PRE-BREEDING DIET, CONDITION AND TIMING OF BREEDING IN A THREATENED SEABIRD, THE MARBLED MURRELET *BRACHYRAMPHUS MARMORATUS*

MICHAEL H. JANSSEN[1], PETER ARCESE[2], T. KURT KYSER[3], DOUGLAS F. BERTRAM[4], LAURA MCFARLANE TRANQUILLA[5], TONY D. WILLIAMS[5] & D. RYAN NORRIS[1]

[1]*Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario, N1G 2W1, Canada (michaelhjanssen@gmail.com)*
[2]*Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia, V6T 1Z4, Canada*
[3]*Department of Geological Sciences and Geological Engineering, Queen's University, Kingston, Ontario, K7L 3N6, Canada*
[4]*Canadian Wildlife Service, 9860 West Saanich Road, Sidney, British Columbia, V8L 4B2, Canada*
[5]*Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada*

Received 15 October 2008, accepted 10 March 2009

SUMMARY

JANSSEN, M.H., ARCESE, P., KYSER, T.K., BERTRAM, D.F., MCFARLANE TRANQUILLA, L., WILLIAMS, T.D. & NORRIS, D.R. 2009. Pre-breeding diet, condition and timing of breeding in a threatened seabird, the Marbled Murrelet *Brachyramphus marmoratus. Marine Ornithology* 37: 33–40.

Marbled Murrelets *Brachyramphus marmoratus* are small, threatened seabirds that nest in old-growth coniferous forests along the west coast of North America and spend most of their lives in nearshore waters. Recent evidence suggests that long-term declines in pre-breeding trophic feeding level may be associated with reduced reproductive success. To test the hypothesis that pre-breeding trophic feeding level positively influences breeding success, we investigated relationships between timing of breeding, female body condition and pre-breeding trophic feeding level. We predicted that females feeding on higher trophic level prey before breeding would be in better condition and would initiate egg production earlier than would females feeding on lower trophic level prey. Egg-producing females were identified based on elevated yolk precursor (vitellogenin) levels, and diet composition was inferred using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) analysis of murrelet and prey tissues during the pre-breeding seasons of 1999, 2000, 2006 and 2007 in Desolation Sound, British Columbia. Contrary to our predictions, females feeding on a higher proportion of low trophic level prey in 2007 were in better condition and were more likely to produce an egg early in the breeding season. However, differences in pre-breeding diet between egg-producing and non-egg-producing females were not consistent among years. Although our results suggest that low trophic level prey in the pre-breeding diet promoted egg production and breeding success in 2007, this was likely not the case in other years studied. To reconcile results presented here and previous work on diet composition and breeding success in the Marbled Murrelet, we propose an alternative hypothesis of diet quality incorporating optimal foraging theory, whereby the net energy gain from feeding on a prey type is a function of its relative availability.

Key words: Marbled Murrelet, *Brachyramphus marmoratus,* diet, egg production, stable isotope analysis, trophic level

INTRODUCTION

Identifying mechanisms causing a population decline is essential for designing effective management strategies for population recovery (Green 1995, Jones 2004, Norris 2004). Marbled Murrelets *Brachyramphus marmoratus* (hereafter "murrelets") are small (*c.* 220 g) seabirds that nest in old-growth coastal coniferous forests along the west coast of North America and spend most of their lives in nearshore coastal waters (Nelson 1997). Murrelets are listed as Threatened in Canada and the United States. Alaska populations are estimated to have declined by 70% over the past 24 years, and limited evidence suggests recent declines in British Columbia as well (Piatt *et al.* 2007). Threats to murrelet populations are thought to include the loss of nesting habitat from widespread logging of old-growth forest (Ralph *et al.* 1995, Burger 2002, Piatt *et al.* 2007), increased nest predation related to terrestrial habitat changes (Nelson & Hamer 1995, Burger 2002) and reduced availability of high-quality prey species (Peery *et al.* 2004, Becker & Beissinger 2006, Becker *et al.* 2007b, Norris *et al.* 2007). Of these potentially competing hypotheses, the mechanisms through which diet composition might influence reproduction and survival are the least well understood and represent a critical information gap.

In many seabirds, shifts in marine communities that affect the availability of forage fish influence the physical condition and breeding success of birds in the affected regions (Crawford & Dyer 1995, Kitaysky *et al.* 1999, Sydeman *et al.* 2001, Bertram *et al.* 2002, Hedd *et al.* 2002, Gjerdrum *et al.* 2003, Lanctot *et al.* 2003, Hedd *et al.* 2006). For Marbled Murrelets in California and British Columbia, analyses of isotope ratios in feathers, used to characterize diet composition during the pre-alternate moult, suggest that the trophic feeding level one to two months before breeding has declined over the past 100 years, with possible links to reduced reproductive success and population growth (Becker & Beissinger 2006, Norris *et al.* 2007). Contemporary field studies also suggest positive relationships between prey availability,

diet composition and annual reproductive success (Peery *et al.* 2004, Becker *et al.* 2007b). However, whether pre-breeding trophic feeding level directly influences breeding success and the mechanisms that underlie potential relationships between diet composition and reproduction remain uncertain.

Here, we examine the hypothesis that trophic feeding level during the pre-breeding period influences breeding success through positive effects on body condition and timing of breeding in female murrelets. In long-lived species such as murrelets, life-history theory predicts a tradeoff between current and future reproduction: When resources are scarce or individuals are in poor condition, birds forego current reproduction to enhance their survival and future reproductive potential (Williams 1966, Goodman 1974). Murrelet eggs weigh 16%–19% of adult body mass and represent a significant energy investment (Nelson 1997). Murrelets are also highly asynchronous breeders (McFarlane Tranquilla *et al.* 2003), and evidence suggests that early nesters achieve higher nest success (Zharikov *et al.* 2006). Taken together, these observations suggest that, during periods within a given season when prey abundance or quality is low, individual murrelets may postpone reproduction until sufficient body reserves have accumulated.

Murrelets take a wide variety of prey (Burkett 1995), but there is some evidence that they preferentially select fish over krill early in the breeding season (Sealy 1975). Forage fish from higher trophic levels contain more energy per item than do smaller fish or macrozooplankton (Becker *et al.* 2007b), and individual murrelets able to find and capture higher trophic level prey during the pre-breeding period may therefore have higher energy reserves and be able to breed earlier than do birds feeding on lower trophic level prey. We predicted that trophic feeding level would be positively associated with body condition and that female murrelets producing eggs early in the breeding season would have fed at higher trophic levels during the pre-breeding period than females not producing eggs early in the breeding period.

To estimate diet, we used stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope signatures in murrelet feathers and their prey. Stable isotopes provide advantages over traditional methods of estimating seabird diet, such as gut content analysis, because they represent assimilated rather than ingested foods, indicate averages over an extended period of tissue formation, and involve minimal impact to the animals being sampled (Tieszen *et al.* 1983, Hobson & Welch 1992).

To identify the females that were producing eggs at the time of capture, we measured plasma vitellogenin (VTG) levels, a lipophosphoprotein yolk precursor that becomes highly elevated in females during egg production (Challenger *et al.* 2001, McFarlane Tranquilla *et al.* 2003, Vezina & Williams 2003).

METHODS

Murrelet capture and sample collection

Field work was conducted in Desolation Sound, British Columbia (50°05′N, 124°40′W), between 6 April and 19 June 2007. Following methods of Whitworth *et al.* (1997) and Vanderkist *et al.* (1999), we captured 169 Marbled Murrelets at night using a dip-net and spotlight. From each bird, we took a small blood sample (0.3–0.8 mL), two brown-tipped breast feathers, and one sixth of the last secondary feather. Blood samples were taken from the brachial vein and stored on ice for four to eight hours before being centrifuged at 12 000 rpm for 10 minutes. Red blood cells and plasma were stored separately at –20°C for further analysis. We also collected red blood cell samples during the early breeding periods of 1999, 2000 and 2006 at the same location using similar capture techniques. Blood samples from those years were stored at –20°C until laboratory analyses.

Prey samples

Potential prey items for isotope analysis were captured in April and May 2007 using either a beach seine or a plankton net. We used a knotless 4 mm stretch-mesh beach seine, 9.2 m in length, with a 3.1 m centre tapering to 1.1 m at the wings. Beach seine sets were conducted within two hours of low slack tide, on tides less than four feet (3.7 m) and at beaches within 10 km of murrelet capture locations. We conducted vertical plankton tows at night from 25 m depth using a two-metre long, 500 μm mesh plankton net with a 50-cm mouth diameter. Plankton sampling occurred less than one kilometre from most murrelet captures. Prey captured included juvenile salmonids *Oncorhynchus* spp.; juvenile rockfish *Sebastes* spp.; Shiner Surfperch *Cymatogaster aggregate*; Krill *Euphausia pacifica*; juvenile Pacific Herring *Clupea harengus*; and larval, juvenile and adult Pacific Sand Lance *Ammodytes hexapterus.*

Stable isotope analysis

To estimate pre-breeding diet, we analyzed brown-tipped breast feathers and red blood cells from females captured early in the breeding season. Brown-tipped breast feathers are grown during the pre-alternate moult in March/April (Nelson 1997). Feathers are metabolically inert after growth and so provide an isotope signature of diet during the period of feather growth (Hobson & Clark 1992). Because murrelets begin breeding in April/May (McFarlane Tranquilla *et al.* 2003), isotope values from new breast feathers indicate the diet of birds over one to two months before breeding. To further evaluate this assumption, we tested whether females producing eggs were more likely to have completed pre-alternate moult than were females not producing eggs.

We analyzed red blood cells to compare pre-breeding diets within and between years, because feather samples were not taken from murrelets captured in 1999 or 2000. The $\delta^{15}N$ and $\delta^{13}C$ from the cellular fraction of avian blood typically provides a measure of diet over the preceding 20–40 days (Hobson & Clark 1993, Bearhop *et al.* 2002, Evans Ogden *et al.* 2004). Furthermore, among all birds captured before 4 May 2007, a strong correlation was observed between both $\delta^{13}C$ values (Spearman $r_s = 0.64$, $P < 0.0001$, n = 41) and $\delta^{15}N$ values ($r_s = 0.66$, $P < 0.0001$, n = 41) in red blood cells and breast feathers, suggesting that isotope signatures from both tissues reflect diet composition during the same time period.

Isotope analysis was conducted at the Queen's Facility for Isotope Research, Kingston, Ontario. Before analysis, feathers were washed in 2:1 chloroform:methanol solution for 24 hours, rinsed in fresh chloroform:methanol solution and left to air-dry for 48 hours. Red blood cells were freeze-dried before analysis. Inorganic carbonate was removed from zooplankton samples by treatment with 10% hydrochloric acid (Drimmie & Heemskere 2005). After 12 hours, the acidic supernatant was removed, and new solution was added. This process was repeated until the supernatant remained acidic after treatment, and samples were rinsed thoroughly with de-ionized water. We subsampled lateral muscle tissue from all fish. Those

tissues and the zooplankton samples were freeze-dried and then ground to a fine powder. Lipids were removed from powdered prey samples by three repeated 30-minute treatments with 2:1 chloroform:methanol solution, samples were then air dried (Bligh & Dyer 1959). Between 0.20 mg and 0.40 mg of each tissue sample was loaded into a tin capsule, combusted and oxidized in a TC Elemental Analyzer (Thermo Finnigan MAT GMBH, Bremen, Germany) and introduced online into a Finnigan MAT Delta Plus XL Isotope Ratio Mass Spectrometer (Thermo Finnigan MAT GMBH, Bremen, Germany). During analysis, we ran four standards [mean ± standard error (SE)]. For carbon, these were the international standard NBS 21 Graphite (–27.7‰ ± 0.1‰, n = 7) and an in-house standard UC-1 Graphite (–25.6‰ ± 0.2‰, n = 7). For nitrogen, we used the international standard RM 8548 Ammonium Sulphate (19.6‰ ± 0.2‰). For both elements, we also used an in-house organic standard: Domestic Chicken *Gallus gallus* blood (δ^{13}C: –20.1‰ ± 0.1‰; δ^{15}N: 3.9‰ ± 0.2‰; n = 17) prepared in the same fashion as murrelet blood. We also ran duplicate tissue samples from the same feather, blood or prey sample (n = 34), which produced a mean [± standard deviation (SD)] difference or repeatability of ±0.2‰ (±0.2) for δ^{15}N and of ±0.1‰ (±0.1) for δ^{13}C. Isotope ratios (R) are expressed in delta units where $\delta = [(R_{sample} / R_{standard}) - 1] \times 1000$. δ^{15}N is the ratio of ^{15}N/^{14}N in the sample relative to air, and δ^{13}C is the ratio of ^{13}C/^{12}C relative to Vienna Pee Dee Belemnite.

Diet composition

Based on their separation along the two isotope gradients, prey samples were separated into three groups labelled as low, mid- and high trophic level prey (Fig. 1). Isotope values within prey species varied significantly with time (M. Janssen, P. Arcese, T.K. Kyser & D.R. Norris unpubl. data), and so we used only prey items captured during the late pre-breeding to early breeding period (1 April/ 4 May). Because we captured only one juvenile Pacific Herring, we used the δ^{15}N and δ^{13}C values from that sample as the means, and we used as standard deviations of δ^{15}N and δ^{13}C the values for Pacific Herring presented in Hobson *et al.* (1994). We incorporated

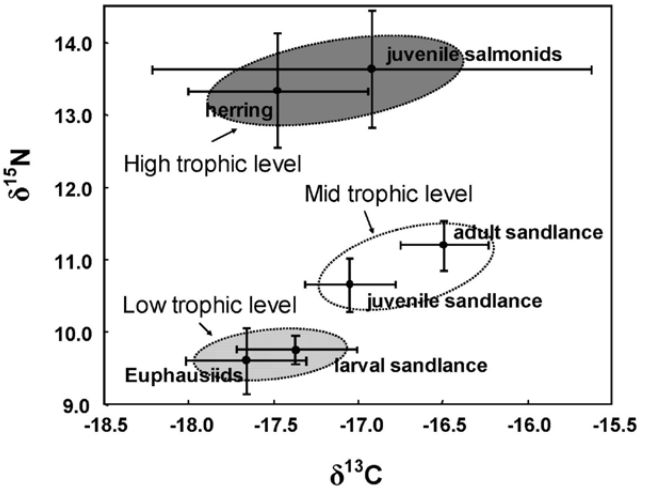

Fig. 1. Mean ± standard deviation δ^{15}N and δ^{13}C values of potential prey items of Marbled Murrelets *Brachyramphus marmoratus* captured 1 April/2 May 2007 in Desolation Sound, British Columbia. Fork lengths of fish were 40–74 mm (juvenile salmonids), 104 mm (Pacific Herring *Clupea harengus*), 95–113 mm (adult sand lance), 45–80 mm (juvenile sand lance) and 32–36 mm (larval sand lance).

δ^{15}N and δ^{13}C values from prey tissue and murrelet feathers into the IsoError dual-isotope, three-source mixing model (Phillips & Gregg 2001) to estimate the relative proportions of low, mid- and high trophic level prey in murrelet diets during the pre-breeding moult. Following other dietary-isotope studies of murrelets (Becker & Beissinger 2006, Becker *et al.* 2007b, Norris *et al.* 2007), we used diet–feather fractionation values of 3.7‰ for δ^{15}N and 1.0‰ for δ^{13}C, which are based on experiments from a closely related species (Common Murre *Uria aalge*; Becker *et al.* 2007a).

Isotope values from tissues of murrelets captured in 1999 and 2006 fell outside the boundaries posed by potential prey captured in 2007, indicating either that isotopic composition of prey species varied between years (Kline 1999) or that the prey consumed by murrelets varied between years. For that reason, we estimated relative proportions of different trophic levels in the diets of murrelets captured in 2007 only.

Sex determination

Because murrelets are sexually monomorphic, we sexed captured birds using genetic molecular techniques (Vanderkist *et al.* 1999). DNA was extracted from red blood cells using the GenElute Blood Genomic DNA Miniprep Kit (Sigma-Aldrich, St. Louis, MO, USA). We used the sex-identification primers developed by Griffiths *et al.* (1998) and a polymerase chain reaction (PCR) protocol modified from Jensen *et al.* (2003), using 5 μL of template DNA in a 15 μL PCR mixture containing 100 ng of each primer, 0.16 mM dNTPs, 4 mM $MgCl_2$, 50 mM KCl, 10 mM Tris–HCl pH 8.3, 0.1% Triton X-100, bovine serum albumin 0.8 mg/mL, and 0.5 U AmpliTaq (Hoffman-LaRoche Ltd., Mississauga, ON, Canada). PCR reactions followed Griffiths *et al.* (1998) and Jensen *et al.* (2003). Reproducibility of the analysis was 100% and was determined from 15 randomly chosen individuals subject to replicate PCR reactions.

Classification of egg producers

Murrelets lay one egg per breeding attempt and vitellogenin becomes elevated during yolk production of the single egg (Vanderkist *et al.* 2000). An assay for vitellogenic zinc was used to determine indirectly the vitellogenin concentration in plasma (Mitchell & Carlisle 1991, Vanderkist *et al.* 2000). Vitellogenic zinc was used as an index of VTG as described and validated for Marbled Murrelets by Vanderkist *et al.* (2000). Conservatively, we considered VTG values above 0.96 mg μL^{-1} as an indication that birds were producing eggs, following McFarlane Tranquilla *et al.* (2003). The inter-assay coefficient of variation for the VTG-Zn assay was 6.3% (n = 9) and the intra-assay coefficient of variation was 5.4% (n = 7).

Body condition

We scaled mass to body size to provide an index of body condition. Among females captured in 2007, those with elevated VTG (237 ± 26 g, n = 52) averaged 26 g heavier than did females not producing eggs (211 ± 17 g, n = 39; Welch's $t = 5.7$, df = 88, $P < 0.0001$), which was likely a result of the additional mass of the developing egg. To facilitate comparisons of mass between egg producers and non-egg producers, we subtracted 26 g from the mass of all egg-producing females. Among female murrelets captured in 2007, unflattened wing chord and tarsus measurements

were weakly correlated (r_s = 0.20, n = 99, P < 0.05), and both were significant predictors (wing: F = 4.9, P < 0.03; tarsus: F = 4.37, P < 0.04) in a least-squares multiple regression predicting female mass (R^2 = 0.11, n = 99, P = 0.005). We therefore took the residuals of this mass–size regression as an index of body condition. Body condition was estimated only for murrelets captured in 2007, because we could not test predictions relating body condition to diet composition in the other three years.

Classifying early breeders

We considered birds captured between 6 April and 4 May 2007—the first third of the egg-laying period in Desolation Sound (McFarlane Tranquilla *et al.* 2003)—as being captured "early" in the breeding season, and we included only those birds in our analyses. This approach reduced the likelihood of erroneously classifying a bird that had already laid an egg as a non-breeder or of classifying a bird that had re-nested as a first-time breeder. Additionally, after 4 May, blood isotope signatures indicated a diet shift towards higher trophic level prey (M. Janssen, P. Arcese, T.K. Kyser & D.R. Norris unpubl. data), and so any influence of pre-breeding diet on body condition or probability of breeding would have been less evident beyond that date.

For analyses among years, we used samples obtained from 6 April through 15 May. This was done partially because of the scarcity of blood samples available from 1999 and 2000, but also because δ^{15}N and δ^{13}C from the cellular fraction of blood provides a window on diet over the preceding 20–40 days (Hobson & Clark 1993, Bearhop *et al.* 2002, Evans Ogden *et al.* 2004). Thus, isotope values from red blood cells of birds captured within the expanded window reflected diet during the early breeding period.

Statistical analyses

We used two-sample t-tests to compare δ^{15}N of red blood cells between egg producers and non-egg producers within years, and diet composition (from breast feathers) between egg-producers and non-egg producers in 2007. Linear least-squares regression was used to investigate relationships between diet and body condition, except where visual inspection of residuals recommended quadratic regression instead. Statistical tests were done using JMP version 5.1.2 (SAS 2004), and we considered P < 0.05 to be statistically significant.

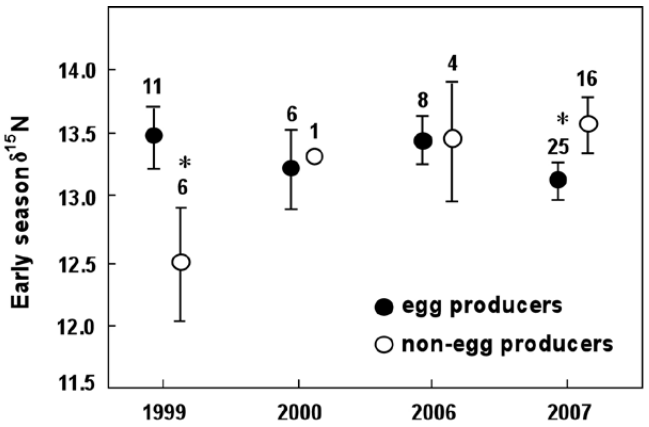

Fig. 2. δ^{15}N from red blood cells of female murrelets captured early in the breeding season in Desolation Sound, British Columbia. Asterisks indicate statistically different values within years; numbers above bars are sample sizes. Error bars show the standard error.

In a few cases, we discuss results that approached significance (0.05 < P < 0.10) and allow the reader to judge their importance. Results are presented as means ± SE or SD, as indicated.

RESULTS

We observed no difference in δ^{15}N of red blood cells between females producing eggs and not producing eggs early in the season in 2000 (t = –0.1, P > 0.9, n = 7) and 2006 (t = 0.02, P > 0.9, n = 12), but a significant variation in δ^{15}N of red blood cells was observed between females in 1999 (t = 2.2, P = 0.04, n = 17) and 2007 (t = –2.0, P = 0.05, n = 41; Fig. 2). Contrary to our predictions, female murrelets producing eggs early in the breeding period in 2007 had a higher proportion of low trophic level prey in the pre-breeding diet than did female murrelets not producing eggs (t = 1.8, P = 0.04, n = 31; Fig. 3). There was no difference, however, in the proportion of mid- (t = –1.08, P > 0.2, n = 31) or high (t = –0.69, P > 0.4, n = 31) trophic level prey consumed between egg producers and non-egg producers (Fig. 3). Body condition of females captured in 2007 was positively related to the proportion of low trophic level prey in the pre-breeding diet (R^2 = 0.31, n = 31, P = 0.005) and negatively related to the proportion of mid-trophic level prey in the pre-breeding diet (R^2 = 0.12, n = 31, P = 0.056; Fig. 4). In addition, we found no evidence of a relationship between the proportion of high trophic level prey in pre-breeding diet and body condition of females (R^2 = 0.006, n = 31, P > 0.5). Finally, we found that females producing eggs were more likely than females not producing eggs to have finished moulting at time of capture (Fisher exact test, one-tailed P = 0.03, n = 32), providing evidence that pre-alternate moult is often completed just before breeding.

DISCUSSION

Isotope signatures from red blood cells of female murrelets captured early in the breeding period suggest that, in 1999 and 2007, females producing eggs were feeding on different prey items than were females not producing eggs; however, there was no evidence of a dietary effect in 2000 or 2006. Moreover, although higher δ^{15}N in red blood cells of egg producers in 1999 suggests that egg producers were feeding at a higher trophic level were than non-egg

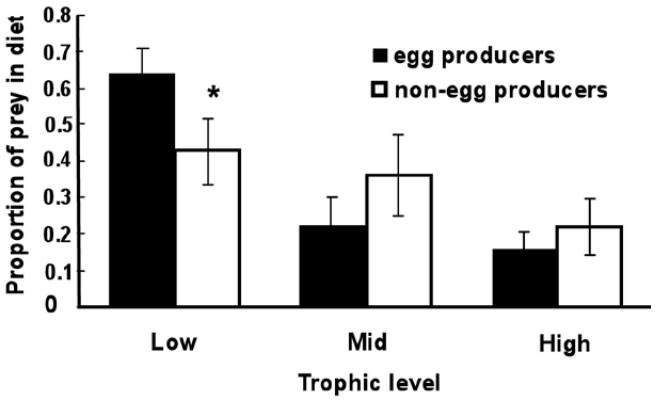

Fig. 3. Results of dual-isotope, three-source mixing model specifying proportion of low, mid- and high trophic level prey in the diets of female Marbled Murrelets *Brachyramphus marmoratus* captured in 2007, as indicated by isotope signatures from brown-tipped breast feathers. Asterisks indicate statistically different values between egg and non-egg producers within a trophic level. Error bars show the standard error.

producers before breeding, the opposite relationship was observed in 2007. Isotope signatures from brown-tipped breast feathers of murrelets captured in 2007 suggest that females that were in better physiological condition and producing eggs early in the breeding season had fed at a lower trophic level during the pre-breeding period than had females in poorer condition and not producing eggs. In Desolation Sound, breeding success of murrelets has been shown to decline as the nesting season progresses (Zharikov *et al.* 2006). In other long-lived seabirds, female body condition is often positively related to breeding success (Chastel *et al.* 1995, Lanctot *et al.* 2003). Our results do not support our stated hypothesis, suggesting rather that the proportion of low trophic level prey before breeding in 2007 was positively related with individual breeding success. Although the absence of prey samples in other years prevented reconstruction of murrelet diets, $\delta^{15}N$ values from red blood cells suggest that the relationships observed in 2007 were absent in 1999, 2000 and 2006, and therefore were not consistent between years.

We did not measure reproductive success, and so it is possible that female pre-breeding diet might have different relationships with other components of successful breeding such as nestling growth or fledging success. Nevertheless, our results from 2007 do not corroborate recent work linking long-term declines in the pre-breeding trophic level of murrelets with reproductive success (Becker & Beissinger 2006, Norris *et al.* 2007). Higher trophic level prey have higher energy content per item (Becker *et al.* 2007b), and it has been suggested that murrelets feeding more on energetically inferior (lower trophic level) prey before breeding have less energy available for reproduction, resulting in reduced population growth rates (Becker & Beissinger 2006, Norris *et al.* 2007). However, similar to our 2007 findings, a recent (1998–2002) study conducted in California found that krill abundance was negatively associated with pre-breeding $\delta^{15}N$, but positively associated with murrelet productivity (Becker *et al.* 2007b), suggesting that murrelet productivity was higher in years in which krill were more prevalent in the pre-breeding diet. Although energy per item is considerably higher for mid- and high trophic level fish than for krill (Becker *et al.* 2007b), the energy per unit mass is relatively similar between trophic levels, and sometimes higher for lower trophic level prey (Vermeer & Cullen 1982, Hedd *et al.* 2002, Becker *et al.* 2007b). Consequently, energy density may be a more relevant metric of prey quality than total energy, and krill may represent higher quality prey than fish early in the breeding season. This hypothesis would predict that females feeding more on lower trophic level prey during the pre-breeding period would be more likely to produce eggs early in the breeding season, and that this relationship would be consistent among years. However, our results are not consistent with this hypothesis (Fig. 2), and we therefore suggest an alternative hypothesis.

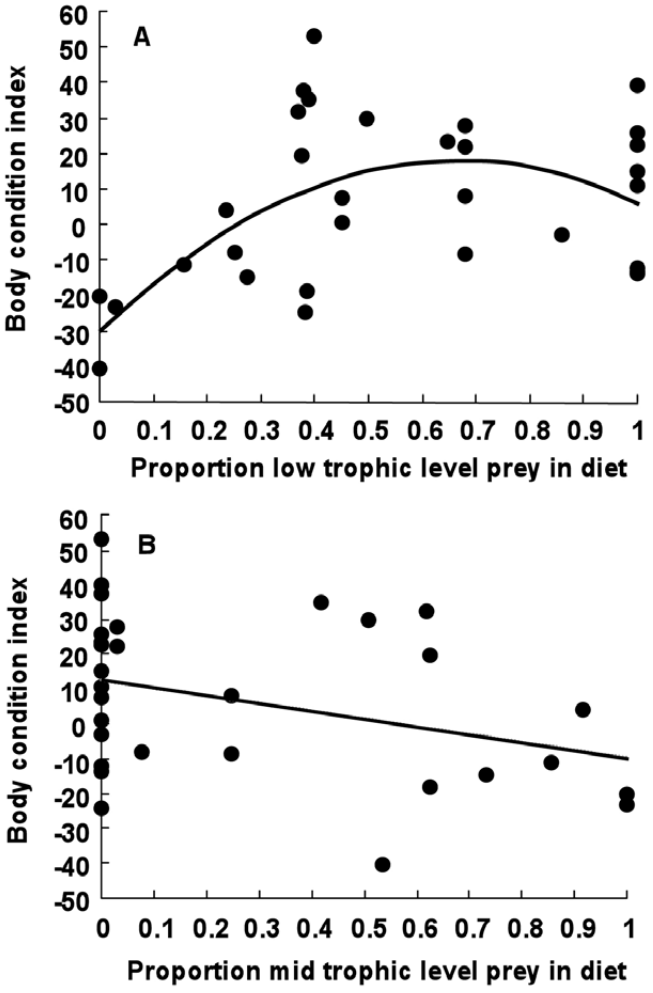

Fig 4. Relationship between body condition and the proportion of (A) low trophic level and (B) mid-trophic level prey in the pre-breeding diet of Marbled Murrelets *Brachyramphus marmoratus* as indicated by stable isotope signatures from breast feathers.

For Marbled Murrelets feeding during the pre-breeding period, we propose that the relative availability of different prey needs to be considered along with energy content, in making inferences about the net energy gain from various prey (Emlen 1966, Becker & Beissinger 2006). The most profitable foraging strategy should maximize the energy gained per unit time spent searching for and handling prey (Holling 1959, Stephens & Krebs 1986). There may therefore be a threshold at which the relative available biomasses of fish and krill result in no benefit of foraging exclusively on one prey type or the other (Fig. 5). However, above the threshold, foraging for fish would be most profitable, as might have been the case historically before possible declines in abundance of Pacific Sardine *Sardinops sagax* and Northern Anchovy *Engraulis mordax* in California (Leet *et al.* 2001) and Eulachon *Thaleichthys pacificus,* Pacific salmon and Pacific Herring in the Georgia Basin of British Columbia (DFO 1999, 2002, 2005; Therriault *et al.* 2009). Interyear diet switching concurrent with changes in relative abundance of high- and low-quality prey species has been observed in other seabirds (Litzow *et al.* 2002, Baillie & Jones 2004, Barrett 2007), and breeding murrelets may adopt the best available strategy in a given year (Fig. 2). If targeting fish when the available prey biomass ratio is fish-biased is more profitable than targeting krill when the ratio is krill-biased, then years in which the best strategy is to target fish should yield higher productivity than years in which targeting krill is the best strategy. Nevertheless, in years with low relative fish availability before breeding, targeting lower trophic level prey might result in higher reproductive success at the individual level despite lower mean productivity at the population level (Fig. 5). Following this hypothesis, it is possible that historic declines in pre-breeding trophic feeding level are associated with declines in overall productivity, whereas lower pre-breeding trophic level in the present study appeared positively associated with female body condition and early laying in 2007.

Diet–feather fractionation values for seabirds can vary significantly between and within species (Becker *et al.* 2007a), but ours is the fourth recent isotope-based dietary study of Marbled Murrelets to use diet–feather fractionation values of 3.7‰ for $\delta^{15}N$ and 1.0‰ for $\delta^{13}C$, and all have produced estimates of diet falling within the boundaries imposed by predicted diet sources (Becker & Beissinger 2006, Becker *et al.* 2007b, Norris *et al.* 2007). Thus, we believe the diet–feather fractionation values used in the present study are robust estimates. Likewise, our isotopic prey map may not accurately represent the actual prey species consumed because we were unable to include all known murrelet prey that occur in Desolation Sound. However, the species that were included (Pacific Sand Lance, euphausiids and juvenile Pacific Herring) are considered the main prey of murrelets in British Columbia, typically comprising 94%–99% of the adult diet (Burkett 1995). In addition, isotope ranges within our trophic level groupings were similar to those obtained by Becker *et al.* (2007b). Thus, it is unlikely that inclusion of isotope signatures from the missing prey species would substantially alter the mean signatures of the three trophic levels identified or the results derived from them. Finally, it is possible that isotope signatures of prey collected nearshore differ from those in the diet of murrelets feeding farther offshore (Kline 1999), but we consider this prospect unlikely. Prey and murrelet samples were collected within 12 km of each other, from essentially the same body of water. Further, radio telemetry suggests only small-scale variability in daytime foraging locations of individual murrelets in Desolation Sound (Lougheed 2000).

Compared with less-experienced or sexually immature females more-experienced females may be more adept at foraging, in better condition and more likely to produce eggs early in the season (Sydeman *et al.* 1991, Ratcliffe *et al.* 1998, Bunce *et al.* 2005).

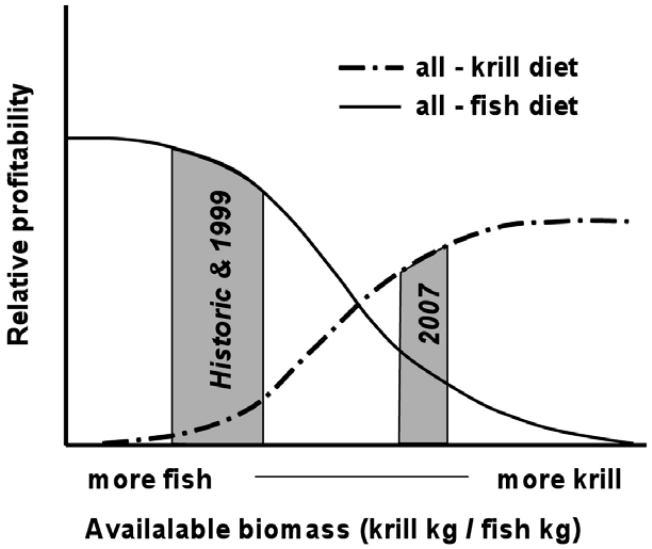

Fig 5. Hypothesized relationship between relative available biomass of fish and krill during the pre-breeding period and the relative profitability of Marbled Murrelets *Brachyramphus marmoratus* targeting only fish or only krill. Relative profitability is the net energy gain per unit time associated with foraging for one prey type relative to the net energy gain per unit time of foraging for the other prey type. Grey bars indicate hypothesized krill-biased biomass ratios in 2007 and fish-biased biomass ratios in 1999 and historical times. Breeding success would be expected to peak when energy gained over unit time is highest.

Because we could not age murrelets beyond their second year, we could not control for this factor. However, we doubt whether age could account for the patterns reported here, because the relationship between diet and early-season egg production was inconsistent among years.

Although we found evidence that pre-breeding diet is at times correlated with female body condition and egg production, there is much still to learn about early-season diet and effects on later stages of reproduction, survival and abundance of murrelets in British Columbia. Priorities for future research include examination of factors affecting the abundance and availability of murrelet prey species; the relationships between prey species availability, diet composition and physiological condition; and whether patterns observed in British Columbia are prevalent throughout the northern range of murrelets. Moreover, there is evidence that diet composition at other times in the annual cycle influences the reproductive success of murrelets (Becker *et al.* 2007b) and other auks (Sorensen *et al.* 2009); thus, further research should investigate murrelet diets during chick rearing and post-fledging in relation to breeding success and overwinter survival. In general, it will be important to weigh carefully the roles of marine versus terrestrial factors on the population dynamics of Marbled Murrelets.

ACKNOWLEDGEMENTS

We thank Sarah Gutowsky, Mark Sloan, Trevor Haynes, Jennifer Barret and Frank Paulson for their dedicated assistance in murrelet and prey sampling. Amy Wilson, Kerry Klassen and Hestor Yueh provided essential aid with laboratory analyses. Two anonymous referees provided suggestions that improved the manuscript. The Canadian Wildlife Service, the Center for Wildlife Ecology at Simon Fraser University, and Cliff Robinson of Parks Canada generously provided field equipment and logistics support. Analyses and field work were funded by the BC Forest Science Program (PA, DRN, DFB), the Endangered Species Recovery Fund (World Wildlife Fund Canada and Environment Canada; DRN, PA, MHJ, DFB), the Canadian Foundation for Innovation (TKK), the Ontario Innovation Trust (TKK), the Natural Sciences and Engineering Research Council of Canada (RN, TDW, TKK, PA, MHJ) and the Canadian Wildlife Service (DFB).

REFERENCES

BAILLIE, S.M. & JONES, I.L. 2004. Response of Atlantic Puffins to a decline in Capelin abundance at the Gannet Islands, Labrador. *Waterbirds* 27: 102–111.

BARRETT, R.T. 2007. Food web interactions in the southwestern Barents Sea: Black-legged Kittiwakes *Rissa tridactyla* respond negatively to an increase in Herring *Clupea harengus. Marine Ecology Progress Series* 349: 269–276.

BEARHOP, S., WALDRON, S., VOTIER, S.C. & FURNESS, R.W. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* 75: 451–458.

BECKER, B.H. & BEISSINGER, S.R. 2006. Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology* 20: 470–479.

BECKER, B.H., NEWMAN, S.H., INGLIS, S. & BEISSINGER, S.R. 2007a. Diet–feather stable isotope ($\delta^{15}N$ and $\delta^{13}C$) fractionation in Common Murres and other seabirds. *Condor* 109: 451–456.

BECKER, B.H., PEERY, M.Z. & BEISSINGER, S.R. 2007b. Ocean climate and prey availability affect the trophic level and reproductive success of the Marbled Murrelet, an endangered seabird. *Marine Ecology Progress Series* 329: 267–279.

BERTRAM, D.F., GOLUMBIA, T., DAVOREN, G.K., HARFENIST, A. & BROWN, J. 2002. Short visits reveal consistent patterns of interyear and intercolony variation in seabird nestling diet and performance. *Canadian Journal of Zoology* 80: 2190–2199.

BLIGH, E.G. & DYER, W.J. 1959. A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology* 37: 911–917.

BUNCE, A., WARD, S.J. & NORMAN, F.I. 2005. Are age-related variations in breeding performance greatest when food availability is limited? *Journal of Zoology* 266: 163–169.

BURGER, A.E. 2002. Conservation assessment of Marbled Murrelets in British Columbia: a review of the biology, populations, habitat associations, and conservation. Technical report series no. 387. Delta, BC: Canadian Wildlife Service, Pacific and Yukon Region. 194 pp.

BURKETT, E.B. 1995. Marbled Murrelet food habits and prey ecology. In: Ralph, C.J., Hunt, G.L., Raphael, M.G. & Piatt, J.F. (Eds). Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152. Albany, CA: US Forest Service, Pacific Southwest Research Station. pp. 223–246.

CHALLENGER, W.O., WILLIAMS, T.D., CHRISTIANS, J.K. & VEZINA, F. 2001. Follicular development and plasma yolk precursor dynamics through the laying cycle in the European Starling (*Sturnus vulgaris*). *Physiological and Biochemical Zoology* 74: 356–365.

CHASTEL, O., WEIMERSKIRCH, H. & JOUVENTIN, P. 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76: 2240–2246.

CRAWFORD, R.J.M. & DYER, B.M. 1995. Responses by four seabird species to a fluctuating availability of Cape Anchovy (*Engraulis capensis*) off South Africa. *Ibis* 137: 329–339.

DFO (DEPARTMENT OF FISHERIES AND OCEANS). 1999. Eulachon. DFO science stock status report B6–06 (1999). Nanaimo, BC: Environment Canada, Department of Fisheries and Oceans. 5 pp.

DFO (DEPARTMENT OF FISHERIES AND OCEANS). 2002. Coho Salmon in Georgia Basin. DFO science stock status report D6–07 (2002). Nanaimo, BC: Environment Canada, Department of Fisheries and Oceans. 6 pp.

DFO (DEPARTMENT OF FISHERIES AND OCEANS). 2005. Stock assessment report on Straight of Georgia Pacific Herring. Scientific advisory report 2005/068. Nanaimo, BC: DFO Canadian Scientific Advisory Secretariat. 5 pp.

DRIMMIE, R.J. & HEEMSKERE, A.R. 2005. Leco combustion of organics. Technical procedure 9.0. Revision 02. Waterloo, ON: University of Waterloo, Department of Earth Sciences, Environmental Isotope Laboratory. 8 pp.

EMLEN, M.J. 1966. The role of time and energy in food preference. *American Naturalist* 100: 611–617.

EVANS OGDEN, L.J., HOBSON, K.A. & LANK, D.B. 2004. Blood isotopic ($\delta^{15}N$ and $\delta^{13}C$) turnover and diet–tissue fractionation factors in captive Dunlin (*Calidris alpina pacifica*). *Auk* 121: 170–177.

GJERDRUM, C., VALLEE, A.M.J., ST. CLAIR, C.C., BERTRAM, D.F., RYDER, J.L. & BLACKBURN, G.S. 2003. Tufted Puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Sciences USA* 100: 9377–9382.

GOODMAN, D. 1974. Natural selection and a cost ceiling on reproductive effort. *American Naturalist* 108: 247–268.

GREEN, R.E. 1995. Diagnosing causes in bird population declines. *Ibis* 137: S47–S55.

GRIFFITHS, R., DOUBLE, M.C., ORR, K. & DAWSON, R.J.G. 1998. A DNA test to sex most birds. *Molecular Ecology* 7: 1071–1075.

HEDD, A., RYDER, J.L., COWEN, L.L. & BERTRAM, D.F. 2002. Inter-annual variation in the diet, provisioning and growth of Cassin's Auklet at Triangle Island, British Columbia: responses to variation in ocean climate. *Marine Ecology Progress Series* 229: 221–232.

HEDD, A., BERTRAM, D.F., RYDER, J.L. & JONES, I.L. 2006. Effects of interdecadal climate variability on marine trophic interactions: Rhinoceros Auklets and their fish prey. *Marine Ecology Progress Series* 309: 263–278.

HOBSON, K.A. & CLARK, R.G. 1992. Assessing avian diets using stable isotopes. I: turnover of ^{13}C in tissues. *Condor* 94: 181–188.

HOBSON, K.A. & CLARK, R.G. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. *Auk* 110: 638–641.

HOBSON, K.A. & WELCH, H.E. 1992. Determination of trophic relationships within a high arctic marine food web using $\delta^{15}N$ and $\delta^{13}C$ analysis. *Marine Ecology Progress Series* 84: 9–18.

HOBSON, K.A., PIATT, J.F. & PITOCCHELLI, J. 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63: 786–798.

HOLLING, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91: 385–398.

JENSEN, T., PERNASETTI, F.M. & DURRANT, B. 2003. Conditions for rapid sex determination in 47 species by PCR of genomic DNA from blood, shell-membrane blood vessels and feathers. *Zoo Biology* 22: 561–571.

JONES, C.G. 2004. Conservation management of endangered birds. In: Sutherland, W.J., Newtone, I. & Green, R.E. (Eds). Bird ecology and conservation, a handbook of techniques. New York: Oxford University Press. pp. 269–302.

KITAYSKY, A.S., WINGFIELD, J.C. & PIATT, J.F. 1999. Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Functional Ecology* 13: 577–584.

KLINE, T.C. 1999. Temporal and spatial variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in pelagic biota of Prince William Sound, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 94–117.

LANCTOT, R.B., HATCH, S.A., GILL, V.A. & EENS, M. 2003. Are corticosterone levels a good indicator of food availability and reproductive performance in a kittiwake colony? *Hormones and Behavior* 43: 489–502.

LEET, W.S., DEWEES, C.M., KLINGBEIL, R. & LARSON, E.J. 2001. California's living marine resources: a status report. Berkeley & Los Angeles, CA: University of California. 594 pp.

LITZOW, M.A., PIATT, J.F., PRICHARD, A.K. & ROBY, D.D. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* 132: 286–295.

LOUGHEED, C. 2000. Breeding chronology, breeding success, distribution and movement of Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. Technical report series no. 352. Delta, BC: Canadian Wildlife Service. 89 pp.

MCFARLANE TRANQUILLA, L.A., WILLIAMS, T.D. & COOKE, F. 2003. Using vitellogenin to identify interannual variation in breeding chronology of Marbled Murrelets (*Brachyramphus marmoratus*). *Auk* 120: 512–521.

MITCHELL, M.A. & CARLISLE, A.J. 1991. Plasma zinc as an index of vitellogenin production and reproductive status in the domestic fowl. *Comparative Biochemistry and Physiology* 100A: 719–724.

NELSON, S.K. 1997. The Marbled Murrelet (*Brachyramphus marmoratus*). In: Poole, A. & Gill, F. (Eds). The birds of North America. No. 276. Philadelphia, PA and Washington, DC: Academy of Natural Sciences and American Ornithologists' Union.

NELSON, S.K. & HAMER, T.E. 1995. Nest success and the effects of predation on Marbled Murrelets. In: Ralph, C.J., Hunt, G.L., Raphael, M.G. & Piatt, J.F. (Eds). Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152. Albany, CA: US Forest Service, Pacific Southwest Research Station. pp. 89–97.

NORRIS, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology* 41: 413–426.

NORRIS, D.R., ARCESE, P., PREIKSHOT, D., BERTRAM, D.F. & KYSER, T.K. 2007. Diet reconstruction and historic population dynamics in a threatened seabird. *Journal of Applied Ecology* 44: 875–884.

PEERY, M.Z., BEISSINGER, S.R., NEWMAN, S.H., BURKETT, E.B. & WILLIAMS, T.D. 2004. Applying the declining population paradigm: diagnosing causes of poor reproduction in the Marbled Murrelet. *Conservation Biology* 18: 1088–1098.

PHILLIPS, D.L. & GREGG, J.W. 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia* 127: 171–179.

PIATT, J.F., KULETZ, K.J., BURGER, A.E., HATCH, S.A., FRIESEN, V.L., BIRT, T.P. & ARIMITSU, A.M.A. 2007. Status review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia. Open-file report 2006-1387. Reston, VA: US Geological Survey. 258 pp.

RALPH, C.J., HUNT, G.L., RAPHAEL, M.G. & PIATT, J.F. 1995. Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152. Albany, CA: US Forest Service, Pacific Southwest Research Station. 420 pp.

RATCLIFFE, N., FURNESS, R.W. & HAMER, K.C. 1998. The interactive effects of age and food supply on the breeding ecology of Great Skuas. *Journal of Animal Ecology* 67: 853–862.

SAS. 2004. JMP IN 1.5.2 for Windows. Cary, NC: SAS Institute, Inc.

SEALY, S. 1975. Feeding ecology of Ancient and Marbled Murrelets near Langara Island, BC. *Canadian Journal of Zoology* 53: 418–433.

SORENSEN, M.C., HIPFNER, M.J., KYSER, T.K. & NORRIS, D.R. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology* 78: 460–467.

STEPHENS, D.W. & KREBS, J.R. 1986. Foraging theory. Princeton, NJ: Princeton University Press.

SYDEMAN, W.J., PENNIMAN, J.F., PENNIMAN, T.M., PYLE, P. & AINLEY, D.G. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food supply. *Journal of Animal Ecology* 60: 135–149.

SYDEMAN, W.J., HESTER, M.M., THAYER, J.A., GRESS, F., MARTIN, P. & BUFFA, J. 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. *Progress in Oceanography* 49: 309–329.

THERRIAULT, T.W., HAY, D.E. & SCHWEIGERT, J.F. 2009. Biologic overview and trends in pelagic forage fish abundance in the Salish Sea (Strait of Georgia, British Columbia). *Marine Ornithology* 37: 3–10.

TIESZEN, L.L., BOUTTON, T.W., TESDAHL, K.G. & SLADE, N.A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. *Oecologia* 57: 32–37.

VANDERKIST, B.A., XUE, X.H., GRIFFITHS, R., MARTIN, K., BEAUCHAMP, W. & WILLIAMS, T.D. 1999. Evidence of male-bias in capture samples of Marbled Murrelets from genetic studies in British Columbia. *Condor* 101: 398–402.

VANDERKIST, B.A., WILLIAMS, T.D., BERTRAM, D.F., LOUGHEED, L.W. & RYDER, J.L. 2000. Indirect, physiological assessment of reproductive state and breeding chronology in free-living birds: an example in the Marbled Murrelet (*Brachyramphus marmoratus*). *Functional Ecology* 14: 758–765.

VERMEER, K. & CULLEN, L. 1982. Growth comparison of a plankton- and a fish-feeding alcid. *Murrelet* 63: 34–39.

VEZINA, F. & WILLIAMS, T.D. 2003. Plasticity in body composition in breeding birds: what drives the metabolic costs of egg production? *Physiological and Biochemical Zoology* 76: 713–730.

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R. & MCIVER, W.R. 1997. A night-lighting technique for at-sea capture of Xantus' Murrelets. *Colonial Waterbirds* 20: 525–531.

WILLIAMS, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's Principle. *American Naturalist* 100: 687–690.

ZHARIKOV, Y., LANK, D.B., HUETTMAN, F., BRADLEY, R.W., PARKER, N., YEN, P.P.W., MCFARLANE TRANQUILLA, L. & COOKE, F. 2006. Habitat selection and breeding success in a forest-nesting alcid, the Marbled Murrelet, in two landscapes with different degrees of forest fragmentation. *Landscape Ecology* 21: 107–120.