THE SUBLETHAL EFFECTS OF SEA LAMPREY PARASITISM ON LAKE TROUT ENERGY BUDGETS, REPRODUCTION, GROWTH, AND WOUND HEALING

By

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ABSTRACT

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Since their introduction into the Laurentian Great Lakes, sea lamprey have had serious negative effects on lake trout populations contributing to population decline. Although the consequences of sea lamprey introduction for lake trout have been studied for decades, there are critical unknowns that remain challenges for lake trout and sea lamprey management. My work focuses on some of these critical unknowns through a combination of experiments addressing the physiology of parasitized lake trout, the accuracy and reliability of sea lamprey wound assessments, and the quantification of the sublethal effects of sea lamprey parasitism in a modeling framework useful for management applications. My first chapter provides a background and description of the critical unknowns surrounding the interactions between sea lamprey and lake trout that my dissertation addresses. My second chapter focuses on problems related to the process of collecting and aggregating sea lamprey wound data from wild fish. The assumptions of consistent and accurate wound classification and reliable wound healing progression that are required for the use of this data is not met. Fisheries management in the Great Lakes depends heavily on these data and models for determining lake trout harvest thresholds, stocking strategies, estimating sea lamprey damage, and for assumptions about lake trout survival that are used in sea lamprey population estimates. Highlighting deficiencies in this process is critical as it allows us to rethink how wound data is collected and used, and provides potential avenues for improving its use going forward. My third chapter addresses the sub-lethal effects of sea lamprey parasitism on lake trout growth, reproduction, and energy storage. Much

research on the interactions between sea lamprey and lake trout has focused on estimating direct mortality on lake trout populations, but an estimated 45-75% of lake trout survive a sea lamprey parasitism event. In our study, severe sea lamprey parasitism resulted in considerable alterations to reproduction and energy storage for siscowet lake trout, but lean lake trout were far less susceptible to these parasitism-driven effects. The difference in response is likely driven by life history differences between these two ecomorphs. This work provides crucial missing information about the effects of sea lamprey parasitism on lake trout in the Laurentian Great Lakes. My fourth chapter focuses on the development of dynamic energy budget (DEB) model to enhance our understanding of the energetic consequences of sea lamprey parasitism. While empirically measured sub-lethal alterations to lake trout reproductive physiology are interesting, it is difficult to understand the implications of stressors in the context of the whole organism. I developed a DEB model that tracks energy allocation for siscowet lake trout, and accounts for parasitism-driven life history alterations. This allows for a better understanding of the energetic mechanisms that lead to skipped spawning following sea lamprey parasitism. Simulations using our developed model highlight the relative importance of parasitism and individual variation in muscle lipid and plasma estradiol concentrations for ovarian development, and closely match empirical observations. This work advances our knowledge of the sub-lethal influences of sea lamprey parasitism and provides tools and guidance for how to measure and estimate these effects going forward.

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CHAPTER 1: INTRODUCTION

Abstract

Lake trout are a historically important species in the Laurentian Great Lakes for commercial, subsistence, and sport fisheries as well as their role as a top predator. The introduction of sea lamprey in the late 1800s resulted in a marked decline of lake trout populations, and spurred a large-scale research, management, and control effort to rehabilitate lake trout stocks. Although these efforts have been largely successful, critical unknowns hinder our ability to reach sea lamprey and lake trout management goals remain. The aim of this chapter is to provide a brief background and description of some of the key unknowns and uncertainties addressed in this dissertation. One current challenge for sea lamprey and lake trout management in the Laurentian Great Lakes is the reliability of wound data used as an indicator of sea lamprey damage. Wound data is collected by direct observation and classification of sea lamprey wounds found on wild lake trout during annual surveys. The classification procedure is subjective, and if wound misclassification is high, the ability to use wound data to inform management decisions may be compromised. An additional challenge is the lack of knowledge about the health and physiology of lake trout that survive sea lamprey parasitism. Currently, our understanding of the interaction between lake trout and sea lamprey focuses on lethal parasitism. However, if lake trout that survive parasitism have reduced growth, reproduction, or survival, sub-lethal parasitism may play a large role in lake trout population dynamics. Finally, we lack methods for modeling the impact of sub-lethal stressors on individual lake trout. Development of these models is challenging, yet essential for understanding population-level consequences of parasitism. This dissertation addresses these critical unknowns and challenges.

Introduction

Lake trout are a historically important species in the Laurentian Great Lakes due to their role as the dominant native salmonine predator, and for their importance for commercial, subsistence, and sport fisheries. Starting in the mid-1940s, lake trout populations rapidly collapsed following the introduction of invasive sea lamprey (Hansen 1999; Muir et al. 2013). This prompted a heavy focus on sea lamprey control, lake trout rehabilitation, and research focusing on understanding the interaction between sea lamprey and lake trout. Lake trout and sea lamprey management in the Laurentian Great Lakes relies on a bi-national effort between Canada and the US, and consists of state, provincial, federal, and tribal natural resources agencies that coordinates management targets, research, stocking, harvest regulations, and invasive species management (Gaden et al. 2008; Muir et al. 2013). Through these efforts, considerable progress has been made towards lake trout recovery. Despite this headway, continued progress towards lake trout rehabilitation faces challenges. Uncertainties inherent in field-collected data and its quality, mismatch between models and empirical measurements, and a lack of information about the effects of parasitism on surviving lake trout all serve as barriers to fully understanding the influence of sea lamprey on lake trout populations (Adams et al. 2020a, 2020b). Thus, it is important to address these critical unknowns to better inform lake trout and sea lamprey management efforts going forward. This dissertation focuses on three critical unknowns: 1) the accuracy and reliability of sea lamprey wound data, 2) the sub-lethal effects of sea lamprey parasitism on lake trout reproduction, growth, and energy storage, and 3) the energetic tradeoffs that occur within a lake trout that is parasitized by a sea lamprey. Each of these unknowns is discussed separately in subsequent chapters of this dissertation. This chapter provides important context justifying why these unknowns are worth studying.

Accuracy and Reliability of Sea Lamprey Wound Data

Since the late 1940s, marks on fish resulting from sea lamprey (*Petromyzon marinus*) parasitism have been recorded and used to inform fisheries management and sea lamprey control in the Laurentian Great Lakes (Eshenroder and Koonce 1984). This information has been used for estimating lamprey-induced mortality of target fish species (Bence et al. 2003; Lantry et al. 2015), evaluating the success of sea lamprey control programs (Adams et al. 2003; Rutter and Bence 2003), and allocating resources for sea lamprey control (Koonce et al. 2004). The procedures for assessing and recording wound data have been modified over time as data quality needs, management priorities, and applications shifted (King Jr. 1980; Eshenroder and Koonce 1984; Ebener et al. 2006; Firkus et al. 2020). Despite these updates, there is currently concern that the accuracy and reliability of wound classification is not sufficient, and that variability in wound records due to misclassification could be adding uncertainty to lamprey damage estimates. Furthermore, there is little information available about healing time and healing progression of these wounds which is useful for attempts to assign wound records to individual cohorts of sea lamprey.

Studies assessing wound classification during workshops found alarmingly high variability among individuals and agencies (Ebener et al. 2003; Nowicki 2008). Wound counts varied three fold among individual assessors (Ebener et al. 2003), indicating that records could be spatially inconsistent depending on which field crew performed the assessment in a given area. Additional evidence suggests that wound healing progression contributes to the difficulty of accurately assessing sea lamprey wounds (Nowicki 2008). In studies modeling simulated sea lamprey wounding rates on lake trout, measurement error of wounding rates contributed considerably to inconsistencies between wound observations and lake trout and sea lamprey population estimates (Adams et al. 2020b, 2020a). Because of these issues, there is a critical need to evaluate the consistency and accuracy of sea lamprey wound assessment. Quantifying misclassification rates and observer agreement is an important next-step for identifying deficiencies in our current use of wound data, and accounting for potential sources of error when wound data is used in modeling efforts. Chapter 2 of this dissertation addresses these critical uncertainties and identifies potential alternatives to our current use of wound data.

Sub-Lethal Effects of Parasitism

Much research on the interactions between sea lamprey (*Petromyzon marinus*) and lake trout (*Salvelinus namaycush*) has focused on estimating direct mortality on lake trout populations from sea lamprey parasitism (reviewed in Swink 2003; Bence et al. 2003). But an estimated 45-75% of lake trout survive sea lamprey parasitism events (Swink 2003; Madenjian et al. 2008). A lake trout that has survived a severe sea lamprey attack is very likely to suffer health repercussions that may result in diversion of energy from normal physiological processes such as growth, immune function, and reproduction, but at present, little is known about these parasitism survivors and how they are affected by a sea lamprey attack. As such, sub-lethal influences on lake trout population dynamics are not explicitly included in population models. Currently, direct mortality from parasitism is incorporated in lake trout population models (Sitar et al. 1999; Bence et al. 2003; Irwin et al. 2012), but other potential indirect effects including susceptibility to secondary infections, reduced reproductive output, and altered growth are often not. This may result in underestimation of the effects sea lamprey exert on lake trout populations, and may ultimately hinder lake trout rehabilitation efforts.

Another concern is that different morphotypes of lake trout could respond differently to sea lamprey parasitism due to differences in life history strategies that may ultimately influence lake trout and sea lamprey management. We are focusing on two morphotypes of lake trout found in Lake Superior, siscowet and lean. Both morphotypes differ in habitat selection (Bronte et al. 2003), diet (Ray et al. 2007), fat content (Eschmeyer and Phillips 1965; Sitar et al. 2008, 2014), and age at maturity (Sitar et al. 2014), all of which could contribute to differential response to parasitism. Siscowet lake trout may be less sensitive to sea lamprey parasitism than the lean morphotype. Siscowets tend to have a higher rate of parasitism and they have more wounds than the lean morphotype suggesting a higher percent survive sea lamprey attacks. Also, siscowets do not show changes in growth trajectories as a result of sea lamprey parasitism, and the two morphotypes show molecular and physiological differences in response to parasitism that suggest a buffering of critical survival physiological processes in siscowets (Sitar et al. 2008; Goetz et al. 2016; Smith et al. 2016). A better understanding of the parasite-host relationship and how it differs between siscowets and leans can contribute to management decisions. For example, if siscowets are less sensitive to sea lamprey parasitism, based on heritable factors and life history, restoration of siscowets may be a viable management avenue to mitigate loss of ecosystem function or buffer negative effects on lean lake trout by absorbing sea lamprey attacks.

Many stressors have negative effects on fish reproduction acting primarily through the Hypothalamus-Pituitary-Gonadal axis (HPG) (Schreck 2010). Briefly, the HPG axis is primarily responsible for regulating reproduction whereby gonadotropin releasing hormone produced in the hypothalamus stimulates follicle stimulating hormone and lutenizing hormone in the pituitary which then trigger gamete maturation and ovulation/spermiation (Ankley and Johnson 2004). Currently, there is evidence that sea lamprey parasitism acts on the HPG axis by suppressing plasma testosterone levels, reducing steroid binding protein function, and suppressing follicle-stimulating hormone levels (Smith et al. 2016). These influences on the HPG axis may alter embryo viability through altered production of sex steroids, reduced egg quality, or reduced sperm viability. Coupled with general stress and effects on energy allocation caused by parasitism, there may be considerable effects on gamete quality, fertilization success, fry survival, and ultimately recruitment success that may have serious implications for lake trout populations. Lake trout are relatively slow growing species and require many years to reach reproductive maturity, making the probability of experiencing an attack prior to spawning substantial, particularly when sea lamprey exceed target levels of suppression.

Sea lamprey parasitism may have significant effects on lake trout growth. The energetic cost of stress and healing associated with parasitism, the use of energy reserves by the sea lamprey, and the alteration of energy allocation to compensate are all mechanisms that can alter long-term growth. Maintaining homeostasis in the face of stressors is energetically costly, and as a result resources typically allocated towards growth may be used counteracting the effects of parasitism (Schreck 2010). But fish may respond to parasitism by allocating more energy towards growth in an attempt to survive the immediate stress inflicted (Barber et al. 2000). This idea may be supported by increased foraging behavior of parasitized fish at the expense of other behaviors (N. Giles 1987). Energy allocation towards growth may also be induced by the parasite to ensure sustained nourishment and prolong the life of the host for the parasite's benefit (Barber et al. 2000). There is evidence that wild-caught lake trout previously parasitized by sea lamprey seem to grow faster than unparasitized lake trout (Smith et al. 2016). Currently, there is only weak evidence of altered lake trout growth following sea lamprey parasitism. Understanding how energy allocation is influenced by sea lamprey parasitism could allow for more refined measures of lake trout reproductive output that depend on sea lamprey abundance. It is therefore important to assess and understand the long-term effects of sea lamprey parasitism on the allocation of energy by lake trout to growth versus reproduction.

Chapter three of this dissertation focuses on identifying and quantifying the sub-lethal effects of sea lamprey parasitism on lake trout reproduction, growth, and energy storage. It also investigates the role of life history in the response to parasitism by comparing physiological alterations of siscowet and lean lake trout. This provides much-needed information about consequences of sea lamprey parasitism that are currently unknown and unaccounted for in fisheries management in the Laurentian Great Lakes. Not only does this project help build understanding of the broad scale implications of sea lamprey parasitism in this specific scenario, but it also provides critical information about the role of life history for lake trout and its importance for modulating the response to stressors in general.

Modeling the Sub-Lethal Effects of Parasitism in the Context of Dynamic Energy Budgets

Empirically measured sub-lethal alterations to lake trout reproductive physiology following sea lamprey parasitism are important, but it is difficult to relate individual alterations to effects on lake trout populations or ecosystem dynamics in the Great Lakes. Despite this difficulty, understanding how individual-level effects influence populations and ecosystems is critical for informing fisheries management in the Great Lakes. One promising approach for modeling the effects of stressors on individuals and bridging to population-level effects are dynamic energy budget (DEB) models. DEB models use generalized theory that can be adapted to the describe energy dynamics, growth, and reproduction of different species under different conditions (Kooijman 2010). They contain three main compartments (reserves, structure, and reproduction buffer) and a series of fluxes that dictate energy allocation to each compartment. DEB models can be parameterized for any organism through a formalized fitting procedure (Lika et al. 2011). Effects of stressors can be modeled by relating damage caused by the stressor to alterations in DEB model parameters. Once a DEB model is developed for an organism, it allows for the exploration of energetic tradeoffs under a variety of scenarios and environmental conditions . A framework for exploring these scenarios is valuable, as other approaches such as Wisconsin Bioenergetics models require empirical data to examine energetic tradeoffs under different conditions. DEB models are explicitly designed to account for how energy allocation responds to varying conditions and therefore avoids this issue. A parameterized DEB model accounting for the effects of stressors can also be used in an individual-based model to capture population dynamics (Martin et al. 2013).

The fourth chapter of this dissertation focuses on the parameterization of a DEB model for siscowet lake trout. I used data collected in chapter three as well as values from the lake trout literature to parameterize the DEB model using the "add my pet" procedure and covariation method where parameter estimates are derived through simultaneously minimizing the weighted sum of squared deviations between provided data and model estimates (Lika et al. 2011). The resulting DEB model is a good fit and describes the energy dynamics of siscowet lake trout through an individual's lifecycle. Then, I use model results from chapter three to inform the alteration of DEB parameters to model the effects of sea lamprey parasitism while accounting for individual differences in muscle lipid and estradiol. The resulting model and parasitism damage sub-models will inform individual-based-modeling to simulate population implications of sublethal parasitism on siscowet populations.

Conclusion

This work makes significant progress towards addressing critical unknowns that are currently hurdles to sea lamprey and lake trout management efforts in the Laurentian Great

Lakes. With more detailed understanding of sea lamprey wound misclassifications and healing progressions, we can better estimate the extent of sea lamprey damage on lake trout stocks, identify potential causes for mismatch between modeled and empirical data, and have greater precision when assigning damage to individual sea lamprey cohorts. Additionally, this information can inform training of wound assessment field crews. Characterization of the sub-lethal effects of sea lamprey parasitism on lake trout physiology allows lake trout management to better understand and estimate the full impact of sea lamprey on lake trout populations and set targets for lamprey control. Modeling sub-lethal effects in the context of dynamic energy budgets provides a more mechanistic understanding of the stressors involved with parasitism, and allows for population-level influences to be explored. Together, these individual projects fill important gaps in our knowledge about the interaction between sea lamprey and lake trout, and are important for assessing the full impact sea lamprey have on lake trout fisheries management in the Laurentian Great Lakes.

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CHAPTER 2: ASSESSING THE ASSUMPTIONS OF CLASSIFICATION AGREEMENT, ACCURACY, AND PREDICTABLE HEALING TIME OF SEA LAMPREY WOUNDS ON LAKE TROUT

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Abstract

Sea lamprey control in the Laurentian Great Lakes relies on records of sea lamprey wounds on lake trout to assess whether control efforts are supporting fisheries management targets. Wounding records have been maintained for 70 years under the assumption that they are a reliable and accurate reflection of sea lamprey damage inflicted on fish populations. However, two key assumptions underpinning the use of these data need thorough evaluation: sea lamprey wounds follow a predictable healing progression, and individuals classify wounds accurately and reliably. To assess these assumptions, we conducted a workshop where experienced professionals examined lake trout with known sea lamprey wounds. For most lake trout, pictures were taken at regular intervals during the healing process. Our evaluation of wound pictures found high variability in healing times and wound progressions that did not conform to the currently used classification system. Participants' wound classification agreement and accuracy were low and misclassification rates were high for most wound types. Training provided during the workshops did not markedly improve these metrics. We assessed wound classification accuracy for the first time and found assumptions of high accuracy and agreement are not met. We recommend misclassification rates be incorporated into models using wound data, sensitivity analyses be conducted to assess the potential impact of wound misclassification on estimates of key metrics (such as sea lamprey-induced mortality for lake trout), and alternative biomarkers be developed to quantify wound status with greater accuracy and precision.

Introduction

Records of wounds (commonly called marks) on lake trout (*Salvelinus namaycush*) resulting from sea lamprey (*Petromyzon marinus*) parasitism have been used to inform fisheries management and sea lamprey control in the Laurentian Great Lakes for over 70 years (Eshenroder and Koonce 1984). Through a coordinated effort involving multiple agencies in the Great Lakes basin, sea lamprey wound data are collected on an annual basis and aggregated for many different uses. Wounding data have been used for estimating sea lamprey-induced mortality of target fish species (Schneider et al. 1996; Sitar et al. 1999; Bence et al. 2003; Lantry et al. 2015), evaluating the success of sea lamprey control program (Adams et al. 2003; Rutter and Bence 2003), allocating resources for sea lamprey control (Koonce et al. 2004; Irwin et al. 2012), and setting fish community targets (Horns et al. 2003). Given the important applications of these data, it is valuable to periodically assess the effectiveness of the standardized wound classification protocol to ensure wound data are accurate and reliably classified.

The procedures for collecting and aggregating sea lamprey wound data on lake trout have changed over time to meet shifting application and data quality needs. Initially, wound data were recorded as the total number of wounded lake trout and the average number of wounds per fish from sporadic netting efforts and creel censuses such as those in the South Bay of Lake Huron (Budd et al. 1969). Information about the size and latency of the wounds was sometimes included, but there was no standardized reporting procedure (Pycha and King 1975; Eshenroder and Koonce 1984). Concerns regarding the uniformity of wound data collection and the lack of clarity in descriptions of the character and age of wounds, prompted the development of the King Jr. (1980) classification system with the goal of standardizing the assessment and recording of wound data. This system classifies sea lamprey wounds as either Type A or Type B with four stages of wound healing (I-IV) (Figure 2.1). A type-A wound is recorded when the skin is broken exposing the underlying musculature, and a type-B wound is recorded when the wound site is abraded, but there is no visible evidence of broken skin. The stage of a wound varies from a very recent wound (stage I) to a nearly fully healed wound (stage IV) (King, Jr. 1980). For example, the most severe wound would be classified as A-I, showing exposed musculature and recent sea lamprey detachment, and the least severe wound would be classified as B-IV, showing a completely healed wound with regenerated scales. Following the development of the classification system, Eshenroder and Koonce (1984) published a report suggesting only large A-I through A-III wounds be reported. Type-A wounds were thought to be more reflective of host mortality, and easier to distinguish from type-B wounds; completely healed stage IV wounds were assumed to be caused by a previous cohort of sea lamprey (Eshenroder and Koonce 1984). The most recent guide (Ebener et al. 2006), incorporated findings from a series of workshops to revise guidelines for reporting multiple wounds, sliding wounds, and wound size in a further effort to improve wound classification agreement among different agencies and field crews. Currently, sea lamprey wound records are used for a variety of applications, with the number of AI-AIII wounds recorded during sampling efforts as the primary observation. The wounding data are then used to estimate both lake-wide lake trout wounding rates (also known as marking rates) that guide sea lamprey control efforts, and sea lamprey-induced mortalities based on area specific wounding rates. More recently, Great Lakes fisheries managers have become interested in wounding rates on other species (e.g., lake whitefish (*Coregonus clupeaformis*)) to quantify impacts on other populations and characterize how availability of other hosts affects lake trout wounding rates.

The use of wound data for fisheries management and research questions relies on two key assumptions. The first assumption is that sea lamprey wounds follow a predictable healing progression transitioning sequentially from stage I to stage IV within the initial wound type. Most current applications that use sea lamprey wound data rely only on A-I through A-III wounds (Rutter and Bence 2003), in an attempt to capture recent wounding by a single cohort of sea lamprey. For example, type-A wounds occurring in the late summer and fall are expected to remain as identifiable A-I through A-III wounds in the following spring surveys. If wound healing time is highly variable, some fast-healing wounds may progress to A-IV before spring surveys begin, while other slow-healing wounds from previous cohorts may still be present as A-I through A-III wounds. If a sizable proportion of wounds follow healing progressions that result in switching wound types (e.g., type-B to type-A), wound records may not be accurate reflections of the true state of sea lamprey wounding. The second assumption is that staff from a variety of different agencies are able to classify wounds accurately and reliably. Given many different state, provincial, tribal, and federal agencies are responsible for collecting sea lamprey wound data, the methods used to assess and record this information as well as the skill-level of individual assessors must be uniform. Inconsistent approaches to wound classification or variation in ability to assess wounds could result in over or under-reporting of wound rates. Furthermore, discrepancies in wound healing progression, as highlighted in the first assumption, will make the accurate and reliable classification of sea lamprey wounds more difficult as the key characteristics used to classify wounds may be obscured or difficult to identify.

The assumption that wounds follow a predictable healing progression and healing time lacks strong evidence. Studies that assessed wound healing times found considerable variation that could confound the ability to identify individual sea lamprey cohorts (Schneider et al. 1996;

Ebener et al. 2003; Nowicki 2008; Lantry et al. 2015). At water temperatures that lake trout experience in the Great Lakes, a substantial proportion of wounds that occur in late summer and fall would heal to stage IV before spring surveys (Bence et al. 2003; Ebener et al. 2003). Nowicki (2008) observed several instances of wounds changing type (from type-B to type-A) or following unexpected progressions (from A-IV to A-III) during the healing process. In field studies that assessed seasonal trends in wound rates during trawl and gill net surveys, little-to-no correlation was found between early stage wounds in early months and later stage wounds in later months (e.g., A-I wounds in July did not correlate with A-II wounds in September), suggesting discrepancies in wound healing progression or seasonal changes in survival of wounded fish (Schneider et al. 1996; Lantry et al. 2015). The relationship between healing time and water temperature may also result in a greater number of recorded wounds for benthic oriented lake trout that spend more time in cooler water where wounds heal more slowly (Bence et al. 2003). Finally, during our ongoing study assessing the sub-lethal effects of sea lamprey parasitism on lake trout, we noticed that many wounds did not appear to follow the healing progression outlined by the King (1980) classification system (Firkus, unpublished results). Often, wounds classified as type-B immediately after sea lamprey detachment appeared to follow a healing progression that would likely lead to identification as type-A after 8 to 12 months of healing (Figure 2.2). Despite known wound classification inconsistencies and the potential for non-conforming wound healing progression, the King (1980) system is currently the most frequently used classification scheme.

Several lines of evidence suggest that wound misclassification is occurring. Following a series of workshops, Ebener et al. (2003) found high variability among individuals and agencies when classifying sea lamprey wounds on lake trout. Counts of A-I through A-III wounds sometimes varied three-fold despite individuals classifying the same group of lake trout. Although training during the workshops somewhat improved overall wound classification agreement, it remained poor for most wound types, with some types having lower observer agreement following training. Observer agreement also varied considerably by wound type (Ebener et al. 2003). Workshops conducted in the mid-2000s also observed poor wound classification agreement (Nowicki 2008). The results from these workshops provide evidence that the assumption of high wound classification agreement among individuals and agencies may not be met. If wounds are consistently misclassified, estimates of sea lamprey damage and sea lamprey-induced mortality (used in fishery catch-at-age models) may not be accurate.

The last revision to the wound classification system guidelines was published over a decade ago (Ebener et al. 2006), yet the extent of wound classification inaccuracy and disagreement since then is currently not well characterized. The key objectives of this study are to quantify observer accuracy and agreement as well as the error associated with wound misclassification rates and overall wound detection rates, evaluate the efficacy of a workshop at improving wound classification agreement and accuracy, highlight wound types and locations that are particularly challenging to identify and classify, estimate healing the time between wound stages, and assess the degree to which wound healing progression conforms to the assumptions of the current classification system. Although similar workshops/studies have been conducted in the past, our study was the first to use fish with known wound histories, thereby permitting estimation of classification accuracy.

Methods

Fish

During October and November 2018, 24 twelve-year-old siscowet and lean lake trout reared and held at the University of Wisconsin-Stevens Point Northern Aquaculture Demonstration Facility (UWSP NADF) were parasitized in a laboratory setting by juvenile sea lamprey collected from Lake Superior. Hatchery lake trout have been used in previous studies (Goetz et al. 2010, 2014, 2016; Smith et al. 2016) and display similar physiological and morphological characteristics as their wild lake trout parents (Goetz et al. 2010). All sea lamprey used were actively parasitic and collected from lake trout hosts in the summer and early-autumn of 2018 by commercial fishing operations. Lake trout used in the study weighed from 2.19 to 5.14kg. Lake trout were removed from their raceways and individually placed in separate 1000L tanks (7-7.6°C), each containing one sea lamprey. Each tank was regularly monitored during the day for sea lamprey attachment. Once attached, sea lamprey were allowed to feed for four days after which they were removed to prevent high lake trout mortality rates; preliminary observations suggest parasitism events lasting over four days have a high likelihood of killing the host (Smith et al. 2016). Following parasitism, wounds were immediately classified as A-I or B-I using the Ebener (2006) classification guidelines, and pictures of the wound site on each lake trout were taken. The lake trout were returned to the raceways and allowed to heal at water temperatures ranging from 7.0 – 7.6°C. Wounds were classified, and pictures of the wound sites were taken every week following parasitism until the start of the workshop to monitor wound healing progression. An additional group of 11 lake trout unexposed to sea lamprey were set aside for workshop participants to classify as well, the first time unwounded fish have been included in a wound classification workshop. Fish were euthanized with an overdose of tricaine methane sulfonate (MS-222) following Michigan State University and University of Wisconsin-Stevens Point approved IACUC (Institutional Animal Care and Use Committee) protocols the day of the workshop to ensure good specimen quality. To supplement the lake trout with known wound history, 16 more freshly wounded lake trout collected during spring field surveys by the Red Cliff Fisheries Department and the Wisconsin Department of Natural Resources were also provided. Although the wound history of fish collected during field surveys was unknown, the wound type and stage for each was classified by two experts prior to use in the workshops to serve as a benchmark following guidelines from Engelhard (1996).

Wound healing time

The time required for a wound to heal to the next stage (e.g., time for an A-I wound to heal to an A-II wound) was assessed using pictures and records taken on a weekly basis for each fish following parasitism. For each fish, the number of days elapsed before transition to the next stage was recorded. A Weibull distribution was fitted to healing time between each stage for both wound types using maximum likelihood estimation with the fitdistrplus package (Delignette-Muller and Dutang 2015) in R 3.6.1 (R Core Team 2019). The mean and standard deviation of the Weibull distribution for time spent in each stage was calculated for each wound type (type-A and type-B). As wounds were only examined on a weekly basis, healing times are approximate. Wounds that resulted in fish mortality (n=5) were not included.

Workshop

On May 21-22, 2019, a workshop was held to evaluate and improve the accuracy and agreement of sea lamprey wound classification on lake trout. Twenty professionals from the Great Lakes Indian Fish and Wildlife Commission, Minnesota Department of Natural Resources, Red Cliff Fisheries Department, Sault Ste. Marie Tribe of Chippewa Indians, US Fish and Wildlife Service, US Geological Survey, and Wisconsin Department of Natural Resources attended. Most attendees were part of field assessment crews or had previous experience with wound classification, but three reported having no prior field experience with sea lamprey wound classification.

The workshop was structured as two separate wound classification trials: one on the first day soon after the participants arrived and one on the second day following debriefing, performance assessment, and additional training. For each trial, participants were presented with a series of lake trout (25 for trial 1, 22 for trial 2) to identify and classify the wounds present on the fish (if any). During the first trial, participants were asked to classify wounds using the procedures they were currently using in the field. During the second trial, participants were asked to incorporate what they had learned during the performance assessment and training when classifying fish. For both trials, participants were not informed whether each lake trout was wounded or not, and no discussion between participants was permitted. To more closely simulate field conditions, the participants were limited to 90 seconds per fish to identify any wounds (if present) and record their classification. Participants were also asked to record the location of each wound and indicate whether the wound would be recorded in their agencies wound survey data.

The performance assessment and training were both designed to refresh participants on the wound classification procedure, highlight wounds that are often difficult to classify, and allow participants to discuss potential causes of variation in classification. Following the first wound classification trial, participants were given presentations about the wound classification system, wounds that are difficult to identify or classify, and how sea lamprey wound data are used to inform fisheries management in the Great Lakes. Participants were also given a hands-on demonstration of how to classify wounds on several fish. Photos of sea lamprey wounds were presented and participants were asked to discuss with the group which classification they would give each fish and why. Before the second trial, participants were also shown the results of the first trial accompanied with pictures of the initial wound and the subsequent pictures of the wound as it healed. Following the second wound classification trial, participants were split into three discussion groups. Each group was asked to discuss 1) what aspects of sea lamprey wound identification most surprised them 2) problems with wound classification 3) how wound classification and the system as a whole could be improved. After discussion within the groups, one person from each group was asked to present their findings to everyone. Key discussion points and findings were summarized. Notes from the group discussions are included in Appendix III. Participants were also given a post-workshop survey where the usefulness of the workshop and general comments were recorded (Appendix IV). Results from the second wound classification trial were compiled and sent to participants via email after the workshop.

Agreement, accuracy, and misclassification statistics

Gwet's First-Order Agreement Coefficient (AC_1) calculated with the R package ragree (Redd 2019) was used to assess the chance-corrected agreement among participants classifying sea lamprey wounds (Gwet 2008). Agreement was assessed overall for all wounds as well as broken down by wound type and wound stage (stage I-III and stage IV). AC_1 values less than 0.20 were considered poor agreement, 0.21-0.40 were fair, 0.41-0.60 were moderate, 0.61-0.80 were substantial, and 0.81-1.0 were considered almost perfect agreement (Landis and Koch 1977). For comparison purposes with previous studies (Ebener et al. 2003), an AC_1 value of 0.4 was considered the minimum satisfactory level of agreement.

Wound classification accuracy was assessed by comparing participant classifications to benchmarks obtained via discussion and consensus of two expert panelists following guidelines from Engelhard (1996). Accuracy was assessed as the percentage of participants who correctly classified both the wound type (type-A or type-B), and wound stage (I-IV) as indicated by the benchmark classifications. Because we were also interested in the ability of participants to distinguish between type-A and type-B wounds, the percentage of participants who correctly classified the wound type (regardless of stage) was also recorded. For fish with multiple wounds, the classification was only considered correct if the participant correctly classified all wounds present. Classifications from fish with multiple wounds were not included when reporting summarized accuracy as it was not possible to determine which wound(s) were incorrectly classified. Since counts of A-I through A-III wounds are often aggregated for lake-wide wounding rate estimations, the percentage of A-I through A-III wounds that were classified within the aggregated A-I through A-III category (even if not exactly correct) was also calculated.

To quantify misclassification rates, wound classification data from both trials were combined. Accuracy and agreement was consistent between trials, so pooling among trials was justified. Wound classification data from fish with multiple wounds were removed from misclassification rate estimates as it was impossible to determine which individual wound was classified by the participant. For each wound type and stage, participants' responses were tabulated to display the percentage of correct and incorrect classifications. Incorrect classifications were further subdivided into the specific misclassified response.

Results

Wound healing time

Healing time from stage I to stage II was similar for both type-A and type-B wounds (Figure 2.3). The time for an A-I wound to heal to an A-II wound was 11±3 days (mean ± standard deviation), and the mean healing time for B-I to B-II was 9±3 days. Progression from stage II to stage III was considerably more variable than from stage I to stage II for both wound types (Figure 2.3). Healing to stage III took approximately half as long on average for type-A wounds (32±12 days) than for type-B wounds (68±33 days). Similarly, healing time from stage III to stage IV was shorter for type-A wounds (45±26) than for type-B wounds (64±20). Overall healing time from stage I to stage IV ranged from 10 to 133 days for type-A wounds (mean 96±15).

Although wounds that resulted in lake trout mortality were not included in wound healing time analysis, two lethal wounds followed uncharacteristic healing progressions. In one instance, a lake trout received multiple type-B wounds from a sea lamprey. The wounds initially appeared mild but during the healing process the wound sites became inflamed and necrotic, ultimately leading to the death of the fish after 21 days (Figure 2.4). Three other instances of a type-B wound resulting in lake trout mortality were observed, but these followed expected type-B wound healing progressions.

Wound classification agreement

For the first wound classification trial, overall agreement among reviewers was “fair” (AC_1=0.36) (Table 2.1). Agreement varied by wound type and stage. Unwounded fish had the highest classification agreement (AC_1=0.79), and fish with multiple wounds had the lowest classification agreement (AC_1=0.15). A-I through A-III wounds had only “slight” agreement (AC_1=0.15). During trial 1, type-B wounds had greater classification agreement than type-A wounds, and earlier stage wounds (I-III) had lower classification agreement than late stage wounds (IV) (Table 2.1). With the exception of type-B wounds (Z-test, z=1.59 p=0.06), agreement was statistically greater than expected by chance ($p<0.05$). Classification agreement was also below the 0.4 threshold for all categories except unwounded fish.

Overall classification agreement improved slightly for trial 2 (AC_1=0.37), but agreement among reviewers remained “fair”. Despite the slight improvement in overall agreement, the improvements were inconsistent across wound types. Although agreement was higher in trial 2 for type-A, stage I-III, and stage IV wounds, it was lower for type-B, unwounded, and fish with multiple wounds (Table 2.1). Agreement was also higher in trial 2 for A-I through A-III wounds (AC_1=0.32), but was more variable than in trial 1. Agreement among observers was statistically greater than chance alone ($p<0.05$) for all categories with the exception of fish with multiple wounds (Z-test, z=1.24, p=0.11) and A-I through A-III wounds (Z-test, z=1.34, p=0.09). Classification agreement remained below the 0.4 threshold for all categories except unwounded fish.

Wound classification accuracy

In the first trial, lake trout wounds were correctly classified 28% of the time (Table 2.2). To break this down further, unwounded fish had the highest classification accuracy (89%), and fish with multiple wounds had the lowest classification accuracy (2%). Participant's ability to correctly classify wounds did not vary by wound type, but was more accurate for early stage wounds (stage I-III) than late stage wounds (Table 2.2). On a coarser scale, participants identified the correct wound type (regardless of stage) 52% of the time. Type-A wounds were correctly classified as type-A 57% of the time, and type-B wounds were correctly classified as type-B 49% of the time. Stage I-III wounds were easier to classify to wound type than stage IV wounds (67% and 25% respectively). Fish with multiple wounds had all wounds correctly identified to wound type 5% of the time. Stage I-III wounds were accurately identified to wound type 67% of the time (Table 2.2). Participants classified A-I through A-III wounded fish within the A-I through A-III category 67% of the time in trial 1, and non-A-1 through A-III fish (unwounded, A-4, and B-I through B-IV) were classified in the A-I through A-III category 5% of the time.

Overall classification accuracy improved slightly in the second trial with 29% of wounds being correctly classified to wound type and stage (Table 2.2). Unwounded fish continued to have the highest classification accuracy, but accuracy declined from the first trial (69%). Accuracy classifying fish with multiple wounds improved to 12%. Type-A and type-B classification accuracy remained similar to trial 1. Accuracy improved slightly over trial 1 for stage I-III wounds. A-I through A-III wounds were more accurately classified in trial 2 (53%). Despite slight improvements in classifying wounds to both type and stage, on a coarser scale, ability to classify the correct wound type (regardless of stage) was worse overall (47%).

However, accuracy to wound type improved for all stage I-III wounds and for A-I through A-III wounds (80 and 83% respectively) (Table 2.2). In trial 2, participants classified A-I through A-III wounded fish within the aggregated A-I through A-III category 81% of the time, and non-A-1 through A-III fish (unwounded, A-4, and B-I through B-IV) were classified in the A-I through A-III category 7% of the time.

Misclassification rates

For most wound types and stages, the majority of misclassifications were off by only one stage. For example, A-II wounds were correctly classified 44% of the time, but were misclassified as A-I 17% of the time and as A-III 12% of the time (Table 2.3). Although wounds going undetected were relatively infrequent for wounds in stage I-III, both A-IV and B-IV wounds were highly likely to be missed and classified as unwounded (64% and 49% respectively). Type-B wounds appeared to be frequently misclassified as type-A wounds at later stages of healing. For example, B-II wounds were classified as A-III or A-IV wounds 34% of the time, and B-III wounds were classified as A-III or A-IV wounds 30% of the time. Participants appeared to distinguish early stage A wounds (I-III) from late stage A wounds (IV) with reasonable success. A-I through A-III wounds were classified as A-IV wounds fewer than 10% of the time (Table 2.3). Note that sample sizes were small for some wound types.

Group discussion

When asked to discuss what aspects of wound classification surprised them the most after seeing the results from trial 1, several themes were commonly expressed (Appendix III).

Multiple groups mentioned having difficulty identifying wounds in unexpected locations such as on fin rays or the operculum. Wounds in unexpected locations were discussed in detail following trial 1, and some participants noted seeing wounds in these locations fairly frequently during field surveys. However, some participants mentioned that knowledge of wounds in unexpected locations may have led them to be more likely to classify a fish as wounded during trial 2, even if no wound was present. Each group also indicated that wound healing progressions where type-B wounds transition into type-A wounds after a skin sloughing event was surprising. The quick healing times of some wounds and the high level of disagreement between classifications of type-A and type-B wounds were also unexpected.

Groups were asked to identify any problems they were encountering with the current wound classification system. One concern mentioned was that most field crews do not have sufficient time to thoroughly assess a fish for sea lamprey wounds which may increase the proportion that are missed. The inherent subjectivity in the wound classification process was also identified as a potential problem for reliable and accurate wound records and was highlighted by the variability in wound classification. Often during field surveys, multiple people will examine a wound and come to a consensus which may reduce variability. Participants also mentioned that the perceived importance of A-I through A-III wounds may result in more attention being paid to those wounds when found in the field. As a result, fewer A-IV or B-I through B-IV wounds may be recorded, and misclassification rates may be higher as an artifact of less time being spent assessing these wounds.

Not all of the recommendations in the most recent guide (Ebener et al. 2006) are universally followed. For example, the reporting guidelines state that wound size should be recorded, so sea lamprey cohorts can be separated (Ebener et al. 2006). Larval sea lamprey typically spend a number of years growing in stream sediment before metamorphosing and migrating to a Great Lake during the fall (Manion and Smith 1978; Hanson and Swink 1989), although outmigration has been observed throughout the year (Applegate and Brynildson 1952). The parasitic juveniles then feed on fish for the next 12-18 months after which they stop feeding and switch energy allocation to spawning, at which point they are considered adults. During April through June, adults are sexually mature and seek out a tributary in which to spawn, and subsequently die (Nowicki 2008). Thus, two cohorts of sea lamprey are present in the lake at a given time. The intent of the classification guide was to omit smaller wounds (less than 20 mm) associated with recently out-migrated juveniles as they are unlikely to cause damage to fish stocks (Ebener et al. 2006). Agency adherence to this guidance is unknown; currently we are aware of only one agency (Ontario Ministry of Natural Resources and Forestry on Lake Huron) recording wound sizes.

Each group was also asked to discuss potential ways wound classification could be improved going forward. All groups identified improving and standardizing wound classification training. Ideas included requiring an online quiz each season prior to field work that must be passed before an individual is authorized to classify wounds, and holding regular “hands-on” workshops. Such approaches may reduce the likelihood of improper techniques or practices being passed down to newly hired staff. Our post-workshop survey indicated participants generally found value in this type of workshop (Appendix IV).

Discussion

Assumptions of consistent wound healing time and progression, high classification agreement among reviewers, and high reviewer accuracy are likely not being met. Wound healing times varied considerably and some wounds did not follow expected healing progressions. Classification agreement was below the minimum threshold for all wound types with the exception of unwounded fish. Reviewer accuracy was also generally low, though A-I through A-III wound classification accuracy did improve following training. The implications of and potential solutions to these issues vary and are discussed in further detail below.

Wound healing time

The wound classification system relies on the assumption that as a wound heals, it will follow a predictable healing pattern transitioning sequentially from stage I to stage IV within the initial wound type. Additionally, it is assumed that the time required to heal from one stage to the next is consistent enough that wounds can be attributed to different cohorts of sea lamprey based on the healing stage. However, studies that have assessed wound healing time have found considerable variation that could influence the ability to separate cohorts (Ebener et al. 2003; Nowicki 2008). Variation in healing time was high enough in wild-caught lake trout that Nowicki (2008) concluded wound classification schemes should not be used as an indicator of time since wounding or of the health of the host fish. Our results provide some support for these previous findings. Healing times in our study did vary, but the variation was stage dependent. Although healing times from stage I to stage II were fairly consistent for both type-A and type-B wounds, healing to later stages had high variation. Despite this variability, all healing times we observed were relatively rapid compared to the assumption that wounds occurring in autumn will remain as A-I to A-III wounds in spring. For the type-A wounds we monitored in our study, nearly all of them would have transitioned to A-IV wounds prior to spring surveys and therefore would not be included in A-I through A-III wounding statistics if they were classified in the field.

Many factors can influence wound healing times. Healing times are known to change with water temperature, which could contribute to the rapid healing we observed. Wounded lake trout in this study were allowed to heal at consistent temperatures of 7-7.6°C, and had similar healing times to those reported at 10°C (Ebener et al. 2003). Wounds occurring on fins, or the operculum also appeared to heal much more rapidly than other wounds which may reduce the likelihood of detection for these wounds. Wounds in such locations have been observed leading to mortality and sub-lethal effects on lake trout (Firkus, unpublished results), so detection of these wounds is still important. Further work quantifying the healing times of wounds on different morphotypes of lake trout from different lakes and water temperatures would be beneficial to understand the implications of healing time for wound records. Regardless, our results add support to previous findings that observed healing times are likely problematic for the assumption that A-I through A-III wounds capture the activity of the most recent cohort of parasitic sea lamprey (Bence et al. 2003; Ebener et al. 2003; Nowicki 2008).

In addition to healing time variation, observations of wounds following healing progressions that do not conform to the classification system may challenge wound data assumptions. Wounds similar to the ones shown in Figures 2.2 and 2.3 show an increase in severity as they heal, either with the wound changing from type-B to type-A or with a type-B wound leading to mortality. Other studies have documented similar findings; either as wound classifications progressing from a later to earlier stage (Nowicki 2008), or as "sloughing B-wounds" where tissue around a type-B wound will slough off exposing underlying musculature and taking on the appearance of a type-A wound (Ebener et al. 2003, 2006). Additionally, four type-B wounds resulted in lake trout mortality during this study. Current use of sea lamprey wound records only consider A-I through A-III wounds under the premise that type-B wounds do not contribute significantly to host mortality (Eshenroder and Koonce 1984; Ebener et al. 2003, 2006). Although it is likely that type-A wounds result in lake trout mortality more frequently, the assumption that type-B wounds do not inflict mortality may not be valid. Adams et al. (This volume) explored this in simulations, and found that increasing the type-B lethality rate from 0 to 24% of the type-A lethality rate (the maximum observed by Swink 2003) did not significantly change the relation between observed wounding rates and underlying true attack rates.

Classification agreement

High wound classification agreement amongst reviewers is an important assumption of the use of sea lamprey wound data. Unreliable and inconsistent classification by individual assessors and field crews could skew sea lamprey damage and fish population estimates. Wound records could also be spatially inconsistent if wound classification varies considerably among field crews covering different geographical areas of the Great Lakes. Likewise, wound records across years could be influenced by low classification consistency, especially if consistency changes over time due to new employees or adoption of new techniques and guidelines. Consistent with our findings, previous studies have found relatively poor classification consistency and agreement, both among agencies and individuals assessing the same lake trout (Ebener et al. 2003; Nowicki 2008). In a prior study, researchers found that even following training, there was a two-fold difference in wounding rate records among agencies, and a four-to-five-fold difference among individual observers assessing the same fish (Ebener et al. 2003). Later workshops where participants classified pictures of wounds also found low observer agreement (Nowicki 2008). Although overall agreement was greater than due to chance, it was only in the “fair” category both before and after training (Landis and Koch 1977). Only unwounded fish had classification agreement that exceeded the 0.4 AC_1 threshold. Thus, the the assumptions of high classification agreement among individuals was not met.

In our study, classification agreement varied by wound type and stage. Classifications of unwounded fish had the highest observer agreement (moderate-to-substantial) suggesting there is little confusion between observers when no wounds are present. Unsurprisingly, agreement was lowest for fish with multiple wounds. Not only is it more difficult to find multiple wounds on a fish, but when they are found, there will be inherently more disagreement by virtue of having more than one wound to classify. Agreement was not consistently higher for type-A or type-B wounds, but early stage wounds (I-III) had consistently lower agreement than stage IV wounds. Part of the reason for higher agreement for stage IV wounds could be attributed to the high misclassification frequency of fish with stage IV wounds as unwounded fish (Table 2.3). If a large proportion of observers classify a stage IV wounded fish as unwounded, agreement would still be high despite poor accuracy.

Classification of sea lamprey wounds is an inherently subjective process, so some degree of inconsistency and disagreement among reviewers and agencies will always be present. However, it is likely that not all of the inconsistency is due to the inherent subjectivity of the classification system. During the group discussions, some participants mentioned that they did not feel training for new hires was sufficient. Currently, there is no coordinated training program available for new hires working on biological crews that assess sea lamprey wounds on fish. As a result, trainees may receive different information depending on the experience of their co-workers and the guidance materials provided. Additionally, wound classification guidelines have been updated several times since originally published, and therefore it may be difficult for fisheries managers and field crew leads to identify the most up-to-date wound classification guide. As a consequence, field crews may be basing their classification practices on different iterations of the wound classification guidelines which could contribute to low consistency and agreement.

Classification accuracy

Fish with known wound histories created a unique opportunity to assess the accuracy of sea lamprey wound classification. We were able to compare participants' classifications with pictures of the wound's healing progression and expert benchmarks to determine if their classifications accurately reflected the known wound type and stage of healing. Previous studies have recorded classification agreement, but classification accuracy has not been previously documented. Accurate wound classification is a critical assumption for the use of wound data. When estimating sea lamprey damage, managers require wound records from the current year's cohort of sea lamprey. To obtain these, generally only records of A-I through A-III wounds are used under the premise that type-B wounds do not contribute significantly to host mortality and stage IV wounds are the result of a previous cohort of sea lamprey no longer present in the lake (Eshenroder and Koonce 1984; Ebener et al. 2003, 2006). The best practice is to record all wounds to allow for adjustments to be made if accuracy is low to the degree that A-I through A-III wounds cannot be distinguished from A-IV or B wounds, and to inform other applications that require consideration of all wound types.

Although the accuracy of specific wound classifications has not been investigated previously, findings of low classification agreement among individual assessors indicates a high rate of wound misclassification (Ebener et al. 2003). The present study found that overall accuracy for all wound types was low both before and after training. Before training, only 28% of wounded fish were correctly classified to both wound type and stage. Following training, 29% were correctly classified. Such low accuracy rates may help explain the discrepancies in records of A-I through A-III wounds observed in other workshops. Accuracy for stage I-III wounds was generally higher than for stage IV wounds (Table 2.2) with a large proportion of participants misclassifying stage IV wounded fish as unwounded (Table 2.3). A-IV wounds were also more frequently classified as B-IV wounds than they were A-type wounds (Table 2.3). Although misclassifying stage IV wounds as the incorrect wound type or as unwounded fish would not have consequences for the current method of estimating sea lamprey damage, it should be accounted for in applications that require all wound stages. Currently, A-I through A-III wounds are aggregated when used to estimate sea lamprey damage, so it is not necessarily critical that wound classifications are correct for both wound type and stage. A-I through A-III wounds were correctly classified as A-I through A-III wounds 81% of the time following training which suggests that these estimates may be reasonably reliable when assessors have been trained. However, pre-training accuracy within the A-I through A-III category, which likely better represents current accuracy rates, was only 67%. Furthermore, the finding that type-B wounds are commonly misclassified as type-A at all stages (Table 2.3) could have implications for sea lamprey damage estimates as counts of A-I through A-III wounds would be inflated and sea lamprey-induced mortality will be overestimated. The degree of classification accuracy necessary for informing management decisions is unknown, but the assumption that wound classification accuracy is high may not be met, particularly when accuracy to wound type and stage is required.

The low accuracy and high rates of misclassification observed during this workshop have a number of potential causes. One factor that likely contributes to wounded fish being classified as unwounded fish is the presence of difficult-to-detect wounds. During the group discussions wound location and visibility were identified as potential factors that could influence classification accuracy. Participants also mentioned that many wounds heal in a manner that makes them difficult to classify accurately. Type-B wounds in which damaged skin sloughed off exposing the underlying musculature was noted as being particularly problematic and may contribute to difficulties with accurately classifying wounds. Varying degrees of severity within each wound type and stage also likely contributes to low accuracy. Small type-A wounds may not leave obvious characteristics indicative of a type-A wound for assessors to identify after the wound has begun healing. Likewise, large type-A wounds may make identification of the stage of healing difficult due to inconsistent healing of the entire wound surface.

Potential solutions

Although the results of this study suggest low wound classification agreement and accuracy among observers, there are several steps that can be taken to improve these metrics. One suggestion that was mentioned and supported during group discussions was to increase and standardize wound classification training for field crews tasked with wound classification surveys. Despite low wound classification agreement and accuracy suggesting that further training is necessary, there is little evidence that single-event workshops improve these metrics. In this study, wound classification agreement and accuracy only improved marginally following training. We did see improvement in the classification of A-I through A-III wounds during our workshop, but variability in agreement and accuracy was high. Other workshops similarly observed little or inconsistent improvement in classification agreement following training (Ebener et al. 2003; Nowicki 2008). Although there is little evidence that wound classification workshops improve wound classification agreement and accuracy, it does not mean that holding regular standardized training would not be beneficial. The group discussions indicated that there were a variety of approaches to handling multiple wounds, wound size, and wound identification among participants suggesting there is still room for standardization. A coordinated effort to develop a standardized training and data recording program may improve agreement and consistency by virtue of everyone receiving the same training. Additionally, it is possible that the training approaches taken in wound classification workshops, including this one, were not effectively designed to meet the goal of improving agreement and accuracy. If more targeted consideration were put into the development of training materials and methods, improvements may be achievable.

Another possibility to reduce the influence of low classification agreement and accuracy would be to incorporate misclassification rates into applications that use wound data. Wounding data are currently used to inform statistical catch-at-age models and provide insight into the binational sea lamprey control program. Misclassification rates for each wound type could inform priors in a Bayesian modeling approach, be used to modify wound records before use, or be incorporated in a sensitivity analysis to quantify the effects of wound misclassification on model estimates. Assessment of misclassification rates give some insight into how wound data might be adjusted to reflect what we know about wound classification accuracy. However, our workshop was held once with a relatively small number of participants and it is therefore likely that a repeat of this workshop in other locations would be necessary to obtain error estimates required for any type of correction factor. Alternatively, Adams et al. (This volume) suggest that statistical catch at age models should incorporate sea lamprey abundance estimates via a functional response model as a way of calibrating observed wounding rates.

Other biomarkers may be more reliable indicators of parasitism status than classification of sea lamprey wounds. If a protein biomarker expressed in parasitized individuals could be identified with a simple, non-invasive, and low cost blood test, difficulties with the use of a subjective classification protocol may be avoided. Similar approaches have been used previously to identify biomarkers indicative of bitumen exposure in sockeye salmon (*Oncorhynchus nerka*) (Alderman et al. 2017), environmental estrogen exposure in Atlantic salmon (*Salmo salar*) (Arukwe et al. 1997), and for a wide array of contaminants in toxicology applications (Gupta 2014). However, finding biomarkers that are cost effective, reliable predictors of ecological effects can be challenging (reviewed in Forbes et al., 2006) and using biomarkers to estimate risk to populations is generally not advised (Hanson 2009). Ideally, any biomarker developed would be a time sensitive measure of parasitism, as most current management applications of wound data attempt to associate wounds with a given year in order to evaluate the success of the sea lamprey control program or direct influences on fish mortality. Despite these challenges, approaches to biomarker identification have become more sophisticated (Song et al. 2008), and if developed could play an important role in estimating parasitism intensity.

Conclusion

The Great Lakes Fishery Commission's sea lamprey control program assists managers in meeting fish community objectives (Gaden et al. 2008), with a goal toward restoration of native lake trout stocks (Treska et al. this volume; Stewart et al., 2003). Records of sea lamprey wounds on lake trout are the primary tool used to evaluate lake trout objectives and assess the effectiveness of the sea lamprey control program (Stewart et al. 2003). Given the importance of wound data for assessing and directing management plans, it is critical that the underlying assumptions behind their use are evaluated and the degree to which the assumptions are met is well characterized. The results of this workshop suggest that wound classification agreement and accuracy are low, and misclassification rates are high for most wound types, consistent with previous workshops assessing similar metrics (Ebener et al. 2003; Nowicki 2008). Because high classification agreement and accuracy are important assumptions of wound data use, the reliability of wound data as an indicator of the success of lake trout rehabilitation and sea lamprey control efforts may merit more critical evaluation.

Despite these concerns, several approaches may improve the reliability of wound data going forward. Although previous efforts, including this workshop, have not demonstrated the ability to markedly improve wound classification accuracy and agreement, a better designed training program adopted by all agencies doing field assessments may be able to improve the reliability of wound data. Additionally, more work characterizing misclassification rates may allow for inaccuracies in wound records to be accounted for in modeling efforts. More work is needed to understand the extent to which current inaccuracies in sea lamprey wound classification can influence the evaluation of fish community targets in the Great Lakes.

APPENDICES

APPENDIX I

Tables

Table 2.1. Classification agreement for workshop participants before training in trial 1, and after training in trial 2 by wound type and stage.

	Agreement (Gwet's AC_1)	
	Trial 1	Trial 2
All Wounds	0.36	0.37
Type-A	0.23	0.34
Type-B	0.30	0.26
Unwounded	0.79	0.57
Multiple Wounds	0.15	0.10
Wound Stage I-III	0.15	0.25
Wound Stage IV	0.23	0.31
A-I through A-III	0.15	0.32

Table 2.2. Percentage of wounds correctly classified by workshop participants before (trial 1) and after (trial 2) training. Classifications from fish with multiple wounds were not included in other categories as it was not possible to determine which wound(s) were incorrectly identified.

	Trial 1			Trial 2		
	% correct (both type and stage)	% correct (type only)	n	% correct (both type and stage)	% correct (type only)	n
All Wounds	28	52	280	29	47	273
Type-A	25	57	181	31	52	153
Type-B	26	49	99	25	39	120
Unwounded	89	89	92	69	69	116
Multiple Wounds	2	5	118	12	19	58
Wound Stage I-III	36	67	180	48	80	97
Wound Stage IV	14	25	100	18	28	176
A-I through A-III	37	67	141	53	83	78

Table 2.3. Comparison of known wound classification with the classifications of workshop participants. The percentage of participants correctly classifying each wound type and stage is presented in bold.

		Known Wound Classification								
		A-I	A-II	A-III	A-IV	B-I	B-II	B-III	B-IV	Unwounded
Participant Classifications (%)	A-I	**36**	17	2	1	-	0	0	0	0
	A-II	21	**44**	9	3	-	0	0	4	0
	A-III	14	12	**62**	3	-	26	10	2	1
	A-IV	0	3	9	**7**	-	8	20	7	2
	B-I	0	2	4	1	-	11	0	2	1
	B-II	0	7	2	1	-	**34**	10	3	0
	B-III	14	3	9	6	-	21	**35**	10	1
	B-IV	7	2	4	16	-	0	25	**23**	16
	Unwounded	7	8	0	63	-	0	0	49	**78**
	Sample Size	1	7	3	6	0	3	1	7	11

APPENDIX II

Figures

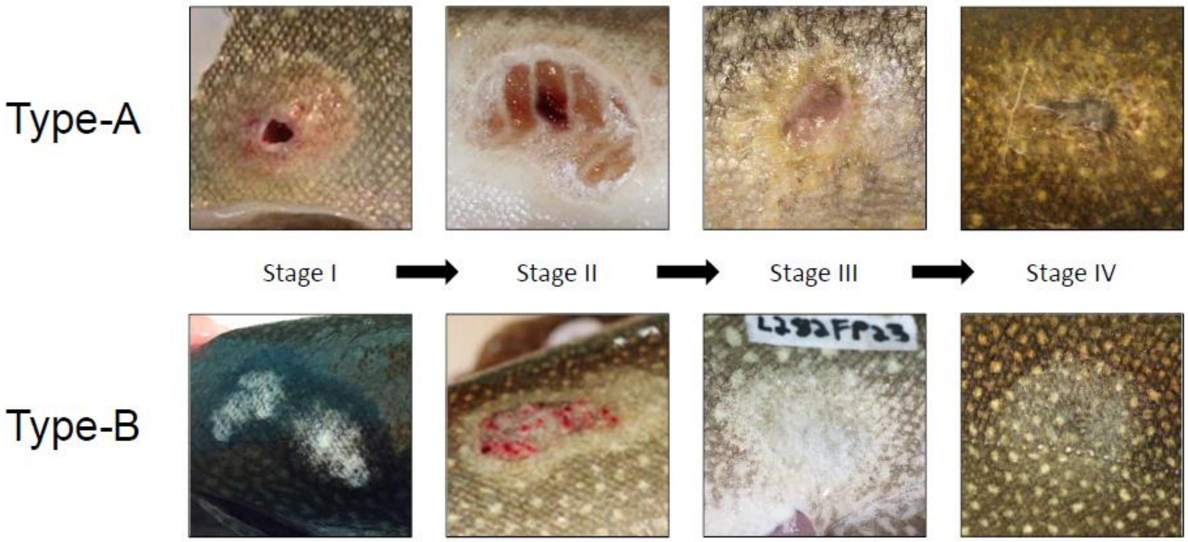

Figure 2.1: Examples of lake trout with sea lamprey wounds for each wound type (A and B) and stage (I-IV) in the King (1980) classification system.

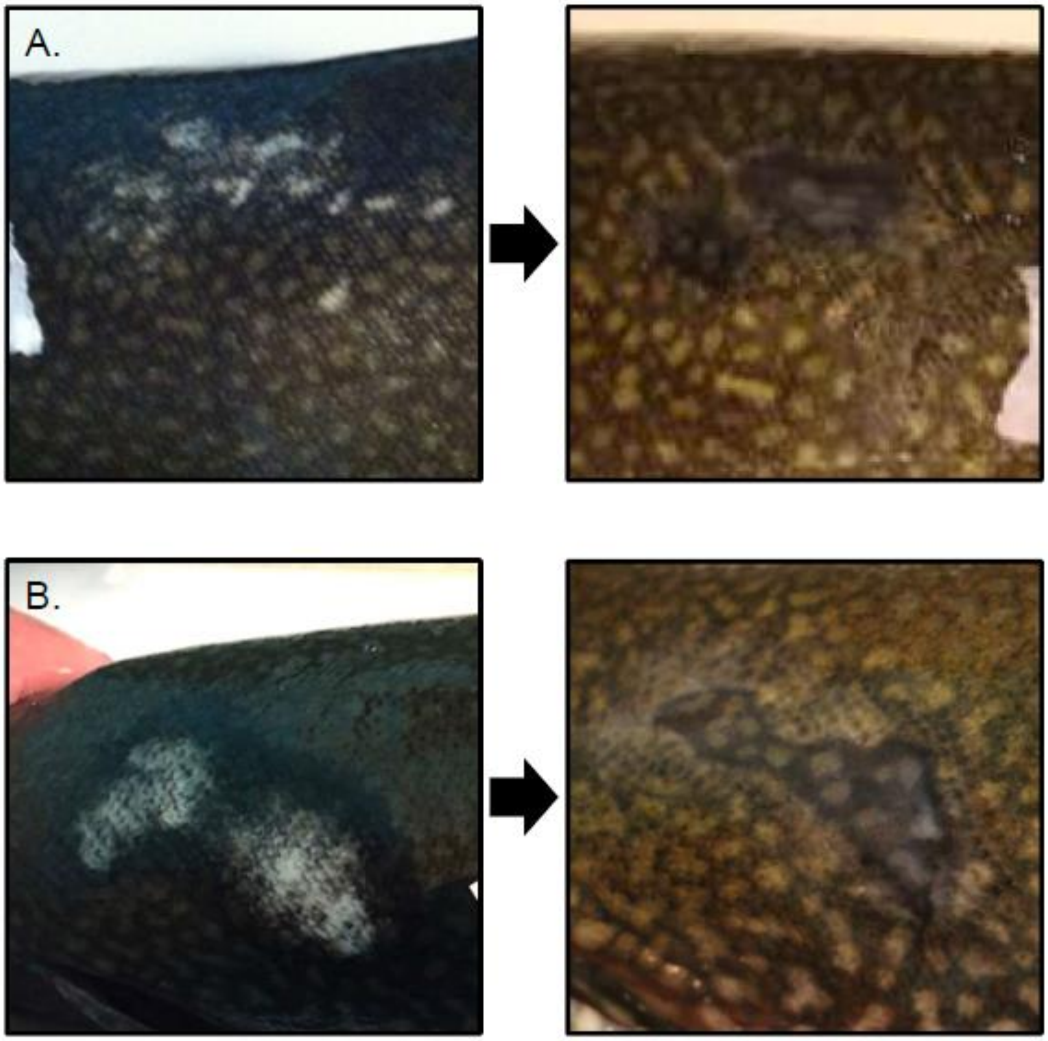

Figure 2.2. Examples of two lake trout (A. and B.) with wounds that were classified as B-I wounds immediately following sea lamprey detachment, but matched an A-IV classification after healing.

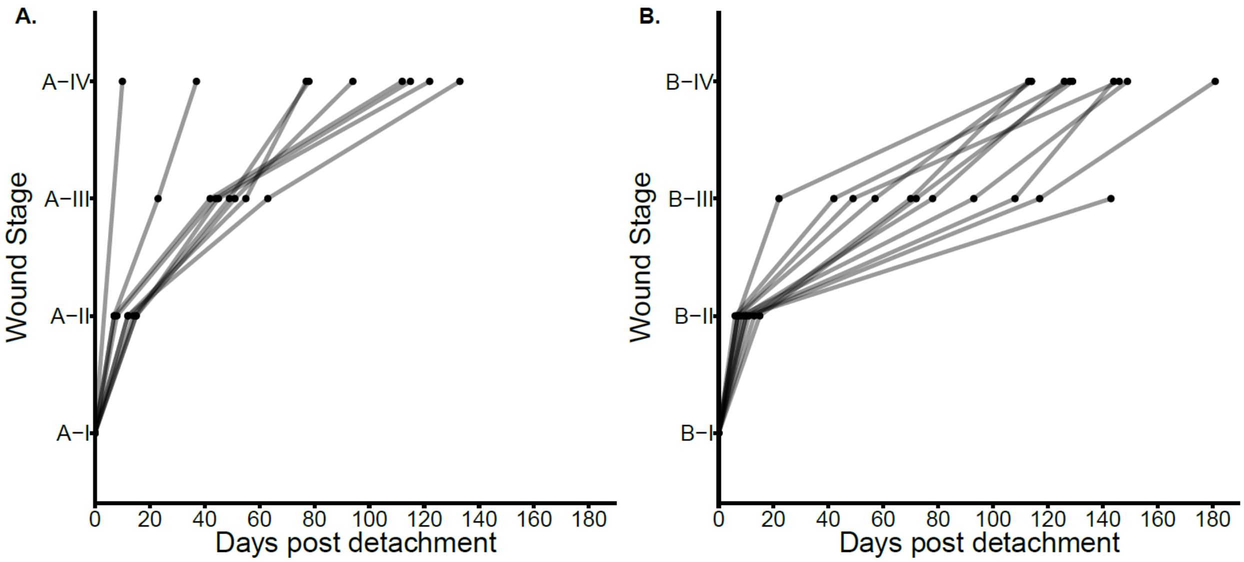

Figure 2.3: Number of days elapsed following sea lamprey detachment for individual type-A (A.) and type-B (B.) wounds to transition to each subsequent stage of the King (1980) wound classification system. Each line tracks a wound on an individual fish with points indicating the day the wound was observed to transition to the designated stage.

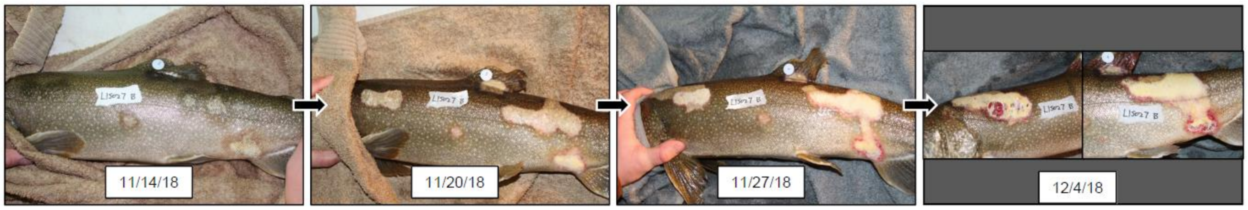

Figure 2.4: A lake trout wound that was classified as B-I following sea lamprey detachment. Over 21 days, the wound became more severe ultimately resulting in mortality.

APPENDIX III

Summary of group discussions

Summary of group discussions

After the second wound assessment trial, participants were split into three separate discussion groups and asked to discuss the following questions. A summary of recorded responses to each question is included below:

1. *What aspects of lamprey wound classification surprised you the most?*

- Wounds on fins
- B wounds morphing into A-looking wounds
- Disagreement on A vs. B classification
- How quickly some wounds healed to being undetectable
- Weird location wounds disappeared quickly
- Finding wounds on fins is just as common as what was observed in the lab setting
- Variations in wounds
- Sloughing skin on B-wounds looking like A-wounds

2. *What are some of the problems with wound classification?*

- Time needed to accurately identify/classify wounds
- Perceived importance of A1-A3 and unimportance of A4, B1-B4
- Subjective
- Sloughing skin B-wounds
- Time constraints may result in missing many hard-to-see marks
- How much differently 2 people can view the same

3. *How can we improve wound classification and the system as a whole?*

- Enforced spring training using online quiz (e.g. lake committee and tech committee require 80% correct before you can classify)
- Hands on workshop every 5 years
- New laminated picture ID key
- Piggybacking training onto occasional technical committee meetings
- Continuing trainings like this, and improve standardization
- Multiple people looking at each fish
- More online quizzes
- Refresh yourself before going out on surveys

APPENDIX IV

Workshop evaluation

Workshop Evaluation Form – Summary of Responses

Below is a summary of responses to the post-workshop evaluation survey. Questions are listed in the order in which they appeared with the percent of respondent's answers provided for each question.

	Strongly agree 1	2	3	4	**Strongly disagree** 5
1. The content was as described in publicity materials	70%	20%	10%	0%	0%
2. The workshop was applicable to my job	85%	15%	0%	0%	0%
3. I will recommend this workshop to other fishery professionals	100%	0%	0%	0%	0%
4. The program was well paced within the allotted time	70%	25%	5%	0%	0%
5. The instructor was a good communicator	85%	15%	0%	0%	0%
6. The material was presented in an organized manner	55%	45%	0%	0%	0%
7. The instructor was knowledgeable on the topic	80%	20%	0%	0%	0%
8. I would be interested in attending a follow-up, more advanced workshop on this same subject	65%	15%	10%	10%	0%

9. Given the topic, was this workshop: ❑ a. Too short (10%) ❑ b. Right length (90%) ❑ c. Too long (0%)

10. In your opinion, was this workshop: ❑ a. Introductory (10%) ❑ b. Intermediate (70%) ❑ c. Advanced (20%)

*many participants noted that it was appropriate for all levels

11. Please rate the following:

	Excellent	Very Good	Good	Fair	Poor
a. Lake trout specimens	50%	30%	20%	0%	0%
b. Slide show	37%	63%	0%	0%	0%
c. Meeting space	45%	35%	20%	0%	0%
d. Presentations	60%	30%	10%	0%	0%
e. The program overall	45%	55%	0%	0%	0%

12. What did you most appreciate/enjoy/think was best about the course? Any suggestions for improvement?

Individual responses listed as separate bullet points:

- Great training, have more!
- The wounds that had pictures with timelines from lamprey removal to present were great! The lake trout heal quicker than I thought.
- Real specimens and next day feedback on classifications. I felt there was more conversation (good thing) during this workshop compared to other workshops I've attended. Something to do

w/# of people?

- Appreciated Tyler leading us through marking and his research. Longer workdays would be fine, lots of travel would be offset by longer working days
- I liked practicing on the specimens both days to get a good feel for the technique
- Discussion of how to improve system training, etc. Maybe should try to do another workshop in a couple years and re-evaluate.
- Great refresher and created some excellent discussion on the topic. Improvement on course: get more people/groups/affiliations working with lamprey wounding involved
- Thought it was good overall, whether advanced or beginner. Presentations were well thought out with plenty of discussion time.
- Overall just getting more training on wounding was very useful. A little more time to discuss different wounds
- Hands on fish samples
- Overall it was a good opportunity to spend time assessing and discussing wounds on actual specimens, not just pictures
- The discussions and feedback from the participants
- Only feedback for improvement would be to hold this workshop a bit later in the season. Some agencies were obligated to spring lake trout surveys at this time of year. Otherwise, nicely done.
- I liked the hands-on quizzes. I would like to see more hands-on training with the fin wounds, also working on live fish.
- Best: hands on wound assessment and walking through the results the next day. Discussion of challenges. One suggestion: bigger screen
- I enjoyed attending this event, would've liked more time in the demonstration facility
- I appreciated being able to interact with other professionals – learning how each agency approaches assessing wounding. Periodically moisten fish with spray bottle – sometimes it could be difficult to see wounds on dried fish.
- The point seemed to be to follow the timeline of the lab wounded fish, yet most scars that caused confusion had no history. Including more fish with history makes for a better fulfilling experience.
- Actual fish with varying degrees of healing. Good mix of presentations, at correct informality level for this group and topic.
- Although very difficult, would've been nicer to do 1/Lake (Superior, MI…). Probably better attendance w/o long drives. Thought everything else was really good, informative. Thank you for hosting this workshop.

LITERATURE CITED

LITERATURE CITED

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CHAPTER 3: THE INFLUENCE OF LIFE HISTORY ON THE RESPONSE TO PARASITISM: DIFFERENTIAL RESPONSE TO NON-LETHAL SEA LAMPREY PARASITISM BY TWO LAKE TROUT ECOMORPHS

Abstract

The energetic demands of stressors like parasitism require hosts to reallocate energy away from normal physiological processes to survive. Life history theory provides predictions about how hosts will reallocate energy following parasitism, but few studies provide empirical evidence to test these predictions. We examined the sub-lethal effects of sea lamprey parasitism on lean and siscowet lake trout, two ecomorphs with different life history strategies. Leans are shorter lived, faster growing, and reach reproductive maturity earlier than siscowets. Following a parasitism event of four days, we assessed changes to energy allocation by monitoring endpoints related to reproduction, energy storage, and growth. Results indicate that lean and siscowet lake trout differ considerably in their response to parasitism. Severely parasitized leans slightly increased their reproductive effort and maintained growth and energy storage, consistent with expectations based on life history given that leans are less likely to survive parasitism and have shorter lifespans than siscowets. Siscowets nearly ceased reproduction completely following severe parasitism and showed evidence of altered energy storage, consistent with a strategy that favors maximizing long term reproductive success. These findings suggest that life history can be used to generalize stressor response between populations and can aid management efforts.

Introduction

Parasitism is an energetically costly stressor for hosts. Coping with the energetic demands of parasitism necessitates diverting energy away from other physiological processes such as growth and reproduction and results in alterations to host physiology and behavior (Barber et al. 2000; Barber 2007; Iwanowicz 2011; Allan et al. 2020). In many studies involving fish under the stress of parasitism, energy is redirected from reproduction and invested in processes that mitigate negative influences on survival such as growth or immune function (Lemly and Esch 1984; Adlerstein and Dorn 1998; Hecker and Karbe 2005). In other cases, in the face of energy limitation reproductive effort is maintained, leading to a decreased probability of survival (Agnew et al. 2000; Wingfield and Sapolsky 2003). The most advantageous response in the face of parasitism-driven energy limitation depends on the life history of the host and the specific stress mechanism of the parasite (Forbes 1993; Agnew et al. 2000; Alvestad 2017). Hosts that are longer lived and have many opportunities to reproduce during their lifetimes, are likely to maximize fitness by diverting resources away from reproduction in the short-term, if by doing so it allows the host to have more opportunities to reproduce in the future. This strategy is only adaptive if the likelihood of surviving parasitism is high, and parasitism does not lead to a future reduction in the ability to reproduce (Forbes 1993). Conversely, if a host has a relatively short lifespan and fewer opportunities to reproduce during its lifetime, diverting resources away from reproduction may not increase fitness as there are fewer opportunities to later compensate for the loss of reproductive effort. These adaptive responses to parasitism are well grounded in life history theory (Forbes 1993; Agnew et al. 2000), but robust empirical evidence supporting these patterns is lacking for most animals (Valenzuela-Sánchez et al. 2021).

A particularly good case for examining life history tradeoffs experienced in the face of parasitism is the interaction between lake trout (*Salvelinus namaycush*) and the invasive sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes. Lake trout in the Laurentian Great Lakes display considerable variability influenced by environmental adaptation, with four currently recognized lake trout ecomorphs differing in appearance, habitat preference, and life history characteristics (Moore and Bronte 2001; Muir et al. 2014; Hansen et al. 2016; Sitar et al. 2020). Lake trout are a preferred host species for sea lamprey in the Laurentian Great Lakes (Harvey et al. 2008; Johnson et al. 2021). Although lake trout mortality following sea lamprey parasitism occurs frequently, an estimated 45-75% of lake trout survive sea lamprey parasitism events (Swink 2003; Madenjian et al. 2008). Lake trout that survive sea lamprey parasitism often make up a large proportion of the total population; evidenced by high rates of lake trout with sea lamprey wounds (Sitar et al. 1997; Rogers et al. 2019). However, little is known about lake trout that survive sea lamprey parasitism. In the short term, sea lamprey parasitism alters plasma sex steroid concentrations (Smith et al. 2016), alters blood chemistry (Edsall and Swink 2001) and results in a transcriptional response involving the regulation of genes involved in inflammation and regulating cellular damage (Goetz et al. 2016). In the longer term, parasitism influences expression of proteins related to immune response, lipid transport, and blood coagulation (Bullingham et al. 2021). It is possible that these health repercussions could lead to a diversion of energy from normal physiological processes such as growth, immune function, and reproduction, and have long-term implications. Furthermore, the response to parasitism may vary depending on the life history characteristics of the lake trout ecomorph that has been parasitized (Smith et al. 2016).

Siscowets and leans are two lake trout ecomorphs found in Lake Superior, that have considerable life history and morphological differences that could influence their response to parasitism. Leans prefer shallower depths and warmer water temperatures, have relatively low muscle lipid content and are faster growing than their siscowet counterparts (Moore and Bronte 2001; Sitar et al. 2020; Chavarie et al. 2021). Leans also experience higher mortality regimes than siscowets (Goetz et al. 2011, 2014). Siscowets generally live deeper in the water column and experience cooler water temperatures (Moore and Bronte 2001; Chavarie et al. 2021). As a result, siscowets are slower growing and reach reproductive maturity much later than leans (Sitar et al. 2014). A high proportion of siscowets also do not put forth a reproductive effort each year ("skipped spawning"). Although leans also display skipped spawning, they do so less frequently (~12% for leans, ~58% for siscowets) (Sitar et al. 2014). Siscowets tend to have a higher rate of observed sea lamprey parasitism in the Laurentian Great Lakes than leans suggesting a higher percent survive sea lamprey attacks (Bence et al. 2003; Horns et al. 2003; Sitar et al. 2008). Additionally, siscowets appear to cope better with parasitism than leans as they do not show altered growth trajectories following parasitism (Smith et al. 2016). The two ecomorphs also show molecular and physiological differences following parasitism that suggest siscowets buffer critical physiological processes important for survival (Sitar et al. 2008; Goetz et al. 2016; Smith et al. 2016).

The objective of this study was to evaluate the influence of lake trout life history on the long-term influence of sea lamprey parasitism on reproduction, growth, and energy storage. We approached this by assessing the sublethal effects of sea lamprey parasitism on growth, energy storage, and the reproductive physiology of siscowet and lean lake trout and comparing the findings with expectations from our conceptual model. We experimentally allowed sea lamprey to parasitize siscowet and lean lake trout that were raised in a common environment and monitored long-term effects on reproductive endpoints. If life history plays an important role in dictating how parasitism stress is addressed, we expected these two ecomorphs to display key differences in their parasitism response that are consistent with expected optimal strategies (Table 1). Briefly, because siscowets are longer lived and less likely to die following parasitism, we expect them to respond to sea lamprey parasitism by diverting energy away from reproduction in the short-term to increase survival, maintain critical lipid reserves, and maximize future reproductive success. Because leans are shorter-lived and less likely to survive parasitism, we expected to observe comparatively less diversion of energy away from reproduction following sea lamprey parasitism as there is less benefit to increasing future reproductive success at the expense of current reproduction. Leans may instead compensate by allocating energy away from growth and storage, and toward surviving the parasitism event and maintaining reproduction. A better understanding of the parasite-host relationship and how it differs between life history strategies, could assist in generalizing responses to stressors and to assist management efforts.

Materials and methods

Study organisms

We used 11-12 year-old siscowet (n=82, 1.93-4.78kg) and lean (n=89, 1.81-5.25kg) ecomorph lake trout raised from eggs collected from wild adult lake trout in Lake Superior in the autumn of 2006. The lake trout were raised in identical laboratory conditions (1.5 x 21 m raceways, 6.8-8.3°C, natural photoperiod), and maintained the morphometric, physiological, and life history differences expected of wild siscowet and lean lake trout (Goetz et al. 2010, 2014). Lake trout were fed a maintenance diet (0.5%) of Rangen 8.0 mm EXTR 450 Trout Feed (Buhl, ID, USA), and excess uneaten food was observed at each feeding. No feed was provided during parasitism trials. Each lake trout had an implanted pit tag allowing for individuals to be tracked.

Actively parasitic sea lamprey used in this study were collected from wild lake trout hosts by commercial fishing operations in summer and early-autumn of 2016 and 2017 from Lake Superior and Lake Huron. Sea lamprey (n=44, 44-241g) were screened for disease prior to transfer into the lab and were kept in flow-through tanks isolated from the lake trout when not in-use for parasitism trials.

Parasitism trials

Parasitism trials were conducted during November through December of 2016 and 2017 following Michigan State University Institutional Animal Care and Use Committee approved protocols. Briefly, individual lake trout were placed in separate 1000 L circular tanks, containing one sea lamprey. Tanks were checked three times daily, and the time of sea lamprey attachment was recorded. Sea lamprey were removed after 4 days of feeding to prevent lethal parasitism (Smith et al. 2016). An additional group of lake trout were individually placed in the 1000 L tanks without sea lamprey for a similar duration as the parasitism trials to serve as controls.

Immediately following each parasitism trial, length, weight, and fat content of the lake trout was measured, and the resulting wound was classified using current sea lamprey wound classification guidelines (Ebener et al. 2006). These wound types were considered separately because the severity of the parasitism event is likely to influence the magnitude of the response to parasitism. After wound assessment, lake trout were transferred back to their raceways and allowed to heal.

Endpoints of interest

To assess changes to growth, length and weight were measured in the October prior to parasitism trials, and in the October the year following parasitism trials. Each lake trout was removed from the raceways and anesthetized with tricaine methane sulfonate (MS-222). Excess water was blotted from each lake trout with paper towels before total length (to nearest cm) and weight (to nearest 10g) were recorded. The difference in length and weight between these time points was used to represent alterations to growth.

Alterations to energy storage was measured by assessing the change in muscle lipid concentrations and the hepatosomatic index (HSI) in the August following parasitism trials. For the change in muscle lipid concentration, each lake trout was measured with a handheld microwave fatmeter (Distell Inc., Model FFM-692, West Lothian, Scotland) immediately after length and weight measurements. Lipid concentrations were again measured in the October prior to parasitism trials, and in the October following parasitism trials, and the difference between these time points was used. To obtain HSI, an indicator of energy storage (Skjæraasen et al. 2012; Goetz et al. 2014; Sitar et al. 2014), a subset of lake trout were lethally sampled in the August following parasitism trials. We sampled 31 siscowets - 17 females (5 type-A wounded, 5 type-B wounded, 7 control) and 14 males (3 type-A wounded, 4 type-B wounded, 7 control) – and 33 leans – 16 females (3 type-A wounded, 5 type-B wounded, 8 control) and 17 males (5 type-A, 7 type-B, 5 control). These lake trout were not used for reproduction or growth analysis. Lake trout were euthanized with an overdose of MS-222, and livers were surgically extracted and weighed. HSI was calculated as $\frac{liver\ weight}{body\ weight} x\ 100$.

Reproduction was measured by obtaining the normalized egg mass, skipped spawning (females), and milt sperm cell concentration (males). Both ecomorphs generally spawn in early October, so from mid-September through early-November, we regularly monitored each lake trout for ovulation and spermiation. The sample sizes for this time point were: 51 siscowets – 29 females (9 type-A wounded, 10 type-B wounded, 10 control) and 22 males (7 type-A wounded, 7 type-B wounded, 8 control) – and 57 leans – 31 females (10 type-A wounded, 10 type-B wounded, 11 control) and 26 males (7 type-A wounded, 9 type-B wounded, 10 control). Any lake trout ready to spawn were stripped of eggs or milt. The total volume of eggs stripped and egg mass was collected from each female. To account for size-related difference in egg production, egg mass was standardized by divided by the wet weight of each individual female. Females that did not produce any eggs were deemed to have skipped spawning (Sitar et al. 2014).

Additional co-variates

Because we were interested in other factors that may contribute to growth, energy storage, and reproduction in addition to sea lamprey parasitism, we collected additional information from lake trout at various time points. At the beginning of each month from July through October following parasitism, we took additional sub-lethal samples measuring length, weight, condition factor, muscle lipid concentration, plasma estradiol and testosterone concentrations, and hematocrit. A 0.5 ml blood sample was taken via heparinized syringe from the caudal vein and centrifuged to separate plasma and packed red blood cells. Each fraction was stored separately at -80°C before plasma sex steroid concentrations were assessed using radioimmunoassays (raw steroid profiles are included in Figs. S4 and S5). Additional blood was collected in a hematocrit tube, centrifuged and blood hematocrit (ratio of packed red blood cell volume to total volume) was recorded. Following sampling, each fish recovered in a MS-222 free holding tank and then returned to the raceways. These additional data were considered as potential co-variates when estimating the influence of parasitism on our endpoints of interest.

Analysis

We were interested in the influence sea lamprey parasitism had on growth, storage, and reproductive outcomes for siscowet and lean lake trout. To assess growth, changes in length and weight were used as endpoints of interest. HSI and muscle lipid concentration were used to assess effects on storage. To assess impacts on reproduction, egg production, milt production and skipped spawning were used as endpoints. Embryo survival was also assessed, but due to small sample sizes for each parental cross combination, only qualitative analysis was used. Because there may be several factors that contribute to growth, storage, and reproductive success besides parasitism, we used Bayesian multiple linear regression to evaluate competing models for each endpoint of interest. Models were fit using JAGS (Plummer 2016) using the jagsUI package (Kellner 2019) with R version 3.6.1 (R Core Team 2019). Each model was fitted with diffuse flat priors on the model parameters, a choice made to be weakly informative, and using 3 Markov chains, 100,000 iterations, a burn-in of 20,000, and a thinning rate of 2. Posterior distributions were assessed for convergence with the Brooks-Gelman-Rubin statistic ($\hat{R}$ values < 1.1 indicated convergence) (Brooks and Gelman 1998) and with visual assessment of posterior distributions. The resulting chains all had effective sample sizes >10000 for all variables, indicating they provided a good characterization of the posterior distribution. For each endpoint of interest, we developed a list of plausible *a priori* candidate models and ranked competing model performance using the deviance information criterion (DIC). Models were run separately for each ecomorph. We assumed that models with ΔDIC < 2 were plausible. Credible intervals were obtained from posterior estimates of parameter values (all three chains combined), and model parameters were deemed significant if 90% credible intervals did not overlap zero (Spiegelhalter et al. 2002).

Results

Growth

Parasitism did not influence growth as measured by change in length for lean or siscowet lake trout. The best performing model estimating change in length for leans included only the presence of a type-A wound, however the 90% credible interval for the parameter estimate included zero. Three models had DIC values within 2 of the best performing model, but none of the parameters had 90% credible intervals not containing zero (Table S1). For siscowets, no candidate models estimating change in length were informative. The best performing model included only initial muscle lipid, but the 90% credible interval contained zero (90%CrI = -0.28 – 0.26). One other model containing only the presence of a type-A wound performed within 2 DIC of the best performing model, but the 90% credible interval also contained zero (Table S1).

Parasitism also did not influence the change in weight following parasitism for lean or siscowet lake trout. The best performing model estimating change in weight for leans included only the initial lipid concentration prior to parasitism, but the 90% credible interval contained zero (90%CrI = -0.007 – 0.004). Two models performed within 2 DIC of the best model but the 90% credible intervals for all parameters contained zero. For siscowets, the best performing model estimating change in weight included the presence of a type-A wound and the presence of a type-B wound, however, the 90% credible intervals for both parameters included zero. A model containing only the presence of a type-A wound had a DIC value within 2, but the 90% credible interval also contained zero (Table S1).

Energy storage

Severe parasitism affected the HSI of female and male siscowet lake trout, but not lean lake trout of either sex. The best performing model for lean HSI included sex. Female leans had HSI values 0.66 (90%CrI = 0.54 – 0.78) higher than male leans (Figure 2). Models including parasitism status did not perform within 2 DIC of the sex only model (Table S1). For siscowet lake trout, the best model included presence of a type-A wound, sex, and an interaction between the two. Female siscowets had HSI values 0.33 (90%CrI=0.14 – 0.51) higher than siscowet males. The effect of a type-A wound depended on sex. For females with type-A wounds, HSI values were 0.55 (90%CrI = 0.14 – 0.96) higher than for control and type-B wounded females. For males with type-A wounds, HSI values were 0.30 (90%CrI = -0.64 – 0.04) lower than control and type-B wounded males, but the 90% credible interval contained zero (Figure 3). Two additional models had DIC values within 2 of the best performing model (Table S1). One had the addition of the presence of a type-B wound, but the 90% credible interval contained zero. The other model included only sex as a predictor, similar to leans. In this model female HSI values were 0.45 higher for than for males (90%CrI = 0.28 – 0.62).

Changes in muscle lipid concentration following parasitism were not influenced by parasitism lean or siscowet lake trout, but were influenced by sex for siscowets. None of the models estimating change in muscle lipid in the year following parasitism for leans had parameter estimates with 90% credible intervals not containing zero. For siscowets, the best performing model included only sex. Female siscowets gained 5.16% less muscle lipid (90%CrI

= -7.70 - -0.63) than male siscowets. No other models had DIC values within 2 of the sex-only model (Table S4).

Egg production

For lean lake trout, severe parasitism and change in length in the year following parasitism influenced egg production. All female leans produced eggs, and the best performing model for estimating normalized egg production included presence of a type-A wound and the change in length in the year following parasitism (Table S1). Leans with a type-A wound were associated with a 0.019g (90%CrI = 0.005 – 0.032) increase in egg weight per g of body weight relative to control and type-B wounded leans. A 1mm increase in length in the year following parasitism was associated with a 0.002g (95%CrI = 0.001 – 0.003) increase in egg weight per g of body weight for leans. For the average weight lean lake trout in our sample (3.05kg), a type-A wound would be associated with a 58g increase in egg mass (17% of the average egg mass for lean females), and a 2.7cm increase in length (average for lean females) is associated with a 16.4g increase in egg mass (5% of the average egg mass for lean females).

For siscowet lake trout, the muscle lipid concentration prior to parasitism affected egg production. The best performing model included the presence of a type-A wound and the percent muscle lipid content prior to parasitism, but only the percent muscle lipid content had a 90% credible interval that did not contain zero (Table S1). Siscowets with type-A wounds were associated with a 0.02g decrease in egg weight per g of body weight relative to control and type-B wounded siscowets, however the 90% credible interval contained zero (90%CrI = -0.043–0.002). A 1% increase in initial muscle lipid content was associated with a 0.003g (95%CrI = 0.001 – 0.005) increase in egg weight per g of body weight. There were 4 additional models that had DIC values within 2 of the best performing model (Table S1). These models contained a combination of initial muscle lipid, presence of a type-A wound, September E2 concentration, and presence of a type-B wound.

Siscowet lake trout had more variable egg production than leans as a large proportion of siscowets skipped spawning (54%). 78% (7 of 9) of siscowets with type-A wounds, 30% (3 of 10) with type-B wounds, and 50% (5 of 10) control siscowets skipped spawning. Parasitism heavily influences the likelihood of skipping spawning, but muscle lipid concentration prior to parasitism and plasma E2 concentration in September also play a role. The most parsimonious model estimating the likelihood of skipped spawning for included the presence of a type-A wound, initial muscle lipid concentration, and plasma E2 concentration in September (Table S1). The odds of skipping spawning for siscowets with type-A wounds are 292 times higher (90%CrI = 11.24 – 14144.26) than control and type-b wounded siscowets (Figure 4A). Every 1% increase in initial muscle lipid concentration decreased the odds of skipping spawning by 24% (90%CrI = 0.61 – 0.92) (Figure 4B). For every 1ng/ml increase in September plasma E2 concentration there was a 50% (90%CrI = 0.31 – 0.73) decrease in the odds of skipping spawning (Figure 4C). For the average siscowet in our sample, the probability of skipping spawning is 98% following parasitism with a type-A wound compared to only 17% when the siscowet was unparasitized or parasitized with a type-B wound. For the effect of muscle lipid concentration, a 10% decrease in initial muscle lipid increases the probability of skipping spawning by 52%. Similarly, a reduction in E2 concentration by 2ng/ml increases the probability of skipping spawning from 24% to 45% for the average siscowet in our sample. One model, adding the presence of a type-B wound as an additional parameter, had a DIC value within 2 of the best performing model (Table S1). However, in this model the 90%CrI for the type-B parameter overlapped with zero.

Milt concentration

For male leans lake trout, parasitism did not influence milt sperm cell concentration but the change in muscle lipid in the year following parasitism did. Every 1% increase in lipid corresponded with a decrease of 0.28 (90%CrI = -0.44 – -0.12) billion sperm cells per ml of milt. A lean gaining 1.8% muscle lipid in the year following parasitism (average change in our sample) would have a milt concentration of 5.32 billion sperm cells per ml, while one with no change in muscle lipid would have 5.83 billion sperm cells per ml. A model including the presence of a type-A wound in addition to change in muscle lipid had a DIC value within 2 of the best performing model (Table S1), however the 90%CrI for the type-A parameter included zero.

For siscowet lake trout, milt concentration was influenced by parasitism, the change in weight during the year following parasitism, and muscle lipid concentration prior to parasitism. The most parsimonious model included the presence of a type-A wound, presence of a type-B wound, change in weight during the year following parasitism, and initial muscle lipid concentration (Table S1). Parasitism leading to a type-A wound corresponded with a decrease of 4.11(90%CrI = -5.64 – -2.58) billion sperm cells per ml of milt. Parasitism leading to a type-B wound corresponded with a decrease of 2.52 (90%CrI = -4.02 – -1.02) billion sperm cells per ml of milt. A 1kg increase in weight in the year following parasitism was associated with an increase of 3.82 (90%CrI = 1.27 – 6.36) billion sperm cells per ml of milt, and a 1% increase in muscle lipid concentration prior to parasitism corresponded with an increase of 0.22 (90%CrI = 0.08 – 0.35) billion sperm cells per ml of milt (Figure 5). With all other parameters held at their averages, an unwounded siscowet would have 4.04 billion sperm cells per ml, a type-A wounded siscowet would have -0.07 billion sperm cells per ml of milt, and a type-B wounded siscowet would have 1.53 billion sperm cells per ml of milt (Figure 5A).

Embryo survival

Due to sample size limitations for parental cross categories, we did not perform statistical analysis for embryo survival. However, for siscowet, no eggs fertilized by males with type-A wounds were viable (Figure S2). This trend was not present for leans (Figure S1).

Discussion

We found that the response to sea lamprey parasitism differed between siscowet and lean lake trout and these differences, with few exceptions, matched the expectations laid out in our life history conceptual model (Table 1). Severely parasitized lean lake trout slightly increased their reproductive effort and maintained growth and energy storage, consistent with expectations based on life history given that leans are less likely to survive parasitism and have shorter lifespans than siscowet lake trout. Siscowets ceased reproduction almost completely following severe parasitism and showed evidence of altered energy storage, consistent with a strategy that favors maximizing long term reproductive success at the expense of current reproduction. These findings suggest that life history can be used to generalize the response to sea lamprey parasitism.

Growth

We expected that growth would be influenced by parasitism for both ecomorphs and that leans would divert energy from growth towards maintaining reproduction and siscowets would reduce growth to maintain energy storage. In many parasite-host interactions involving fish hosts, energy limitation from parasitism results in reductions of host growth (Britton et al. 2011;

Godwin et al. 2017; Fjelldal et al. 2019). We did not find evidence that lean or siscowets were significantly altering growth in response to parasitism. One important consideration is that the age 12 lake trout used in this laboratory study were approaching their growth asymptotes and had small annual growth rates. As a result, changes in length or weight over time would likely be subtle and thus difficult to detect. Additionally, evaluations of wild lake trout have found evidence of faster growth rates following severe parasitism (Smith et al. 2016) which could make identifying short-term reductions in growth difficult. Therefore, we conducted additional parasitism trials and monitored growth on a small group of 5-year-old lake trout. While sample sizes were not large enough for statistical analysis, the observed trends appear to support the presence of an initial reduction in growth followed by growth compensation (Figure S3).

Energy storage

We predicted that following parasitism, leans would reduce energy allocation towards storage while siscowets would maintain storage energy allocation. Because leans have fewer opportunities to reproduce over their lives than siscowets, we would expect them to prioritize reproduction over energy storage. However, we did not observe any alteration to muscle lipid concentration or HSI for lean lake trout resulting from parasitism. Similarly, siscowets did not significantly alter muscle lipid concentration following parasitism. Although siscowets have high muscle lipid content that could be available to mobilize following parasitism, lipid storage likely plays an important role in reducing the costs of maintaining neutral buoyancy at the depths they inhabit (Henderson and Anderson 2002; Goetz et al. 2014). Lipid storage is also hypothesized as an important siscowet life history strategy for building energy reserves sufficient for reproduction (Goetz et al. 2014), similar to Northeast Arctic cod (Skjæraasen et al. 2012). Given the functional role of muscle lipids for siscowet lake trout, parasitism effects on storage are more likely to be expressed in the HSI. For siscowets, HSI was influenced by an interaction between parasitism and sex. Sex differences in HSI have been well documented in lake trout (Goetz et al. 2017) and are likely underpinning the differential response to parasitism. Male siscowet HSI is seasonally consistent, and therefore, the reductions in HSI we observed following severe parasitism (Figure 2) is likely an indication of energy limitation. Female siscowet HSIs vary seasonally as liver weight is influenced by vitellogenin production during gamete development with higher HSI in the summer than in fall when reproduction is occurring (Goetz et al. 2017). We sampled HSI in late summer when female lake trout are beginning to ramp up gamete development for reproduction. The higher HSI values observed in type-A wounded female siscowets could be an indication that they are not mobilizing energy for reproduction. Alternatively, wild lake trout that skip spawning have been found to have lower HSI values than spawning lake trout (Sitar et al. 2014). Because a considerable number of control and type-B wounded siscowets also skipped spawning (see below) any effect of parasitism on HSI might be obscured. Also possible is that siscowets that skip spawning following type-A parasitism may be allocating energy towards reproduction differently than siscowets that skip spawning without the major stressor. Lake trout that skip spawning have been observed to undergo normal gonadal development until August where the maturation process stops and oocyte degeneration and resorption begins (Goetz et al. 2011; Sitar et al. 2014). Further work is necessary to identify the specific mechanisms at play.

Reproduction

We expected female leans would maintain their reproductive effort while siscowets would divert energy away from reproduction to maximize future reproductive success. Female leans parasitized with type-A wounds produced more eggs than control and type-B wounded fish. An increased investment in egg production following severe parasitism makes sense because leans have fewer opportunities to reproduce over their lifespan (Chu and Koops 2007) and are more likely to die following parasitism than siscowets (Horns et al. 2003; Sitar et al. 2008). Therefore, reproductive success is maximized by investing in reproduction in the short-term. The less severe type-B parasitism was is not sufficient to elicit an increase in reproductive investment. This is not surprising as mortality from type-B wounds are less frequent (Eshenroder and Koonce 1984) and the optimal life history strategy would not favor short-term reproduction. Surprisingly, the increased investment in reproduction following type-A parasitism did not result in any observed adverse trade-offs for growth and storage in lean lake trout. However, preliminary growth data suggests that the trade-offs may exist in younger fish (Figure S3).

For female siscowet lake trout, the most striking influence on reproduction was the increased incidence of skipped spawning following severe parasitism. The increased odds of skipping spawning (292 times greater) for type-A wounded females was particularly large considering spawning was assessed approximately 1 year following a relatively brief parasitism event. Skipping spawning is common in many long-lived fish species that rely on energy reserves to support gamete development or experience energy limitation (Rideout and Tomkiewicz 2011), and has been well-documented in siscowet lake trout (Goetz et al. 2011; Sitar et al. 2014). Our results largely align with observations of wild lake trout in Lake Superior. In southern Lake Superior, 58% of siscowet lake trout were observed to skip spawning (Sitar et al. 2014). The control and type-B wounded siscowets in our laboratory study skipped spawning at rates of 30% and 50% respectively, while 78% of type-A wounded siscowets skipped spawning. The likelihood of skipping spawning also depended on lipid concentration prior to parasitism and plasma E2 concentrations in September (when plasma E2 peaks for lake trout) (Foster et al. 1993). Siscowets maintain high muscle lipid reserves and differ considerably in energy processing and storage dynamics compared to leans (Goetz et al. 2014; Sitar et al. 2020). These differences are heritable and are likely an adaptation for accumulating sufficient energy until a threshold is reached and reproduction proceeds. Our results make sense in this context as the energy limitations presented by severe sea lamprey parasitism would compete with the ability to accumulate energy for reproduction. Muscle lipid concentration prior to parasitism influenced skipped spawning and further suggests that there is some baseline rate of skipped spawning that depends on a lipid storage threshold - parasitism demands a greater stored lipid requirement for successful reproduction. The presence of September E2 concentrations in the best performing model is consistent with observations of reduced plasma E2 concentrations in other skip spawning fish (Skjæraasen et al. 2009; Pierce et al. 2017). Estradiol modulates hepatic production and gonadal uptake of the egg yolk protein vitellogenin (Tyler and Sumpter 1996), and is therefore critical for gonadal development and may be useful as an early biomarker of skipped spawning.

We evaluated effects on male reproduction by assessing influences on milt concentration. For lean males, parasitism status did not have an effect. The change in muscle lipid concentration in the year following parasitism best predicted milt concentration and indicates that the more energy a lean invests in storage (regardless of parasitism status), the less energy is available to invest in milt production. The lack of parasitism effects matches our expectations that leans will maintain reproductive output following parasitism so that short-term reproductive success is maximized. While our results do not indicate evidence of a parasitism driven change in reproductive output, they may highlight a life history tradeoff between energy storage and reproduction for male leans.

Male siscowet milt concentration was influenced by parasitism status change in weight in the year following parasitism, and initial muscle lipid concentration. Interestingly, siscowet milt concentration was the only endpoint where type-B parasitism was distinguished from control fish. Effects on milt concentration matched our expectations based on the severity of parasitism with type-B wounds being associated with a smaller reduction in milt concentration than type-A wounds. Similar to our observations with female egg production and skipped spawning, we expected male siscowets to also reduce reproductive effort following parasitism to maximize future reproductive success. There were striking visual differences in milt with most of the parasitized males with type-A wounds having nearly transparent milt compared to the milky white color of control male milt (Figure 6). These dramatic changes in milt quality were surprising given these effects were observed approximately 1 year after a brief (4 day) sea lamprey attack. In lake superior, siscowets have been observed with very low GSI and no signs of spermatogenesis during normal spawning (Goetz et al. 2011) suggesting that some male siscowets skip spawning in a similar manner to females. Although we did not observe males with no sperm cells in their milt, sperm counts were very low and the collected milt failed to successfully fertilize eggs, effectively skipping spawning.

Gamete production is generally more energetically demanding for females than males, so we expected to see more subtle effects on male reproduction. However, similar severe effects on male reproduction have been observed in closely related Arctic trout with high macroparasite loads (*Salvelinus alpinus*) (Skarstein et al. 2001). Sperm cells are antigenic, and part of the role of testosterone in male fish is to suppress the autoimmune response that would otherwise attack sperm cells (Hillgarth et al. 1996). Given the considerable cross-talk between the immune system and the hypothalamus-pituitary-gonadal axis (Segner et al. 2017), it is possible that testosterone and other androgens produced during sperm development would suppress immune function and inhibit the fish's ability to sufficiently cope with parasitism. This dynamic may provide a further incentive for male siscowets to forgo reproduction. Similar to female siscowets, muscle lipid concentration prior to parasitism was predictive of milt. We also hypothesize that this is due to the life history of siscowets whereby stored lipid reserves are required for reproduction independent of parasitism. This is supported by findings that wild siscowets with higher energy storage (as measured by HSI) were more likely to spawn (Sitar et al. 2014). The change in weight in the year following parasitism was also positively associated with milt concentration in our model. We found that change in weight was not significantly associated with parasitism status, but instead we suggest this effect is simply due to the positive relationship between size and reproductive output.

The finding that parasitism increases the incidence of skipped spawning for male and female siscowets has important implications for life history theory. Skipped spawning is thought to be an adaptation by some fish species to energy resource limitation, density-dependence, or suboptimal environmental conditions (Rideout et al. 2005). Under these conditions, skipping spawning allows for energy reserves to be built and future reproductive success to be maximized when energetic and environmental conditions are likely more favorable (Rideout et al. 2005; Rideout and Tomkiewicz 2011). Our findings that muscle lipid reserves measured one year before spawning were an important factor for estimating the likelihood of skipping spawning independent of parasitism support this idea. The relatively high rate of skipped spawning in control fish (50%) was still surprising, given the fact that food was abundantly available and energy resource limitation due to a lack of food would be unlikely. One explanation is that skipped spawning is not solely a response to environmental conditions, but also a programed response to adaptations siscowets have for living in consistently low water temperatures that leave less energy available to allocate towards reproduction (Goetz et al. 2014). Thus skipped spawning naturally occurs at some baseline rate for siscowet lake trout, and environmental factors that limit energy storage increase the likelihood of skipping (Goetz et al. 2021). Another possibility is that under high food availability, skipped spawning may be more common as individuals can opportunistically increase growth and take advantage of the future benefits of increased body size for reproductive output when food availability may be lower (Jørgensen et al. 2006; Rideout and Tomkiewicz 2011). It is likely that all of these factors play a role in skipped spawning, and sea lamprey parasitism simply increases the likelihood that a fish will skip due to energy limitation.

Study limitations

There are several important limitations with our study that should be considered when comparing the physiological responses we observed under laboratory conditions to lake trout in the field. One limitation is that lake trout in our laboratory conditions were provided with ample easy-to-access food. If parasitism had an influence on feeding behavior or ability to capture prey fish, we likely would not have observed these effects under laboratory conditions. The presence of ample food under laboratory conditions could obscure effects on growth, energy storage, and reproduction that would result from an inability to capture sufficient prey in the wild. An additional limitation is that we removed sea lamprey from hosts after 4 days of feeding to prevent lethal parasitism. In the wild, sea lamprey feeding duration is much more variable, and appears to depend on water temperature and sea lamprey body size (Swink 1993, 2003). The environmental conditions provided in our study also do not necessarily match conditions experienced by wild lake trout. Siscowet lake trout in particular are adapted to live in deep water and experience high pressure (up to 41 atmospheres), low light, and relatively constant water temperatures (4°C) (Sitar et al. 2008). However, the siscowet ectomorph displays diel vertical migration behavior which periodically exposes them to lower pressures, higher light intensity, and warmer water temperatures (Keyler et al. 2019). The conditions provided by the raceway environment were generally warmer (6.8-8.3°C), lower pressure, and lighter than the siscowet ecomorph would typically experience while not vertically migrating in the wild. Consequently, there could be an influence on the response to parasitism or environmental cues important for the physiological functions we observed. For example, the lower water temperatures experienced by siscowet lake trout in the wild is often attributed to their higher survival following sea lamprey parasitism (Bence et al. 2003; Sitar et al. 2008), and therefore the warmer water temperatures in our study may result in more severe consequences for siscowet lake trout than would be expected in the wild.

Despite these limitations, our observations are largely mirrored in observations of field caught lake trout. For example, the rates of skipped spawning we observed for siscowet lake trout are in-line with observations of wild lake trout in southern Lake Superior (Sitar et al. 2014). Wild siscowet lake trout that had experienced parasitism did not display altered growth trajectories, similar to our observations (Smith et al. 2016). Nevertheless, the differences in laboratory versus natural conditions should be considered when extrapolating these results to inform the management of wild lake trout.

Conclusion

Our results indicate that siscowet and leans differ in their response to parasitism, and these different responses largely match our expectations given the different life histories of these two ecomorphs. Because lean lake trout are relatively short lived (Chu and Koops 2007), reach reproductive maturity faster (Sitar et al. 2014), and are less likely to survive parasitism (Horns et al. 2003; Sitar et al. 2008), maximizing short-term reproduction makes sense. For siscowet lake trout, forgoing reproduction so that energy can be stored for future reproduction is more advantageous as it maximizes lifetime reproduction in the long run. This study is the first time we are aware of that these life history tradeoffs have been empirically examined in the context of sea lamprey parasitism.

Currently, the sub-lethal effects of sea lamprey parasitism are not considered in lake trout management plans or population models, and wounded fish are assumed to reproduce and function like unparasitized lake trout. This means that many of the potential consequences of sea lamprey parasitism are not accounted for when informing the management of the fishery. For example, records of sea lamprey wounds observed on lake trout captured during biological monitoring surveys are used as a standardized metric of sea lamprey damage in the Great Lakes (Treska et al. 2021). These marking rates inform sea lamprey control efforts and estimated rates of lake trout mortality. A target of fewer than 5 A-I through A-III marks per 100 lake trout over 533mm in length (2 A-I marks per 100 lake trout over 432mm for Lake Ontario) was developed based on the maximum level of sea lamprey-induced mortality fisheries managers were willing to accept (Treska et al. 2021). If the sublethal effects of sea lamprey parasitism were also considered when setting this target, the target marking rate may need to be lowered. Our research suggests the inclusion of the sublethal effects of parasitism would help refine and improve these targets.

APPENDICES

APPENDIX I

Tables

Table 3.1. Conceptual model of expected relative energy allocation in siscowet and lean lake trout with and without sea lamprey parasitism.

Energetic category	Morphotype	Energy allocation	Change in energy allocation under parasitism
Growth	Lean	High	Decrease
	Siscowet	Low	Decrease
Storage	Lean	Low	Decrease
	Siscowet	High	Maintain
Reproduction	Lean	High	Maintain
	Siscowet	Low	Decrease

APPENDIX II

Figures

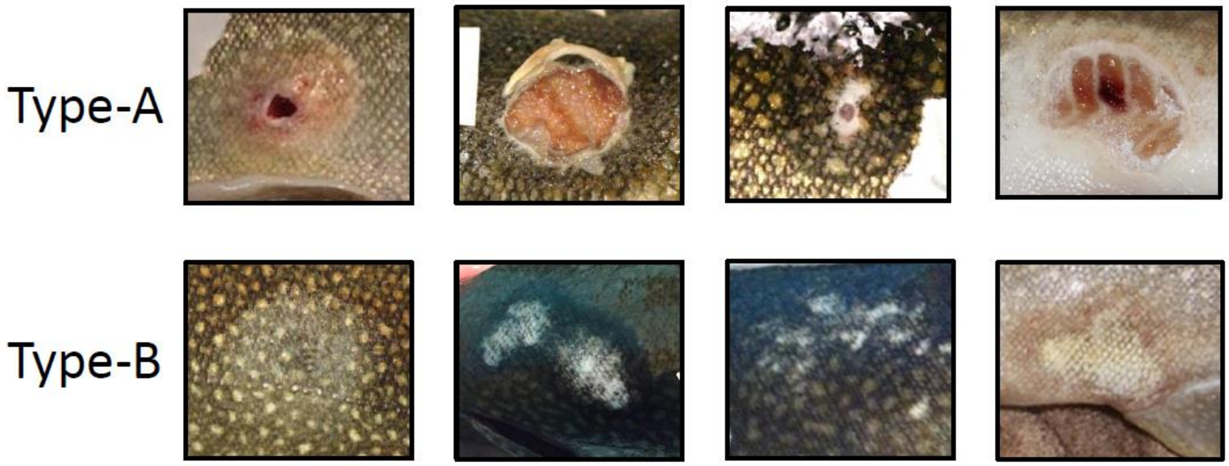

Figure 3.1. Examples of difference in parasitism severity of type-A and type-B wounds

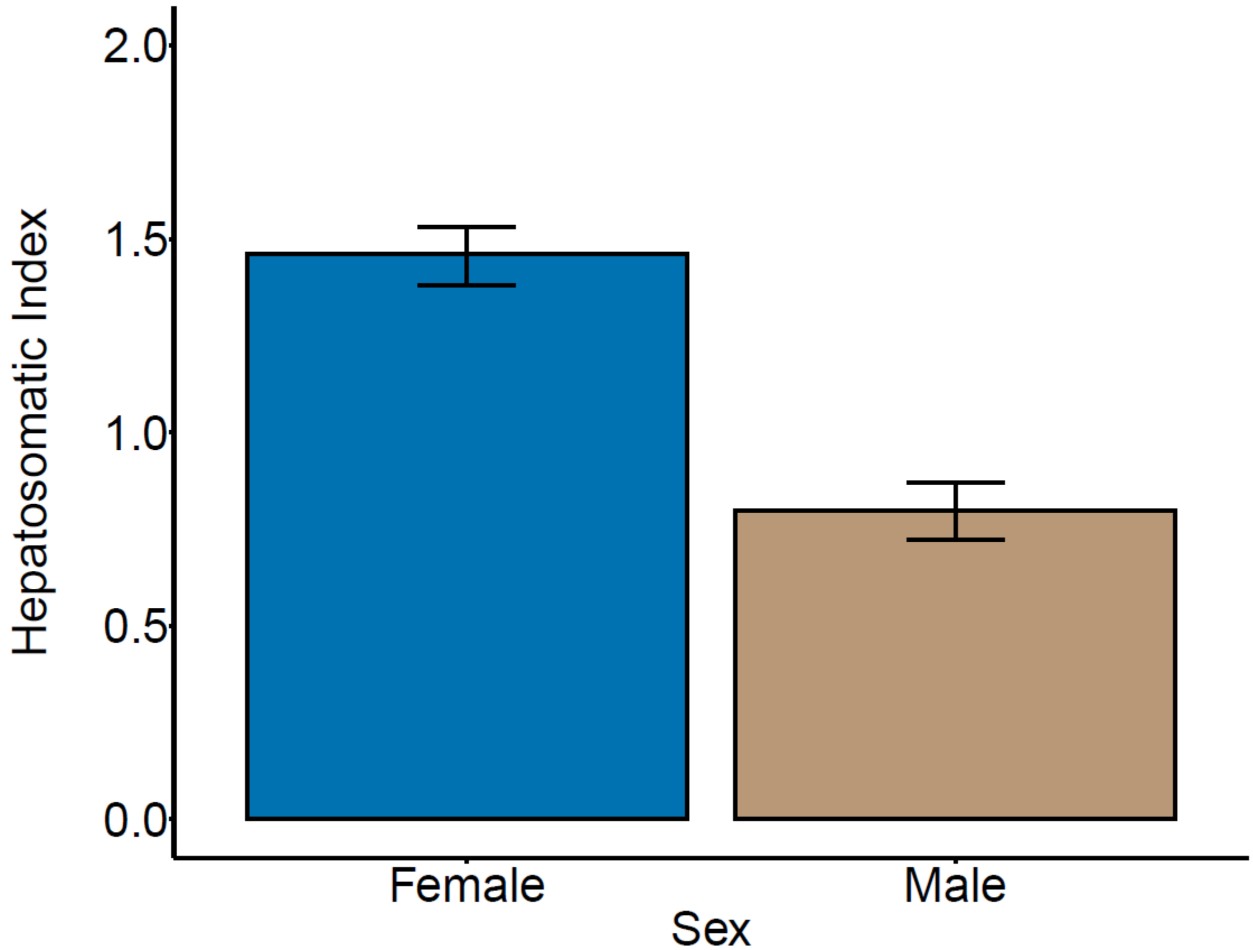

Figure 3.2. Marginal effect of sex in the most parsimonious model estimating hepatosomatic index for lean lake trout. The height of the bar indicates the posterior mean, and error bars represent 90% credible intervals.

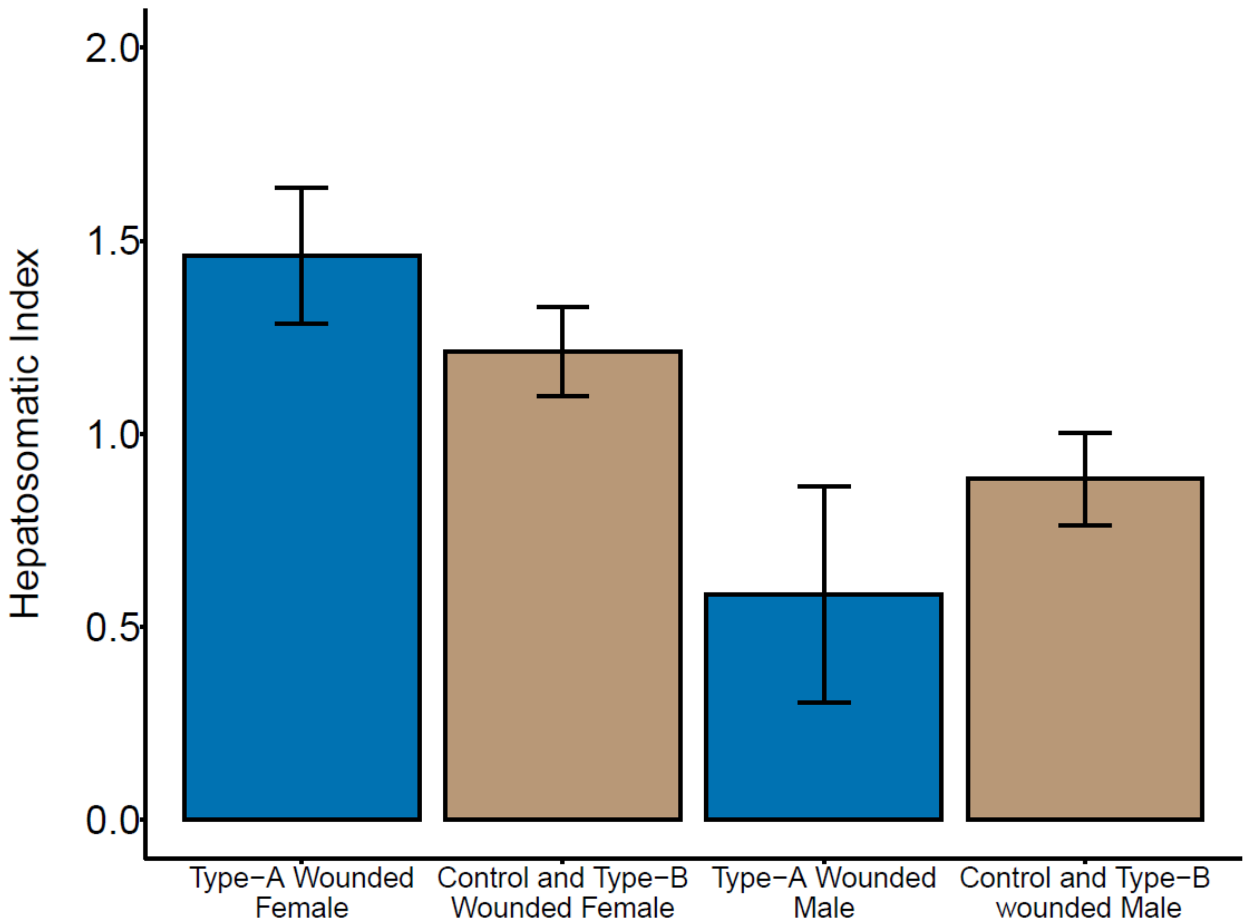

Figure 3.3. Hepatosomatic index estimates from the most parsimonious model for siscowet lake trout. The height of the bar indicates the posterior mean, and error bars represent 90% credible intervals.

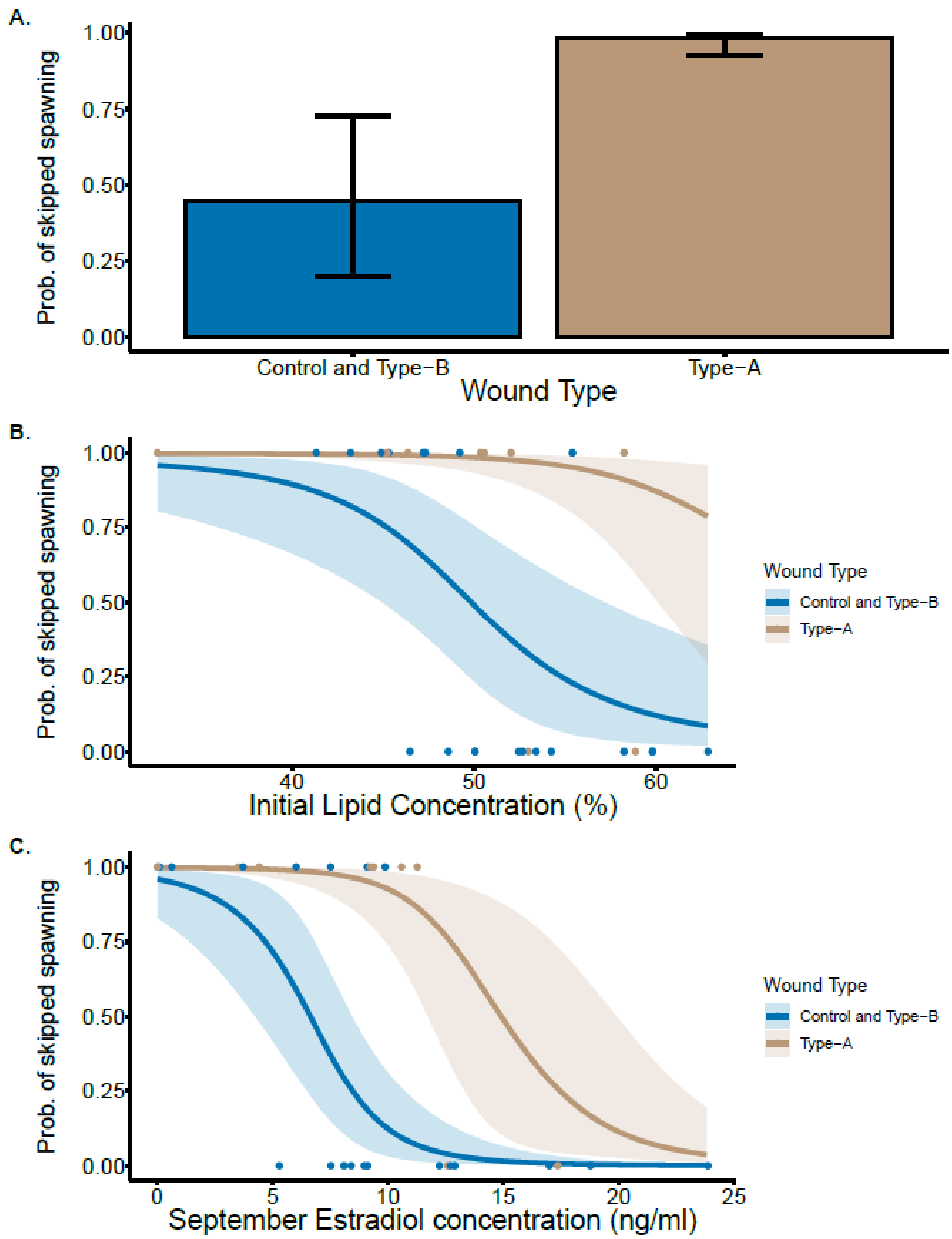

Figure 3.4. The influence of parasitism (A), initial lipid concentration (B), and September estradiol concentration (C) on the probability of skipping spawning for siscowet lake trout. Each panel shows the relationship between the probability of skipping spawning and the indicated variable calculated from the posterior chains of the most parsimonious model with all other variables held at their average values. For the influence of parasitism (A), the height of the bar indicates the posterior mean, and error bars represent 90% credible intervals. For the influence of initial lipid concentration (B) and September estradiol concentration (C), lines indicate the calculated probability of skipping spawning over a range of values for the indicated variable for type-A wounded and type-B wounded/control treatments, shaded areas indicate 90% credible intervals, and dots are observations of spawning.

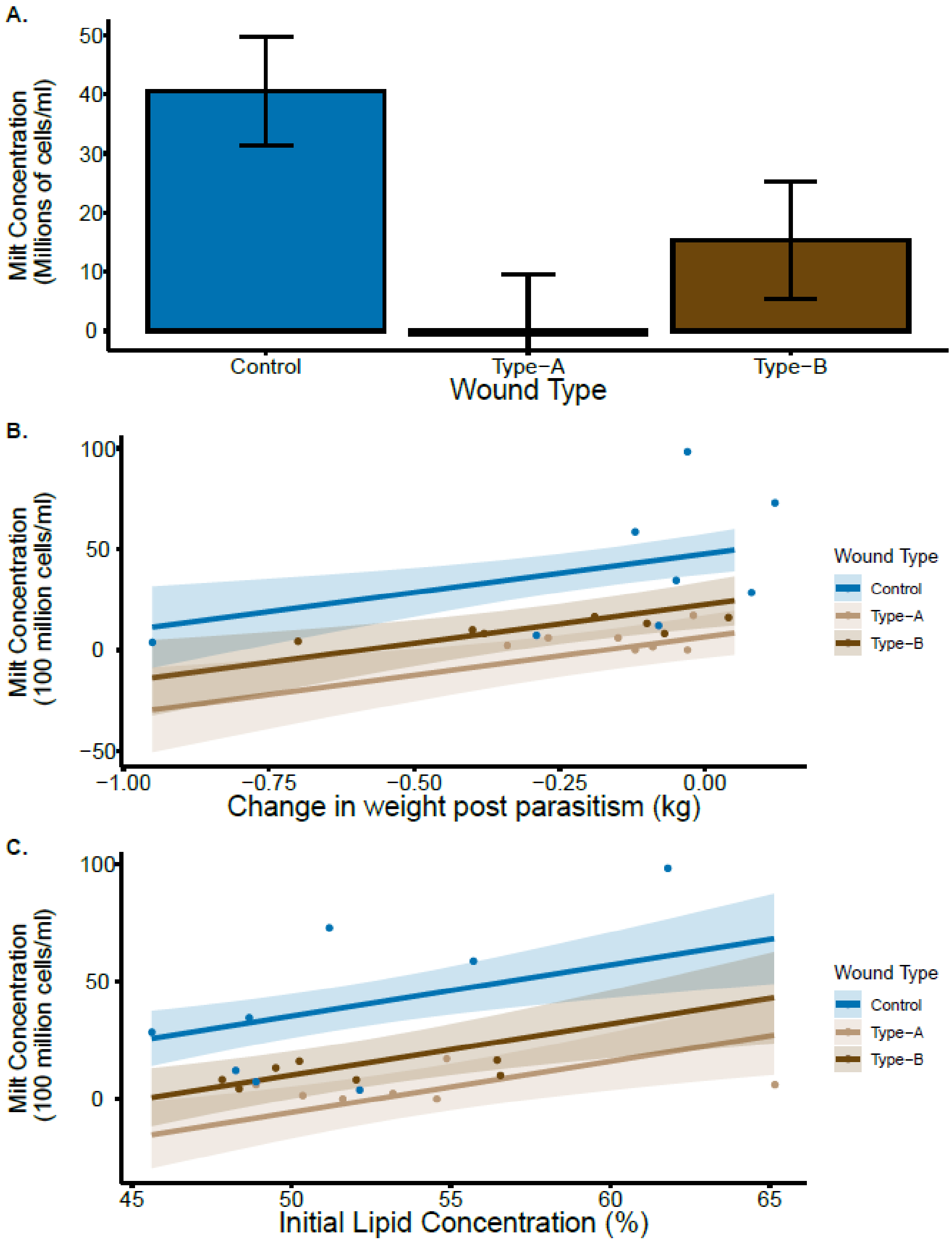

Figure 3.5. The influence of parasitism (A), change in weight following parasitism (B), and initial lipid concentration (C) on milt sperm cell concentration for siscowet lake trout. Each panel shows the relationship between milt sperm cell concentration and the indicated variable calculated from the posterior chains of the most parsimonious model with all other variables held at their average values. For the influence of parasitism (A), the height of the bar indicates the posterior mean, and error bars represent 90% credible intervals. For the influence of the change in weight following parasitism (B) and initial lipid concentration (C), lines indicate the calculated milt sperm cell concentration over a range of values for the indicated variable for type-A, type-B, and control treatments, shaded areas indicate 90% credible intervals, and dots are observed values. The location of observed values on the plot does not account for the influence of other variables.

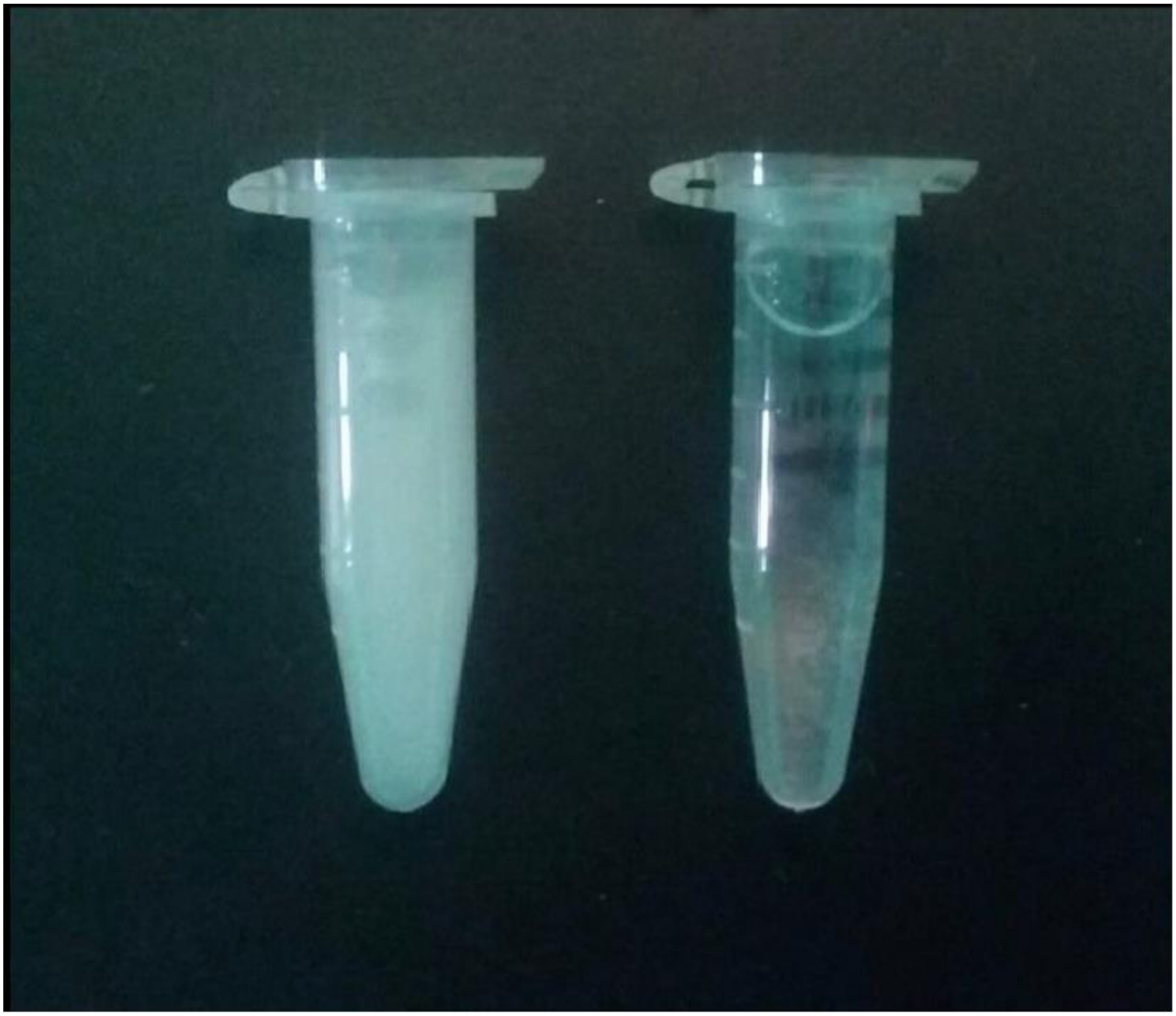

Figure 3.6. Examples of milt sampled from a siscowet control male (left) and a type-A wounded male (right).

APPENDIX III

Supplementary materials

Table S3.1. Model performance of the top 5 candidate models for each of our endpoints of interest as ranked by the deviance information criterion (DIC).

Model Type	Ecomorph	Parameters	DIC	Δ DIC
Change in Length	Siscowet	LipInit	397.6	0
		sex	397.7	0.1
		woundA	398.5	0.9
		woundA + LipInit	399	1.4
		woundA + woundB	399.6	2
	Lean	woundA	362.6	0
		LipInit	363.5	0.9
		woundA + sex	364.2	1.6
		woundA + LipInit	364.2	1.6
		woundA + woundB	364.7	2.1
Change in Weight	Siscowet	woundA + woundB	30.3	0
		woundA	31.6	1.3
		woundA + woundB + sex	32.6	2.3
		woundA + woundB + LipInit	32.6	2.3
		LipInit	33.3	3
	Lean	LipInit	-9.3	0
		woundA	-9.1	0.2
		woundA + woundB	-7.5	1.8
		woundA + LipInit	-7	2.3
		woundA + sex	-6.8	2.5
Normalized egg production	Siscowet	woundA + LipInit	156.158	0
		LipInit	156.453	0.295
		woundA + Esep + LipInit	156.508	0.35
		LipInit + Esep	156.91	0.752
		woundA + woundB + LipInit	157.926	1.768
	Lean	woundA + deltL	131.365	0
		deltL	134.695	3.33
		deltWt	137.339	5.974
		deltLip	138.073	6.708
		woundA + deltWt	138.361	6.996
Change in muscle lipid	Siscowet	sex	319.7	0
		woundA + sex	321.9	2.2
		woundA + woundB + sex	322.6	2.9
		woundA	330.8	11.1
		woundA + woundB	331.5	11.8

Table S3.1 (cont'd)

	Lean	LipInit	392.2	0
		woundA	393.1	0.9
		woundA + woundB	394.7	2.5
		woundA + LipInit	394.5	2.3
		woundA + sex	395.2	3
Normalized egg production	Siscowet	woundA + LipInit	156.158	0
		LipInit	156.453	0.295
		woundA + Esep + LipInit	156.508	0.35
		LipInit + Esep	156.91	0.752
		woundA + woundB + LipInit	157.926	1.768
	Lean	woundA + deltL	131.365	0
		deltL	134.695	3.33
		deltWt	137.339	5.974
		deltLip	138.073	6.708
		woundA + deltWt	138.361	6.996
Skipped Spawning	Siscowet	woundA + LipInit + Esep	20.136	0
		woundA + woundB + LipInit + Esep	21.353	1.217
		woundA + woundB + Esep	26.633	6.497
		LipInit + Esep	28.175	8.039
		deltWt + Esep + LipInit	28.28	8.144

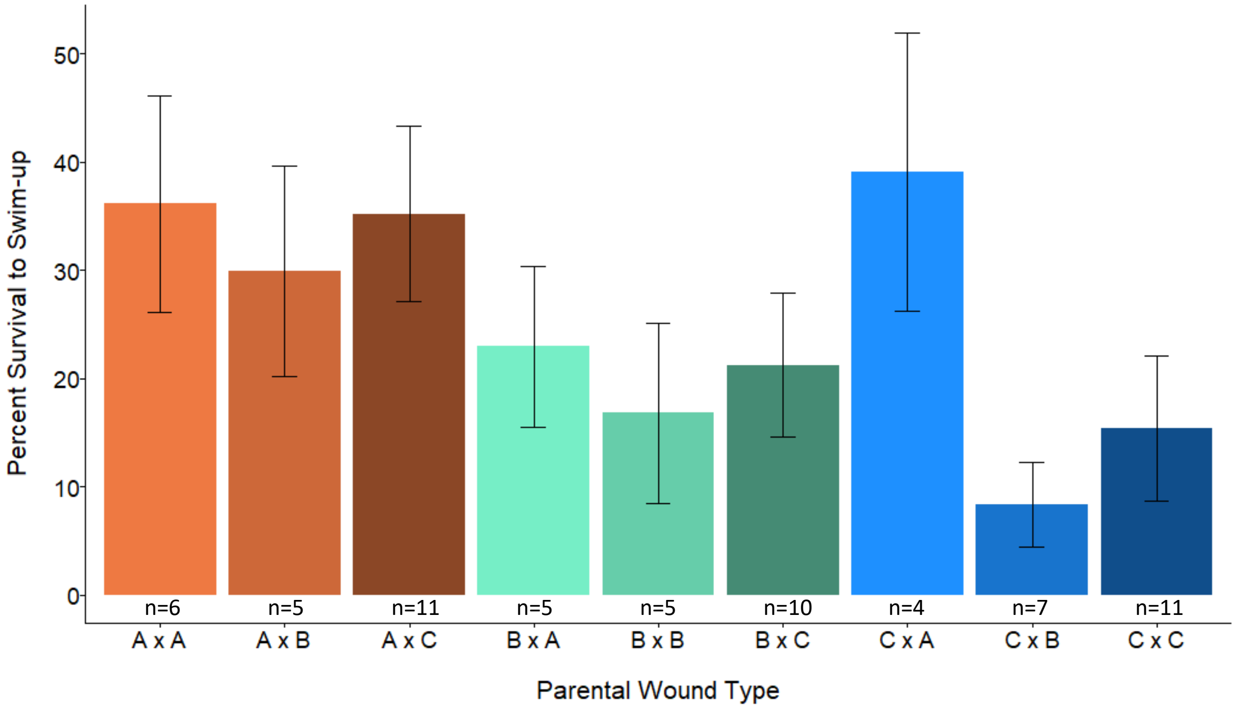

Figure S3.1. Embryo survival to swim-up for lean lake trout by parental wound type. Error bars indicate standard error of the mean. Parental wound types are indicated as follows (female x male). A refers to type-A, B refers to type-B, and C refers to control. For example, “A x C” indicates eggs from a type-A wounded female and milt from a control male were used in the cross.

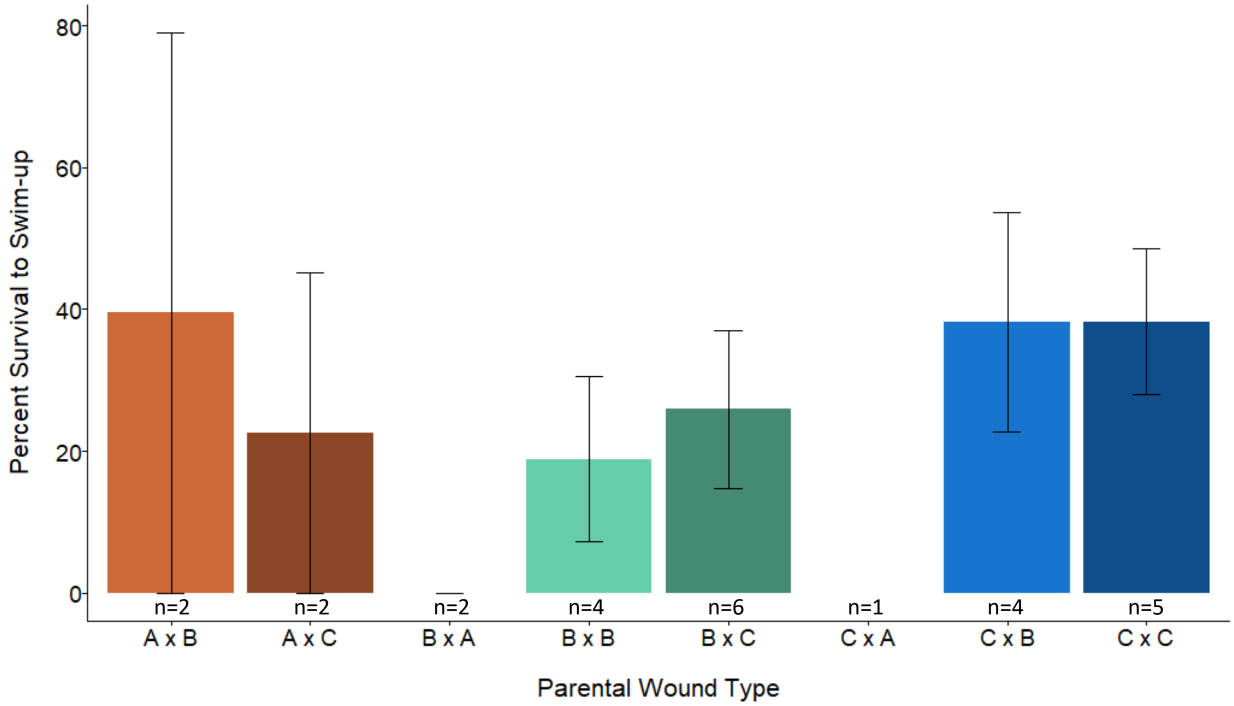

Figure S3.2. Embryo survival to swim-up for siscowet lake trout by parental wound type. Error bars indicate standard error of the mean. Parental wound types are indicated as follows (female x male). A refers to type-A, B refers to type-B, and C refers to control. For example, "A x C" indicates eggs from a type-A wounded female and milt from a control male were used in the cross.

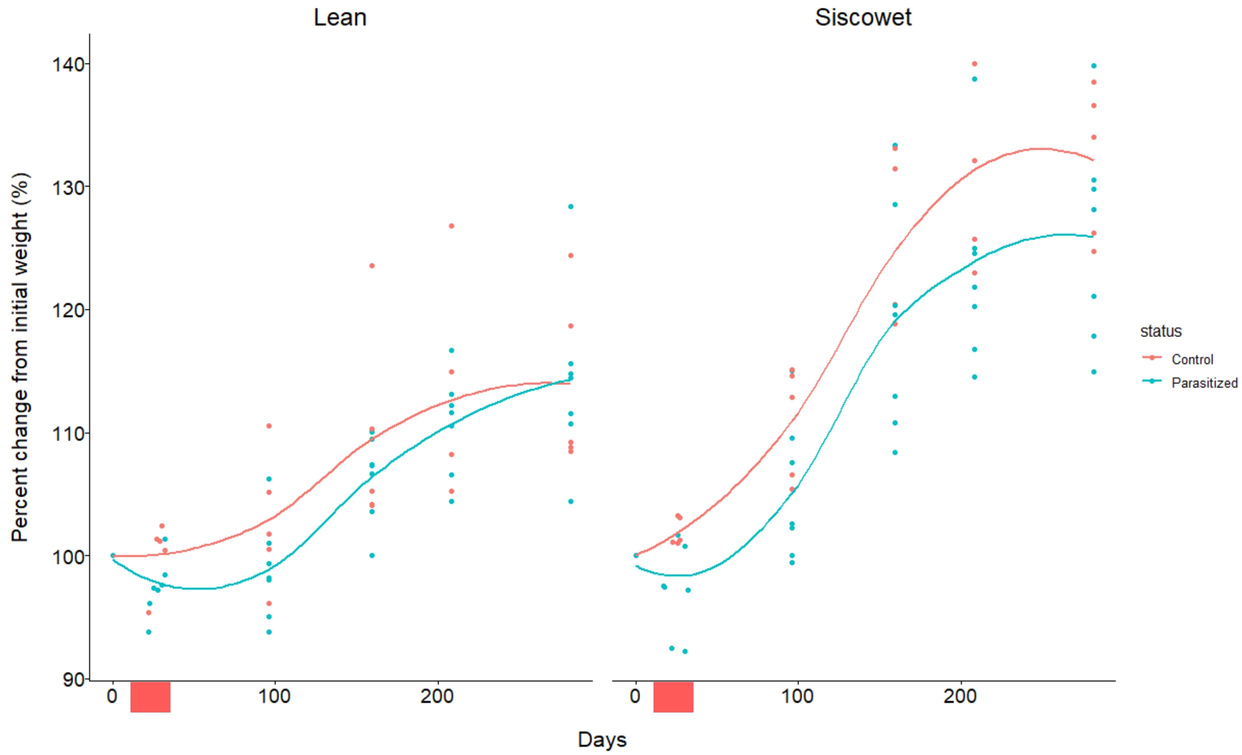

Figure S3.3. Percent change in weight for 5 year old lean and siscowet lake trout from a companion study. Change in weight is relative to weights just prior to parasitism. Boxes on the X-axis indicate the time that parasitism trials took place. Trend lines indicate loess smoothed regressions for parasitized and control categories.

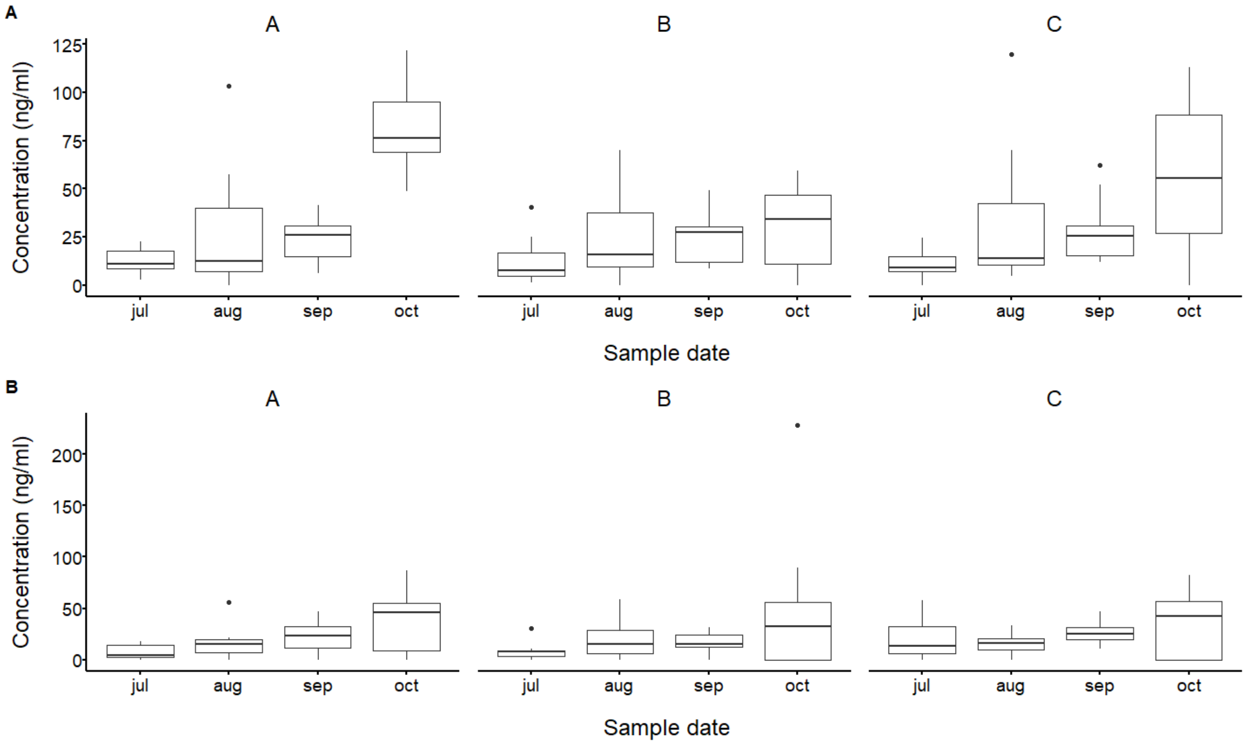

Figure S3.4. Testosterone (T) profiles for female lean (A) and siscowet (B) lake trout by parasitism status. Boxes indicate interquartile range, thick horizontal lines indicate medians, vertical lines indicate highest and lowest values, and dots indicate outliers. Type-A wounded, type-B wounded, and control fish profiles are indicated by A, B, and C respectively.

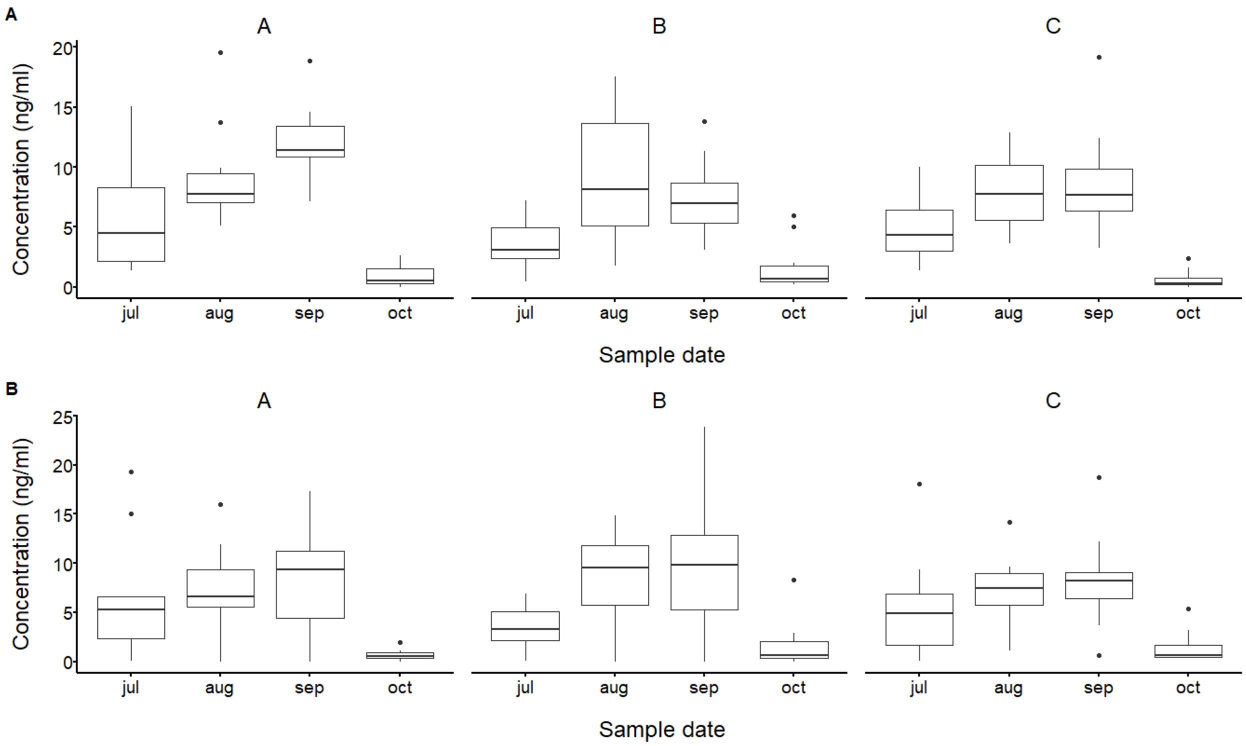

Figure S3.5. Estradiol (E2) profiles for female lean (A) and siscowet (B) lake trout by parasitism status. Boxes indicate interquartile range, thick horizontal lines indicate medians, vertical lines indicate highest and lowest values, and dots indicate outliers. Type-A wounded, type-B wounded, and control fish profiles are indicated by A, B, and C respectively.

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CHAPTER 4: THE CONSEQUENCES OF SEA LAMPREY PARASITISM ON LAKE TROUT ENERGY BUDGETS

Abstract

This study focuses on the development of a Dynamic Energy Budget model for siscowet lake trout and its use to enhance our understanding of the energetic consequences of sea lamprey parasitism. While empirically measured sub-lethal alterations to lake trout reproductive physiology can be striking, it is difficult to relate individual physiological alterations resulting from sea lamprey parasitism to effects on lake trout populations or ecosystem dynamics in the Great Lakes. To bridge between individual and population effects, we developed a Dynamic Energy Budget model that tracks energy allocation for siscowet lake trout, and account for parasitism-driven life history alterations. The model is parameterized to reflect the changes in allocation of energy towards growth and reproduction observed in lake trout following sea lamprey parasitism. This allows us to gain a better understanding of the energetic mechanisms that lead to skipped spawning following sea lamprey parasitism.

Introduction

One of the most consequential stressors for lake trout (*Salvelinus namaycush*) in the Laurentian Great Lakes is parasitism from non-native sea lamprey (*Petromyzon marinus*). Sea Lamprey are large ectoparasites that feed by attaching to host fish with a suction-cup-like mouth, mechanically removing scales and tissue with rasping mouthpart structures, and consuming blood and tissue (Lennon 1954). Lake trout are the preferred host species for non-native sea lamprey in the Laurentian Great Lakes (Harvey et al. 2008; Johnson et al. 2021). Following parasitism, hosts face a series of complications including osmotic imbalances from a large open wound (Ebener et al. 2006; Goetz et al. 2016; Firkus et al. 2020), low hematocrit from loss of blood (Edsall and Swink 2001), and introduced compounds from sea lamprey buccal gland secretions (Goetz et al. 2016). Often, sea lamprey parasitism is lethal to lake trout (Swink 1990, 2003; Madenjian et al. 2008), but those that survive are faced with energetic deficits and alterations to reproductive and growth physiology (Goetz et al. 2016; Smith et al. 2016; Chapter 3). Accordingly, when sea lamprey were introduced to the Laurentian Great Lakes in the late 1800s following construction of the Welland Canal, lake trout populations sharply declined (Hansen 1999; Muir et al. 2013).

Understanding the sublethal effects of sea lamprey parasitism on host lake trout physiology is critical for estimating the consequences for lake trout populations. Empirical measurements of sublethal effects at the molecular, cellular, or tissue level of biological organization provide important information, but they cannot alone inform about the consequences at the individual level. One valuable tool for modeling the energetic consequences of stressors at lower levels of biological organization and linking them to individual effects is dynamic energy budget theory (Kooijman 2010; Martin et al. 2013). Dynamic energy budget (DEB) theory provides a modeling framework based on evolutionary, chemical, and thermodynamic principles that describes the metabolic dynamics and energy partitioning of an individual organism through its entire life cycle (Kooijman 2010; Sousa et al. 2010; Jusup et al. 2017). DEB models are adaptable and can be developed for any species; a similar model framework can be used for a wide variety of species, but model parameters are estimated to predict observed biological responses for each species individually and can be altered to account for stressors that influence a species physiology. The models contain three main compartments (reserves, structure, and reproduction buffer) and a series of fluxes that dictate energy allocation to each compartment (Figure 4.1). Once parameterized, a DEB model can describe energy dynamics, and estimate growth, reproduction, and life history characteristics under different environmental conditions such as temperature and feeding regimes, and stressors including contaminants, disease, and parasitism at any point in an organisms life cycle (Kooijman 2010). Any stressor that alters physiological processes can be represented by a change in one or more DEB model parameters (Jager 2019). Because these models consider the whole organism and can simultaneously account for stress acting on multiple physiological functions, they are well suited to assimilating empirically measured sublethal effects at lower levels of biological organization to understand how they will influence individuals and populations.

The objectives of this study are twofold. First, we aim to parameterize a DEB model for siscowet lake trout using available life history data from the literature. Lake trout display tremendous variation throughout their range, exemplified by the existence of a least four currently recognized lake trout ecomorphs in Lake Superior alone that are distinguished in appearance, habitat preference, metabolism, and life history characteristics (Moore and Bronte 2001; Goetz et al. 2014; Muir et al. 2014, 2016; Sitar et al. 2020). A general lake trout DEB model has previously been developed using data from an inland strain of lake trout (Kooijman 2019), but because the metabolic dynamics and response to sea lamprey parasitism differ so dramatically for the siscowet ecomorph (Goetz et al. 2010, 2014, 2016; Smith et al. 2016; Sitar et al. 2020; Chapter 3), it is necessary to develop a separate siscowet-specific model. The second objective is to use the parameterized DEB model for siscowet lake trout to explore the effects of sea lamprey parasitism on reproduction, growth, and other life history characteristics. In prior studies, we have empirically measured the influences of sea lamprey parasitism on siscowet lake trout growth, reproduction, energy storage, and gene expression (Goetz et al. 2016; Smith et al. 2016; Chapter 3). Based on these studies, we know that the siscowet lake trout response to parasitism depends largely on muscle lipid concentration, plasma estradiol concentration, and parasitism status (Chapter 3). These measured effects can be used to inform how different DEB parameters are stressed under parasitism, and allow alterations to reproductive output, growth, and energy storage to be estimated within the context of the whole lake trout energy budget. Once the effects of parasitism are modeled, they can be used to explore the effects of parasitism under a variety of scenarios and ultimately inform stock-recruitment relationships, individual-based models, and other tools critical for the management of lake trout in the Laurentian Great Lakes.

Methods

General model description

The general structure, equations, and assumptions of DEB models have been thoroughly covered previously (Sousa et al. 2008, 2010; Kooijman 2010; Jusup et al. 2017). Briefly, energy enters an organism through uptake of food (with a fraction removed as feces) and enters a reserve pool. Energy is mobilized from the reserve at a given rate and allocated towards somatic growth and reproduction following the κ rule. The κ rule states that a fixed portion (κ) of mobilized energy is allocated towards somatic growth, while the remaining fraction (1-κ) is allocated towards reproduction. For both somatic growth and reproduction, maintenance processes (e.g. protein turnover, activity, respiration, immune function, etc.) are paid first, before remaining energy can be allocated to growth or the reproduction buffer that allows for gamete production. This structure is described in the model by four state variables (reserve E, structural volume V, reproduction buffer E_R, and maturity E_H), and a series of differential equations and model parameters that dictate energy flux to each compartment (Kooijman 2010). A generalized overview of these processes is shown in Figure 4.1. We used an “abj” typified DEB model that accounts for metabolic acceleration during early development between birth and metamorphosis (Marques et al. 2018). The abj DEB models differ from 'standard' DEB models by allowing for the rapid increase in respiration and change in body shape that occurs during the larval stages of most fish species, and include one additional parameter, ${E_H}^j$ or the maturity threshold at metamorphosis (Kooijman 2014; Lika et al. 2014).

State variables in DEB models represent an aggregation of complex physiological functions, and therefore model parameters cannot be directly measured. Instead, we indirectly estimated them from empirical data using the "add my pet" procedure (Marques et al. 2018) and covariation method (Lika et al. 2011) implemented in MatLab (The Math Works Inc. 2020) with the software package DEBtool (available at https://add-my-pet.github.io/DEBtool_M/docs/index.html). Briefly, parameter estimates are derived through simultaneously minimizing the weighted sum of squared deviations between provided data and model estimates. Model goodness of fit was evaluated with the mean relative error (MRE) and symmetric mean squared error (SMSE) (Marques et al. 2019). Lower MRE and SMSE indicate better model predictions.

Data for model parameterization

Data used for parameter estimation was obtained from published literature from both laboratory studies and surveys of wild populations (Table 4.4, Appendix III). Because there are many lake trout ecomorphs with very different life histories, only data collected specifically from the siscowet ecomorph was included for parameter estimation. Age-at-puberty, total length-at-puberty, wet weight-at-puberty, maximum reproduction rate, length-number of eggs, time-length, time-wet weight, length-wet weight, and time-gonadal mass were obtained from observations of wild siscowet lake trout surveyed in Lake Superior (Miller and Schram 2000; Goetz et al. 2011, 2017; Sitar et al. 2014; Hansen et al. 2016; Froese and Pauly 2021). Additional information such as length-at-birth, age-at-birth, and egg weight were obtained from laboratory rearing studies (Smith et al. 2016; Firkus et al. Unpublished). Because there is not sufficient information available to estimate all model parameters, values from a generalized animal (termed pseudodata) were used to guide the estimation procedure for energy conductance, allocation fraction to soma, reproduction efficiency, volume-specific somatic maintenance, maturity maintenance coefficient, growth efficiency, and maintenance ratio following guidelines detailed in Kooijman (2010) and Lika et al. (2011) (Table 4.4). Briefly, pseduodata serves a similar role to a prior in Bayesian parameter estimation, and gives a reasonable starting point when no species-specific information is available.

Implementing effects of parasitism, muscle lipid concentration, and estradiol concentration

In the case of sea lamprey parasitism, empirical evidence suggests siscowet lake trout reduce reproductive output (Chapter 3) and plasma sex steroid concentrations (Smith et al. 2016; Chapter 3) following parasitism. For siscowet lake trout that survive sea lamprey parasitism, a common outcome is skipped spawning whereby an individual forgoes reproductive output completely and instead allocates energy towards surviving the stress associated with the parasitism event. In addition to parasitism, energy storage in the form of muscle lipids also plays an important role in the reproductive success of siscowet lake trout and the likelihood of skipping spawning (Sitar et al. 2014; Goetz et al. 2017; Chapter 3).

In the context of dynamic energy budgets, any stressor that alters physiological processes must be reflected by a change in one or more model parameters (Jager 2019). Therefore, we must identify the physiological mode of action (pMoA) that describes the specific physiological mechanism, and thus the specific DEB parameter(s), through which sea lamprey parasitism influences life history (Ashauer and Jager 2018). Once the appropriate DEB parameter(s) are identified, a relationship between the stressor and model parameter, termed damage, must be developed. In toxicology applications, the relationship between damage function is typically expressed as 'linear-with-threshold' model that approximates a dose-response curve (Jager 2019). Because sea lamprey parasitism is a binary stressor (parasitism either occurs or does not occur), our relationships between parasitism and the target DEB parameters are also binary. Also, because individual variation in muscle lipid and estradiol concentration is not necessarily the result of some form of damage, a 'linear-with-threshold' relationship is also unlikely to best represent what we are trying to capture. The changes to a particular DEB parameter cannot be experimentally derived, and therefore must be developed based on best judgement and an approximation of the desired response based on empirically observed changes to length, weight, and egg production (Chapter 3). A detailed description of our process for implementing parasitism stress, muscle lipid variation, and estradiol variation is outlined below and summarized in Table 4.1.

After developing these parasitism and individual variation driven modifications to the siscowet lake trout DEB parameters, our goal was to explore a variety of scenarios by varying muscle lipid concentration, parasitism status, and plasma estradiol concentration. Simulations were run only for female lake trout and for each simulated individual we started the simulation year at a weight of 1.73kg. These scenarios can help inform how individual siscowet lake trout will respond to parasitism, which can be explored later in population models.

Influence of parasitism

One of the key effects observed in siscowet lake trout following parasitism is the reduction of egg production and increased incidence of skipped spawning (see Chapter 3, Figure 3.4). Thus, parasitism should alter DEB parameters in a way which leads to a marked reduction of reproductive investment. Many DEB parameters can influence reproduction, but not all are likely candidates given what we know about parasitism. We expect siscowet lake trout will favor allocating energy towards somatic functions over reproduction during parasitism due to the need to meet the demands of parasitism-driven increases in somatic maintenance (Goetz et al. 2016). Observations that growth is not reduced in siscowets following parasitism (Chapter 3), and observations that reproduction is severely reduced (or ceased) in parasitized siscowets (Chapter 3) further support this idea. Because of these observed effects, parasitism altering the portion of energy that is allocated to soma vs reproduction is a plausible pMoA. Although we observe high rates of skipped spawning in parasitized siscowets, we know that some "normal" reproductive development occurs prior to spawning, but at some point, oocytes cease further development and are resorbed (Goetz et al. 2011; Sitar et al. 2014). Therefore, we expect allocation to soma (represented in DEB by the parameter κ) to increase, but we do not expect all energy to be allocated to soma. Our DEB model of an unparasitized siscowet has a κ value of 0.52. To simulate parasitism, we increased κ by 40% to 0.73, a considerable increase, but not unreasonable given the increase in somatic maintenance, repair processes, and the sharp reduction in reproduction observed following parasitism.

Energy invested to soma must first pay somatic maintenance costs. Somatic maintenance can be either volume-specific or surface-area-specific. Volume-specific somatic maintenance represents the costs for maintaining somatic functions such as concentration gradients, turnover of structure, and movement costs, and the parameter $[\dot{p}_M]$ is multiplied by the cubed structural length of the individual (Kooijman 2010) (Table 4.1). Because parasitism creates an open wound in the lake trout, the costs for maintaining concentration gradients, repairing tissue, replacing lost blood cells, and turning over necrotic tissue will be considerably increased. Thus, an increase in volume-specific somatic maintenance is a likely pMoA. For unparasitized siscowets, the estimated volume-specific somatic maintenance parameter $[\dot{p}_M]$ is 31.59 J/d.cm^2. While we cannot directly measure how much this will increase following parasitism, increasing maintenance costs 2.5 times (78.98) is not unreasonable given the magnitude of damage caused by parasitism. Surface-area-specific somatic maintenance $[\dot{p}_T]$ generally represents costs associated with endothermic heat-loss. Because lake trout are ectotherms, this form of maintenance is negligible and represented as 0 in our unparasitized siscowet DEB model and is left unchanged following parasitism.

Energy allocated to reproduction must pay maturity maintenance $\dot{k}_J$ prior to investment in reproductive processes. Maturity maintenance is the costs associated with maintaining a certain level of maturity and are proportional to the total energy invested to maturation. Maturity maintenance also includes regulation and protection functions such as the immune system (Kooijman 2010). Because parasitism results in a mounted immune response and greater regulatory and protection overheads (Goetz et al. 2016), we expect maturity maintenance to increase in parasitized siscowets (Table 4.1). The unparasitized maturity maintenance coefficient is 0.002. It is impossible to measure how parasitism increases this parameter, so we must use our best judgement based on our data. Because of the observed increase in immune function gene expression (Goetz et al. 2016) and observed decrease in reproduction, we will assume that parasitism increases maturity maintenance by 90% (to 0.0038).

Influence of muscle lipid concentration

In addition to the effects of parasitism-induced stress, lipid storage also plays a key role in reproduction for siscowet lake trout. Surveys of wild lake trout found that siscowet lake trout that skipped spawning had significantly lower energy reserves (Sitar et al. 2014). In laboratory settings, muscle lipid concentration prior to parasitism was a significant predictor of egg production and the likelihood of skipping spawning (Chapter 3). Therefore, accounting for individual variation in muscle lipid is important for accurately modeling the influence of parasitism. Lipid storage has no direct analogue in the DEB framework, but is most likely analogous to the reserve compartment as this is thought to primarily consist of polymers and lipids (Kooijman 2010). The energy conductance parameter $\dot{V}$ controls the rate of energy mobilization from the reserve. Increasing $\dot{V}$ increases the rate at which reserves are depleted and mobilized for use. We would expect that siscowet lake trout with low muscle lipid storage would mobilize energy from the reserve at a much lower rate to allow lipid to accumulate (Table 4.1). This seems especially likely given the functional role of lipid for maintaining neutral buoyancy at the depths siscowet lake trout inhabit (Henderson and Anderson 2002; Goetz et al. 2014). From laboratory studies, we know that every 10% decrease in muscle lipid content is associated with an approximate 44% reduction in egg mass for siscowet lake trout (Chapter 3), and we aimed to approximate that change by modifying $\dot{V}$. The resulting modifying equation is $\dot{V} = 0.017(\frac{L}{50.67})^2$, where L is the lipid concentration of the modeled individual, 0.017 is the $\dot{V}$ parameter estimated for an unparasitized siscowet lake trout, and 50.67 is the average lipid concentration in the siscowet lake trout sample from Chapter 3. In this equation, as an individual deviates from the average lipid concentration, $\dot{V}$ is increased or decreased accordingly. This relationship produced the desired effect on reproductive output and serves as a reasonable representation of the influence of muscle lipid independent of parasitism.

Influence of plasma estradiol concentration

In addition to muscle lipid concentrations, reproductive hormone dynamics also play a critical role in reproduction, and are influenced by stress. To account for this, we implemented an egg module to the DEB model that allows reproductive hormone dynamics to dictate the conversion of energy in the reproduction buffer into eggs. A similar approach is outlined in Murphy et al. (2018) and Muller et al. (2019), however we simplified this approach so that estradiol concentration was the only required input. A list of sub-model parameters and their description is provided in Table 4.2. In this sub-model, energy allocated to reproduction is accumulated in the reproduction reserve (M_R), and is then converted into egg mass (M_{OV}). Energy enters M_R at a rate of $\dot{j}_R = (1-\kappa)\dot{j}_{EC} - \dot{j}_{EJ}$ where $\dot{j}_{EC}$ is the flux of reserve mobilization and $\dot{j}_{EJ}$ is the maturity maintenance rate. The energy available for egg production is equal to the maximum allocation to reproduction:

$$\dot{j}_R = \left((1-\kappa)\dot{j}_{EC_m} - \dot{j}_{EJ}\right) \quad (1)$$

where $\dot{j}_{EC_m}$ is the maximum mobilization rate from reserve. Data for estradiol (E2) was obtained from laboratory studies of siscowet lake trout (Chapter 3) as ng/ml of plasma. These data were linked to the model variable that accounts for the mass of estradiol (M_{E2}) using the following equation:

$$[E2] = \frac{10^9 w_{E2} M_{E2}}{V_{pl}} \quad (2)$$

where $[w_{E2}]$ is the molecular weight of estradiol (272.38 g/mol) and V_{pl} is the total volume of plasma in a lake trout in ml given by the following equation:

$$V_{pl} = \frac{\beta_{pl} W_W}{100} \tag{3}$$

where W_W is the wet weight and β_{pl} is the proportionality constant (2.86%). M_R is combined with E2 to synthesize the egg yolk protein vitellogenin (Vtg) using the synthesizing units concept (Brandt et al. 2004; Muller, Klanjšček, et al. 2019). Vtg synthesis follows sequential-complementary transformation, and therefore estradiol provides the signal for Vtg production. Conversion of M_R to Vtg proceeds as follows:

$$y_{Vtg,H} E2 + y_{Vtg,R} R \rightarrow Vtg \tag{4}$$

where $y_{Vtg,H}$ and $y_{Vtg,R}$ are coupling coefficients and represent the amount of Vtg synthesized per mol of E2 and per mol of reproductive reserve respectively. Vtg synthesis rate is calculated as:

$$j_{VtG} = \left(\left(y_{Vtg,R} j_R \right)^{-1} + \left(y_{Vtg,H} j_H \right)^{-1} \right)^{-1} \tag{5}$$

where j_H and j_R are the specific arrival rates of estradiol and reproductive reserve respectively; $j_H = b_H m_{E2}$ while j_R is given in eq. (1). The specific transformation rates are explained as;

Estradiol:

$$j_{\bar{H}} = y_{Vtg,H} \left(\left(y_{Vtg,R} j_R \right)^{-1} + \left(y_{Vtg,H} j_H \right)^{-1} \right)^{-1} \tag{6}$$

And reproductive reserve:

$$j_{\bar{R}} = y_{Vtg,R} \left(\left(y_{Vtg,R} j_R \right)^{-1} + \left(y_{Vtg,H} j_H \right)^{-1} \right)^{-1} \tag{7}$$

Vtg production occurs in the liver, and the processes involved are proportional to the volume-specific mass of structure (M_V). M_V dynamics are:

$$\frac{dM_v}{dt} = rM_V \quad (8)$$

The dynamics of the mass of the reproductive reserve (M_R) are:

$$\frac{dM_R}{dt} = (1-\kappa)\dot{j}_{EC} - k_J M_H^P - \dot{j}_{\bar{R}} M_V \quad (9)$$

The dynamics of the mass of the ovaries (M_{OV}) is described as:

$$\frac{dM_{OV}}{dt} = \kappa_R j_{Vtg} M_v \quad (10)$$

where κ_R is the fraction of mass fixed in eggs. The dynamics of the reserve density m_E is described as:

$$\frac{dm_E}{dt} = j_{EAm}\left(f - \frac{m_E}{m_{Em}}\right) \quad (11)$$

Results

DEB model parameters

Parameterization of the siscowet lake trout DEB model was successful and resulted in reasonable primary parameters (Table 4.3). Predictions from the parameterized DEB model matched the provided data well and resulted in an acceptable overall goodness of fit as measured by the mean relative error MRE (0.133) and the symmetric mean squared error SMSE (0.155) (Table 4.4). Wet weight at metamorphosis and ultimate wet weight was underestimated (RE=0.996 and 0.158 respectively) and age at puberty was overestimated (RE=0.124) compared to the observed data (Table 4.4). Estimates for fecundity-at-length, fecundity-at-weight, length-weight, length-time, and weight-time were all reasonable with relatively low residual error (Figure 4.2, Table 4.4). Gonadal wet mass-time had a worse fit, and underestimated gonadal mass at the end of the year (Figure 4.2, Table 4.4).

Parasitism and muscle lipid concentration

One scenario we were interested in exploring was the combined influence of muscle lipid concentration and parasitism on reproduction and growth outcomes. Both factors are known to influence reproduction and the likelihood of skipping spawning, but we have little information about how they interact. In our first scenario, we altered parasitism status and lipid concentration (40%, 50%, and 60%) while holding estradiol constant. For unparasitized siscowet lake trout, varying lipid alters gonadal mass. The muscle lipid concentration for the average siscowet lake trout in our data (50%) resulted in an ovarian weight of 148g just prior to spawning (270 d). A 10% reduction in muscle lipid resulted in a reduction of ovarian mass to 110g, while a 10% increase in muscle lipid increased ovarian mass to 174g (Figure 4.3B). Adding the influence of parasitism reduced ovarian mass regardless of muscle lipid concentration. Under average muscle lipid concentrations (50%) and parasitism, ovarian weight was 74g at the time spawning would normally occur. A 10% reduction in muscle lipid resulted in a resulted in ovarian mass reduced to 14g, while a 10% increase in muscle lipid increased ovarian mass to 117g (Figure 4.3B)

Growth was also influenced by both parasitism and muscle lipid concentration in our tested scenarios. In the scenarios that included parasitism, growth was greater than for unparasitized scenarios with the same lipid concentration (Figure 4.3C). At 50% muscle lipid concentration, the parasitism scenario resulted in an end-of-year weight of 1928g, while the unparasitized scenario resulted in an end-of-year weight of 1903g (Figure 4.3C). In all scenarios, a 10% change in muscle lipid concentration generally resulted in an ~30g difference in end-of-year wet weight (Figure 4.3C).

Parasitism and estradiol concentration

We also wished to examine the interaction between individual variation in estradiol concentration and parasitism for siscowet lake trout. In this scenario, we provided two separate estradiol regimes taken from estradiol profiles of laboratory raised fish (Foster et al. 1993; Chapter 3) (Figure 4.4A) and observed the effects on ovarian mass for parasitized and unparasitized individuals while keeping muscle lipid constant (50%). Differences in estradiol regime resulted in a 12g difference in ovarian mass (136 vs 148g) in the unparasitized simulations, and a negligible difference in ovarian mass in the parasitized simulations (Figure 4.4B).

Discussion

Parasitism is a complex stressor for host species, and influences multiple physiological processes simultaneously. Capturing the full extent of these effects, and their implications for the whole organism, is challenging with empirical measurements alone. DEB theory allows us to cumulatively incorporate empirical measurements of the effects of parasitism into one coherent framework that allows the consequences for many different processes to be evaluated simultaneously. In this paper, we successfully developed and parameterized a DEB model that captures the energy dynamics of siscowet lake trout. The model reproduced key life history features specific to the siscowet lake trout ecomorph, and produced model estimates that adequately matched field and laboratory collected data. We also developed modifications to key DEB parameters to capture the effects of sea lamprey parasitism, and the influence of individual variation in muscle lipid concentration and estradiol profiles. Using these modifications, we explored several scenarios and evaluated their influence on ovarian mass and growth.

DEB model for unparasitized siscowet lake trout

Lake trout ecomorphs display considerable life history variation (Moore and Bronte 2001; Goetz et al. 2014; Muir et al. 2014, 2016; Sitar et al. 2020), so it is important that this variation was accounted for in our DEB model. The parameterized model ultimately did a good job of capturing the specific life history of siscowet lake trout with a few exceptions. Age-at-puberty was underestimated in the model (3647 days, compared to an observed 4161 days). Part of the reason for this discrepancy may be due to difficulties differentiating immature lake trout from skipped spawning individuals in the field (Goetz et al. 2011; Sitar et al. 2014). This difficulty coupled with the high rates of skipped spawning for siscowet lake trout (Sitar et al. 2014) may explain why observed puberty data was higher than our model estimates. Additionally, siscowet lake trout display a tremendous amount of variation in age-at-puberty in the wild, with some reaching puberty as late as age 19 (Sitar et al. 2014). Therefore an approximately one year underestimation for age-at-puberty is not too concerning. Wet weight at metamorphosis was also a poor fit in our model (RE=0.99). The data we used for metamorphosis was based on modeled post-hatch growth when the initial burst of growth appeared to taper. There is little published information about lake trout metamorphosis, and some evidence indicates that lake trout have a very brief metamorphosis phase (Marsden et al. 2021), which may mean our model estimates are more reasonable than the provided data.

For some parameters with little information, we relied on pseudo-data following guidelines detailed in Kooijman (2010) and Lika et al. (2011). Pseudo-data serves as a starting point for parameter estimation when there is no available data. The estimation process can help hone in on better species-specific estimates for these parameters as the model fits to other provided data. In most cases, our use of pseudodata resulted in reasonable fits with the exception of allocation fraction to soma and volume-specific somatic maintenance. The resulting estimate for allocation fraction to soma (0.52) was smaller than our provided pseudodata value (0.8) and smaller than typical values for most salmonid species in the add_my_pet database (Table 4.4). Volume-specific somatic maintenance was estimated at 31.59 which is higher than the provided pseudo-data. Given what we know about the life history of siscowet lake trout, a lower allocation fraction to soma and higher volume-specific somatic maintenance makes sense. Siscowet lake trout are relatively long lived and slow growing compared to other salmonids and lake trout ecomorphs, and likely require significantly higher energy investment to maintain body condition (Goetz et al. 2014; Hansen et al. 2016; Muir et al. 2016). Additionally, siscowet lake trout invest a considerable amount of energy into lipid reserves which are not included as a part of soma in DEB models. As a consequence, these estimate deviations from the pseudo-data make sense.

Influence of parasitism and individual variation

The alterations to DEB parameters we implemented are not necessarily a true representation of how sea lamprey parasitism influences the energy budget of a siscowet lake trout. Because the metabolic parameters in DEB models are abstract, include many processes, and cannot be directly measured, the process for implementing stress is inherently arbitrary

(Jager 2019). Regardless, the alterations we implemented do a reasonable job of describing the effects on growth, reproduction, and energy storage observed from the empirical data, and at the very least serve as plausible hypotheses for future experimental work. They also allow us to examine the consequences of parasitism on reproduction and growth under a variety of scenarios.

The first scenario we were interested in was the interaction between muscle lipid concentration and parasitism, and its influence on reproduction and growth. Under the scenarios we tested, lipid concentration had a heavy influence on reproduction regardless of parasitism status. At the lowest lipid simulation (40%), ovarian mass reached 110g just prior to spawning. This is low relative to the observed data from wild siscowet lake trout, but is likely a reasonable representation of individuals with low muscle lipid concentration. Studies of wild and laboratory raised siscowet lake trout, indicate unparasitized individuals skip spawning at some baseline rate as a part of their life history, and that skipping is at least partially dependent on muscle lipid concentration (Goetz et al. 2011; Sitar et al. 2014; Chapter 3). Therefore, we would expect low lipid levels to result in lower-than-typical ovarian weight to reflect the increased likelihood of skipping spawning.

As expected, parasitism reduced ovarian mass at all lipid concentrations, and only at lipid concentrations of 60% did ovarian mass exceed 100g. The threshold for skipping spawning is a gonadosomatic index below 3. In our simulations this would mean any lake trout with ovarian mass lower than 57g would be deemed a skipped spawner. In our simulations, a parasitized siscowet lake trout would require a muscle lipid concentration of at least 47% to reach that threshold. Average siscowet lake trout muscle lipid concentrations range from 29 to 64% depending on the size and depth inhabited by the individual (Sitar et al. 2020), so a substantial proportion of wild fish may not meet that threshold.

Interestingly, in our simulations, parasitism resulted in increased growth relative to our unparasitized simulations with the same muscle lipid conditions. This is largely due to our choice to have parasitism significantly increase the allocation fraction to soma (κ). Because parasitism increases somatic maintenance costs, allocating energy away from reproduction to meet these demands is a good strategy. Furthermore, it is likely an adaptive strategy to allocate the majority of remaining energy after paying maintenance to growth following parasitism, as the relationship between body size and egg production means that any growth that can be added in a year of skipped spawning will lead to greater reproductive output in future years. The lean ecomorph of lake trout appear to increase growth following parasitism relative to their unparasitized counterparts as estimated from long-term field-collected sampling efforts (Smith et al. 2016), but this trend has not been identified in siscowet lake trout. The simulated changes in growth we observed are also relatively small biologically. A 20-30g difference in wet weight over the course of a year between parasitized and unparasitized individuals is not dramatic, and likely would not be noticeable in field-sampled fish in the long-term.

Estradiol profile had a much more subtle effect on reproduction in our simulations. For unparasitized individuals, the two estradiol profiles we tested resulted in only a 12g difference in ovarian mass. In the scenarios tested, the low estradiol profile represented the averages of lake trout who were observed to skip spawning. We therefore expected this scenario to result in a greater decrease in ovarian mass than we ultimately observed. There are several potential explanations for why the changes we observed in these scenarios was subtle. First, our sub-model assumes that estradiol contributes to ovarian mass synthesis at the same rate regardless of other conditions. It is possible that when lake trout skip spawning, plasma estradiol plays a different role outside of gonadal development. We generally think of estradiol in terms of its role in modulating hepatic production and gonadal uptake of Vtg. (Tyler and Sumpter 1996), but it also plays a key role in regulating immune functions in fish (Cabas et al. 2018). If this is the case, the same amount of estradiol could result in different ovarian mass depending on what proportion is used for gonadal development relative to other functions. Therefore, this assumption may require re-evaluation in future studies. Second, the relative influence of estradiol on egg production is relatively small in comparison to the influence of muscle lipid concentration and parasitism (Chapter 3), and therefore more dramatic changes in plasma estradiol may be necessary to drive large changes in ovarian mass.

Model limitations

It is important to highlight the limitations of this model and resulting simulations. First, the alterations to the DEB model implemented to represent parasitism are not directly measured. Because DEB model parameters often represent a combination of many physiological processes, there is not a direct empirical measurement for each parameter. Instead, we were required to rely on our best judgement and implement changes to DEB parameters that matched or knowledge of the physiological modes of action caused by parasitism and that resulted in changes to endpoints we were able to empirically observe. Thus, the changes we implemented are putative. Other processes that we did not consider could be important. Our model therefore only serves as a reasonable hypothesis for how parasitism, muscle lipid, and estradiol concentration influence lake trout energy budgets. Likewise, our simulation results reflect the decisions we made when developing the relationships between parasitism, muscle lipid, estradiol, and respective DEB parameters. Despite these limitations, our model and simulation results provide testable hypotheses that can drive empirical research going forward.

Conclusions

The DEB model presented in this paper can play an important role in modeling lake trout populations and evaluating the influence of other stressors besides parasitism. Coupled with parameterized DEB models for other lake trout ecomorphs, and individual based model that used these DEBs could be a valuable tool for modeling lake trout populations and assessing the relative contribution of different ecomorphs to lake trout populations in the Laurentian Great Lakes. If developed, this model could also evaluate the influence of changing environmental conditions or other stressors on lake trout populations. Because lake trout ecomorphs in the Great Lakes have widely varying life histories, a model that accounts for those differences would be much more powerful than traditional stock-recruitment population models.

Modeling the effects of sea lamprey parasitism on lake trout in the context of DEB models is a powerful tool that allows for the entire energy budget of the organism to be accounted for. Parasitism is a complex stressor that influences many different physiological functions and interacts with the life history of the host, and understanding the cumulative effects on growth and reproduction is challenging. The DEB model we parameterized for siscowet lake trout allows us to explore these cumulative effects and interactions of sea lamprey parasitism, and are a step towards accounting for the sublethal effects of sea lamprey parasitism in lake trout population models. If integrated into an individual-based-model, this approach could model lake trout populations while accounting for individual variation both among and between lake trout ecomorphs. Additionally, simulations evaluating the effects on reproduction and growth can be developed to adjust stock-recruitment model parameters such as spawning stock biomass, or spawners-per-recruit. This is a promising approach for incorporating the sublethal effects of parasitism and other stressors into population models going forward. Additionally, these efforts help identify knowledge gaps in our mechanistic understanding of sea lamprey parasitism, and can provide us with testable hypotheses that can inform future empirical studies.

APPENDICES

APPENDIX I

Tables

Table 4.1. Alterations to original DEB parameters due to parasitism, variation in muscle lipid concentration, and variation in plasma estradiol concentration.

Source	Affected Parameter	Original Value	Changed Value	Unit	Justification
Parasitism	κ	0.5205	0.73	–	Parasitism requires more energy to be allocated to soma to meet increased somatic maintenance demands and optimize future reproductive success
	$[\dot{p}_M]$	31.59	78.98	$J\ cm^{-3}\ d^{-1}$	The open wound created by parasitism increases costs for maintaining concentration gradients, repairing tissue, replacing lost blood cells, and turning over necrotic tissue
	$\dot{k}_J$	0.002	0.0038	d^{-1}	Parasitism results in a mounted immune response and increased regulatory and protection overheads which are part of maturity maintenance
Muscle lipid concentration	$\dot{v}$	0.017	Varies	$cm\ d^{-1}$	Lake charr with lower muscle lipid concentration mobilize energy from reserve at a lower rate to allow lipid stores (part of reserve) to increase
Plasma estradiol concentration	estradiol sub-model	-	-	-	Estradiol dictates the conversion of energy in the reproduction buffer into ovarian mass, and therefore differences in estradiol profile must be accounted for (see eq. 1-11)

Table 4.2. State variables and parameters used in the estradiol sub-model and associated units. Quantities in moles are converted to grams or to Joules using the respective molecular weights and chemical potentials.

	Symbol	Value	Unit	Interpretation
State Variables				
	M_V		mol/ml	mass of structure
	M_E		mol/ml	mass of reserve
	m_E		–	scaled reserve density
	M_R		mol/ml	mass of reproductive reserve
	M_{E2}		mol/ml	mass of estradiol
	m_{E2}		–	scaled mass of estradiol
	E2		ng/ml	concentration of estradiol in plasma
	V_{pl}		ml	total volume of plasma
	$y_{Vtg,H}$	19613000	mol VtG/mol E2	coupling coefficient, E2
	$y_{Vtg,R}$	6.0464	mol VtG/mol R	coupling coefficient, reproductive reserve
	b_H	1	d^{-1}	signal
Molecular weights, chemical potentials, and densities				
	w_E	23.9	g/mol	molecular weight of dry reserve
	w_V	23.9	g/mol	molecular weight of structure
	μ_E	550000	J/mol	chemical potential of the reserve
	d_E	0.2	g/cm^3	specific density of dry reserve
	d_V	0.2	g/cm^3	specific density of structure

Table 4.3. Primary abj DEB parameters estimated for siscowet lake trout at a reference temperature of T=20.0°C

Symbol	Value	Unit	Interpretation
z	10.74	–	Zoom factor
$[\dot{F}_m]$	6.5	$1 d^{-1} cm^2$	Maximum specific searching rate
$\{\dot{p}_{am}\}$	652.09	$J\,cm^{-2}\,d^{-1}$	Specific maximum assimilation rate
$\dot{v}$	0.01717	$cm\,d^{-1}$	Energy conductance
κ	0.5205	–	Allocation fraction to soma
κ_X	0.8	–	Digestion efficiency of food to reserves
κ_P	0.1	–	Defecation efficiency of food to faeces
κ_R	0.95	–	Reproduction efficiency
$[\dot{p}_M]$	31.59	$J\,cm^{-3}\,d^{-1}$	Volume-specific somatic maintenance rate
$\{\dot{p}_T\}$	0	$J\,cm^{-3}\,d^{-2}$	Surface-specific somatic maintenance
$[E_G]$	5227	$J\,cm^{-3}$	Specific costs for structure
$\dot{k}_J$	0.002	d^{-1}	Maturity Maintenance rate coefficient
E^h_H	0.0674	J	Maturity threshold at hatching
E^b_H	33.91	J	Maturity threshold at birth
E^j_H	82.19	J	Maturity threshold at metamorphosis
E^p_H	$6.35\ 10^5$	J	Maturity threshold at puberty
$\ddot{h}_a$	$3.64\ 10^{-8}$	d^{-2}	Weibull aging acceleration
T_A	8000	K	Arrhenius temperature
T_{Ref}	293.15	K	Reference temperature
δ_M	0.1058	–	Shape coefficient

Table 4.4. Comparisons of model predictions with observed life history data provided to the model and relative errors (mean of relative differences between model predictions and data used in calibration). Data with a symbol beginning with 'psd' indicates that psuedodata was used.

Observed data	Predicted estimates	Relative Error	Data symbol	Units	Description	Observed data source
127	124.8	0.017	ab	d	age at birth	(Firkus et al. Unpublished)
151	152.5	0.010	aj	d	age at metamorphosis	(Firkus et al. Unpublished)
4161	3647.0	0.124	ap	d	age at puberty	(Sitar et al. 2014)
18250	18240.0	<0.001	am	d	life span	(Froese and Pauly 2021)
2.775	2.775	<0.001	Lb	cm	length at birth	(Firkus et al. Unpublished)
44.3	40.43	0.087	Lp	cm	total length at puberty	(Sitar et al. 2014)
150	135.9	0.094	Li	cm	ultimate standard length	(Froese and Pauly 2021)
0.065	0.072	0.102	Ww0	g	egg wet weight	(Smith et al. 2016)
36.3	0.151	0.996	Wwj	g	wet weight at metamorphosis	(Firkus et al. Unpublished)
680	724.9	0.066	Wwp	g	wet weight at puberty	(Sitar et al. 2014)
32700	27520	0.158	Wwi	g	ultimate wet weight	(Froese and Pauly 2021)
46.58	56.40	0.211	Ri	#/d	maximum reproduction rate	(Goetz et al. 2011)
0.02	0.017	0.142	psd.v	cm/d	energy conductance	Pseudodata
0.8	0.521	0.349	psd.kap	-	allocation fraction to soma	Pseudodata
0.95	0.950	0	psd.kap_R	-	reproduction efficiency	Pseudodata
18	31.59	0.755	psd.p_M	J/d.cm^3	volume-specific somatic maintenance	Pseudodata
0.002	0.002	0	psd.k_J	1/d	maturity maint rate coefficient	Pseudodata
0.8	0.801	0.001	psd.kap_G	-	growth efficiency	Pseudodata
0.3	0.331	0.103	psd.k	-	maintenance ratio	Pseudodata

APPENDIX II:

Figures

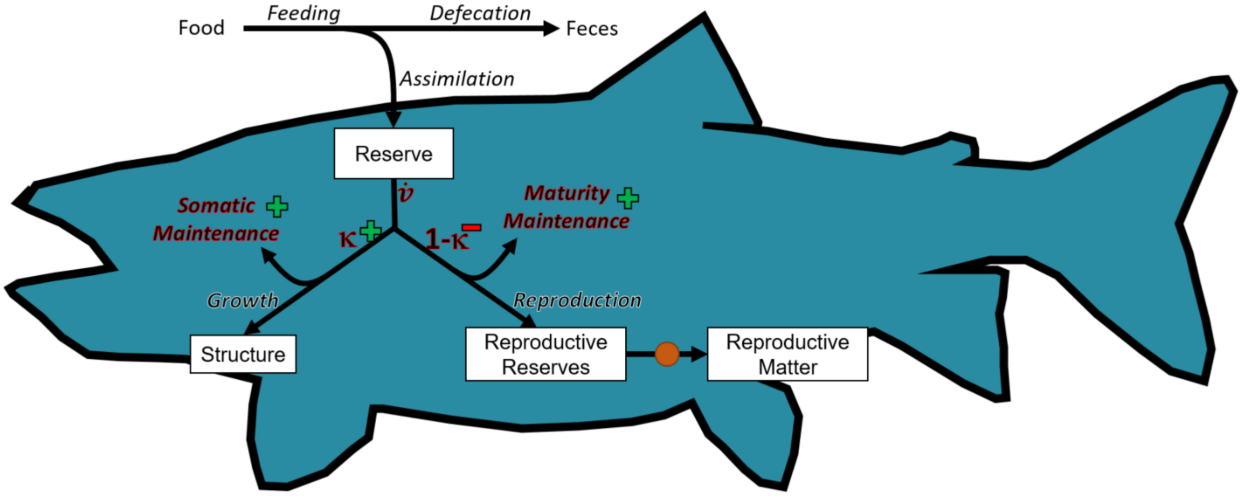

Figure 4.1. General overview of the structure of our Dynamic Energy Budget model. Words highlighted in red indicate the components of the model that were altered to simulate the effects of parasitism and muscle lipid concentration, and + and – indicates the direction of change when parasitism is added. The orange circle between reproductive reserves and reproductive matter represents the estradiol sub-model that allows differences in plasma estradiol concentration to influence ovarian mass synthesis.

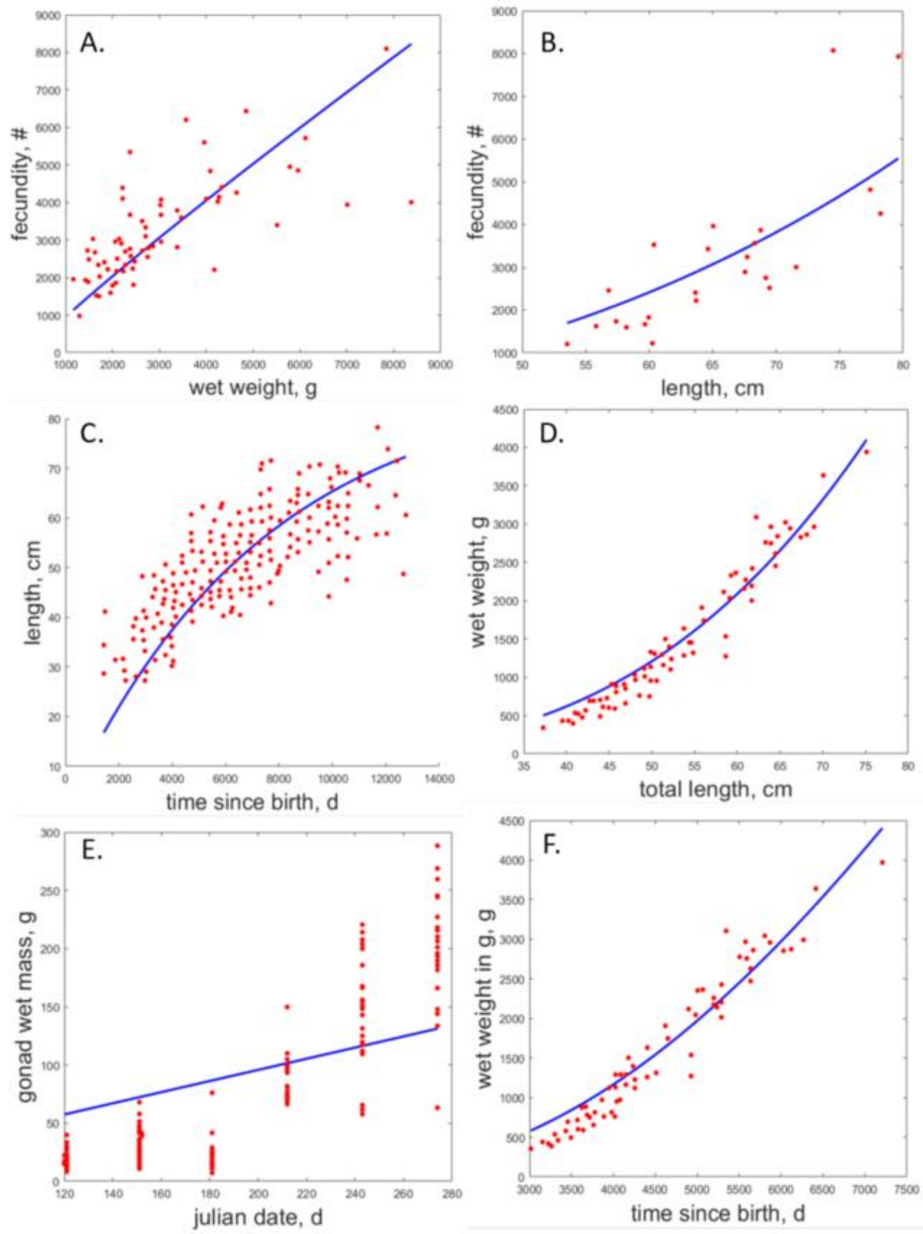

Figure 4.2. DEB model fits (blue) to provided univariate data (red). The relationship between fecundity and wet weight (A), fecundity and length (B), length and time since birth (C), wet weight and total length (D), gonadal mass and time of year (E), and wet weight and time since birth (F).

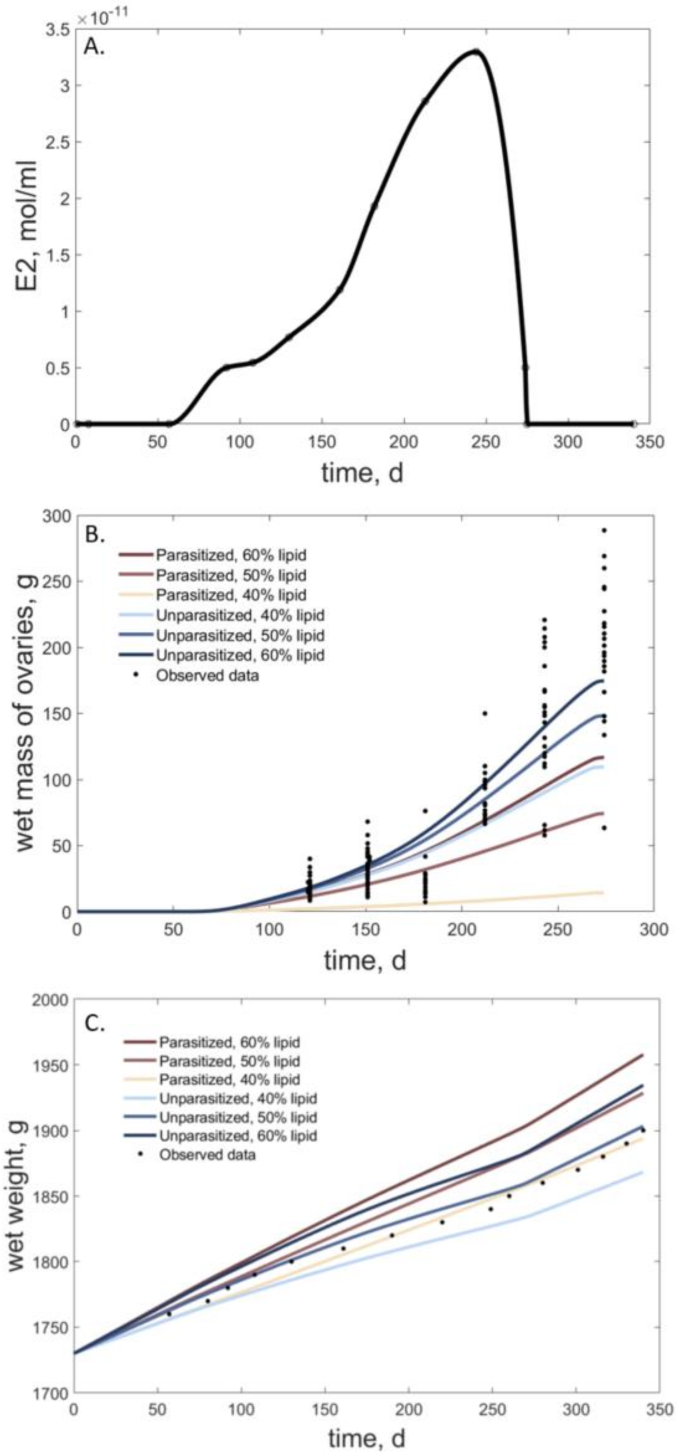

Figure 4.3. Simulation of varied ovarian mass and growth outcomes under different parasitism status and muscle lipid concentration scenarios. All scenarios were run with the same estradiol concentrations (A). Wet mass of ovaries (B) and wet weight (C) from wild lake trout is plotted with black dots, while simulated outcomes are plotted in varying shades of blue representing unparasitized scenarios, and brown representing parasitized scenarios.

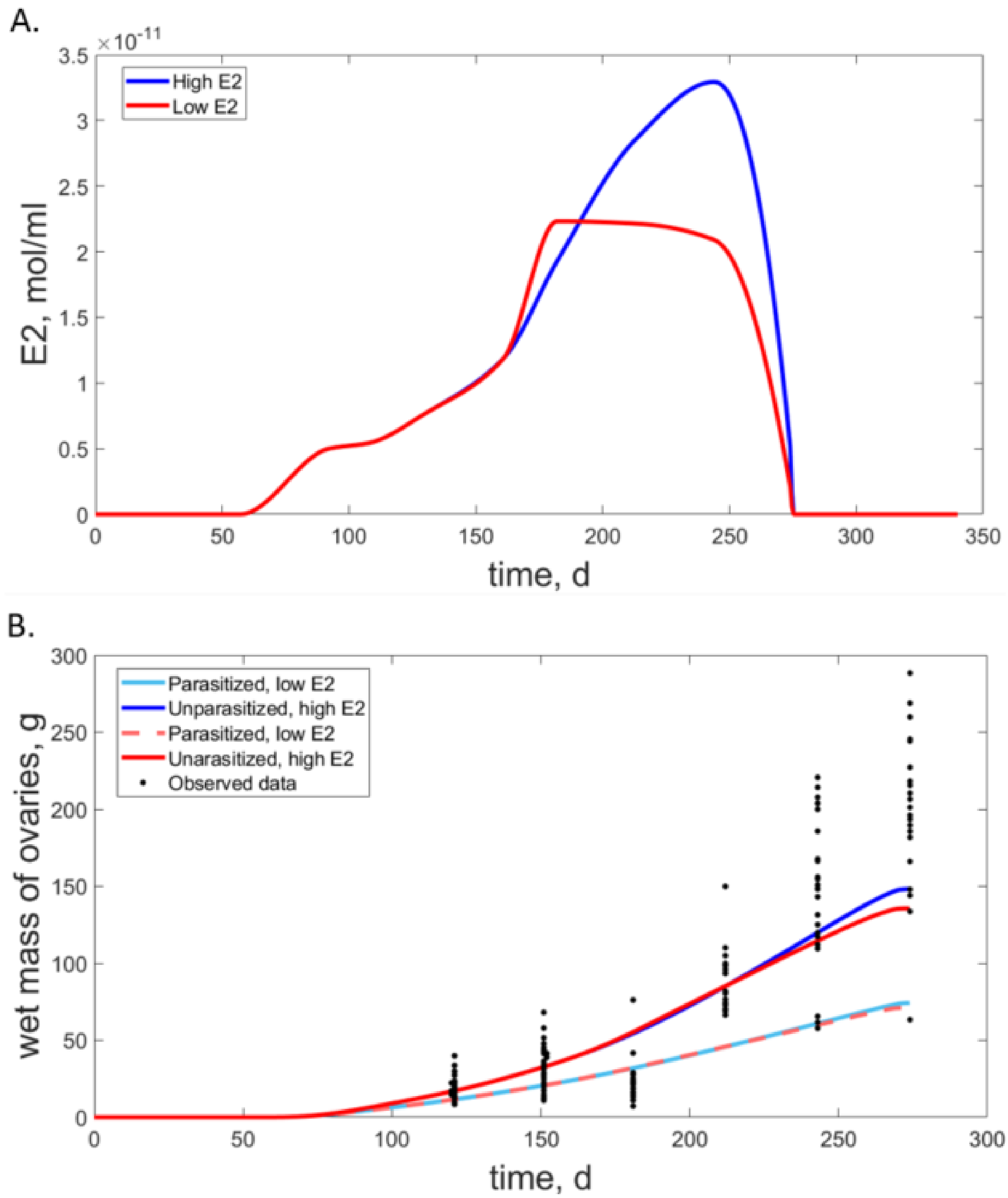

Figure 4.4. Wet mass of ovaries (B) under two different estradiol profiles (A) and parasitism regimes (light red and blue indicate parasitism).

APPENDIX III

Data for parameter estimation

Appendix III – Data used for parameter estimation. Included below is the data used for parameter estimation of the base model. Data is provided in the Matlab language and follows standard Add_my_pet mydata file formatting. For non-formatted references see table 4.4.
Zero Variate Data:

```
% zero-variate data

data.ab = 127 ;    units.ab = 'd';    label.ab = 'age at birth';             bibkey.ab
= 'Firkus';
  temp.ab = C2K(7);  units.temp.ab = 'K'; label.temp.ab = 'temperature';
  comment.ab = 'based on swim-up time (start of feeding) of my control siscowet
crosses';

data.aj = 151 ;    units.aj = 'd';    label.aj = 'age at metamorphosis';
bibkey.ah = 'Guess';
  temp.aj = C2K(8);  units.temp.aj = 'K'; label.temp.aj = 'temperature';
  comment.aj = 'guess based on growth rate and Wwj data';

data.ap = 11.4*365; units.ap = 'd'; label.ap = 'age at puberty'; bibkey.ap =
'Sitar2014';
    temp.ap = C2K(5); units.temp.ap = 'K'; label.temp.ap = 'temperature';

data.am = 50*365;  units.am = 'd';   label.am = 'life span';              bibkey.am =
'fishbase';
  temp.am = C2K(5); units.temp.am = 'K'; label.temp.am = 'temperature';

data.Lb = 27.75e-1; units.Lb = 'cm'; label.Lb = 'length at birth'; bibkey.Lb='Firkus';
  temp.Lb= C2K(7);  units.temp.ah = 'K'; label.temp.ah = 'temperature';

data.Lp = 44.3;     units.Lp = 'cm';  label.Lp = 'total length at puberty';bibkey.Lp =
'Sitar2014';
  comment.Lp = 'estimated';

data.Li = 150;    units.Li = 'cm';  label.Li = 'ultimate standard length';  bibkey.Li
= 'fishbase';

data.Ww0 = 6.5e-2; units.Ww0 = 'g';   label.Ww0 = 'egg wet weight';    bibkey.Ww0 =
'guess';
  comment.Ww0 = 'based on egg diameter of 5 mm: pi/6*0.5^3; 5mm estimate from
Smith2016';

data.Wwj = 36.3;   units.Wwj = 'g';   label.Wwj = 'wet weight at metam';
bibkey.Wwp = 'guess';
  comment.Wwj = 'based on length-weight regression of L50 from model 1. Wrong';

data.Wwp = 680;    units.Wwp = 'g';   label.Wwp = 'wet weight at puberty';
bibkey.Wwp = 'SitaJaso2014';
  comment.Wwp = 'based on length-weight regression of L50 from model 1';

data.Wwi = 32.7e3;   units.Wwi = 'g';   label.Wwi = 'ultimate wet weight';
bibkey.Wwi = 'fishbase';

data.Ri = 17000/365; units.Ri = '#/d'; label.Ri = 'maximum reprod rate';   bibkey.Ri =
'Goetz2011';
  temp.Ri = C2K(5);  units.temp.Ri = 'K'; label.temp.Ri = 'temperature';
  comment.Ri = 'Paper states a relationship of 1167egg/kg.  Our ultimate weight is
much higher than the range of data, so this is inferred';
```

Uni-Variate Data:

```
% uni-variate data

%length-number of eggs
data.LN= [... %length (mm), number of offspring (#)
535.4085603 1206.542394
558.1712062 1623.382499
568.0933852 2459.82264
573.9299611 1738.43996
582.1011673 1598.27165
602.5291829 1224.595059
596.692607  1666.907972
599.6108949 1829.472446
636.381323  2408.017374
636.9649805 2221.925618
603.6964981 3526.830151
646.3035019 3430.504027
650.3891051 3965.071034
675.4863813 2893.358067
694.7470817 2519.771966
691.8287938 2752.55633
715.7587549 3006.515247
677.2373541 3242.059542
683.07393   3567.18849
687.7431907 3869.152113
774.1245136 4815.944258
782.2957198 4257.171297
796.3035019 7930.504027
744.9416342 8074.020451];
data.LN(:,1) = 0.1 * data.LN(:,1); % convert mm to cm
units.LN = {'cm', '#'}; label.LN = {'length', 'fecundity'};
temp.LN = C2K(7); units.temp.LN = 'K'; label.temp.LN = 'temperature';
bibkey.LN = {'Goetz2011'};
comment.LN ='data extracted from figure, temperature estimated and may need to be
revised';

%wet weight-number of eggs
data.WwN = [... $ wet weight (kg), number of eggs (#)
1.2949640287769792, 976.3535784917876
1.1654676258992787, 1956.9491816905029
1.4244604316546763, 1932.0129553727493
1.4820143884892083, 1883.9748917997058
1.71223021582734, 1500.5875777465662
1.6546762589928061, 1524.7212588494913
1.956834532374101, 1595.230588437611
2, 1786.2936742239617
2.0719424460431632, 1857.7201983433115
1.4964028776978413, 2481.5271288944896
1.4676258992805735, 2720.6856029120936
1.5827338129496393, 3030.983977758031
1.6258992805755401, 2672.246266731632
1.7266187050359711, 2026.4266674309947
1.8273381294964022, 2408.49551434549
1.899280575539569, 2216.9738312935297
1.6978417266187051, 2337.2982888589468
2.4460431654676267, 1808.4209922898299
2.431654676258992, 2238.757201410186
2.4748201438848927, 2429.820287196537
2.388489208633093, 2573.590529966463
2.374100719424458, 2764.88291438562
2.273381294964029, 2693.5710395826754
```

```
2.187050359712229, 2909.0544297629604
2.143884892086332, 3028.74831608816
2.057553956834532, 2957.379116627013
2.100719424460431, 2503.0238757201405
2.086330935251798, 2168.4198457966704
2.23021582733813, 2167.846599214652
2.273381294964029, 2335.0053025308807
2.7482014388489215, 2548.2530310412985
2.6330935251798557, 2716.0423055977517
2.8633093525179856, 2834.647023417121
2.7625899280575528, 2787.2395310842912
2.7050359712230208, 3098.225801828652
2.7050359712230208, 3337.2696265298473
2.6330935251798557, 3504.886927111693
2.374100719424458, 3673.2494482501643
2.215827338129495, 4104.158903952533
2.215827338129495, 4391.011493593967
3.0359712230215816, 3670.6125139728865
3.0215827338129486, 3933.618045802399
3.0359712230215816, 4076.9870159649145
3.3812949640287773, 3788.7586345266373
3.4676258992805753, 3597.1796268164762
3.3812949640287773, 2808.678953251736
3.0359712230215816, 2953.481039869297
4.172661870503598, 2207.916535297656
3.9999999999999982, 4097.05064633552
4.244604316546761, 4024.3629797357316
4.273381294964027, 4143.770242769926
4.330935251798559, 4406.489151308433
4.086330935251796, 4837.742554960014
4.647482014388489, 4261.801714007277
5.784172661870501, 4950.500157642808
5.956834532374101, 4854.194731863909
5.5107913669064725, 3397.8044655908707
3.956834532374101, 5603.198715927656
3.568345323741008, 6202.35604345209
2.374100719424458, 5346.5562211585275
4.848920863309351, 6436.29797357333
6.115107913669062, 5714.121929547995
7.007194244604316, 3941.643497950641
8.37410071942446, 4007.910802831837
7.841726618705033, 8097.68121757574];
data.WwN(:, 1) = 1000*data.WwN(:, 1);
units.WwN = {'g', '#'}; label.WwN = {'wet weight', 'fecundity'};
temp.WwN = C2K(7); units.temp.WwN = 'K'; label.temp.WwN = 'temperature';
bibkey.WwN = {'Goetz2017'};
comment.WwN ='data extracted from figure, temperature estimated and may need to be
revised';


%length-wetweight
data.LW = [...% total length (cm), weight (kg)
    37.27979274611399 0.34090909090909083
    39.53367875647668 0.43181818181818166
    40.233160621761655 0.43181818181818166
    40.777202072538856 0.3977272727272725
    41.865284974093264 0.4772727272727275
    41.01036269430051 0.5340909090909092
    41.398963730569946 0.5227272727272725
    42.25388601036269 0.5681818181818183
    42.72020725388601 0.6931818181818183
    43.18652849740933 0.6931818181818183
    43.96373056994818 0.4886363636363633
```

```
    44.27461139896373 0.6136363636363642
    45.673575129533674 0.5909090909090908
    44.97409326424871 0.6022727272727275
    44.74093264248704 0.7272727272727266
    43.96373056994818 0.704545454545455
    45.284974093264246 0.9090909090909092
    45.829015544041454 0.8863636363636367
    45.829015544041454 0.8068181818181825
    46.917098445595855 0.6590909090909092
    46.917098445595855 0.8522727272727275
    46.76165803108808 0.9090909090909092
    48.549222797927456 0.7613636363636367
    48.082901554404145 0.9659090909090908
    49.71502590673575 0.75
    50.56994818652849 0.954545454545455
    49.870466321243526 0.954545454545455
    49.170984455958546 1.0113636363636358
    49.093264248704656 1.1136363636363633
    48.005181347150256 1.0340909090909092
    49.870466321243526 1.1363636363636367
    51.34715025906735 1.1590909090909092
    52.2020725388601 1.1022727272727275
    52.27979274611398 1.2386363636363642
    52.04663212435233 1.3977272727272725
    51.58031088082902 1.5
    51.19170984455958 1.295454545454545
    50.33678756476684 1.3068181818181817
    49.870466321243526 1.329545454545455
    53.75647668393782 1.2840909090909092
    54.84455958549223 1.3181818181818183
    53.75647668393782 1.6363636363636358
    54.611398963730565 1.4545454545454541
    54.37823834196891 1.4545454545454541
    56.0880829015544 1.7386363636363633
    55.854922279792746 1.9090909090909092
    58.652849740932645 1.5340909090909092
    58.652849740932645 1.2727272727272725
    59.119170984455955 2.034090909090909
    58.41968911917098 2.1136363636363633
    59.818652849740936 2.3636363636363633
    59.27461139896373 2.329545454545455
    61.6839378238342 2
    61.6839378238342 2.1931818181818183
    61.76165803108808 2.420454545454546
    60.82901554404145 2.159090909090909
    60.98445595854922 2.2727272727272725
    64.48186528497409 2.454545454545454
    64.48186528497409 2.6136363636363633
    64.71502590673575 2.840909090909091
    63.93782383419689 2.75
    63.3160621761658 2.7613636363636362
    63.93782383419689 2.9659090909090913
    62.2279792746114 3.090909090909091
    66.19170984455958 2.9431818181818183
    65.64766839378238 3.022727272727273
    68.13471502590673 2.8636363636363638
    68.98963730569947 2.9659090909090913
    67.43523316062175 2.8295454545454546
    70.07772020725389 3.6363636363636362
    75.12953367875647 3.943181818181818];
data.LW(:, 2) = 1000*data.LW(:, 2); %convert kg to g
units.LW = {'cm', 'g'}; label.LW = {'total length', 'wet weight'};
```

```
temp.LW = C2K(5); units.temp.LW = 'K'; label.temp.LW = 'temperature'; %assuming 5C,
may have to revise
bibkey.LW = 'Miller2000';

% Time _ length
data.tL_H = [...
    3.927392739 344.3714668
    8.151815182 272.8752083
    8.283828383 290.6904552
    7.227722772 280.8417475
    6.171617162 272.9732379
    6.03960396  292.7817534
    5.907590759 316.550665
    5.115511551 314.6096788
    9.207920792 314.4070843
    10.2640264  324.2557919
    11.05610561 312.335392
    10.92409241 302.4409372
    8.151815182 332.2811489
    8.01980198  354.0698624
    7.887788779 373.8783779
    6.96369637  356.1023429
    6.96369637  381.8449172
    7.227722772 397.6734307
    8.283828383 399.6013463
    8.01980198  413.475803
    4.059405941 411.6916642
    10.79207921 359.873215
    10.92409241 342.0448976
    10  355.9520308
    9.075907591 379.7601542
    13.03630363 391.4452831
    16.20462046 403.1696239
    16.99669967 411.0512041
    17.92079208 405.0648629
    17.12871287 418.9654609
    21.08910891 428.6703918
    18.97689769 444.6165409
    19.9009901  460.4123779
    20.95709571 470.2610855
    21.74917492 488.0436559
    21.88118812 493.9777146
    22.01320132 503.8721694
    22.80528053 521.6547397
    23.86138614 531.5034474
    23.06930693 541.4436493
    25.97359736 491.7949221
    27.02970297 442.2376891
    28.87788779 475.8095612
    29.00990099 521.3475803
    27.95379538 523.3800608
    27.02970297 509.5644218
    34.68646865 487.4031958
    32.97029703 568.6762736
    31.91419142 566.748358
    29.9339934  558.9255955
    28.87788779 570.8590661
    27.02970297 557.0891743
    25.04950495 551.2466098
    23.86138614 557.2460216
    25.97359736 624.4681894
    27.02970297 620.4555109
    27.02970297 632.336699
```

27.95379538	624.3701598
29.00990099	624.3178773
29.00990099	650.0604516
32.04620462	622.1873673
33.89438944	645.8582492
34.02640264	715.1586446
33.10231023	738.966768
32.04620462	782.5834069
30.1980198	689.6055942
30.1980198	675.7442081
31.12211221	665.7974708
34.95049505	606.2020063
27.29372937	662.0265987
27.16171617	679.8549162
28.08580858	691.6903572
27.95379538	703.5780806
28.74587459	691.6576806
26.10561056	707.6299709
25.04950495	703.7218573
23.99339934	689.9127537
21.08910891	715.7991047
20.1650165	709.9042578
20.0330033	698.0296049
20.95709571	658.3798974
20.0330033	648.5246544
23.06930693	634.5129562
23.72937294	630.5198837
23.86138614	646.3549325
24.91749175	648.2828481
23.86138614	658.2361206
23.99339934	612.6850309
25.04950495	600.7515603
23.72937294	592.8961213
22.93729373	610.7571153
22.01320132	594.9612783
21.08910891	600.9476195
20.1650165	593.0725746
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20.0330033	620.8018822
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17.78877888	611.0119923
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18.97689769	458.477927
18.05280528	478.3256543

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21.08910891	515.7991047
20.95709571	533.6274221
23.06930693	567.1862236
24.91749175	575.0155214
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27.95379538	586.7463974
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28.87788779	598.5818384
26.89768977	588.7788779
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12.37623762	490.4878607
11.05610561	464.8106395
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13.96039604	531.9935954
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14.88448845	571.5518086
19.10891089	593.124857
19.10891089	565.4020848
17.92079208	565.4609025
16.20462046	563.5656635
16.20462046	547.7240793
17.52475248	549.6389243
18.97689769	551.5472339
19.9009901	549.5212888
20.95709571	559.3699964
20.95709571	575.2115806
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17.78877888	529.8238735
16.46864686	527.9090285
15.28052805	527.9678463
14.09240924	512.1850799
15.54455446	510.1329935
16.46864686	512.0674444
17.39273927	512.0216972
18.58085809	509.9826814
18.58085809	496.1212953
17.39273927	494.199915
16.46864686	492.2654642
14.88448845	494.3240859
13.30033003	494.4025096
11.32013201	401.4312322
12.90429043	413.2339967
15.94059406	472.4896252
15.80858086	442.7931902
15.80858086	454.6743783
14.88448845	436.8983433
14.88448845	450.7597294
14.88448845	472.5419077
13.03630363	470.6532039
11.98019802	466.7450904
11.32013201	450.9361827
11.18811881	433.1209359
11.98019802	425.1609319
11.05610561	419.266085
10	427.2391596

```
    10.2640264  454.9488612
    13.96039604 458.7262687
    13.96039604 442.8846845
    13.96039604 425.0629023
    13.03630363 435.0096396
    12.77227723 446.9038983
    3.927392739 286.9457243];
data.tL_H(:,1) = 365 * data.tL_H(:,1); % convert yr to d
data.tL_H(:,2) = 0.1 * data.tL_H(:,2); % convert mm to cm
units.tL_H = {'d', 'cm'};     label.tL_H = {'time since birth', 'length'};
temp.tL_H = C2K(5); units.temp.tL_H = 'K'; label.temp.tL_H = 'temperature';
bibkey.tL_H = {'Hansen16'};

% Time _ GSI
data.tMass_ov = [...
    121, 2.209302325581394
121, 1.860465116279066
121, 1.651162790697672
121, 1.5116279069767415
121, 1.651162790697672
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121, 1.2325581395348806
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120, 0.8139534883720927
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121, 0.5348837209302317
121, 0.4651162790697647
121, 0.8139534883720927
121, 0.7441860465116257
121, 0.8837209302325562
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121, 1.0930232558139537
121, 1.1627906976744171
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121, 1.3023255813953476
121, 1.0930232558139537
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121, 0.8139534883720927
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121, 0.8139534883720927
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152, 2.139534883720927
151, 2
151, 1.930232558139533
```

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151, 1.441860465116278
151, 1.372093023255811
151, 1.2325581395348806
151, 1.2325581395348806
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151, 1.372093023255811
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181, 1.1627906976744171
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212, 4.441860465116278
212, 4.372093023255811
212, 3.953488372093023
212, 4.162790697674417
212, 4.023255813953487
212, 3.813953488372089
212, 3.604651162790695
212, 3.7441860465116257
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243, 3.1162790697674403
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274, 7.930232558139535
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274, 10.162790697674417
274, 10.511627906976745
274, 10.372093023255815
274, 10.790697674418604
274, 11.069767441860465
274, 11.279069767441861
274, 11.69767441860465
274, 11.558139534883722
274, 12.186046511627907
274, 13.162790697674419
274, 13.093023255813954
274, 13.162790697674419
274, 13.930232558139537
274, 14.418604651162791
274, 15.465116279069768
274, 10.511627906976745
];
data.tMass_ov(:,2) = (data.tMass_ov(:,2).*(1760 + (140/365)*data.tMass_ov(:,1))/100);
units.tMass_ov = {'d', 'g'};     label.tMass_ov = {'julian date', 'gonad wet mass'};
temp.tMass_ov = C2K(5); units.temp.tMass_ov = 'K'; label.temp.tMass_ov =
'temperature';
bibkey.tMass_ov = {'Goetz2011'};

data.tWw_ov = [...
    0, 1760
    365, 1900];
units.tWw_ov = {'d', 'g'};     label.tWw_ov = {'julian date', 'Wet weight (grams)'};
temp.tWw_ov = C2K(5); units.temp.tWw_ov = 'K'; label.temp.tWw_ov = 'temperature';
bibkey.tWw_ov = {'Goetz2011'};


%time-WetWeight
 data.tWw = [...%time since birth (days), wet weight (g)

8.267368671368168, 0.3560308247935966
8.647030847087326, 0.44122258800448844
8.83652752903758, 0.42032593429295506
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8.941698187519973, 0.3887282914830532
9.152764050621625, 0.46310016571670687
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9.574282699324499, 0.4954409327695508
9.47000378993364, 0.6963520030913966
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9.975068181649291, 0.5912445101696546
9.786128842881244, 0.7179620560761553
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10.186579919296706, 0.7502730981592816
10.102476833101727, 0.7819004659389011
10.060899031709113, 0.8876619081944321
9.934437863666428, 0.8769014691566275
10.355454903505317, 0.8140034332340029
10.650122243937966, 0.7615091367125668
11.008270972823949, 0.7620144611977677
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11.368537605802315, 1.1646391760238384
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11.601507055964687, 1.3977721135196592
11.454591393135019, 1.5033849309266012
12.064269100150854, 1.2608589029999928
12.359493783765709, 1.3141854986735222
12.066219801288579, 1.6312320256823734
12.740995191986151, 1.7485862061278024
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13.417108206321016, 2.1199105278411494
13.71328037334562, 2.3531326402461223
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14.492000267524729, 2.2060832150527245
14.490997049796757, 2.0156056091017858
14.34419285560353, 2.142382604947721
14.239022197121136, 2.1739802477576218
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15.44143437841373, 2.4719730691774346
15.442270393187039, 2.630704407469884
15.316533771281222, 2.757511128285538
15.084901944756144, 2.7783483320576368
15.275513313070812, 2.9690934627360344
15.527766837337536, 2.8636292701776807
14.644210690585359, 3.1057688734979596
15.907930621920677, 3.044059836364041
16.076025325674202, 2.9596409223658107
16.517887000527622, 2.854444254534915
16.770809336612988, 2.8759651326105207
17.171706287574217, 2.9929328884496194
17.575389954446482, 3.639005105263549
19.747077663914634, 3.9701115429488647
];
```

```
data.tWw(:,1) = data.tWw(:,1)*365;  % convert years to days
data.tWw(:,2) = data.tWw(:,2)*1000; % convert kg to g
units.tWw = {'d', 'g'};     label.tWw = {'time since birth', 'wet weight in g'};
temp.tWw = C2K(5); units.temp.tWw = 'K'; label.temp.tWw = 'temperature';
```

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