristics best identified species' elasticity patterns.

Data

Life-history data for all aquatic species assessed as Special Concern, Threatened, or Endangered by COSEWIC were compiled, totaling 143 wildlife species. Individual designatable units (DU) were included only if life-history data were available at the DU level and if there were significant differences in life-history characteristics among DUs. Each DUs will be considered as a wildlife species in the analysis. Taxa included were: freshwater fishes, marine fishes, sharks and skates, freshwater mussels, marine mammals, and marine turtles (Table 1).

Data required to build the matrix population models were: longevity, T_{max}; age-at-first reproduction, T_{mat}; reproductive information including: mean fecundity, f, sex ratio φ, and spawning periodicity, Ψ; and stage-specific survival rates, σ_i. If species-specific data were unavailable, parameters were estimated with relationships from the literature (see Appendix for taxa-specific methodology for parameter estimation).

Table 1. Species count within taxa included in analysis

Taxa	N
Freshwater Fishes	65
Marine Fishes	18
Sharks and Skates	29
Marine Mammals	18
Freshwater Mussels	11
Marine Turtles	2

Population model

Each COSEWIC-assessed species' life cycle was represented with a female-only, post breeding, stage-based matrix model with annual projection intervals. Three model structures were used (Figure 12). The majority of species were modelled using a 3-stage matrix with stages representing young-of-the-year (age-0; YOY) or calves (marine mammals), juvenile, and adult females (Figure 12a). Early maturing species (age-of-maturity < 2) were modelled using a 2-stage matrix representing YOY and adult females (Figure 12b). An additional matrix structure was applied to semelparous species consisting of 3-stages (YOY, juvenile, and adult) but delayed reproduction following metamorphosis and prevented repeat spawning (Figure 12c).

Required stage-specific matrix elements for population projection are fertility, F, which represents the mean number of female offspring produce per female per annum, P_i, which represents the probability of surviving and remaining in stage i, and G_i, the probability of surviving and transitioning to stage $i + 1$ (Caswell 2001). F is a function of fecundity, f, the average number of eggs produced per female, the sex ratio φ, and the spawning periodicity, Ψ, the number of years between spawning events:

$$F = \frac{\varphi f}{\Psi}. \tag{1}$$

P_i and G_i are a function of stage-specific survival rate, σ_i, and the transition probability, τ_i (estimated from the inverse of stage duration, $\tau_i = D_i{}^{-1}$), where:

$$P_i = \sigma_i(1 - \tau_i) \tag{2}$$

$$G_i = \sigma_i \tau_i \ . \tag{3}$$

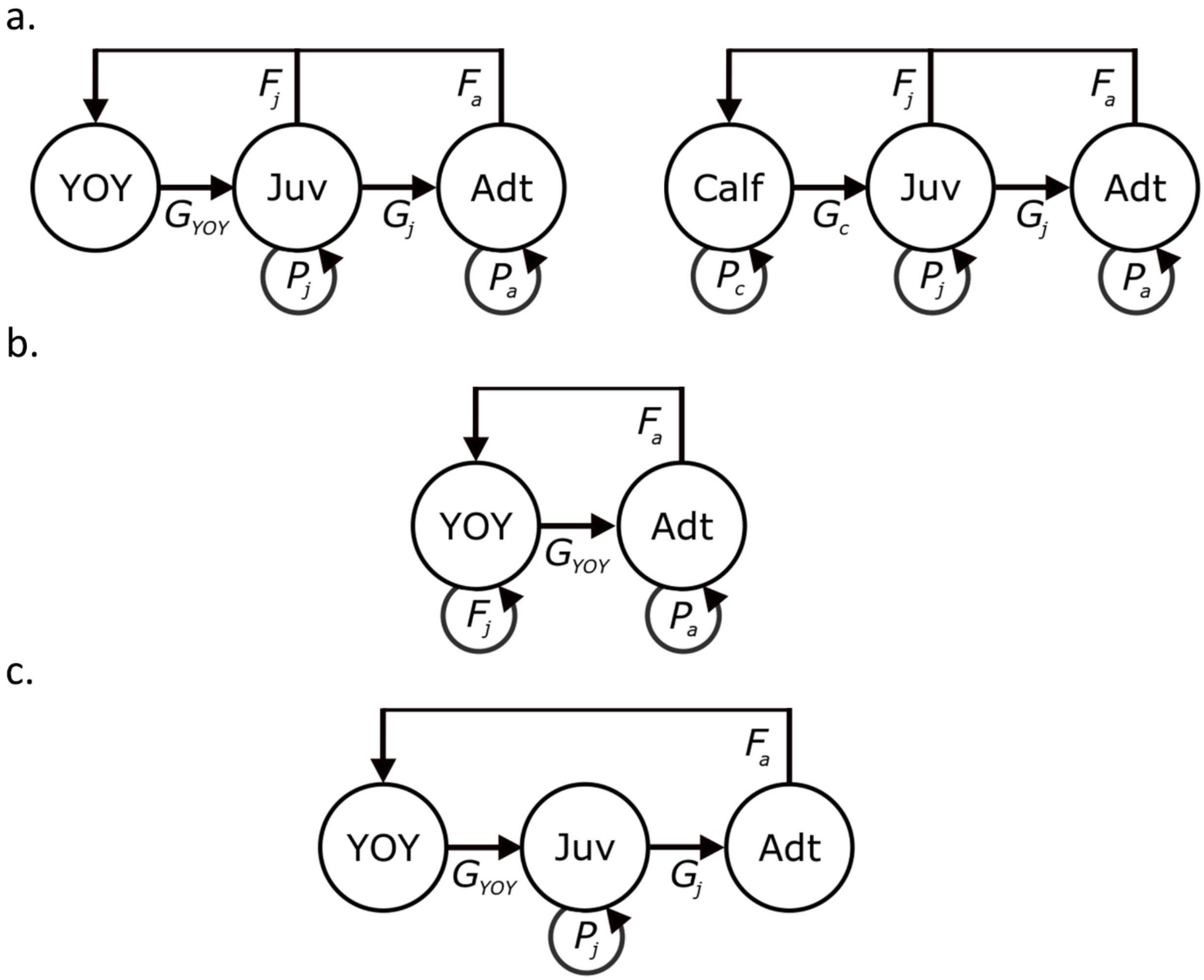


Figure 12. Life history diagrams representing population models used in analysis for: a) 3-stage species and marine mammals, b) 2-stage species, and 3) semelparous species.

The dominate eigenvalue of the matrix represents the population growth rate, λ, the rate of change in population size annually ($N_{t+1} = \lambda N_t$). The value of λ gives an indication of the relative status of the population. A λ > 1 indicates a population growing exponentially, λ < 1 indicates a population declining exponentially, and λ = 1 indicates a stable population. The relative impact of changes to vital rates on λ can be calculated deterministically through sensitivity analysis and estimation of elasticities. Elasticities quantify the proportional change in λ following a proportional change in a vital rate (v). Elasticities are calculated by taking the scaled partial derivatives of λ with respect to a vital rate (Caswell 2001):

$$\varepsilon_v = \frac{v}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{i,j}}\frac{\partial a_{i,j}}{\partial v}, \qquad (4)$$

where a_{ij} is the projection matrix element in row i and column j. Elasticities are additive; as such, the effect of perturbations acting on multiple vital rates can be assessed by summing the elasticities of the affected vital rates. Elasticity analysis was used to determine the impacts of changes to vital rates on COSEWIC-assessed species for populations under different trajectories (booming, growing, stable, declining and crashing) to assess the response of species to anthropogenic actions. A stable population is one with constant population size and $\lambda = 1$. Declining and crashing populations represent populations decreasing in size at a rate commensurate with the COSEWIC definitions of Threatened and Endangered species respectively (a 50% or 70% decline in population size over 3 generations or 10 years, whichever is longer). Booming populations represent maximum possible population growth (See appendix for methods to determine specie-specific r_{max}). Growing populations represent those experiencing a level of growth that could be maintained over a longer term; estimated as the geometric mean between crashing, stable, and booming rates (as per Vélez-Espino and Koops 2009). Taxon-specific methods were utilized to achieve different population growth rates and were chosen to reflect threats and life-history characteristics specific to each taxon.

The λ of increasing (growing and booming) populations for most taxa were achieved by increasing YOY survival, σ_0, such that the correct λ resulted. This, in effect, implies that density-dependence acts entirely in the first year of life. This method was applied to all taxa except marine mammals. As calf survival for marine mammals was already high it is unlikely that population growth would result solely from density-dependence early in life. Instead, increasing (growing and booming) population growth rates were achieved using a multistep process. Density-dependence in marine mammals may act on periodicity where good conditions may allow more frequent spawning in cetaceans (Williams et al. 2013). Therefore periodicity was decreased to a minimum value, mean gestation length. If the desired λ was not yet achieved calf survival was increased until it equalled juvenile survival. If the desired λ had still not been achieved the entire survival schedule was increased. This resulted in all species reaching the desired λ with $\sigma_i < 1$.

Methods to achieve decreasing population growth (declining and crashing) were selected to simulate the dominant taxon-specific threats. Freshwater fish populations are most threatened by habitat degradation (Venter et al. 2006). It was assumed that this likely impacts each life stage equally and survival rates across stages were decreased proportionally to realize the target λ. Declines in population size for marine fishes and freshwater mussels were achieved via reductions in adult survival rate. This represents threats to the adult stage from overharvest (marine fishes, Venter et al. 2006) and biofouling of adults from invasive dreissenid mussels (Zanatta et al. 2015). The remaining taxa were assumed to be vulnerable as by-catch, from fishing gear entanglements, or boat strikes (marine mammals, DFO 2016; sharks and skates, Venter et al. 2006; and turtles, DFO 2017b). These events are likely to affect both juvenile and adult individuals therefore survival rates for those stages were decreased proportionally to achieve the target λ.

Analysis

Elasticity estimates were made for each species under all 5 levels of population growth for the vital rates: fertility, juvenile survival, and adult survival. The elasticity values for fertility and YOY survival rate are identical and therefore only fertility rate elasticities are presented. In total there were 715 observations (143 species at 5 growth rates).

Following the general approach from Young and Koops (2011) species were grouped into clusters using k-means clustering (Hartigan and Wong 1979) of elasticity values with the kmeans function in R 3.5.0 (R Core Team 2018). Life-history characteristics that were important in determining group membership were identified with random forests, using the randomForest library (Liaw and Wiener 2002). Finally, using the 5 most important predictor variables, determined from random forest analysis, a single decision tree was created as a demonstration of how elasticity patterns can be predicted from life-history characteristics. The decision tree was fit using recursive partitioning and the rpart library (Therneau and Atkinson 2018) in R. To fit random forest and decision tree models the data set was partitioned into training and testing data sets, representing 70% and 30% of the data respectively. The data were partitioned such that the group proportions were maintained between the original and partitioned data sets using the createDataPartition function in the caret library (Kuhn 2018). The training data set was used to fit each of the models and the testing data set was used to make out-of-sample predictions as an estimate of the accuracy of model predictions.

Decision trees function by partitioning a data set using an input variable with the goal of increasing homogeneity of groups. The process is continued until the benefit of further divisions is below a certain threshold. Decision trees were used due to their simplicity and ease of interpretation. They suffer from reduced predictive accuracy relative to random forests and sensitivity to randomly generate data division between training and testing data sets.

Random forests extend decision trees by building many hundreds of trees with a random subsample of observations (with replacement) and variables. Predictions are made using majority rule from the multiple decision trees created. Random forests are robust and highly predictive and were utilised to determine important variables (Williams 2011). They, however, are not as easily interpreted as decision trees.

The threats affecting populations leading to population decline likely impact elasticity patterns. Therefore the method used to achieve population decline may influence elasticity group assignment. To determine how differing threats influence elasticity patterns, the above analysis was repeated, simulating a variety of different threats. Across all species, various vital rates were reduced alone and in combinations to achieve declining and crashing population growth rates simulating threats affecting different life stage. This included reducing each stage-specific survival rate independently, reducing YOY and juvenile survival to simulated impacts to early life/pre-adulthood, reducing juvenile and adult survival to simulated threats later in life, and reducing all three survival rates to simulating threats affecting all life stages. Impacts to the juvenile stage were not applied to species where $T_{mat} < 2$.

RESULTS

Elasticity patterns of aquatic SAR in Canada were grouped using k-means clustering. With k-means clustering the desired number of clusters must be specified prior to analysis. An examination of within group sum-of-squares can be used to determine the optimum number of groups (when there is no improvement as group number increases), which indicated that elasticity patterns should be divided into 4 groups (Figure 13).

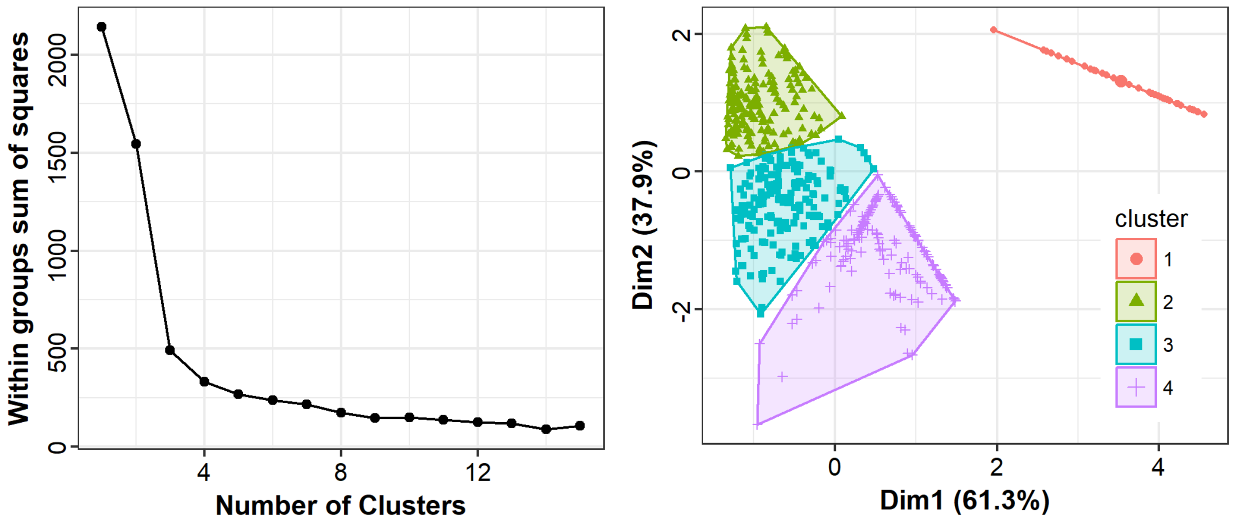


Figure 13. Results of k-means cluster analysis of species' elasticity patterns. Left panel: within group sum of squares pattern with number of clusters created indicating that 4 clusters provides that optimum number of clusters. Right panel: cluster pattern plotted as the two dominate axes from principal component analysis of vital rate elasticities.

The assigned groups represent distinct elasticity patterns (Table 2, Figure 14). Group 1 represents reproduction-sensitive species (or YOY survival sensitive) and is made up exclusively of early-maturing species ($T_{mat} < 2$), as such, there is no juvenile stage ($\varepsilon_j = 0$). Group 2 represents species that are predominantly sensitive to perturbations to adult survival. Group 3 represents species that are primarily sensitive to perturbations to juvenile and adult survival with lower sensitivity to reproduction. Group 4 represents species that are mainly sensitive to early life stages (reproduction/YOY survival and juvenile survival) with somewhat lower sensitivity to adult survival. The magnitude of stage-specific elasticities indicates the relative, proportional effect on population growth. Therefore members of groups 1 and 2 demonstrate much greater sensitivity to stage-specific vital rates (reproduction or adult survival respectively) than members of groups 3 or 4.

Table 2. Elasticity groups determined from cluster analysis of stage-specific vital rate elasticities. F represents fertility, σ_0 represents YOY/calf survival rate, σ_j represents juvenile survival rate, and σ_a represents adult survival rate. Values indicate group elasticity means and standard deviations in brackets.

Group	N	F/σ_0	σ_j	σ_a
1: Reproduction/YOY survival sensitive	65	0.80 (0.11)	0 (0)	0.20 (0.11)
2: Adult survival sensitive	232	0.11 (0.07)	0.30 (0.04)	0.67 (0.06)
3: Juvenile/adult survival sensitive	214	0.15 (0.07)	0.43 (0.07)	0.44 (0.06)
4: Early life sensitive	204	0.33 (0.08)	0.44 (0.08)	0.22 (0.08)

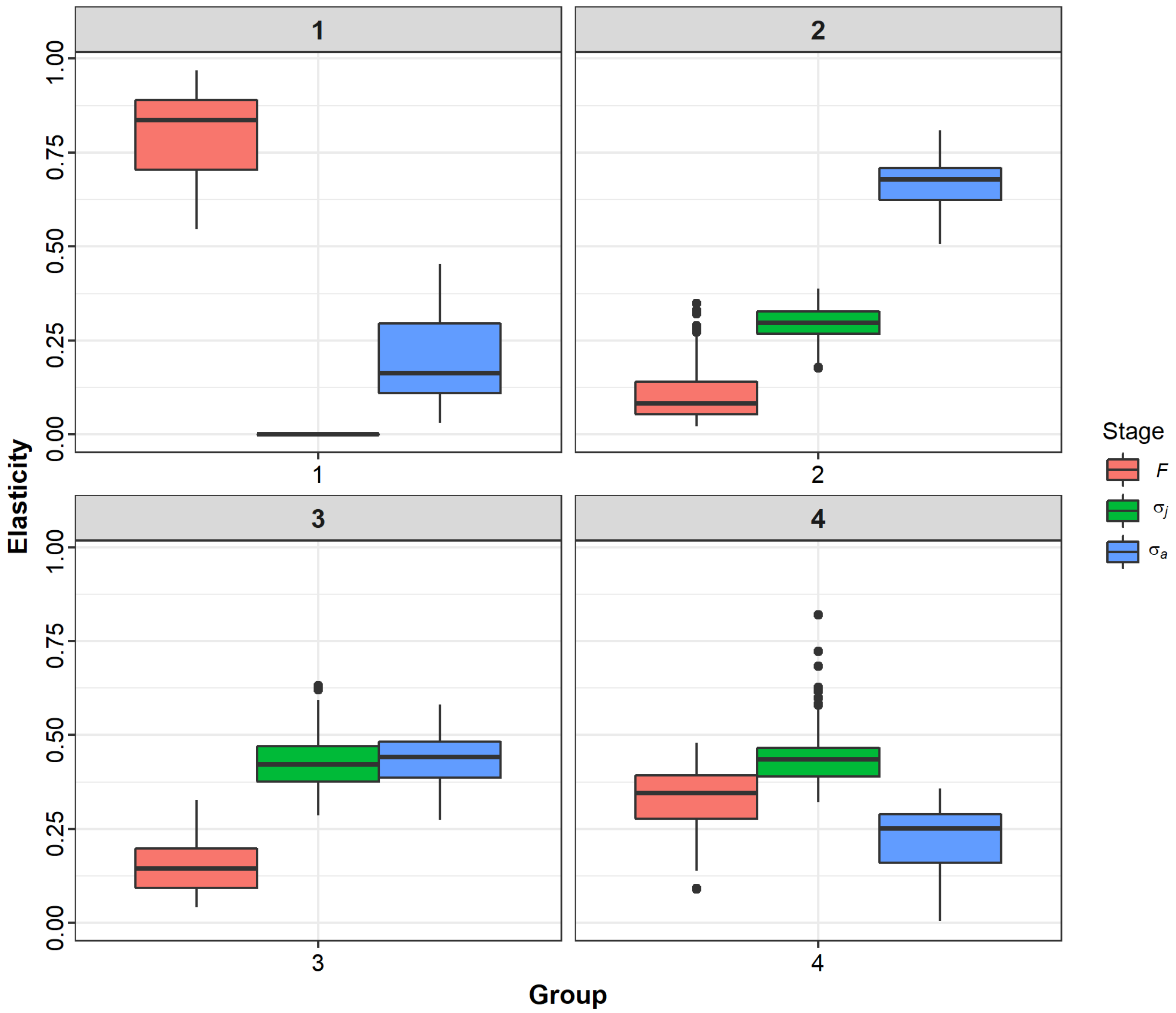


Figure 14. Elasticity patterns of identified groups (1-4) for aquatic species-at-risk across taxa. F represents fertility, σ_j represents juvenile survival rate, and σ_a represents adult survival rate.

Group membership within species varied with population growth rate (Figure 15). Across all species 41.9% were assigned to at least 2 different elasticity groups when population growth rate differed. Marine mammals and freshwater mussels were primarily categorized in group 2 as sensitive to adult survival. Sharks and skates and turtles were primarily categorized in group 3 as sensitive to juvenile and adult survival. 79% of marine fishes were assigned to different elasticity pattern groups when experiencing different population growth rates. Under stable population growth conditions the majority of species ($N = 14$) were categorized in group 2; however, all semelparous species were categorized as group 4, early life sensitive. Under booming population growth conditions the majority of marine fish species ($N = 24$) were categorized as group 4. While growing, declining and crashing the majority of marine fishes were categorized as group 3 ($N = 22$, 13, and 15 respectively). Freshwater fishes represented the largest taxon with 65 species assessed as at risk by COSEWIC and were the taxon with the greatest diversity of elasticity patterns; however, only 35% of freshwater fishes had elasticity patterns that differed among population growth rates. All species with $T_{mat} < 2$ were categorized as group 1 across all population growth rates. The greatest numbers of freshwater fishes were categorized as group 4, especially while booming. Group 2 had the lowest membership among freshwater fishes, adult survival sensitive, with no freshwater fish assigned to group 2 while experiencing booming population growth.

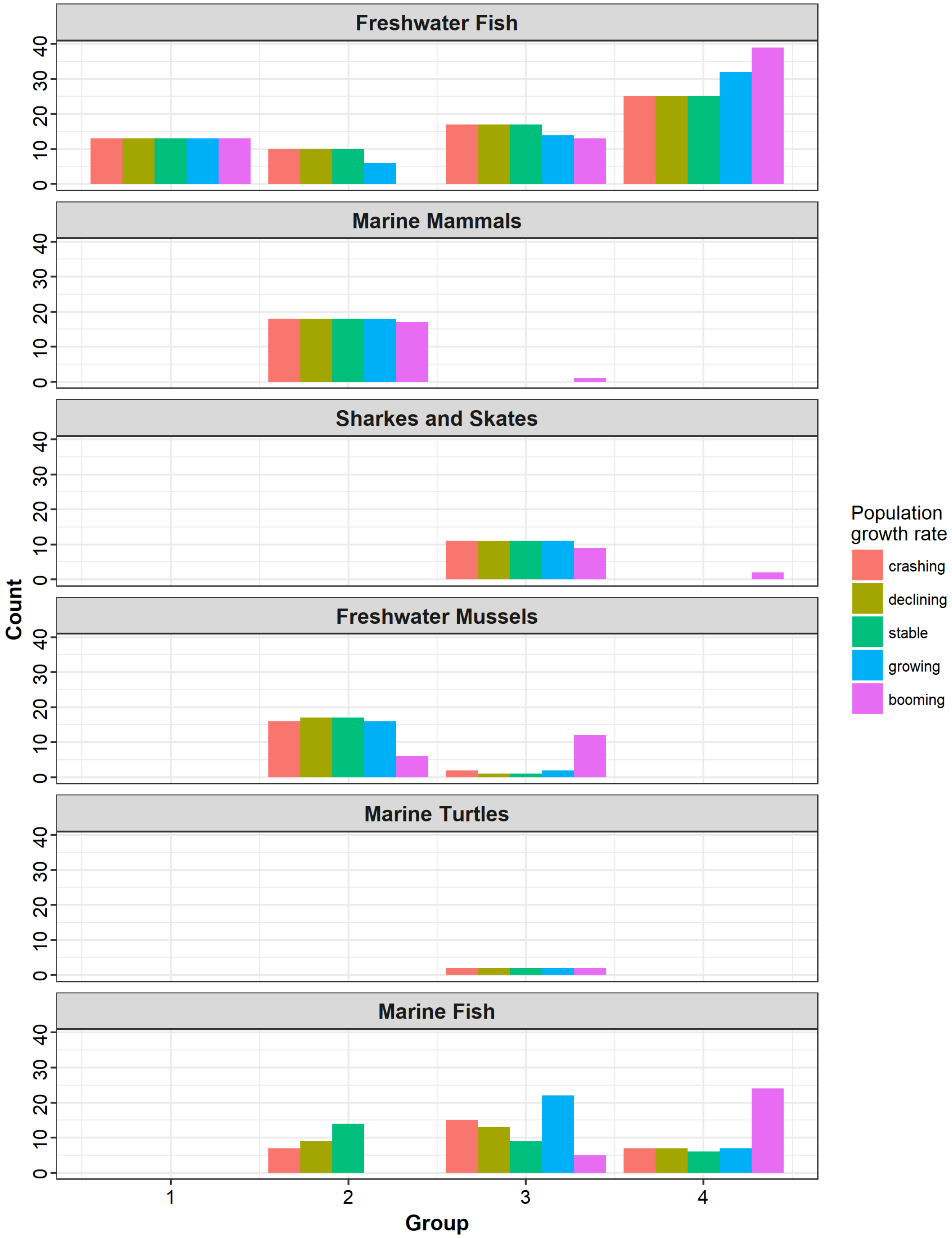


Figure 15. The number of species identified within each elasticity group (1-4) for each taxa and population growth rate class.

Random forests were used to determine which life-history variables (Table 3) were most important in determining elasticity group membership. Variable ranking was based on the decrease in scaled out-of-bag prediction accuracy and gini index (a measure of group purity) when a variable was excluded from model fitting (Figure 16). There was agreement between mean accuracy decrease and gini index decrease in the 5 most important predictor variables: λ value, age-at-maturity, taxa, adult survival (σ_a), and adult stage length (or reproductive life span). Categorical description of population state (λ class), semelparity, and COSEWIC status were not important predictors of elasticity group membership. The random forest model was 91.1% accurate in predicting out-of-sample species elasticity group membership.

Table 3. Life history variables and definitions considered in random forest analysis of elasticity group membership.

Variable	Definition	Units
Lambda	Population growth rate	NA
Taxa	Species groups	Categorical
Age at Maturity	Age at which 50% of the population is reaches maturity	years
Adult Survival	Annual proportions of mature individuals that survive	proportion
Adult Stage Length	Average number of years the adult stage lasts ($T_{max} - T_{mat}$)	years
Fertility	Average number of female offspring produced annually ($F = \frac{\varphi f}{\Psi}$)	eggs
Maximum Length	Maximum length achieved by individual of the species	cm
Lambda Class	Population growth category: booming, growing, stable, declining, or crashing	Categorical
Status	COSEWIC status	Categorical
Semelparous	Species dies after spawning	Yes/No

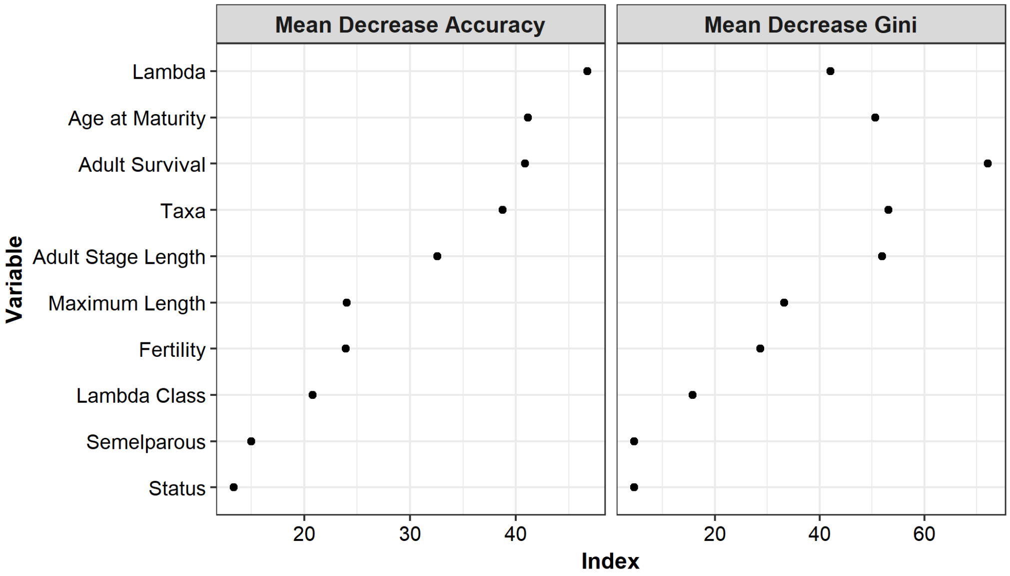


Figure 16. Results of random forest analysis ranking variable importance with two scaled metrics. Mean decrease in accuracy measures the change in out-of-box prediction accuracy when the variable was excluded. Mean decrease Gini measures the change in the gini index (a measure of group purity) when the variable was excluded.

The 5 most important predictors were used in a single decision tree as a demonstration of how these variables can be used to predict a species' elasticity patterns (Figure 17). The model was 84% accurate in predicting out-of-sample group membership. The main division of the tree was taxa predicting that all marine mammals and freshwater mussels were members of elasticity group 2, though with only 90% accuracy of within-sample predictions. Other taxa were divided based on adult survival rate, age-at-maturity, and population growth rate. Species in elasticity group 1 could be identified when age-at-maturity was < 1.5 with 100% within-sample accuracy. Group 4 species typically had low adult survival rate ($\sigma_a < 0.68$ or < 0.89 when $\lambda > 1.2$) and age-at-maturity > 1.5. Species in group 2 that were not marine mammals or freshwater mussels were identified as having high adult survival ($\sigma_a > 0.94$) and low population growth ($\lambda > 1.1$). Group 3 membership was predicted with the least success (72% accuracy for out-of-sample predictions) though the model indicated that these species typically had $\sigma_a > 0.89$ when $\lambda > 1.2$, $\sigma_a < 0.94$ when $\lambda < 1.2$, or $\lambda > 1.1$ when $\sigma_a > 0.94$.

Inclusion of taxa as a predictive variable may not be desirable, especially if the diversity of COSEWIC-assessed species within a taxon is not representative of the taxon as a whole. An additional decision tree was fit excluding taxa as a predictor (Figure 18). The resultant tree was somewhat less predictive (77.5% accuracy for out-of-sample predictions). The main division of the tree was adult survival rate dividing species into those with greater or lower adult survival (≥ 0.68). Species with lower adult survival are then divided into elasticity groups 1 or 4 depending on if age-at-maturity was less than or greater than 1.5 years. Species with greater adult survival can be divided into elasticity groups 2, 3, or 4. Group 2 species were more likely to have low population growth rate (< 1.1) and adult stage length > 14 years. Group 3 species were more likely to have adult stage length < 14 years if population growth rate was < 1.1 or adult stage length ≥ 4.5 years if λ was between 1.1 and 1.4. Species with high population growth rate (> 1.4) or short adult stage length (< 4.5) when λ was between 1.1 and 1.4 were classified as having group 4 elasticity patterns.

The type of threat (assessed as the vital rate impacted) had an influence on elasticity group membership (Figure 19). Across all taxa 35.3% of species changed group membership when affected by differing threats. The impact of threat type on group membership was greater with greater decreases in population size. 38.5% of species were assigned to at least 2 elasticity groups when experiencing crashing λs while 23.1% of species were assigned to at least 2 elasticity groups when experiencing declining λs. The most marked effects of threats on elasticity group membership was from threats affecting the adult stage. Reduced adult survival resulted in reduced elasticity values for adult survival and a large shift in group membership towards group 4. As well, there was an increase in species being assigned to group 2 (adult survival sensitive) and decrease in group 3 (juvenile and adult survival sensitive) membership when juvenile survivorship was decreased (with threats to juvenile and young stages). There was, however, little influence of threat type in predicting group membership when included in random forest analysis, ranking 7th and 8th in accuracy and gini index metrics out of 10 predictors (Figure 20). This analysis incorporated only declining and crashing trajectories and therefore lambda was not an important predictor. Adult survival, however, increased in importance relative to the previous random forest analysis.

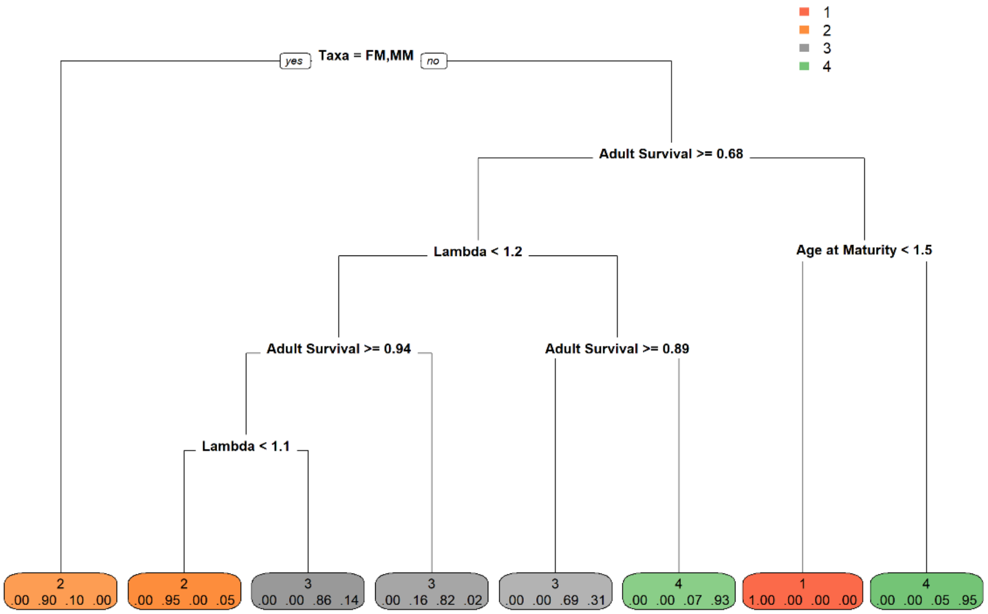


Figure 17. Decision tree analysis results predicting group membership from the 5 most important predictor variables determined from random forest analysis (Figure 5). Branches to the left of each node indicate agreement. Boxes at each leaf indicate the dominate group with the colour corresponding to group purity and the values indicate the in sample prediction success order from group 1 to 4.

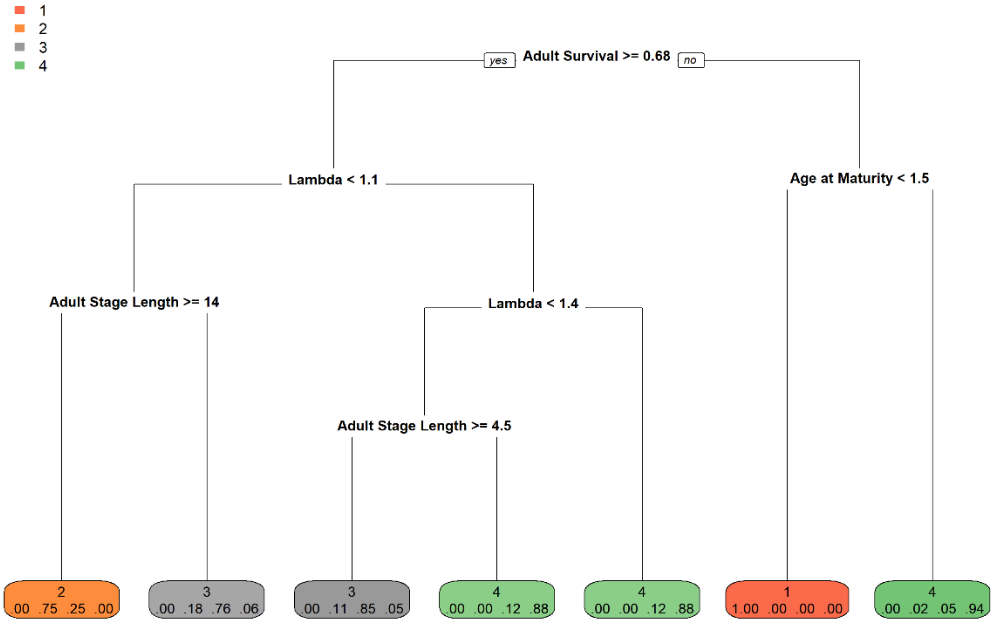


Figure 18. Repeated Decision tree analysis results predicting group membership from the most important predictor variables, excluding taxa, determined from random forest analysis (Figure 5). Branches to the left of each node indicate agreement. Boxes at each leaf indicate dominate group with the colour corresponding to group purity and the values indicate the in sample prediction success order from group 1 to 4.

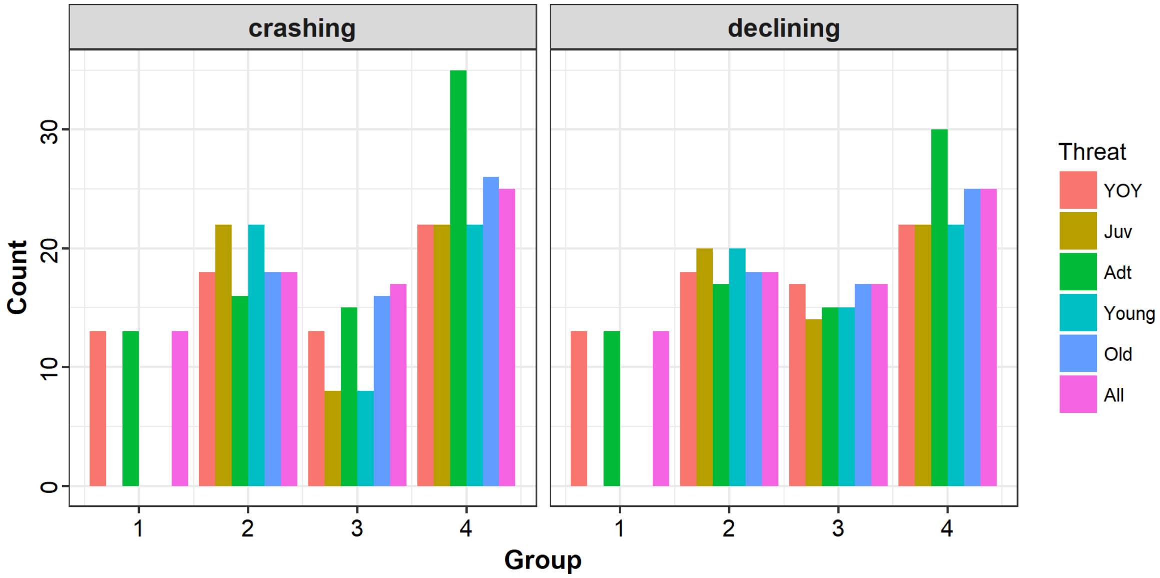


Figure 19. The number of species, across taxa, assigned to each elasticity pattern group when population decrease (crashing or declining) has resulted from threats affecting different life stages.

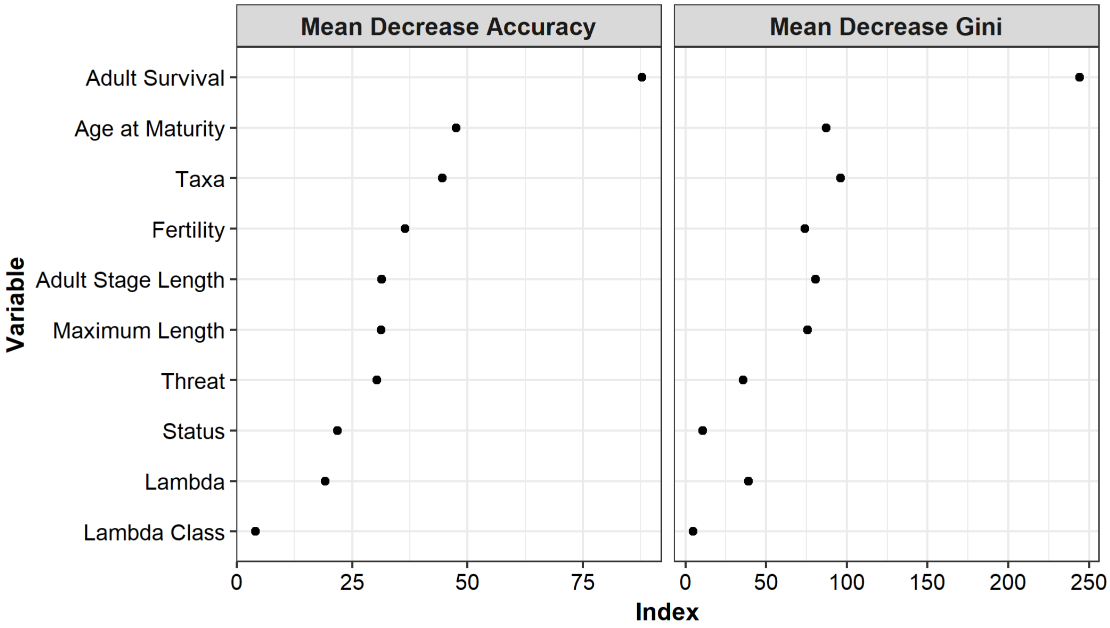


Figure 20. Results of random forest analysis of crashing and declining populations under differing threats. Mean decrease in accuracy measures the change in out-of-box prediction accuracy when the variable was excluded. Mean decrease Gini measures the change in the gini index (a measure of group purity) when the variable was excluded.

DISCUSSION

Based on this analysis, aquatic species-at-risk in Canada can largely be categorized into four elasticity patterns describing how population growth rate is expected to respond to vital rate (fertility, juvenile survival and adult survival) perturbations. Furthermore, group membership can be determined with a high degree of accuracy (91% from random forests or 84% and 78% from independent decision trees) from a few life-history traits: adult survival rate, age-at-maturity, population growth rate, adult stage length/reproductive life span and taxa. This will allow early identification of how a SARA-listed species is expected to respond to management actions or anthropogenic harm prior to completion of population modelling or when data limitations prevent parameterization of a detailed population model. In these instances, knowledge of just a few life-history traits will allow for determination of a suite of elasticity values. Moreover, when data are severely limited, expert opinion may suffice to determine if a trait is likely to be above or below a certain threshold (e.g. if reproductive life span exceeds 14 years). This can then guide management actions while further species-specific data are collected.

For example, a species such as Deepwater Sculpin (*Myoxocephalus thompsonii*), which is listed as Special Concern in the Great Lakes, is not well studied and little is known about its life-history traits. It is thought to live at least 7 years and mature at age-3; however, fecundity and survival rates are unknown (COSEWIC 2017). Therefore there is insufficient information to adequately parameterize a population model to inform recovery actions or estimate the impact of harm. If, however, adult survival rate is estimated from literature allometries (e.g. Hoenig 1983) as 0.438, this value and the assumption that age-at-maturity is > 1.5 years can be used to predict that Deepwater Sculpin likely falls into elasticity group 4. If it is assumed that the mean elasticity values from group 4 apply to Deepwater Sculpin, preliminary elasticity values could be assumed to be 0.33, 0.44, and 0.22 for YOY survival/fertility, juvenile survival, and adult survival respectively. This approach provides an initial indication of how the population may respond to life stage-specific perturbations and the ability to quantify these changes. For example, the population may be most sensitive to harm to the juvenile stage and a 10% mortality action on this stage would be estimated to result in a 4.4% reduction in population growth. This method of evaluating harm to SARA-listed aquatic species is meant to provide a guide when other species-specific information is not available. It is not meant to supplant more data intensive methodologies of measuring harm (e.g., existing population models) and should be revisited following additional research when population models can be adequately parameterized.

Including taxa as a predictor in the classification tree served simply to isolate particular taxa where the majority of species were categorized in a single elasticity pattern group. This result may not be desirable when identifying how harm may affect newly assessed SAR; especially if life-history characteristics differ from the majority of previously assessed species within a taxa. Removing taxa from the classification tree resulted in a slight decrease in predictive accuracy (78 vs. 84% out-of-sample prediction accuracy). It may be more prudent to create taxon-specific models to improve accuracy. Among species at risk, within-taxon life-history diversity for marine mammals, turtles and freshwater mussels was less than among the fishes. As a result, for these species it was not possible to discern taxon-specific elasticity patterns or identify the life-history traits (other than λ) that influence them. Extending this analysis outside of SAR may allow for increased diversity of life-history traits and elasticity patterns, which could then be modelled with greater success.

Previous analyses have identified patterns in elasticities and predictive responses for specific taxonomic groups. Heppell et al. (2000) found that with simplified population models of mammalian species a complete set of elasticities could be determined from estimates of age-at-maturity, adult survival and λ (Heppell et al. 2000; Caswell 2001). As well, early maturing species with large litters (“fast” mammals) typically had high fertility and low adult survival elasticities (i.e. group 1 or group 4 species) while “slow” mammals with low fertility and high juvenile and adult survival rates (similar to marine mammals modelled here) had much lower fertility and high adult survival elasticities (i.e. group 2 species).

Vélez-Espino et al. (2006) applied elasticity analysis to 88 species of freshwater fishes. Freshwater fishes were grouped into four categories based on their elasticity patterns: i) species sensitive to adult survival; ii) species sensitive to total survival; iii) species sensitive to juvenile survival; and, iv) species sensitive to juvenile survival and fertility/YOY survival (Vélez-Espino et al. 2006). They also determined that across species the magnitude of adult survival elasticities was related to life span and fertility/YOY survival elasticities were related to age-at-maturity when population growth was stable. Elasticity patterns have also been related to body size in freshwater fishes (van der Lee and Koops 2016).

Young and Koops (2011) explored patterns in Unionid mussel elasticities through population models based on extremes of life-history characteristics (i.e. survival rates, age-at-maturity, fecundity and longevity). The analysis of Young and Koops (2011) allowed for greater variation in life-history traits than the analysis in this document, including much greater λ values than were considered here. Resultant elasticity patterns corresponded with groups 2, 3, and 4 from the current analysis (groups 2, 1, and 3 respectively in Young and Koops 2011). The elasticity patterns of group 2 were most frequently identified in Young and Koops (2011), as they were in the current analysis. Population growth rate was not included as a predictor to categorize elasticity patterns but the other life-history characteristics determined to be important were: fecundity, age-at-maturity, and the relative survival between the juvenile and adult stage.

The analysis in this section was subject to several limitations that may have influenced the results. Foremost were data limitations for species-specific life-history traits. As many of the species included in the analysis are rare and not well researched there were significant gaps in data availability for many species; this was especially true for freshwater mussels. These gaps were typically filled in through parameter estimation from taxon-specific relationships. These relationships, however, reflect taxon-wide mean estimates and therefore may under-represent the diversity in life-history characteristics when applied broadly throughout the analysis. Every effort was made to avoid using such relationships, though it was necessary in some cases.

The effects of perturbations to vital rates on population growth rate in this analysis reflect permanent changes, such as through permanent habitat changes from a w/u/a. Therefore, estimates may not accurately represent the impacts of transient or temporary harm (i.e. when the w/u/a leads to a short term impact on one or several vital rates). Elasticity estimates may reflect the immediate impacts of these activities but will not capture the long-term impacts of these projects and the resulting risk to population recovery or persistence. It is likely that elasticities from permanent perturbations will over-estimate the impacts of transient harm.

As well, the matrix models incorporated in this analysis are deterministic and density-independent. The deterministic elasticity values from mean matrix models are likely good approximations of those of stochastic models (Caswell 2001). Therefore it is unlikely that the general trends from this analysis would differ with inclusion of stochasticity. The impacts of density dependence on a population’s response to perturbations, however, are less clear. Compensatory density-dependence can diminish the effects of harm as assumed in many fisheries models (i.e. stock-recruitment curves, Hilborn and Walters 1992). Alternatively, small changes in vital rates or life history characteristics in a density-dependent environment can cause permanent state changes or bifurcations in trajectories with significant long-term impacts (i.e. changes in equilibria, Caswell 2001). Inclusion of density-dependence or environmental/demographic stochasticity is beyond the scope of this generic analysis. However when assessing harm with more rigorous species-specific methods, these factors should be considered.

It is likely that elasticity patterns of alternative population growth rates in the initial decision tree (Figure 17) were influenced by the assumed threats (decrease in vital rates) that result in population decline. For example, the choice to reduce the entire survival schedule of freshwater fishes to create population decline (simulating broad-scale habitat impacts) resulted in elasticity patterns identical to stable populations, while reducing adult survival rate of marine fishes (simulating fishing mortality) resulted in reduced adult survival elasticities relative to stable populations. While attempts were made to apply harm in a manner that reflected taxon-specific threats, the application across all species within a taxon may not be appropriate. As a result, the elasticity patterns produced from the initial analysis by alternative (non-stable) population growth rates represent hypotheses of threats and may differ from population-specific results when threats differ.

Examining how elasticity patterns change when a population experiences different threats indicated that certain threats can lead to significant changes in elasticity patterns. There was a tendency for species with reduced adult survival (e.g. from fishing mortality) to become more sensitive to juvenile survival and species with reduced juvenile survival (e.g. from degraded rearing habitat) to have increased sensitivity to adult survival. In these scenarios populations are facing threats and the elasticities quantify the effects of perturbations with those threats still in effect. Mitigation or recovery efforts that return the population to its initial state would result in elasticity patterns of growing and/or stable populations. However if the threats can not be removed (e.g. ongoing bycatch mortality) these simulation results provide insight into how population growth can be best stimulated. While the active threat caused a change in group assignment (Figure 18) threat type was not a dominant predictor of group membership. Instead adult survival (natural and threat mortality) was highly predictive of group membership. Adult survival was an important predictor in the initial tree (Figures 16 and 17) therefore threat type may not greatly impact the tree.

In conclusion, the elasticity patterns of species-at-risk in Canada were grouped into 4 categories: group 1, species sensitive to reproduction/YOY survival; group 2, species sensitive to adult survival; group 3, species sensitive to juvenile and adult survival; and group 4, species sensitive to early life (reproduction/YOY survival and juvenile survival). Knowledge of a species' elasticity pattern allows for inferences to be made about how a population may react to harm or management actions designed to stimulate population growth. When lacking detailed population models or demographic data, we found that elasticity group membership can be reliably predicted with few life-history characteristics: adult survival, adult stage length, age-at-maturity, and population growth rate. This analysis provides a framework to guide management decisions for species-at-risk when assessing harm and recovery actions in instances when alternative methods are unavailable.

SECTION 5: OFFSETTING CONSIDERATIONS FOR SARA-LISTED SPECIES

Sections 2, 3, and 4 provide the basic components to identify the nature and extent of habitat change from the w/u/a, the associated vital rate shifts, and population responses. These components provide a useful stand-alone framework for evaluating the impact of an individual w/u/a on the trajectory of a SARA-listed species, and when combined with allowable harm reference points, provide a framework to make determinations about the impact of a w/u/a under Section 73. However, in addition to these components, DFO's Species at Risk program has requested guidance on the potential use of biodiversity offsets to counterbalance residual effects to SARA-listed species. To provide advice, the basic theory behind biodiversity offsetting is reviewed. Then, the extent to which policy involving offsetting for imperilled species exists on a global scale is described. Finally, an interpretation of where and how the offsetting process could apply to a given w/u/a while satisfying the conditions of Section 73 is shown.

Biodiversity offsetting is a relatively new and evolving technique used globally to counterbalance the unavoidable residual environmental effects of development projects. When pursued, offsetting is the third phase of a three-tiered mitigation hierarchy that begins with: 1) avoiding project impacts, such as through site relocation; 2) the application of mitigation measures, such as redesign of the project if relocation is not possible; and, 3) offsetting losses when avoidance and mitigation measures result in residual environmental impacts (Gardner et al. 2013).

Offsetting aims to balance expected losses with gains at the impact site or elsewhere by some form of human-mediated compensation measure. Offsets can be in-kind (losses replaced with similar gains, e.g., habitat loss is balanced with habitat gain through restoration) or out-of-kind (e.g., habitat losses are replaced with, for example, control of an invasive species that is limiting productivity). In general, offsets take the form of habitat, biological, or chemical manipulations that are intended to provide, at minimum, an equivalent gain to what has been lost. Offset calculations are typically evaluated through a purpose-built accounting framework (e.g., see the use of 'Equivalent Adults' as a useful metric within DFO's Fish and Fish Habitat Protection Program; Bradford et al. 2016).

There is considerable scientific debate about the effectiveness of offsetting (see Walker et al. 2009 and Gardner et al. 2013, and references therein), with criticisms mainly concerning: 1) lack of empirical evidence for effectiveness (Gibbons and Lindenmayer 2007); 2) concerns that the eventual opportunity to offset residual impacts relaxes the level of rigour applied to other stages of the mitigation hierarchy (Clare et al. 2011); and, 3) the idea that offsetting involves the "exchange [of] certain and almost immediate losses for uncertain future gains" (Laitila et al. 2014). However, offsetting has been applied successfully to counterbalance losses to fisheries productivity in Canada (Loughlin and Clarke 2014; Bradford 2017; see below). Offsetting has also been applied successfully for imperilled species, with success often tied to the rigour of implementation. For example, following the construction of infrastructure to support the Olympic games in Sydney, Australia, offsetting was initiated to balance losses to endangered frog populations. Intensive offset requirements (a 19:1 like-for-like habitat creation ratio and intensive pre- and post-monitoring with mark-recapture studies) led to a 19-fold increase in pond area and a 1.2 – 3.5 fold increase in population size during follow-up monitoring (Pickett et al. 2013).

The 2012 amendments to the *Fisheries Act* introduced the concept of offsetting as a means to balance residual productivity losses resulting from development activity. The theory and application of offsetting has been reviewed by DFO science as it pertains to achieving no net loss in fisheries productivity (see Clarke and Bradford 2014; Loughlin and Clarke 2014; Bradford et al. 2016). In particular, Loughlin and Clarke (2014) provide examples of offsets applied successfully in a fisheries context. However, unlike the *Fisheries Act*, the *Species at Risk Act* does not include the term 'offset', 'offsetting', 'compensate', or 'compensation'. Draft policy from

Environment and Climate Change Canada (ECCC, undated), including the proposed SARA permitting policy (Government of Canada 2016), indicate that the use of biodiversity offsets (also termed conservation allowances; ECCC, undated) may be considered when evaluating projects under Section 73; however, scientific advice about implementation has not been developed.

To understand the prevalence of offsetting for imperiled species and the potential differences in offsetting policy compared with more basic offsetting scenarios, Bhathal et al. (unpublished manuscript) conducted a global review of 73 federal jurisdictions with biodiversity offsetting programs in place for aquatic or terrestrial species. These encompassed three classes of regulations: environmental impact assessments, endangered species policies, and other regulations and policies. Of the 73 reviewed jurisdictions, 72% indicated through general policy statements that biodiversity offsetting could be used in scenarios involving imperiled species, and that additional rigour should be applied in these scenarios. However, in general, differences in evaluation criteria or the increased level of offsetting rigour for situations involving imperiled species were not provided. Only five jurisdictions provided measurable differences in how offsets should be implemented for endangered species (Table 4). South Africa provided the greatest difference in terms of how offsetting for endangered species should differ from generic scenarios, with predetermined offset ratios based on the status of a given population (Table 5).

Table 4. Summary of federal jurisdictions outlining offsetting requirements for endangered species (includes terrestrial or aquatic; Bhathal et al., unpublished manuscript). Short forms in Offset Goal are no net loss (NNL) and net gain (NG).

Region	Country	Jurisdiction	Legal Instrument with Biodiversity Offset	Year	Offset Goal	Offset Metric	Equivalence	Offset Longevity	Offset Type	Offset Context	Ecosystem Type
North America	United States of America	National	Compensatory mitigation for losses of aquatic resources mitigation banks for wetlands under Section 404	2008	NNL	Based on lost aquatic resources; ratio by acreage or linear foot	In kind (for difficult to replace resources)	Long term Management/ Perpetuity	Permittee responsible; mitigation bank; ILF	Watershed approach (to the extent appropriate and applicable) Landscape	Wetlands, streams and other aquatic resources
North America	United States of America	National	Guidance for the establishment, use, and operation of conservation banks Endangered and threatened wildlife and plants; Endangered Species Act compensatory mitigation policy, 2016	2003 2016	NNL NG	Based on species and habitat value; Equivalent metrics to be used whenever possible (≥1:1 ratio for area supporting nest site or family group)	In kind	Perpetuity	Permittee responsible; mitigation bank; ILF	Landscape	Terrestrial and freshwater (endangered species)
Caribbean Central & South America	Colombia	National	Manual for the allotment of compensation for the loss of biodiversity	2012	NNL NG	Area (Aggregate-ratio Compensation Factor)	In kind	Project duration	One-off	Landscape	Terrestrial
Africa	Western Cape (South Africa)	Provincial	Western Cape biodiversity offsets guidelines	2007	NNL	Area (ratio: conservation, species, functionality and ecosystem services-based multipliers)	In kind	Perpetuity	One-off; payments in-lieu	Landscape	Terrestrial and wetland
Africa	KwaZulu-Natal (South Africa)	Provincial	Concise guidelines biodiversity offsets in KwaZulu Natal	2013	NNL	Area (ratio-conservation, species, functionality and ecosystem services-based multipliers)	In kind	Duration of project or in perpetuity	One-off; payments in-lieu	Landscape	Terrestrial wetland and coastal ecosystems
Australia, New Zealand, and Oceana	Australia	National	Environmental offset policy	2012	NNL NG	Area of community (start area and future area, both in hectares and quality); Area of habitat; Number of features (e.g., habitat trees); Condition of habitat (in terms of quality); Birth rate; Mortality rate; Number of individuals	In kind*	Flexible; timing is dependent on factoring	One-off and payments in-lieu, exploring biobanking	Landscape	Terrestrial (some aspects relevant to the marine environment)

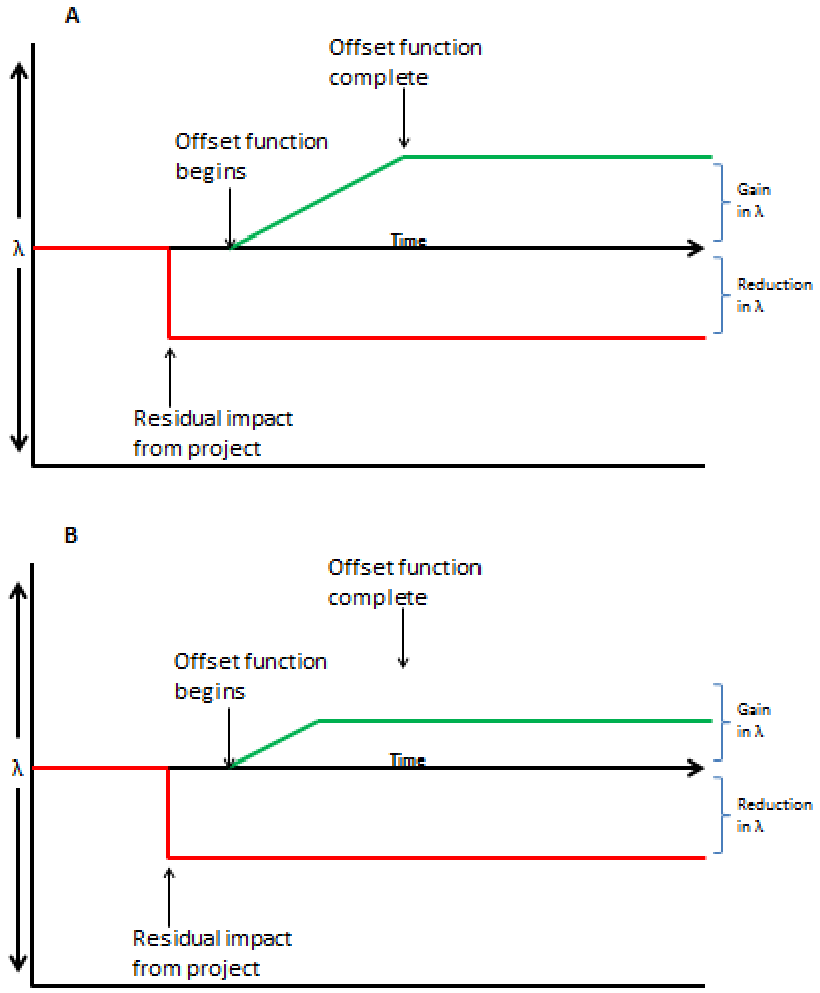
Table 5. Offset ratio rules established to support endangered species policy in South Africa (Bhathal et al., unpublished manuscript).

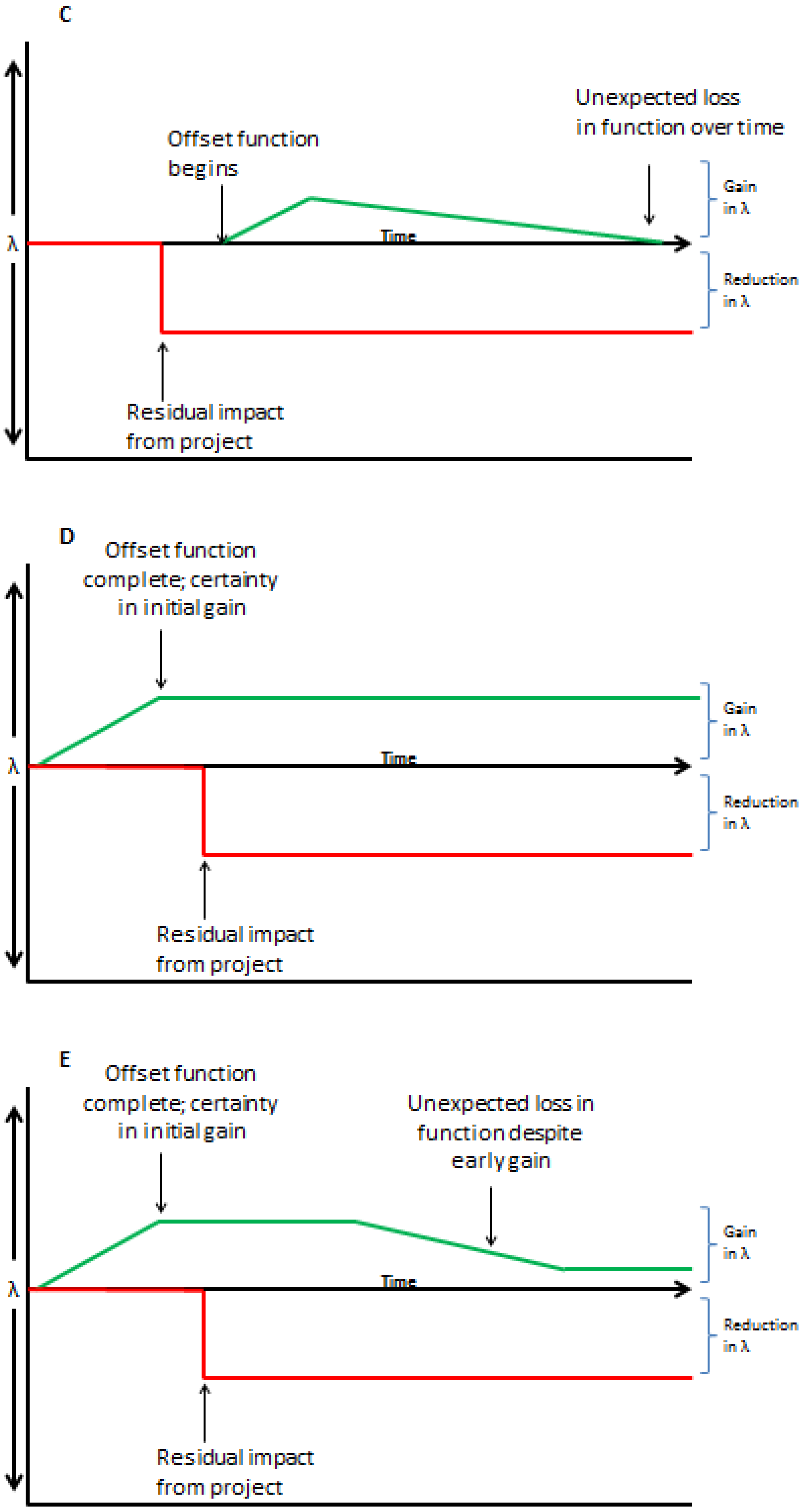
Province	Offset Category	Ecosystem Type	Offset Ratio
Western Cape	General Biodiversity Offsets	Least Threatened	No offset required
	Imperilled Species Offsets	Critically Endangered (only in exceptional circumstances)	30:1
		Endangered	20:1
		Vulnerable	10:1
KwaZulu Natal	General Biodiversity Offsets	Least Threatened	No offset required
	General Biodiversity Offsets	Critically Endangered (only in exceptional circumstances)	30:1
		Endangered	25:1
		Vulnerable	5:1
		Near Threatened	3:1

Considerations for understanding the suitability of an offset have been reviewed by Pilgrim et al. (2013), Gardner et al. (2013), and Poulton (2018). In particular, Pilgrim et al. (2013) established a weight-of-evidence framework to consider whether impacts from a project can be offset based on the vulnerability of the object (e.g. habitat or population or species) in question, the irreplaceability of that object, and the available opportunities for implementing offsets. Here, several conceptual scenarios were developed to consider whether and how offsets could balance residual impacts to population growth rate for a SARA-listed species, and the associated uncertainties. In the first scenario (Figure 21, A), a w/u/a is permitted to proceed because review of an offsetting plan determines a high likelihood that the offset will eventually balance residual losses. The offset is initiated during or immediately following the residual impacts of the project; however, offset function (in terms of measurable changes to population growth) does not occur until some point in the future. This is a relatively common scenario for non-SARA species, where the uncertainty associated with the delay in function is often handled with multipliers (e.g., offset ratios), such that short-term losses will eventually be balanced or surpassed. In this scenario, there are several considerations and potential outcomes that relate to satisfying Section 73(3)(c). The first relates to offset function that is less than expected based on the review of the offsetting plan. In Figure 21 (B), the offset provides consistent ecological function into the future, but at a reduced intensity relative to what was needed to balance residual losses. In Figure 21 (C), the offset suffers from increasingly reduced function through time, eventually reaching a state where biological function is no longer supported by the offset, despite longstanding changes to population growth imposed by the w/u/a.

To reduce uncertainties related to function and permanency of the offset, one approach could involve implementing the offset in advance of the project's residual impacts, such that the gains expected from the offset are fully functioning and can be identified and measured prior to authorizing residual loss (Figure 21, D). Here, uncertainty about initial gain in function is reduced, provided that suitable monitoring of offset function can occur. However, the possibility exists that an eventual loss of function through time may occur (Figure 21, E), or an unexpected loss of function due to interactions with other offsets and/or changes in environmental conditions that interact with the offset but not the species (Figure 21, F). Lastly, the possibility also exists that offsets applied prior to residual impacts may have unexpected negative effects (e.g., failure during construction that unexpectedly impacts the species), leading to population declines during implementation of the offset despite best intentions. Significant monitoring data related to the long-term function of offsets in aquatic ecosystems would help understand the general feasibility of achieving population gains under each scenario, and were not available at the time of this review.

Assessing the suitability of an offset can occur by evaluating the probability of achieving population growth due to the offset, relative to population losses due to the residual impact. The three-panel framework presented in Figure 3 can be used to evaluate the changes in habitat and populations owing to the offset, as well as the net difference between predicted residual impact and offset.

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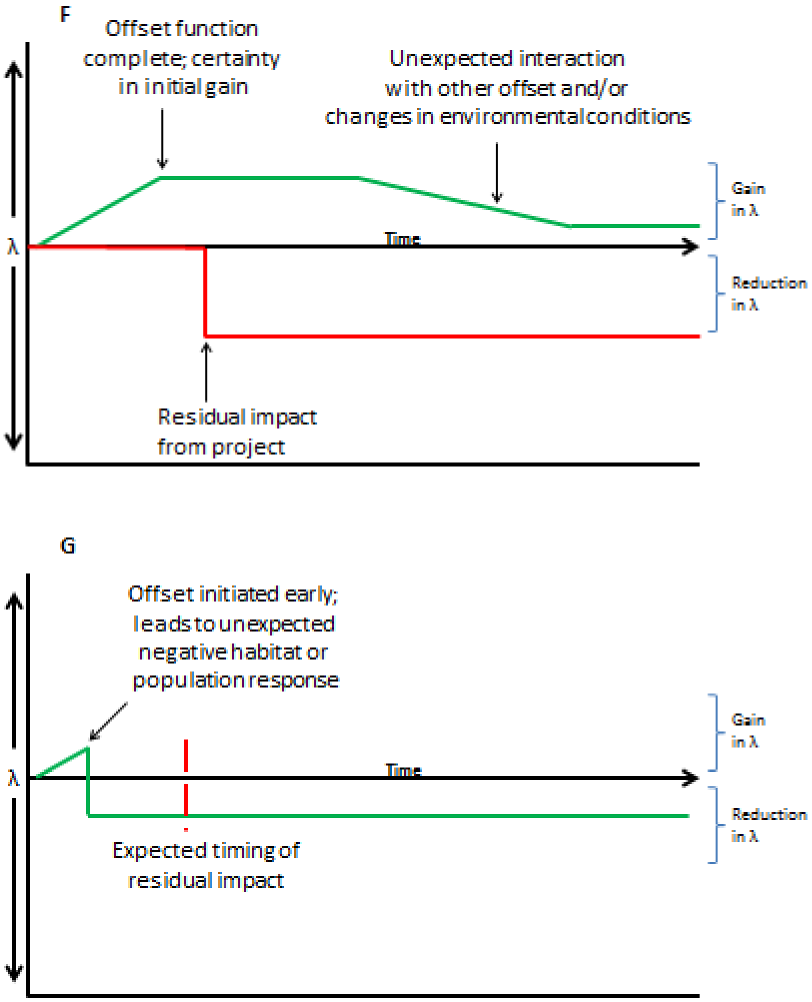

Figure 21. Potential offsetting considerations for SARA-listed species. Panel (A) represents a common scenario where the offset is initiated when the project is initiated and offset function is not fully realized until after the project's residual impact has occurred. Uncertainties relate to whether offset function will be perpetually reduced (B), or (C) degrade through time. An alternative approach (D) may involve implementing the offset in advance of residual impacts, which reduces uncertainty about initial offset function because it can be monitored prior to the residual impact occurring. However, even when offsets are implemented in advance of residual impacts, they may experience (E) long-term reductions in function through time, or (F) unexpected interactions with other offsets or changing environmental conditions. A final scenario (G) may involve implementing the offset in advance where the offset leads to unexpected, negative perturbations to habitat or populations, such as a critical failure of the offset during construction.

SECTION 6: INTEGRATION OF FRAMEWORK COMPONENTS IN SUPPORT OF SECTION 73

Bradford et al. (2015) identified the importance of establishing "the risk of what to whom" when developing scientific frameworks to support decision-making. The integration of framework components in this document can be used to determine the probability, *p*, that an individual w/u/a, *i*, will lead to a given change in the population growth rate, λ, of a SARA-listed species. Changes in the population imposed by the w/u/a can be evaluated against existing estimates of allowable harm and the ability to meet recovery targets, whether existing estimates of allowable harm are generic (e.g., maintain population growth, as in maximum allowable harm estimates) or prescriptive (e.g., years to recovery, when recovery targets are available). However, decisions around an individual w/u/a must also consider all other sources of harm and the effect of recovery measures over the permitting period. Therefore, a three-step integration of framework components is proposed (Figure 22), which involves: 1) Identifying the pre-impact state of habitat and the population, including how habitat influences population productivity; 2) identifying the change in habitat and population imposed by the individual w/u/a (steps 1 and 2 informed by Sections 2, 3, and 4, outlined in Figure 3, with or without an offset); and, 3) identifying the change in habitat and population imposed by all other w/u/a's, threats, and recovery measures over the permitting period. Additional information about these steps is as follows:

1. **Identify the pre-impact state of the population and habitat**
    a. Population state
        i. The population's state prior to the w/u/a can be informed by available monitoring data; where monitoring data is lacking, several approaches to estimate baseline trajectory have been described (e.g., assumed rate of decline based on COSEWIC criterion A; see Vélez-Espino and Koops 2007; van der Lee et al. 2020). Population state can be evaluated directly as the measured or inferred λ, or by inferring one of the five states presented in Section 4 (booming, growing, stability, declining, crashing). This step should also determine whether an existing population model exists for the species. In cases where existing population models are lacking, Section 4 provides an approach to estimate vital rate elasticities given basic knowledge of life history parameters.
    b. State of habitat
        i. Understanding the baseline state of habitat requires identifying the habitat variables that are important to the population. The habitat stressor categories identified in DFO (2014a) can provide guidance about the suite of conditions to assess (e.g., food supply, EMF, noise, flow), recognizing that certain features will be more relevant for certain species, and other features not identified in DFO (2014a) may also be important. Ideally, an assessment can be made of current vital rate function in relation to the habitat variables of interest.
2. **Identify the change in habitat and population imposed by the w/u/a**
    a. State of habitat
        i. Changes to the state of habitat can be informed by DFO's Pathways of Effects, which will determine which habitat variables are likely to be affected by the w/u/a. In cases where the activity falls outside of the Pathways of Effects framework, an estimate must be made of which habitat variables are affected by the w/u/a. In all cases, the habitat variables influenced by the project must be assessed in terms of changes in their intensity, spatial extent, and the duration/frequency of change. In some cases, the w/u/a may pose direct impacts to vital rates, such as animal strikes during construction. These can occur in conjunction with habitat changes, or independently of habitat changes. In the case of direct impacts to vital rates, an estimate of which vital rate(s) are impacted, the intensity of change, duration/frequency of change, and proportion of the population receiving the change must be made.
    b. Effect of habitat changes on vital rates

        i. The expected changes to habitat will form the basis for estimating changes to vital rates, based on habitat-vital rate functions for each taxon. Estimating changes to vital rates must consider: 1) the number and identity of habitat variables influenced by the w/u/a, 2) which vital rates they influence (e.g., a single rate will be influenced by multiple habitat variables), and 3) the nature of interactions between habitat stress and vital rate responses (e.g., Figure 23). Although assuming additive effects is the simplest solution, it is not the most precautionary. Simple rules or best practices could be developed to adhere to a precautionary parameterization. Functions to relate the degree of sub-lethal effects (if any) can also be incorporated as appropriate for the taxon, for example, following King et al. (2015). Ultimately, the intensity and frequency/duration of the vital rate shifts must be estimated, as well as the proportion of the population affected.
    c. Changes in population productivity
        i. The estimated vital rate changes can be combined with existing population models to determine the consequence to the population. In cases where population models do not exist, the population models presented in Section 4 can be used to determine the potential change in population growth under different assumed population states. However, in all cases, special attention is needed on how to incorporate transient shifts in vital rates (e.g., see Young and Koops 2013). Once the shift in population productivity has been estimated from the w/u/a (e.g., Figure 24), a comparison can be made against existing estimates of allowable harm and/or recovery targets.
        ii. In cases where offsetting has been proposed, a comparison can be made of the change in productivity with and without the offset measures and in relation to allowable harm and recovery targets.

3. **Estimate the change in population productivity imposed by all other w/u/a's over the permitting period.**
    a. To ensure that survival or recovery of the wildlife species is not jeopardized, an individual w/u/a cannot be assessed in isolation. Thus, an assessment must be made of the change in population productivity of all other w/u/a over the permitting period. Two approaches exist to consider the cumulative effects posed by multiple w/u/a: 1) a first-come first-served approach, where development impacts are assessed based on the order of application until the quota of allowable harm is reached; or, 2) hind-casting techniques, where the expected level of development (e.g., using past SARA permits as a record) is projected to define the subset of harm that can be permitted over the permitting period.
4. **Estimate the change in population productivity imposed by non-w/u/a factors over the permitting period (threats and recovery measures)**
    a. Similar to step 3a, additional information must be considered as to changes in habitat and population productivity over the permitting period from other relevant factors, such as the effect of threats and recovery measures on habitat and population productivity.
5. **Combine information in steps 1 through 4 and make decision about individual w/u/a**

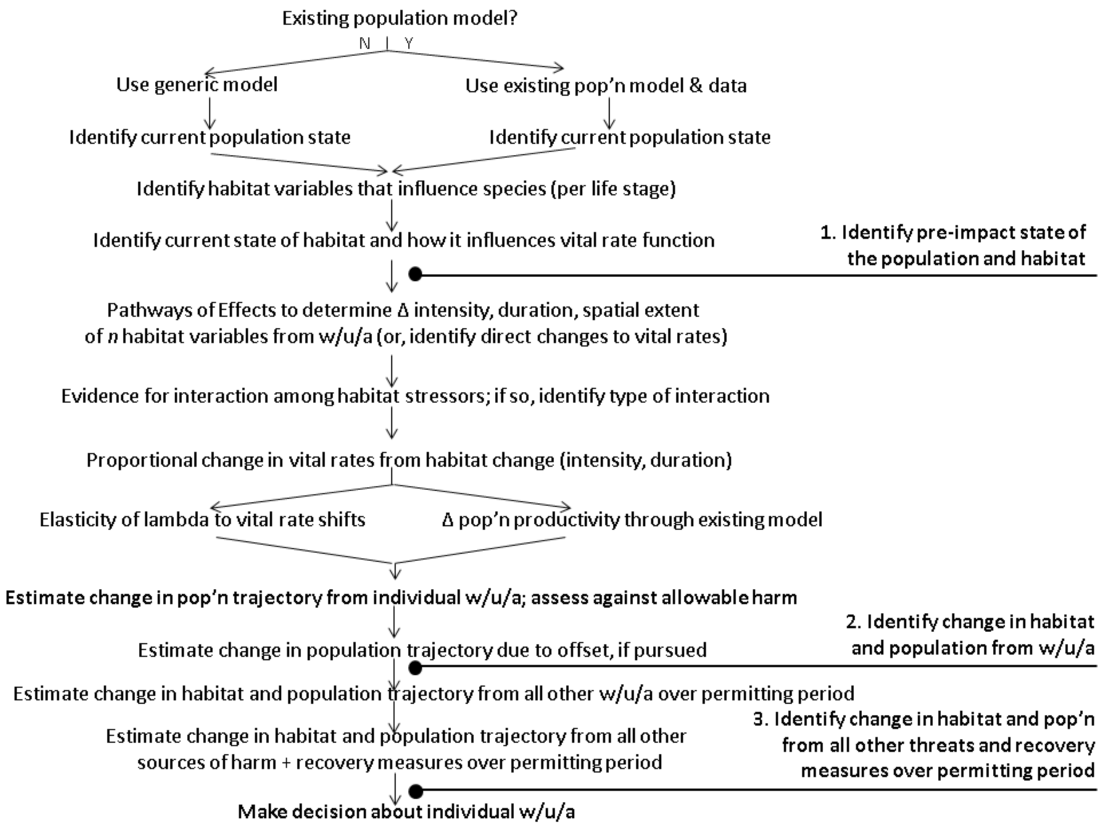

Figure 22. Conceptual framework to evaluate the harm of an individual w/u/a to a SARA species in relation to all other sources of harm and recovery measures over the permitting period. Steps 1 and 2 follow the three-component framework for evaluating an individual w/u/a shown in Figure 3.

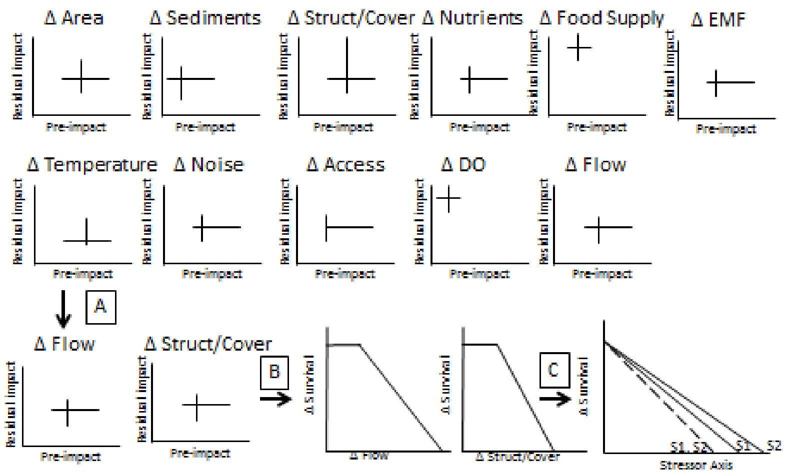

Figure 23. Conceptual framework to relate the suite of habitat changes imposed by a w/u/a to vital rate shifts. Boxes describe A, the subset of habitat variables that influence the vital rate, b) the shape of the flow / survival and structure cover / survival response functions, and C, the choice of aggregation of two factors (in this case, additive effects are assumed).

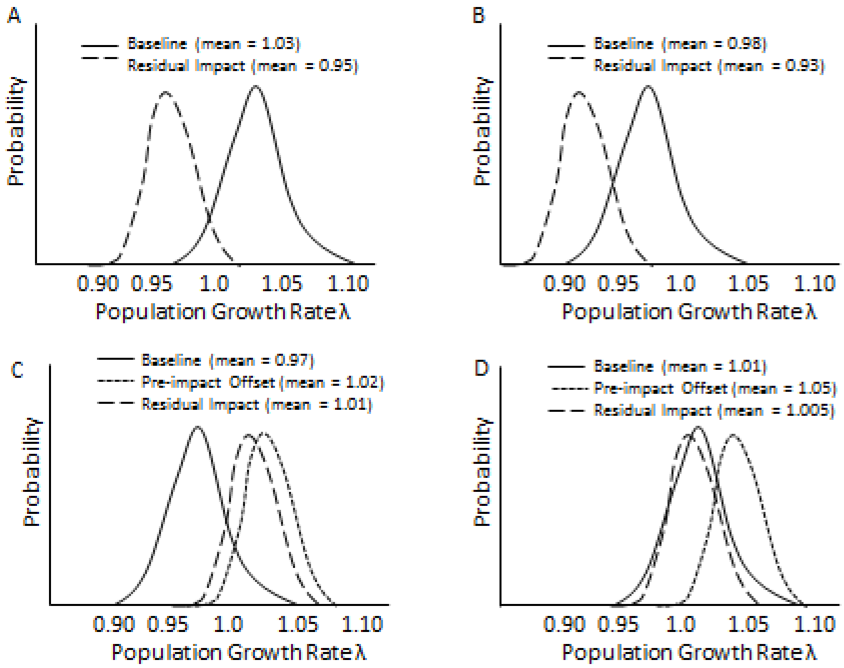

Figure 24.Four hypothetical scenarios describing baseline and the residual impacts to population growth rate from a w/u/a. In panel A, baseline condition suggests a high likelihood of a growing population (λ >1); residual impact estimates the high likelihood of a declining population (λ < 1). In panel B, the baseline scenario suggests a moderately high likelihood of a declining population; residual impacts increase the likelihood of decline. In panel C, baseline population growth rate suggests decline, but offsets enacted before the project result in a high likelihood of growth, with residual impacts reducing growth only slightly; in panel D, baseline population growth rate has a high likelihood of being positive; pre-impact offsets increase growth further, but residual impacts suggest a slight loss over baseline. Interpretation of decision points within these scenarios requires knowledge of existing estimates of allowable harm and the specificity of the recovery target (maintain growth or time-based recovery).

FINAL CONSIDERATIONS AND UNCERTAINTIES

This document presents components of a science-based framework to determine whether an individual w/u/a will jeopardize the survival or recovery of a SARA-listed species. The framework builds on existing science advice around the concept of allowable harm, while translating the effects of the project to changes in population productivity through vital rate functions, and by considering additional w/u/a and threats and recovery measures that may impact SARA-listed species over the permitting period.

Significant work will be required to operationalize the framework into a decision support tool. For example, although the information required for each stage of the assessment framework has been described, there will be challenges for compiling information to quantitatively assess each step in the framework, especially given the data-limited nature of most SARA-listed species. Basic information such as the current state of a population or its habitat and the role of habitat on vital rate function will be limited for many SARA-listed species, yet is sorely needed to operationalize the framework. Considerable work is also needed to determine how behavioural and sub-lethal components can be incorporated into population responses. In these situations, promising approaches proposed by NRC (2005) and King et al. (2015) use expert elicitation to establish index values. In other cases, meta-analytic approaches may be needed to establish statistical relationships between habitat and vital rate function, applicable to a range of taxa. Methods to establish presumed rates of population decline and growth are presented here, several of which have been used in RPAs to inform allowable harm. A key part of operationalizing the framework is to ensure that decisions are sufficiently precautionary when information is lacking.

The population models in Section 4 do not consider or assume density-dependent effects, and thus assume no relief from compensation as a result of development impacts. This represents a precautionary viewpoint, but further examination of the suitability of this assumption is warranted. Significant data limitations prevented a fulsome evaluation of the effectiveness of offsetting for SARA-listed species. Detailed, long-term monitoring datasets that include suitable experimental designs (e.g., before-after, control-impact) are needed to assess whether offsetting measures for SARA species have achieved their intended benefits on habitat, vital rate function, and population responses.

Despite the significant challenges to operationalize a science-based decision support framework, such work is justified to ensure that Section 73(3) permitting decisions under the *Species at Risk Act* are based on sound, defensible, science-based criteria, and thus will ensure that w/u/a do not jeopardize the survival or recovery of SARA-listed species.

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APPENDIX

ESTIMATION OF LIFE HISTORY PARAMETERS USED IN ELASTICITY ANALYSIS

LIFE HISTORY PARAMETERS

Life history data for all aquatic species assessed by COSEWIC as Special Concern, Threatened, or Endangered were compiled to parameterize species-specific matrix population models. Required data were, Longevity, T_{max}; age-at-maturity, T_{mat}; reproductive information including: mean fecundity, f, sex ratio, φ, and spawning periodicity, Ψ; and stage-specific survival rates, σ_i. If species-specific data were unavailable, parameters were estimated with taxa-specific relationships from the literature.

Freshwater Fishes

Survival rate, if unknown, was estimated from a relationship predicting instantaneous adult mortality, M, from von Bertalanffy growth function, VBGF, coefficients (Then et al. 2015 adapted from Pauly 1981):

$$M = 4.188k^{0.73}{L_\infty}^{-0.33}, \qquad \text{(A1)}$$

where L_∞ is asymptotic length and k is the growth coefficient. If the VBGF coefficients were not available for a particular species they were estimated from (Froese and Binohlan 2000):

$$L_\infty = 1.148{L_{max}}^{0.984}, \qquad \text{(A2)}$$

and (FishBase, Froese and Pauly 2018):

$$k = 10.8{L_\infty}^{-0.615}. \qquad \text{(A3)}$$

Juvenile mortality can be back calculated from adult mortality assuming that mortality is an inverse function of length (Lorenzen 2000). If a species follows a VBGF growth pattern juvenile survival rate can be estimated as (van der Lee and Koops 2016):

$$\sigma_j = \left[\left(\frac{L_1 e^{-k(T_{mat}-1)}}{L_{mat}}\right)^{\frac{ML_{mat}}{kL_\infty}}\right]^{\frac{1}{T_{mat}-1}}, \qquad \text{(A4)}$$

where L_1 and L_{mat} represent length at age-1 and age-of-maturity respectively. YOY survival was solved for such that the population would experience a $\lambda = 1$.

Maximum population growth rate, the λ used for booming populations, was estimated from a relationship predicting the intrinsic rate of increase (r_{max}) for freshwater fish (Randall and Minns 2000):

$$r_{max} = 2.64{W_{mat}}^{-0.35}. \qquad \text{(A5)}$$

Where W_{mat} is weight at age-of-maturity and $\lambda = e^{r_{max}}$. Weight was estimated from length using the length-weight regression ($W = aL^b$). If the regression coefficient were unavailable, mean values from species-specific prior distributions were used (Froese et al. 2014). To ensure realistic levels of population growth a maximum value of 2.5 was imposed for a booming population.

Marine Fishes

Unknown vital rates were estimated in the same manner as freshwater fishes.

The λ for booming populations were estimated from a relationship predicting the intrinsic rate of increase (r_{max}) for marine fishes (Hutchings et al. 2012):

$$r_{max} = 0.925 {W_{mat}}^{-0.102}. \quad \text{(A6)}$$

Sharks and Skates

Adult survival was available for all but one COSEWIC-assessed species (bluntnose sixgill shark) for which a cross species average was used. Juvenile survival was assumed to equal adult survival. YOY survival was solved for such that the population would experience λ = 1.

Estimates of species-specific r_{max} were available from literature reports.

Marine Mammals

Stage-specific survival rates were unknown for several marine mammal species. Adult survival rates were assigned following Taylor et al. (2007) where default survival rates were based on longevity:

$$\sigma_a = \begin{cases} 0.986 \; if \; T_{max} \geq 60 \\ 0.960 \; if \; 50 \leq T_{max} < 60. \\ 0.950 \; if \; T_{max} < 50 \end{cases} \quad \text{(A7)}$$

Juvenile survival was estimated by fitting a linear relationship between known adult and juvenile survival rates:

$$\sigma_j = 1.57\sigma_a - 0.5664 \; (n = 6; r^2 = 0.86; p = 0.008) \; . \quad \text{(A8)}$$

Calf survival, σ_0, was again solved for such that the matrix model resulted in a $\lambda = 1$.

Population growth rates for booming populations were determined by species type. Cetacean r_{max} was set to 0.04 and seal r_{max} was 0.12 (Wade 1998). Maximum growth rates for other species such as sea otter and walrus were taken from the literature.

Freshwater Mussels

Freshwater mussels represented the most data-limited taxa included in the analysis with many parameters requiring estimation for several species. Longevity can be estimated as a function of maximum length (Haag 2012):

$$T_{max} = 0.643 {L_{max}}^{0.815}. \quad \text{(A9)}$$

Both longevity and age-at-maturity can be estimated as a function of the von Bertalanffy growth coefficient, k (Haag 2012):

$$T_{max} = 4.735k^{-0.0941}, \quad \text{(A10)}$$

$$T_{mat} = 0.690k^{-1.031}. \quad \text{(A11)}$$

Inserting equation A10 into A11 allows age-at-maturity to be estimated as a function of longevity:

$$T_{mat} = 0.126 {T_{max}}^{1.096}. \quad \text{(A12)}$$

Mean annual fecundity can be estimated from adult length (Haag 2013):

$$f = e^{-0.672} {L_a}^{3.146}. \quad \text{(A13)}$$

Adult instantaneous mortality is related to longevity (Haag 2012):

$$M_a = 4.171 T_{max}^{-1.070}, \qquad \text{(A14)}$$

and juvenile survival can be predicted from adult survival (fit to data from Haag 2012):

$$S_j = 0.952 S_a - 0.0566 \; (n = 11; r^2 = 0.61; p = 0.005). \qquad \text{(A15)}$$

Maximum population growth rate of freshwater mussels is unknown. Due to their high fecundity, the potential exists for a relatively high rate of population growth similar to marine fishes. We therefore chose 1.4 as a potential maximum applied across species.

Marine Turtles

Only two species of marine turtles have been COSEWIC-assessed as Special Concern, Threatened, or Endangered: loggerhead and leatherback turtles. Species-specific data were available to parameterize the matrix model. YOY survival was solved for such that the population would experience $\lambda = 1$.

Maximum population growth rate was assumed to be 1.1 (Warden et al 2017).

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