A QUANTITATIVE REVIEW OF MARINE MORTALITY AND AN INVESTIGATION INTO OF THE EFFECT OF MIGRATION ON SOCKEYE SALMON (*ONCORHYNCHUS NERKA*)

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[redacted]

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Preface

The following report was written in two chapters as by the design of my primary thesis advisor, Dr. Scott Hinch. The first chapter explores research methods regarding the survivorship of sockeye salmon (*Oncorhynchus nerka*) though a quantitative review of the literature, while the second chapter is an analysis of morphological and reproductive changes in sockeye salmon as a result of migrations. Data in the first chapter were collected by myself though and exhaustive review of the literature. Data used in chapter 2 were provided by Charlotte Whitney which was collected as a part of their master's thesis. The examination of two topics in this paper allowed for a broader appreciation of the diversity of sockeye salmon research, which I found greatly stimulating.

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CHAPTER 1: A quantitative review of research trends regarding the marine phase of sockeye salmon (Oncorhynchus nerka): historical trends and recommendations for the future

Abstract

Marine mortality has remained a poorly understood component of Pacific salmon life-history indicating a need for the re-evaluation of research practices. 45 peer-reviewed journals were retrieved from 1965 to 2010 that addressed the topic of survivorship of sockeye salmon (*Onchorhynchus nerka*) during the marine phase of migration. To accurately describe the historical trends in research, four topics were quantified in the review: (1) the geographic location of the study, (2) the marine life stage, (3) the type of research question, and (4) the sampling level. Regional trends over the entire time series indicated British Columbia produced the most research followed closely by Alaska, Washington and Oregon, Russia and Japan. Research on the sub-adult and estuarine life stages were significantly less abundant in the literature compared to those that examined adults and coastal-migrating juveniles. All articles in the search (100%) addressed population characteristics. Morphological/physiological, abiotic, and biotic research questions were close to equally addressed in more than 50% of articles, while only 22% of articles examined abiotic factors. Most articles relied solely on population based sampling or individual based sampling with few choosing to incorporate both methods into methodology. Only 9 articles returned in the search used telemetry. Recommendations for future research include an increased attention to anthropogenic factors and pathogens affecting marine mortality, an emphasis on international collaboration, and the shifting

population research toward an interdisciplinary approach as proposed in Cooke, Hinch *et al.* (2008).

Key words

Ocean survivorship, populations, salmonids, abiotic, biotic, pathogens, climate change, telemetry

Introduction

Pacific salmon are iconic for the Pacific Northwest and yet there is very little known about the factors that influence survival during the marine phase of their migration. Pacific salmon spend the majority of their lives in the ocean; yet, historically freshwater habitat has

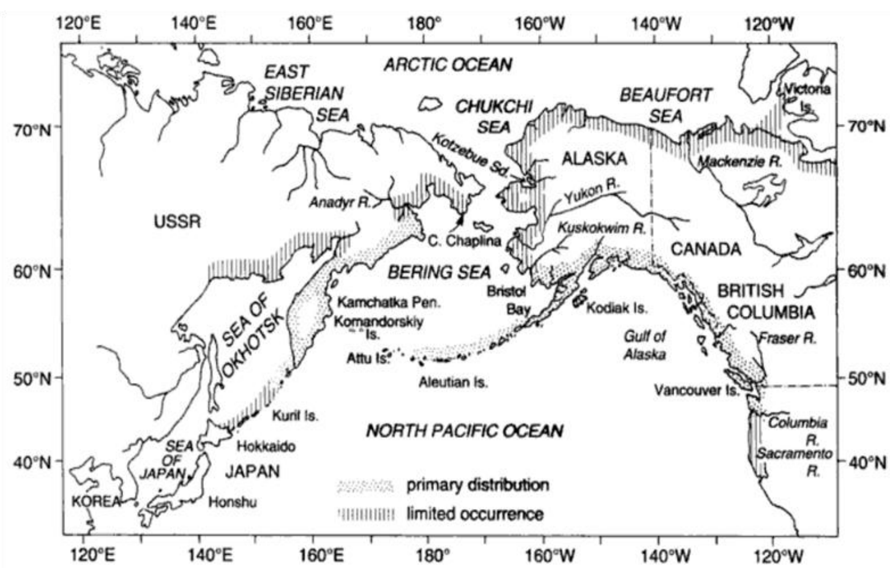


Figure 1: An image of sockeye salmon (*Oncorhynchus* nerka) spawning habitat distribution from Burgner (1991).

received the bulk of interest by researchers due to a higher and more variable mortality during the salmon lifecycle when compared to the ocean environment (Burgner 1991) and difficulties of studying the life-history of salmon during the marine phase was also much harder to undertake compared to freshwater habitat (Percy 1992). Ocean mortality, however, might not be trivial. Thorne and Ames (1987) estimated the variability of ocean survivorship was between 4-20% based on presmolt and spawner population estimates and other research has indicated the early marine stage as the largest source of mortality for juvenile salmon (Kline and Willette 2002). Questions still remain regarding the location and timing juvenile salmon experience high marine mortality as well as whether deep sea habitats are sought out as precisely as natal spawning grounds (Payne, Andrews et al. 2010).

Sockeye salmon (*Oncorhynchus nerka* Walbaum) exhibit the largest range of life-history characteristics (Hinch, Cooke et al. 2006) and are also generally well-studied due to their economic importance as a food fish. Commercially viable populations of sockeye salmon spawn in The United States, Canada, and Russia. (Burgner 1991) In North America, large numbers return to the Columbia River to as far north as the Kuskowim River in Western Alaska. On the Asian side of the Pacific Ocean, large populations of sockeye spawn on the Kamchatka Peninsula with small populations occurring as far south as Hokkaido Island, Japan. (See figure of sockeye spawner abundance) The two most productive spawning grounds in the North Pacific rim occur in the Bristol Bay watershed in Alaska and the Fraser River drainage in British Columbia, Canada. British Columbia has numerous other highly productive systems including the Skeena River, Nass River, Somass River, and the Smith inlet areas, while Alaska has the Chignik, Karuk and Copper River tributaries of the Cook Inlet. The two most productive rivers in

Russia include the Ozernaya River and the Kamchatka River, both of which lie in the Kamchatka peninsula. (Burgner 1991)

The sockeye salmon life cycle is unique compared to other anadromous salmonids as juvenile sockeye generally rear in lakes for a year before they venture to the ocean; however this is not always typical. Harrison river populations close to the ocean behave more similarly to pink salmon (*Oncorhynchus gorbuscha*) and rear in stream areas and migrate to sea soon after emergence. An extreme example of lake rearing can be observed in populations of Kokanee, which are a variant of sockeye salmon that complete their entire lifecycle in freshwater without ever visiting the sea. Ocean residency of typical sockeye can range from one to four years before they return as adults to spawn and die in their natal stream. Precision of homing instinct is more important for sockeye salmon compared to other Pacific salmon in both run timing and location of natal spawning grounds and is attributed to their specialization to lake environments. (Burgner 1991)

Although globally sockeye salmon are considered unthreatened, many populations are experiencing a decline, while the status of some populations in Russia, Alaska and BC are unknown (IUCN 2008). Rresearch has received criticism for being overly focused on models, producing "office biologists" with little physical experience with the species they study (Lichatowich 1999) The objective of the paper was to survey the types and methods of research questions that were conducted on the marine phase of sockeye salmon and then determine where gaps existed in the research. Through this understanding, recommendations for future research that addressed important oversights could be proposed.

Methods

Field based research publications that assessed the marine survival of sockeye salmon were collected from 1965-2011. Due to the number of articles it was not feasible to conduct a quantitative review examining all seven species of Pacific salmon; therefore sockeye salmon were selected due to their uniquely large range of life history characteristics and the amount research conducted. Articles returned from key terms “sockeye”, “*Oncorhyncus nerka*”, “surviv*”, “mort*”, “marine”, “ocean”, “pelagic”, “deep sea”, and “sea” were accepted or rejected based on whether they explicitly mentioned the key terms in the abstract and/or title. Articles were then only included if they contained field data. Articles that did not complete their own field collection of data, but used stock-recruitment data were included. If the abstract was not available, the paper was not included thus eliminating papers published prior to 1965 due to limitations of the electronic databases. Conference proceedings, symposiums, technical reports and books were not assessed. Relevant papers that met the criteria but did not appear in the searches with ISI and AFSA were sought out and included in the results.

Four categories evaluated: (1) the geographic location of the study, (2) the marine life stage, (3) the type of research question, and (4) the sampling level (individuals, populations, or both). Papers analyzed in the meta-analysis were scored “1” if they fit the criteria or “0” if they did not. This allowed for quantitative and qualitative analysis of the scope of research published, rather than simply a qualitative analysis characteristic of most literature reviews.

The geographic location of an article was assigned based on where the study took place. Due to Alaska’s location north of Canada and separation from Washington and Oregon, it was treated separately as its own distinct region. Articles were therefore distinguished based on whether they occurred in (1) Washington or Oregon, (2) British Columbia, (3) Alaska, or (4) Japan or Russia. The marine life stage was broken down into 4 categories as well: (1) estuarine juveniles, (2) coastal-migrating juveniles, (3) Sub-adults, and (4) adult returners. The research question category characterized articles based on the hypothesis examined. Subcategories for each research question were used to clarify the topics that received the most and least attention. A summary of research questions and sub-categories can be seen in (appendix table?). None of the categories evaluated in the meta-analysis were mutually exclusive; therefore if a paper fit in more than one of the categories, it was scored for all that it applied to.

Comment [U1]: Should I make an appendix table with all the papers and their data?

Results

45 articles were returned in the search spanning from 1982 to 2011. Only 4 articles were published prior to 1990, while greater than 56% of articles returned in the search were published in the last 10 years (Figure 2).

Geographic Region of Study

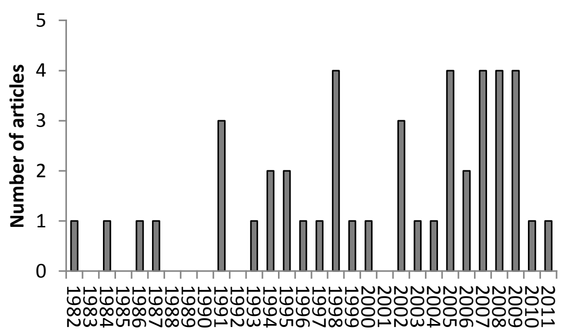


Figure 3: Total number of peer-reviewed journal articles regarding sockeye salmon (*Oncorhynchus nerka*) ocean survivorship by year.

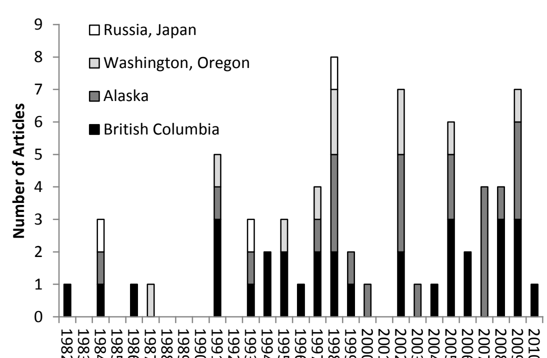


Figure 3: Number of peer-reviewed journal articles regarding sockeye salmon (*Oncorhynchus nerka*) ocean survivorship by year and region of study.

The largest number of articles (31) looked at British Columbia populations, with Alaska coming in second (23) followed by Washington and Oregon (9) and lastly Russia and Japan (3). Many articles looked at more than one region.

Life Stage

Most research looked at the adult life stage with coastal migrating juveniles as the second most researched. Very little research on the sub-adult or estuarine life stage has been conducted. Research on coastal migrating juveniles has increased since the mid-1990s.

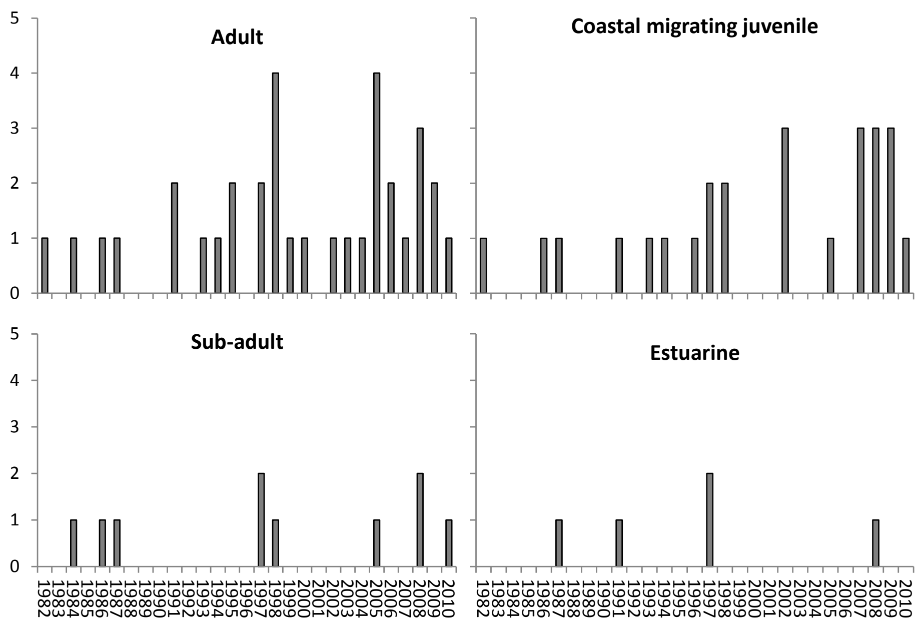


Figure 4: Number of peer-reviewed journal articles regarding sockeye salmon (Oncorhynchus nerka) ocean survivorship by life stage.

Telemetry

Only 9 articles used telemetry. Radio tags were the most popular method followed by acoustic and coded wire tags (CWT). No passive tags were used in any of the research articles and no articles were returned that used telemetry prior to 1998. Beginning in 2005, telemetry seemed to increase in use. The type of tag used also changed over the years with a shift from CWT to radio and lastly acoustic tags.

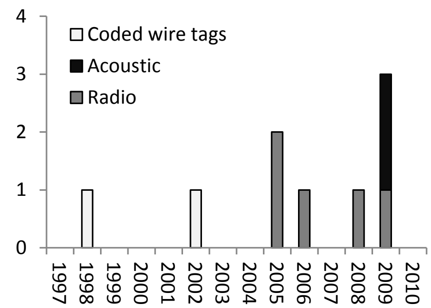
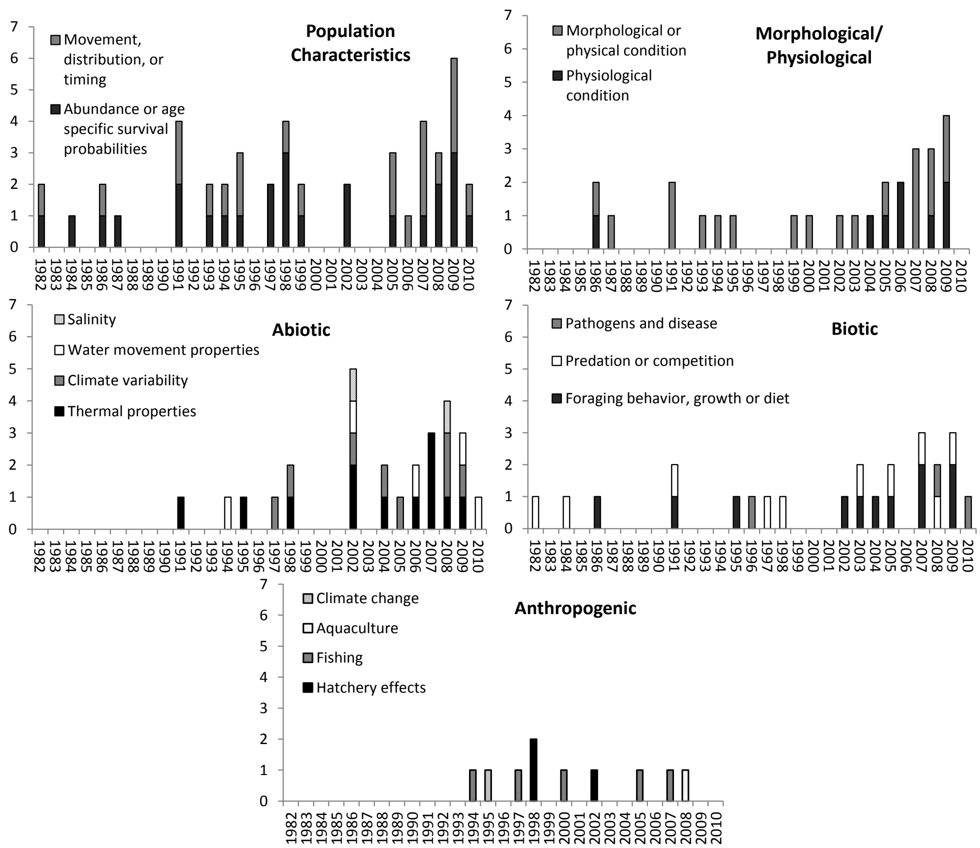


Figure 5: Number of peer-reviewed journal articles regarding sockeye salmon (*Oncorhynchus nerka*) ocean survivorship and telemetry method used. No articles that used telemetry were returned in the search prior to 1998.

Research Question

Trends in research questions indicate that interest in specific research questions has changed over time and also varied in overall popularity (**Error! Reference source not found.**Figure 6). All articles (100%) looked at population characteristics as part of their research question. The two subcategories of population characteristics were represented relatively equally over the time series as well as in total number of articles. Another 59% of articles looked at morphological/physiological characteristics with the bulk addressing morphological characteristics as opposed to physiological condition. Similarly, 59% of articles looked at abiotic factors with thermal properties as the most popular subcategory. Biotic research questions were addressed in 52% of articles with the majority of focus on foraging behavior, growth, diet, predation and competition. The least addressed research question was the anthropogenic

Figure 6: Number of peer-reviewed journal articles regarding sockeye salmon (*Oncorhynchus nerka*) ocean survivorship by research question (population characteristics, morphological/physiological, abiotic, biotic and anthropogenic) showing relative subcategories over time.



category which was discussed in only 22% of articles. The main focuses of research within the anthropogenic category were fishing effects (commercial and recreational) and hatchery effects.

Population versus Individual Level Sampling

Most articles (60%) looked exclusively at populations, while another 24% looked exclusively at individual sockeye salmon. Only 13% of all articles in this meta-analysis used both individual sampling combined with population based sampling within their methods (Figure 7).

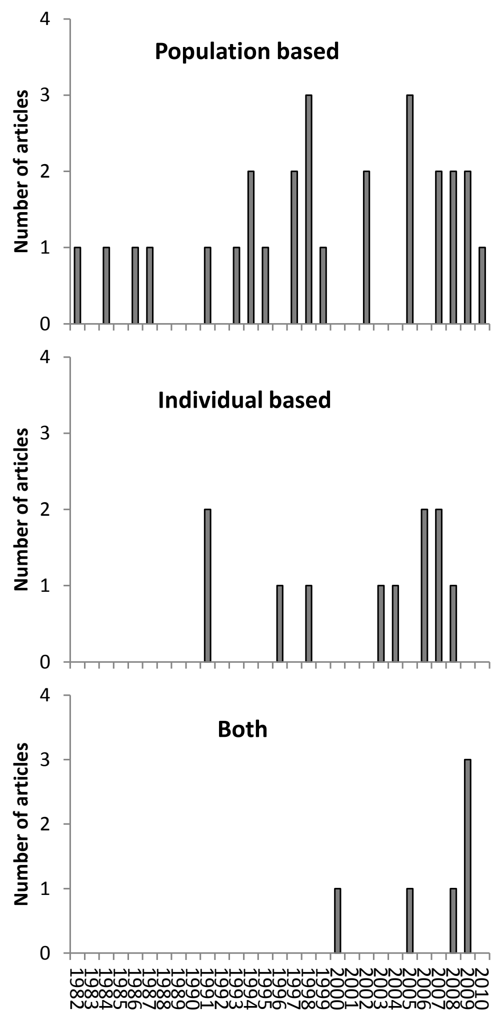


Figure 7: Number of peer-reviewed journal articles regarding sockeye salmon (*Oncorhynchus nerka*) ocean survivorship and sampling level indicating trends in research on populations, individuals or both.

Discussion

Region of Study

British Columbia remained the dominant region for marine research on sockeye salmon with Alaska at a close second. Both regions showed an increasing number of publications; however other areas like Washington/Oregon and Japan and Russia did not show an increasing trend in research. Regional inequalities regarding research have caused limitations in the present understanding the marine phase of sockeye salmons life history. One of the reasons British Columbia populations might have been the best studied in the marine phase could be due to ideal geography of the Georgia Strait. Migrating juveniles are forced to funnel out of the

Strait of Juan De Fuca or the Queen Charlotte straight allowing researchers to document their migration using telemetry. Sockeye salmon are also economically and culturally important in this region. The Fraser River is not only one of the most productive sockeye rivers in British Columbia, but also flows through densely populated metropolitan cities with universities and government offices. Images of plentiful runs of salmon in cedar lined rivers are part of BC's global image of wild natural beauty. This attracts a tourist industry that grossed 13.8 billion dollars in 2008 alone (Henshaw 2010). This leads to public pressure for sustainable practices and likely increased funding for sockeye research. Alaska populations of sockeye salmon were second to British Columbia in terms of total amounts of research even though natural are much more abundant. Similar to British Columbia, Alaska has a commercial fishery for sockeye as well as an expanding tourist industry that brought in almost 900,000 visitors to the state in 2002 with 300,000 fishing licenses (1/3 of the number of visitors) issued that same year (USDA 2005). Research on Alaskan populations might be less prevalent, even though sockeye salmon abundance is greater, due to the general assumption that fisheries are well managed and underexploited; therefore research efforts by the limited pool of salmon experts might be diverted to research in other areas, such as those undergoing declines. Washington and Oregon populations were studied in only 9 articles returned in the search. Populations of sockeye in these US states are not as plentiful as those in British Columbia or Alaska which might be explain the lack of articles on these populations. Three articles were returned in the search for Japanese and Russian populations of sockeye. This could be an underestimate if articles were not available in English and therefore not returned in the searches of the electronic databases. It is also possible that marine research on sockeye salmon in these countries is rare; however, due to the high abundances of sockeye salmon in Russia and the importance of sockeye as a food fish in Japanese culture, I would expect lack of research to be indicative at least partially of translation issues.

The unique adaptations of sockeye to localized environments make it necessary to understand the geographical range of the species. The disparity in amounts of research between regions indicates the need for an international collaboration to increase the amount of research on in the Pacific Ocean habitat. Of the 80 genetically distinct subpopulations reported on in the International Union for the Conservation of Nature State of the Salmon Report (2008), 26 (33%) lacked sufficient data for assessment. Russia and Alaska both had 10 subpopulations that were “data deficient” while British Columbia had 6. Research has focused on the most productive systems while it is well understood that stability of populations, considering eminent climate change and habitat destruction, is reliant on the bank of genetic diversity provided by uniquely adapted populations, not just the large ones. With the variety of life history traits exhibited by sockeye salmon populations, it is necessary to understand the unique adaptations and habits of these subpopulations if we are to be effective at managing them. (IUCN 2008)

Telemetry and Life Stage

Technological improvements to telemetry have likely helped to increase the number of marine studies in the past decade, while future developments seem promising. Recognizing the need for better monitoring of marine migration patterns and survival, David Welch and his associates proposed the Pacific Ocean Shelf Tracking System (POST) in 2001. The ambitious project began strategic placement of acoustic tag receiver lines in locations throughout the west coast as far north as Port Gravina, Alaska and as far south as Point Reyes, California with a large amount of focus on waters surrounding Vancouver Island, British Columbia. (Payne, Andrews et al. 2010) Lines can detect individuals as small as 10 centimetres (Payne, Andrews et al. 2010) increasing the ability to study early marine migration in juvenile fish. Preliminary results correlating survival to anthropogenic, abiotic, and biotic factors present an interesting diversity in the location and degree of mortality; however definitive conclusions require multi-year analyses. (Payne, Andrews et al. 2010) In the past, telemetry experiments have focused on the adult life stage and generally only explained either reported “observed traits” of populations, or “relationships” between an environmental variable and the results of tagging studies (e.g. timing and success of migrations). Telemetry methods, whether acoustic, radio, or CWT when combined with other disciplines can be used to determine the mechanistic reasons for fish migration; for example, tagging studies can be combined with genetic methods to determine the population the fish originated from and hence stock-specific migratory routes. Other fields that could be combined with telemetry might include physiology and behaviour. (Cooke, Hinch et al. 2008)

Research Questions

The total number of peer-reviewed scientific articles regarding marine survivorship of sockeye salmon showed an increasing trend, while emphasis also shifted toward previously untouched areas of research. All of the research regarding sockeye salmon addressed population characteristics as part of their research question likely due to the use of search term “surviv*” which predisposed articles returned in the search to fit within the subcategory of abundance or age specific survival probabilities. Regardless of the large amount of research already present on the topic, there is still much that is not understood. Through pending results from POST it is eminent that an increase in the quality and quantity of the information on movement, distribution, age specific survival probabilities, and abundance will occur in the near future. Some improvements would include better understandings of stock size and identification of “survival bottlenecks” as well as answer questions regarding the juvenile mortality and ocean habitat issues. (Payne, Andrews et al. 2010) Efforts for future research appear to be heading in the right direction for improving our understandings of population characteristics. Morphological and physiological research (addressed in over 50% of articles) can be combined with telemetry studies enabling the researcher to draw conclusions about the mechanisms of marine survival, abundance, and migration. Biotic and abiotic research questions, present in over half of articles, showed an increasing trend in popularity since 2004. The thermal properties subcategory was the most popular of the research questions in the abiotic group likely due to hype surrounding the climate change. Salinity was only examined in 2 papers; however the importance of this factor with regards to sockeye marine survival were unclear (REF MUETER 2002). Subcategories of biotic research questions (1) predation and competition, (2) foraging behaviour, and (3) growth and diet, received similar attention (≈10 articles each) however pathogens and disease was only addressed in 3 articles. Results from the June 2010 workshop on the decline of sockeye salmon proposed that marine pathogens were a possible a contributor to the poor returns of sockeye salmon observed in 2009 in the Fraser River. (Dr. Randall M. Peterman, personal communication, Nov 19, 2010) More research focused on this area would be recommended. The anthropogenic category was the least popular research question with the fewest articles returned in the search. This was surprising, since this category included climate change as a subcategory. This effect might have been caused by the methodology of the analysis requiring the intention to assess the effects of climate change to be stated within the abstract. Papers that discussed climate change in the discussion, though directly applicable were not included in anthropogenic category. No papers in the analysis examined pollution or introduced species, while only one paper was returned for climate change and aquaculture.

Study approach

Although this quantitative review included all papers that analyzed field data, many of the papers presented in this analysis relied exclusively on available stock-recruitment data to produce correlational or observational studies. These types of correlations can be useful to preliminary understandings of factors that affect marine survival as they allow for a relatively cheap assessment of a variable (or multiple variables); however, integration of individual based sampling (e.g. genetic assays, physiological or morphological condition) with population based data (as mentioned in the discussion regarding telemetry) would be recommended in order to provide evidence of the mechanistic causes of observed patterns rather than simply reporting correlations and hypothetical musings regarding the cause. (Cooke, Hinch et al. 2008) Fortunately, it appears the number of studies combining both individual and population based sampling have increased since the publication of (Cooke, Hinch et al. 2008)).

Discussion of limitations with methods

During the process of eliminating papers, it was evident that many reviews proposed important hypotheses not yet addressed or validated by field studies. One such paper proposed mortality imposed by salmon sharks as high as 12.6-25.2% of the 1989 run in the North Pacific with sockeye as the number one prey item among salmonids. (Nagasawa 1998) This would be a noteworthy sum of ocean related mortality. Field studies have been conducted on salmon shark predation, but written in Japanese without translation and therefore not captured by the databases used for this analysis. Fortunately, bilingual researchers identified this gap and reviewed the Japanese articles in English; therefore the lack of field studies in this instance was due to the language barrier of the database not lack of research. (Ishida, Ueno et al. 1998) Another limitation to the analysis was the inability to access papers prior to 1965 online. A few articles that fit the criteria might not have been included in the analysis due to the lack of presence in electronic form.

Another problem encountered regarded the use of the search terms “surv* and mort*” as that many papers that addressed ocean issues with salmon might not have explicitly stated whether the results were about mortality rather than just a change in the fish. For example, in (Hamon, Foote et al. 2000) they discussed the effect of fishing on size dynamics of sockeye salmon, but from the abstract did not relate this explicitly to survivorship even though this intuitively changes the survivorship of the species. Small individuals fit through the holes in the fishing net, but maybe aren’t as successful in spawning grounds or during migration.

Summary and recommendations

The results of the quantitative analysis indicate many positive developments regarding the recent history of marine sockeye salmon research, such as the increasing quantity of articles, the potential uses of POST, and the growing number of articles combining population and individual based sampling; however, there are still areas that need to be improved. Gaps in the research indicate the need for increased understanding of the roll pathogens and anthropogenic factors might have on marine survival. Future research endeavours (and to those that fund them) should be encouraged to continue supporting the freedom of research creativity through the balanced funding of innovative and interdisciplinary projects, while also provisioning funds for “priority issues” which might include the gaps in research questions mentioned earlier as well as declining, worrisome or data deficient populations. Internationally, this would implicate collaboration with researchers in Japan and Russia to mutually protect the vitality of sockeye salmon within their Pacific Ocean habitat. Part of this collaboration would include the translation of research into Japanese, English, and Russian, which although idealistic and expensive, might be worth the effort if the sharing of scientific knowledge would improve management of the species throughout its marine range.

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CHAPTER 2: The effect of migration on morphological and reproductive features of Sockeye salmon (Oncorhynchus nerka) from the Fraser River watershed

Abstract

Populations of sockeye salmon (*Oncorhynchus nerka*) from the Fraser River watershed are unique in their adaptability to both coastal and distant freshwater spawning grounds as far as 1000 kilometers inland (Hinch and Rand 1998). Differences in morphology were found between 8 populations of sockeye salmon that underwent varying degrees of migratory work. Populations that underwent long migrations had a smaller fork length, smaller ovary mass, and also a smaller individual egg dry mass. Results of this analysis agree with the those found in Crossin *et al.* (2004) and increase the confidence in the theory that migratory challenge creates a selective pressure on morphology and reproductive anatomy of sockeye salmon.

Key Words: Energetics, migration dry egg weight, evolution, morphology, salmon

Introduction

Sockeye salmon (*Oncorhynchus nerka*) populations are ideal for studying the evolutionary effects of migration due to the precise nature of their homing instinct resulting in reproductively isolated populations with varying degrees of migratory challenge. (Crossin, Hinch et al. 2004) Sockeye salmon are semelparous and die following spawning; hence, energy reserves are close to exhaustion following migration and reproduction (Brett 1995).

Additionally, feeding activity ends just prior to river entry shifting the metabolism into a catabolic state lasting for up to a month. Sockeye must consequently rely only on endogenous energy reserves accumulated during ocean feeding for the extent of their freshwater migration (Hinch, Cooke et al. 2006). Especially challenging or long migrations can drain over half the total somatic reserve (Brett 1995) and if energy is depleted too quickly, mortality and has been documented to occur (Rand and Hinch 1998). Migration and swimming speed are also critical to the arrival of individuals during ideal spawning conditions avoiding high flows caused by spring freshet and high temperatures experienced in midsummer months (Webb 1995) while, differences in individual migration speeds have attributed to differences in size (Hinch and Rand 1998). Selection in long migrating populations might therefore favour biological trade-offs between somatic energy reserves accumulated during ocean residency, morphology, and reproductive characteristics that maximize fitness and survival. (Crossin, Hinch et al. 2004)

To determine the cause of differences observed in morphology between five populations of Fraser River sockeye salmon, Crossin *et al*. (2004) correlated variables of migratory challenge (e.g. distance to spawning grounds, discharge rates, elevation, river slope, work and temperature) to measured physiological and morphological features. Populations with long migrations had smaller more fusiform bodies, fewer numbers of eggs, and reduced ovary mass compared to populations with shorter migrations similar to findings in (Kinnison, Unwin et al. 2001; Kinnison, Unwin et al. 2003). Unlike other studies that used distance to spawning grounds to indicate migratory challenge, (Crossin, Hinch et al. 2004) used a an index of work calculated for each population based on a factor of migratory distance (D_M) and migratory elevation (E_M) resulting in the stronger correlations to morphology and physiology.

Conclusions supported the life-history theory that longer migrations resulted in selection for increased size efficiency; however, compromises in body size were not sufficient to mitigate losses in mass of ovaries. (Crossin, Hinch et al. 2004)

Migration affects males and females differently in terms of energetic costs and hence prioritization of energy reserves associated with reproduction is also different. Females swam more slowly than males and were more energetically efficient, which would be expected since females generally have a higher energetic cost of migration (Rand and Hinch 1998). Migratory distance correlations to reproductive characteristics of females within introduced populations of chinook salmon (*Oncorhynchus tshawytscha*) in New Zealand indicated that migrating populations displayed overall reduced investment in ovarian mass and smaller egg size; however, overall numbers of eggs either increased or stayed the same. (Kinnison, Unwin et al. 2001) Environmental trade-offs in male chinook salmon between secondary sexual traits (e.g. hump depth and snout length) with those necessary for increased migratory and reproductive success (e.g. tissue energy and testes size) indicated that migratory distance had no distinguishable influence on of testes size, but individuals that underwent short migrations showed significantly larger humps, and longer snouts than long migrating populations (Kinnison, Unwin et al. 2003). Since males invest less energy into gonads, energy can therefore be allocated to features that attract mates such large humps and snouts, aggressive displays towards other males, and a longer life expectancy. (Kinnison, Unwin et al. 2003)

Differences in observed phenotypes are thought to be heritable and the result of evolution to migratory challenge rather than phenotypic plasticity caused by differing environmental conditions (Kinnison, Unwin et al. 2001; Kinnison, Unwin et al. 2003). Captive experiments using artificial swim channels indicated that females that were exercised had lower fat content than those that were not exercised; however, groups that were not exercised did not show an increased provision of energy to reproduction (Patterson, Macdonald et al. 2004). Allocation to reproduction was therefore not likely phenotypically plastic among individuals experiencing differing environments, but rather a result of evolution. In another attempt to estimate the evolutionary effects of migratory challenge, Kinnison *et al.* (2003) (Kinnison, Unwin et al. 2001) Many streams have with similar migratory challenge; also share other environmental characteristics (gravel size, river depth, etc) (Kinnison, Unwin et al. 2003).

Previous studies correlating migration challenge to morphological and reproductive characteristics only looked at a small number of populations within a single year (Crossin, Hinch et al. 2004), under experimental conditions (Kinnison, Unwin et al. 2001), or outside the natural range of sockeye salmon spawning habitat (Kinnison, Unwin et al. 2003). The objective of this research was to look at a larger number of populations (8 total) to confirm some of the results in found in the literature (Crossin, Hinch et al. 2004) for an additional year. Fork length, ovary mass and egg mass were measured to assess the basic hypothesis that populations with long and arduous migrations should have adaptations to conserve the most energy and therefore should also have a shorter body length and smaller egg size.

Methods

Sockeye salmon were collected from 8 populations within the Fraser River watershed with varying migration distance and challenge as well as run timing (Figure 1, Table 1). Sampling dates occurred from late August to November 2010 (Figure 1: **Map from Patterson *et al.* 2007 showing the sampling location of the eight populations of sockeye salmon in the Fraser River**

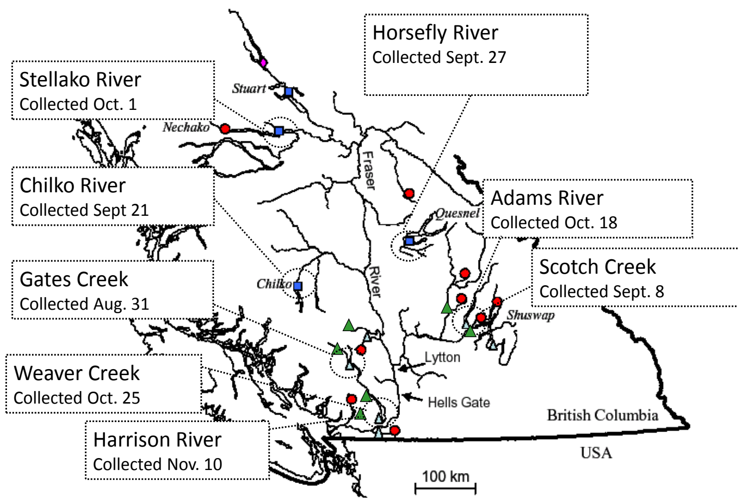

Figure 8: Map from Patterson *et al.* 2007 showing the sampling location of the eight populations of sockeye salmon in the Fraser River watershed and their respective sampling dates.

Table 1: Environmental characteristics and migration work indices for seven populations of Fraser River sockeye salmon. Environmental data presented for Adams, Quesnel, and Early Stuart populations was used for Scotch, Horsefly, and Sellako populations respectively.

Population	Early Stuart	Gates	Nechako	Quesnel	Chilko	Lower Adams	Weaver	Harrison
Run Timing Group	Early Stuart	Early Summer	Summer	Summer	Summer	Late	Late	Late
Migration Distance (D_M) (km)	1071	364	958	796	642	480	117	121
Migration Elevation (E_M) (m)	690	280	716	728	1174	346	32	10
Work ($0.001E_MD_M$)	739	102	686	579	754	166	4	1

watershed and their respective sampling dates. Figure 1**Table 1**). Morphological characteristics such as fork length, total weight, and ovary weight were recorded in the field while, eggs were transported back to lab facilities at UBC where dry mass of eggs were measured.

Index of migratory work was used based on methods in Crossin *et al.* (2004) to best represent the relative difficulty of passage reflective of the migratory challenge of the individual population (Table 1**Error! Reference source not found.**). Exact environmental characteristics of migration were not available for Scotch, Horsefly, and Stellako populations; therefore

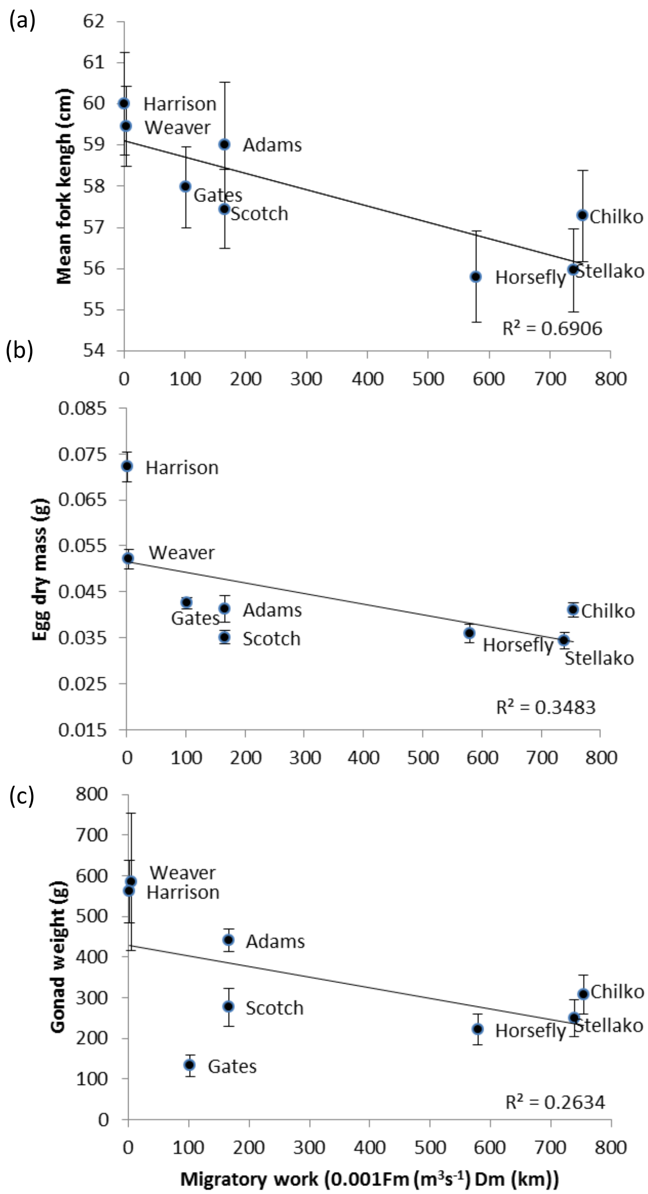

Figure 9: (a) Mean fork length (g) with 95% confidence intervals (α=0.05). (Weaver, n=20; Harrison, n=19; Scotch, n=20; Adams, n=20; Gates, n=20; Chilko, n=15; Horsefly, n=15; Stellako, n=15) **(b)** Mean of egg dry mass (g) with 95% confidence intervals (α=0.05). (Weaver, n=20; Harrison, n=19; Scotch, n=20; Adams, n=20; Gates, n=20; Chilko, n=15; Horsefly, n=15; Stellako, n=15) **(c)** Mean of ovary weight (g) with 95% confidence intervals (α=0.05). (Weaver, N=20; Harrison, n=19; Scotch, n=10; Adams, n=20; Gates, n=20; Chilko, n=15; Horsefly, n=15; Stellako, n=15)

environmental characteristics from populations that shared the same migratory route were used as surrogates (Table 1). Migratory work was compared to sample population means for fork length, ovary mass and dry egg mass by a general linear model. Two-sided t-tests were used to calculate 95% confidence intervals.

Results

Mean fork length, dry egg dry mass, and ovary weight were found to decrease with increased migratory work with R^2 values equalling 0.6906, 0.3483, and 0.2634 respectively (Figure 2). Strongest trends were yielded when correlating fork length to migratory work.

Discussion

Sockeye salmon undergo rigorous migrations that can result in mortality (Rand and Hinch 1998). Energy reserves are generally lower in these populations (Kinnison, Unwin et al. 2001; Kinnison, Unwin et al. 2003; Crossin, Hinch et al. 2004); therefore size, ovary investment, and egg size are compromised. One of the limitations of this analysis is that we did not look at the somatic energy of populations. This limits our ability to confirm the evolutionary principle that selection favoured individuals that were more efficient in terms of body morphology. Measurements of horizontal body width were also not available to validate Criossin *et al.* (2004) conclusions regarding fusiformity.

Dry egg mass might be a better indicator of energy investment than wet egg mass since it removes the effect that water content might have on egg size.

Lloyd (1987) looked at egg number-size relationships in relation to parental care. Parental care increased the fitness of offspring by enhancing their chance of survival; however, costs of care were increased with larger broods. Based on life-history theory, larger eggs were expected to have a greater chance of survival compared to smaller eggs, but also sustaining a higher cost to the parent. Given a fixed amount of parental care, Lloyd theorized that egg number and size would be expected to reach ratio giving the offspring the maximum fitness. Trends seen in sockeye salmon reproductive characteristics indicate that offspring size-number trade-offs might be function of parental care and might help explain the trends in dry egg mass found in this study as well as offer a hypothesis for the results seen in Kinnison *et al.* (2001). If sockeye with long migrations were less able to extend parental care through nest guarding due to energy demands associated with their migration, this might lead to a reduction in size of eggs in favour of egg number.

Although it is likely that some of the differences observed in sockeye populations were caused by genetic divergence produced by migratory effort, the extent of this effect is unknown. Other factors besides migratory costs might account for the similarities in reproductive traits being more highly selected for. (Kinnison, Unwin et al. 2003; Crossin, Hinch et al. 2004) Crossin *et al.* (2004) proposed an alternative hypothesis to explain the morphological differences observed. If individual populations were not specifically adapted to their rivers for the migration challenge, then morphology might be reflective of differences in maturity at river entry. Crossin *et al.* (2004) argued that if this were the case, rivers with similar run timing and therefore of similar maturity level should be expected to have similar morphology, but this was not the case. Our results agree with those presented in Crossin *et al.* (2004) as we found significant differences in morphology of dry egg mass and gonad weight between populations Chilko and Horsefly and also Weaver and Adams populations which both exhibit similar run timing. Confidence intervals (α=0.05) of mean fork length for Chilko and Horsefly as well as Weaver and Adams populations overlapped; however the sample means showed a consistent decrease as expected with increasing migratory challenge. This indicates that differences in populations with similar run timing and therefore similar maturity still showed morphological and reproductive changes consistent with migratory work.

Consideration of the effects of commercial fishing might have on populations might also be causing some of the trends observed in the analysis. Long term results of commercial fishign generally cause similar effects as migratory effort: large mortality and selective pressure on growth rate, size at sexual maturity, and reproductive yield. (Andersen and Brander 2009) Argument regarding the extent of selective pressure and evolutionary change exerted by commercial fisheries on salmon morphology and reproductive yield ranges from slow (Andersen and Brander 2009) to more drastic evolutionary change. The likelihood that commercial fishing caused the trends seen in this analysis are low; however, worth mentioning since no papers were found that described the relative harvest rates on individual populations of sockeye salmon in the Fraser River watershed. Studies conducted over multiple years would help increase the confidence that variation in migratory challenge is the significant evolutionary driver affecting morphological and reproductive change observed in Fraser River populations.

Considering the high energetic costs of migration, what might the effects of global warming have on sockeye populations? Crossin *et al.* (2004) calculated degree-days to determine the cumulative temperature experienced for each population within their individual migratory pathways based on the temperature of river segments and the number of days spent within the segment. Degree-days produced significant, but weaker correlations on morphological and energetic features when compared to other environmental factors such as migratory distance, elevation, work, and river slope; nevertheless, temperature effects should not be discounted. With expected increases of 1.1-6.4 °C during the 21st century (IPCC 2007), the effects might be more extreme reductions in size and reproductive capacity.

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Chapter 1 Appendix

Reference	Geographic Location of Study				Marine Life Stage				Study Approach			Telemetry			
	WA, OR	BC	AK	Russia/ Japan	Estuarine	Coastal-migrating juveniles	Sub-adult	Adult	Population based	Individual based	Both	Radio	Acoustic	CWT	Passive
(Peterman 1982)	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0
(Peterman and Wong 1984)	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0
(Brett 1986)	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0
(Thorne and Ames 1987)	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0
(Welch, Margolis et al. 1991)	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
(Hsieh, Warren et al. 1991)	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0
(Healey 1991)	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0
(Koenings, Geiger et al. 1993)	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0
(Cass and Wood 1994)	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
(Peterman, Marinone et al. 1994)	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0
(Hinch, Healey et al. 1995)	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
(Johnson, Baylock et al. 1996)	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0

(Myers, Bradford et al. 1997)	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0
(Beamish, Mahnken et al. 1997)	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0
(Peterman, Pyper et al. 1998)	0	1	1	0	0	1	0	1	1	0	0	0	0	0	0
(Downton and Miller 1998)	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0
(Mahnken, Ruggerone et al. 1998)	1	1	1	1	0	1	1	1	1	0	0	0	0	1	0
(Fryer 1998)	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
(Pyper, Peterman et al.)	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0
(Hamon, Foote et al. 2000)	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0
(Mueter, Ware et al. 2002)	1	1	1	0	0	1	0	1	1	0	0	0	0	0	0
(Kline and Willette)	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0
(Mueter, Peterman et al. 2002)	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0
(Ruggerone, Zimmermann et al. 2003)	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0
(Crossin, Hinch et al. 2004)	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
(Pyper, Mueter et	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0

al. 2005)															
(Cooke, Crossin et al. 2005)	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0
(English, Koski et al. 2005)	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0
(Ruggerone , Farley et al. 2005)	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
(Rand, Hinch et al. 2006)	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
(Cooke, Hinch et al. 2006)	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0
(Quinn, Hodgson et al. 2007)f	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0
(Farley, Murphy et al. 2007)	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0
(Farley, Murphy et al. 2007)	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0
(Ruggerone , Nielsen et al. 2007)	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
(Martinson, Helle et al. 2008)	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0
(McKinnell 2008)	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0
(Hanson, Cooke et al. 2008)	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0
(Morton, Routledge et al. 2008)	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
(Welch, Melnychuk	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0

et al. 2009)															
(Martinson, Helle et al. 2009)	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
(Crossin, Hinch et al. 2009)	0	1	0	0	0	0	0	1	0	0	1	1	1	0	0
(Sturdevant, Sigler et al. 2009)	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0
(Rensel, Haigh et al. 2010)	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0
(Tucker, Trudel et al. 2009)	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0

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