CONTRASTING DIET, GROWTH, AND ENERGY PROVISIONING IN LOONS BREEDING SYMPATRICALLY IN THE ARCTIC

By

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ABSTRACT

Red-throated (*Gavia stellata*) and Pacific (*G. pacifica*) loons breed throughout Arctic Alaska, often on adjacent lakes. Despite having similar life histories and distributions, these species have contrasting population trends in Alaska. Red-throated Loon populations have fluctuated dramatically over the past 3 decades, while the population trend of Pacific Loons has remained stable. These species-specific, population-level differences may be related to the foraging behaviors of breeding adults: Red-throated Loons feed on marine fishes using central place foraging behavior, while Pacific Loons feed primarily on freshwater prey captured from their breeding lakes. In this dissertation, I examined how differences in diet composition during the breeding season were associated with individual fitness parameters, namely adult body condition, chick growth performance, and breeding success. I used results from this research to address the hypothesis that interspecific differences in foraging behaviors contribute to the contrasting population dynamics of Pacific and Red-throated Loons breeding in Alaska.

Using stable isotopes and fatty acid biotracers of diet, I found that the diet of breeding Pacific Loons was composed of a mix of freshwater and marine prey, and that variation in diet composition was related to the size of the breeding lake. Pacific Loons nesting on small lakes consumed more marine prey, suggesting that small lakes were not profitable foraging habitat, but their use for nesting was enabled by the close proximity of marine foraging habitat. In contrast, Red-throated Loons nested on very small lakes and ate a diversity of marine fishes. Despite differences in diet, both species had similar body condition during late-incubation, indicating that their diets met adult energy requirements, and adults maintained similar lipid reserves despite differences in foraging behavior.

I found that Red-throated Loon chicks grew rapidly, yet were only 66% of adult body mass when they departed their natal lakes for the sea at fledging. This pattern of chick growth reduced the length of the postnatal period, and, consequently, the amount of time adults had to fly to marine habitat to capture fish for their chicks. Red-throated Loons provisioned their chicks with sufficient energy to support high growth rates. Other loon species which do not fly to the sea to capture fish for their chicks, like the Pacific Loon, likely do not face similar selection pressure for reduced parental energy investment through rapid chick growth. In Red-throated Loons, the total energy demands of chicks over the postnatal period were reduced at the expense of increased daily energy demands during the period of rapid growth. Given this pattern of chick growth, variation in the availability of high-energy content prey exerts a strong influence on breeding success.

Pacific Loons provisioned their chicks mostly freshwater invertebrates with low-lipid content. Consequently, Pacific Loon brood provisioning rates were much higher than those of Red-throated Loons, which provisioned their chicks large-bodied marine fishes. Brood-rearing Pacific Loons commonly departed their breeding lakes for marine habitat, presumably to forage for themselves; however, parents rarely fed their chicks marine fishes, suggesting that central place foraging was not an energetically profitable provisioning behavior for larger-bodied Pacific Loons. Reproductive success over 3 years was higher in Red-throated Loons than Pacific Loons due to higher chick survival rates. Estimates of maximum energy provisioning rates for broods demonstrated that the provisioning rates and diet composition of Red-throated Loons could more easily meet peak brood energy requirements than the provisioning rates and diet composition of Pacific Loons. Thus, lower survival of Pacific Loon chicks was associated with lower maximum energy provisioning rates.

The use of both freshwater and marine prey may insulate Pacific Loons from changes in either foraging habitat. Further, Arctic lakes provide a reliable source of invertebrate prey for chicks, but a diet of invertebrates may limit chick production rates because of their small size and low lipid content. Although meeting maximum brood energy requirement by provisioning freshwater invertebrates was difficult for Pacific Loons, particularly for adults rearing the maximum brood size of 2 chicks, chick production rates were sufficient to maintain a stable population trend. Red-throated Loons' specialization on marine prey strongly links their energy intake to the availability of marine fishes, which can vary suddenly and dramatically with ocean climate. Foraging conditions for Red-throated Loons in this study supported high chick growth rate and high chick production rates. Low chick growth rate and low chick production documented at other sites in Alaska indicate that Red-throated Loon breeding success is highly variable. Low chick production rates may contribute to Red-throated Loon population dynamics in Alaska if the availability of important forage fish species is low over multiple breeding seasons. Pacific Loons may be better suited than Red-throated Loons to adapt to the changing Arctic environment given the flexibility of their foraging behavior and diet. Because Pacific and Red-throated loon chicks in coastal tundra habitat rely on different types of prey, chick survival can function as a sensitive indicator of changes in lentic and marine habitats in the Arctic.

DEDICATION

To the teachers, mentors, and colleagues that have encouraged my interests and helped me along the way.

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INTRODUCTION

How similar species that co-occur in space and time (i.e., are sympatric) differ in their use of resources is a fundamental question in ecology (Brown and Wilson 1956, Hutchinson 1957, Hardin 1960, Lack 1968, Schoener 1974). MacArthur's (1958) foundational study of sympatrically breeding warblers demonstrated that closely-related species using the same habitat partitioned resources at fine-scales, for example when feeding in the same tree, by foraging in different areas of the tree and by using different foraging behaviors. Further, MacArthur (1958) correlated population dynamics with niche breadth by showing Cape May Warblers (*Setophaga tigrina*) with a specialized diet of spruce budworms (*Choristoneura fumiferana*) tracked the increases and decreases of its prey population, while sympatric species with more generalized diets maintained stable populations. Thus, partitioning resources that regulate or limit populations can lead to divergent population trends in closely related species occurring in the same habitat.

Pacific (*Gavia pacifica*) and Red-throated (*G. stellata*) loons are species of large-bodied waterbirds that share many life history traits. Both species spend most of their annual cycle on coastal marine habitat (Okill 1994, Russell and Lehman 1994, Rizzolo and Schmutz 2012). During the breeding season (June–September), adults nest on islands and shorelines of lakes in the same coastal tundra habitat, often with one species nesting on a lake immediately adjacent to the other species (Davis 1972, Petersen 1976, Bergman and Derksen 1977, Mallek and Groves 2011, Stehn et al. 2013). In both species, males and females incubate the 2-egg clutch, eggs hatch asynchronously, and chicks leave the nest within 24 hours of hatching and remain in the natal lake until they fledge from the lake to the sea (Johnson and Johnson 1935; Bundy 1976, 1978; Petersen 1989, Dickson 1994). During the postnatal period, chicks of both species depend on their parents for their food intake (Reimchen and Douglas 1984, Petersen 1989, Eberl and Picman 1993, Kertell 1996).

Given the similarities between species, comparative studies have focused on how sympatrically breeding Pacific and Red-throated loons partition resources. These studies have shown that Pacific Loons breed on lakes with a larger average surface area than those used by Red-throated Loons (Davis 1972, Petersen 1976, Bergman and Derksen 1977, Dickson 1994). Further, to feed themselves, and to provision their chicks, Red-throated Loons use central place foraging behavior (Orians and Pearson 1979) to fly between their breeding lakes and separate foraging habitat (often nearshore marine habitat; Reimchen and Douglas 1984, Eberl and Picman 1993). During brood-rearing, Red-throated Loons return to their breeding lakes after foraging trips carrying a single fish in their bills to provision their brood (Bergman and Derksen 1977, Reimchen and Douglas 1984, Eriksson et al. 1990, Eberl and Picman 1993, Ball 2004). In contrast, Pacific Loons forage for themselves, and to provision their brood, within their territorial breeding lakes (Petersen 1989, Kertell 1996). Thus, Pacific and Red-throated loons partition breeding habitat by lake size and foraging habitat by location. Because their use of different foraging habitats leads to diets composed of different prey species, Bergman and Derksen (1977) concluded that each loon species functions as an indicator of changes in their respective foraging habitat.

The degree to which Pacific Loons rely only on prey from their freshwater territorial lakes, however, is apparently variable. Davis (1972) observed Pacific Loons breeding in lakes adjacent to Hudson Bay provisioning their chicks marine fishes. Andres (1993) observed Pacific Loons on the Arctic Coastal Plain of Alaska flying between marine habitat and breeding habitat at rates equivalent to those of Red-throated Loons. Pacific Loons raising chicks on the Arctic Coastal Plain, however, rarely, if ever, provisioned marine fishes to their broods (Bergman and Derksen 1977, Kertell 1996). Factors associated with variation in brood provisioning behavior in Pacific Loons have not been determined, but brood-rearing Arctic Loons (*G. arctica*), a sister species to Pacific Loons which breeds primarily in Asia, delivered prey captured away from the breeding lake to chicks < 4 days old and to broods in small lakes (Jackson 2003). A better understanding of how well Pacific Loons may serve as indicators of change in freshwater habitats requires more information on the diet of adults and chicks, and factors associated with variation in foraging and provisioning behaviors.

Despite similarities in the distributions and many life-history traits of Pacific and Red-throated loons, their populations in Alaska have shown contrasting trends. Red-throated Loon numbers in Alaska have fluctuated dramatically over the past three decades (Mallek and Groves 2011, Stehn et al. 2013), including a > 50% decline from 1977 to 1993 (Groves et al. 1996), while the population trend of Pacific Loons has remained stable (Groves et al. 1996, Mallek and Groves 2011). In response to the Red-throated Loon population decline and perceived threats to habitats, the U. S. Fish and Wildlife Service listed this species as a Bird of Conservation Concern, a designation applied to species that without conservation action are likely to become candidates for Endangered Species Act listing (USFWS 2008). Effective conservation of loons in Alaska, however, is limited by our poor understanding of the factors regulating their abundance (McCaffery 2000).

The consequences of resource partitioning by Pacific and Red-throated loons are poorly understood. The diet composition of breeding adults has not been quantified because adults consume prey while underwater. Thus, the species of prey in the diet and their nutritional value are unknown. Adult diet composition may affect body condition (i.e., fat reserves), especially when available foraging time is limited during incubation (Choinière and Gauthier 1995, MacCluskie and Sedinger 2000) and when environmental conditions are energetically demanding (Birt-Friesen et al. 1989, Piersma et al. 2003). Foraging behavior may also select for an optimal amount of lipid reserve during breeding. Red-throated Loons may use lipid stores facultatively (Norberg 1981, Moreno 1989) to reduce body mass and the energetic expense of flying to marine foraging habitat, whereas the cost of flight may play a less important role in determining optimal fat stores for Pacific Loons that do not undertake energetically expensive provisioning flights. In Chapter 1 of this dissertation, I use biochemical indicators of diet to examine sources of variation in diet and to obtain quantitative estimates of proportional diet composition. I evaluate diet composition in the context of the lipid content of prey and examine the consequences of diet composition on adult body condition.

Differences in provisioning behavior and chick diet composition may influence chick growth, survival, and ultimately, chick production rates (Springer et al. 1986, Litzow et al. 2002, Wanless et al. 2005, Piatt et al. 2007). Red-throated Loons make an interesting model species for studying chick growth given the central place foraging behavior of provisioning adults, which is a behavioral trait not shared with other loon species. Further, some species of high-latitude breeding birds have chicks with very high energy requirements due to cold air temperatures and the high energy expenditure associated with precocial development (Hodum and Weathers 2003, Schekkerman et al. 2003, Tjørve et al. 2007). Red-throated Loons have semi-precocial chicks that enter a cold aquatic habitat where thermoregulatory demands are likely high and may produce high chick energy requirements (Fournier et al. 2002). Although chicks are mobile after hatching, they depend on their parents for their entire food intake, thus high chick energy requirements must be met through adult provisioning effort. The provisioning effort of Red-throated Loon parents is likely high given their central place foraging behavior and high wing loading during flight. Thus, chick production in Red-throated Loons may be more sensitive to food availability than that of Pacific Loons that provision their young from breeding lakes (Davis 1972, Eberl and Picman 1993, Ball 2004). In Chapter 2, I quantify the growth and energy requirement of Red-throated Loon chicks to examine the hypothesis that Red-throated Loon chicks are energetically expensive for adults to raise.

Provisioning rate and diet composition regulate brood energy intake. Thus, differences in provisioning behavior and prey choice between sympatrically breeding species may affect reproductive success (Lance and Roby 1998, Gall et al. 2006). The maximum daily energy requirement of the brood represents period of highest provisioning effort required of parents of dependent young (Weathers 1996), and may differ between foraging habitats. In Chapter 3, I address the question of how easily brood energy demands are met in Pacific and Red-throated loons. I quantify chick diet composition, the provisioning rate of broods, and reproductive success. I use estimates of chick provisioning rates and the energy values of prey in the chick diet to examine how diet and provisioning behavior may limit chick survival.

The research described in this dissertation was designed to improve our understanding of breeding loons on the Arctic Coastal Plain of Alaska and to inform decisions related to oil and gas development in the Chukchi Sea (Federal Register 2008) by quantifying marine habitat use. This research was funded primarily through the Outer Continental Shelf Program of the Bureau of Ocean Energy Management and the U.S. Geological Survey through an intra-agency agreement (M07RG13414) granted to Joel Schmutz of the USGS Alaska Science Center; Joel is coauthor on all manuscripts in this dissertation. In additional to obtaining funding, Joel also contributed to study design of the research described in all 3 chapters. John Speakman of the University of Aberdeen was a collaborator on Chapter 3, and as such is a coauthor on that chapter. John provided valuable input on doubly labeled water methodology, laboratory analyses, and study design.

The study site for this research was located around the village of Point Lay (69°44′N, 163°00′W), bounded by the Kokolik River to the north and the Epizetka River (locally known as the Qipigsatqaq River) to the south. This site was selected based on the high densities of breeding Pacific and Red-throated loons in the area detected during non-systematic surveys conducted on foot at 4 sites on the Chukchi Sea coast in 2007 (Mitliktavik: 70°25′N, 160°29′W; Icy Cape 70°17′N, 161°53′W; Utukok River, 70°03′N, 162°20′W; and Point Lay). Data for the study were collected over 3 summers, June–September 2008–2010. Results from this research will significantly advance our knowledge of the ecology of loons on the Arctic Coastal Plain and our understanding of how these populations may be affected by changes in their prey related to climate change and anthropogenic disturbance.

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CHAPTER 1

VARIABLE USE OF MARINE PREY BY SYMPATRICALLY BREEDING LOONS[1]

1.1 Abstract

Pacific (*Gavia pacifica*) and Red-throated (*G. stellata*) loons breed sympatrically in Arctic Alaska, often on adjacent lakes. These species have similar breeding life history traits, but contrasting foraging behaviors. Pacific Loons feed in both freshwater and marine habitats, but their diet composition has not been well described. Red-throated Loons feed away from the breeding lake, typically in marine habitat. We used stable isotopes and fatty acids to examine sources of variation in loon diets and to quantify diet composition. We also estimated body condition of loons, by measuring total body water, and measured the lipid content of prey. As expected, Red-throated Loon diet was composed entirely of marine fishes. Pacific Loon diet included a mix of freshwater and marine prey, and the amount of marine fishes in the diet decreased with increasing surface area of the breeding lake. The corresponding increase in freshwater prey with increasing lake area was driven by the amount of ninespine stickleback (*Pungitius pungitius*) in the diet. Most freshwater fishes and invertebrates had lower lipid content than marine fishes, however, freshwater ninespine stickleback contained as much lipid as some marine fishes. We conclude that local foraging was not profitable for Pacific Loons breeding in small, shallow lakes because of insufficient prey. The proximity of marine habitat, however, permitted Pacific Loons to augment their diet with marine fishes. Larger, deeper lakes likely supported greater freshwater fish abundance, which made local foraging profitable. Although we found no association between diet and body condition in either species, the more diverse diet of Pacific Loons may insulate this species from changes in the availability of either freshwater or marine prey. In contrast, the inflexible reliance on marine prey by Red-throated Loons likely couples their body condition, and ultimate breeding success, to marine foraging conditions.

1.2 Introduction

During incubation, birds must invest both time and energy in warming their eggs (Williams 1996). The need to incubate constrains available foraging time and forces adults to

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[1] Rizzolo, D.J. and J.A. Schmutz. Variable use of marine prey in sympatrically breeding loons from the Arctic. Prepared for submission in Ecosphere.

concentrate foraging behavior during incubation breaks, which can increase off-nest energy expenditure (Dearborn 2001, Cresswell 2004). The demands of incubation are apparent in the loss of body mass, often caused by declines in lipid reserves (Choinière and Gauthier 1995, MacCluskie and Sedinger 2000), and increased stress response (Kitaysky et al. 1999) during the incubation period. Individuals with higher body condition (i.e., greater lipid reserves) at the start of the breeding season may initiate nests earlier (MacCluskie and Sedinger 2000) and have higher hatching rates (Barbraud and Chastel 1999). Further, the energetic cost of incubation is exceptionally high in some Arctic-nesting species (Birt-Friesen et al. 1989, Piersma et al. 2003). The energetic demands of incubation are fueled by food intake, which is used to regain body condition lost during each incubation bout (Chaurand and Weimerskirch 1994, Weimerskirch 1995). Thus, diet composition prior to and during incubation is critically important for maintaining body condition and successful reproduction, even in species with biparental incubation (Adams et al. 1991, Cresswell et al. 2003).

Pacific (*Gavia pacifica*) and Red-throated (*G. stellata*) loons are species of large-bodied, waterbirds with Holarctic distributions that overlap during most of the annual cycle (Barr et al. 2000, Russell 2002). These species breed sympatrically on lakes on the Arctic Coastal Plain of Alaska where they typically lay a 2-egg clutch that both adults in the breeding pair incubate. These species differ, however, in their foraging behaviors during the breeding season. Red-throated Loons feed exclusively away from their breeding lakes on fishes, often in marine habitat (Bergman and Derksen 1977, Eberl and Picman 1993); Pacific Loons feed primarily in their breeding lakes on fishes and invertebrates (Bergman and Derksen 1977, Petersen 1989, Kertell 1996). Pacific Loons breeding near the coast may also forage in marine habitat (Andres 1993). The importance of specific prey species to Pacific and Red-throated loons is unknown because diet composition during the breeding season has not been well described. As with most dive-feeding species that consume prey underwater, direct observation of the types of prey consumed usually is not possible. Most diet studies have focused on prey species fed to chicks because they can been seen when carried in the adult's bill (Reimchen and Douglas 1984, Kertell 1996); however, the prey species consumed by adults may differ from those fed to chicks, particularly for central-place foraging species that face high energy demands during provisioning trips (Orians and Pearson 1979, Ydenberg 1994, Wilson et al. 2004).

Loon foraging behavior may contribute to contrasting population trends of Pacific and Red-throated loons in Alaska. Red-throated Loon numbers on coastal tundra breeding habitat in Alaska have fluctuated dramatically over the past 3 decades, including a > 50% decline between 1976 and 2001 (Groves et al. 1996, Mallek and Groves 2011, Stehn et al. 2013). In contrast, Pacific Loons are more abundant and have had a stable population trend over the same period and in the same habitat (Mallek and Groves 2011, Stehn et al. 2013). Summer diet may play a role in these divergent population trends (Ball 2004, Ball et al. 2007). Diet composition directly affects individual energy balance and the nutritional resources available for building energy reserves and for supporting reproduction (Ricklefs et al. 1996). A thorough understanding of an animal's diet requires knowledge of what species of prey are consumed and their biochemical composition. Differences in energy content among forage fishes are driven primarily by differences in lipid content (Anthony et al. 2000, Ball et al. 2007). Thus, intra- and inter-specific variation in the amount of lipid-rich prey in the diet of loons may lead to variation in body condition (i.e., lipid reserves). Further, foraging behavior may also select for an optimal amount of lipid reserves during breeding. Red-throated Loons may use lipid stores facultatively (Norberg 1981, Moreno 1989) to reduce body mass and the energetic expense of flights to marine foraging habitat.

Biochemical tracers of diet (hereafter "biotracers"), such as stable isotopes and fatty acids, provide valuable insights into the diet composition of elusive species, like loons (Hobson 1993, Bearhop 1999, Iverson et al. 2007, Wang et al. 2007). Diet inferences from stable isotopes are based on consistent and predictable differences in stable isotope concentrations among prey species. For example, the stable isotope ratio of carbon ^{13}C:^{12}C indicates carbon sources (e.g., atmospheric carbon dioxide and seawater bicarbonate; Hobson 1987), and can be used to infer the proportions of freshwater and marine prey in the diet of a consumer (Bearhop 1999). The stable isotope ratio of nitrogen ^{15}N:^{14}N changes predictably with increasing trophic level due to the preference for the lighter isotope in biochemical reactions (Minagawa and Wada 1984). The time scale over which stable isotopes integrate diet is determined by the turnover rate of the sampled tissue. For the components of blood, red blood cells integrate diet over a period of around 1 month, whereas plasma integrates diet over several days (Hobson and Clark 1993).

Fatty acids, the primary building blocks of lipids, also provide diet inference. The proportional fatty acid composition of lipid (hereafter "fatty acid signature") varies among species (Budge et al. 2002, Iverson et al. 2002) and long-chain (> 14 carbons) fatty acids from prey are predictably deposited in the lipid of monogastric consumers (Budge et al. 2006, Williams and Buck 2010). Fatty acids from avian adipose tissue integrate diet over a period of > 3 weeks (Williams et al. 2009, Wang et al. 2010). Both stable isotopes and fatty acids can be used qualitatively, for example to examine temporal and spatial variation in biotracers among species of predators and prey (Williams et al. 2008, Wang et al. 2009), and quantitatively, to estimate the composition of prey species in the diet of a consumer (Iverson et al. 2004, Moore and Semmens 2008). These techniques are relevant to understanding how the foraging behaviors of Pacific and Red-throated loons affect their diet composition and body condition.

In this study, we measured the carbon and nitrogen stable isotope ratios of plasma and red blood cells, and the fatty acid signatures of adipose tissue from sympatrically breeding Pacific and Red-throated loons. We examined how well biotracers differentiated between species of prey and species of loons. We also estimated the proportional diet composition of loons and examined sources of variation in diet estimates. Specifically, we were interested in the relative contributions of freshwater and marine prey to the diet of Pacific Loons, and the proportion of high-lipid marine fish species in the diet of Red-throated Loons. To examine the hypothesis that diet and foraging behavior affects loon lipid reserves, we examined adult body condition in relation to loon species and diet composition.

1.3 Methods

1.3.1 Loon sampling

This study was conducted near the village of Point Lay, Alaska (69° 44’N, 163° 00’W). Breeding loons arrive in June to initiate nests, eggs hatch in mid- to late-July, and chicks fledge in late-August to mid-September. We sampled breeding adult Pacific and Red-throated loons, and Red-throated Loon chicks, during three consecutive summers, June–September in 2008–2010. We captured adult loons on breeding lakes using bow nets set at nest sites (Salyer 1962), suspended dive nets (Okill 1981, Uher-Koch et al. 2016), and vertical mist nets at the breeding lake (Zicus 1975). We captured Red-throated Loon chicks using suspended dive nets. We have no data for Pacific Loon chicks because we were unable to capture them on their larger brood-rearing lakes. Upon capturing a bird, we measured total culmen length, diagonal tarsus length, flattened wing length, and body mass (Dzubin and Cooch 1992). We used the live biopsy technique of Iverson et al. (2004) as modified by Wang et al. (2010) to remove approximately 100 mg of subcutaneous adipose tissue, which we placed in chloroform containing the antioxidant butylated hydroxytoluene. Samples were stored frozen at -20° C at the field site and -80 °C at the laboratory until analysis. We also collected blood samples from adults and chicks from either the jugular vein or the medial metatarsal vein into untreated Vacutainers (Becton, Dickinson and Company, USA). Whole blood samples were centrifuged to separate red blood cells and plasma at the field camp and frozen at -20 °C until analysis.

1.3.2 Prey sampling

We collected marine fishes near Point Lay using: (1) an otter trawl (3.1 m × 1.6 m opening, 1.5 cm mesh size) towed from a 4.9 m skiff with an outboard motor, (2) beach seine (36.9 m × 3.0 m, 10 cm mesh), and (3) variable mesh gill net (38 × 1.8 m with mesh size 1.5–6.5 cm). We captured fishes and invertebrates from freshwater lakes used for breeding by Pacific Loons using variable mesh gill nets, minnow traps (Gee-style galvanized steel, 2.5 cm opening, 6 mm mesh), and hand-held sweep nets (500 micron mesh). Collections were made June–September 2008–2010. We weighed and measured total length of captured fishes and invertebrates and froze them whole in the field at -20 °C. Small invertebrates collected from the same lake and of the same order were grouped in composite 10 g samples for analysis. Samples from 2009 and 2010 were analyzed for fatty acid composition, and samples from all 3 years were analyzed for carbon and nitrogen stable isotope ratios. Fishes were identified to species based on Mecklenburg et al. (2002), and invertebrates were identified to order based on Smith (2001); we refer to both prey species and orders as species for simplicity, despite the difference in level of taxonomic identification.

We obtained additional samples of species not collected from Point Lay, but observed provisioned to chicks (i.e., slender eelblenny *Lumpenus fabricii*, Pacific sand lance *Ammodytes hexapterus*), or known to be important prey to piscivorous marine birds (i.e., capelin *Mallotus villosus*, Arctic cod *Boreogadus saida*) from two surveys conducted in the Chukchi Sea: (1) the Alaska Monitoring and Assessment Program (AKMAP) Chukchi Sea coast survey at sites within 40 km of Wainwright, Alaska (140 km northeast of Point Lay) in September 2011, and (2) the Chukchi Sea Environmental Studies Program (CSESP) pelagic fish survey conducted 220 km offshore from Wainwright in August–September 2011 (Goodman et al. 2012). Fishes from these surveys were received frozen and were processed and analyzed with samples collected at Point Lay. We obtained additional fatty acid composition data for Alaska blackfish (*Dallia pectoralis*) from lakes in the central Arctic Coastal Plain, 260 km east of Point Lay, sampled in 2009 and 2010 (Haynes et al. 2015). These samples were analyzed for fatty acid composition in the same laboratory and using the same methods as samples collected at Point Lay.

1.3.3 Stable isotope analysis

We homogenized whole, frozen prey samples using a laboratory blender and mortar and pestle, desiccated samples by freeze-drying, and extracted lipids using the Folch technique (Folch et al. 1957). We removed lipids from loon plasma samples by rinsing samples with a 20:1 methanol:chloroform solution and separating the lipid-free plasma from the solvent using centrifugation. Lipid-free plasma was freeze-dried. Loon red blood cell samples were freeze-dried, but not lipid extracted, because samples had low C:N ratios (< 3.5), indicating low lipid content. To obtain stable isotope ratios, we analyzed red blood cells and plasma from adults, but only analyzed red blood cells from chicks.

Ratios of ^{13}C:^{12}C and ^{15}N:^{14}N in samples were measured with continuous flow isotope ratio mass spectrometry (CFIRMS) using an elemental analyzer (Costech ESC 4010) and continuous flow interface (Thermo Scientific Conflo IV) with a Delta V^{Plus} mass spectrometer. Stable isotope ratios were reported in delta (δ) notation in parts per thousand (‰) deviation from international standards as: $\delta X = [(R_{sample}/R_{standard})-1] \times 1000$, where R is the ratio of ^{13}C:^{12}C or ^{15}N:^{14}N. Standards were atmospheric N_2 for nitrogen and Vienna Peedee Belemnite for carbon. Instrument precision was < 0.2 ‰. Laboratory analyses were done by the Alaska Stable Isotope Facility at the University of Alaska Fairbanks (ASIF-UAF).

1.3.4 Fatty acid analysis

We used a 1.5 g aliquot of thawed fish or invertebrate homogenate for fatty acid analysis. Lipids in prey homogenate and loon adipose tissue were quantitatively extracted using the Folch technique (Folch et al. 1957) as modified by Iverson et al. (2001). Lipids were transesterified into fatty acid methyl esters (FAME) using an acid catalyst (Budge et al. 2006). Thin layer chromatography was used to detect fatty alcohols derived from wax esters, and wax ester alcohols were converted to their respective fatty acids per Budge et al. (2006). FAMEs were stored in hexane until analysis. Fatty acid composition of samples was quantified using gas-liquid chromatography on a gas chromatograph (Varian Autosystem II Capillary FID) fitted with a 30 m × 0.25 mm diameter column (50% cyanopropyl methylpolysiloxane film). Each chromatogram was manually assessed for correct peak identification and integration of peak areas. Fatty acids were described using standard nomenclature of carbon chain length:number of double bonds and location (n-x) of the double bond nearest the terminal methyl group. Individual fatty acids were expressed as percentages of total fatty acids. Analysis and identification of all FAME was performed in S.J. Iverson's laboratory at Dalhousie University.

1.3.5 Body condition analysis

We measured total body water (TBW) of adult loons using the deuterium dilution method (Lifson and McClintock 1966, Speakman 1997, Visser et al. 2000, Mata et al. 2006). We collected 0.5–2.0 mL of blood from the medial metatarsal vein of loons to determine naturally occurring levels of deuterium (*background* sample). We then injected a dose of deuterium oxide into the peritoneal cavity. We used deuterated water containing either 35.4 atom percent (AP) of deuterium (2008), or 99.9 AP (2009, 2010) and injected 0.6 to 2.3 g, depending on body mass. Birds were held for 90 minutes after injection to allow equilibration of the deuterium into the body water pool. We then collected an additional (*equilibration*) blood sample. At the field camp, we separated plasma from red blood cells using a centrifuge and stored plasma and red blood cell samples frozen in cryovials at -20 °C in the field and -80 °C in the laboratory until analysis.

We determined concentrations of deuterium in blood plasma using CFIRMS. Prior to analysis, we diluted *background* plasma samples to reduce plasma viscosity by pipetting 100 uL of plasma into 200 uL of distilled water, and *equilibration* plasma samples by pipetting 100 uL of plasma into 1.9 mL of distilled water. Sample vials were loaded into a liquid autosampler (CTC Analytics A200SE), which injected 0.2 uL of each sample into an on-line pyrolysis, thermochemical reactor elemental analyzer (TCEA; Finnigan ThermoQuest) coupled to a continuous flow (Conflo IV) Delta V^{Plus} IRMS (Finnigan). Gas concentrations of ^{18}O and ^{2}H (CO and H_2) from each sample were measured relative to calibrated reference gases (CO and H_2) and reported in delta notation as parts per thousand (‰). For quality control, we ran working standards after every seventh sample. Four replicate measurements were taken of each sample and standard. We made 2–4 replicate dilutions of most samples, depending on the volume of plasma available; deuterium concentrations varied little among dilutions (average coefficient of variation of replicate dilutions was 3%). Instrument precision was < 3.0‰ for hydrogen. We converted deuterium concentrations of diluted samples back to their original concentrations using the measured concentration of deuterium in the diluted sample, the concentration of deuterium in 5 replicate samples of distilled water, and the known volumes of plasma and distilled water used in the dilution. Laboratory analyses were performed by ASIF-UAF.

We converted equilibrium concentrations of deuterium in plasma samples to estimates of TBW based on the amount of injectate (Q_d, moles), isotopic enrichment of the injectate (R_d, in ppm), and the enrichment of the *background* and *equilibration* samples (C_{bg}, C_{eq}, respectively, in ppm), according to the plateau method equation in Speakman et al. (2001):

$$\mathrm{TBW} = 18.02 \cdot Q_d \cdot (R_d - C_{eq}) / (C_{eq} - C_{bg}) \qquad \text{Eq. 1.1}$$

where 18.02 is the molar mass of water. We used TBW to estimate percent lean body mass assuming a water content of lean tissue of 0.70, which is within the range of values measured in species of waterfowl using carcass lyophilization (62.8–73.3% Eichhorn and Visser 2008). TBW values were corrected for the positive bias of the deuterium dilution method relative to tissue carcass analysis (8%; Speakman et al. 2001, Mata et al. 2006). We calculated percent body lipid as 100 − percent lean (Pace and Rathbun 1945). Values of percent lean and percent lipid were used to calculate a fat index for each sampled bird as: grams lean tissue/grams fat (Tulp et al. 2009).

1.3.6 Statistical analyses

1.3.6.1 Statistical approach

We analyzed biotracer data using qualitative and quantitative methods. First, we used qualitative analyses to examine differences in biotracers from prey and loons in relation to factors such as species, year, sex, and age. For fatty acids, qualitative analyses also identified which specific fatty acids were most correlated with group separation. Second, we used biotracer values from loons and their potential prey to get estimates of loon diet composition using quantitative models. We used quantitative diet estimates from these models to further examine variation in diet related to species, sex, age, and characteristics of loon breeding lakes. Finally, we examined the consequences of diet composition by relating body condition to stable carbon and nitrogen isotope values measured from the same individuals. Agreement between diet composition estimates from these two independent biotracer methods permits greater confidence in the validity of results.

1.3.6.2 Stable isotopes

We examined differences between prey species $\delta^{13}C$ and $\delta^{15}N$ values separately using general linear models (GLMs) to specify different groupings of prey samples. For $\delta^{13}C$, we fit GLMs that grouped samples by habitat (freshwater, marine) and species-habitat (marine fishes, freshwater fishes, freshwater invertebrates) categories, as well as a model that included the 18 species separately. For $\delta^{15}N$, we fit GLMs that grouped prey by diet-habitat categories: herbivorous-freshwater (Anostraca, Coleoptera, Diplostraca, Trichoptera), carnivorous-freshwater (Notostraca, Alaska blackfish, ninespine stickleback *Pungitius pungitius*), and carnivorous-marine (all marine fishes).

For loon plasma and red blood cells, we examined differences in stable isotope ratio values between sample type (plasma, red blood cells) by calculating the average difference between stable isotope values of red blood cells and blood plasma within each individual bird. We fit GLMs relating variation in average $\delta^{13}C$ and $\delta^{15}N$ of loon plasma and red blood cells to *species*, *year*, and *sex*. We composed candidate model sets for each isotope that included all combinations of the main effects of *year*, *species*, and *sex*, and the interactions *species* × *year* and *species* × *sex*. For Pacific Loons, we fit a GLM relating $\delta^{13}C$ of plasma to lake surface area (*area*) to examine the hypothesis that individuals breeding on smaller lakes would consume more marine prey than individuals breeding on large lakes. For Red-throated Loons, we fit a GLM relating $\delta^{15}N$ from red blood cells of adults and chicks, for which we only analyzed red blood cell samples, to examine differences between adults and chicks (*age*) and the effect of distance from the coast (*distance*). We hypothesized that birds breeding farther from the coast, and thus incurring higher flight costs, would select more energy-dense marine prey species (Orians and Pearson 1979, Ydenberg 1994), which tended have higher $\delta^{15}N$ values (see Results).

1.3.6.3 Bayesian mixing models

We used a Bayesian mixing model (BMM; Moore and Semmens 2008) to estimate the proportion of prey types in the diets of loons based on stable isotope values in plasma for adult Red-throated and Pacific loons. We fit the BMM using the MixSIAR package in Program R

(Parnell et al. 2013). The model adjusts stable isotope ratios of prey for changes related to discrimination against heavier isotopes during assimilation and metabolism by the predator using trophic enrichment factors (TEFs; Hobson and Clark 1992). TEFs are measured from predators maintained on controlled diets. The model also incorporates uncertainty in TEFs into the uncertainty diet estimate uncertainty using the standard deviations of TEFs. No loon-specific TEFs have been measured, therefore, we used TEFs from the seabird literature calculated as the average of TEF values from 5 experimental studies (Hobson and Clark 1992, Bearhop et al. 2002, Cherel et al. 2005, Barquete et al. 2013, Chiaradia et al. 2014), and the standard deviations of the average values ($\delta^{13}C = 0.02 \pm 1.25$, $\delta^{15}N = 3.02 \pm 0.74$). We combined prey into 3 source groups based on similarities in $\delta^{13}C$ and $\delta^{15}N$ values: (1) freshwater fishes and invertebrates, (2) least cisco (*Coregonus sardinella*), (3) marine fishes, and calculated average isotope values and standard deviations across species included in each prey group. We chose to group prey species due to similarities in stable isotope ratios among some species and uncertainty in the trophic enrichment factors (TEFs) used in the model. Grouping species also can increase the accuracy of diet proportion estimates from BMMs (Ward et al. 2011). In all models, we used the residual × process error structure (Stock and Semmens 2016) and generalist priors.

We compared the diets of Red-throated and Pacific loons by fitting a model to the combined plasma $\delta^{13}C$ and $\delta\ ^{15}N$ data from both species. The model included *individual* as a random effect and *species* as a fixed effect. We compared posterior distributions of diet proportions between species and examined variation in diet composition among individuals.

For Pacific Loons, we examined sources of variation in individual diets by comparing 4 BMMs using the Deviance Information Criteria (DIC; Spiegelhalter et al. 2002). The first model included *individual* and *year* as random effects. The second model included *individual* as a random effect and *sex* as a fixed effect. The third model included only *individual* as a random effect. Of these 3 models, we used the model with the lowest DIC value and added lake surface *area* (in ha) as a continuous covariate (Francis et al. 2011). We hypothesized that the proportion of freshwater prey would increase with increasing lake size. BMM results are presented as the average (95% credible interval). We did not estimate diet proportions of Red-throated Loons using BMMs because of the similarity among stable isotope values of marine fishes and the uncertainty around trophic enrichment values (Fig. 1.1A).

1.3.6.4 Qualitative fatty acid analysis

We used discriminant function (DF) analysis (Tabachnick and Fidell 2007) to examine how accurately fatty acid signatures classified prey samples by *species*, and loon samples by *species*, *sex*, *year*, and for Red-throated Loons, *age* (adult, chick). DF analysis was applied using Bayes discriminant rule and uninformative prior probabilities of group membership. Quadratic DFs were used to calculate group-specific covariance matrices because the data consisted of unequal group sample sizes and within group covariance matrices were not homogenous (Bartlette's test $P < 0.001$ for all analyses). We did not include prey species with < 10 samples.

Only fatty acids entirely or predominantly derived from diet ("extended dietary" fatty acids, Iverson et al. 2004) were considered in analyses. We ranked fatty acids in the average signature of each species (prey and loons) in descending order by variance, excluding the fatty acid 22:5n-3, because it may be an intermediate of fatty acids 20:5n-3 and 22:6n-3 (Williams et al. 2008). We used a forward selection procedure to choose the fatty acids included in the final DF used to infer group differences. Fatty acids that improved the classification success of the DF, based on jackknife cross validation, were retained in the DF. Fatty acids were added to the DF until either classification success reached a maximum, or the maximum sample size supported by DF analysis ($n-1$ of the smallest group) was reached.

For Pacific Loons, we applied DFs to loon fatty acid signatures to separate samples in relation to *sex* and *year*. We started by adding the fatty acids found to separate freshwater and marine prey species, followed by fatty acids with the highest variances. For Red-throated Loons, we examined differences related to *sex*, *year*, and *age*, starting with the fatty acids that separated marine fish species, followed by those with the highest variances. We applied the same stopping rule as used in the analyses of prey species.

For each fatty acid signature, fatty acid percentages were transformed to meet DF analysis assumptions of multivariate normality and non-collinearity using the natural logarithm of the ratio of a given fatty acid to the geometric mean of all fatty acids in the signature: ln(fa/geometric mean) (Aitchison 1982, Kucera and Malmgren 1998). We assessed the significance of the final DF for each dataset based on a multivariate F-test and only drew inferences from DFs that reliably separated species (F-test statistic $P < 0.05$). For DFs that reliably separated groups, we determined which fatty acids were important to group separation by assessing DF loadings, which quantify correlations between fatty acids and the fitted DFs, and present average DF scores to visualize group separation.

1.3.6.5 Quantitative fatty acid signature analysis (QFASA)

We estimated the proportional contribution of each potential prey species to the diet of Red-throated and Pacific loons using quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004). The QFASA model estimates the proportion of each fatty acid in the consumer diet by finding the mixture of prey fatty acids that results in a predicted fatty acid signature for the predator that most closely matches its observed fatty acid signature. We used the Kullback-Leibler (KL; Iverson et al. 2004, Meynier et al. 2010) distance as the statistical measure of the distance between the observed and predicted fatty acid signatures. KL distance values are calculated based on the summed distance between observed and predicted proportions for each fatty acid in the signature of each predator. QFASA weights the best mixture of prey fatty acids by the lipid content of each prey species to arrive at estimates of diet proportions for each individual predator in the data set.

QFASA accounts for differential deposition, mobilization, and biosynthesis of fatty acids during lipid metabolism using calibration coefficients (CCs). CCs are determined from controlled feeding experiments and are calculated as the ratio of the amount of each fatty acid in the consumer to that of each fatty acid in the prey. We used CCs measured from two prior studies of marine piscivores: (1) captive Common Murre (*Uria aalge*) chicks reared on a monotypic diet of Atlantic silversides (*Menidia menidia*; Iverson et al. 2007), and (2) wild Tufted Puffin (*Fratercula cirrhata*) chicks from Kodiak Island, Alaska, reared on a controlled diet of Pacific herring (*Clupea pallasii*; Williams et al. 2009). Both Common Murres and Tufted Puffins are marine birds that have mixed diets of fishes and invertebrates.

We applied QFASA using 4 sets of CCs: (1) Common Murre, (2) Tufted Puffin, (3) the average of these two sets, and (4) CCs set to equal 1.0 (i.e., indicating no metabolic alteration of the fatty acids by the consumer). We also compared diet composition estimated with QFASA using 3 different sets of fatty acids: (1) *extended dietary* set (Iverson et al. 2004, n = 40 fatty acids), (2) fatty acids entirely derived from diet (*dietary set*, Iverson et al. 2004, n = 32 fatty acids), and (3) the subset of extended dietary fatty acids with mean proportions ≥ 1.0% of the average fatty acid composition of loons (*high-mean*, n = 14 fatty acids).

Because the two loon species had different sets of potential prey, we fit QFASA separately to data from each species. We fit QFASA with each combination of fatty acid subset and calibration coefficient for a total of 12 QFASA models (4 CCs × 3 fatty acid sets). We compared fit of QFASA models based on the KL distance of each QFASA model (Meynier et al. 2010). To compare QFASA models with differing numbers of fatty acids, we scaled the average KL distance of each model formulation by the number of fatty acids in the model to quantify the average distance between the observed and predicted fatty acid in the signature. The model with the lowest scaled KL distance value was selected as the inferential model.

Prey species may have similar fatty acid signatures (Budge et al. 2002, Iverson et al. 2002, Dissen 2015), which makes it impossible for QFASA to estimate their relative contribution to the diet accurately. We examined overlap of fatty acid signatures among prey species using simulations that treated each prey species as both the predator and prey in the QFASA model (i.e., prey-on-prey simulations; Wang et al. 2010). In the simulation, the fatty acid signature of each prey species was randomly split into two groups, one treated as a predator fatty acid signature and the other treated as a prey fatty acid signature along with all other prey fatty acid signatures. The QFASA model was then fit, without calibration coefficients, to estimate diet composition given the predator fatty acid signature subsample and all prey fatty acid signatures. We repeated this process 1000 times for each prey species with ≥ 4 samples. We used results to calculate average estimated diet proportions for all prey species given each predator subsample. Prey species with fatty acid signatures that were distinct (i.e., with little overlap of fatty acid signatures of other species) were estimated as the main component of the diet when used as the predator in the model. Based on these simulation results, we summed loon diet proportion output by QFASA models into groups of prey with similar fatty acid signatures.

We used QFASA estimates of Pacific and Red-throated loon diet proportions to examine sources of variation in the estimated diet. For Pacific Loons, we used QFASA output to examine variation in the summed proportions of high-lipid prey (i.e., prey species with lipid content ≥ 3.0 g lipid per g wet mass, see Results) and the summed proportion of freshwater prey. We examined variation in each of these response variables using GLMs that included *year*, *sex*, and lake surface *area* as explanatory variables. For Red-throated Loons, we used a GLM to examine variation in the summed proportions of high-lipid content fishes in association with *year*, *sex*, and *distance* to the coast. Model sets for each response variable were composed of all possible combinations of the main effects of explanatory variables and an intercept-only null model. Diet proportion values were logit transformed.

1.3.6.6 Prey lipid content

We examined differences in prey lipid content (i.e., the lipid proportion of wet mass) using GLMs that specified different prey groupings, including species, habitat (marine, freshwater), and species-habitat categories (marine fishes, freshwater fishes, freshwater invertebrates). Proportional fat values were logit transformed.

1.3.6.7 Body condition

We examined variation in fat index in relation to *species* (Pacific Loon, Red-throated Loon), *year* (2008, 2009, 2010), and *sex* using GLMs. Sex was determined using genetic analysis of blood samples collected in 2009 and 2010 for Red-throated Loons (Griffiths et al. 1998) and Pacific Loons (Guzzetti et al. 2008). Genetic analyses were done at the Molecular Ecology Laboratory at USGS Alaska Science Center. We used measurements from individuals with genetically-determined sex to determine the sex of birds sampled in 2008 using DF analysis. The fitted DF estimated sex of unknown samples based on body mass, tarsus length, and culmen length of known-sex individuals. To examine sources of variation in average fat index, we used GLMs that included *species*, *sex* and *year* as main effects, in addition to *year* × *sex*, *year* × *species*, and *sex* × *species* interactions. The set of candidate models was composed of all combinations of the main effects explanatory variables, and the 2-way interactions of interest listed above, in addition to an intercept-only null model.

For Pacific Loons, we used GLMs relating variation in average fat index to $\delta^{15}N$, $\delta^{13}C$, and lake surface *area*. We hypothesized that fat index would increase with the amount of marine fishes in the diet, and thus would be positively associated with $\delta^{15}N$ and negatively associated with $\delta^{13}C$. For Red-throated Loons, diet composition also may influence their body condition. High-lipid species like Arctic cod, slender eelblenny, and least cisco had higher $\delta^{15}N$ values than low-lipid species like Arctic flounder (*Liopsetta glacialis*), threespine stickleback (*Gasterosteus aculeatus*), and fourhorn sculpin (*Myoxocephalus quadricornis*; see Results). To examine the hypothesis that the fat index of Red-throated Loons was associated with high-lipid fishes, we fit GLMs relating variation in average fat index to $\delta^{15}N$ values in plasma, and *distance* to coast. For both species, we composed candidate model sets using all combinations of main effects of explanatory variables and included intercept-only null models.

For all analyses using GLMs, selection of the inferential model was based on Bayesian Information Criteria values (BIC; Schwarz 1978, Raftery 1995). We gauged the strength of support from the data for the inferential model relative to the other candidate models on the basis of model posterior probabilities (Link and Barker 2006). Model posterior probabilities closest to 1.0 indicate more support for a given model relative to the other models in the candidate set. We present estimated means with 95% confidence intervals, unless otherwise stated.

1.4 Results

1.4.1 Prey sampling

For stable isotope and fatty acid analyses, we collected 9 species of marine fishes, 4 species of freshwater fishes, and 5 orders of freshwater invertebrates (Table 1.1). Sample sizes for stable isotope and fatty acid analyses differ because samples collected in 2008 were not analyzed for fatty acids. Average fatty acid proportions for each prey species are provided in Appendices 1.1 and 1.2, and for loon species in Appendix 1.3.

1.4.2 Stable isotopes

Freshwater fishes and invertebrates had lower $\delta^{13}C$ values than marine fishes (Fig. 1.1A). Least cisco, all captured in marine or brackish water habitats, had $\delta^{13}C$ values similar to freshwater species. The model that grouped $\delta^{13}C$ samples by species was most supported by the data (model posterior probability = 1.0). Freshwater fishes and invertebrates had lower $\delta^{15}N$ values than marine fishes. The model that grouped $\delta^{15}N$ samples by species was most supported by the data (model posterior probability = 1.0). Anostraca, Trichoptera, and Coleoptera had the lowest $\delta^{15}N$ values, with intermediate values for ninespine stickleback, Notostraca, Diplostraca, Arctic grayling (*Thymallus arcticus*), and Alaska blackfish; marine fishes had the highest $\delta^{15}N$ values (Fig. 1.1A).

Red blood cell and plasma samples paired by individual loon had similar $\delta^{13}C$ and $\delta^{15}N$ values. For Red-throated Loons (n = 36), the average difference between red blood cell and plasma stable isotope ratios was 0.24 (0.11, 0.37) for $\delta^{13}C$ and -1.07 (-1.35, -0.78) for $\delta^{15}N$. Pacific Loon (n = 29) red blood cell and plasma also had small differences ($\delta^{13}C$ = 0.22: -0.41, 0.85; δ^{15}N = -1.11: -1.59, -0.62). All differences, except Pacific Loon δ^{13}C, were bound away from zero; however, these small differences were less than differences between marine and freshwater habitats (~ 4.5 ‰ for δ^{13}C), and trophic levels (~ 3 ‰ per trophic level for δ^{15}N), and thus these differences do not indicate significant changes in diet between the time scales integrated by plasma and red blood cells.

For both δ^{13}C and δ^{15}N values of loon plasma, models including only species were most supported by the data (δ^{13}C species model posterior probability = 0.88, δ^{15}N species model posterior probability = 0.86), indicating blood plasma values of δ^{13}C and δ^{15}N differed between species, but not between years or sexes. Plasma δ^{13}C was lower in Pacific Loons (-21.62: -22.38, -20.87) than in Red-throated Loons (-18.19: -18.84, -17.53). Similarly, plasma δ^{15}N values were lower in Pacific Loons (13.7: 13.11, 14.29) than in Red-throated Loons (17.49: 16.95, 18.02). The range of values for δ^{13}C and δ^{15}N were broader for Pacific Loons (9 ‰ for both isotopes) than Red-throated Loons (3 ‰ for both isotopes; Fig. 1.1B).

Pacific Loon plasma δ^{13}C was negatively associated with lake surface area (β_{area} = -0.06: -0.09, -0.03). Across the range of lake surface areas, δ^{13}C decreased from -20.8 (-21.8, -19.9) for a lake of 0.2 ha, which is in the range of marine prey, to -29.1 (-32.7, -25.5) for a lake of 128 ha, which is consistent with freshwater prey. When the two data points from the largest lake in the data set (128 ha) were removed to constrain inference to lakes ≤ 14 ha, the effect of lake surface area remained significant (β_{area} = -0.3: -0.55, -0.13) with estimates ranging from -19.6 (-21.0, -18.4) for a 0.14 ha lake to -24.0 (-26.0, -22.1) for a 13 ha lake. There was no association between lake surface area and δ^{15}N of Pacific Loon plasma (β_{area} = -0.1: -0.05, 0.01).

For Red-throated Loons, δ^{15}N of red blood cells was similar between adults (16.4: 16.2, 16.6) and chicks (16.5: 16.3, 16.7). Adult red blood cell δ^{15}N increased with distance from the coast ($\beta_{distance}$ = 0.15: 0.06, 0.24). Over the range of distances in the data, δ^{15}N showed only a minor increase from 16.2 (16.05, 16.41) at 0.25 km, to 17.01 (16.61, 17.41) at 5.5 km. The magnitude of this difference is less than the expected change of ~3‰ associated with changes in trophic level.

For both adult Pacific and Red-throated loons, stable isotope results from red blood cells were similar to those of plasma, and therefore RBC results are not presented.

1.4.3 Bayesian mixing model

Stable isotope ratios of Red-throated Loon plasma, after adjusting prey values for trophic enrichment, were clustered near the average value of marine fishes; in contrast, those of Pacific Loons had a much broader range, with individual values similar to both low trophic level freshwater invertebrates and to higher trophic level marine fishes (Fig. 1.1B). These differences were reflected in diet proportion estimates from the mixing model. The estimated average diet of Red-throated Loons was composed exclusively of marine prey (1.0; 95% credible interval: 0.99, 1.0). In contrast, the estimated average diet of Pacific Loons was composed of 0.22 (95% credible interval: 0.07, 0.38) freshwater prey and 0.77 (95% credible interval: 0.60, 0.90) marine prey; least cisco was absent from the estimated diet (Fig. 1.2).

Diet proportions varied considerably among individual Pacific Loons (Fig. 1.3). The model including *individual* and *year* as random effects fit the data better (DIC = 315.7) than models including a random *individual* effect and *sex* fixed effect (DIC = 319.4), and the model including only the random *individual* effect (DIC = 320. 4). Adding lake surface *area* as a continuous covariate to the best fitting model improved model fit (DIC = 292.4) and indicated that the proportion of freshwater prey in the diet increased with lake area (Fig. 1.4). Individuals breeding on lakes < 10 ha had diets composed of mostly marine prey; in contrast, individuals breeding on lakes > 10 ha had diets composed of mostly freshwater prey. This effect remained when 2 samples from the largest lake (128 ha) in the data set were removed and the model was refit, constraining inference to lakes ≤ 14 ha.

1.4.4 Qualitative analysis of fatty acids

The final DF separating prey species correctly classified 79% of individuals and included 5 fatty acids (Fig. 1.5A). The fit of the discriminant function was statistically significant ($F_{60,\,814} = 66.3$, $P < 0.0001$), indicating that the fatty acids in the final DF successfully separated some species when considered simultaneously. The first linear discriminant explained 55.2% of the between-group variation in the data and the second explained 34.3% of the remaining between-group variation. The first linear discriminant separated freshwater invertebrates (Notostraca, Diplostraca) from all fishes (Fig. 1.6A) and was correlated with the fatty acids c20:1n-9 (0.43) and c22:6n-3 (0.35), which were low in aquatic invertebrates. The second linear discriminant separated Alaska blackfish from all other species with group separation correlated with fatty acids c20:1n-9 (0.41) and c20:5n-3 (0.26), which were lower in Alaska blackfish than other species (Fig. 1.6A). Jackknife cross validation identified species with the lowest successful classification rates as: saffron cod (*Eleginus gracilis*) and slender eelblenny (both 50%). All other species had error rates of 71% or less.

When considering only marine fishes, the DF including 7 FA (Fig. 1.5B) reliably separated some species ($F_{20, 56} = 0.002$, $P < 0.0001$), with a correct classification of 70%. The first linear discriminant explained 51% of the between-group variation and separated Arctic cod from all other species (Fig 1.6B). The first discriminant was correlated with fatty acids c18:1n-9 (0.60) and c18:1n-7 (0.47), both of which were lower in Arctic cod compared to all other species, and c20:1n-9 (-0.47), which was higher in Arctic cod than all other species. The second linear discriminant explained 34% of the remaining variation and separated Arctic flounder, slender eelblenny, and fourhorn sculpin from all other species. Separation along the second discriminant function was correlated with the fatty acids c18:1n-7 (0.66), and c20:5n-3 (0.52), both higher in slender eelblenny and fourhorn sculpin, and c20:1n-9 (-0.36) and c22:1n-11 (-0.38), which were lower than in other species. Species with the lowest correct classification were slender eelblenny (30%), threespine stickleback (69%), fourhorn sculpin (69%), and saffron cod (50%). Arctic flounder (94%) and least cisco (93%) had the highest correct classification rates; classification rates of all other species were $\geq$ 70%.

The final DF applied to fatty acid data from both loon species ($F_{8,44} = 17.65$, $P < 0.0001$) had a successful classification rate of 92% and included 7 fatty acids (Fig. 1.5C). Species separation was correlated with c18:2n-6 (-0.47), which was higher in Pacific Loons, and c18:1n-7 (0.39), which was higher in Red-throated Loons. The DFA applied to the original data set with jackknife cross validation correctly classified 91% of Pacific Loon samples and 93% of Red-throated Loon samples.

For Pacific Loons, neither *sex* ($F_{7,14} = 0.74$, $P = 0.65$), nor *year* ($F_{7,14} = 1.13$, $P = 0.40$) were reliably separated using fatty acids. For Red-throated Loons, the final DFA that reliably separated males from females ($F_{6,24} = 0.53$, $P = 0.01$) included the fatty acids c22:6n-3, c20:1n-9, c22:1n-11, c20:5n-3, c18:1n-9, and c18:1n-7. This DF had a classification success of 74%. Separation was correlated with 22:6n-3 (0.57), and 20:5n-3 (0.43), which were higher in females than males. The DF correctly classified 73% of males and 75% of females.

Adult Red-throated Loon samples were reliably separated by *year* ($F_{6,24}$=5.17, $P < 0.01$) with the DF that included the fatty acids c22:6n-3, c20:1n-9, c22:1n-11, c20:5n-3, c18:1n-9, c18:1n-7, and c20:1n-9. This separation was most correlated with the fatty acid c22:6n-3 (-0.17), which was higher in 2009 than 2010. The fitted DF had a classification success rate of 79% and, when applied to the data with jackknife cross validation, successfully assigned 100% of samples from 2009 and 58% samples from 2010 to the correct year.

The final DF applied to Red-throated Loon adult and chick fatty acid profiles ($F_{2,16}$ = 20.61, $P < 0.01$) included the fatty acids c18:1n-9 (0.77) and c22:1n-11 (-0.75) and had a correct classification rate of 97%. Group separation was correlated with c18:1n-9 (0.89), which was higher in chicks than adults, and c22:1n-11 (-0.87), which was higher in adults than chicks. Jackknife cross validation had a correct classification rate of 92% for adults and 96% for chicks.

1.4.5 QFASA

Prey-on-prey modeling of marine and freshwater species showed that 2 species groupings had similar fatty acid signatures: (1) capelin, Pacific sand lance, and rainbow smelt (*Osmerus mordax*), and (2) saffron cod and fourhorn sculpin; all other prey species were correctly classified at ≥ 68% (Table 1.2).

The QFASA model with the lowest scaled KL distance for Pacific Loons included calibration coefficients measured from Common Murre chicks applied to the *extended dietary* set of fatty acids (Table 1.3). Diet proportion estimates varied among models (Fig. 1.7A); however, models consistently showed that the average Pacific Loon diet was composed of a mix of freshwater and marine prey. Estimates from the top model indicate the average proportional diet of adult Pacific Loon diet was composed of 0.55 (0.42, 0.69) freshwater prey and 0.45 (0.30, 0.60) marine prey. The freshwater invertebrates Notostraca (0.20: 0.12, 0.27) and Anostraca (0.14: 0.04, 0.24), both crustaceans, were important freshwater prey. Freshwater fishes, including ninespine stickleback (0.09: 0.01, 0.17) and threespine stickleback (0.09: 0.04, 0.13), composed the remainder of the freshwater portion of the diet. A diversity of fishes composed the marine portion of the diet, with the groups saffron cod–fourhorn sculpin group (0.13: 0.07, 0.27), capelin–Pacific sand lance–rainbow smelt (0.12: 0.06, 0.20), and slender eelblenny (0.10: 0.03, 0.17) forming the largest components. For individual Pacific Loons for which we had both stable isotope BMM and QFASA estimates, the summed proportions of marine prey estimated with

QFASA were lower than the BMM estimates in 20 of 22 cases; however, the estimates from both biotracers showed the same pattern among individuals (Fig. 1.3).

For adult Red-throated Loons, QFASA fit with Common Murre calibration coefficients and the *extended dietary* set of fatty acids had the lowest scaled KL distance (Table 1.3). Average proportional diet composition estimates from the top models (Fig. 1.7B) show the species groups capelin–Pacific sand lance–rainbow smelt (0.40: 0.31, 0.49) and saffron cod–fourhorn sculpin (0.17: 0.8, 0.26), as well as slender eelblenny (0.22: 0.16, 0.28) composed the largest components of the diet. For Red-throated Loon chicks, the QFASA model that included average CCs and the *dietary* set of fatty acids best fit the data (Table 1.3). Arctic flounder (0.28: 0.20, 0.36), slender eelblenny (0.26: 0.17, 0.36), and the saffron cod–fourhorn sculpin group (0.25: 0.15, 0.35) were the largest components of the diet (Fig. 1.7C).

The proportion of high-lipid content prey in the diet of Pacific Loons was associated with lake area (β_{area} = 0.04: 0.004, 0.073; model posterior probability 0.34). This association was driven by three samples collected from the large lakes > 30 ha. When these 3 samples were removed from the data set, the effect of area was larger and had greater uncertainty (β_{area} = 0.29, -0.03, 0.61). The model *sex* + *area* ranked second (model posterior probability 0.30), however, the parameter estimate for *sex* indicated no difference between males and females (β_{male} = 1.91, -0.59, 4.39). Models including *year* received little support (model posterior probability < 0.10).

The proportion of freshwater prey in the QFASA predicted diet of Pacific Loons increased with lake area (β_{area} = 0.02: 0.0002, 0.035; model posterior probability 0.37). The effect of lake area remained significant when the data set was reduced to lakes < 30 ha (β_{area} = 0.21: 0.08, 0.35; Fig. 1.8). The increase in freshwater prey with lake surface area was driven by the proportion of ninespine stickleback in the diet. When summarized by lake size, ninespine stickleback composed 0.01 (0, 0.35) of the proportional diet in lakes < 14 ha (n = 18). In the small sample of Pacific Loons breeding on lakes ≥ 13 ha (n = 4), ninespine stickleback composed 0.40 (0.11, 0.68) of the diet. Models including *year* and *sex* all ranked below the null model, indicating no support for these effects.

For Red-throated Loons, the proportion of high-energy content prey in the QFASA estimated diet was higher for females (0.98: 0.94, 0.99) than for males (0.83: 0.53, 0.95). The most supported model included only *sex* (model posterior weight 0.37). The second ranked model included *sex*, *distance*, and *year* (posterior model weight 0.24); however, the effects of *distance* and *year* had confidence intervals overlapping zero (β_{2010} = 1.34: -0.70, 3.37; $\beta_{distance}$ = -0.16: -0.41, 0.73).

1.4.6 Prey lipid content

The model grouping lipid content values of prey by species received the most support (model posterior probability = 1.0), indicating that the proportion of tissue wet mass that was lipid varied among species (Fig. 1.9). Marine species with the highest lipid content were Arctic cod (0.058: 0.047, 0.072), Pacific sand lance (0.054: 0.041, 0.070), and least cisco (0.038: 0.032, 0.044). Freshwater species with the highest lipid content included ninespine stickleback (0.054: 0.043, 0.067) and Arctic grayling (0.040: 0.025, 0.065). Freshwater invertebrates had low lipid content (all < 0.02). Alaska blackfish (0.012: 0.009, 0.014) and fourhorn sculpin (0.018: 0.015, 0.022) had the lowest lipid content of all fishes.

1.4.7 Body composition

Variation in average fat index of Pacific and Red-throated loons (n = 63) was most related to *year* (model posterior probability = 0.85). Across both species, average fat index was lower in 2008 (0.06: 0.03, 0.08) than either 2009 (0.13: 0.11, 0.16) or 2010 (0.14: 0.11, 0.16). There was no association between *species* and fat index (β_{PALO} = 0.009: -0.02, 0.04; model *species* + *year* posterior probability = 0.13). Red-throated Loon average fat index (0.11: 0.09, 0.12; n = 39) was similar to that of Pacific Loons (0.11: 0.09, 0.14; n = 24).

Variation in the average fat index of Pacific Loons for which there also were $\delta^{13}C$ measures (n = 29) was not related to concentration of $\delta^{13}C$ or $\delta^{15}N$ in plasma, nor the surface *area* of the lake (null model posterior weight = 0.54). Similarly, variation in fat index of Red-throated Loons (n = 37) was not related to $\delta^{13}C$ or $\delta^{15}N$ in plasma or *distance* to the coast from the breeding lake (null model posterior probability = 0.52).

1.5 Discussion

Diet composition, estimated using stable isotopes and fatty acids, was different in sympatrically breeding Pacific and Red-throated loons. As expected, the diets of Red-throated Loon adults and chicks were composed entirely of marine prey. In contrast, a mix of freshwater and marine prey was included in the diet of Pacific Loons, the proportions of which varied among individuals. This individual variation was related to the surface area of the breeding lake.

Pacific Loons breeding in small lakes (< 10 ha) consumed mostly marine prey, while those breeding in larger lakes consumed mostly freshwater prey. Despite the low lipid content of most freshwater prey species relative to marine species, body condition was similar between loon species and was not associated with diet composition. Thus, both loon species met their energy requirements using different prey during a period when available foraging time was constrained by the requirements of incubation.

The accuracy of biotracer diet estimators depends on meeting the assumptions of the models. Both BMM and QFASA models assume that all potential prey are included in the model and that sampled prey are representative of the prey consumed by the predators (Iverson et al. 2004, Moore and Semmens 2008). To address this assumption, we sampled prey from aquatic habitats in the study area using multiple sampling methods. We also used other surveys in the region to obtain prey species that we failed to collect. Both model types require consistent - between-species variation in biotracer values that is greater than the within-species variation (Phillips and Gregg 2001, Iverson et al. 2004). To address this assumption, we grouped prey species based on similarities in biotracer values. Lastly, both models assume that conversion factors (TEFs, CCs) accurately account for changes to biotracers during predator metabolism. We lacked conversion factors specific to either loon species, but used those from the literature we thought were most appropriate for loons, and either included uncertainty in conversion factors in the model estimates (BMM), or selected from multiple conversion factors based on model fit (QFASA). Despite these approaches, we acknowledge that the lack of conversion factors specific to either loon species adds uncertainty regarding the accuracy of diet proportion estimates that can only be resolved by obtaining species-specific TEF and CC values. The consistency in diet composition results between both stable isotopes and fatty acids, however, provides weight of evidence supporting the validity of our diet estimates.

Most results from loon biotracers were consistent across both stable isotopes and fatty acids. Individual variation in Pacific Loon diet, ranging from mostly marine to mostly freshwater prey, was demonstrated by the $\delta^{13}C$ and $\delta^{15}N$ of plasma, as well as BMM and QFASA diet estimates. In contrast, the stable isotopes in Red-throated loon plasma showed little variation and reflected higher trophic level marine prey. The difference in diet composition between loon species was seen in their fatty acid signatures. Pacific Loon diet was associated with the surface area of breeding lakes in both stable isotope and fatty acid results. The absence of year and sex differences in the diet of Pacific Loons also was consistent across both biotracers, as were age and sex differences in Red-throated Loons. The only result that was not consistent was the effect of year in adult Red-throated Loon diet, which was only apparent in the qualitative analysis of fatty acids. Agreement between stable isotope and fatty acids has been demonstrated in marine mammals (Hooker et al. 2001, Herman et al. 2005) and marine birds (Williams et al. 2008). Few studies, however, have employed multiple biotracers to produce independent estimates of diet composition (Tucker et al. 2008).

Biotracers distinguished among prey species at different resolutions. Stable isotopes provided a course-scale picture of prey in terms of freshwater, brackish, and marine prey. This scale was useful for estimating the more diverse diet of Pacific Loons, but not that of Red-throated Loons. For Red-throated Loons, BMM output would be strongly influenced by TEFs given the similarity in stable isotope values among many marine fishes (Bond and Diamond 2011). Fatty acids provide higher resolution estimates of diet because of the larger number of fatty acids used in the model (40 *extra-dietary* fatty acids) than stable isotopes (C and N). To examining qualitative differences in fatty acid signatures using all fatty acids with DFA requires the number of samples per prey type to be one greater than the number of available fatty acids. Thus, obtaining sufficient sample sizes may be difficult and expense of laboratory analyses will likely be high. QFASA does not face sample size constraints, but assumes the mean fatty acid signature for each prey group is representative of that prey population, which makes sampling design critical to valid inferences. For loons, fatty acids provide a more detailed understanding of diet, but require more laboratory time and greater expense.

The use of marine habitat during the breeding season has been documented in Pacific Loons (Davis 1972, Andres 1993), as well as in other loon species (Eriksson and Sundberg 1991, Jackson 2003, Schmutz et al. 2014). For incubating Pacific Loons, the proportion of marine prey in the diet decreased with increasing lake surface area. This change in diet composition with lake surface area may have been related to the costs and benefits associated with foraging locally in the breeding lake compared to central place foraging for marine prey. Foraging for marine prey incurs the cost of flight to and from the foraging habitat (Pennycuick et al. 1989, Bryan et al. 1995, Norberg 1996). All lakes in the study area were within 7 km of the coast; however, even short flights require additional energy expenditure compared to foraging in the breeding lake. Further, foraging away from the breeding lake carries additional costs because territory and nest site defense is not possible when adults are away foraging. Thus, foraging in the breeding lake should be the preferred feeding strategy if sufficient prey are available to meet adult energy requirements. That the diet of Pacific Loons breeding on small lakes included less freshwater prey suggests that foraging in the breeding lake was either not profitable, or was less profitable than feeding in marine habitat.

The small, and typically shallow, lakes that are abundant on the Arctic Coastal Plain (Sellmann et al. 1975, Hinkel et al. 2005) may provide limited prey for breeding loons. Shallow lakes freeze completely during winter (Jeffries et al. 1996) and cannot support overwintering fish populations. Both prey sampling and brood provisioning observations (Chapter 3) suggest that large-bodied freshwater fishes were either absent or rare in loon breeding lakes. Freshwater invertebrates are abundant in lakes without fishes (Mallory et al. 1994, Rautio and Vincent 2006, Schilling et al. 2008), but invertebrates are small and have low lipid content. Small-bodied fishes colonize small lakes during spring floods (Haynes et al. 2014), but are likely in low abundance. Thus, maintaining a positive energy balance by feeding on freshwater fishes and invertebrates may be difficult for a large-bodied, diving bird, like the Pacific Loon. Marine fishes, in contrast, were larger and had higher lipid content than most freshwater prey. This difference in prey size and lipid content, in addition to the proximity of marine foraging habitat, likely explains why Pacific Loons breeding in lakes with small surface areas had diets that included higher proportions of marine prey.

Ninespine stickleback and Arctic grayling were exceptions to the pattern of low-energy densities in freshwater prey; both species had lipid contents similar to high-lipid content marine fishes. Arctic grayling were not an important component of the estimated diet; however, ninespine stickleback comprised 0.09 of the average proportional diet estimated by QFASA and its prevalence in the diet varied among individuals from 0 to 0.74. The proportion of ninespine stickleback in the diet of Pacific Loons was higher in lakes with surface areas > 10 ha than in smaller lakes. Larger lakes in the study site may provide overwintering habitat for populations of small fishes, like ninespine stickleback, but not larger fishes, like least cisco (Reynolds 1997, Haynes et al. 2014). We hypothesize that as lakes get larger, the net energy gain of foraging locally on ninespine stickleback matches or exceeds the profitability of foraging in marine habitat for Pacific Loons.

The diet of Red-throated Loons was composed entirely of marine prey. Red-throated Loons also bred on small sized lakes (Chapter 3). Red-throated Loons may have been responding to the same selection pressure as Pacific Loons by using marine foraging habitat; however, there is evidence that foraging behavior is an inflexible trait in this species. Red-throated Loons breeding in areas farther from the coast exhibit central place foraging by flying to larger lakes and rivers to feed (Eriksson and Sundberg 1991). In the southern portion of their breeding range, Red-throated Loons breed on large fish-bearing lakes; however, they still forage using only central place foraging behavior and do not feed within their breeding territories (Reimchen and Douglas 1984). Thus, central place foraging appears to be a specialized foraging behavior in breeding Red-throated Loons and they may lack individual foraging plasticity.

High-lipid content fish species apparently composed a large proportion of the diet of adult Red-throated Loons. Pacific sand lance, a high-lipid species, was grouped with capelin and rainbow smelt, both species with lower-lipid content, but this species group comprised the largest portion of the diet. Slender eelblenny, another high-lipid content species, was also an important part of the estimated diet. Both adult males and females had diets composed of > 0.80 of species-groups that included high-lipid species. The proportion of high-lipid prey was greater in females than males, and may reflect an increased energy requirement in females necessary to recover from the energetic expense of egg production (Carey 1996). Apparent differences between sexes in diet proportions from QFASA may also result from differences in lipid metabolism between males and females due to egg production (Surai et al. 2001), rather than sex-related differences in diet composition. Further, lipid content is only one component of the energy content of fish, because energy content increases rapidly with fish length (Anthony et al. 2000, Ball et al. 2007). Thus, absent sex-specific CCs for QFASA and data on the length of fish consumed, our diet proportion estimates should be interpreted cautiously when making inferences regarding sex-related differences in diet composition and diet energy content.

The diet of Red-throated Loon chicks differed from that of adults. Chicks had greater proportions of the saffron cod–fourhorn sculpin group and Arctic flounder, and less of the capelin-Pacific sand lance-rainbow smelt group and Arctic Cod. These differences, however, are confounded with time as chicks were sampled later in the breeding season than adults, and fish availability may vary over the course of the summer (Haldorson and Craig 1984). Chicks in the study population had high growth rates and high survival probabilities (Rizzolo et al. 2015) that were likely fueled by the availability of high-lipid content fishes, like slender eelblenny. Observations of fish species provisioned to chicks (Chapter 3) estimated a higher proportion of least cisco in the diet (0.33) than what was estimated by QFASA. Differences between observed diet and the QFASA estimated diet might be related to several factors. QFASA integrates diet over a period of weeks, thus the QFASA estimated diet of chicks reflects fish provisioned over the entire postnatal period, whereas provisioning observations document diet during a portion of a given day. Chick diet also varied between broods and differences in estimates may result from sampling variation. Provisioning observations are also subject to errors in species identification (Elliott et al. 2008).

Pacific and Red-throated loons had similar body condition, despite differences in foraging behavior and diet composition. The body condition of Red-throated and Pacific loons was lower in 2008 than either 2009 or 2010; unfortunately, we did not sample loon adipose tissue in 2008 and have no detailed diet composition estimates for the year of lower body condition. We sampled loons during late-incubation (average day of capture was day 25 of the 26-day incubation period). By this stage in the incubation period, it is likely that any birds in poorer condition had already failed in their breeding attempt. Individuals sampled in late-incubation, demonstrated little variation in body condition, indicating that the foraging strategies and diet compositions documented in this study supported adult energy requirements.

Red-throated Loons that successfully hatch their clutch go on to provision their brood using central place foraging, while Pacific Loons feed chicks mostly freshwater prey (Chapter 3). Thus, Red-throated Loons might be expected to carry lower lipid reserves than Pacific loons to reduce body mass heading into the period of frequent provisioning flights. This was not the case, and Red-throated Loons had similar body condition to Pacific Loons, suggesting that either flight costs are already reduced adequately by their lower body mass, or maintaining lipid reserves during brood rearing is adaptive for persevering through periods of poor foraging conditions.

Species with generalized diets have greater adaptive capacity (Bennett and Owens 1997). The use of both freshwater and marine prey by breeding Pacific Loons may insulate them from changes in either foraging habitat. Specialization of Red-throated Loons on marine prey ties their energy intake to the availability of marine fishes during the breeding season. Due to increasing global temperatures (IPCC 2013), both lentic and marine habitats are changing (Grebmeier et al. 2006, Mueller et al. 2009, Grebmeier 2012, Grosse et al. 2012). The foraging and diet flexibility of Pacific Loons may permit them to more readily adapt to the changing Arctic environment than Red-throated Loons.

1.6 Acknowledgements

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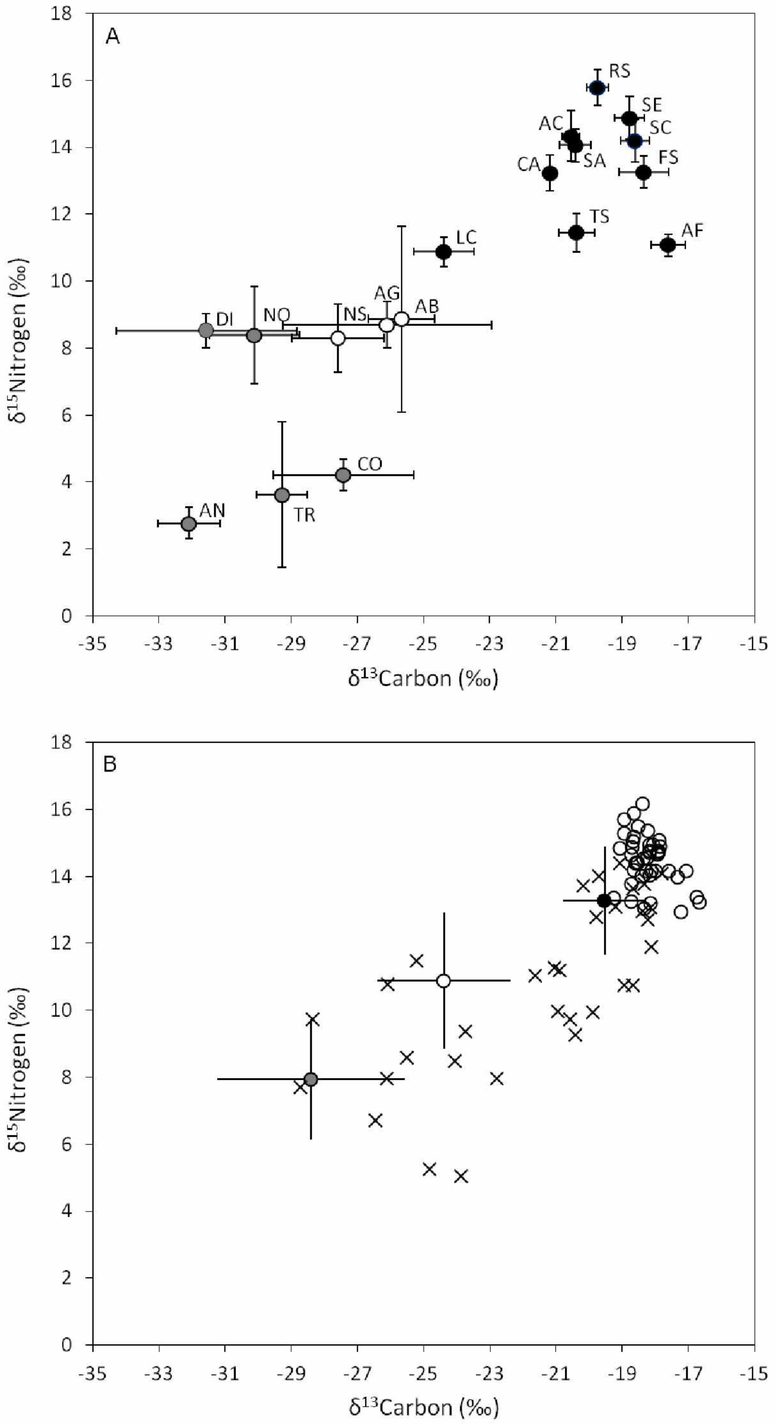


Figure 1.1 Stable isotope biplots of loons and their prey. (A) Average carbon and nitrogen stable isotope ratios (circles) of marine (black) and freshwater fishes (white) and invertebrates (gray) sampled from the Arctic Coastal Plain, Alaska, 2008–2011. Error bars are 95% confidence intervals. (B) Average ± SD stable isotope ratios (circles) for prey groups used to estimate diet

Figure 1.1 cont.

proportions using Bayesian mixing models: marine fishes (black), least cisco (white), and freshwater fishes and invertebrates (gray). Plasma values for Red-throated (○) and Pacific loons (×) were adjusted for trophic enrichment ($\delta^{13}C$ = -0.02, $\delta^{15}N$ = -3.02). Species codes: Alaska blackfish (AB), Anostraca (AN), Arctic cod (AC), Arctic flounder (AF), Arctic grayling (AG), capelin (CA), Coleoptera (CO), Diplostraca (DI), fourhorn sculpin (FS), least cisco (LC), ninespine stickleback (NS), Notostraca (NO), Pacific sand lance (SA), rainbow smelt (RS), saffron cod (SC), slender eelblenny (SE), threespine stickleback (TS), Trichoptera (TR).

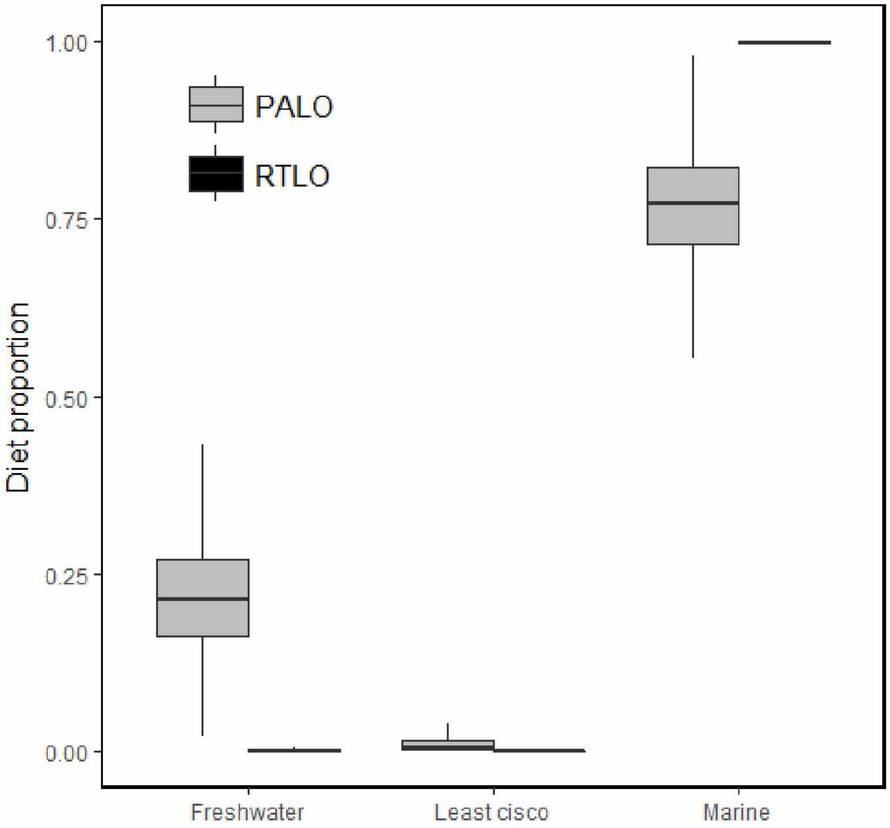


Figure 1.2 Bayesian mixing model diet estimates. The bounds of the shaded boxes indicate the 25th and 75th percentiles, the upper and lower lines indicate the 2.5th and 97.5th percentiles of model posterior distributions. Red-throated Loon diet proportions were estimated at proportion boundaries, 0.0, 0.0, and 1.0 for freshwater, least cisco, and marine prey, respectively. Species codes: Pacific Loon (PALO), Red-throated Loon (RTLO).

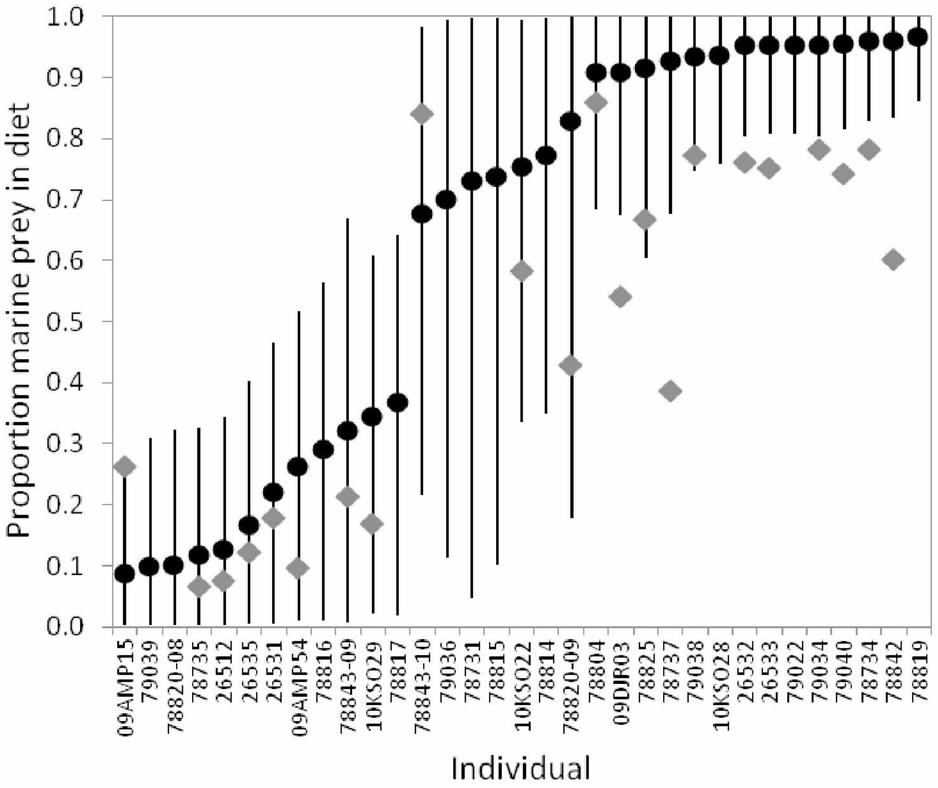


Figure 1.3 Proportion of marine prey in the estimated diet of Pacific Loons. Circles indicate average values and lines indicate 95% credible intervals estimated using a stable isotope Bayesian mixing model; diamonds are QFASA model estimates of summed marine prey.

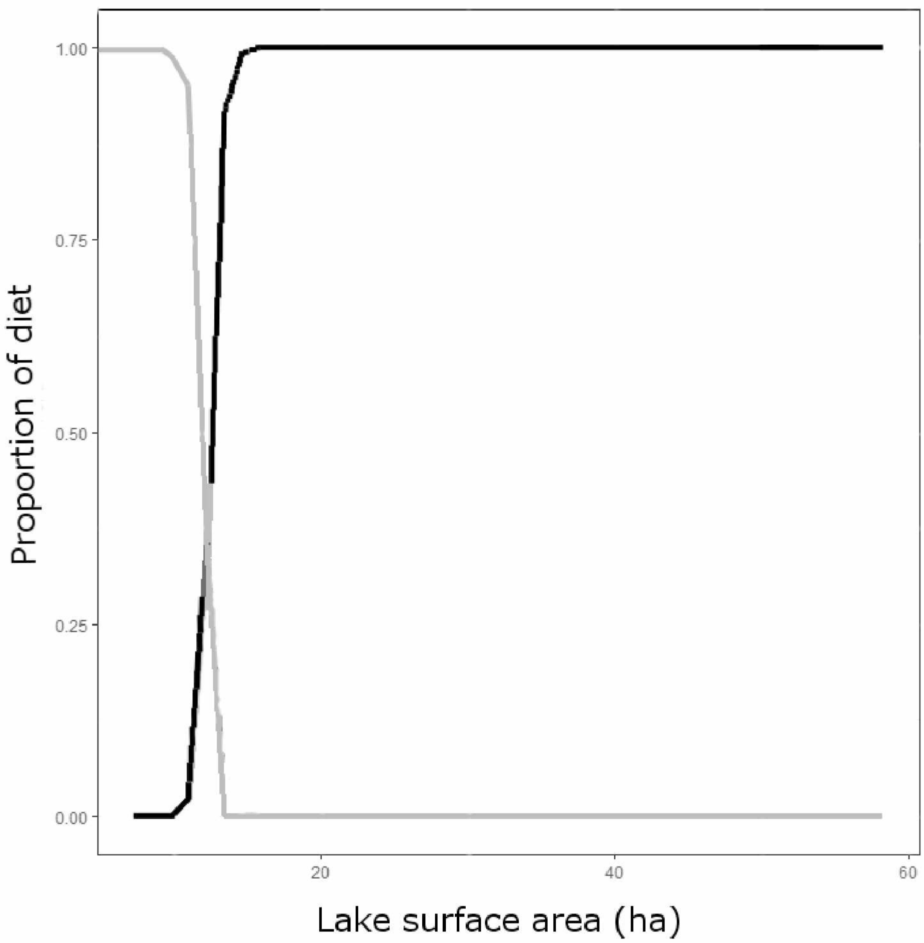


Figure 1.4 Pacific Loon diet in relation to lake surface area. Average diet proportions of freshwater prey (black line) and marine prey (gray line) estimated using a stable isotope Bayesian mixing model.

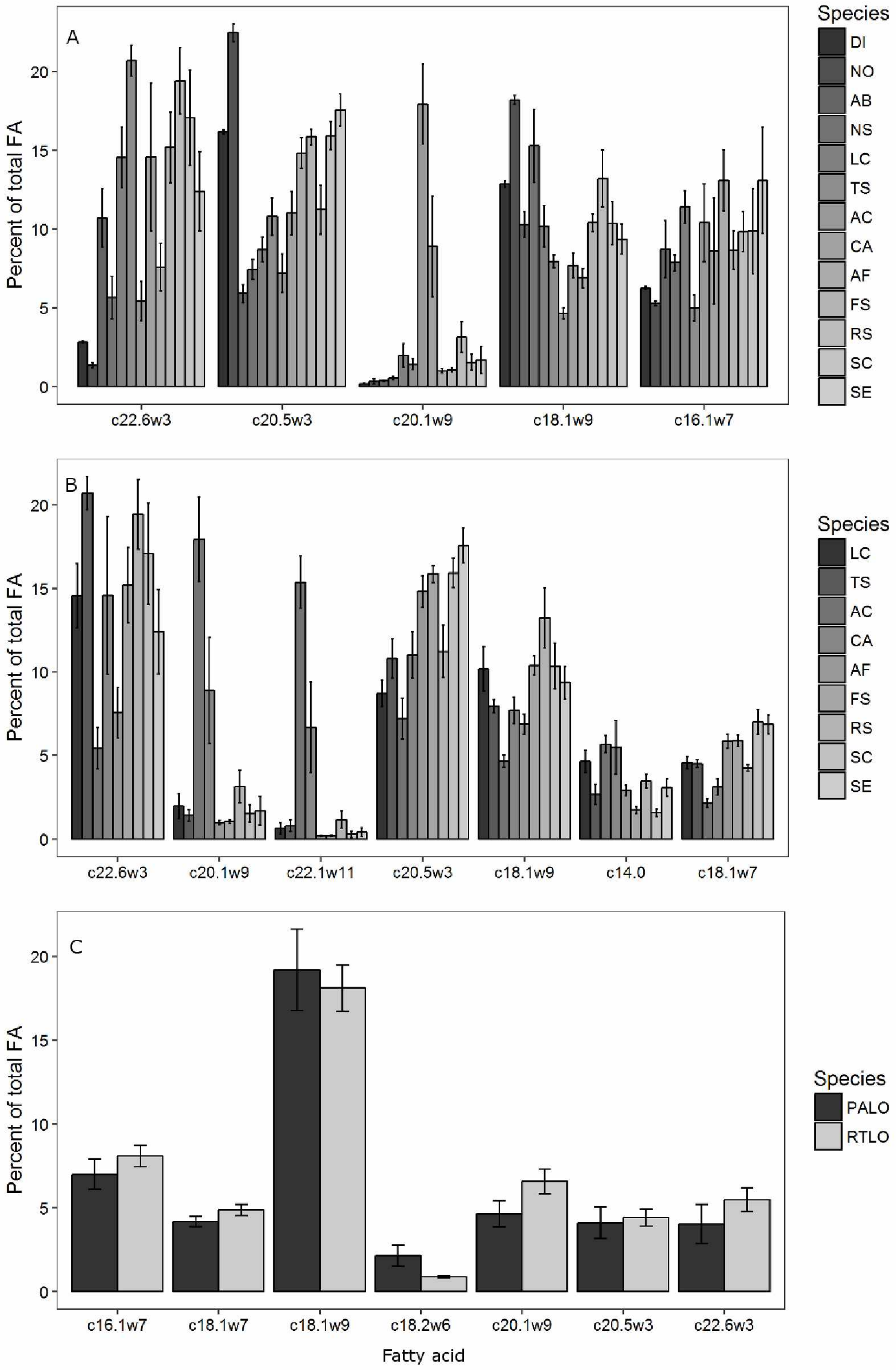


Figure 1.5 Fatty acid signatures of fish, invertebrates, and loons. Percentage of total fatty acids separating (A) marine fishes, freshwater fishes, and freshwater invertebrates; (B) marine fishes;

Figure 1.5 cont.

and (C) Pacific and Red-throated loons from the Chukchi Sea and Arctic Coastal Plain, Alaska. Species codes: Alaska blackfish (AB), Arctic cod (AC), Arctic flounder (AF), capelin (CA), Diplostraca (DI), fourhorn sculpin (FS), least cisco (LC), ninespine stickleback (NS), Notostraca (NO), Pacific Loon (PALO), rainbow smelt (RS), Red-throated Loon (RTLO), saffron cod (SC), threespine stickleback (TS), slender eelblenny (SE). Error bars are 95% confidence intervals.

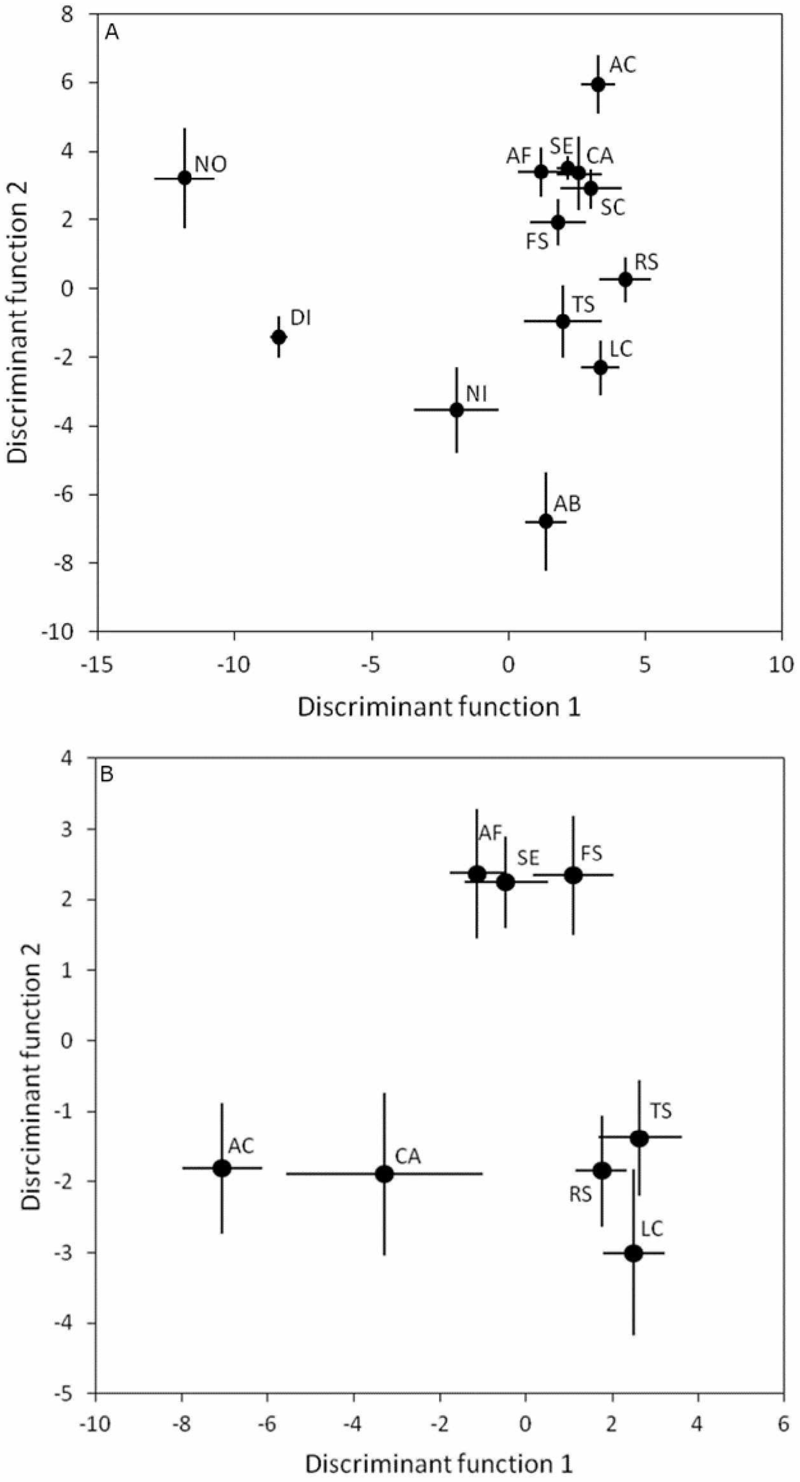


Figure 1.6 Discriminant function scores of fishes and invertebrates. Average ± SD discriminant function scores by species from the discriminant function separating (A) marine fishes, freshwater fishes, and freshwater invertebrates; and (B) marine fishes based on fatty acids.

Figure 1.6 cont.

Species codes: Alaska blackfish (AB), Arctic cod (AC), Arctic flounder (AF), Arctic grayling (AG), capelin (CA), Diplostraca (DI), fourhorn sculpin (FS), least cisco (LC), ninespine stickleback (NS), Notostraca (NO), Pacific sand lance (SA), rainbow smelt (RS), saffron cod (SC), slender eelblenny (SE), threespine stickleback (TS).

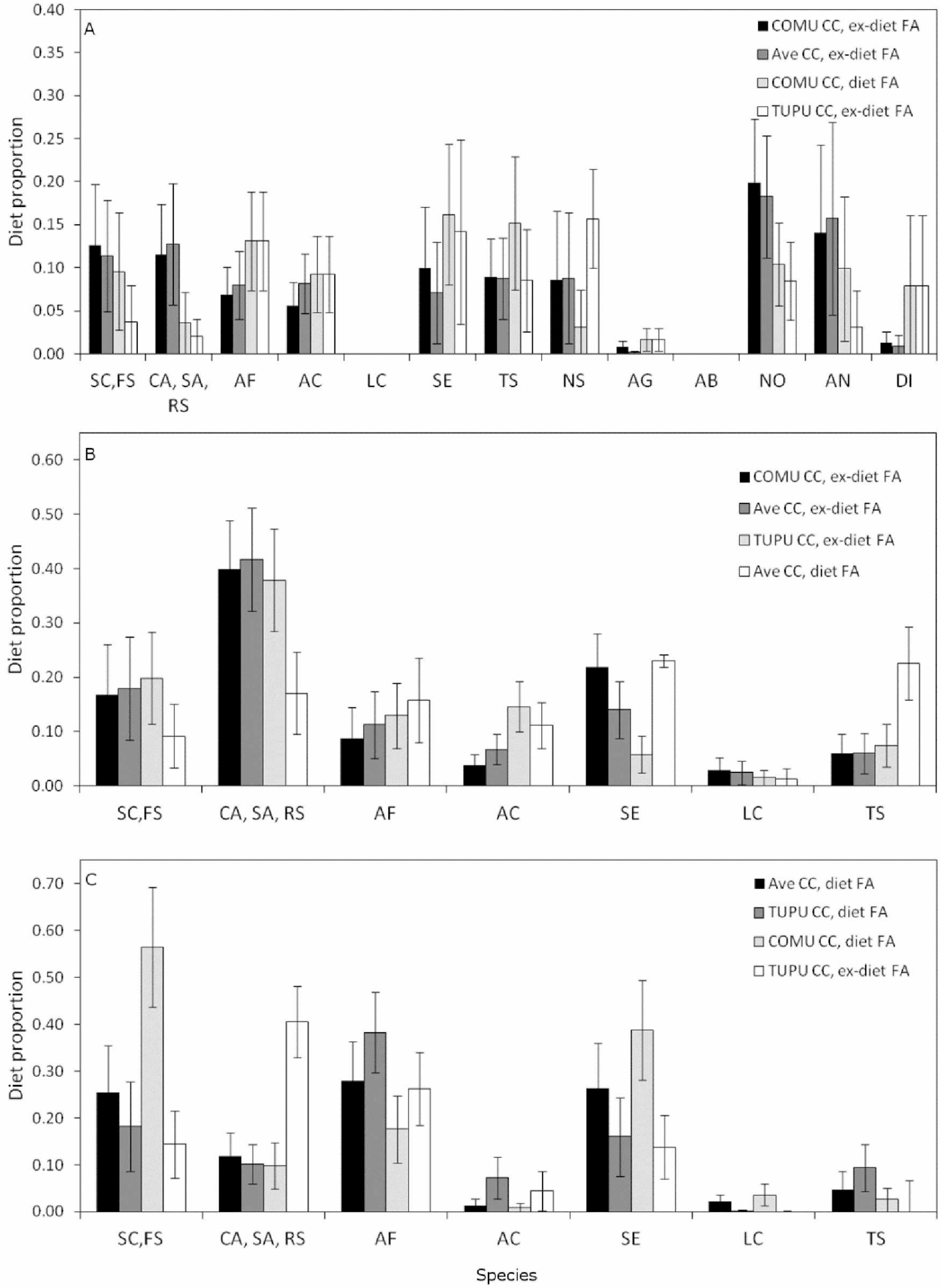


Figure 1.7 Loon QFASA diet estimates. Average proportions of prey species in the diet of (A)

Figure 1.7 cont.

adult Pacific Loons, (B) adult Red-throated Loons, and (C) Red-throated Loon chicks estimated by quantitative fatty acid signature analysis using different combinations of calibration coefficients (CC) and fatty acid sets (FA). Model estimates are ordered by decreasing fit from left to right. Error bars are 95% confidence intervals. Species codes: Alaska blackfish (AB), Anostraca (AN), Arctic cod (AC), Arctic flounder (AF), Arctic grayling (AG), capelin (CA), Diplostraca (DI), fourhorn sculpin (FS), least cisco (LC), ninespine stickleback (NS), Notostraca (NO), Pacific sand lance (SA), rainbow smelt (RS), saffron cod (SC), slender eelblenny (SE), threespine stickleback (TS).

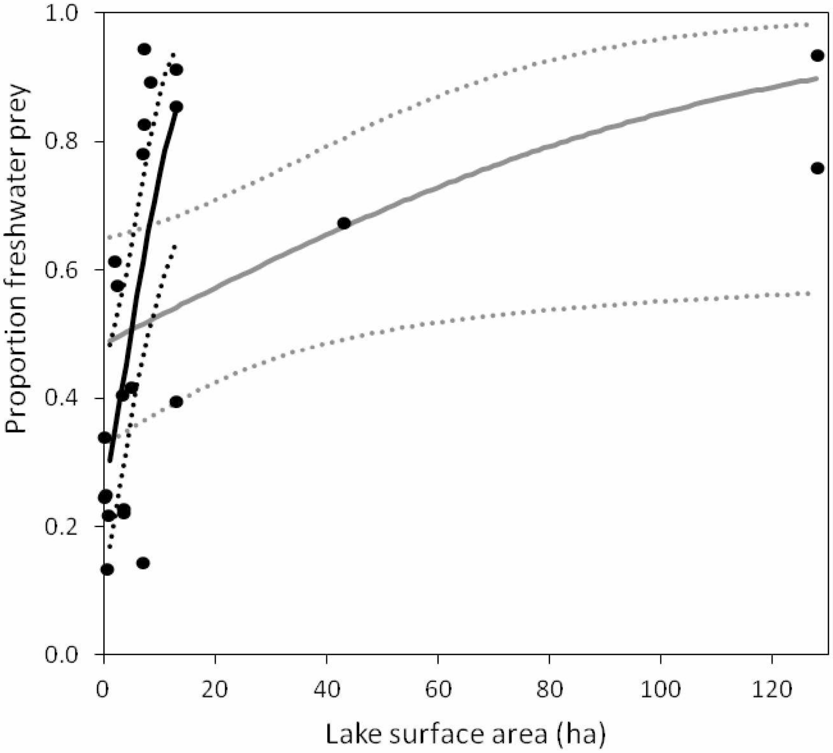


Figure 1.8 Proportion of freshwater prey in the QFASA estimated diet of Pacific Loons in relation to lake surface area. Points are QFASA predicted proportions, solid lines are model predicted values for all lakes in the complete data set (gray line) and data set reduced to lakes < 40 ha (black line). Broken lines are 95% confidence intervals.

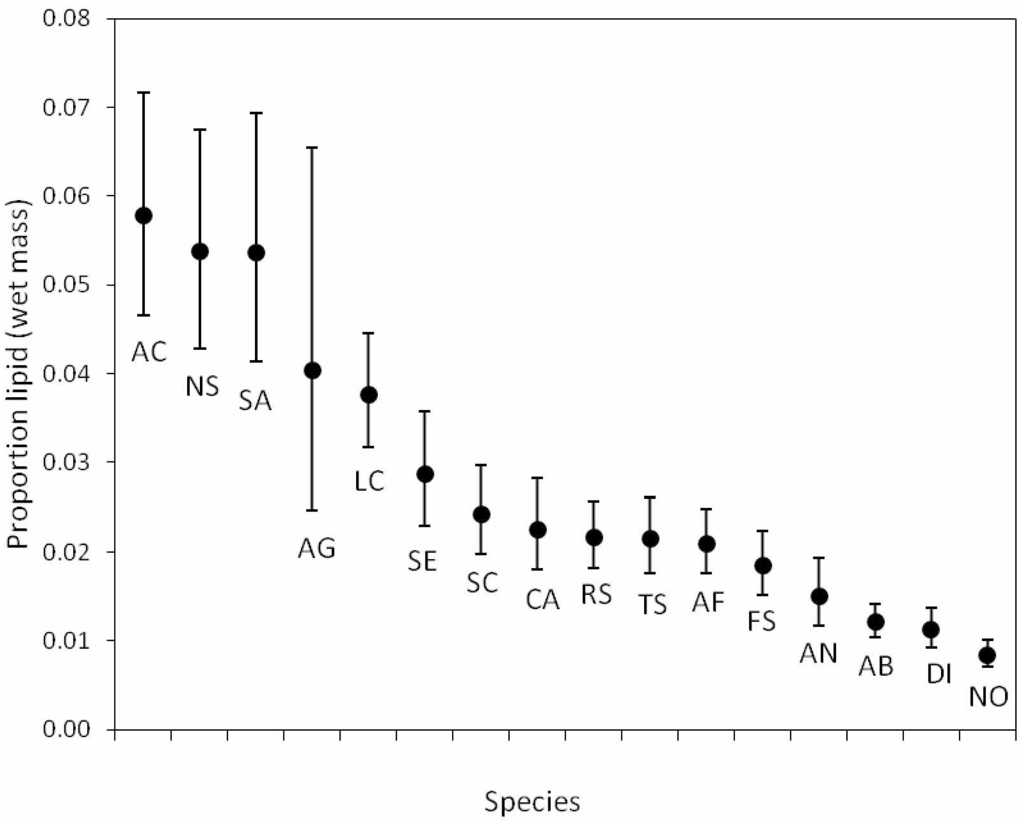


Figure 1.9 Prey lipid content. Lipid proportion of wet mass of marine fishes and freshwater fishes and invertebrates sampled from the Arctic Coastal Plain, Alaska, 2008–2011. Species codes: Alaska blackfish (AB), Anostraca (AN), Arctic cod (AC), Arctic flounder (AF), Arctic grayling (AG), capelin (CA), Diplostraca (DI), fourhorn sculpin (FS), ninespine stickleback (NS), Notostraca (NO), Pacific sand lance (SA), least cisco (LC), saffron cod (SC), slender eelblenny (SE), rainbow smelt (RS), threespine stickleback (TS).

Table 1.1 Fish and invertebrate samples collected from freshwater and marine habitats in the northwestern Chukchi Sea and Arctic Coastal Plain, Alaska. Sampling locations include: nearshore marine and lentic habitats near Point Lay, nearshore marine habitat near Wainwright (CSESP), offshore marine habitat near Wainwright (AKMAP), and central Arctic Coastal Plain lentic habitat (NPRA). Sample sizes for stable isotope analysis (n_{SI}) and fatty acid analysis (n_{FA}) are indicated.

Prey type	Species	Sampling location	n_{SI}	n_{FA}
Fish: marine	Arctic cod (*Boreogadus saida*)	AKMAP	4	10
		CSESP	12	18
	Arctic flounder (*Liopsetta glacialis*)	Point Lay	18	22
	Capelin (*Mallotus villosus*)	AKMAP	10	10
		CSESP	6	10
	Fourhorn sculpin (*Myoxocephalus quadricornis*)	Point Lay	16	13
	Least cisco (*Coregonus sardinella*)	Point Lay	19	17
	Rainbow smelt (*Osmerus mordax*)	Point Lay	13	18
	Saffron cod (*Eleginus gracilis*)	Point Lay	11	12
	Pacific sand lance (*Ammodytes hexapterus*)	AKMAP	8	7
	Slender eelblenny (*Lupenus fabricii*)	AKMAP	11	9
		CSESP	4	3
		Point Lay	1	1
	Threespine stickleback (*Gasterosteus aculeatus*)	Point Lay	13	9
Fish: fresh	Alaska blackfish (*Dallia pectoralis*)	NPRA	24	20
		Point Lay	3	2
	Arctic grayling (*Thaymallus arcticus*)	Point Lay	2	2
	Ninespine stickleback (*Pungitius pungitius*)	Point Lay	12	9
	Threespine stickleback (*Gasterosteus aculeatus*)	Point Lay	11	4
Inverts: fresh	Fairy shrimp (Order Anostraca)	Point Lay	3	3
		NPRA	0	5
	Aquatic beetle adults (Order Coleoptera)	Point Lay	2	0
	Clam shrimp (Order Diplostraca)	Point Lay	14	13
	Tadpole shrimp (Order Notostraca)	Point Lay	20	15
	Caddisfly larvae (Order Trichoptera)	Point Lay	4	0

Table 1.2 Matrix of prey similarity values based on prey-on-prey modeling with QFASA. The diagonal shows the probability of correctly identifying each prey type based on its fatty acid signature. Off-diagonal values indicate the probability of a prey type being incorrectly identified as another prey type. Species codes: Alaska blackfish (AB), Anostraca (AN), Arctic cod (AC), Arctic flounder (AF), capelin (CA), Diplostraca (DI), fourhorn sculpin (FS), least cisco (LC), ninespine stickleback (NS), Notostraca (NO), Pacific sand lance (SA), rainbow smelt (RS), saffron cod (SC), slender eelblenny (SE), threespine stickleback (TS).

Species	AB	AC	AF	CA	DI	AN	FS	LC	NO	RS	RS	SC	SA	SE	TS
AB	0.86	0.00	0.01	0.00	0.01	0.02	0.01	0.01	0.01	0.04	0.00	0.01	0.00	0.00	0.03
AC	0.00	0.87	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.01	0.00
AF	0.01	0.00	0.91	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.02
CA	0.00	0.09	0.00	0.46	0.00	0.00	0.01	0.02	0.00	0.00	0.16	0.02	0.15	0.06	0.00
DI	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
AN	0.00	0.00	0.00	0.00	0.10	0.73	0.00	0.03	0.03	0.09	0.00	0.00	0.00	0.00	0.00
FS	0.01	0.00	0.05	0.00	0.00	0.00	0.68	0.00	0.01	0.00	0.01	0.20	0.00	0.02	0.01
LC	0.01	0.00	0.01	0.01	0.00	0.00	0.00	0.79	0.02	0.00	0.06	0.03	0.01	0.03	0.00
NS	0.05	0.00	0.01	0.00	0.03	0.00	0.00	0.00	0.86	0.00	0.00	0.00	0.00	0.00	0.00
NO	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00
RS	0.00	0.02	0.00	0.01	0.00	0.00	0.02	0.01	0.01	0.00	0.80	0.08	0.00	0.01	0.00
SC	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.05	0.51	0.00	0.11	0.00
SA	0.00	0.06	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.86	0.00	0.00
SE	0.00	0.00	0.06	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.02	0.13	0.01	0.70	0.00
TS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00

Table 1.3 QFASA model results from Pacific and Red-throated loon fatty acid signatures. For each species and age-class, models including different combinations of calibration coefficients (CC) and sets of fatty acids (FA) were fit to the data and compared based on Kullback-Leibler (KL) distanced scaled by the number of fatty acids (KL_{scaled} Distance). Models from each set with the smallest KL_{scaled} distance most closely fit the data.

Species	CC	FA set	n_{FA}	KL Distance	KL_{scaled} Distance (1×10^{-3})
Pacific loon adult	Murre	Ex-dietary	40	0.13	3.29
	Average	Ex-dietary	40	0.15	3.73
	Murre	Dietary	32	0.16	4.89
	Puffin	Ex-dietary	40	0.22	5.49
	Average	Dietary	32	0.18	5.50
	Murre	High-mean	14	0.11	7.63
	Puffin	Dietary	32	0.27	8.31
	Average	High-mean	14	0.14	9.70
	Null	Ex-dietary	40	0.45	11.18
	Puffin	High-mean	14	0.22	15.45
	Null	Dietary	32	0.50	15.76
	Null	High-mean	14	0.43	30.37
Red-throated Loon adult	Murre	Ex-dietary	40	0.10	2.52
	Average	Ex-dietary	40	0.11	2.64
	Puffin	Ex-dietary	40	0.14	3.39
	Average	Dietary	32	0.11	3.42
	Murre	Dietary	32	0.11	3.48
	Puffin	Dietary	32	0.14	4.36
	Null	Dietary	32	0.07	4.91
	Null	Ex-dietary	40	0.08	5.76
	Null	High-mean	14	0.12	8.26
	Puffin	High-mean	14	0.28	8.74
	Average	High-mean	14	0.38	9.55
	Murre	High-mean	14	0.33	23.85
Red-throated loon chick	Average	Dietary	32	0.06	1.76
	Puffin	Dietary	32	0.06	1.81
	Murre	Dietary	32	0.07	2.14
	Puffin	Ex-dietary	40	0.11	2.66
	Average	Ex-dietary	40	0.11	2.72
	Murre	Ex-dietary	40	0.12	2.98
	Puffin	High-mean	14	0.08	5.53
	Average	High-mean	14	0.08	5.61
	Murre	High-mean	14	0.08	6.03
	Null	Dietary	32	0.21	6.50
	Null	Ex-dietary	40	0.42	10.39
	Null	High-mean	14	0.34	24.05

Appendix 1.1 Average (± SE) fatty acid percent composition of marine fishes. Samples were collected from Kasegaluk Lagoon and the Chukchi Sea, Alaska, 2008–2011. Samples sizes are in parentheses with species names.

Fatty acid	Arctic cod (10)	Arctic flounder (17)	Capelin (10)	Fourhorn sculpin (13)	Least cisco (14)	Rainbow smelt (17)	Saffron cod (12)	Slender eelblenny (10)	Threespine stickleback (13)
14:0	5.67 (0.27)	2.91 (0.15)	5.49 (0.82)	1.73 (0.11)	4.64 (0.34)	3.46 (0.21)	1.57 (0.12)	3.08 (0.26)	2.66 (0.30)
16:0	11.49 (0.4)	14.13 (0.21)	16.41 (0.91)	16.67 (0.51)	17.34 (0.43)	16 (0.52)	15.77 (0.54)	14.73 (0.23)	17.31 (0.52)
16:1n-7	10.4 (1.25)	13.1 (0.99)	8.62 (1.72)	8.67 (0.63)	11.42 (0.52)	9.83 (0.65)	9.87 (1.38)	13.1 (1.73)	4.98 (0.42)
16:2n-6	0.1 (0.01)	0.07 (0.01)	0.07 (0.01)	0.06 (0.005)	0.09 (0.01)	0.05 (0.004)	0.06 (0.004)	0.1 (0.01)	0.07 (0.01)
16:2n-4	0.13 (0.01)	0.35 (0.02)	0.25 (0.03)	0.34 (0.03)	0.23 (0.01)	0.41 (0.02)	0.24 (0.02)	0.29 (0.04)	0.42 (0.04)
16:3n-6	0.46 (0.05)	0.41 (0.03)	0.31 (0.05)	0.3 (0.03)	0.43 (0.03)	0.28 (0.03)	0.3 (0.03)	0.49 (0.06)	0.26 (0.03)
17:0	0.12 (0.01)	0.63 (0.02)	0.23 (0.04)	0.6 (0.04)	0.42 (0.03)	0.22 (0.02)	0.43 (0.04)	0.32 (0.04)	0.52 (0.06)
16:3n-4	0.34 (0.04)	0.71 (0.15)	0.24 (0.04)	0.19 (0.02)	0.24 (0.02)	0.18 (0.03)	0.25 (0.05)	0.38 (0.06)	0.15 (0.02)
16:4n-3	0.32 (0.07)	0.13 (0.01)	0.18 (0.01)	0.12 (0.01)	0.16 (0.01)	0.18 (0.01)	0.09 (0.01)	0.12 (0.02)	0.18 (0.02)
16:4n-1	0.32 (0.12)	0.17 (0.02)	0.32 (0.09)	0.12 (0.01)	0.13 (0.02)	0.17 (0.05)	0.09 (0.01)	0.04 (0.02)	0.07 (0.01)
18:0	1.2 (0.11)	3.89 (0.21)	2.2 (0.33)	4.74 (0.24)	3.46 (0.13)	3.34 (0.25)	4.14 (0.3)	3.14 (0.18)	5.28 (0.3)
18:1n-9	4.65 (0.19)	6.88 (0.31)	7.69 (0.41)	10.4 (0.28)	10.18 (0.67)	13.23 (0.92)	10.35 (0.69)	9.37 (0.49)	7.95 (0.2)
18:1n-7	2.14 (0.13)	5.85 (0.22)	3.11 (0.25)	5.87 (0.17)	4.56 (0.19)	4.25 (0.1)	7.01 (0.38)	6.86 (0.29)	4.51 (0.12)
18:2n-6	0.57 (0.04)	0.9 (0.12)	0.8 (0.04)	1.02 (0.09)	2.33 (0.2)	0.77 (0.02)	0.69 (0.04)	0.77 (0.04)	1.4 (0.13)
18:2n-4	0.18 (0.01)	0.21 (0.02)	0.18 (0.03)	0.17 (0.01)	0.28 (0.03)	0.12 (0.02)	0.2 (0.02)	0.22 (0.01)	0.12 (0.01)

Appendix 1.1 continued...

Fatty acid	Arctic cod (10)	Arctic flounder (17)	Capelin (10)	Fourhorn sculpin (13)	Least cisco (14)	Rainbow smelt (17)	Saffron cod (12)	Slender eelblenny (10)	Threespine stickleback (13)
18:3n-6	0.15 (0.01)	0.2 (0.02)	0.13 (0.02)	0.2 (0.02)	0.31 (0.04)	0.09 (0.01)	0.18 (0.02)	0.25 (0.03)	0.21 (0.02)
18:3n-4	0.06 (0.01)	0.28 (0.05)	0.07 (0.01)	0.12 (0.01)	0.12 (0.01)	0.06 (0.003)	0.11 (0.01)	0.11 (0.01)	0.07 (0.003)
18:3n-3	0.3 (0.03)	0.5 (0.04)	0.48 (0.03)	0.48 (0.05)	1.84 (0.22)	0.35 (0.01)	0.31 (0.04)	0.35 (0.05)	0.85 (0.21)
18:3n-1	0.05 (0.01)	0.19 (0.04)	0.1 (0.03)	0.26 (0.03)	0.15 (0.01)	0.22 (0.01)	0.24 (0.02)	0.23 (0.02)	0.23 (0.02)
18:4n-3	1.19 (0.13)	0.35 (0.03)	1.21 (0.16)	0.46 (0.04)	2.06 (0.32)	0.54 (0.05)	0.57 (0.05)	1.47 (0.12)	0.98 (0.15)
18:4n-1	0.15 (0.01)	0.04 (0.01)	0.11 (0.01)	0.03 (0.004)	0.09 (0.02)	0.05 (0.01)	0.07 (0.01)	0.22 (0.02)	0.07 (0.01)
20:1n-11	2.76 (0.58)	2.37 (0.14)	0.74 (0.15)	0.44 (0.09)	0.34 (0.04)	0.69 (0.24)	0.34 (0.05)	0.59 (0.06)	1.75 (0.39)
20:1n-9	17.94 (1.3)	0.99 (0.06)	8.9 (1.63)	1.05 (0.06)	1.97 (0.38)	3.14 (0.5)	1.53 (0.26)	1.69 (0.43)	1.42 (0.18)
20:1n-7	0.9 (0.21)	4.41 (0.3)	0.56 (0.09)	1.24 (0.19)	0.5 (0.06)	0.64 (0.03)	1 (0.08)	1.48 (0.11)	0.26 (0.02)
20:2n-6	0.14 (0.01)	0.37 (0.03)	0.19 (0.01)	0.34 (0.04)	0.37 (0.02)	0.21 (0.004)	0.33 (0.01)	0.31 (0.02)	0.26 (0.01)
20:3n-6	0.04 (0.002)	0.17 (0.01)	0.05 (0.003)	0.15 (0.01)	0.18 (0.02)	0.08 (0.003)	0.14 (0.01)	0.1 (0.01)	0.13 (0.01)
20:4n-6	0.2 (0.02)	2.84 (0.24)	0.53 (0.08)	2.77 (0.12)	1.26 (0.15)	1.31 (0.11)	2.17 (0.17)	1.6 (0.11)	2.3 (0.23)
20:3n-3	0.04 (0.002)	0.18 (0.04)	0.07 (0.01)	0.17 (0.04)	0.18 (0.02)	0.08 (0.01)	0.11 (0.01)	0.09 (0.01)	0.12 (0.01)
20:4n-3	0.29 (0.02)	0.24 (0.01)	0.35 (0.02)	0.29 (0.01)	0.75 (0.05)	0.34 (0.01)	0.35 (0.01)	0.37 (0.02)	0.51 (0.05)
20:5n-3	7.21 (0.63)	14.82 (0.49)	11.02 (0.7)	15.86 (0.25)	8.69 (0.4)	11.23 (0.8)	15.93 (0.46)	17.57 (0.53)	10.8 (0.6)
22:1n-11	15.37 (0.8)	0.19 (0.01)	6.68 (1.39)	0.18 (0.03)	0.64 (0.18)	1.16 (0.27)	0.28 (0.09)	0.4 (0.14)	0.8 (0.17)

Appendix 1.1 continued...

Fatty acid	Arctic cod (10)	Arctic flounder (17)	Capelin (10)	Fourhorn sculpin (13)	Least cisco (14)	Rainbow smelt (17)	Saffron cod (12)	Slender eelblenny (10)	Threespine stickleback (13)
22:1n-9	2.28 (0.21)	0.15 (0.02)	1.00 (0.18)	0.18 (0.01)	0.27 (0.05)	0.36 (0.04)	0.23 (0.02)	0.23 (0.04)	0.23 (0.03)
22:1n-7	0.51 (0.08)	0.33 (0.01)	0.24 (0.04)	0.13 (0.02)	0.16 (0.02)	0.1 (0.01)	0.14 (0.01)	0.17 (0.02)	0.05 (0.002)
22:2n-6	0.03 (0.004)	0.02 (0.003)	0.02 (0.01)	0.02 (0.004)	0.04 (0.002)	0.03 (0.002)	0.02 (0.002)	0.02 (0.003)	0.02 (0.003)
21:5n-3	0.19 (0.03)	0.19 (0.01)	0.24 (0.01)	0.18 (0.01)	0.22 (0.01)	0.22 (0.01)	0.28 (0.02)	0.5 (0.03)	0.16 (0.01)
22:4n-6	0.03 (0.005)	0.42 (0.02)	0.04 (0.01)	0.29 (0.03)	0.15 (0.01)	0.08 (0.004)	0.17 (0.02)	0.2 (0.04)	0.17 (0.02)
22:5n-6	0.02 (0.01)	0.3 (0.02)	0.17 (0.03)	0.36 (0.02)	0.68 (0.22)	0.19 (0.01)	0.29 (0.02)	0.25 (0.02)	0.41 (0.05)
22:4n-6	0.02 (0.004)	0.03 (0.003)	0.05 (0.01)	0.04 (0.003)	0.08 (0.01)	0.03 (0.003)	0.03 (0.003)	0.05 (0.003)	0.09 (0.01)
22:5n-3	0.55 (0.03)	3.04 (0.15)	0.87 (0.07)	2.14 (0.12)	2.05 (0.12)	1.27 (0.03)	1.59 (0.15)	1.33 (0.12)	5.46 (0.17)
22:6n-3	5.42 (0.64)	7.57 (0.78)	14.58 (2.41)	15.19 (1.15)	14.56 (0.98)	19.43 (1.07)	17.07 (1.54)	12.4 (1.28)	20.7 (0.51)

Appendix 1.2 Average (± SE) fatty acid percent composition of freshwater fishes and invertebrates. Samples were collected from the Arctic Coastal Plain, Alaska, 2008–2011. Samples sizes are in parentheses with species names.

Fatty acid	Alaska blackfish (22)	Diplostraca (13)	Ninespine stickleback (24)	Notostraca (15)
14:0	1.54 (0.21)	4.03 (0.10)	1.91 (0.13)	1.36 (0.05)
16:0	16.17 (0.25)	14.1 (0.06)	15.95 (0.28)	12.21 (0.12)
16:1n-7	8.72 (0.93)	6.25 (0.05)	7.86 (0.26)	5.29 (0.08)
16:2n-6	0.08 (0.01)	0.19 (0.004)	0.15 (0.01)	0.08 (0.003)
16:2n-4	0.27 (0.02)	0.22 (0.01)	0.2 (0.01)	0.15 (0.01)
16:3n-6	0.26 (0.05)	0.61 (0.01)	0.19 (0.01)	0.2 (0.02)
17:0	0.76 (0.05)	0.9 (0.01)	0.72 (0.02)	1.71 (0.02)
16:3n-4	0.11 (0.02)	0.34 (0.01)	0.09 (0.01)	0.16 (0.01)
16:4n-3	0.3 (0.03)	0.15 (0.01)	0.14 (0.01)	0.13 (0.01)
16:4n-1	0.26 (0.04)	0.13 (0.002)	0.15 (0.02)	0.07 (0.003)
18:0	6.39 (0.31)	2.58 (0.06)	5.33 (0.15)	5.74 (0.11)
18:1n-9	10.3 (0.41)	12.86 (0.1)	15.29 (1.19)	18.2 (0.14)
18:1n-7	4.35 (0.14)	2.89 (0.03)	6.93 (0.31)	5.34 (0.05)
18:2n-6	5.83 (0.5)	4.85 (0.04)	5.55 (0.21)	3.28 (0.11)
18:2n-4	0.07 (0.01)	0.14 (0.03)	0.1 (0.04)	0.13 (0.01)
18:3n-6	0.76 (0.09)	0.38 (0.03)	0.53 (0.03)	0.1 (0.01)
18:3n-4	0.12 (0.01)	0.08 (0.02)	0.07 (0.01)	0.16 (0.01)
18:3n-3	3.19 (0.38)	11.43 (0.06)	4.06 (0.15)	7.7 (0.07)
18:3n-1	0.17 (0.02)	0.13 (0.01)	0.08 (0.004)	0.13 (0.01)
18:4n-3	0.76 (0.13)	4.22 (0.02)	1.05 (0.13)	1.46 (0.04)
18:4n-1	0.15 (0.03)	0.02 (0.002)	0.04 (0.003)	0.04 (0.004)
20:1n-11	0.33 (0.05)	0.11 (0.01)	0.21 (0.02)	0.11 (0.02)

Appendix 1.2 continued...

Fatty acid	Alaska blackfish (22)	Diplostraca (13)	Ninespine stickleback (24)	Notostraca (15)
20:1n-9	0.37 (0.02)	0.17 (0.01)	0.53 (0.05)	0.31 (0.08)
20:1n-7	0.85 (0.06)	0.09 (0.01)	0.37 (0.04)	0.21 (0.02)
20:2n-6	0.65 (0.05)	0.13 (0.005)	0.54 (0.05)	0.17 (0.01)
20:3n-6	0.47 (0.04)	0.22 (0.002)	0.42 (0.03)	0.12 (0.01)
20:4n-6	6.35 (0.54)	2.52 (0.01)	4.23 (0.38)	2.03 (0.11)
20:3n-3	0.21 (0.02)	0.09 (0.01)	0.36 (0.02)	0.09 (0.01)
20:4n-3	0.52 (0.03)	0.77 (0.01)	0.79 (0.06)	0.79 (0.02)
20:5n-3	5.9 (0.3)	16.19 (0.07)	7.44 (0.32)	22.47 (0.28)
22:1n-11	0.09 (0.01)	0.18 (0.02)	0.11 (0.01)	0.33 (0.1)
22:1n-9	0.11 (0.02)	0.08 (0.01)	0.07 (0.01)	0.26 (0.02)
22:1n-7	0.11 (0.01)	0.03 (0.01)	0.03 (0.004)	0.12 (0.03)
22:2n-6	0.04 (0.01)	0.01 (0.002)	0.04 (0.01)	0.01 (0.003)
21:5n-3	0.07 (0.01)	0.34 (0.002)	0.08 (0.01)	0.14 (0.005)
22:4n-6	0.75 (0.08)	0.07 (0.004)	0.47 (0.03)	0.06 (0.003)
22:5n-6	1.26 (0.16)	0.49 (0.003)	0.72 (0.06)	0.25 (0.004)
22:4n-6	0.04 (0.002)	0.01 (0.001)	0.15 (0.01)	0.02 (0.005)
22:5n-3	2.46 (0.17)	0.43 (0.02)	2.88 (0.23)	0.25 (0.01)
22:6n-3	10.71 (0.95)	2.82 (0.02)	5.65 (0.68)	1.35 (0.09)

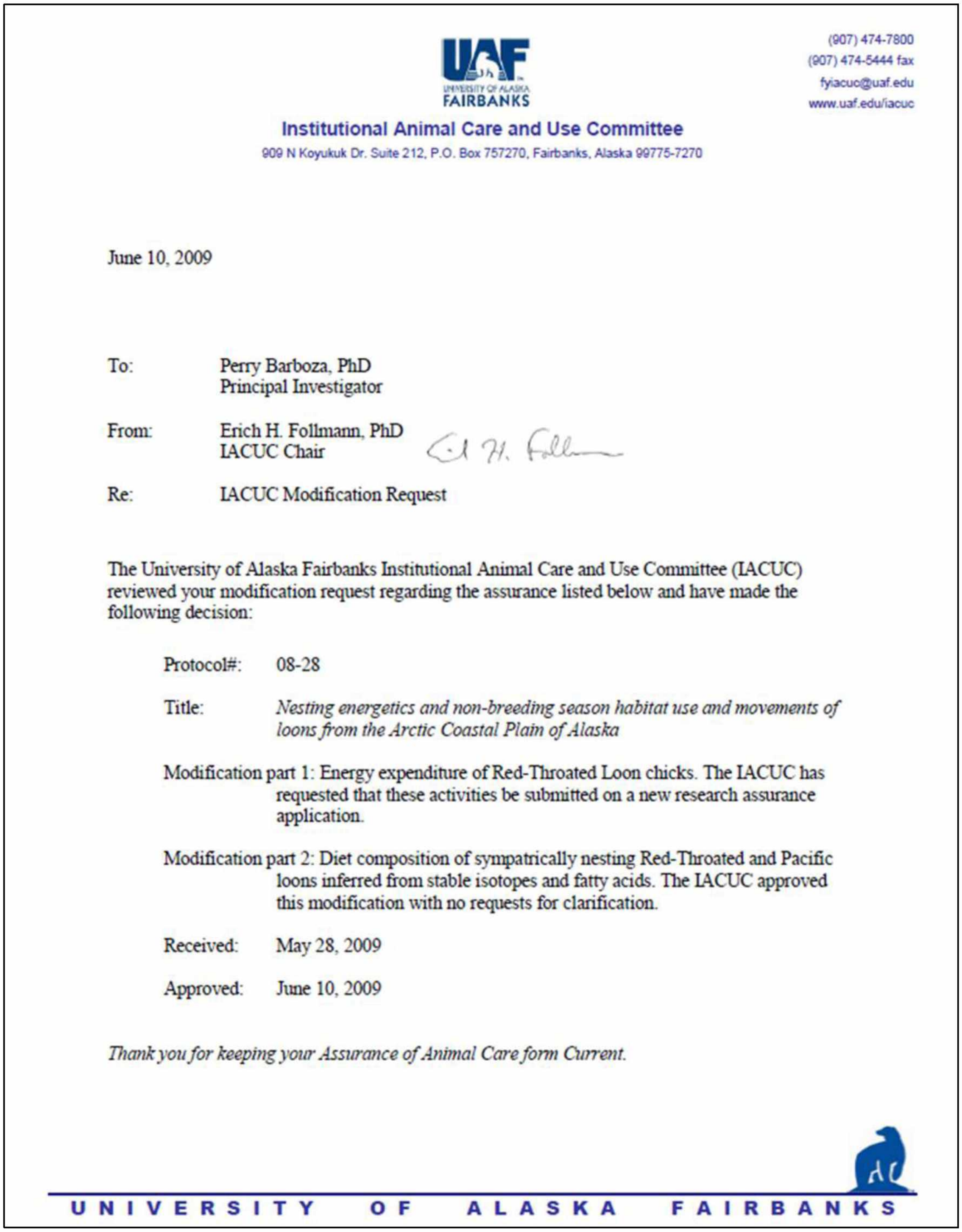
Appendix 1.3 Average (± SE) fatty acid percent composition of adipose tissue samples. Samples were collected from Pacific and Red-throated loons from the Arctic Coastal Plain, Alaska, 2008–2010. Samples sizes are in parentheses with species names.

Fatty acid	Pacific Loon (23)	Red-throated Loon (35)
14:0	2.32 (0.2)	2.75 (0.16)
16:0	15.26 (0.72)	16.82 (0.42)
16:1n-7	7.17 (0.47)	8.08 (0.31)
16:2n-6	0.04 (0.004)	0.05 (0.02)
16:2n-4	0.28 (0.02)	0.27 (0.01)
16:3n-6	0.26 (0.01)	0.28 (0.01)
17:0	0.32 (0.02)	0.22 (0.02)
16:3n-4	0.11 (0.01)	0.11 (0.005)
16:4n-3	0.12 (0.02)	0.13 (0.04)
16:4n-1	0.12 (0.02)	0.12 (0.01)
18:0	7.58 (0.32)	7.42 (0.2)
18:1n-9	18.87 (1.23)	17.95 (0.69)
18:1n-7	4.18 (0.15)	4.85 (0.16)
18:2n-6	2.09 (0.31)	0.88 (0.03)
18:2n-4	0.12 (0.01)	0.12 (0.005)
18:3n-6	0.1 (0.005)	0.08 (0.004)
18:3n-4	0.15 (0.01)	0.13 (0.01)
18:3n-3	1.57 (0.42)	0.44 (0.08)
18:3n-1	0.12 (0.01)	0.16 (0.01)
18:4n-3	0.48 (0.05)	0.38 (0.03)
18:4n-1	0.07 (0.02)	0.07 (0.01)
20:1n-11	7.83 (1.08)	5.99 (0.58)
20:1n-9	4.66 (0.39)	6.67 (0.35)
20:1n-7	1.06 (0.12)	1.27 (0.09)
20:2n-6	0.25 (0.01)	0.24 (0.01)
20:3n-6	0.1 (0.01)	0.09 (0.01)

Appendix 1.3 continued...

Fatty acid	Pacific loon (23)	Red-throated loon (35)
20:4n-6	0.95 (0.07)	0.82 (0.06)
20:3n-3	0.07 (0.01)	0.16 (0.1)
20:4n-3	0.19 (0.02)	0.17 (0.01)
20:5n-3	4.3 (0.51)	4.46 (0.25)
22:1n-11	7.94 (1.14)	6.25 (0.59)
22:1n-9	0.81 (0.07)	0.81 (0.1)
22:1n-7	0.19 (0.02)	0.17 (0.02)
22:2n-6	0.03 (0.003)	0.03 (0.004)
21:5n-3	0.14 (0.01)	0.18 (0.01)
22:4n-6	0.18 (0.02)	0.21 (0.07)
22:5n-6	0.13 (0.01)	0.1 (0.005)
22:4n-6	0.02 (0.003)	0.03 (0.01)
22:5n-3	1.14 (0.08)	1.11 (0.06)
22:6n-3	4.27 (0.61)	5.55 (0.34)

Appendix 1.4 Institutional Animal Care and Use Committee approval from the University of Alaska Fairbanks for adult loon diet studies, 2008–2010.



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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 10, 2009

To: Perry Barboza, PhD
Principal Investigator

From: Erich H. Follmann, PhD
IACUC Chair

Re: IACUC Modification Request

The University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC) reviewed your modification request regarding the assurance listed below and have made the following decision:

Protocol#: 08-28

Title: *Nesting energetics and non-breeding season habitat use and movements of loons from the Arctic Coastal Plain of Alaska*

Modification part 1: Energy expenditure of Red-Throated Loon chicks. The IACUC has requested that these activities be submitted on a new research assurance application.

Modification part 2: Diet composition of sympatrically nesting Red-Throated and Pacific loons inferred from stable isotopes and fatty acids. The IACUC approved this modification with no requests for clarification.

Received: May 28, 2009

Approved: June 10, 2009

Thank you for keeping your Assurance of Animal Care form Current.

UNIVERSITY OF ALASKA FAIRBANKS

CHAPTER 2

FAST AND EFFICIENT: POSTNATAL GROWTH AND ENERGY EXPENDITURE IN AN ARCTIC-BREEDING WATERBIRD, THE RED-THROATED LOON (*GAVIA STELLATA*)[2]

2.1 Abstract

Environmental conditions can exert a strong influence on the growth and energy demands of chicks. We hypothesized that postnatal growth in a cold, aquatic environment would require a high level of energy metabolism in semiprecocial Red-throated Loon (*Gavia stellata*) chicks. We measured body mass growth and daily energy expenditure (DEE) of free-ranging chicks in the Arctic. We used daily gains in body mass and DEE to estimate daily metabolizable energy (DME, kJ d^{-1}) and total metabolizable energy (TME, kJ $chick^{-1}$). Chicks gained body mass quickly with a logistic growth rate constant 57% greater than the allometric prediction, yet were only 60% of adult body mass at fledging. Males grew at a rate similar to females, but for a slightly longer duration and so reached an asymptotic body mass 23% heavier, and tarsus length 8% longer, than females. Chick growth performance was similar between first- and second-hatched chicks within broods of two, suggesting that food availability was not limited. DEE increased in proportion to body mass and DME peaked at 1214 kJ d^{-1} on day 25 post-hatching. Over the average 49-day postnatal period, TME was 49.0 MJ, which is within the range of error of the allometric prediction. Parents provided 58.6 MJ as food to meet this energy requirement. Given this chick energy requirement and the range of energy content of prey observed in chick diet, selecting prey with higher energy content would greatly reduce adult provisioning effort. Red-throated Loon chicks did not have a high postnatal energy requirement, but rather grew quickly and fledged at a small size with the effect of reducing the length of the postnatal period, and consequently, parental energy investment in chicks.

2.2 Introduction

Growing chicks must ingest sufficient energy to support the costs of tissue synthesis, tissue maintenance, dietary thermogenesis, activity, and thermoregulation (Weathers 1996). The

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[2] Published as Rizzolo, D.J., J.A. Schmutz, and J.R. Speakman. 2015. Fast and efficient: postnatal growth and energy expenditure in an Arctic-breeding waterbird, the Red-throated Loon (*Gavia stellata*), The Auk: Ornithological Advances, 132, 657–670.

sum of these energetic costs over the postnatal period, from hatching until fledging, represents the total expense of producing a fledgling. In species with chicks that self-feed, the chicks must acquire sufficient food to meet this requirement; otherwise, parent(s) must acquire and provision it to their chicks (Nice 1962). Chick energy requirement is most related to body mass because metabolic rate, which scales positively with body mass, is a dominant pathway of energy expenditure (Drent et al. 1992, Klaassen 1994). However, each pathway of energy expenditure may vary in relation to life history traits and the environment (Weathers 1992). Accordingly, some species are more energetically expensive to produce than others, even after accounting for body mass (Schekkerman and Visser 2001, Hodum and Weathers 2003). Species with high chick energy demands require a high food intake to maintain energy balance (Klaassen et al. 1992, Benowitz-Fredericks and Kitaysky 2005). Under conditions of restricted food intake, growing birds must allocate limited energy among competing metabolic demands (Dunn and Brisbin 1980, Konarzewski 1995). Consequently, if energy intake is limited, growth may be compromised with potential effects on chick survival and recruitment into the breeding population (Lindén et al. 1992, Schmutz 1993, Sedinger et al. 1995).

How chick energy allocation is related to mode of development and the environment is unclear. Weathers (1992) showed that most variation in the total energy metabolism of chicks in a diverse group of 30 species was explained by body mass and length of the postnatal period. Drent et al. (1992) showed that the combined energy costs of thermoregulation and activity made up ~ 30% of a chick's total energy budget in a small, but diverse group of 14 species. However, most species examined in these reviews were either altricial or semiprecocial and remained at or near the nest until fledging. In contrast, the total energy requirements of some precocial, self-feeding shorebird chicks exceeded allometric predictions by 29–39% at a middle latitude breeding site (Schekkerman and Visser 2001). Total energy requirements were even higher (up to 107% > predicted) at high-latitude breeding sites for both precocial (Schekkerman et al. 2003, Tjørve et al. 2007) and semiprecocial chicks (Hodum and Weathers 2003). High energy requirements in chicks that experience cold operative temperatures, or that leave the nest site after hatching to follow parents or feed, suggests that mode of development can interact with the environment to create energy-demanding chick life histories.

Loons (family Gaviidae) are waterbirds whose semiprecocial young enter aquatic habitat shortly after hatching. The thermoregulatory demands of residing on water may be particularly important for loon chicks. Common Loon (*Gavia immer*) chicks had similar rates of energy expenditure at 10 days and 21 days post-hatching, suggesting the cost of thermoregulation may have been exceptionally high in young chicks (Fournier et al. 2002). Of all species in the Gaviidae, the Red-throated Loon (*Gavia stellata*; Fig. 2.1) has the farthest north breeding distribution, up to 83° N (Barr et al. 2000), and is unique among its congeners in that chicks, in broods of two, rely exclusively on parental provisioning for energy intake during the entirety of the postnatal period (Reimchen and Douglas 1984, Eberl and Picman 1993). Breeding Red-throated Loons do not capture prey from within their breeding lakes, which are often small and devoid of fish, but instead fly to foraging sites in coastal marine habitat or larger lakes (Johnson and Johnson 1935, Eriksson et al. 1990) up to 20 km from the breeding lake (Davis 1972). Because chicks do not self-feed, parental provisioning effort must be sufficient to meet the energy requirements of both chicks in the brood, else chicks may grow at reduced rates and brood size may be reduced by starvation (Okill and Wanless 1990, Eberl and Picman 1993, Ball 2004). Their reliance on adult provisioning for energy intake and use of aquatic habitat make the Red-throated Loon an interesting model species for examining postnatal growth and energy requirement.

We quantified growth in free-ranging Red-throated Loon chicks from the Arctic Coastal Plain of Alaska. To determine if parents were able to meet the energy requirement of their brood, we examined differences in growth performance associated with sex and chick status (first-hatched senior chicks, second-hatched junior chicks, or solitary singleton chicks). We used the doubly-labeled water method to quantify postnatal daily energy expenditure (DEE, kJ d^{-1}) and examined DEE for differences in sex and chick status independent of body mass. We used daily gains in body mass and DEE to estimate daily metabolizable energy (DME, kJ d^{-1}) and total metabolizable energy (TME, MJ $chick^{-1}$) and examined how easily parents were able to meet chick energy requirements given prey species observed in the chick diet. We hypothesized that Red-throated Loon chicks would metabolize more energy than predicted from their body mass at fledging.

2.3 Methods

2.3.1 Study site

We conducted this study at a site on the Chukchi Sea coast of the Arctic Coastal Plain of Alaska, near the village of Point Lay (69° 44'N, 163° 00'W) during two consecutive summers, June to September in 2009 and 2010. The habitat at the study site is dominated by thermokarst with abundant ice-wedge polygons and thaw lakes ranging in size from 0.02–50 ha. Small (0.02–0.80 ha) thaw lakes are numerous and occur in association with river deltas and dry lakebeds (Jorgenson and Shur 2007). The main vegetative communities at the site are tussock-sedge, dwarf-shrub, and moss (Gallant et al. 1995). The Arctic Coastal Plain has a polar climate characterized by monthly average temperatures < 10°C throughout the year. Average daily (± 1 SD) air temperature at the study site during the brood rearing period (July and August) was 7.9 ± 3.7°C in 2009 and 7.8 ± 3.3°C in 2010. (NOAA 2014). In a sample of lakes used by brood-rearing loons ($n = 16$), average water temperature was 7.4 ± 2.0°C.

2.3.2 Chick growth

We used aerial photography to identify areas of suitable breeding habitat and systematically searched these areas on foot for active nests. Upon discovering an active nest, we recorded its coordinates using hand-held Global Positioning Systems and floated eggs in water to determine the extent of embryo development (Rizzolo and Schmutz 2007). We used estimated embryo age (i.e., the number of days of incubation) to calculate a predicted hatching date for each nest assuming a 26-day incubation period and 48-hour hatching interval for eggs within a typical 2-egg clutch (Barr et al. 2000). We began capturing chicks using mist nets floated horizontally on the surface of the breeding lake (Okill 1981) 10 days after hatching, when chicks were able to effectively dive to avoid predators. We attempted to capture all active chicks at approximately weekly intervals until fledging to collect morphometric data (Dzubin and Cooch 1992). We marked each chick with a uniquely numbered metal tag attached to the webbing of its foot. Morphometric data included body mass (± 1 g), length of exposed culmen (± 0.5 mm), length of diagonal tarsus (± 0.5 mm), folded-flattened wing length (± 1 mm), and length of the outermost primary feather (± 1 mm). We determined fledging dates by visiting most brood lakes every 2 days late in the brood rearing period to count the chicks present on the lake. Absent any sign of depredation at the brood lake (e.g., carcass or feathers), we considered a chick that disappeared from the brood lake after the earliest documented age of fledging (38 days; Barr et al. 2000) to have fledged.

2.3.3 Daily energy expenditure

We measured daily energy expenditure (DEE, kJ d^{-1}) in each of the 2 years using the doubly labeled water (DLW) technique (Lifson and McClintock 1966, Nagy 1980, Butler et al. 2004). In each year, we selected broods for inclusion in the DLW study using random selection stratified by brood size (1 or 2 chicks). We attempted to measure the DEE of each chick on 3 occasions during the postnatal period, at approximately 10 days, 28 days, and 38 days post-hatching, to capture nonlinearities in the association between DEE and body mass; however, we were not able to sample all chicks at these exact ages. We dosed chicks in the *pectoralis* muscle with a solution of DLW containing 65.2 atom percent excess (APE) oxygen-18 (^{18}O) and 35.4 APE Deuterium (^{2}H). Dose volumes varied in relation to chick body mass and ranged from 0.2 mL to 1.5 mL DLW. We measured doses on an electronic balance (± 0.002 g) and weighed the syringe used to inject the DLW immediately before and after the injection to correct for any residual solution remaining in the syringe. Prior to administering the dose, we collected a background blood sample to determine naturally occurring levels of ^{18}O and ^{2}H in the blood of each chick (method 'A' in Speakman and Racey 1987). After DLW dosing, we held chicks for 1 hour for equilibration of the isotopes into the body water pool (Król and Speakman 1999, Visser et al. 2000), after which we collected an initial blood sample and returned chicks to their brood lake. We recaptured chicks 48 hours after the initial blood sample to collect the final blood sample for calculating rates of change in ^{18}O and ^{2}H concentrations. Samples were collected as close as possible to 48 h after the initial sample to minimize circadian effects (Speakman and Racey 1988). Measurements were made across two days to minimize the potential day to day variability in DEE (Speakman et al. 1994, Berteaux et al. 2014). We collected blood samples from the medial metatarsal vein by venipuncture into 6–10 untreated microhematocrit tubes each filled with 10–15 µL of blood and immediately flamed-sealed and stored tubes at 5° C. In addition, we collected ~20 µL of blood from each chick into an Eppendorf tube containing Longmire buffer for genetic determination of sex (Guzzetti et al. 2008). We collected morphometric data during each DLW capture and at age ~ 21 days.

Concentrations of ^{18}O and ^{2}H in blood samples were determined by isotope ratio mass spectrometry (IRMS) using methods described by Speakman and Król (2005). Blood samples were vacuum distilled into glass Pasteur pipettes (Nagy 1983) and the water obtained was used for determination of ^{2}H:^{1}H and ^{18}O:^{16}O ratios. The enrichment of ^{2}H was determined from hydrogen gas produced by online chromium reduction of water (Morrison et al. 2001). For analysis of the ^{18}O enrichment in blood samples, water distilled from blood was equilibrated with CO_2 gas using the small sample technique (Speakman et al. 1990). IRMS determination of ^{2}H:^{1}H and ^{18}O:^{16}O ratios was done using isotopically characterized gases of H_2 and CO_2 in the reference channels of the IRMS. Four subsamples of each blood sample were analyzed and average values of enrichments were used for calculations. Injectate enrichment was determined by serial dilution with tap water and IRMS analysis of 5 subsamples of each DLW solution used (Speakman 1997). All isotope enrichments were measured in per mil (δ) relative to working standards and converted to parts per million using the established ratios for these reference materials.

We calculated DEE using Speakman's eq. 7.17 (Speakman 1997) that assumes ^{2}H and ^{18}O dilute into a single dilution space and a fixed evaporation of 25% of the water flux. This equation has been validated in precocial chicks (Visser and Schekkerman 1999). We estimated percent body water pool (i.e., total body water, %TBW) using the dilution space of ^{18}O and the plateau technique (Speakman 1997, Mata et al. 2006). We converted rates of CO_2 production (mol d^{-1}) to DEE (kJ d^{-1}) by assuming an energy equivalent of 27.33 J mL^{-1} for a diet comprised primarily of fat and protein (Gessaman and Nagy 1988), as is the piscivorous diet of Red-throated Loons (Barr et al. 2000).

2.3.4 Statistical analyses

2.3.4.1 Growth

To quantify the growth of each morphometric, we limited the analysis to chicks captured on ≥ 4 occasions for measurements. We selected the growth model that best fitted data for each morphometric. Candidate growth models for each morphometric included the Gompertz, the logistic, the von Bertalanffy (Ricklefs 1967), and the Janoschek (Gille and Salomon 1995). These models express a sigmoidally shaped relationship between the morphometric and chick age.

The Gompertz, logistic, and von Bertalanffy models differ with regard to the placement of the inflection point of the curve, which corresponds to the day of maximum growth rate, relative to the asymptote (Ricklefs 1967). Other parameters in these models include asymptotic size (A, g), and growth rate constant (K, d^{-1}), which is the rate at which the slope of the curve changes with age and therefore is positively associated with growth rate. For both the Gompertz and logistic models, the parameter T estimates the age corresponding to the inflection point; in the von Bertalanffy model, T corresponds to the size at hatching. The Janoschek model includes 4 parameters: size at hatching (W_0), asymptotic size (A), age at which 50% of asymptotic size is reached (t_{50}), and a shape parameter (p; Gille and Salomon 1995). We fit the Janoschek model to data from each morphometric with W_0 set to the hatchling measurements of Davis (1972; n = 11 hatchlings: body mass = 55 g, tarsus length = 26.1 mm, culmen length = 9.9 mm), or from 2 hatchlings opportunistically measured at our study site (wing length = 23.9 mm, outermost primary length = 0 mm). For body mass, we compare our estimate of growth rate constant to that predicted using Ricklefs' (1979) equation based on 190 species representing all modes of development.

For each morphometric, we selected the growth model with the lowest Bayesian Information Criteria (BIC; Schwarz 1978) value and compared the strength of support for candidate models from the data based on posterior model weights (Link and Barker 2006). We used multilevel, non-linear, mixed-effects models (Sockman et al. 2008) fitted in the NLMIXED procedure of Program SAS (SAS 2009) to examine the association between growth curve parameters and sex and chick brood status: first-hatched "senior", second-hatched "junior", or solitary "singleton" chicks. Singleton chicks either hatched from clutches with a single egg, or resulted from partial depredation during incubation or chick rearing. Multilevel models estimate non-linear model parameters and examine variation in these parameters in relation to explanatory variables. We examined variation in growth parameters of the non-linear growth models (e.g., model parameters A, K, and T) that were most supported by the data for each morphometric. For each morphometric, we included a model that permitted each parameter to vary with "sex," a model that allowed each parameter to vary with "status," and a model that allowed each parameter to vary with both "sex" and "status" as additive effects; we included a random "individual" effect on A in all models to account for repeated measurements on chicks. We used

BIC posterior model weights to select the model that best described sources of variation in growth curve parameters for each morphometric.

2.3.4.2 Daily energy expenditure

We estimated the power curve relating DEE to body mass using a linear mixed-effects model. We $\log_{10}$ transformed both DEE and body mass and included “individual” as a random effect in all models to account for repeated measurements on chicks. We examined how the relationship between DEE and body mass varied with sex and chick status by including “sex” and “status” in models as interactions with “mass.” We did not include “sex” and “status” main effects because we assumed all chicks share a common intercept value, but may differ in the slope of the relationship between DEE and body mass. We fitted models that included “sex” and “status” independently and in combination, as well as a model that included only “mass” and based model selection on BIC posterior model weights.

2.3.4.3 Energy requirement

We determined the average metabolizable energy requirement of a Red-throated Loon chick based on the logistic growth model relating body mass to chick age and the power model relating DEE to chick body mass. We calculated daily metabolizable energy (ingested food energy minus excretory energy, DME, kJ day^{-1}; Weathers 1992) as the daily sum of DEE (kJ d^{-1}) at age-specific body masses and retained energy (RE, kJ g^{-1} d^{-1}) deposited as daily gains in body mass. We estimated body tissue energy (TE, kJ g^{-1}) based on measurements of %TBW of chicks using dilution of ^{18}O and the plateau method (Speakman 1997, Mata et al. 2006). We did not collect chicks to measure whole body composition in the laboratory and instead assumed the water fraction of lean tissue (w, %) changed during postnatal growth according to the equation: $w = 79.86 - 9.55 \times$ proportion of adult body mass attained (Schekkerman and Visser 2001). For adult body mass, we used average adult body mass adjusted for sex differences (1614 g), average male adult body mass (1741 g), and average female body mass (1424 g; body masses from n = 40 adults captured from the study population). We calculated percent lean body mass as the quotient of %TBW and w, and percent fat mass as 100 − percent lean body mass. We used lean and fat fractions to calculate the energy content of tissue assuming energy equivalents of 5 kJ g^{-1} fresh mass for lean tissue and 38 kJ g^{-1} fresh mass for fat (Weathers 1996).

We determined the relationship between the mass-specific tissue energy content of chicks and chick body mass using a linear mixed effects model that included “individual” as a random effect. We summed DME from hatching to the average age at fledging (49 days) to determine total metabolizable energy (TME, MJ chick^{-1}) for the postnatal period. We compared our estimate to that predicted by the equation of Weathers (1992; eq. 8) to examine the hypothesis that Red-throated Loon chick TME was higher than predicted given their body mass and the length of their postnatal period.

We determined the amount of energy a chick needed to ingest to meet its DME given the inefficiencies of energy assimilation (i.e., daily energy intake, DEI, kJ day^{-1} chick^{-1}) using estimates of assimilation efficiency (AE, proportion of ingested energy assimilated) from Common Loon chicks fed trout (*Oncorhynchus mykiss*; Fournier et al. 2007). Estimated assimilation efficiency of Common Loon chicks at 32% and 53% of the age of asymptotic body mass increased from 0.64 to 0.83 (Fournier et al. 2007). We applied these AE estimates to Red-throated Loon chicks by assuming an incremental increase in AE from 0.64 to 0.83 between ages 10 and 17 days (32% and 53% of the age of asymptotic body mass for Red-throated Loons, respectively). We summed estimates of DEI over the postnatal period to determine the total amount of energy a chick ingested to meet its TME demand (gross energy intake, GEI, MJ chick^{-1}). We made these calculations at the average values of DEE and body mass as well as at their lower and upper confidence limits to set a range of plausible values given the data (we report these as the "plausible range" of DME, TME, and GEI). We calculated the portion of the energy budget required for growth of tissue as the sum of RE and the energy used for biosynthesis divided by TME, assuming the cost of biosynthesis was 33% of RE (Ricklefs 1974).

As a heuristic exercise, we examined the influence of diet energy content on parental foraging effort given the energy requirement we quantified for a Red-throated Loon chick. We calculated the number of fish required to meet chick DEI given a diet at either limit of the range of prey energy content we observed in chick diets. We observed both rainbow smelt (*Osmerus mordax*) and least cisco (*Coregonus sardinella*) provisioned to chicks by their parents in the present study population (D.J. Rizzolo, personal observation); these species also were fed to chicks on the Bering Sea coast of Alaska (Ball 2004). Least cisco is a relatively energy-rich species with an average energy density of 5.2 kJ g^{-1} wet mass (Ball et al. 2007), whereas rainbow smelt has a lower average energy density of 3.1 kJ g^{-1} wet mass (Ball et al. 2007).

The size of prey that a chick is able to ingest changes with age as chick body size increases; further, the energy content of fish also varies with fish body length. To account for these factors, we used chick age-specific fish sizes (mm wk^{-1}; Ball 2004) and fish length-specific estimates of energy content (kJ mm^{-1} length; Ball et al. 2007) to calculate the energy content of least cisco and rainbow smelt ingested by a chick between weeks 1 to 7 of the postnatal period. We assumed that once a chick reached the age when it consumed the maximum fish size observed (145 mm fish length at chick age 3 wk; Ball 2004), that parents continued to provision fish of this size for the remainder of the postnatal period. We then calculated the number of least cisco or rainbow smelt at chick age-specific fish sizes that would be required to meet the DEI of a chick for each day of the postnatal period. Given that each fish eaten by a chick represents an individual foraging trip that one parent must make, we believe this exercise will demonstrate the potential range of effect that diet energy content can have on adult provisioning effort given chick energy demands.

2.4 Results

2.4.1 Growth

We measured 36 chicks (20 female, 16 male) from 25 broods (12 pairs of siblings, 13 singletons). We knew with certainty the hatching date of 22% of the chicks we measured and calculated the hatching date of 16% based on the observed hatch date of their sibling, assuming a 48-hour hatching interval; we estimated hatching date using egg flotation for the remaining 62% of chicks. We captured chicks an average of 6 times during the postnatal period (range: 4–9 times) for 228 measurements that occurred 7–50 days post-hatching. Average length of the postnatal period, from hatching to fledging, was 49 days (range: 42–55 days, n = 17). All chicks included in the analysis survived to fledging or were still active when last checked (minimum age of 40 days when last observed). The average interval between the last capture occasion for a chick and fledging was 6 days (range: 1–14 days).

The nonlinear growth model most supported by the data varied by morphometric measurement (Table 2.1). Body mass, tarsus length, and wing length grew at the fastest rates and were best described by the logistic model, while slower growth of the culmen and primary feather were best described by the von Bertalanffy model (Fig. 2.2). The estimated logistic growth rate constant for body mass (K = 0.16, 95% CI: 0.15, 0.17) was 57% greater than the allometric prediction (0.10; Ricklefs 1979). Lengths of the culmen, wing, and primary feather at fledging were all below model-predicted asymptotic size and all morphometric measurements other than tarsus length were less than adult size at fledging (Fig. 2.2). Variation in growth of body mass and tarsus length was associated with sex of the chick (posterior model weights for models including "sex" = 1.0; Table 2.2); chick status was unrelated to growth for any morphometric (posterior model weights for all models including "status" = 0.0; Table 2.2). Male asymptotic body mass was 23% heavier and tarsus length was 8% longer than female measurements due to males growing at a similar rate to females, but for a slightly longer duration (Table 2.3).

2.4.2 Daily energy expenditure

We measured DEE of 25 chicks (10 male, 15 female) from 18 broods (7 pairs of siblings, 11 singletons). Average (± 1 SD) duration of the DEE interval was 48.3 h (± 3.9 h). We were able to measure DEE on 3 occasions within the postnatal period for 16 chicks, on 2 occasions for 7 chicks, and on 1 occasion for 2 chicks. Chicks not sampled on all 3 occasions either were depredated, entered the study late to replace depredated chicks, had failed DLW injections, or could not be located at the time of recapture during a given sampling occasion. The average age of chicks was 12 days (range: 8–19 days) at the early sampling occasion, 30 days (range: 23–34 days) at the middle sampling occasion, and 40 days (range: 33–47days) at the late sampling occasion. We did not sample chicks younger than 7 days old and instead extrapolated outside of the data from age of the youngest chick sampled for DEE to age 1 day. Of the 25 chicks sampled for DEE, 22 successfully fledged, 2 chicks were depredated, and 1 was still alive when last checked. The average age at fledging for sampled chicks was 49 days (range: 43–55 days).

Average (± 1 SD) levels of ^{2}H and ^{18}O in background blood samples were 152.3 ppm (± 2.1 ppm, n = 25) and 1987.1 ppm (± 6.1 ppm, n = 25), respectively. Estimates of %TBW based on ^{18}O dilution space declined with chick body mass (g) as described by the linear equation with estimated parameters (±1 SE): $\%TBW = 76.8\ (\pm 1.17) - 0.0097\ (\pm 0.0014) \times \text{body mass}$. DEE varied with chick body mass (g) according to the equation: $DEE = 11.89\ (\pm 3.6) \times M^{0.65\ (\pm 0.05)}$ (Fig. 2.3). Variation in DEE was not explained by "sex" or "status." The model that included only "mass" was most supported by the data (posterior model weight = 0.98), and had much more support from the data than the next best model that included "status" (posterior model weight < 0.02). Thus, we found no evidence that sex or chick status had effects on DEE independent of body mass.

2.4.3 Energy requirement

Estimated energy content of chick tissue based on %TBW measurements increased with chick body mass (g) according to the linear equation estimated with parameters (±1 SE): tissue energy (kJ g^{-1}) = 6.6 (± 0.46) + 0.0015 (± 0.0005) × body mass. DME peaked at 1214 kJ (plausible range: 1094–1339 kJ) at 25 days (Fig. 2.4). This value represents the maximum DME per chick that parents had to meet through their combined provisioning effort. DME values over an average postnatal period length (49 days) summed to a TME of 48.9 MJ (plausible range: 44.8–52.9 MJ). This empirical estimate based on DEE and RE measurements is 22% greater than TME estimated based on fledging body mass and length of the postnatal period (40.2 MJ; Weathers 1992; eq. 8), but is within the range of error of the predictive equation. DME values adjusted for age-specific assimilation efficiency summed to a GEI of 58.6 MJ (plausible range: 53.8–63.4 MJ), which is the amount of energy parents provisioned as food over the course of the postnatal period to meet a chick's TME requirement. When calculated based on sex-specific body mass growth curves and estimates of RE, the TME of males was 12% greater than females (male: 52.0 MJ; female: 46.4 MJ). Based on average DEE and body mass, chicks allocated 20% of TME for the synthesis and accumulation of tissue during growth and used the remaining 80% to meet the combined costs of resting metabolism, dietary thermogenesis during digestion, thermoregulation, and activity (Fig. 2.4).

Assuming chick diet was composed entirely of energy-rich least cisco, adults would need to provision an average of 8.9 fish day^{-1} (range: 3.0–10.6 fish day^{-1}) to meet the daily energy requirement of 1 chick, or in total 438 fish over the entire postnatal period (Fig. 2.5). In contrast, assuming chick diet was composed entirely of lower energy content rainbow smelt, parents would need to provision an average of 17 fish day^{-1} (range 5.8–20.4 fish day^{-1}), or in total, 842 fish over the postnatal period. The average difference in the number of fish required to meet chick daily energy requirement between these fish species was 8.2 fish day^{-1} (range: 2.7–9.8 fish day^{-1}). Every extra fish represents 1 additional foraging trip parents would be required to make.

2.5 Discussion

During the postnatal period, Red-throated Loon chicks gained body mass at a rate that was higher than predicted given their asymptotic body mass, and metabolized an amount of energy similar to that predicted given their asymptotic body mass and length of their postnatal period. High growth rate and near-average energy requirement were unexpected given the semiprecocial mode of development and use of aquatic habitat of this species, as well as the high latitude climate of the study site. Although growth rate for body mass was high, asymptotic body mass and sizes of all morphometrics, other than tarsus length, were less than those of adults. Thus, chicks had not completed growth before fledging. Rapid growth to a size at fledging that was less than adult size reduced the length of the postnatal period.

Variation in Red-throated Loon chick growth was most related to the sex of the chick, but not chick status. The effect of sex on chick growth was apparent in the asymptotic size of both body mass and tarsus length. Sexually dimorphic body mass consequently raised the TME of males by 12% compared to females. A difference in energy requirement between male and female chicks may affect parental provisioning effort (Harding et al. 2009) and chick growth performance (Daunt et al. 2001, Laaksonen et al. 2004), particularly when energy intake is limited.

The absence of an effect of chick status on growth or DEE indicates parents provisioned both chicks in their brood with adequate energy to support equivalent patterns of growth and energy expenditure. In contrast, Ball (2004) found growth in Red-throated Loon body mass, culmen length, and tarsus length was less in junior chicks compared to senior and singleton chicks at a site on the Bering Sea coast in years when the availability of energy-rich prey was low (Ball et al. 2007). Compared to our results, average body mass at fledging was 17% lower and sizes at fledging of all other morphometrics were smaller by 4–10% in the Bering Sea study (Ball 2004). The availability of energy-rich prey may underlie this difference in growth performance. During the Bering Sea study, chicks were provisioned low-to-moderate energy species of fish and no junior chicks survived to fledging (Ball 2004). In the present study, relatively high-energy least cisco were frequently fed to chicks and over half of broods that survived to fledging included 2 chicks (D.J. Rizzolo, personal observation).

Red-throated Loon chicks gained body mass at a rapid rate. Common Loon chicks also gain body mass rapidly, with a logistic growth rate constant (0.09 day^{-1}) that was 27% greater than predicted by the Ricklefs (1979) equation (0.07 day^{-1}; Fournier et al. 2007). In Red-throated Loons, the logistic growth rate constant for body mass gain was even higher, 57% greater than predicted. Thus, although Red-throated Loons are semiprecocial with a high degree of functional maturity at hatching, their body mass growth rate was similar to that of an altricial species of similar size.

The rate of postnatal growth in Red-throated Loons raises the question: why grow so fast? Rapid growth as a mechanism to reduce predation risk during the postnatal period (Lack 1968, Case 1978, Remeš and Martin 2002) seems unlikely given that chick survival in Red-throated Loons is high after the first week post-hatching when chicks are most vulnerable (Ball 2004). A limited ice-free season on breeding lakes is another potential explanation; however, the duration of the ice-free summer throughout most of its range is substantially longer than the total time required for incubation and chick rearing (Walsh et al. 1998). Further, Red-throated Loons nest sympatrically in portions of their range above 70° N latitude with Yellow-billed Loons (*Gavia adamsii*), which need more than 100 days to hatch and fledge their young (North 1994), suggesting that a seasonal constraint on fledging time was unlikely even prior to the current pattern of climate warming in the Arctic (Hinzman et al. 2005).

An important consequence of rapid growth is the reduction in chick TME that results both from decreasing the length of the postnatal period and having a low body mass at fledging (Weathers 1992). Rapid growth reduces chick TME because growth rate and postnatal period length are positively correlated (Ricklefs 1968). Most energy expenditure late in the postnatal period is related to maintenance, activity, and thermoregulation, thus shortening the postnatal period reduces the sum of these costs (Weathers 1992). Further, fledging at a body mass that is less than that of adults reduces TME because resting metabolic rate increases with body mass (Drent et al. 1992, Klaassen and Bech 1992). The trade-off to reducing TME by increasing growth rate is an increased peak daily energy requirement; however, peak daily energy demand increases with growth rate at a lesser rate than TME decreases (Weathers 1992). Thus, growing fast and fledging small makes a fledgling energetically less expensive to produce, but requires a high daily energy intake to achieve.

The Red-throated Loon is the only species of loon that provisions chicks exclusively by flying between brood-rearing habitat and separate foraging habitat (McIntyre 1994). Consequently, brood-rearing adults incur the cost of flight during provisioning, which is likely high given their high wing loading (Lovvorn and Jones 1994). In addition to reducing chick TME, a low postnatal asymptotic body mass may enable chicks to optimize their wing loading for flight (Wright et al. 2006) and fledge before flight feather growth is completed. After chicks fledge from natal habitat to the sea, parents no longer incur provisioning flight costs. In this respect, Red-throated Loons are similar to seabirds that also must leave their chicks to forage in the marine environment. The chicks of high-latitude breeding seabirds, specifically species in the family Alcidae, fledge across a broad range of body sizes (15–100% of adult size), and ages (25–60 days; Sealy 1973; Ydenberg 1989). Achieving postnatal asymptotic body mass relatively quickly and at a size less than adults are likely adaptations to reduce adult provisioning effort.

The costs of thermoregulation in the chicks of some species breeding at high latitudes are substantial and evident in high rates of energy metabolism. Semiprecocial Fulmarine petrel (family Procellaridae) chicks at 68° S latitude had TME values 33–73% greater than predicted (Hodum and Weathers 2003). TME in precocial, self-feeding shorebird chicks at 73–75° N latitude was elevated 89–107% above predicted values (Schekkerman et al. 2003, Tjørve et al. 2007). These species grew rapidly, but contrary to the inverse relationship between length of the postnatal period and TME shown by Weathers (1992), had exceptionally high rates of energy metabolism, in part due to the high costs of thermoregulation. We predicted Red-throated Loon chicks would have a similarly high postnatal TME; however, we found TME was not substantially elevated given their adult body mass and length of postnatal period. Thus, despite residing in cold-water lakes and experiencing low operative temperatures, Red-throated Loon chick TME was near its predicted value.

To achieve energy efficiency during the postnatal period, Red-throated loon chicks may limit their energy expenditure behaviorally. Parents brood young chicks frequently for the first several days after hatching (Barr et al. 2000). Brooding reduced the energy requirement of Arctic Tern (*Sterna paradisaea*) chicks by 26% during the first 10–11 days of their postnatal period (Klaassen et al. 1989) and 19% during the first 16 days in Black-legged Kittiwakes (*Rissa tridactyla*; Gabrielsen et al. 1992). Throughout the postnatal period, loon chicks regularly rest onshore with one parent (Barr et al. 2000), thus reducing the time spent on water. As chicks grow, they gain the thermoregulatory benefits of increased body mass (Calder 1974, Visser and Ricklefs 1993, Williams et al. 2007) and complete juvenal plumage. Further, because Red-throated Loon chicks do not forage for themselves, they can reduce their activity in response to periods of low energy intake. Thus, in Red-throated Loons, adaptations to growth in an aquatic, high-latitude environment do not include a high TME. Instead, chicks apparently have the flexibility to moderate energy demand behaviorally because they are parent-fed and benefit from reduced thermoregulatory costs of rapidly increased body mass.

In Red-throated Loons, parents provision the energy required to meet chick DME over the postnatal period, thus provisioning effort is closely coupled with chick DME and the energy density of prey. The energy content of food is less important when chick daily energy requirements are low and thus more easily met (Degen et al. 1992). However, a high growth rate for body mass increases peak daily energy requirements (Weathers 1992). Breeding success of piscivorous marine birds is often correlated with prey quality and availability (Springer et al. 1986, Litzow et al. 2002, Wanless et al. 2005, Piatt et al. 2007). Our provisioning rate estimates correspond with observed provisioning rates (9–23 trips d^{-1} across studies, average 13.9 trips d^{-1}; Davis 1972, Reimchen and Douglas 1984, Eberl and Picman 1993) and demonstrate that the number of fish per day a chick requires to meet its daily energy demand differed greatly between fish species at opposite ends of the spectrum of prey energy content. At the peak DME, parents provisioning lower energy content rainbow smelt would be required to make twice as many foraging trips per chick than would parents provisioning higher energy content least cisco. If the upper limit on fish required per chick at peak DME corresponds with a ceiling on adult provisioning effort (Drent and Daan 1980), then provisioning higher energy content least cisco would permit successfully fledging both chicks in the brood, whereas access to only lower energy content rainbow smelt would result in brood reduction. We found the combined DME of both chicks in a 2-chick brood exceeds the DME of a single chick at 10 days post-hatching, given the observed difference in growth rate of the junior and senior chicks through the first 14 days of growth (-63%; Ball 2004). Consistent with this, brood reduction in Red-throated Loons is typically observed between 10–14 days post-hatching and is often attributed to the starvation of the junior chick (Gomersall 1986, Okill and Wanless 1990, Eberl and Picman 1993, Ball 2004).

Hypotheses explaining patterns of growth in chicks include energy limitation (Ashmole 1963, Lack 1968, Case 1978), diet composition (Roby 1991), tissue level constraints (Ricklefs 1983, Ricklefs et al. 1994), and seasonal peaks in energy availability (Sedinger and Raveling 1986, Lepage et al. 1998, Schekkerman et al. 2003). Here we describe a pattern in growth that is best explained in relation to parental investment in chicks. In Red-throated Loons, which are a high wing-loading species, rapid growth and low fledgling body mass reduce the adult provisioning period by reducing the total energy requirement of the chick and thus the total number of provisioning trips required of parents. Total energy demands of chicks are reduced at the expense of increased daily energy demands. We show that given chick diet composition, chick daily energy requirements are more easily met when adults select prey with high-energy content. Under these circumstances, variation in the availability of high-energy prey should exert a strong influence on reproductive success. Accordingly, Red-throated Loon productivity is highly variable and often low (Rizzolo et al. 2014). However, the life history strategy of the Gaviidae emphasizes high adult survival over fecundity (Nilsson 1977, Evers 2004, Grear et al. 2009, Schmutz 2014) and can accommodate years of low productivity without causing population decline. Thus, natural selection should favor patterns of chick growth and energy allocation that increase adult survival even at the expense of chick survival.

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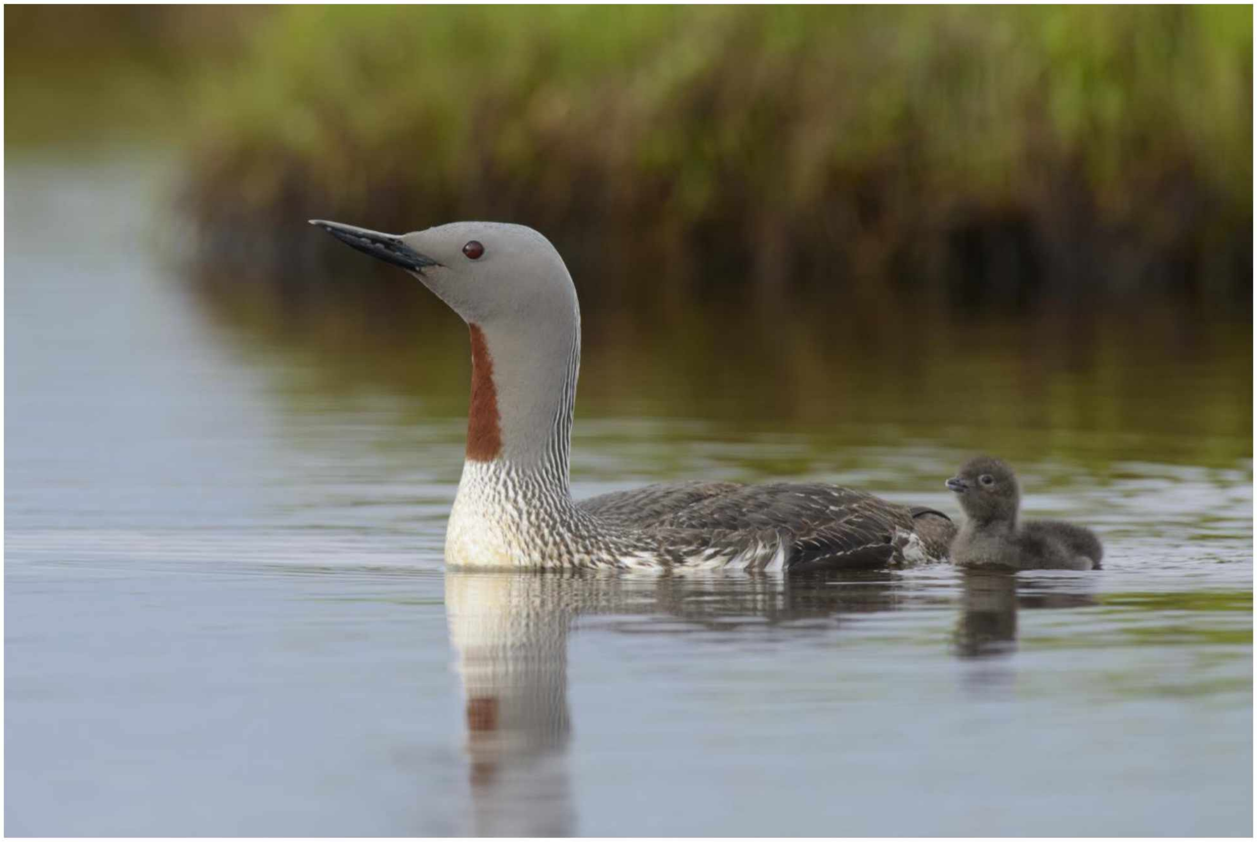


Figure 2.1 A parent Red-throated Loon (*Gavia stellata*) with its chick. Photo credit: Gerrit Vyn.

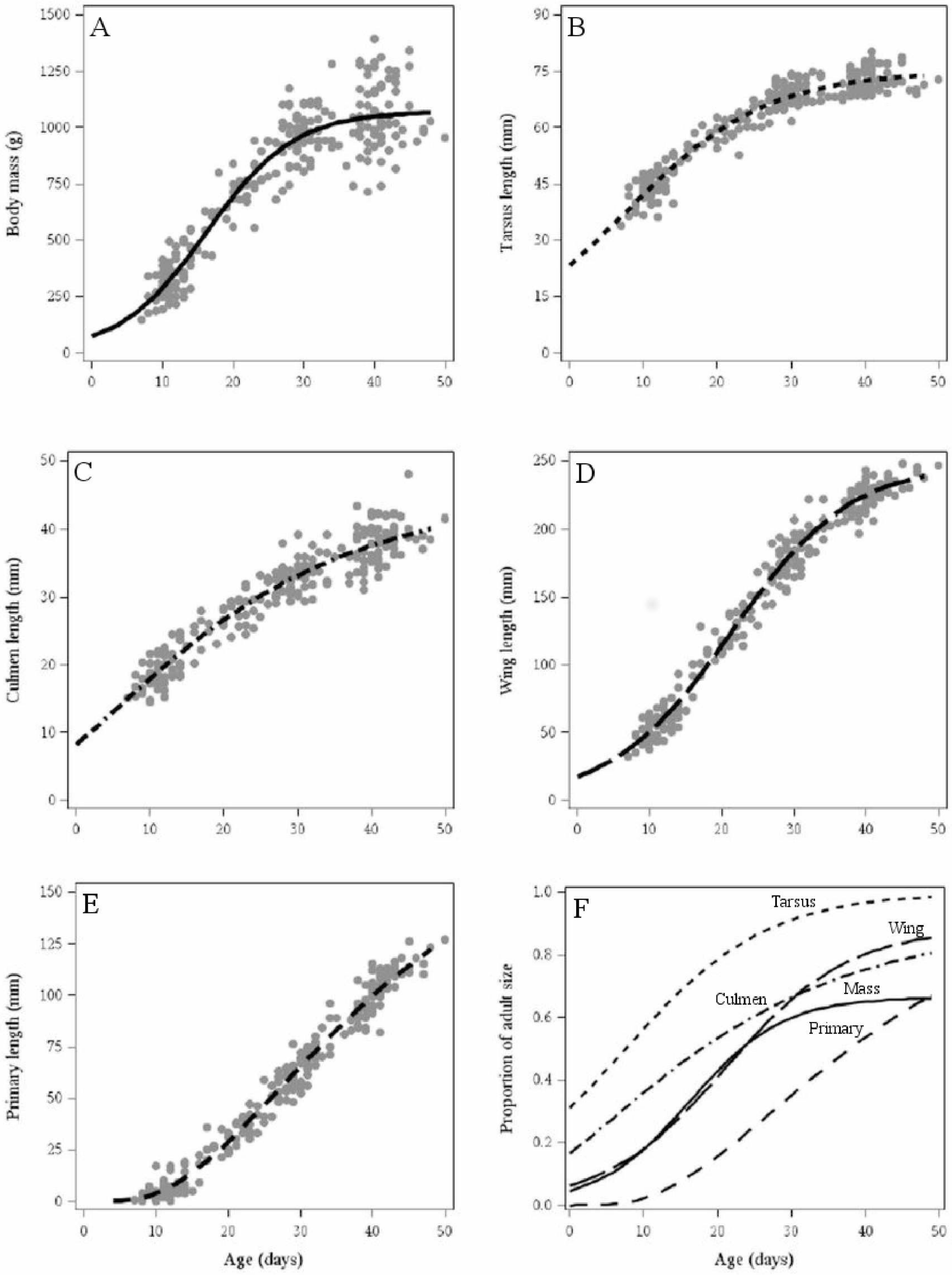


Figure 2.2 Growth plots. Measurements of (A) body mass, (B) tarsus length, (C) culmen length,

Figure 2.2 cont.

(D) wing length, (E) outer-most primary feather length, and (F) all morphometrics as proportion of adult size in relation to age of Red-throated Loon chicks from Point Lay, Alaska in 2009 and 2010. Lines are estimates from the best-fitting growth model for each morphometric. Measurements are from 36 chicks from 25 broods.

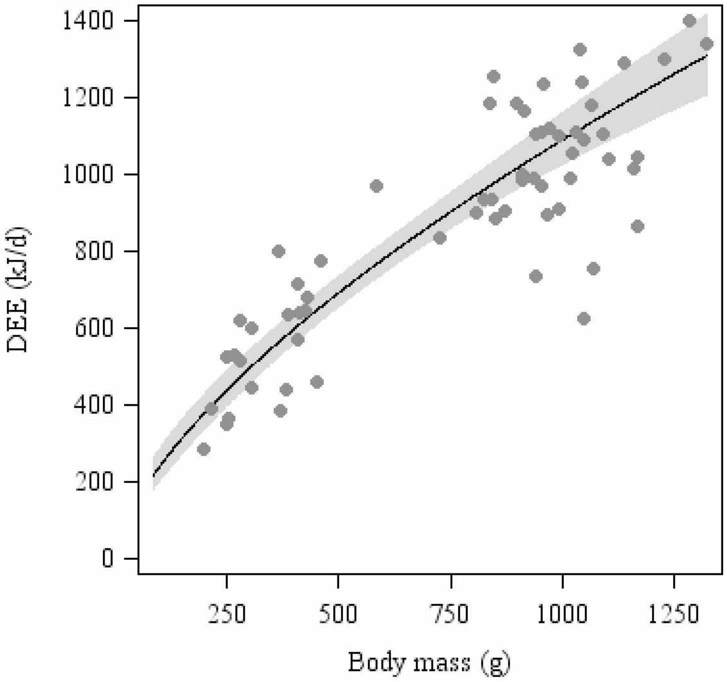


Figure 2.3 Daily energy expenditure (DEE). DEE in relation to body mass during postnatal growth in Red-throated Loon chicks from Point Lay, Alaska in 2009 and 2010. Points are DEE measurements (66 measurements from n = 25 chicks) with the fitted mean (line) and 95% confidence interval (shaded area).

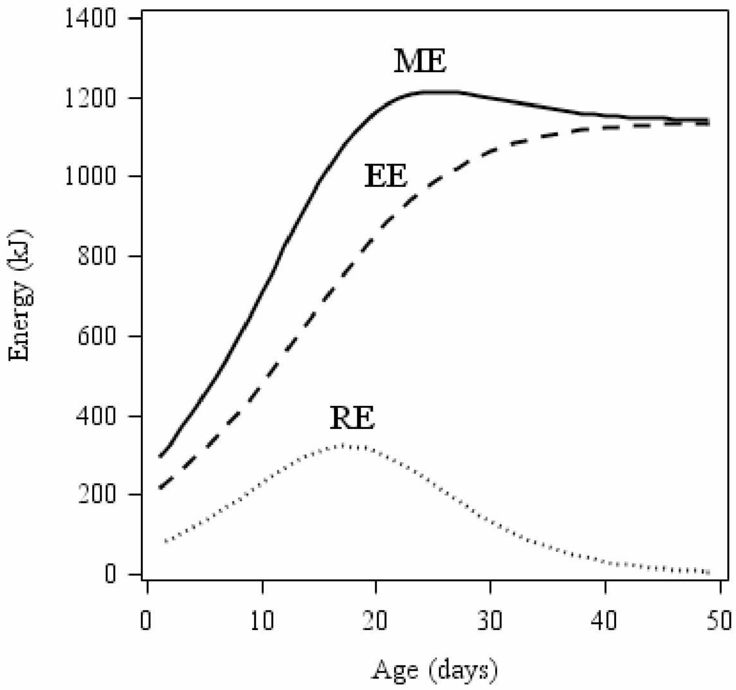


Figure 2.4 Energy budgets. Energy budgets of Red-throated Loon chicks from Point Lay, Alaska in 2009 and 2010, growing at the average growth rate for body mass from hatching to the average age of fledging. Estimates of metabolizable energy (solid line; ME, kJ d^{-1}), shown partitioned into its components: energy expenditure (dashed line; EE, kJ d^{-1}), and retained energy of new tissue (dotted line; RE, kJ d^{-1}) for each day of the postnatal period.

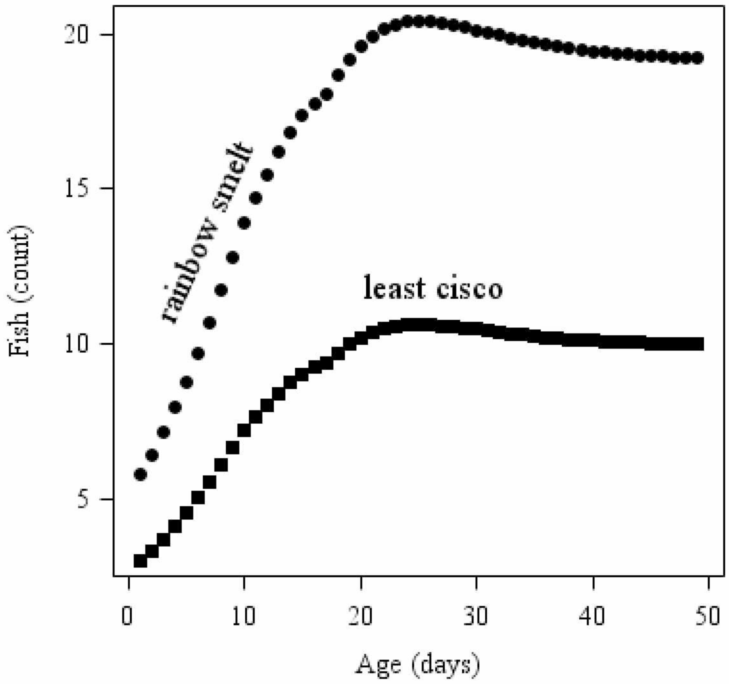


Figure 2.5 Fish intake. Daily intake of a high-energy content forage fish species (squares; least cisco, *Coregonus sardinella*) and a lower energy content species (circles; rainbow smelt, *Osmerus mordax*) required to meet the daily metabolizable energy requirement of a Red-throated Loon chick during the postnatal period.

Table 2.1 Growth model results. Best-fitting nonlinear models and associated parameter estimates (95% confidence intervals) describing growth of body mass (g), tarsus length (mm), culmen length (mm), wing length (mm), and primary feather length (mm) of Red-throated Loons from Point Lay, Alaska in 2009 and 2010. Bayesian Information Criterion posterior model weights (BICw_i) indicate strength of support for the model from the data relative to the other models considered with values closer to 1.0 indicating stronger support. Model parameters include asymptote (A), growth rate constant (K, d^{-1}), and inflection point (T, d) for all models other than the von Bertalanffy for which T is size at hatching (T, mm).

Morphometric	Model	BIC w_i	A	K	T
Mass	Logistic	0.81	1071 (1025, 1118)	0.161 (0.148, 0.173)	16.3 (15.8, 16.8)
Tarsus	Logistic	0.85	74.8 (73.5, 76.1)	0.105 (0.098, 0.111)	7.6 (7.2, 7.9)
Culmen	von Bertalanffy	0.57	45.4 (43.4, 47.5)	0.049 (0.044, 0.054)	16.9 (14.5, 19.3)
Wing	Logistic	0.63	247.5 (241.9, 253.2)	0.121 (0.117, 0.126)	21.2 (20.8, 21.7)
Primary	von Bertalanffy	0.99	186.4 (171.3, 201.4)	0.044 (0.041, 0.048)	-2.9 (-3.9, -1.9)

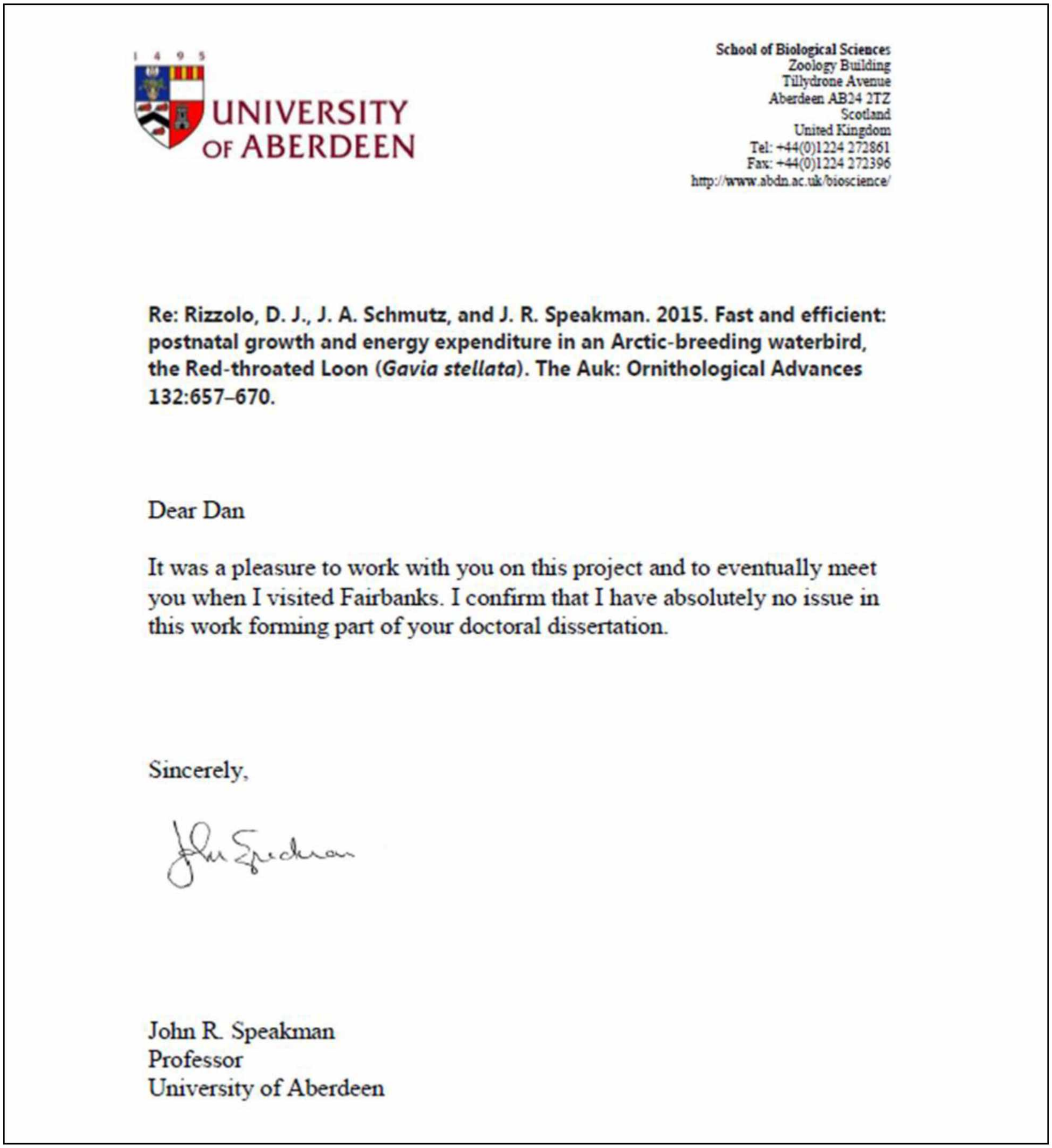
Table 2.2 Growth model selection results. Ranking of multilevel nonlinear mixed effects models used to examine variation in parameters describing growth in Red-throated Loons from Point Lay, Alaska in 2009 and 2010. Models with Bayesian Information Criterion (BIC) posterior model weights (BICw_i) close or equal to 1.0 were more strongly supported by the data.

Morphometric	Model	k	Deviance	BIC	BIC w_i
Mass	SEX	8	2620.3	2663.7	1.00
	Null	5	2657.8	2684.9	0.00
	SEX + STATUS	14	2621.0	2697.0	0.00
	STATUS	11	2655.2	2714.9	0.00
Tarsus	SEX	8	990.5	1033.9	1.00
	Null	5	1023.5	1050.7	0.00
	SEX + STATUS	14	981.2	1057.2	0.00
	STATUS	11	1017.3	1077.0	0.00
Culmen	Null	5	836.2	863.4	0.98
	SEX	8	827.8	871.2	0.02
	STATUS	11	824.3	884.0	0.00
	SEX + STATUS	14	808.7	884.7	0.00
Wing	Null	5	1611.1	1638.3	0.99
	SEX	8	1604.5	1648.0	0.01
	STATUS	11	1607.1	1666.9	0.00
	SEX + STATUS	14	1599.9	1675.9	0.00
Primary	Null	5	1349.8	1376.9	0.99
	SEX	8	1342.3	1385.7	0.01
	STATUS	11	1339.9	1399.7	0.00
	SEX + STATUS	14	1334.5	1410.5	0.00

Table 2.3 Growth parameters. Logistic model parameter estimates (95% confidence intervals) for body mass and tarsus length growth in male and female Red-throated Loon chicks from Point Lay, Alaska in 2009 and 2010.

		Estimates	
Morphometric	Parameter	Male	Female
Body mass	A	1202 (1143, 1260)	975 (928, 1022)
	K	0.15 (0.14, 0.17)	0.17 (0.15, 0.19)
	T	17.3 (16.6, 18.1)	15.4 (14.8, 16.0)
Tarsus	A	78.5 (76.5, 80.2)	72.3 (71.0, 73.7)
	K	0.10 (0.09, 0.11)	0.11 (0.10, 0.12)
	T	8.2 (7.7, 8.6)	7.1 (6.7, 7.6)

Appendix 2.1. Permission from co-author John Speakman to include manuscript in the dissertation.



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Re: Rizzolo, D. J., J. A. Schmutz, and J. R. Speakman. 2015. Fast and efficient: postnatal growth and energy expenditure in an Arctic-breeding waterbird, the Red-throated Loon (*Gavia stellata*). The Auk: Ornithological Advances 132:657–670.

Dear Dan

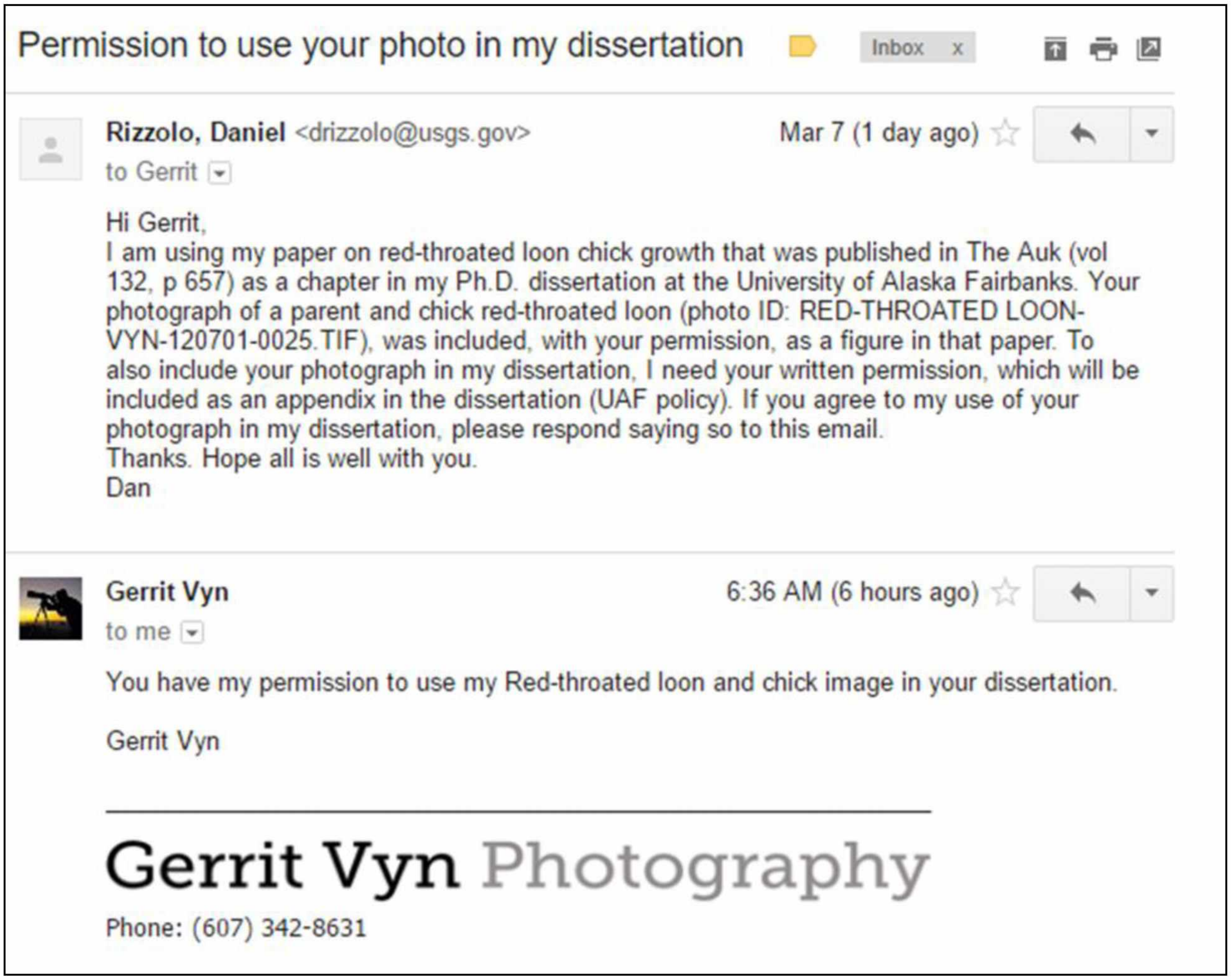
It was a pleasure to work with you on this project and to eventually meet you when I visited Fairbanks. I confirm that I have absolutely no issue in this work forming part of your doctoral dissertation.

Sincerely,

John Speakman

John R. Speakman
Professor
University of Aberdeen

Appendix 2.2. Permission from Gerrit Vyn to include his photograph as Figure 2.1 in the dissertation.



Permission to use your photo in my dissertation

Rizzolo, Daniel <drizzolo@usgs.gov>
to Gerrit

Mar 7 (1 day ago)

Hi Gerrit,
I am using my paper on red-throated loon chick growth that was published in The Auk (vol 132, p 657) as a chapter in my Ph.D. dissertation at the University of Alaska Fairbanks. Your photograph of a parent and chick red-throated loon (photo ID: RED-THROATED LOON-VYN-120701-0025.TIF), was included, with your permission, as a figure in that paper. To also include your photograph in my dissertation, I need your written permission, which will be included as an appendix in the dissertation (UAF policy). If you agree to my use of your photograph in my dissertation, please respond saying so to this email.
Thanks. Hope all is well with you.
Dan

Gerrit Vyn
to me

6:36 AM (6 hours ago)

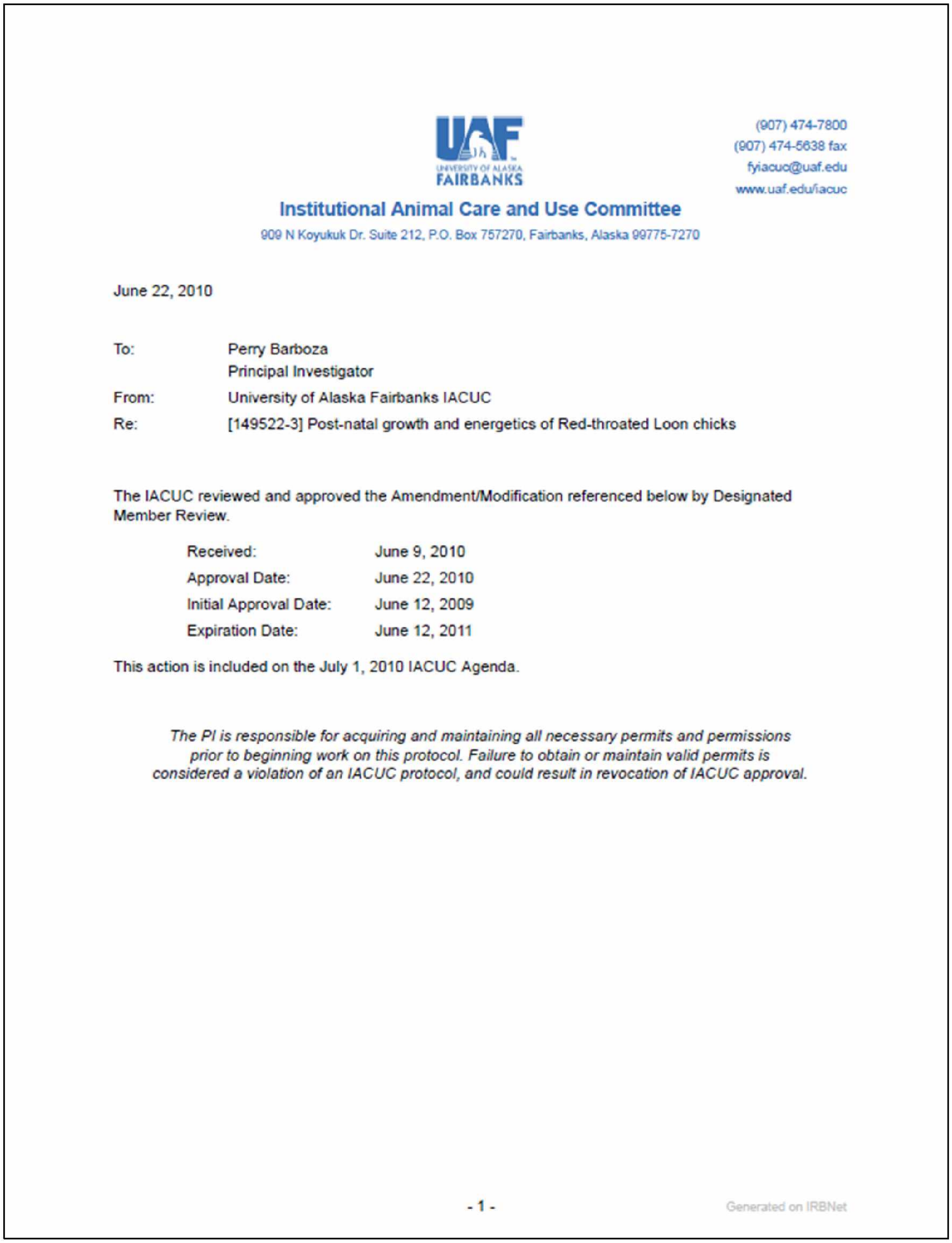
You have my permission to use my Red-throated loon and chick image in your dissertation.

Gerrit Vyn

Gerrit Vyn Photography

Phone: (607) 342-8631

Appendix 2.3 Institutional Animal Care and Use Committee approval from the University of Alaska Fairbanks for loon chick studies, 2009–2010.



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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 22, 2010

To: Perry Barboza
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [149522-3] Post-natal growth and energetics of Red-throated Loon chicks

The IACUC reviewed and approved the Amendment/Modification referenced below by Designated Member Review.

Received:	June 9, 2010
Approval Date:	June 22, 2010
Initial Approval Date:	June 12, 2009
Expiration Date:	June 12, 2011

This action is included on the July 1, 2010 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

CHAPTER 3

CONTRASTING ENERGY PROVISIONING RATES AND BREEDING SUCCESS IN SYMPATRIC LOONS[3]

3.1 Abstract

Sympatric Pacific Loons (*Gavia pacifica*) and Red-throated Loons (*G. stellata*) raise young on lakes throughout the Arctic, but their provisioning behaviors are markedly different. To examine the hypothesis that differences in provisioning are associated with differences in reproductive success, we quantified provisioning rates and chick production rates in Pacific and Red-throated loons breeding in Arctic Alaska. Both species had low egg survival probabilities in 2 of the 3 years (Pacific Loon average [lower, upper 95% confidence limit] = 0.48 [0.18, 0.78]; Red-throated Loon average = 0.61 [0.33, 0.90]). Chick survival was higher in Red-throated (average = 0.99 [0.94, 1.0]) than Pacific loons (average = 0.68 [0.42, 0.93]) in all 3 years. Pacific Loon broods were provisioned almost entirely (96%) freshwater invertebrates, while Red-throated Loon broods were provisioned marine fishes. In both species, provisioning rates were higher for 2-chick broods than 1-chick broods. Pacific Loon provisioning rate increased with lake surface area, suggesting invertebrate abundance increased with lake size. Red-throated Loon provisioning rate decreased with distance from the marine coast; however, most (67%) breeding lakes were within 2 km of the coast where provisioning rates were high. Estimates of maximum energy provisioning rates for broods demonstrated that Red-throated Loons could more easily meet peak brood energy requirements than Pacific Loons. Thus, lower survival of Pacific Loon chicks was associated with lower maximum energy provisioning rates. The apparent coupling of Red-throated Loon chick survival with the availability of marine forage fishes suggests that their population dynamics are influenced by changes in ocean climate that affect fish communities. Reliance on lower-quality, but abundant, freshwater prey by Pacific Loon chicks supported levels of chick production sufficient to maintain a stable population trend. Their reliance on different prey types makes sympatrically breeding Pacific and Red-throated loons sensitive indicators of changes in lentic and marine habitats in the Arctic.

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[3] Rizzolo, D.J. and J.A. Schmutz. 2017. Contrasting energy provisioning rates and breeding success in sympatric loons from the Arctic. Prepared for submission in The Auk: Ornithology Advances.

3.2 Introduction

The rate at which adult birds provision young varies with prey abundance (Cairns 1987, Piatt et al. 2007), the ease of capturing and handling prey (Lifjeld and Slagsvold 1988), the nutritional value of available prey (Wright et al. 1998), and limits on adult provisioning effort (Drent and Daan 1980). Closely related species may use different foraging behaviors to exploit available prey resources within the same habitat type (MacArthur 1958). Consequently, differences in provisioning behavior and prey choice may affect reproductive success (Lance and Roby 1998, Gall et al. 2006).

Pacific Loons (*Gavia pacifica*) and Red-throated Loons (*G. stellata*) are closely related species of waterbirds with broadly overlapping breeding and non-breeding distributions (Barr et al. 2000, Russell 2002). Both species are common on coastal tundra habitat throughout much of the Arctic and Subarctic, but differ in the size of lakes they use for breeding and in their foraging behavior (Davis 1972, Bergman and Derksen 1977). Pacific Loons are larger-bodied (average body mass 2.2 kg) than Red-throated Loons (average body mass 1.6 kg) and use breeding lakes to forage for themselves and their chicks (Bergman and Derksen 1977, Petersen 1989, Kertell 1996). Pacific Loons in coastal habitat may also use nearshore marine habitat for foraging (Andres 1993), but the importance of marine resources to breeding adults and growing chicks is poorly understood (Andres 1993, Kertell 1996). Red-throated Loons use very small, often fishless, lakes for breeding, and do not forage in their breeding lakes. Typically, Red-throated Loons forage in nearshore marine habitat both for themselves and their brood, which they provision with a single fish captured during each provisioning trip and carried back to the brood in their bill (Reimchen and Douglas 1984, Eriksson et al. 1990).

Habitat use and foraging behaviors are important to understanding how resource availability may influence population dynamics in these congeneric species that frequently breed on adjacent lakes. Red-throated Loon numbers on coastal tundra breeding habitat in Alaska have fluctuated dramatically over the past 3 decades, including a > 50% decline between 1976 and 2001 (Groves et al. 1996, Mallek and Groves 2011, Stehn et al. 2013). In contrast, Pacific Loons are more abundant and have had a stable population trend over the same period and in the same habitat (Mallek and Groves 2011, Stehn et al. 2013). Use of different prey to raise young may contribute to these divergent population trends (Ball 2004, Ball et al. 2007, Rizzolo et al. 2014, 2015).

To better understand how differences in resource use may underlie population-level differences in sympatrically breeding loons, we quantified breeding success, provisioning behavior, and chick diet composition of Pacific and Red-throated loons at a site on the Arctic Coastal Plain of Alaska. We hypothesized that in coastal tundra habitat, Pacific Loons would have the behavioral flexibility to provision their brood with both freshwater and marine prey, insulating them from changes in prey availability in one or the other habitat. The reliance of Red-throated Loons on marine prey may closely couple their populations with changes in the marine environment that affect the availability of fishes. We predicted that differences in brood provisioning behavior and diet composition between species would lead to disparate chick production rates. We used estimates of chick provisioning rates and the energy content of prey species observed fed to chicks, to calculate maximum energy provisioning rates for both species. To examine how energy provisioning may influence breeding success, we compared maximum energy provisioning rates to the maximum brood energy requirements of each species.

3.3 Methods

3.3.1 Study site

We conducted this study near the village of Point Lay, Alaska (69° 44'N, 163° 00'W) on the Chukchi Sea coast of the Arctic Coastal Plain, during three consecutive summers, June to September 2008–2010. The habitat at the study site is dominated by thermokarst with abundant lakes ranging in size from 0.02–130 ha. Small (0.02–0.80 ha) lakes are numerous and occur in association with river deltas, tundra polygons, and drained thermokarst lake basins (Jorgenson and Shur 2007). The main vegetative communities at the site are tussock-sedge, dwarf-shrub, and moss (Gallant et al. 1995). The Arctic Coastal Plain has a polar climate characterized by monthly average temperatures < 10°C throughout the year. The photoperiod at the study site, including civil twilight, is 24 hours from when loons arrive on the breeding grounds in early-June until mid-August, after which it declines to 17 hours in mid-September, when most loon chicks have fledged.

3.3.2 Breeding success

We systematically searched areas of suitable loon breeding habitat for active nests and broods throughout each summer. Upon finding a nest, we floated eggs in water to determine the extent of embryo development (Rizzolo and Schmutz 2007), and used estimated embryo age to predict the hatch date for each nest assuming a 26-day incubation period and 48-hour hatch interval for eggs within a typical 2-egg clutch. We periodically revisited breeding lakes to monitor the fates of eggs and chicks. We classified an egg as having survived the interval between visits during incubation if it was still present in the nest, or if it had hatched and a chick was present in the breeding lake. After hatch, any chicks still present up to the age of earliest potential fledging were considered fledged. Loon chicks leave the nest shortly after hatch, but remain in or near their natal lake for at least 42 days for Red-throated Loons (Barr et al. 2000), or 54 days for Pacific Loons (Russell 2002). Any egg missing before its predicted hatch date, or chick missing before its earliest fledging date, was classified as failed.

3.3.3 Brood observations

We randomly selected broods for provisioning observations from the sample of known active broods, stratified by species and brood size (1 or 2 chicks in the brood). We observed loon families from portable blinds setup within 100 m of brood rearing lakes, and conducted observations of each family over 3 days that were consecutive, unless interrupted by inclement weather. In 2008, observation sessions were 12 hours long and started at 08:00, 10:00, and 12:00 Alaska Daylight Savings Time (ADST) for each brood over the 3 days of observation. In 2009 and 2010, observation sessions were 8 hours long and started at 08:00, 12:00, and 16:00 ADST over the 3 days of observation. Occasionally, we stopped observations before we completed the session due to inclement weather or the presence of bears near blinds.

We used binoculars and spotting scopes to observe loon families. We recorded departure and arrival times for each trip away from the breeding lake made by a brood-rearing adult, but we did not include short trips during which adults immediately returned to the breeding lake or landed at an adjacent lake. For some broods, one or both adults were color-banded and we recorded the band combination of the departing adult. For non-banded individuals, we used the larger size of the male compared to the female to determine the sex of the departing adult. If observers could not determine the sex of the provisioning adult, sex was recorded as. Upon returning to the brood-rearing lake, we recorded whether the returning adult was carrying a fish in its bill, and if so, identified the fish species and recorded its size relative to the adult gape length (length from the tip of the bill to the corner of the mouth). If observers could not identify the species of fish provisioned, they recorded the species as unknown.

We recorded the brood provisioning behavior of Pacific Loons foraging in their breeding lakes using portable computers. We recorded the start and end times of brood provisioning behavior, the number of prey fed to the brood, the type of prey (invertebrates, fish, or unidentified prey), and the sex of the provisioning adult. Adults and chicks infrequently went out of the observer's view while provisioning. Typically, families were out of view when they entered dense vegetation to rest, after provisioning had clearly ended. Families sometimes, however, went out of view during provisioning bouts when, for example, they swam behind an island, or entered a cove not visible from the observation blind. In these instances, chicks were being provisioned when they went out of sight and were typically still being provisioned when they came back into the observer's view, thus we assumed that chicks were being provisioned continuously during time spent out of sight. We included the duration of time out-of-sight in provisioning time when calculating adult provisioning effort. We did not include time out-of-sight when calculating chick intake rates, because we could not count the number of prey items provisioned during this time.

To aid identification of prey species, we collected reference specimens of freshwater and marine fishes and invertebrates from the study area (Chapter 2). We identified species based on taxonomic keys in Mecklenburg et al. (2002) and invertebrates according to Smith (2001). We used reference specimens of marine fishes to train observers in the identification of species and estimation of fish size relative to gape length by attaching specimens to a loon decoy and viewing them through a spotting scope from 75 m away.

3.3.4 Statistical analyses

We examined sources of variation in all response variables of interest by composing sets of candidate statistical models. We drew inferences from candidate models based on posterior model weights calculated using Bayesian Information Criterion statistics (BIC, Schwarz 1978, Raftery 1995). Posterior model weights sum to 1.0 across a set of candidate models and quantify the amount of support for a given model from the data relative to the other models considered; as such, posterior model weights close to 1.0 indicate greater support for a model from the data (Link and Barker 2006).

3.3.4.1 Breeding success

We used egg and chick monitoring data to estimate daily survival probabilities of eggs and chicks. We used generalized linear mixed-effects models to relate the binomially distributed response variable (egg or chick alive, egg or chick failed) to explanatory variables using a logit link to obtain maximum likelihood estimates of parameters (Rotella et al. 2004, Stephens et al. 2005, Rizzolo et al. 2014). We included a unique breeding attempt identification variable as a random effect in models to account for the correlated fates of eggs within a clutch, or chicks within a brood. We confirmed that variance inflation factors ($\hat{c}$) calculated for our most parameterized models were ≤ 1.0, which provides a conservative assessment of model fit to the data (McCullagh and Nelder 1989, Burnham and Anderson 2002).

We conducted separate analyses for breeding stage (egg, chick) and species. We included a categorical variable for year (*year*) in all models to permit a temporal comparison of survival estimates. We included an indicator variable for days following researcher activity at nests or brood lakes (*observer*) to account for the effect of observation on egg and chick survival (Rotella et al. 2004), because loon breeding success is negatively associated with observer disturbance at the nest site (Rizzolo et al. 2014, Uher-Koch et al. 2015). Under this approach, observer effects on survival are accounted for in model estimates by inclusion of the observer parameter in the model (Rotella et al. 2004). Our candidate model sets included potential sources of within season variation: egg age and chick age as both linear and quadratic trends (*age*, age^2), and day of the season centered on median nest initiation date, as both linear and quadratic trends (*day*, day^2). For Red-throated Loons, we evaluated the effect of the distance from the breeding lake to the nearest marine coast in km (*distance*). For Pacific Loons, we examined the effect of lake surface area in hectares (*area*). Candidate model sets included all combinations of *age*, age^2, *day*, day^2, and lake covariates added to the *year* + *observer* base model. *Day* was not included in models of Pacific Loon egg or chick survival because of a high correlation with *age* (Pearson correlation, $r \geq 0.75$), thus we included only *age*.

To estimate survival over the entire breeding period, from nest initiation to chick fledging, we estimated daily survival probabilities from the combined dataset of eggs and chicks (Rizzolo et al. 2014). We included explanatory variables in the model that were supported in the separate analyses of egg and chick survival. We calculated productivity as survival over the breeding period × 2, assuming a clutch size of 2 for the population.

3.3.4.2 Provisioning behaviors

We examined food provisioning from both the perspective of the brood (intake rates) and brood-rearing adults (adult provisioning rates; Table 3.1). For Pacific and Red-throated loons, we summarized data from each observation session into counts of marine fishes provisioned to the brood to estimate *brood intake rate*. Using observations during which the sex of both adults was known, we summarized the total number of marine fishes provisioned by sex to estimate *adult provisioning rate*. We used all trips away from the brood-rearing lake with known departure and arrival times to estimate *trip duration*. We summarized the count of adult Pacific Loon departures from the brood-rearing lake by each member of the brood-rearing pair to estimate *adult lake departure rate*.

We calculated *freshwater prey intake rates* of Pacific Loon broods as the count of freshwater prey ingested by the brood divided by the total time the brood was in view and being provisioned during each observation session. To calculate *freshwater prey provisioning rate* by adults, we divided the count of freshwater prey each adult provisioned to the brood by the total time the brood was provisioned while in sight of the observer. We calculated the *proportion of time the brood was provisioned* by dividing the total time the brood was provisioned by the total duration of the observation session. For each adult in a pair, we also calculated the *proportion of time spent provisioning* by dividing the total time spent provisioning by the total time the brood was provisioned.

3.3.4.3 Statistical models

To obtain unbiased estimates of the provisioning rates of interest, we examined variation in provisioning response variables related to potentially influential explanatory variables (Table 3.2). To examine sources of variation in *brood intake rate* of marine fish provisioned to Pacific and Red-throated loon broods, and *adult lake departure rate* by Pacific Loons, we used generalized linear mixed-effects models (Bolker et al. 2009) with a Poisson distribution and natural logarithmic link to the data (Poisson mixed models), because the data consisted of counts of fish provisioned. All Poisson mixed models included the natural logarithm of the length of the observation session (in hours) as an offset to account for unequal observation session lengths. Each Poisson mixed model also included either a brood identification (for brood intake rate) or individual identification (for adult provisioning effort) variable as a random effect to account for repeated observations on broods or adults (Littell et al. 2006).

For Pacific Loons, we analyzed variation in *freshwater prey intake rates* of broods, *adult provisioning rate* of freshwater prey, *proportion of time the brood was provisioned*, and *proportion of time spent provisioning* by adults using linear mixed effects models (Littell et al. 2006), because Poisson mixed models fit raw count data poorly. We square root transformed *brood intake rate* and *adult provisioning rate* to better meet linear model assumptions of normal distribution and constant variance. *Proportion of time the brood was provisioned* and *proportion of time spent provisioning* by adults met linear model assumptions without transformation. Linear mixed effects models included either a brood identification variable or adult identification variable as a random effect to account for repeated observations on broods and individual adults.

For each provisioning response variable, we composed a set of candidate models that included explanatory variables potentially related to variation in that response variable (Table 3.1). Candidate model sets were composed of all combinations of the main effects of the explanatory variables of interest. We then used explanatory variables supported in the analysis of brood intake rates in models of adult provisioning rate with the addition of *sex* to test for differences in provisioning between males and females.

In all analyses, we ensured models fit the data by inspecting residual plots of linear models and examining deviance residual distributions for Poisson mixed models. We evaluated the effects of model explanatory variables and model-based estimates of response variables using parameter estimates and 95% confidence intervals. We present results as mean (lower 95% confidence limit, upper 95% confidence limit), unless otherwise stated.

3.3.4.4 Chick diet composition

We summarized the prey species composition of Pacific and Red-throated loon brood diets as the proportion of each prey type provisioned to the brood averaged over all broods with complete provisioning data. We converted estimates of the length of marine fishes provisioned to broods by multiplying the fish length, estimated in bill gape lengths, by the average adult gape length. To examine whether chicks consumed larger fish as they aged, we used a model that included covariates for chick age, fish species, and their interaction. We compared the fit of this model to a model including only fish species. We also fit a model with brood size to see if the average size of fish provisioned to chicks was larger for broods of two than broods of one.

3.3.4.5 Brood energy intake

We used our estimates of provisioning rates and the prey species we observed provisioned to broods to estimate maximum brood energy intake (DEI_{max}, kJ; Table 3.3). We used calculations of DEI_{max} to examine how easily brood peak energy requirements could be met given a range of prey energy content. For Pacific Loons, we used estimates of freshwater prey intake rate (I_f) of broods, proportion of time provisioned freshwater prey (P_f), and intake rate of marine fishes per day (I_m). We calculated DEI_{max} of broods using freshwater prey energy content values (E_f, kJ per item) and marine fish energy density values (E_m, kJ per fish) at 3 levels of diet energy content: (1) broods ingesting only low-energy freshwater prey (tadpole shrimp, order Notostraca), and (2) broods ingesting the average diet of 95.6% Notostraca and 4.1% ninespine stickleback (*Pungitius pungitius*), and (3) broods ingesting only ninespine stickleback (Table 3.3). In all 3 scenarios, the energy content of marine prey was held constant at the average value of fish observed in the marine component of Pacific Loon brood diets, as the average energy content of marine fish species in the diet estimated at the average observed lengths and weighted by their proportional contribution to the diet. Maximum daily energy intake of 1- and 2-chick Pacific Loon broods was calculated as:

$$DEI_{max}\ (\text{kJ/day}) = [(I_f \times P_f \times E_f) + (I_m \times E_m)] \times 24 \qquad \text{(Eq. 3.2).}$$

For Red-throated Loon broods, we calculated DEI_{max} using estimated values of the intake rate of marine fishes (I_m). We calculated DEI_{max} at 3 levels of diet energy content (E_m): (1) low-energy content rainbow smelt (*Osmerus mordax*), (2) the energy content of the average diet, and (3) high-energy content least cisco (*Coregonus sardinella*; Table 3.3). Maximum daily energy intake of Red-throated Loon broods was calculated as:

$$DEI_{max}\ (\text{kJ/day}) = I_m \times E_m \times 24 \qquad \text{(Eq. 3.1).}$$

To estimate the energy content of prey, we used equations relating total energy content to fish total length of marine fishes (least cisco; rainbow smelt; Arctic flounder, *Liopsetta glacialis*; saffron cod, *Eleginus gracilis*) from Ball et al. (2007), estimates of energy density (kJ per gram wet mass) of slender eelblenny (*Lumpenus fabricii*) and fourhorn sculpin (*Myoxocephalus quadriconis*) from Anthony et al. (2000), and energy content per gram dry mass of Notostraca from Davis and Smith (1998) (Table 3.4). Lipid content measured from fish and invertebrates collected at the study site were similar to lipid content in published measurements (Chapter 2); we assumed the ash-free lean dry matter content was also similar.

We compared DEI_{max} values to brood peak daily metabolizable energy estimates. For Red-throated Loons, pDME was measured in the study population (1214 kJ: Rizzolo et al. 2015). We used an allometric equation (Weathers 1992, eq. 12) to estimate Pacific Loon pDME (1583 kJ) assuming an asymptotic chick mass of 70% of adult body mass. Pacific Loon peak DME values were adjusted for assimilation efficiency using 0.775 for fish diets (a chick age-weighted average based on Fournier et al. 2007), 0.739 for invertebrate diets (Castro et al. 1989), and 0.774 for a diet composed of 96% fish and 4% invertebrates. Two-chick brood DEI_{max} was calculated as twice the value of single chicks.

3.4 Results

3.4.1 Breeding lakes

Loons used a diversity of lakes for breeding, ranging from small, water-filled thaw pits in ice-wedge polygon networks, to large lakes in drained thermokarst lake basins. Pacific Loons nested on lakes with a larger average surface area and nested on a broader range of lake sizes than Red-throated Loons (Table 3.5). For both species, breeding lakes were located near to the marine coast (Table 3.5); most breeding lakes (67%) were within 2 km of the coast.

3.4.2 Egg survival

We monitored the survival of 283 Pacific Loon eggs from 179 clutches over the 3 years of the study. Daily egg survival probabilities decreased with *age* ($\beta_{age} = -0.11$: -0.17, -0.06; *age* model posterior model weight 0.78; Table 3.6). Observer visits to monitor egg fate were associated with a decrease in egg survival ($\beta_{observer} = -2.10$: -3.05, -1.14). Egg survival until hatch was similar in all years (Fig. 3.1A): 2008 = 0.40 (0.04, 0.76), 2009 = 0.53 (0.27, 0.79), 2010 = 0.51 (0.24, 0.79).

For Red-throated Loons, we monitored the survival of 338 eggs from 204 clutches over the 3 years of the study. Daily survival probability of Red-throated Loon eggs decreased with *age* ($\beta_{age} = -0.14$: -0.08, -0.02; *age* model posterior model weight 0.93; Table 3.6). Observer visits were associated with decreased daily survival probability of eggs ($\beta_{observer} = -3.98$: -5.03, -2.91). The probability of an egg surviving to hatch (Fig. 3.1A) was highest in 2009 (0.84: 0.69, 0.99), while 2008 and 2010 had lower and similar egg survival (2008 = 0.45: 0.10, 0.84; 2010 = 0.53: 0.21, 0.86).

3.4.4 Chick survival

We monitored the survival of 96 Pacific Loon chicks from 78 broods over 3 years. Daily survival probability of Pacific Loon chicks increased with *age* ($\beta_{age} = 0.11$: 0.06, 0.15; *age* model posterior model weight 0.82; Table 3.6). Observer visits to check chick status were not associated with chick daily survival probability ($\beta_{observer} = -0.69$: -2.47, 1.09). Chick survival to fledging was similar between years: 2008 = 0.72: 0.48, 0.96; 2009 = 0.65: 0.39, 0.91; 2010 = 0.66: 0.39, 0.92; Fig. 3.1B). Of the 38 broods in which both eggs successfully hatched, 9 (24%) either fledged both chicks or had chicks that were still alive and older than 28 days when last checked.

For Red-throated Loons, we monitored the survival of 121 chicks from 91 broods over the 3 years of the study. Daily survival probability of Red-throated Loon chicks was high in all years and did not vary with any of the explanatory variables included in the model set. The base model *year* + *observer* was most supported by the data (posterior model weight 0.77). Parameter estimates showed no support for observer effects on chick daily survival probability ($\beta_{observer} = -0.69$: -5.66, 4.28). Chick survival was high and similar across years (2008 = 0.98: 0.90, 1.0; 2009 = 0.99: 0.97, 1.0; 2010 = 0.99: 0.96, 1.0; Fig. 3.1B). Of 42 broods in which both eggs hatched, 30 (71%) either successfully fledged both chicks or both were still alive and older than 28 days when last checked.

3.4.5 Productivity

Productivity rates for Pacific Loons were similar in all years (2008 = 0.60: 0.23, 0.97; 2009 = 0.51: 0.16, 0.86, 2010 = 0.57: 0.21, 0.94 chicks per pair; Fig. 3.1C). Productivity rates for Red-throated Loons were similar in all years (2008 = 0.79: 0.42, 1.16, 2009 = 1.06: 0.68, 1.44, 2010 = 0.95: 0.58, 1.31 chicks per pair; Fig. 3.1C), and higher than the rates of Pacific Loons.

3.4.6 Provisioning behavior

3.4.6.1 Brood intake rate

We conducted 516 hours of brood observation during 59 observation sessions of 25 Pacific Loon broods. Pacific Loon broods were provisioned almost exclusively from the breeding lake. During observation sessions, we recorded a total of 227 hours of freshwater brood provisioning. The average observation length was 8.8 ± 2 (SD) hours. Observed chicks ranged in age from 8 to 48 days old (average 25 ± 9 [SD] days). For Red-throated Loons, we documented all provisioning events during 52 observation sessions of 26 broods totaling 458 hours. The average observation length was 8.8 ± 2 (SD) hours. Observed chicks ranged in age from 6 to 44 days old (average 24 ± 10 [SD] days). We observed only marine fishes provisioned to Red-throated Loon broods.

Prey intake rate of Pacific Loon broods increased with lake area, but not brood size. The model *brood* and the model *brood + area* received similar support from the data (posterior model weights 0.23 and 0.24, respectively; Table 3.6). Prey intake rate was similar for broods with one chick (4.5: 3.4, 5.7 items per min) and 2 chicks (3.8: 2.6, 5.1 items per minute), and increased in association with lake area ($\beta_{area} = 0.02$: 0.001, 0.044). Across the range of lake sizes in the sample of observed breeding pairs, brood intake rate increased from a rate of 3.6 (2.5, 4.8) prey items per minute in lakes with a surface area of 0.68 ha to 8.1 (4.2, 13.2) items per minute in lakes with a surface area of 43 ha; intake at the mean lake surface area of 6.87 ha was 4.1 (3.1, 5.3.) items per min (Fig. 3.2). The surface area of most lakes in the sample (90%) was < 10 ha. At a lake area of 10 ha, provisioning rate was 4.4 (3.0, 5.3) items per minute. When data points from the 3 large lakes in the sample were removed, model estimates were not significantly different (intake rate at 10 ha lake = 5.8: 4.1, 8.0 items per minute).

Although prey intake rate was unrelated to brood size, Pacific Loon broods with 2 chicks were provisioned for 36% longer than broods with just one chick (proportion of time provisioned: 2-chicks = 0.53: 0.43, 0.62; 1-chick = 0.39: 0.32, 0.47). The base model that included only *brood* was most supported by the data (posterior model weight 0.29; Table 3.6). The model *brood + age* also received some support (posterior model weight 0.19; Table 3.6), but provided little evidence that provisioning time increased with chick age ($\beta_{age} = 0.5\times10^{-2}$: -0.6×10^{-3}, 0.01). The model *brood + pfish* received some support (posterior weight 0.11; Table 3.6), but provided no evidence that proportion of fish in the brood diet was associated with brood provisioning time ($\beta_{pfish} = -0.33$: -1.77, 0.27).

Pacific Loon parents delivered at least one marine fish during 31 of 58 observation sessions (17 out of 25 broods). Brood size was not related to marine fish provisioning rate (1-chick brood = 0.07: 0.03, 0.13; 2-chick brood = 0.10: 0.05, 0.20; *brood* model posterior model weight 0.49; Table 3.6). The models *area* and *brood* + *daylight* received some support from the data (posterior model weights 0.12 for both models; Table 3.6), but neither the effect of lake area (β_{lake} = 0.02: -0.02, 0.07), nor day length ($\beta_{daylight}$ = -0.15: -0.45, 0.13) were supported. The average rate of marine fish intake by a Pacific Loon brood was 0.08 (0.05, 0.13) fish per hour.

Fish intake rate of Red-throated Loon broods increased in association with brood size and proximity of the brood-rearing lake to the coast (Fig. 3.3). Two models explaining variation in brood intake rate received similar support from the data: the base model that included only *brood* (posterior model weight 0.35; Table 3.6), and the model *brood* + *distance* (posterior model weight 0.34; Table 3.6). Estimates from the brood size model indicate that broods with two chicks were provisioned at a rate 45% greater than broods with one chick (0.81: 0.64, 1.02 vs. 0.51: 0.40, 0.66 fish per hour, respectively). The *brood* + *distance* model indicated that brood provisioning rate decreased farther from the coast ($\beta_{distance}$ = -0.20: -0.434, -0.002). Across the range of distances from the coast at which we observed broods, average provisioning rate decreased from 0.80 (0.57, 1.02) fish per hour at 0.4 km to 0.28 (0.02, 0.54) fish per hour at 5.2 km from the coast. However, 97% of Red-throated Loon breeding lakes at which we conducted observations were 1.7 km or less from the coast. At the distance of 1.7 km, provisioning rate was 0.57 (0.41, 0.73) fish per hour. The *brood* + *distance* model provided similar estimates of provisioning rate by brood size at average distance (1.1 km) from the coast (2 chicks = 0.77: 0.59, 0.94; 1 chick = 0.53: 0.40, 0.66). Removing the 3 data points from far lakes (> 2 km) and refitting the model did not significantly change model parameter estimates (provision rate estimates at 1.1 km differed by < 2%).

3.4.6.2 Adult provisioning effort

Pacific Loon females provisioned 3.7 (2.9, 4.6) items per minute, while males provisioned at less than half that rate, 1.6 (0.9, 1.9) items per minute (n = 118 observations of 25 broods). Female Pacific Loons also provisioned the brood for over twice as much time as males (0.43: 0.38, 0.49; 0.21: 0.15, 0.27, respectively). Adults provisioned broods with 2 chicks (0.30: 0.22, 0.39) for a longer proportion of the observation than broods with only 1 chick (0.21: 0.15, 0.29). Adult provisioning time was not associated with chick age (β_{age} = 0.002: -0.003, 0.007). In contrast to the female-biased provisioning rate of freshwater prey, brood-rearing male Pacific Loons delivered marine fishes at a higher rate (0.06: 0.03, 0.10 fish per hour) than females (0.02: 0.01, 0.04 fish per hour; n = 58 observations of 24 broods). For Red-throated Loons, we found no difference in provisioning rate between males (0.31: 0.23, 0.41 fish per hour) and females (0.27: 0.20, 0.37 fish per hour; n = 82 observations of 42 broods).

3.4.6.3 Provisioning trip duration

Brood-rearing Pacific Loons departed rearing lakes 168 times (104 trips by males, 45 trips by females, and 19 trips by adults of unknown sex) during 57 observation sessions. Males departed the breeding lake more frequently than females; the model *sex* received the most support from the data (posterior model weight 0.56; Table 3.6). Female lake departure rate (0.08: 0.05, 0.12 departures per hour) was 58% lower than that of males (0.19: 0.14, 0.27 trips per hour). Models including *age*, *area*, and *distance* were not supported by the data (posterior model weights of all other models < 0.10). We measured the durations of 129 trips away from breeding lakes made by 36 adult Pacific Loons. Trip durations ranged from 10 min to 7.5 hours. Average trip duration was 58.9 minutes (48.4, 72.3) and did not vary with any of the covariates we considered (posterior model weight of null model = 0.99; Table 3.6).

We measured the durations of 457 trips away from breeding lakes made by 57 chick-rearing adult Red-throated Loons. Trip durations ranged from 6 min to 8.5 hours. The model *brood* + *distance* was most supported by the data (posterior model weight 0.51; Table 3.6); however, 95% confidence intervals around the effects of *distance* (β_{distance} = 0.07: -0.08, 0.21) and *brood* (β_{single} = 0.21: -0.03, 0.45) included zero. Trip duration was also unrelated to *daylight* (model *distance* + *daylight* posterior weight 0.22, β_{light} = -0.06: -0.13, 0.03) and *age* (model *distance* + *age* posterior weight 0.10, β_{age} = 0.01: -0.01, 0.02). Models including *sex* and *fish* were not supported by the data (posterior model weights of all other models < 0.04). The model estimated median trip duration was 38.2 min (33.4, 43.6 min).

3.4.6.4 Brood diet composition

The diet of Pacific Loon broods was composed of 93.6% invertebrates; only 2.1% were freshwater fishes, 0.2% were marine fishes, and 4% were not identified (Fig. 3.4). Most often, invertebrates provisioned to broods were too small to be identified; however, we did note that large Notostraca (*Lepidurus* arcticus) were a common type of prey. Sweep net samples of brood-rearing lakes collected mostly crustaceans, which we often encountered in high abundance. Larval Trichoptera (caddisfly) and adult Coleoptera (family Dytiscidae) also were present. We collected ninespine stickleback, threespine stickleback, and Alaska blackfish from lakes. The sizes of marine fishes provisioned to chicks were similar for 1-chick (101: 77, 131 mm) and 2-chick (98: 74, 129 mm) broods.

For Red-throated Loons, brood diet was composed of a diversity of marine fishes and was dominated by cisco and cod (Fig. 3.5). During observations, we identified species to order; however, during prey sampling we collected only 1 species from each order and assume these were the species fed to broods. We did not collect Pacific sand lance at Point Lay; however, this species is easily identified by its color and body shape. We found no evidence that the size of fish provisioned to Red-throated Loon broods increased with chick age (posterior model weight of species model 1.0). For Red-throated Loons, average fish length was larger for broods of 2 (163: 146, 180 mm) than broods of 1 (147: 132, 161 mm).

3.4.6.5 Energy provisioning

The estimated energy content of the average brood diet for Pacific Loons was similar to low-energy content prey (Table 3.3). Thus, meeting peak brood energy requirements given low- or average-energy density prey was difficult (Fig. 3.6). For 1-chick broods, maximum energy intake was 62% and 75% of brood requirements given a diet of solely low-energy content Notostraca, or the average diet of 95.6% invertebrates and 4.2% freshwater fish, respectively. Maximum energy intake of 2-chick broods decreased to 35% and 47% of the peak energy requirement of 2-chick broods given low- and average-energy content diets, respectively. In contrast, a diet composed of all ninespine stickleback provisioned at the observed rates would greatly exceed brood requirements. Marine fish species contributed 2–14% of the broods' energy requirements given the average energy content of marine fish observed in the diet and provisioning rates for marine fishes.

Maximum energy intake rates for Red-throated Loon broods exceeded, or nearly met, peak brood energy requirements given average- and high-energy content diets for both 1- and 2-chick broods (Fig. 3.6). Maximum energy intake given the low-energy content diet was only 47% and 37% of peak energy requirements for 1- and 2-chick broods, respectively. Given the provisioning rates estimated in this study, and the prey species we observed fed to broods, Red-throated Loon broods were able to achieve high rates of chick production. However, if the available prey are restricted to low-energy density species, our calculations indicate brood energy requirements would not be met and chick production rates would be low.

3.5 Discussion

Pacific and Red-throated loons nesting sympatrically in coastal tundra habitat had contrasting energy provisioning strategies. Pacific Loons provisioned small, energy-poor prey captured within the breeding territory, at a high rate. Red-throated Loons provisioned large, relatively energy-rich fish captured in marine habitat, at a much lower rate. Despite the close proximity to marine habitat, Pacific Loons made little use of marine prey to provision broods. These differences in brood provisioning behavior were associated with differences in breeding success. Red-throated Loon annual rate of chick production was higher than that of Pacific Loons.

Differences in chick production rates between the species were not consistently related to egg mortality during incubation, as egg survival was similar between species. Egg daily survival probability in both Red-throated and Pacific loons was negatively associated with egg age and observer activity at nests. Similarities in egg daily survival probability parallel similarities in the reproductive biology of these species with regard to nest site selection, clutch size, and incubation behavior: both species typically lay a 2-egg clutch on the shores of lakes and islands, and both sexes incubate and rarely leave the nest unoccupied, unless disturbed (Bundy 1976, Petersen 1989).

High abundance of small mammals in Arctic food webs may reduce predation on tundra nesting birds through frequency-dependent predation (Petersen 1979, Bêty and Gauthier 2002, Gauthier et al. 2004). Annual egg survival estimates were similar between species in 2008 and 2010, with just under half of all eggs surviving to hatch. Egg survival estimates diverged in 2009, when Red-throated Loon egg survival was high (84%) and Pacific Loon egg survival remained consistent at around 50%. This difference in egg survival may be related to a differential response to small mammal abundance at the study site. In 2009, tundra vole (*Microtus oeconomus*) apparent abundance increased markedly compared to 2008 or 2010. Further, in 2009 we anecdotally noted very high productivity of some common tundra nesting species (e.g., Long-tailed Duck *Clangula hyemalis*, Willow Ptarmigan *Lagopus lagopus*). Arctic foxes (*Vulpes lagopus*) and red foxes (*V. vulpes*), both present at the study site, are important predators on Red-throated Loon eggs (Bergman and Derksen 1977, Petersen 1979, Dickson 1993, Rizzolo et al. 2014), and Red-throated Loons may have benefited from the high tundra vole abundance we observed in 2009 through reduced egg predation by foxes that consumed voles rather than eggs.

Pacific Loon egg survival did not show a corresponding increase in 2009, although both species were exposed to the same potential nest predators. Consistent egg survival in Pacific Loons, even in the presence of high small mammal abundance, may have been due to plumage coloration (Haskell 1996). Plumage is more conspicuous in Pacific Loons than Red-throated Loons, and there is evidence that Parasitic Jaegers (*Stercorarius parasiticus*), an important nest predator, remember visual cues to nest locations to increase their predation success on loon nests (Enquist 1983).

In contrast to egg survival, annual chick survival of Red-throated Loons was 36–53% higher than that of Pacific Loons. Estimates of chick survival for Red-throated Loons were near 1.0 in all years. For Pacific Loons, just over half of chicks survived to fledge in each year and their chick daily survival probability was positively associated with chick age, which is consistent with increased size and functional maturity of chicks (Barr 1996, Rizzolo et al. 2015). Most Red-throated Loon pairs (71%) that hatched two eggs successfully raised both chicks to fledging. In contrast, few Pacific Loon pairs (24%) successfully fledged two chicks. Consistently higher chick survival led to higher productivity rates in Red-throated Loons compared to Pacific Loons in all years. Survival of dependent young requires sufficient energy intake to support growth and development (Weathers 1996), and adult attendance for brooding and predator defense, suggesting a difference in either energy provisioning or adult attendance may underlie these differences in chick survival (Bukacinski et al. 1998).

Red-throated Loons provisioned their broods exclusively with marine fishes, while Pacific Loons relied on freshwater invertebrates. Features of brood-rearing lakes were associated with provisioning rates in both species. Red-throated Loon broods were provisioned fewer fish as distance from the coast increased. Higher provisioning rates of Red-throated Loon broods located closer to foraging habitat have been associated with higher chick survival (Eberl and Picman 1993). We documented high chick survival and found no association between chick daily survival probability and distance to the coast, possibly because most (67%) breeding lakes were located within 1.7 km of the coast where provisioning rates were high.

Freshwater prey intake of Pacific Loon broods increased with lake surface area. Most lakes on the coastal margin of the Arctic Coastal Plain freeze completely in winter (Jeffries et al.

1996, Hinkel et al. 2012) and cannot support overwintering fish populations. Macrozooplankton (e.g., Anostraca, Diplostraca) abundance is high in small-sized Arctic lakes (Rautio and Vincent 2006), and invertebrate abundance is higher in lakes lacking fish (Mallory et al. 1994, Schilling et al. 2009). Thus, high brood provisioning rates of Pacific Loons likely reflect high abundance of invertebrate prey. Increased provisioning rate of freshwater prey with increasing lake area suggests that either invertebrate abundance (O'Brien et al. 2004) or capture efficiency increased with lake area.

The two loon species showed different patterns of investment in the brood by males and females in the brood-rearing pair. Provisioning rates were similar in male and female Red-throated Loons, while in Pacific Loons, provisioning effort was highly skewed toward the female. Prior studies of sex-specific provisioning behavior in Red-throated Loons have had mixed findings. In a small sample of Red-throated Loons breeding on Haida Gwaii Island, males and females had similar provisioning rates in the first 6 days following hatch, after which male provisioning rate decreased to less than half that of the female (Reimchen and Douglas 1985). However, similar to our study, males and females in Sweden had equivalent provisioning rates (Eriksson et al. 1990). Similar brood provisioning rates in males and females may be a reflection of high brood rearing costs (Jones et al. 2002) associated with central-place foraging behavior in a species with high flight costs (Lovvorn and Jones 1994). In Pacific Loons, Petersen (1989) also found evidence of female-biased provisioning in western Alaska. This difference was attributed to males requiring time to restore body condition lost during early incubation, when males spent more time incubating than females (Petersen 1989); however, body condition during incubation did not differ between males in females in this population (Chapter 1).

Both species adjusted provisioning behavior to brood size. Red-throated Loons raising two chicks provisioned their brood at a rate 45% greater than those with only one chick. Intake rate of Pacific Loon broods did not change in association with brood size; rather the parents spent more time provisioning broods of two than broods with only one chick. The provisioning rate for Red-throated Loon broods with two chicks was lower than found in previous studies in which estimates were 82–98% greater than rates for 1-chick broods (Eriksson et al. 1990, Eberl and Picman 1993). The provisioning rates we documented were associated with high Red-throated Loon chick survival, and, correspondingly, a high proportion of 2-chick broods that survived to fledging. Thus, Red-throated Loons were able to meet the higher energy demands of raising 2-chicks without a near doubling of provisioning rate. This suggests that the higher brood energy requirement of a 2-chick brood was met by increasing the size of fishes provisioned to chicks, or by selecting fish species with higher energy content. Consistent with this hypothesis, Red-throated Loons provisioned larger fish to broods of two than to broods of one.

Brood provisioning rates of Pacific Loons were associated with moderate chick survival (68%). Few broods, however, were able to successfully fledge 2 chicks, despite 2-chick broods being provisioned for 36% longer than 1-chick broods. Most chick mortality occurred early in brood-rearing, as indicated by the increase in chick survival with age. Lower chick survival may be due to the high proportion of time broods were provisioned, which potentially exposed young chicks to predators. Young Red-throated Loon chicks typically rest with an adult between provisioning events (Eberl and Picman 1993, Ball 2004), making them less visible to predators compared to Pacific Loon chicks that must follow provisioning adults in open water. Insufficient energy intake may have also contributed to chick mortality through starvation or compromised ability to detect and avoid predators (Hatch and Hatch 1990).

Our estimates of maximum brood energy intake rate demonstrated that the peak energy requirement of Pacific Loon broods were much harder to meet than those of Red-throated Loons, given the provisioning rates and prey types we observed. The maximum energy intake of Red-throated Loon broods provisioned the average diet was 98% and 78% of peak brood energy requirement for 1-chick and 2-chick broods, respectively. To fully meet these requirements, average energy content of prey would have to increase by only 2% (to 121 kJ per fish) for 1-chick broods, and 28% (to 152 kJ per fish) for 2-chick broods. Minor increases in energy content would be easily achieved given that fish energy content can increase rapidly with fish length (Ball et al. 2007, Anthony et al. 2000). Our estimates of the lengths of provisioned fish were coarse-scale given that provisioning events occurred quickly. Alternatively, brood peak daily energy requirements could also be reduced by slowing chick growth rate (Romano et al. 2006, Lyons and Roby 2011), as has been documented in western Alaska (Ball 2004) in years with apparently low energy availability (Ball et al. 2007). Chicks in the present study, however, had high growth rates (Rizzolo et al. 2015). High chick survival and 2-chick brood fledging rates indicate that Red-throated Loon broods received sufficient energy to meet their requirements at the study site during the years of this study.

The maximum energy intake rates of Pacific Loon broods were 75% and 47% of the estimated peak requirements for 1-chick and 2-chick broods, respectively. Peak brood requirements for 1-chick broods could be met by increasing the average energy content of prey from 0.48 kJ to 0.68 kJ, which corresponds to increasing the proportion of ninespine stickleback in the diet from 4% to 32%. For 2-chick broods, the average energy content of prey would have to increase from 0.48 to 1.1 kJ per prey item, which could be achieved by increasing the proportion of ninespine stickleback in the diet to 50%. Marine fishes composed a small component of the brood diet and as such, increases in the energy content and provisioning rate of marine prey would need to be unrealistically high (> 400%) to meet the peak energy requirements of 1-chick and 2-chick broods.

It is surprising that brood-rearing Pacific Loons did not provision more ninespine stickleback or marine fishes, given the high-energy content of these prey types. Ninespine stickleback are ubiquitous in lakes on the Arctic Coastal Plain, but must re-colonize shallow lakes during flooding caused by the spring thaw (Haynes et al. 2014), and so are likely in low abundance in shallow lakes. A low abundance of ninespine stickleback likely makes them a less profitable prey type compared to highly abundant invertebrates. Further, high flight costs associated with higher wing loading during flight (Storer 1958, Lovvorn and Jones 1994) may make central place foraging to marine foraging habitat unprofitable for Pacific Loons.

Boom or bust years of productivity are common for Red-throated Loons, ranging from near total failure (e.g., zero hatched nests during one year in western Alaska, Rizzolo et al. 2014), to very high chick production rates (e.g., 1.5 chicks per pair in Finland; Lokki and Kalevi 1984). Low availability of energy-rich prey in some years has been proposed as a mechanism for low chick survival in Red-throated Loons (Gomersall 1986, Ball 2004, Ball et al. 2007). Pacific Loons (Kertell 1996), and other loon species that breed on fishless lakes and provision chicks invertebrates (Common Loon: Gingras and Paszkowski 1999, Alvo 2009; Arctic Loon, *G. arctica*: Jackson 2003, 2005), have moderate-to-low chick survival rates. Limited energy availability likely precludes high chick survival rates in fishless lakes (Gingras and Paszkowski 2006). Our results for Pacific Loons are consistent with the limited productivity documented in these other loon species.

Pacific and Red-throated loons breeding sympatrically in Arctic Alaska relied on different prey resources to provision their young. Chick survival in these species was associated with the energy content of available prey in their respective foraging habitats. Thus, variation in prey availability in these foraging habitats has implications for chick survival. Variation in ocean climate (e.g., El Nino Southern Oscillation, Mysak 1986; Pacific Decadal Oscillation, Mantua et al. 1997) can dramatically and rapidly restructure marine communities (Anderson and Piatt 1999, Litzow 2006). Productivity of marine birds varies in association with the availability of energy-rich forage fish (Springer et al. 1986, Litzow et al. 2002, Wanless et al. 2005, Piatt et al. 2007). Variation in the availability of marine forage fishes has been evoked as a hypothesis explaining changes in Red-throated Loon abundance on Alaskan breeding grounds (Ball 2004, Ball et al. 2007, Rizzolo et al. 2014, 2015). Further, a link between adult survival and ocean climate may also contribute to Red-throated Loon population dynamics (Schmutz 2014). Thus, population dynamics in Red-throated Loons are apparently closely related to ocean conditions.

In contrast to the marine environment, shallow, high-latitude lakes, like those on the Arctic Coastal Plain, provide predictable and abundant invertebrate prey (O'Brien et al. 2004). Persistent fish populations are absent from shallow lakes, which permits high abundance and large body size of invertebrates (O'Brien et al. 2004). Thus, although freshwater invertebrates are small and energy-poor relative to fishes, they provide breeding Pacific Loons a reliable food resource capable of supporting moderate rates of chick survival in most years. Moderate, but consistent, productivity may explain the stable population trend of Pacific Loons on tundra habitats in Alaska (Larned et al. 2010, Mallek and Groves 2011). In all years of this study, Pacific Loon productivity estimates were above the level required to maintain a stable population trend (0.47 chicks per pair; Nilsson 1977).

Pacific and Red-throated loons breeding sympatrically in coastal tundra habitat may serve as indicators of change in their respective foraging habitats through changes in chick survival (Bergman and Derksen 1977). We found that marine prey comprised a small component of the overall energy intake of Pacific Loon broods, consistent with the findings from a site further east on the Arctic Coastal Plain (Kertell 1996). Frequent use of marine habitat by adult Pacific Loons (this study, Andres 1993) suggests that marine prey may be important to breeding adults during brood-rearing. Red-throated and Pacific loons breeding sympatrically meet brood energy requirements using prey captured in separate habitats that may respond differently to natural and anthropogenic change.

Lentic habitat (Mueller et al. 2009, Grosse et al. 2012, Alexeev et al. 2016) and marine habitat (Grebmeier et al. 2006, Grebmeier 2012) in the Arctic are undergoing unprecedented changes related to increasing global temperatures (IPCC 2013). The effects of these changes on the prey species used by breeding loons are unclear. Variation in marine conditions in the north Pacific Ocean formerly occurred over decadal time scales (Mantua et al. 1997). Increased variability in ocean climate may reduce prolonged periods of prey shortage for breeding Red-throated Loons, potentially stabilizing their population trend. Longer length of the open water season and increasing water temperature in Arctic lakes are increasing lake depth (Arp et al. 2015, 2016) and may make more lakes that froze completely in the past, deeper and suitable to support overwintering fish populations. Because of their territorial behavior on breeding lakes and the long life span of adults, loon population structure includes a cohort of non-breeding adults (Grear et al. 2009). Non-breeding adult Pacific Loons seeking breeding habitat may increase competition with Red-throated Loons as small lakes become deeper and suitable for overwinter fish populations. Monitoring chick survival of sympatrically breeding loons can serve as a valuable tool for elucidating changes in lentic and marine habitats of the Arctic.

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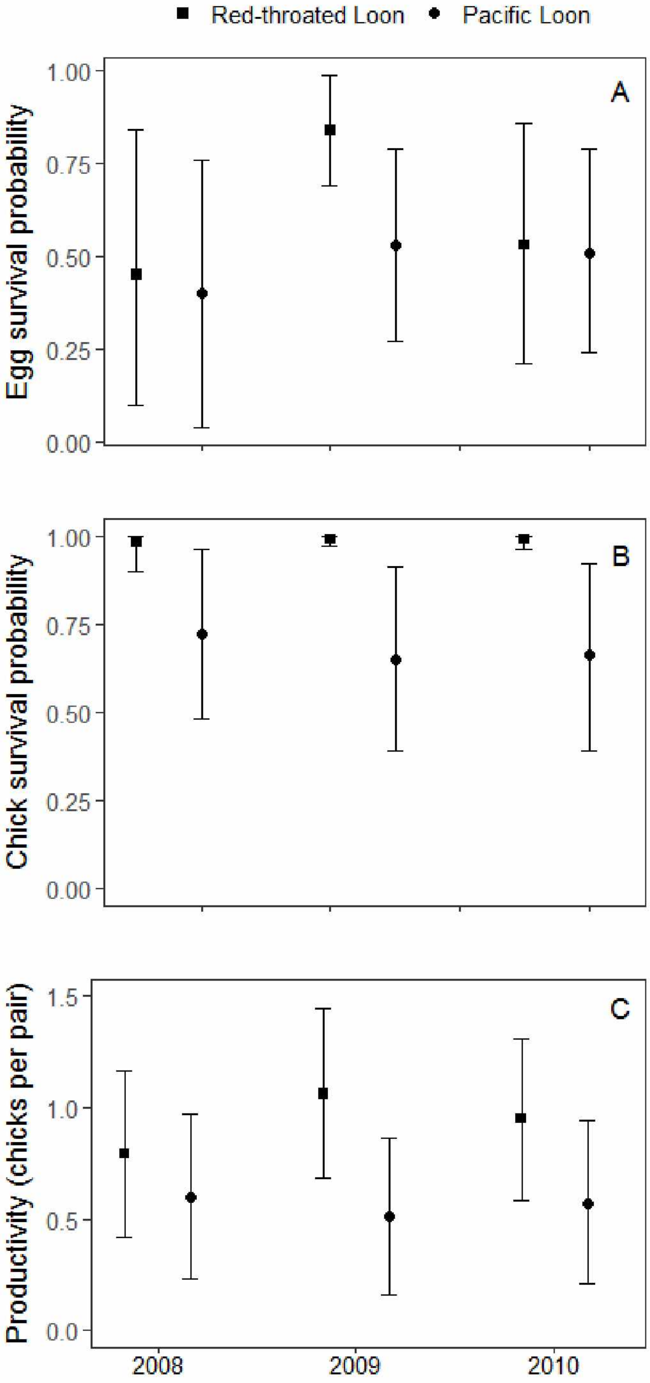


Figure 3.1 Estimates of breeding success. Annual estimates of (A) egg and (B) chick survival probability and (C) productivity for Pacific (circles) and Red-throated (squares) loons breeding near Point Lay, Alaska 2008–2010.

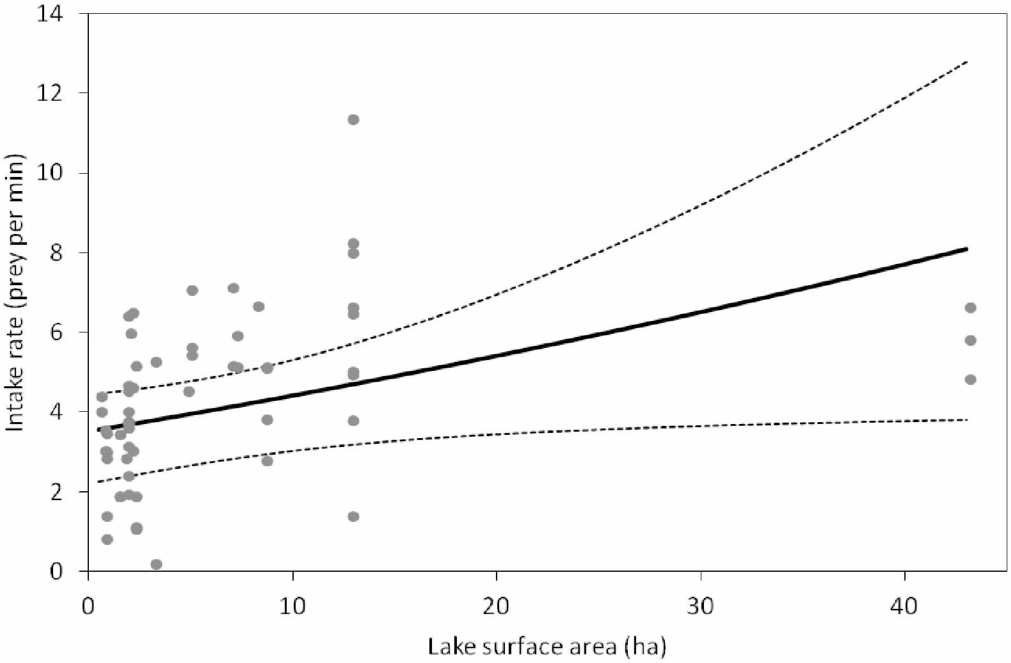


Figure 3.2 Pacific Loon brood food intake rate across the range of lake surface areas. Solid line is model fitted values and broken lines are 95% confidence intervals.

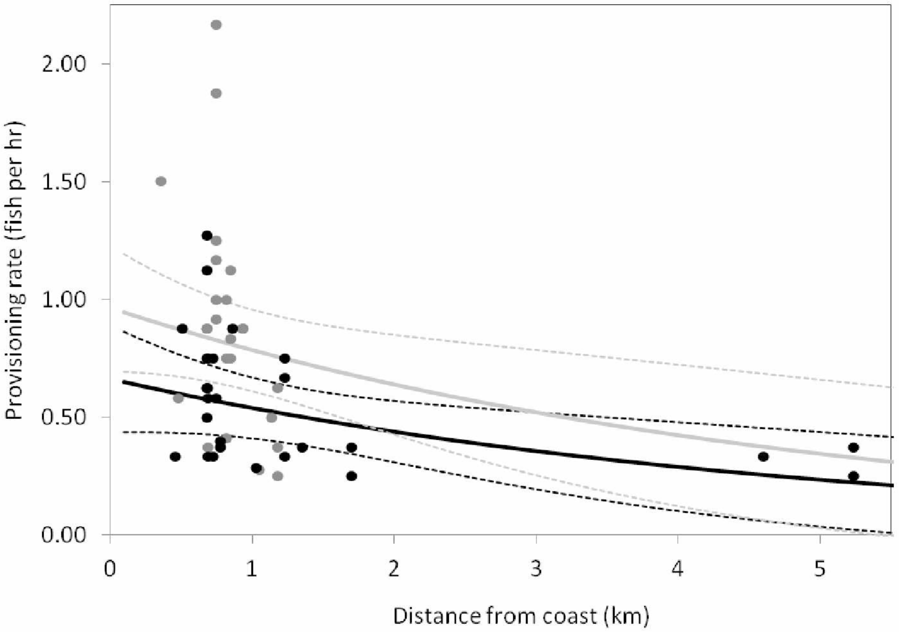


Figure 3.3 Red-throated Loon brood provisioning rates. Estimates for broods with 1 chick (black) and 2 chicks (gray) in relation to the distance from the brood rearing lake to the nearest marine coast. Solid lines are model fitted values and broken lines indicate 95% confidence intervals.

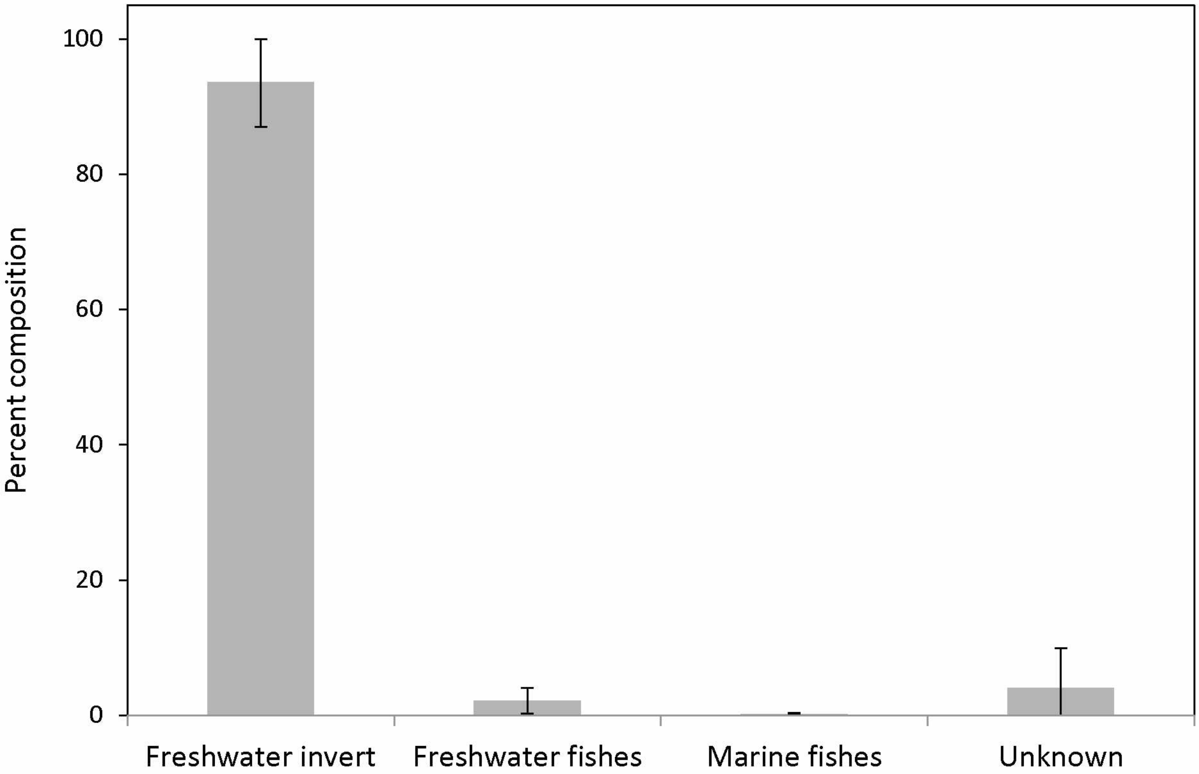


Figure 3.4 Percent composition of prey types provisioned to Pacific Loon broods near Point Lay, Alaska, 2008–2010. Error bars are 95% confidence intervals.

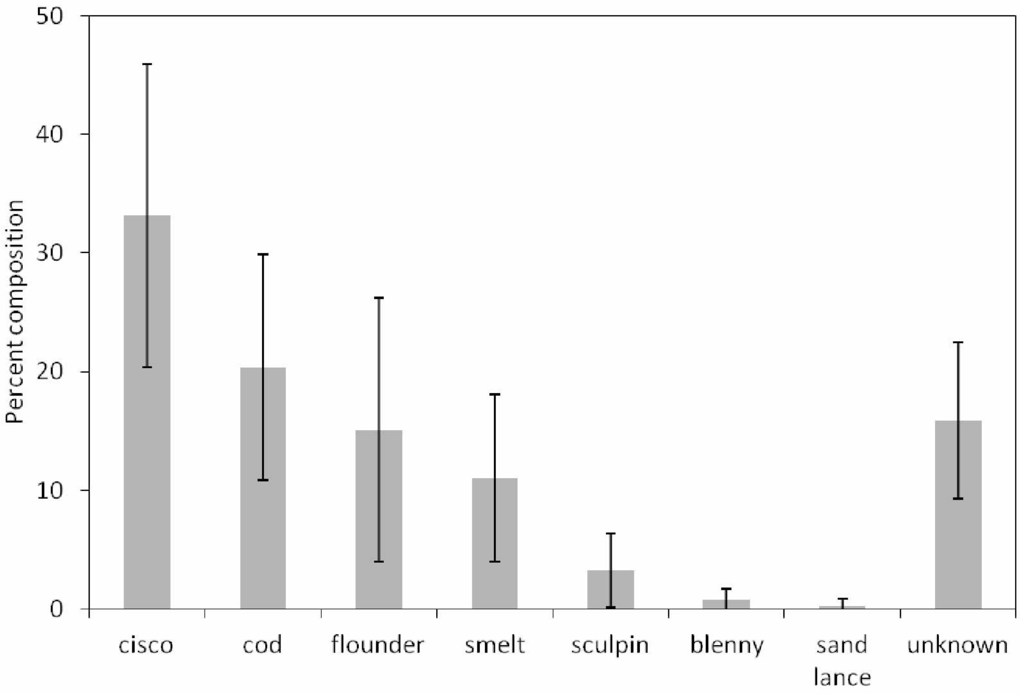


Figure 3.5 Percent composition of prey types provisioned to Red-throated Loon broods near Point Lay, Alaska, 2008–2010. Error bars are 95% confidence intervals.

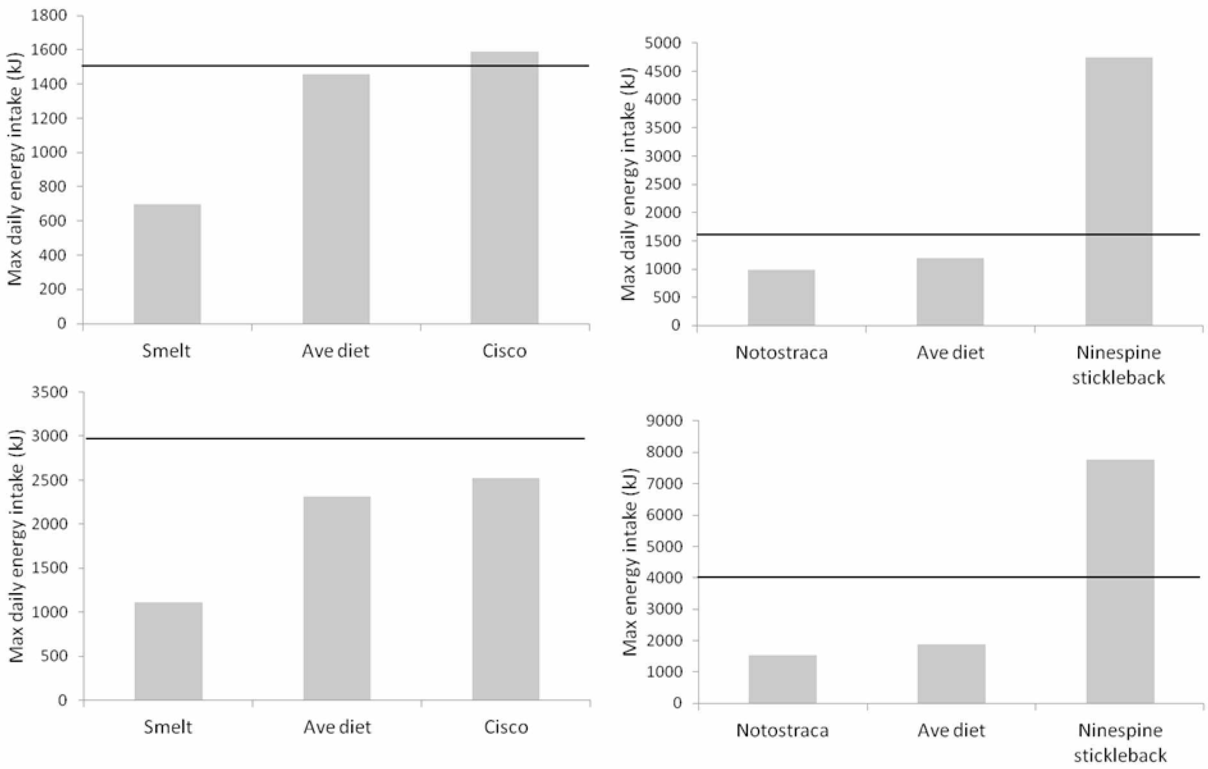


Figure 3.6 Brood energy intake rates. Estimates of maximum energy intake rate for Red-throated Loon (left columns) and Pacific Loon (right columns) broods. Estimates are based on energy content of low-, high-, and average-energy content diets and observed provisioning rates for 1-chick (top row) and 2-chick (bottom row) broods. Horizontal lines represent peak energy requirements of broods.

Table 3.1 Provisioning response variables, statistical models, and explanatory variables used to estimate provisioning parameters for Pacific and Red-throated Loons breeding near Point Lay, Alaska 2008–2010.

Species	Response variables	Statistical model	Explanatory variables
Pacific Loon	Brood marine fish intake rate	mixed Poisson	*brood, age, distance, area, light*
	Brood freshwater prey intake rate (square root transformed)	mixed linear	*brood, age, light, pfish*
	Brood proportion of time provisioned	mixed linear	*brood, age, area, light, pfish*
	Adult freshwater prey provisioning rate (square root transformed)	mixed linear	*sex, area*
	Adult marine fish provisioning rate	mixed Poisson	*sex, brood*
	Adult proportion of time spent provisioning	mixed linear	*sex*
	Adult lake departure rate	mixed Poisson	*sex, brood, age, area, distance*
	Adult trip duration	mixed linear	*brood, sex, age, distance, area, light, fish*
Red-throated Loon	Brood marine fish intake rate	mixed Poisson	*brood, age, distance, light*
	Adult marine fish provisioning rate	mixed Poisson	*brood, distance*
	Adult trip duration	mixed linear	*brood, sex, age, distance, light, fish*

Table 3.2 Variables used to explain variation in the provisioning rates of Pacific and Red-throated loons breeding near Point Lay, Alaska 2008–2010.

Explanatory variable	Description
brood	Indicator variable distinguishing between broods with 1 chick from broods with 2 chicks
age	Age of chicks as the number of days since hatching
distance	Distance from the brood rearing lake to the nearest marine coast in kilometers
area	Surface area of the brood rearing lake in hectares
daylight	Length of the photoperiod, including twilight in hours, on the observation day
sex	Indicator variable for the sex of the provisioning adult
pfish	Proportion of fish (freshwater and marine) in the brood diet during the observation session
fish	Indicator variable for trips away from the brood rearing lake by a Pacific Loon that resulted in a marine fish being brought back for the brood

Table 3.3 Parameter values used to calculate maximum daily energy intake (DEI_{max}) of Pacific and Red-throated loon broods. Parameters include: intake rate of marine fishes (I_m), energy content of marine fishes (E_m), intake rate of freshwater prey (I_f), proportion of time spent provisioning freshwater prey (P_f), and energy content of freshwater prey (E_f). DEI_{max} values were calculated assuming 24 hours of daylight.

Species	Brood size	Diet type	I_m (fish/hr)	E_m (kJ/fish)	I_f (prey/hr)	P_f (prop of day)	E_f (kJ/fish)	DEI_{max} (kJ)
Red-throated Loon	One	Low	0.51	57	--	--	--	698
		Average	0.51	119	--	--	--	1457
		High	0.51	130	--	--	--	1591
	Two	Low	0.81	57	--	--	--	1108
		Average	0.81	119	--	--	--	2313
		High	0.81	130	--	--	--	2527
Pacific Loon	One	Low	0.12	49	275	0.32	0.4	981
		Average	0.12	49	275	0.32	0.5	1192
		High	0.12	49	275	0.32	2.18	4741
	Two	Low	0.12	49	275	0.32	0.4	1536
		Average	0.12	49	275	0.32	0.5	1885
		High	0.12	49	275	0.32	2.18	7762

Table 3.4 Prey species used to calculate maximum daily intake rate of Pacific and Red-throated loon broods.

Prey type	Species	Total length[a] (mm)	Wet mass (g)[b]	Energy content (kJ)
Fishes	Least cisco (*Coregonus sardinella*)	154 ± 4	63	129[c]
	Saffron cod (*Eleginus gracilis*)	177 ± 5	21	126[c]
	Arctic flounder (*Liopsetta glacialis*)	145 ± 7	25	121[c]
	Rainbow smelt (*Osmerus mordax*)	173 ± 8	23	103[c]
	Fourhorn sculpin (*Myoxocephalus quadricornis*)	153 ± 13	24	84[d]
	Slender eelblenny (*Lumpenus fabricii*)	211 ± 15	28	139[d]
	Ninespine stickleback (*Pungitius pungitius*)	35 ± 1[b]	0.5	2.2[c]
Invertebrates	Fairy shrimp (Anostraca)	10 ± 0.4[b]	0.1	0.04[e]
	Clam shrimp (Diplostraca)	8 ± 3[b]	0.1	0.04[e]
	Tadpole shrimp (Notostraca)	16 ± 2[b]	1.6	0.41[e]

[a] Estimated from brood provisioning observations.
[b] Measurements from sampled prey.
[c] Estimated using Ball et al. (2007) equations relating total length to energy content.
[d] Estimated from Anthony et al. (2000) measurements of energy density (kJ/g wet mass).
[e] Estimated from energy density (kJ/dry mass) measurements from Davis and Smith (2001) and converted to energy density of wet mass based on invertebrate water content from Davis and Smith (1998).

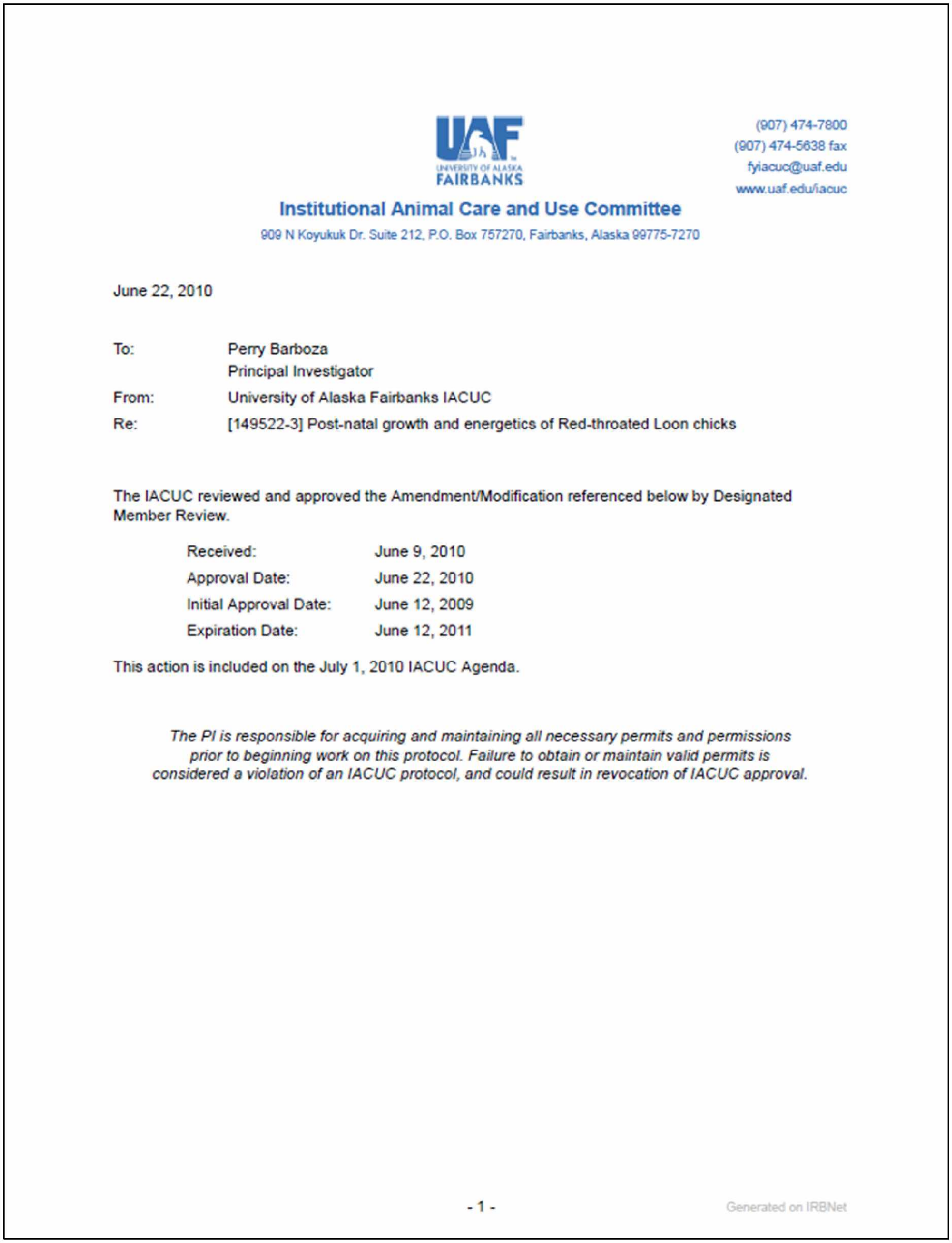
Table 3.5 Breeding lake characteristics. Surface area and distance to the nearest marine coast for Pacific and Red-throated Loon breeding lakes at Point Lay, Alaska.

		Surface area (ha)		Distance to coast (km)	
Species	n	Average (95% CI)	Range	Average (95% CI)	Range
Pacific Loon	119	8.2 (1.7, 11.7)	0.01–128.15	2.0 (1.6, 2.3)	0.13–7.90
Red-throated Loon	144	0.3 (0.2, 0.4)	0.001–3.470	1.9 (1.6, 2.2)	0.22–6.74

Table 3.6 Model selection results. Statistical models that received the most support from the data (based on model posterior weights) for explaining variation in breeding success and provisioning rates of Pacific and Red-throated loons breeding near Point Lay, Alaska 2008–2010.

Species	Response variable	Model	k	Deviance	Weight
Red-throated Loon	Egg survival	age	6	667.8	0.93
	Chick survival	null	5	96.3	0.85
	Brood intake rate	BROOD	3	242.1	0.35
		BROOD + distance	4	238.2	0.34
		BROOD + age	4	240.5	0.11
	Adult provisioning rate	BROOD + SEX + distance	5	324.6	--
	Trip duration	distance + BROOD	5	1068.3	0.51
		distance + daylight	5	1069.9	0.23
		distance + age	5	1070.8	0.15
Pacific Loon	Egg survival	day + day^2	7	516	0.89
		age	6	529.9	0.05
	Chick survival	age	6	171.9	0.82
	Brood intake rate: freshwater	BROOD + lake	5	96.3	0.26
		BROOD	4	100.4	0.26
		BROOD + pfish	5	97.9	0.12
		BROOD + pfish + lake	6	94.1	0.11
	Brood intake rate: marine	BROOD + SEX	5	232.3	0.58
		BROOD + SEX + daylight	6	200.3	0.15
	Brood provisioning time	BROOD	4	-29.4	0.29
		BROOD + age	5	-32.6	0.19
		BROOD + pfish	5	-31.5	0.11
	Adult provisioning rate	SEX + lake	6	187.3	--
	Adult provisioning time	SEX + BROOD + age	7	-103.8	--
	Trip duration	null	3	273.3	0.99

Appendix 3.1 Institutional Animal Care and Use Committee approval from the University of Alaska Fairbanks for loon chick studies, 2008–2010.



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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 22, 2010

To: Perry Barboza
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [149522-3] Post-natal growth and energetics of Red-throated Loon chicks

The IACUC reviewed and approved the Amendment/Modification referenced below by Designated Member Review.

Received:	June 9, 2010
Approval Date:	June 22, 2010
Initial Approval Date:	June 12, 2009
Expiration Date:	June 12, 2011

This action is included on the July 1, 2010 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

CONCLUSIONS

Consistent with previous studies, Red-throated and Pacific loons breeding sympatrically at Point Lay partitioned breeding and foraging habitats. Differences in foraging behavior and diet composition, however, were not related to body condition in incubating adults, as both species maintained similar body condition. Red-throated Loons achieved their body condition with a diet dominated by high-lipid content fishes, notably slender eelblenny. In contrast, Pacific Loons achieved their body condition by feeding on a diversity of fishes and invertebrates. Individual Pacific Loons altered their foraging behavior in relation to the availability of prey in their breeding lake. Pacific Loons in small lakes consumed a high proportion of marine prey, while those in large lakes relied more on freshwater prey. In contrast to adult diet during incubation, Pacific Loon chicks were fed freshwater prey, mostly invertebrates. Further, differences in provisioning behavior and chick diet between Pacific and Red-throated loons were associated with differences in chick production rates. Thus, adult body condition during late-incubation was less sensitive to differences in foraging behavior and diet than the survival of chicks during brood rearing.

Are differences in foraging behavior and diet between Pacific and Red-throated loons associated with their contrasting population trends in Alaska? Inferences drawn from the results of this research are limited by sampling design to this site and environmental conditions during the years of the study. Patterns in chick growth and chick production rates documented at Point Lay, however, are consistent with mechanisms hypothesized to regulate Red-throated Loon population abundance (Ball 2004, Ball et al. 2007, Rizzolo et al. 2014, 2015) and general patterns of loon productivity (Alvo et al. 1988, Gingras and Paszkowski 1999, Jackson 2003). High growth and chick production rates at Point Lay and the presence of high-lipid content fish species, notably slender eelblenny, in the diet of adults and chicks support the hypothesis that Red-throated Loon productivity is sensitive to the availability of high-energy content marine fishes. When the availability of high-lipid content marine fish was limited at a site on the Bering Sea coast of Alaska (Ball et al. 2007), however, Red-throated Loon chick growth rate and survival were low (Ball 2004). Taken together, results from Point Lay and Ball (2004) bracket a wide range of reproductive success and prey availability for Red-throated Loons, and support an association between breeding success and chick diet.

The reliance of breeding Red-throated Loons on marine prey makes them ecologically similar to piscivorous seabirds whose breeding success is correlated with prey quality and availability (Springer et al. 1986, Litzow et al. 2002, Wanless et al. 2005, Piatt et al. 2007). Abundance and community composition of ecologically important species of fish can vary dramatically with ocean climate (Hare and Mantua 2000), with consequent effects on breeding bird populations (Anderson and Piatt 1999). The life history traits of loons, however, lie towards the slow end of the fast–slow life history continuum (i.e., long life-span, long juvenile non-breeding life stage, low fecundity; Nilsson 1977, Evers 2004, Grear et al. 2009), and variation in reproductive success has less of an impact on loon populations than variation in adult survival. Therefore, periods of poor productivity would have to be prolonged over multiple years to induce a decline in the breeding population independent of changes in adult survival because of the low turnover rate of breeding adults. Changes in the availability of marine prey associated with the Pacific Decadal Oscillation (Mantua et al. 1997, Minobe 1997) provide a potential mechanism for bottom-up effects on Red-throated Loon populations because changes in the marine ecosystem occur at decadal timescales.

The productivity of loons relying on freshwater prey in breeding lakes to raise chicks apparently is also sensitive to prey availability. Pacific Loons at Point Lay had lower chick production rates than sympatric Red-throated Loons due to differences in chick survival. Estimates of maximum brood provisioning rates for Pacific Loons indicated that peak chick energy requirements were difficult for parents to meet, particularly for broods with 2 chicks, given a diet of freshwater invertebrates, which were abundant in lakes, but were small and lipid-poor. This result is consistent with reduced productivity in both Arctic Loons (Jackson 2003, 2005) and Common Loons (Alvo et al. 1988; Gingras and Paszkowski 1999, 2006) limited to provisioning their chicks freshwater invertebrates. These results suggest the suitability of a given lake for breeding is related to the availability of sufficient prey for the brood. For Pacific Loons, adults used marine resources during incubation and chick rearing (inferred from lake departure rates), but did not provision their chicks marine fishes. The cost of provisioning flights may make central place provisioning behavior unprofitable given body mass of Pacific Loons, which is greater than that of Red-throated Loons. Thus, the lower limit on size of lakes suitable for breeding Pacific Loons may be set by the availability of prey, rather than the minimum lake surface area required for taking off to fly (Petersen 1979).

Indicators of environmental change in the Arctic are critical for understanding the ongoing effects of increasing average global temperature. Both marine (Grebmeier et al. 2006, Grebmeier 2012, Gall et al. 2017) and lentic (Mueller et al. 2009, Grosse et al. 2012) habitats in the Arctic are undergoing substantial changes. Arctic lakes are warming and maximum lake ice thickness is declining (Arp et al. 2015, 2016). These processes have the potential to make small lakes, that historically had frozen completely during winter, suitable for overwintering fish populations. Thus, lakes previously suitable only for Red-throated Loons that do not need freshwater prey to successfully raise chicks, may become suitable for breeding Pacific Loons if fish become more abundant. Pacific Loons are larger than, and behaviorally dominant to, Red-throated Loons (Davis 1972), and thus changes in Arctic lakes have the potential to increase breeding habitat for Pacific Loons at the expense of Red-throated Loons. Changes in water temperature and water depth in lakes may also increase variation in the abundance of prey in lakes where prey abundances are typically temporally stable.

In marine habitats of the Arctic, reduced extent of summer sea ice (Laxon et al. 2013) and earlier spring sea ice retreat have been associated with changes in the community structure of seabirds in pelagic habitat (Gall et al. 2017) and reduced productivity of sea ice dependent species (Moline et al. 2008). The dynamics of nearshore marine habitat in the Chukchi Sea are complex and poorly understood (Weingartner et al. 2005, Danielson et al. 2014). The timing of the formation of warm Alaska Coastal Water in the spring, however, was associated with reproductive success of seabirds at Cape Lisburne through effects on the timing of the availability of important forage fish species (Springer et al. 1984). Similar effects on Red-throated Loons are possible, but require longer-term monitoring to elucidate.

Results presented in this dissertation support the conclusion of Bergman and Derksen (1977) that Pacific and Red-throated loons on coastal tundra habitat serve as indicators of change in their respective foraging habitats. Loons fit the role of indicator species well because they are conspicuous and widely distributed in coastal tundra habitat. Chick survival was more sensitive to variation in diet than adult body condition. Thus, chick survival could serve as a valuable monitoring tool for assessing changes in marine and freshwater habitats where Pacific and Red-throated loons breed sympatrically.

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