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Quantitative methods for analysing cumulative effects on fish migration success: a review

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It is often recognized, but seldom addressed, that a quantitative assessment of the cumulative effects, both additive and non-additive, of multiple stressors on fish survival would provide a more realistic representation of the factors that influence fish migration. This review presents a compilation of analytical methods applied to a well-studied fish migration, a more general review of quantitative multivariable methods, and a synthesis on how to apply new analytical techniques in fish migration studies. A compilation of adult migration papers from Fraser River sockeye salmon *Oncorhynchus nerka* revealed a limited number of multivariable methods being applied and the sub-optimal reliance on univariable methods for multivariable problems. The literature review of fisheries science, general biology and medicine identified a large number of alternative methods for dealing with cumulative effects, with a limited number of techniques being used in fish migration studies. An evaluation of the different methods revealed that certain classes of multivariable analyses will probably prove useful in future assessments of cumulative effects on fish migration. This overview and evaluation of quantitative methods gathered from the disparate fields should serve as a primer for anyone seeking to quantify cumulative effects on fish migration survival.

Key words: antagonistic; cumulative impacts; multivariable; non-additive; synergistic.

INTRODUCTION

Migrating fishes are exposed to a myriad of biological (*e.g.* pathogens and predators) and physical (*e.g.* extreme temperatures, flows and currents) stressors that can reduce their *en route* survival. Because fish migrations tend to be cyclical and predictable in both timing and location (Lucas & Baras, 2001), fisheries exploit such patterns, which creates additional challenges (*e.g.* gear and boat avoidance behaviours, stress from capture and release on non-target species) for migratory individuals (Froese & Torres, 1999; McDowall, 1999). When exposed to a stressor, fishes respond in a rather predictable manner with the elevation of circulating glucocorticoid concentrations (the primary response), which leads to a suite of adaptive physiological

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and behavioural changes (secondary and tertiary) that should increase the chance of overcoming the stressor in the short term (Mazeaud *et al.*, 1977). When stressors persist (*i.e.* become chronic), the biological responses in fishes become detrimental (Barton, 2002).

Complicating matters is the fact that exposure to multiple stressors sometimes create combined effects that can alter survival during activities such as migration (Crain *et al.*, 2008). The combined effect of multiple stressors is commonly referred to as a cumulative effect (Crain *et al.*, 2008) and is here considered synonymous with cumulative impact. Two or more stressors can combine to produce the following three general outcomes: (1) additive, the combined effect is the simple sum of the individual stressors, (2) synergistic, the combined effect is greater than the sum of the individual stressors and (3) antagonistic, the combined effect is less than the sum of the individual stressors (Folt *et al.*, 1999; Crain *et al.*, 2008). For migrating fishes, cumulative effects can include both the combined effect of a single stressor repeatedly applied over time (repeated interactions with fishing gear or predators during a migration), and the combined effect of multiple stressors applied simultaneously or at different points in space or time (*e.g.* fisheries interactions combined with a high-flow event and cold shock), that affect fish survival or a surrogate of survival (*e.g.* fish health). The above is an inclusive description of cumulative effects, but this review will focus on examining different quantitative methods for assessing the combined effect of multiple stressors that are relevant to fish migration studies.

Fraser River sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) are a well-studied aggregate population of anadromous fish, which migrate every year from the ocean to their freshwater spawning grounds to reproduce and then die (Burgner, 1991). Extensive research has demonstrated that exposure to adverse physical conditions (*e.g.* high water temperature) and biological factors (*e.g.* pathogens) during spawning migration can lead to premature mortality, either *en route* to the spawning ground or at the spawning grounds (Cooke *et al.*, 2008). Even within a system with well-documented multiple stressors, however, the majority of research has focused on relationships between *O. nerka* migration success and exposure to only one or two stressors (*e.g.* high temperature and discharge). As the number of identified stressors and factors that mediate the stress response grows, the need for adequate methods to assess the cumulative effects of stressors on migration success for *O. nerka* and other migratory fishes becomes more pressing. Addressing this methodology gap for assessing cumulative effects will be crucial for future management and viability of fish populations, especially due to the anticipated changes to the biological and physical stressors associated with further human development and climate change (IPCC, 2007; USEPA, 2007).

The ability to quantify cumulative effects relies on both a good study and on different multivariable methods (not to be mistaken for multivariate methods, which involves the analysis of multiple outcomes or responses) available for analysing the combined effects of two or more predictor variables on a single response. Simply quantifying the cumulative effect, however, is not always sufficient for fish migration research. In practice, researchers may need to better understand how two or more variables combine (additive, synergistic or antagonistic) to influence survival. Furthermore, multivariable methods are not all equal in dealing with the types of relationships among predictor and response variables. Currently no clear approach or guideline exists on which method to use in order to best quantify cumulative effects.

Towards achieving that goal, this review represents the following: (1) a compilation of what is currently being applied within a single well-studied fish migration system, with an emphasis on the identification of areas where the application of multivariable statistical approaches could be improved or expanded, (2) a review of other potentially useful multivariable methods that are available from the fisheries science, biological and medical realms and (3) a synthesis of both the compilation and review with recommendations on how to apply multivariable methods to study cumulative effects on fish migration success. This overview and evaluation of quantitative methods gathered from a diverse range of scientific fields should serve as a primer for anyone seeking to quantify cumulative effects of multiple variables to fish migration success. Indeed, this framework could also be applied to other migratory animals.

COMPILATION OF MULTIVARIABLE PAPERS ON FRASER RIVER *ONCORHYNCHUS NERKA*

BACKGROUND

Fraser River *O. nerka* comprise several hundred distinct spawning populations experiencing differences in migration timing (July to November), distances (50–1150 km), elevation (10–1000 m) and thermal conditions (4–22° C) (Burgner, 1991). Therefore, population differences in physiology, behaviour and morphology, such as thermal tolerance, energy use, swim strategies and body shape are thought to be local adaptations in response to migratory stressors (Crossin *et al*., 2004*a*; Eliason *et al*., 2011). Even within a population, individual variability in response to changing migratory stressors will probably drive the future evolution of these populations (Reed *et al*., 2011). Numerous studies have examined the effects of multiple variables on migration success of Fraser River *O. nerka* and this relatively large body of research now offers an excellent opportunity for assessing several, commonly used, multivariable statistical methods. The lessons learned from this comparatively well-studied system (Hinch *et al*., 2005) on the current ability to quantify the effects of multiple variables are probably exportable to other fish migration studies, or even to studies of other taxa.

COMPILATION METHODS

Research articles were compiled using an internal Fisheries and Oceans Canada (*i.e.* DFO; the federal science-based government agency responsible for fisheries research and management) database that has kept track of Fraser River *O. nerka* publications (accessed by D. A. P. in September 2011). Papers published since 1990 that focused on upstream spawning migration and had a minimum of two predictor variables (continuous or categorical) used to describe a migratory stress response were selected. These papers included examples where more than one predictor variable was a migratory stressor (*e.g.* temperature and pathogens), and examples of where a single stressor was analysed along with other non-stress factors (*e.g.* stock and sex). Both types of examples were assumed to showcase multivariable statistical methods that could be used to study cumulative effects. The response could either be lethal or involve sub-lethal outcomes. Sub-lethal outcomes that could potentially affect fish migration success were categorized as physiological (including a variety of disease states and health conditions) or behavioural responses. The specific focus of this compilation was on the range of quantitative methods currently being applied and to determine the range and type of different predictors and response variables being used.

COMPILATION RESULTS

A total 56 papers dealing with multiple predictor variables related to spawning migration success in Fraser River *O. nerka* from 1990 to 2011 were found (Table I). There were a total of five different multivariable statistical methods used (see Table II for brief description). The majority of papers presenting multivariable analyses applied multifactor analysis of variance (MFANOVA) (Table I and Fig. 1). A few articles used multiple linear regression (MLR), a generalized linear model (GLM), non-linear regression (NLR) or survival analysis (SA) to address migration success (Table I and Fig. 1).

Interestingly, not all of the papers used traditional analyses (Table I). In several cases unique simulation type models were built to describe the relationship between two or more variables. This included very system-specific simulation models that were constructed based on known relationships and interactions between stressors (Hague *et al*., 2011; Reed *et al*., 2011). Several articles also used ordination methods for both variable reduction (*e.g.* principle component analysis; Macdonald *et al*., 2010) and visual interpretation of multivariable interactions (non-metric multi-dimensional scaling; Cooperman *et al*., 2010). Another approach included categorical data analysis techniques, such as the contingency χ^2 or Fisher's exact test (Roscoe *et al*., 2011). Ordination methods encountered, however, were not used as multivariable models of cumulative effects, and simulation models were not readily adaptable to other systems, therefore neither approach was included in subsequent discussions.

Over one third of all papers in the database applied non-multivariable approaches (Table I). Many of these papers chose a series of univariable analyses to describe or infer the individual effect of two or more variables separately. These univariable methods included *t*-tests, one-way ANOVAs, simple linear regressions, and correlation analyses (Table I).

Twenty-two of the papers dealt directly with mortality, 20 papers dealt exclusively with sub-lethal responses, and 19 papers reported on both sub-lethal responses and mortality (Table I). Only 16 papers dealt with sub-lethal effects on behaviour compared to 27 papers dealing with physiological responses. The behavioural end points focused on changes in timing (Cooperman *et al*., 2010), migration rate (Hanson *et al*., 2008), or holding behaviour (Mathes *et al*., 2010). The physiological responses were more variable and included energy use, cardio-vascular performance, disease, osmoregulation, reproduction and general stress response. For most of the physiological response variables used, a biological rationale was provided for how the sub-lethal effect related to overall survival during migration, although in some cases such links are speculative and tenuous.

For the two most common physical predictor variables used, water temperature and discharge (Table I), there were examples applied to describe a direct effect on survival, and sub-lethal effects on behaviour and physiology. The biological predictors spanned the range of biological organization levels and include the following

TABLE I. Classification of all *Oncorhynchus nerka* papers found within the Fisheries and Oceans Canada (DFO) database

Model	Physical predictor	Biological predictor	Response variables			Reference
MFANOVA	Discharge	Activity, heart rate, sex			P	Clark *et al.* (2010)
MFANOVA	Handling	Physiology, stock, sex	L	B		Cooke *et al.* (2005)
MFANOVA		Stock, physiology	L			Cooke *et al.* (2006*b*)
MFANOVA		Timing, sex, stock			P	Cooke *et al.* (2008)
MFANOVA		Physiology, stock, sex	L	B		Crossin *et al.* (2007)
MFANOVA	Temperature	Sex	L	B	P	Crossin *et al.* (2008)
MFANOVA		Stock, sex, physiology	L	B		Crossin *et al.* (2009*a*)
MFANOVA		Stock, sex, physiology, timing	L	B	P	Crossin *et al.* (2009*b*)
MFANOVA		Physiology, sex, timing	L	B		Donaldson *et al.* (2010)
MFANOVA	Year, location	Sex		B		Hinch & Rand (1998)
MFANOVA		Osmoregulation, timing	L			Jeffries *et al.* (2011)
MFANOVA	Temperature	Sex, timing, holding	L		P	Mathes *et al.* (2010)
MFANOVA	Discharge	Handling			P	Pon *et al.* (2009*a*)
MFANOVA	Location, handling	Sex	L	B	P	Roscoe *et al.* (2011)
MFANOVA	Location, discharge	Stock			P	Shrimpton *et al.* (2005)
MFANOVA	Temperature	Behaviour	L	B	P	Steinhausen *et al.* (2008)
MFANOVA	Temperature	Pathogens	L		P	Wagner *et al.* (2005)
MFANOVA	Salinity	Activity			P	Wagner *et al.* (2006)
MLR	Temperature, discharge	Abundance, timing	L			Gilhousen (1990)
MLR, MFANOVA	Temperature	Stock, sex, physiology		B		Hanson *et al.* (2008)
MLR, PCA	Discharge, temperature	Abundance, stock, timing	L			Macdonald *et al.* (2010)
MLR, GLM	Temperature			B		Roscoe *et al.* (2010)
GLM	Temperature, location, year		L			Martins *et al.* (2011)
GLM	Temperature, location	Stock	L			Martins *et al.* (2012)
GLM, NLR	Year	Timing, sex	L			Bradford *et al.* (2010*b*)
GLM, MFANOVA		Physiology, pathogens	L		P	Bradford *et al.* (2010*a*)
GLM, MFANOVA	Discharge, handling	Sex, physiology	L		P	Patterson *et al.* (2004)
NLR	Temperature, discharge				P	Rand *et al.* (2006)
SA		Genomics, stock, sex	L			Miller *et al.* (2011)

TABLE I. Continued

Model	Physical predictor	Biological predictor	Response variables			Reference
SA	Discharge	Sex	L			Nadeau *et al*. (2010)
Simulation models	Temperature	Stock	L			Hague *et al*. (2011)
Simulation models	Location, discharge	Activity			P	Hinch *et al*. (1996)
Simulation models	Discharge, temperature		L	B		Reed *et al*. (2011)
Non-multivariable	Temperature	Energy, timing, physiology	L	B		Cooke *et al*. (2004*a*)
Non-multivariable		Physiology, energetics	L			Cooke *et al*. (2006*a*)
Non-multivariable		Physiology, energetics	L			Cooke *et al*. (2009)
Non-multivariable		Physiology	L	B	P	Cooperman *et al*. (2010)
Non-multivariable	Year, SST, NPI	Stock, L_s			P	Crossin *et al*. (2004*b*)
Non-multivariable	Location	Stock			P	Crossin *et al*. (2004*a*)
Non-multivariable	Location, discharge	Migration rate, stock, timing		B		Donaldson *et al*. (2009)
Non-multivariable		Handling	L	B	P	Donaldson *et al*. (2011)
Non-multivariable	Temperature	Timing, stock, physiology			P	Eliason *et al*. (2011)
Non-multivariable	Temperature	Stock, physiology	L			Farrell *et al*. (2008)
Non-multivariable	Discharge	Swim behaviour	L			Hinch & Bratty (2000)
Non-multivariable	Discharge	Stock		B		Hinch & Rand (2000)
Non-multivariable		Stress, sex, timing			P	Hruska *et al*. (2010)
Non-multivariable		Longevity, timing, size	L			Hruska *et al*. (2011)
Non-multivariable	Location	Stock			P	Kelly *et al*. (2011)
Non-multivariable	Temperature	Stock			P	Lee *et al*. (2003*a*)
Non-multivariable	Temperature	Stock			P	Lee *et al*. (2003*b*)
Non-multivariable	Temperature, discharge		L	B		Macdonald (2000)
Non-multivariable	Temperature, discharge	Disease	L	B	P	Macdonald *et al*. (2000)
Non-multivariable	Temperature, discharge		L			Macdonald *et al*. (2007)
Non-multivariable	Temperature	Species			P	MacNutt *et al*. (2006)
Non-multivariable		Behaviour, physiology	L			Pon *et al*. (2009*b*)
Non-multivariable		Behaviour, physiology	L			Young *et al*. (2006)

MFANOVA, multifactor analysis of variance; MLR, multiple linear regression; PCA, principal component analysis; GLM, generalized linear model; SA, survival analysis; NLR, non-linear regression; L lethal; B, behaviour; P, physiology; NPI, North Pacific Index; SST, sea surface temperature; L_s, standard length.

TABLE II. Model classifications along with descriptions and examples of appropriate routines in R statistical software (www.r-project.org) and references that can act as an initial guide for choosing between different techniques. Models are ordered in the list according to their classifications

Model	Numerical or categorical response variable	Non-linear relationships must be specified in the modelling process	Interactions must be specified in the modelling process	Parametric, non-parametric or semi-parametric technique	Description	R package guide	Reference for fish migration (**) and fishes	Reference or texts for method details
BAT	Either	No	No	Non-parametric	Creates multiple bootstrapped classification and regression trees and then averages the results.	ipred	Knudby *et al.* (2010)	Breiman (1996), De'ath (2007), Prasad *et al.* (2006)
RF	Either	No	No	Non-parametric	Similar to BATs except a random set of predictor variables are used to build each tree.	randomForest	Knudby *et al.* (2010)	Breiman (2001), De'ath (2007), Prasad *et al.* (2006)
BOT	Either	No	No	Non-parametric	A sequence of simple classification and regression trees where each tree improves prediction ability	gbm	Elith *et al.* (2008), Leathwick *et al.* (2006*a*), Leathwick *et al.* (2008)	De'ath (2007), Moisen *et al.* (2006), Sutton (2005)
MARS	Either	No	No	Semi-parametric	Partitions data-space into regions then fits a regression line to each region.	earth	Elith & Leathwick (2007), Leathwick *et al.* (2005), Leathwick *et al.* (2006*b*)	Friedman (1991), Hill & Lewicki (2007), Prasad *et al.* (2006)
ANN	Either	No	No	Non-parametric	Complex, predictive modelling technique inspired by the neural architecture of the brain.	neuralnet	Olden & Jackson (2001), Palialexis *et al.* (2011)	Carling (1992), Gutierez-Estrada *et al.* (2009), Hill & Lewicki (2007)

TABLE II. Continued

Model	Numerical or categorical response variable	Non-linear relationships must be specified in the modelling process	Interactions must be specified in the modelling process	Parametric, non-parametric or semi-parametric technique	Description	R package guide	Reference for fish migration (**) and fishes	Reference or texts for methods in detail
CART	Categorical	No	No	Non-parametric	A method for determining a set of decision rules about how different predictor variables influence a response variable.	tree & rpart	**Ostergren *et al*. (2011), Ruppert *et al*. (2010), Vignon & Sasal (2010)	De'ath & Fabricious (2000), Harrell (2001), Prasad *et al*. (2006)
CLA	Categorical	No	No	Non-parametric	Can be used to classify a response based on values of predictors.	stats or cluster	Grossman *et al*. (1998), Hinz *et al*. (2009)	Everitt *et al*. (2011), Hill & Lewicki (2007), Romesburg (2004)
SVM	Categorical	No	No	Non-parametric	Projects the predictors into higher dimensional space to find a linear classifier.	e1071	Knudby *et al*. (2010)	Hastie *et al*. (2009), Hill & Lewicki (2007), Moguerza & Munoz (2006)
GLM	Categorical	Yes	Yes	Parametric	Similar to MLR except predictor variables are linearly related to the expected value of a response through a link function.	glm() function	**Bradford *et al*. (2010*a*), Cheng & Gallinat (2004), Martins *et al*. (2011)	Harrell (2001), Hill & Lewicki (2007), McCullagh & Nelder (1989)
GAM	Numerical	Yes	Yes	Semi-parametric	Similar to a GLM except that unspecified functions relate the predictor variables to the expected value of a response.	mgcv	Leathwick *et al*. (2006*b*), Knudby *et al*. (2010), Stoner *et al*. (2001)	Hastie & Tibshirani (1990), Hastie *et al*. (2009), Hill & Lewicki (2007)

TABLE II. Continued

Model	Numerical or categorical response variable	Non-linear relationships must be specified in the modelling process	Interactions must be specified in the modelling process	Parametric, non-parametric or semi-parametric technique	Description	R package guide	Reference for fish migration (**) and fishes	Reference or texts for methods in detail
SA	Numerical	Yes	Yes	All types exist	Suite of methods which model time until an event (e.g. mortality).	survival	**Miller *et al*. (2011), Nadeau *et al*. (2010), **Zabel *et al*. (2006)	Allison (2010), Harrell (2001), Hill & Lewicki (2007)
NLR	Numerical	Yes	Yes	Parametric	Similar to MLR except predictor variables are non-linearly related to the response variable through a known function.	nls() function	**Bradford *et al*. (2010*b*), Laetz *et al*. (2009)	Hill & Lewicki (2007), Huet *et al*. (1996), Smyth (2002)
GWR	Numerical	Yes (inadequate at modelling non-linearities)	Yes	Parametric	An extension of MLR used when model parameters are not constant over the spatial extent of study.	spgwr		Austin (2007), Foody (2004), Fotheringham *et al*. (1998)
SEM	Numerical	Yes (functional relationships assumed to be linear)	Yes	Parametric	A form of pathway analysis which analyses the magnitude of direct and indirect relationships between variables.	sem		Austin (2007), Grace (2008), Palmores *et al*. (1998)
QR	Numerical	Yes	Yes	Parametric	Form of MLR which estimates the median or other quantiles of the response variable.	quantreg	Cade & Noon (2003), Dunham *et al*. (2002)	Austin (2007), Koenker & Basset (1978), Koenker & Hallock (2001)

TABLE II. Continued

Model	Numerical or categorical response variable	Non-linear relationships must be specified in the modelling process	Interactions must be specified in the modelling process	Parametric, non-parametric or semi-parametric technique	Description	R package guide	Reference for fish migration (**) and fishes	Reference or texts for methods in detail
MLR	Numerical	Yes	Yes	Parametric	Models the relationship between two or more predictor variables and a response variable by fitting a linear equation to observed data.	lm() function	**Gilhousen (1990), **Hanson *et al.* (2008), **MacDonald *et al.* (2010)	Harrell (2001), Hill & Lewicki (2007), Zar (1984)
MFANOVA	Numerical	Yes	Yes	Parametric	Assesses the average contribution (main effect) of a few predictors and interactions between variables to the overall mean of a response.	aov() function	Blake & Duffy (2010), Clarieaux & Lagardere (1999), Ginot *et al.* (2006)	Hill & Lewicki (2007); Roberts & Russo (1999), Zar (1984)

MFANOVA, multifactor analysis of variance; MLR, multiple linear regression; QR, quantile regression; SA, survival analysis; GLM, generalized linear model; GAM, generalized additive model; NLR, non-linear regression; MARS, multivariate adaptive regression splines; CART, classification & regression trees; BAT, bagging tree; BOT, boosted tree; RF, random forest; CLA, cluster analysis; ANN, artificial neural network; GWR, geographically weighted regression; SEM, structural equation modelling.

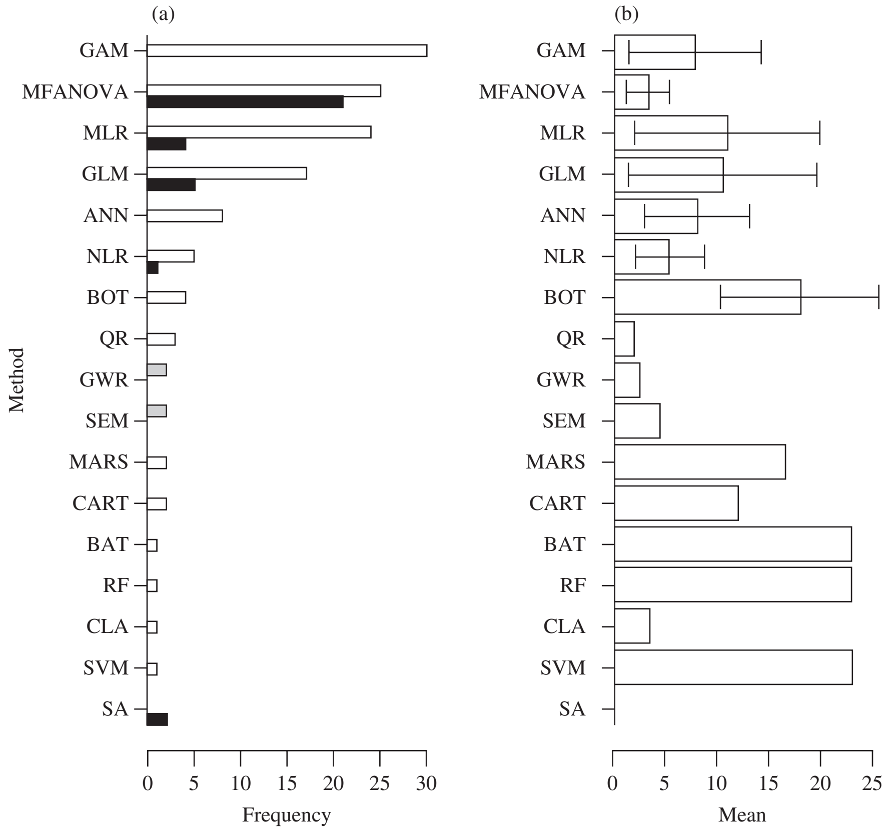

FIG. 1. (a) Frequency distribution for multivariable methods used within the Fraser River *Oncorhynchus nerka* literature (■), fisheries literature (□) and other biological science literature (▩) along with (b) mean ± S.D. for number of predictors used in the fisheries and other biological science literature. MFANOVA, multifactor analysis of variance; MLR, multiple linear regression; QR, quantile regression; SA, survival analysis; GLM, generalized linear model; GAM, generalized additive model; NLR, non-linear regression; MARS, multivariate adaptive regression splines; CART, classification & regression trees; BAT, bagging tree; BOT, boosted tree; RF, random forest; CLA, cluster analysis; ANN, artificial neural network; GWR, geographically weighted regression; SEM, structural equation modelling.

examples; fish abundance (Macdonald *et al*., 2010), aerobic performance (Hague *et al*., 2011), energy density (Rand *et al*., 2006), pathogen presence (Wagner *et al*., 2005), ion levels (Bradford *et al*., 2010*a*; Jeffries *et al*., 2011), and transcriptional gene expression (Miller *et al*., 2011).

REVIEW: QUANTITATIVE METHODS APPLIED WITHIN FISHERIES SCIENCES

REVIEW BACKGROUND

The three most intriguing results from the search of multivariable papers dealing with Fraser River *O. nerka* migration were the ubiquitous use of MFANOVAs, the limited number of multivariable methods used, and the non-ideal application of univariable techniques to deal with multivariable issues. These areas clearly speak to the need to review and consider adopting alternative and in some cases more appropriate quantitative methods for dealing with multivariable problems. This stimulated the need to review the fisheries, biological and medical literature to look for other multivariable methods being used to investigate cumulative effects.

REVIEW METHODS

Fisheries science

The main purpose of this key-word based, systematic literature search was to find additional multivariable methods that could be used to assess cumulative effects on *O. nerka* and other migratory fishes. In order to reduce the large number of articles available for review and also to ensure that techniques were suitable for analysing cumulative effects to fish migration success, the search was restricted to articles from fisheries science literature analysing effects on fishes. Two search engines, the ISI Web of Knowledge (WOK) and Aquatic Sciences and Fisheries Abstracts (ASFA), were used and included articles published from 1900 to August 2011.

A large number of article titles, abstracts or texts contain words like ‘cumulative’ or ‘fish’, therefore the search was restricted to identify articles which contained at least four keywords from the following three groupings: (fish or fishes) AND (statistic* or quantitative or math* or multivar* or numerical) AND [(cumulative or synergy* or additive or non-additive or antagonistic or interaction) SAME (impact* or effect* or stress* or pressure* or result* or consequence* or outcome* or response*)]. The Boolean operator ‘SAME’ denotes that a keyword from each subgroup must be identified in the same sentence within an article’s title, keywords or abstract. Hence, one keyword was required from the first two groups and two keywords were required from the third group. In the ASFA search, the operator ‘NEAR’ was used instead of SAME to yield similar results. The ASFA search was further restricted so that words from the second and third groupings were required within the abstracts of papers returned. Furthermore, the WOK search was restricted to only identify articles found within the Web of Science (WOS) online database pertaining to Fisheries Science, Ecology, Oceanography, Marine and Freshwater Biology and Environmental Science categories.

After these criteria were imposed, over 900 articles remained and were added to a database. All duplicate articles and those that did not use quantitative, multivariable techniques to analyse fish responses were removed from the database.

Non-fisheries literature

Fisheries-based literature contains a variety of different studies using multivariable techniques. Other methods not common to fisheries sciences, hereafter described as novel methods, however, might be found within research journals of other disciplines. Therefore, two searches were conducted using the WOK to find methods uncommon in fisheries research.

The first search looked for methods used in general biology and was restricted to identify scientific journal articles published from January 2007 to August 2011 which contained at least three keywords from the following two groupings: (statistic* or quantitative or math* or multivaria* or numerical) AND [(cumulative or synergy* or additive or non-additive or antagonistic or interaction) SAME (effect* or stress* or pressure* or result* or consequence* or outcome* or response*)]. The search was further refined to identify only articles from the WOS in the fields of Ecology and Biology; however, this restriction still identified >2200 different papers. Hence a random sample of 150 papers from the 2200 was examined.

Another expectation was that the field of medicine would contain a wealth of literature using novel techniques to assess cumulative effects uncommon to any ecological or biological science. A second search was conducted using the MEDLINE database for articles published from January 2007 to August 2011 using the same keyword groupings as in the above search through biological sciences. Again, these search criteria returned thousands of papers, so a random sample of 150 papers was examined from these search results.

Each multivariable method found within the various searches was classified based on the following categories: categorical and numerical (*i.e.* continuous or discrete) response variables; whether or not a researcher needs to specify or test for non-linearities and interactions in the modelling process; and whether a model type is parametric, non-parametric or semi-parametric (*i.e.* having both parametric and non-parametric components). Methods that do not require researchers to test for or specify how non-linearities and interactions are included in a model are especially useful when modelling a large number of variables with potentially complex relationships.

A number of papers identified in the literature searches mentioned the use of novel quantitative methods but failed to describe that method with sufficient detail. Therefore reference sections and statistical textbooks were searched to locate more comprehensive descriptions of each method and examples of usage within fisheries sciences. Several of these references, along with short descriptions of each method are provided to assist in reader comprehension. Additionally, some examples of functions or packages with free R statistical software (www.r-project.org) that can be used to perform each method are provided.

REVIEW RESULTS

The systematic search of fisheries science literature identified 88 articles that used multivariable methods to study fishes (Appendix) and 14 distinct multivariable methods (Fig. 1). Only two of these articles using two distinct methods (MLR and GLMs) analysed fish migration success. Ten of the 14 methods identified were not applied to study Fraser River *O. nerka* (Fig. 1) and 42 out of 87 articles found in this literature search used at least one of these 10 methods (Appendix). The majority of articles that applied these 10 techniques, with the exception of those using generalized additive models (GAM), artificial neural networks (ANN) and cluster analysis (CLA), were published after the year 2005. The most common technique used for analysing effects of multiple variables within these articles was GAMs (30 papers), followed by MFANOVA (25 papers), MLR (24 papers) and then GLMs (17 papers) (Fig. 1). The number of predictor variables used in conjunction with GAMs, MLR, GLMs, ANNs NLR and BOTs varied throughout the literature while MFANOVA studies typically used the fewest predictors (Fig. 1). Other methods were used too infrequently in studies to get any real sense of the range of number of predictor variables used.

The search using a random sample of 150 papers in general biology found an additional three papers that discussed two unique methods not found within the searches of fisheries science literature. These methods were structural equation modelling (SEM) and geographically weighted regression (GWR). No unique methods examining cumulative effects were found in the search of 150 randomly selected medical papers.

Overall, the search through DFO's database, fisheries science and biological literature yielded a total of 17 different multivariable methods that could be used to assess cumulative effects on fish migration success (Table II). Five techniques are able to model either numerical or categorical response variables, eight can only model numerical responses and four can model only categorical response (Table II). Eight techniques do not require a researcher to specify non-linearities and interactions (Table II). Seven methods were parametric, seven were non-parametric, two techniques are considered semi-parametric and one (SA) has all three forms (Table II).

DISCUSSION

The compilation using the Fraser River *O. nerka* system identified only a few multivariable methods that could be used in analyses of cumulative effects on fish migration. The widespread use of MFANOVAs for multivariable analyses possibly reflects their appealing simplicity and robustness as well as easy implementation within various readily available statistical software packages. MFANOVAs are not suited to dealing with large numbers of predictor variables (Ginot *et al.*, 2006) and their extensive use is also probably related to the fact that Fraser River *O. nerka* migration studies have typically analysed the effects of only a few predictor variables. While the use of MFANOVA may have been justified in these cases by specific study limitations or goals, researchers wishing to study cumulative effects using a much broader set of predictor variables should consider using more suitable techniques.

Only a few studies analysed survival using GLMs (*i.e.* logistic regression) or survival analysis techniques, despite the interest in the effects of multiple stressors on migration success of Fraser River *O. nerka*. For example, survival data were usually analysed with χ^2-type tests (Mathes *et al.*, 2010; Roscoe *et al.*, 2011) or used as a categorical predictor to compare the physiology of fish that were successful or failed on their migration (Crossin *et al.*, 2009*a*; Donaldson *et al.*, 2010). These approaches are useful for comparing characteristics between successful and unsuccessful fish, but they cannot be used for predicting survival and elucidating how the odds of survival vary with changes in stressors and underlying physiology. Miller *et al.* (2011) provides an example of using survival analysis to both discriminate the physiologies amongst fate groups as well as calculate the odds of survival as a function of the underlying gene expression patterns.

Another interesting observation in the Fraser River *O. nerka* literature was the common application of several univariable tests to problems that could be dealt with using multivariable techniques (Pon *et al.*, 2009*b*; Hruska *et al.*, 2010). While the application of univariable procedures may have been justified by limitations or the research goals for each of these studies, these authors missed the opportunity to determine how a predictor variable influences the response in the presence of another explanatory variable and whether these variables interact with one another to produce synergistic or antagonistic effects (Kaplan, 2009). Future research should therefore avoid using univariable methods when multivariable approaches are an option in order to improve understanding of cumulative effects.

The breadth of potential relationships between biophysical factors and migratory success at different levels of biological organization that have been explored in Fraser River *O. nerka* makes it a reasonable surrogate for studying other fish migrations. The predictor variables ranged in variety of aquatic environments from coastal marine, to large rivers and lake environments. The lethal response criteria also covered both immediate and delayed mortality associated with cumulative effects. The range of sub-lethal responses for physiology was considerably more varied than behaviour, which is probably a reflection of the difficulty in assessing fish behaviour in the wild as well as a lack of analytical techniques for characterizing fish behaviour and spatial ecology across broad spatial scales. Collectively, this information should be of benefit to other migration studies for examples of what to do and what to avoid in multivariable analysis of cumulative effects.

The search through fisheries science and biology literature yielded information on 12 multivariable techniques that have not been used to study Fraser River *O. nerka* migration success. Several reasons may explain the lack of adoption of these alternative methods within the Fraser River system and potentially elsewhere in the fish migration literature. Foremost, fish migration researchers may be unfamiliar with their use. The majority of these techniques (with the exception of GAMs and ANNs) appear to have only been applied in fields of fisheries research very recently (since 2005 in the search results) and infrequently (if at all). Therefore, techniques, such as BOTs, random forests (RF) and SVMs were possibly unknown to scientists modelling cumulative effects to *O. nerka*. Many methods, such as ANNs, GAMs and SVMs are also fairly complex and computationally intensive and past researchers may have lacked the necessary knowledge, time and computer power to run these models. These computational restrictions, however, no longer apply as all methods outlined in this review can be run quickly and easily on a standard laptop with free software packages such as R (Table II).

Finally, even in the case of such a well-studied system like Fraser River *O. nerka*, data can be sparse or limiting. Complex techniques can sometimes require large amounts of data to properly build and parameterize the model. For example, ANNs often require thousands of data cases to be trained properly (Hill & Lewicki, 2007). The adoption of more simple methods, like MFANOVAs, is understandable in situations where data are less available, and where justification for a much more complex method does not exist. These limitations, however, are becoming less restrictive with the adoption of new technologies available to researchers that can assist in data collection, information sharing and data collation. Examples of each include: recent advances in electronic tagging technologies, such as the development of miniaturized and multi-sensor tags (*i.e.* which records variables related to fish behaviour, physiology and environmental conditions) that enable researchers to collect data on migrating fishes that was unattainable in the past (Cooke *et al.*, 2004*b*, 2012); the recent development of the free, online database, Movebank (www.movebank.org), allows researchers to easily share and track animal movement data (Kranstauber *et al.*, 2001); and the push by regional, national and international science communities or governments to collate physical and biological information into large accessible databases (*e.g.* work on ecosystem management : Canadian Aquatic Biomonitoring

Network Database, www.ec.gc.ca;). Improvements to data management and accessibility in conjunction with readily available software (*i.e.* R) should facilitate the adoption of the quantitative multivariable methods techniques described in fisheries science.

The searches through the ecological and biological science literature yielded two additional multivariable techniques, SEM and GWR, whereas the search through the medical literature did not result in any additional techniques. This lack of results from the medical field was contrary to the original expectation that the medical field would contain information on a number of techniques not used in ecology or biology. A simple explanation could be that the sample of 150 papers may have been too small to capture any novel techniques being used in the field of medicine.

Each of the 12 additional techniques found within the searches are applicable to assessing cumulative effects to fish migration success. Quantile regression (QR) and GAMs each provide useful extensions of the typical MLR model. QR for example, is an alternative form of MLR that approximates the median and other quantiles of a response variable as opposed to the mean. Estimating a number of regression quantiles can potentially reveal multiple rates of change (slopes) between a predictor and response variable, therefore providing a more complete picture of how variables relate to fish migration success in the presence of ecological stressors or limiting factors (*e.g.* prey availability) (Cade & Noon, 2003). GAMs could be used to predict survival based on a number of variables in a similar manner as a GLM. Their use of non-parametric smoothers can help provide excellent fit to the data in the presence of non-linear relationships (Hill & Lewicki, 2007). The relationships modelled by GAMs, however, can be difficult to interpret, making them less useful for researchers interested in exploring potential relationships within a system (Elith *et al.*, 2008).

Non-parametric methods, such as multivariate adaptive regression splines (MARS), tree-learning methods, ANNs and SVMs and CLA all differ in terms of their underlying mechanics. Each of these methods, however, can inherently model or take into account non-linear relationships and interactions between variables to assess or predict cumulative impacts of multiple variables to fish migration (Prasad *et al.*, 2006; De'ath, 2007; Hill & Lewicki, 2007). Hence, they do not require a researcher to specify these types of relationships when building the model and are all excellent choices when a researcher needs to model a large number of predictor variables with complex relationships and interactions. SVMs, CLA and CART, however, are only useful for categorizing a response variable (Moguerza & Munoz, 2006; Hill & Lewicki, 2007). Furthermore, the relationships modelled by some of these methods (*e.g.* SVMs, CLA, RFs, BATs and ANNs) can, like GAMs, be difficult or impossible to interpret making them more suited for predictive purposes.

The first technique found in the general biology search, GWR, is a relatively new technique that allows model parameters to vary spatially (Austin, 2007) and could be applied to situations where the effects of stressors to fish survival vary across migratory locations. For example, the effects of high water temperatures to Fraser River *O. nerka* are possibly exacerbated in areas where fish cannot find thermal refugia in the form of lakes or cold tributaries (Donaldson *et al.*, 2009). GWR, however, has difficulty distinguishing between non-linear relationships and spatial non-stationarity (Austin, 2007) and is therefore not suited to modelling complex relationships between predictor and response variables. The second technique, SEM, is a form of pathway analysis that could easily be applied to problems in fisheries science. SEM provides information on the magnitude of direct and indirect relationships between variables (Palmores *et al.*, 1998). A possible application would be to help analyse how land use factors like deforestation or agricultural activity indirectly influence fish migration survival by influencing freshwater stressors like extreme water temperatures and pollution. The main problem is that functional relationships modelled in SEM are assumed to be linear and therefore is less suitable to situations involving complex relationships between variables (Austin, 2007).

Finally, a cautionary note regarding searching explicitly for papers that deal with cumulative effects and cumulative impacts. A major reason why the WOK and ASFA literature searches found no Fraser River *O. nerka* papers from the DFO database was that none of the *O. nerka* papers reviewed make specific reference to being a cumulative effects assessment. There are probably numerous papers in fisheries science or other disciplines that deal with multivariable approaches that are suitable for assessing multiple stressors in fish migration, but do not necessarily portray themselves as cumulative effects methodology. Therefore it is important in searching for examples of different methods for assessing multivariable techniques that are relevant to fish migration success, to have a sense of the potential methods available. This reinforces the importance of this review paper.

CONCLUSION

Researchers are becoming aware of the ever-increasing number of biological and environmental stressors (*e.g.* dissolved oxygen, pathogens, predators and contaminants) that could potentially affect fish migration success. As the number of potential stressors, moderating factors and interactions grows, so does the need to adopt a wider range of multivariable techniques for analysing and predicting their effects. As exemplified by this review, a number of different quantitative techniques could be used to model cumulative effects of different variables to fish migration success. With such a wide range of techniques available the best technique to use in each situation will depend on a number of factors like: availability of data, complexity of relationships between variables and the overarching goal of the research. The use of promising new methods outlined in this review (*e.g.* CART, MARS, RFs or BOTs), however, can help researchers to move past using MFANOVAs to both predict actual survival and to describe the potential cumulative effects. Therefore, while little has been done in the past to formally quantify cumulative effects to migration success of fishes, the use of newer quantitative methods, in combination with ever increasing computing power will enable researchers to gain much better insight into the cumulative effects of multiple variables to fish migration success.

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APPENDIX. List of all references found using the Web of Knowledge and Aquatic Science and Fisheries Abstracts search engines classified by multivariable method used and general class of predictor and response variables

Reference	Methods	Response classes	Predictor classes
De Raedemaecker *et al*. (2010)	MFANOVA	Habitat preference or distribution	Habitat characteristics
Del Toro-Silva *et al*. (2008)	MFANOVA	Physiology	Environmental stressors
Evans & Neff (2009)	MFANOVA	Physiology	Genetics
Ginot *et al*. (2006)	MFANOVA	Survival, demographics	Biological stressors
Growns *et al*. (2006)	MFANOVA	Assemblage or community structure	Spatial and temporal variables
Locham *et al*. (2010)	MFANOVA	Assemblage or community structure	Habitat characteristics
Mairesse *et al*. (2007)	MFANOVA	Physiology	Behaviour, stocking biomass
Reilly *et al*. (1992)	MFANOVA	Behaviour	Habitat characteristics, physiology
Rodd & Reznick (1997)	MFANOVA	Demographics	Environmental stressors, physiology, demographics
Slawski *et al*. (2008)	MFANOVA	Assemblage or community structure	Environmental stressors, habitat characteristics
Steele *et al*. (1998)	MFANOVA	Survival, demographics	Environmental stressors
Strecker *et al*. (2011)	MFANOVA	Physiology	Habitat characteristics, temporal and spatial variables
Trabelsi *et al*. (2011)	MFANOVA	Behaviour, survival, physiology	Environmental stressors, behaviour
Williams *et al*. (2002)	MFANOVA	Assemblage or community structure	Environmental stressors, habitat characteristics, temporal variables
Cabral *et al*. (1998)	MLR	Behaviour	Environmental stressors, habitat characteristics
Claramunt & Wahl (2000)	MLR	Physiology	Environmental stressors, habitat characteristics, temporal variables
Crozier *et al*. (2010)	MLR	Physiology	Environmental stressors
Lindegren *et al*. (2011)	MLR	Survival, demographics	Environmental stressors, survival
Maceina (1992)	MLR	Physiology	Habitat characteristics, demographics
Magnan *et al*. (1994)	MLR	Behaviour	Environmental stressors, habitat characteristics, physiology, temporal variables
Pyle *et al*. (2005)	MLR	Assemblage or community structure, physiology	Environmental stressors
Raffenberg & Parrish (2003)	MLR	Survival, physiology	Environmental stressors
Rorvik *et al*. (2003)	MLR	Survival	Biological stressors, behaviour
Stevens *et al*. (2010)	MLR	Assemblage or community structure	Environmental stressors, habitat characteristics

APPENDIX. Continued

Reference	Methods	Response classes	Predictor classes
Vadas & Orth (2001)	MLR	Habitat preference or distribution	Environmental stressors, habitat characteristics
Holbrook & Schmitt (2003)	MLR, MFANOVA	Survival	Habitat characteristics
Riginos & Nachman (2001)	MLR, MFANOVA	Genetics	Habitat characteristics, spatial variables
Seenappa & Devaraj (1995)	MLR, MFANOVA	Physiology	Physiology
Wille *et al*. (2002)	MLR, MFANOVA	Physiology	Environmental stressors, physiology
Dunham *et al*. (2002)	QR	Survival, demographics	Habitat characteristics
Planque & Buffaz (2008)	QR	Survival, demographics	Environmental stressors, habitat characteristics
De Zwart *et al*. (2006)	GLM	Survival, demographics	Environmental stressors, habitat characteristics
Goncalvez *et al*. (2008)	GLM	Behaviour	Environmental stressors
Magaud *et al*. (1997)	GLM	Survival	Environmental stressors
Malins *et al*. (2004)	GLM	Genetics	Environmental stressors
Marr *et al*. (1998)	GLM	Survival	Environmental stressors
Theriault *et al*. (2007)	GLM	Behaviour	Physiology, genetics
Tsitsika & Maravelias (2006)	GLM	Catch	Fishing characteristics, temporal variables
Young *et al*. (2010)	GLM	Habitat preference or distribution	Habitat characteristics
Galvez *et al*. (2007)	GLM, MFANOVA	Physiology	Environmental stressors
Jeschke & Strayer (2006)	GLM, MLR	Habitat preference or distribution	Human affiliation, propagule pressure, hunting, physiology
Brenden *et al*. (2007)	GAM	Assemblage or community structure	Habitat characteristics
Buission *et al*. (2008)	GAM	Habitat preference or distribution	Environmental stressors, habitat characteristics
Carol *et al*. (2006)	GAM	Assemblage or community structure	Environmental stressors, habitat characteristics
Ciannelli *et al*. (2004)	GAM	Survival	Environmental stressors, habitat characteristics
Dingsor *et al*. (2007)	GAM	Survival, demographics	Environmental stressors
Hernandez *et al*. (2009)	GAM	Habitat preference or distribution	Environmental stressors, habitat characteristics, genetics
Jowett & Davey (2007)	GAM	Habitat preference or distribution	Habitat characteristics
Kai & Marsac (2010)	GAM	Assemblage or community structure	Habitat characteristics
Katara *et al*. (2011)	GAM	Assemblage or community structure	Environmental stressors, habitat characteristics
Kupschus (2003)	GAM	Habitat preference or distribution	Environmental stressors, habitat characteristics, temporal variables

Appendix. Continued

Reference	Methods	Response classes	Predictor classes
Lorance *et al*. (2010)	GAM	Catch	Fishing characteristics, temporal variables
Swartzman *et al*. (1992)	GAM	Habitat preference or distribution	Environmental stressors, habitat characteristics
Zagaglia *et al*. (2004)	GAM	Catch	Environmental stressors, habitat characteristics
Zhang *et al*. (2010)	GAM	Survival	Environmental stressors, habitat characteristics
Auth *et al*. (2011)	GAM	Assemblage or community structure	Environmental stressors, habitat characteristics
Esteves *et al*. (2009)	GAM, MFANOVA	Physiology	Environmental stressors, habitat characteristics, physiology
Cury *et al*. (1998)	GAM, MLR	Catch	Environmental stressors
Bacheler *et al*. (2009)	GAM, GLM	Habitat preference or distribution	Environmental stressors
Cheng & Gallinat (2004)	GAM, GLM	Catch	Environmental stressors, habitat characteristics
Jobling *et al*. (2009)	GAM, GLM	Physiology	Environmental stressors
Stoner *et al*. (2001)	GAM, GLM	Habitat preference or distribution	Environmental stressors, habitat characteristics
Yee (2010)	GAM, GLM, QR	Physiology, catch	Fishing characteristics, temporal and spatial variables
Claireaux & Lagardere (1999)	NLR, MFANOVA	Physiology	Environmental stressors, habitat characteristics
Laetz *et al*. (2009)	NLR, MFANOVA	Physiology	Environmental stressors
Ayllon *et al*. (2009)	NLR, MLR	Habitat preference or distribution	Environmental stressors, habitat characteristics
Blanc (2005)	NLR, MLR, MFANOVA	Physiology	Environmental stressors, genetics
Leathwick *et al*. (2005)	MARS, GLM	Habitat preference or distribution	Environmental stressors, habitat characteristics
Leathwick *et al*. (2006*b*)	MARS, GAM	Habitat preference or distribution	Environmental stressors, habitat characteristics
Ruppert *et al*. (2010)	CART	Assemblage or community structure	Environmental stressors, habitat characteristics
Vignon & Sasal (2010)	CART	Physiology	Environmental stressors, habitat characteristics, physiology
Elith *et al*. (2008)	BOT	Habitat preference or distribution	Environmental stressors, habitat characteristics
Leathwick *et al*. (2008)	BOT	Habitat preference or distribution	Environmental stressors, habitat characteristics
Leathwick *et al*. (2006*a*)	BOT, GAM	Assemblage or community structure	Environmental stressors, habitat characteristics, fishing characteristics

APPENDIX. Continued

Reference	Methods	Response classes	Predictor classes
Grossman *et al*. (1998)	CLA, MLR	Assemblage or community structure	Environmental stressors, habitat characteristics
Diaz *et al*. (2003)	CLA, GLM	Survival, demographics	Environmental stressors, habitat characteristics, physiology
Knudby *et al*. (2010)	SVM, BOT, RF, BAT, GAM	Assemblage or community structure, survival, demographics	Environmental stressors, habitat characteristics
Brosse *et al*. (1999)	ANN	Habitat preference or distribution	Environmental stressors, habitat characteristics
Erbe & King (2009)	ANN	Behaviour	Environmental stressors
Olden & Jackson (2001)	ANN	Habitat preference or distribution, survival, demographics	Environmental stressors, habitat characteristics
Palialexis *et al*. (2011)	ANN	Habitat preference or distribution	Environmental stressors, habitat characteristics
Yanez *et al*. (2010)	ANN	Survival	Environmental stressors, habitat characteristics
Gutierrez-Estrada *et al*. (2009)	ANN, GAM, MLR	Catch	Environmental stressors, habitat characteristics
Lee *et al*. (2009)	ANN, GAM, MLR	Survival, demographics	Environmental stressors, habitat characteristics
Megrey *et al*. (2005)	ANN, GAM, NLR, MLR	Survival, demographics	Environmental stressors, habitat characteristics
Foody (2004)	GWR	Assemblage or community structure	Environmental stressors
Austin (2007)	SEM, GWR	Case studies	Case studies
Palmores *et al*. (1998)	SEM	Survival	Environmental stressors, habitat characteristics

MFANOVA, multifactor analysis of variance; MLR, multiple linear regression; QR, quantile regression; SA, survival analysis; GLM, generalized linear model; GAM, generalized additive model; NLR, non-linear regression; MARS, multivariate adaptive regression splines; CART, classification & regression trees; BAT, bagging tree; BOT, boosted tree; RF, random forest; CLA, cluster analysis; ANN, artificial neural network; GWR, geographically weighted regression; SEM, structural equation modelling.