

Contribution to the Theme Section 'Forensic methods in conservation research'



Concurrent declines in nestling diet quality and reproductive success of a threatened seabird over 150 years

Sarah Gutowsky^{1,*}, Michael H. Janssen¹, Peter Arcese², T. Kurt Kyser³,
Danielle Ethier⁴, Michael B. Wunder⁵, Douglas F. Bertram⁶,
Laura McFarlane Tranquilla⁷, Cecilia Lougheed⁸, D. Ryan Norris¹

¹Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario N1G 2W1, Canada

²Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada

³Department of Geological Sciences and Geological Engineering, Queen's University, Kingston, Ontario K7L 3N6, Canada

⁴Trent University, 1600 West Bank Drive, Peterborough, Ontario K9J 7B8, Canada

⁵Department of Integrative Biology, University of Colorado Denver, PO Box 173364, Denver, Colorado 80217-3364, USA

⁶Environment Canada, c/o Institute of Ocean Sciences, 9860 West Saanich Road, PO Box 6000, Sidney, British Columbia V8L 4B2, Canada

⁷Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

⁸Fisheries and Oceans Canada, 200 Kent Street, Ottawa, Ontario K1A 0E6, Canada

ABSTRACT: Successful conservation of threatened species is often hindered by a lack of long-term data required to identify the vital rates contributing to population decline and the extrinsic factors influencing those rates. Museum collections can provide a valuable resource for reconstructing the historic demography and diet of otherwise elusive species. Here, we used age ratios (the relative number of hatch-year to after-hatch-year individuals) to examine the hypothesis that population declines in a threatened seabird, the marbled murrelet *Brachyramphus marmoratus*, are due to declines in reproductive success over the past 150 yr. We also used stable-nitrogen isotopes to examine the hypothesis that variation in reproductive success over this period is related to the quality of food received by young in the nest. Age ratios from at-sea surveys conducted from 1994 to 2001 were significantly lower than museum collection age ratios for the period 1860 to 1950. Stable-nitrogen isotope values indicated that the trophic feeding level of marbled murrelet nestlings declined significantly (−2.6‰) from 1854 to 2008. Our results suggest that the reproductive success of marbled murrelets breeding in the Salish Sea has declined over the past 150 yr and that declines in nestling diet quality may be partly responsible. Overall, our results support the idea that managers should consider the quality of both nesting and marine foraging habitat as they attempt to improve reproductive success and population growth rate in this threatened species.

KEY WORDS: Marbled murrelet · Stable isotopes · Age ratios · Diet reconstruction · Museum specimens · *Brachyramphus marmoratus* · Salish Sea

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Successful conservation of threatened species requires proper identification of the demographic vital rates that drive population trends and the extrinsic fac-

tors that influence those vital rates (Green 1995, Norris 2004). Accomplishing these objectives can be challenging, particularly when long-term data are not available (Caughey 1994). Marbled murrelets *Brachyramphus marmoratus* (Alcidae; hereafter 'murrelets')

*Email: sgutowsk@uoguelph.ca

are currently listed as Endangered under the IUCN Red List of Threatened Species and threatened under the Committee on the Status of Endangered Wildlife in Canada. In Alaska, populations are estimated to have declined by 70 % over the past 25 yr, and available evidence indicates that similar declines have occurred in the Salish Sea (Piatt et al. 2007, Bower in press). Murres are a secretive species that typically nest on the high limbs of large trees up to 100 km inland (Nelson 1997), making it particularly challenging to study their breeding biology and identify the demographic rates contributing to their decline.

Here, we used age ratios, or the relative number of hatch-year to after-hatch-year birds, to examine the hypothesis that declines in murrelet abundance are due in part to declines in productivity. Much evidence now suggests that the reproductive success of murres in British Columbia and California is limited by the availability of nesting habitat in old-growth forest (Ralph et al. 1995, Burger 2002, Piatt et al. 2007), nest predation (Nelson & Hamer 1995, Peery et al. 2004), and prey availability (Becker & Beissinger 2006, Norris et al. 2007). Murrelet productivity estimated from age ratios was shown to have declined by nearly an order of magnitude in central California from 1892 to 2003 (Beissinger & Peery 2007). Thus, we predicted that contemporary estimates of productivity in the Salish Sea from at-sea surveys conducted from 1994 to 2001 would be lower than historic estimates derived from museum age ratios collected from 1860 to 1950 in the same region.

We also examined the hypothesis that variation in murrelet productivity is related to the quality of food received by young in the nest. In several species of alcids, nestling diet quality is positively related to body condition (Davoren & Montevecchi 2003), growth rate (Bertram et al. 2002, Litzow et al. 2002, Wanless et al. 2005, Hedd et al. 2006), and fledging date (Harfenist 1995, Ydenberg et al. 1995, Morbey & Ydenberg 1997), all of which can contribute to a successful nesting attempt and thus increase age ratios. Furthermore, Janssen (2009) found that diet quality during development was positively associated with growth and body condition of juvenile murres. Related evidence also suggests that adult trophic feeding level during the 1 to 2 mo prior to breeding has shown strong temporal declines in both California and British Columbia (Becker & Beissinger 2006, Norris et al. 2007), and it is possible that nestling diet composition has also changed over the last century. Thus, we predicted that declines in murrelet nestling diet quality have occurred concurrently with observed declines in productivity and adult trophic feeding level over the last 150 yr.

To test our prediction above, we analyzed stable-nitrogen isotopes ($\delta^{15}\text{N}$) in juvenile breast feathers col-

lected from museum specimens and contemporary at-sea captures from the Georgia Basin. In marine ecosystems, $\delta^{15}\text{N}$ values in predators predictably reflect the isotopic composition of their prey, because $\delta^{15}\text{N}$ is enriched at higher trophic levels (Hobson et al. 1994). Because feathers are metabolically inert, their isotopic signatures are indicative of the food ingested as feathers grow (Hobson & Welch 1992, Hobson et al. 1994). Brown-tipped breast feathers of hatch-year murres are grown in the nest (Nelson 1997), and therefore contain isotopic signatures that indicate nestling diet composition.

MATERIALS AND METHODS

Estimating productivity. We recorded hatch-year (HY; 0 to 1 yr-old) and after-hatch-year (AHY; >1 yr-old) murres from museum specimens that were collected between August and February 1860 to 1950 in the Salish Sea (from the north end of the Strait of Georgia to the west coast of the Strait of Juan de Fuca and the south end of Puget Sound; $50^{\circ} 60' - 47^{\circ} 15' \text{N}$, $121^{\circ} 58' - 125^{\circ} 29' \text{W}$) and from at-sea surveys conducted in Desolation Sound, British Columbia ($50^{\circ} 58' \text{N}$, $124^{\circ} 48' \text{W}$), in August 1994 to 2001. The age class of museum specimens was determined in the hand using plumage characteristics (as described by Beissinger & Peery 2007). At-sea surveys were conducted according to protocol outlined in Lougheed et al. (2002). The vessel crew changed between years (1994–1995, 1996–1998, and 1998–2001) but with significant overlap in personnel between years, such that the survey methodology was taught directly from outgoing to incoming crew. Here we define productivity, R , as the number of offspring produced per adult or subadult. To estimate R , we used the ratio of HY to AHY birds (HY/AHY), where the standard error SE_R was estimated as: $[(\text{HY} \times \text{AHY})/(\text{HY} + \text{AHY})^3]^{1/2}$ (Ricklefs 1997, Beissinger & Peery 2007).

Both historic and contemporary samples were corrected for the proportion of nestlings that had not fledged in August by dividing the number of juveniles detected by the proportion of young expected to have fledged at the time of collection or sampling (Beissinger & Peery 2007). This proportion was derived from breeding chronologies of murres in Desolation Sound, as estimated from vitellogenin, a yolk protein precursor that indicates whether or not females are producing eggs (McFarlane Tranquilla et al. 2003). McFarlane Tranquilla et al. (2003) estimated that the peak fledging period in 1999 and 2000 occurred on $31 \text{ July} \pm 20 \text{ d}$ ($\pm 1 \text{ SD}$ of mean fledge date). For each observation, we calculated a z -value ($[\text{observation date} - \text{mean fledge date}]/\text{SD}$), which was used to esti-

mate the proportion of juveniles that fledged in August from either the historic sample or at-sea surveys. The new HY value was used to derive date-corrected estimates of contemporary and historic R -values. Similar corrections applied by Beissinger & Peery (2007) in central California were found to result in only small biases in R estimates when incorporating annual variation in timing of breeding in simulation analyses (Peery et al. 2007). Thus, we considered that this correction provided the best estimate of R for both historic and contemporary productivity because it accounted for the approximate proportion of individuals fledged at the time of collection or observation.

Because the number of observations of individual birds used to estimate contemporary R -values was considerably larger than that available for the historic estimate ($n = 1522$ and 174, respectively), we used a bootstrapping technique where 10 000 random subsamples of date-corrected HY/AHY ratios were drawn with replacement from the contemporary data set. We then examined where the historic R estimate fell within this distribution of contemporary R -values, with the p -value indicating the proportion of contemporary R estimates that were greater than the historic R estimate.

Feather sample collection and isotope analysis. Stable isotopes in breast feathers of 64 HY murrelets were measured from specimens collected in the Salish Sea from 1854 to 2002 ($n = 34$) from 10 museum collections (see 'Acknowledgements' for a complete list of museums from which feather samples and age ratios were obtained) and from feathers collected during at-sea captures conducted in Desolation Sound in 2008 ($n = 30$).

Isotope analysis was conducted at the Queen's Facility for Isotope Research, Kingston, Ontario, Canada. Before analysis, feathers were washed in 2:1 chloroform: methanol solution for 24 h, rinsed in fresh chloroform:methanol solution, and left to air-dry for 48 h. Between 0.20 to 0.40 mg of each feather sample were loaded into a tin capsule, then combusted and oxidized in a TC elemental analyzer and introduced online into a Finnigan MAT Delta Plus XL isotope ratio mass spectrometer. Two in-house standards were run to quantify measurement error—EIL 61 KNO_3 and an organic standard, domestic chicken *Gallus gallus* blood—and duplicate samples were run from the same feather sample to produce a mean ($\pm \text{SD}$) difference or repeatability, which was $\pm 0.3\%$. Nitrogen isotope ratios are expressed relative to air as δ units (‰), where $\delta^{15}\text{N} = [({^{15}\text{N}}/{^{14}\text{N}}_{\text{sample}})/({^{15}\text{N}}/{^{14}\text{N}}_{\text{air}}) - 1] \times 1000$.

Nestling diet statistical analysis and interpretation. We examined the variation in HY breast feather $\delta^{15}\text{N}$ using a generalized linear mixed-effects model (GLMM) with restricted maximum likelihood protocol

(REML), with year as a fixed effect and site as a random effect.

To relate changes in feather isotopes to changes in nestling diet quality, we reviewed $\delta^{15}\text{N}$ and energy content (kJ fish $^{-1}$) values of potential prey. Potential prey items likely present either currently or historically in the Georgia Basin included salmon species (*Salmonidae*), Pacific herring *Clupea pallasi*, smelt species (*Osmeridae*), northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and Pacific sand lance *Ammodytes hexapterus*. We used isotope values from prey samples collected during the nesting period (June to August; Nelson & Hamer 1995, McFarlane Tranquilla et al. 2003), and from California (Becker et al. 2007), Oregon (Miller 2006), and British Columbia (Janssen 2009). To determine whether a change in $\delta^{15}\text{N}$ values in feathers indicated a change in nestling diet composition, we calculated a mean difference in $\delta^{15}\text{N}$ values for each potential prey item relative to sand lance, based on within-study differences in $\delta^{15}\text{N}$. Differences in $\delta^{15}\text{N}$ values were calculated for fish from within the same study to avoid sampling variation related to geographic location (Kline 1999) and sample preparation (Søreide et al. 2006). Observations of fish holding behaviour suggest that fish between 80 and 100 mm are the most common size range of fish fed to nestlings, although nestlings are also fed prey between 60 and 135 mm (Burkett 1995, Kuletz 2005, Janssen 2009). We therefore used energetic values of potential prey species 80 to 100 mm in length from published sources to provide a relative index of energy content between prey types. Due to the scarcity of published $\delta^{15}\text{N}$ values of potential prey species, we used $\delta^{15}\text{N}$ values from forage fish between 60 and 140 mm. We report both energy content and the number of sand lance deliveries required to equal a single delivery of each prey species (see Table 1).

RESULTS

Productivity

Bootstrapped estimates of contemporary (1994 to 2001) murrelet productivity from random subsamples of 174 observations ranged from 0.13 to 0.37 offspring per adult or subadult. The contemporary estimate obtained by pooling all data ($n = 1522$) from 1994 to 2001 was 0.21 ± 0.03 ($\pm 1 \text{ SE}_R$), falling at about the center of the bootstrapped distribution (Fig. 1). In comparison, the historic value of R estimated from data collected during the period 1860 to 1950 ($n = 174$) was 0.35 ± 0.01 , which was $>99.99\%$ of the bootstrapped contemporary estimates ($p = 0.0011$; Fig. 1).

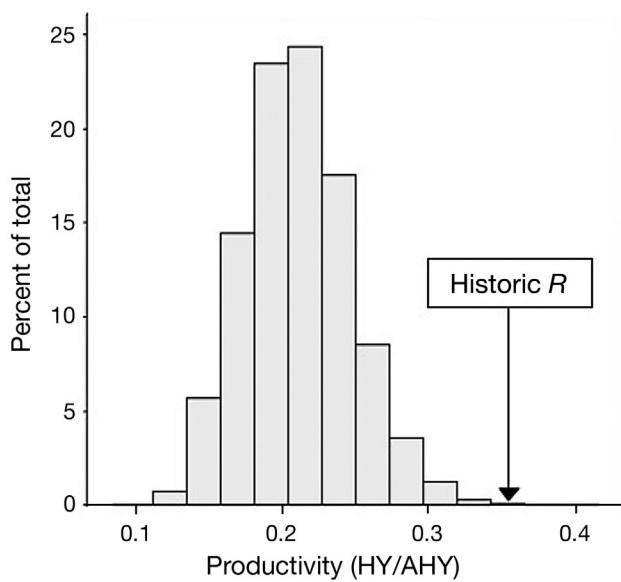


Fig. 1. *Brachyramphus marmoratus*. Distribution of contemporary (1994–2001) marbled murrelet productivity (number of offspring per adult or subadult; R) estimates generated from random subsampling of at-sea survey observations in Desolation Sound, British Columbia (repeated 10 000 times; subsample $n = 174$). The historic (1860–1950) R estimate generated from museum collections ($R = 0.35 \pm 0.01$ SER) was significantly higher than the contemporary distribution ($p = 0.0011$, $n = 174$). HY: hatch-year; AHY: after-hatch-year

Nestling diet

Our GLMM with year as a fixed effect and site as a random effect found a strong negative trend in $\delta^{15}\text{N}$ values over time in murrelet feathers grown in the nest, indicating a drop in nitrogen by 2.6‰ over 154 yr (slope estimate for year = -0.017 , $\text{SE} = 0.0028$, $r^2 = 0.38$, $t = -6.04$, $p < 0.0001$; Fig. 2). Based on previously published and unpublished values, the total range of $\delta^{15}\text{N}$ values between the highest and lowest trophic level prey species was 2.1‰ (Table 1). Pacific sand lance had the lowest $\delta^{15}\text{N}$ value of the potential prey species considered, and salmon species had the highest. Sand lance also had the lowest energy content per individual fish (kJ fish^{-1}), and northern anchovy, Pacific sardine and Pacific herring had the highest (Table 1).

DISCUSSION

Our comparisons of age ratios from museum specimens and at-sea surveys suggest that the productivity of murrelets in the Salish Sea has declined by nearly 50% over the past 150 yr. These results corroborate several recent studies suggesting that contemporary rates of reproduction in murrelets have declined

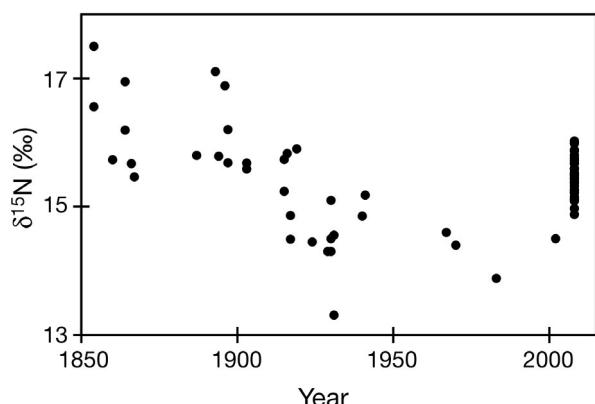


Fig. 2. *Brachyramphus marmoratus*. Stable-nitrogen isotope ($\delta^{15}\text{N}$) values in hatch-year marbled murrelet breast feathers from the Salish Sea collected between 1854 and 2008 ($n = 64$). Samples from 2008 were collected in Desolation Sound, British Columbia, from live birds; all other feather samples were from museum specimens. The slope estimate of year from a general linear mixed effects model was -0.017 ± 0.0028 ($\pm \text{SE}$; see 'Results' for full details)

throughout their range over the last century. Estimates of historic productivity in California (0.30; Beissinger & Peery 2007), together with our estimate of historic productivity from the Salish Sea (0.35), are both much higher than more recent estimates from California, Alaska, and British Columbia. Beissinger & Peery (2007) used museum collections and contemporary surveys to infer a decline in murrelet productivity of nearly an order of magnitude in central California between 1892 and 2003 (0.30 to 0.032). In Alaska, Anderson & Beissinger (1995) found average age ratios of 0.016 during surveys conducted in 1993, and Kuletz (2005) reported similar values (average = 0.043) for the period 1995 to 1999. In Desolation Sound, Lougheed et al. (2002) reported average age ratios of 0.13 from 1996 to 1998, and we report similar values for the same area from 1994 to 2001 (0.21). Low productivity estimates might be expected because murrelets are a relatively long-lived species that may defer breeding until several years of age, and produce a maximum of only one young per year (Piatt et al. 2007). However, the available evidence now suggests that productivity estimates based on recent data are substantially lower than those estimated from historic data in the Salish Sea and central California.

Although other demographic rates may also have changed through time, much evidence now suggests that murrelet population declines have, at least in part, been facilitated by a reduction in reproductive success over time. Annual survival estimates from mark-recapture studies (Cam et al. 2003, Peery et al. 2006) are similar or higher to that expected based on relationships of survival, adult size, and clutch size within the

Table 1. Stable-nitrogen isotope ($\delta^{15}\text{N}$) and energetic (kJ fish $^{-1}$) values for potential prey items of marbled murrelet nestlings. $\delta^{15}\text{N}$ values of fish (60 to 140 mm length) are reported relative to $\delta^{15}\text{N}$ values of Pacific sand lance. Differences were calculated between samples from the same study, and were then used to generate the mean difference across studies. Energetic values are for average-sized nestling prey items (80 to 100 mm length). 'Sand lance delivery equivalent' is the number of single sand lance deliveries to the nest required to equal a single delivery of a given prey species; 'Source' indicates the source for $\delta^{15}\text{N}$ and energetic values, respectively

Prey species	Mean $\delta^{15}\text{N}$ difference	Energy content (kJ fish $^{-1}$)	Sand lance delivery equivalent	Source	
				$\delta^{15}\text{N}$	Energetic values
Salmon species	2.1	24	2.4	Miller (2006) ^a	Anthony et al. (2000)
Smelt species	1.7	40	4.0	Miller (2006) ^a	Anthony et al. (2000)
Pacific herring	1.7	32	3.2	Miller (2006) ^a	Foy & Norcross (1999)
Pacific sardine	1.3	58	5.8	Becker et al. (2007) ^b	Dahdul & Horn (2003) ^c
Northern anchovy	1.2	58	5.8	Miller (2006) ^a , Janssen (2009) ^d , Becker et al. (2007) ^b	Janssen (2009) ^d
Pacific sand lance	0	10	1.0	Miller (2006) ^a , Janssen (2009) ^d , Becker et al. (2007) ^b	Janssen (2009) ^d

^aCrescent City, California to Newport, Oregon; ^bAño Nuevo Bay, Monterey Bay, and Farralones, California; ^cAnchovy and sardine are expected to have equal energy content; ^dDesolation Sound, British Columbia

Alcidae (De Santo & Nelson 1995). Additionally, Beissinger & Peery (2007) found that AHY survival did not differ between contemporary and historic estimates, while productivity declined significantly over the same time period. Taken together, these studies imply that the observed declines in age ratios may be the result of murrelet populations currently experiencing lower reproductive rates than during the first half of the last century.

Our results also provide evidence that the diet of nestling murrelets has changed over the past 150 yr. Stable-nitrogen isotopes from HY breast feathers declined by 2.6‰ from 1854 to 2008 (Fig. 2). In marine food webs, $\delta^{15}\text{N}$ increases between trophic levels (Hobson et al. 1994). Thus, the negative trend in $\delta^{15}\text{N}$ indicates a decline in nestling trophic feeding level. The magnitude of this estimated decline (2.6‰) corresponds to the full range of $\delta^{15}\text{N}$ values estimated across potential prey species, where the difference between the lowest and the highest $\delta^{15}\text{N}$ values was 2.1‰ (Table 1). Contemporary diet studies consistently report Pacific sand lance as comprising a large proportion of nestling diet, and also list northern anchovy and Pacific herring as important prey (Burkett 1995, Kuletz 2005, Janssen 2009). Our results suggest that, in the Salish Sea, the proportion of lower trophic level species such as sand lance have likely increased in nestling diet over the past 150 yr, whereas higher trophic level species, such as Pacific herring and northern anchovy, or species now rare or missing from the ecosystem (including Pacific sardine, smelt species, and eulachon *Thaleichthys pacificus*), probably comprised a greater proportion of the diet historically.

A diet shift towards lower trophic level prey could have important energetic consequences for nestlings.

For example, Pacific sand lance had the lowest energetic value of all potential prey species we considered, whereas energy content generally increased in species at higher trophic levels (Table 1). In contrast, the 2 most common nestling prey species other than sand lance, Pacific herring and northern anchovy, had approximately 3 and 6 times more energy per fish, respectively (Table 1). Because nestlings receive an average of only 3 single-fish feedings per day (Nelson & Hamer 1995), and nests are often 12 to 100 km from foraging locations (Hull et al. 2001), it seems unlikely that parents can compensate for reductions in the availability of high quality prey by increasing foraging effort at lower trophic levels and increasing frequency of energetically expensive, high predation-risk feeding trips (Stearns 1992, Kuletz 2005). Additionally, there is some evidence that the average size of sand lance fed to nestlings is smaller than the average length of other prey types (anchovy and herring) (Kuletz 2005, Janssen 2009). If this was also the case historically, then our relative index of diet quality (Table 1) is likely conservative and may underestimate the difference in energy content between prey types. Thus nestlings fed primarily sand lance during the last few decades probably experienced much lower energy-provisioning rates than nestlings historically fed higher trophic level prey.

Among other alcids, energy-provisioning rate is often positively related to nestling growth (e.g. Bertram et al. 2002, Romano et al. 2006) which, in turn, is positively associated with chick-rearing success and overall reproductive success (e.g. Litzow et al. 2002, Wanless et al. 2005). Additionally, diet quality of nestlings and fledglings was positively associated with growth and body condition of HY murrelets in Desola-

tion Sound, suggesting that diet composition during development may have important consequences for juvenile survival (Janssen 2009). These studies, together with our results, provide some support for the hypothesis that a shift away from energetically superior, high trophic level prey species may have negatively influenced the reproductive success and population growth of murrelets in the Salish Sea.

Our results suggest that concurrent declines in nestling diet quality and reproductive success have occurred in the Salish Sea over the past 150 yr. These declines may be due to changes in the distribution and abundance of high quality prey species (e.g. Becker & Beissinger 2006, Becker et al. 2007) or changes in the timing of peak availability of these species (e.g. Suryan et al. 2006). Fisheries data provide clear evidence of changes in distribution, abundance, and peak timing in a number of higher $\delta^{15}\text{N}$, energetically superior fish species, particularly Pacific herring, Pacific sardine, eulachon, and a number of salmon species in the Georgia Basin over the past 100 yr (Beamish et al. 2004, Therriault et al. in press). Although the effects of commercial fisheries, climate, and the indirect effects of humans on murrelet prey remain largely unstudied, we suggest that future research in this area is essential for developing reliable recovery plans that address both marine and terrestrial impacts on murrelet populations.

Our use of age ratios as an index of productivity relies on several key assumptions and cautions addressed in detail in the following studies. In California, evidence suggests that North American collectors were unlikely to purposefully target one age class over another, that one age class was not more easily collected than the other (Beissinger & Peery 2007), and that biases arising from mistakes in aging are negligible (Peery et al. 2007). Lougheed et al. (2002) suggested that age ratios in Desolation Sound may be biased low because of differences in the timing and rates of emigration of HY and AHY birds throughout the breeding season. Interestingly, their age ratios corrected for emigration during the period 1996–1998 (0.13) were much lower than our uncorrected estimate for 1994–2001 (0.21), and correspond to the lower tail of the contemporary R distribution (Fig. 1), leading us to believe that our R -value is a conservative estimate of contemporary productivity.

Additionally, our use of age ratios generated from both at-sea surveys and collection requires that these 2 methods result in comparable productivity estimates. Beissinger & Peery (2007) found nearly identical age ratios from at-sea captures where individual birds were dip-netted from a small boat and at-sea surveys where birds were observed from a distance. Our at-sea surveys were conducted in the nearshore waters and

fjords of Desolation Sound, and represent similar areas and conditions which would have been accessible to museum collectors throughout the Salish Sea. We suggest that museum collectors approaching murrelets likely obtained a sample representative of the Salish Sea murrelet population comparable to that obtained by at-sea surveys in Desolation Sound, resulting in comparable methods for generating age ratios. Finally, it is imperative to clarify that both historic and contemporary HY/AHY age ratios do not provide true estimates of fecundity, as they include non-breeding AHY birds, which cannot be distinguished from breeding AHY birds. Thus age ratio results should only be used as a comparative index of productivity over time.

The use of nitrogen isotopes as indicators of diet is also subject to several issues which need to be addressed. It has been suggested that variation in $\delta^{15}\text{N}$ may be due to factors unrelated to diet, such as prevalence of nitrates, horizontal advection, and El Niño events, which could cause shifts in isotope signatures at the prey base. Although we were unable to test this directly, previous studies have found little change in zooplankton $\delta^{15}\text{N}$ in central California over a 50-yr period (Rau et al. 2003), and no evidence of correlation between adult murrelet $\delta^{15}\text{N}$ signatures in the Salish Sea and large-scale ocean climate variables over the past century (Norris et al. 2007). It has also been suggested that physiological factors such as nutritional status and growth can potentially complicate the dietary interpretation of $\delta^{15}\text{N}$ signatures (Williams et al. 2007, Sears et al. 2009). Sears et al. (2008) found that both growth and food restriction in captive rhinoceros auklet *Cerorhinca monocerata* chicks resulted in 0.37 to 0.55% depletion in $\delta^{15}\text{N}$. This effect is small relative to the change in $\delta^{15}\text{N}$ values in nestling breast feathers seen in the present study (−2.6%). Sears et al. (2008) suggested that the variability of $\delta^{15}\text{N}$ feather signatures seen in wild birds due to differences in diet likely obscures the magnitude of the effect of nutritional status, and does not invalidate the use of feather isotopes in making ecological inferences. Thus, we are confident that the majority of variation in $\delta^{15}\text{N}$ values presented in the present study can be attributed to variation in murrelet nestling diet composition.

To date, murrelet conservation efforts have been focused strongly on protecting terrestrial nesting habitat, the loss of which is a significant threat faced by many populations, particularly in the Salish Sea (Piatt et al. 2007). However, murrelets spend most of their lives foraging in nearshore waters where the distribution and abundance of energetically superior, high trophic level prey species have changed over the past 100 yr. Declines in adult and nestling trophic feeding level over the past century have also now been documented in the Salish Sea over this same time period

(Norris et al. 2007, present study). $\delta^{15}\text{N}$ in the pre-breeding diet of adult murrelets decreased by 2.0‰ between 1889 and 1996 (Norris et al. 2007), and also decreased in nestling diets by 2.6‰ between 1854 and 2008 (present study). In California, $\delta^{15}\text{N}$ in adult pre-breeding diets decreased by 1.4‰ between 1895 and 2002 (Becker & Beissinger 2006). Overall, these declines represent decreases in trophic feeding level in both adult and nestling murrelets that may influence reproductive success via their influence on egg production (Becker & Beissinger 2006, Janssen et al. 2009) and fledging success (Becker et al. 2007, Janssen 2009). However, due to the secretive nesting behaviour of murrelets, it has been difficult to document reproductive success in relation to diet quality. As we and others (Becker & Beissinger 2006, Beissinger & Peery 2007, Norris et al. 2007) have shown, museum specimens can provide valuable information on long-term changes in reproductive success and diet that can fill gaps in knowledge based solely on contemporary fieldwork and observations. New insights based on this work add to a growing body of evidence suggesting that the successful recovery of marbled murrelets will require the conservation of high quality foraging areas as well as nesting habitat.

Acknowledgements. We thank the Field Museum (Chicago), Royal BC Museum (Victoria), Smithsonian National Museum of Natural History (Washington), National Museum of Ireland, University Museum of Zoology (Cambridge), Canadian Museum of Nature (Ottawa), Museum of Comparative Zoology (Harvard University), American Museum of Natural History (New York), Cowan Museum (University of British Columbia), and San Diego Museum of Natural History for their generous provision of feather samples and age ratio data. K. Klassen kindly assisted with stable isotope analysis and G. Mitchell provided generous statistical support. Funding for this project was provided by the BC Forest Science Program (P.A., D.R.N., D.B.), Natural Sciences and Engineering Council (D.R.N., P.A., S.G., M.H.J., T.K.K.), Canadian Foundation for Innovation (T.K.K.), and the Ontario Government (T.K.K.). All field work was approved by the animal care committee at the University of Guelph.

LITERATURE CITED

Anderson HL, Beissinger SR (1995) Preliminary observations on juvenile:adult ratios of marbled murrelets in Auke Bay, southeast Alaska. *Northwest Nat* 76:79–81

Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *J Exp Mar Biol Ecol* 248:53–78

Beamish RJ, Benson RM, Sweeting RM, Neville CM (2004) Regimes and the history of the major fisheries off Canada's west coast. *Prog Oceanogr* 60:355–385

Becker BH, Beissinger SR (2006) Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conserv Biol* 20:470–479

Becker BH, Peery MZ, Beissinger SR (2007) Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. *Mar Ecol Prog Ser* 329:267–279

Beissinger SR, Peery MZ (2007) Reconstructing the historic demography of an endangered seabird. *Ecology* 88: 296–305

Bertram DF, Columbia T, Davoren GK, Harfenist A, Brown J (2002) Short visits reveal consistent patterns of interyear and intercolony variation in seabird nestling diet and performance. *Can J Zool* 80:2190–2199

Bower JL (in press) Changes in marine bird abundance in the Salish Sea: 1975–2007. *Mar Ornithol* 37

Burger AE (2002) Conservation assessment of marbled murrelets in British Columbia: a review of the biology, populations, habitat associations, and conservation. CWS, Pacific and Yukon Region, BC Tech Rep Ser No. 387

Burkett EB (1995) Marbled murrelet food habits and prey ecology. In: Ralph CJ, Hunt GL, Raphael MG, Piatt JF (eds) *Ecology and conservation of the marbled murrelet*. US Dep Agric For Serv Gen Tech Rep PSW-152, p 223–246

Cam E, Lougheed LW, Bradley RW, Cooke F (2003) Demographic assessment of a marbled murrelet population from capture-mark-recapture and radio telemetry data. *Conserv Biol* 17:1118–1126

Caughley G (1994) Directions in conservation biology. *J Anim Ecol* 63:215–244

Dahdul WM, Horn MH (2003) Energy allocation and postnatal growth in captive elegant tern (*Sterna elegans*) chicks: responses to high- versus low-energy diets. *Auk* 120: 1069–1081

Davoren GK, Montevecchi WA (2003) Consequences of foraging trip duration on provisioning behaviour and condition of common murres *Uria aalge*. *J Avian Biol* 34:44–53

De Santo TL, Nelson SK (1995) Comparative reproductive ecology of the Auks (family alcidae) with emphasis on the marbled murrelet. In: Ralph CJ, Hunt GL, Raphael MG, Piatt JF (eds) *Ecology and conservation of the marbled murrelet*. US Dep Agric For Serv Gen Tech Rep PSW-152, p 33–47

Foy RJ, Norcross BL (1999) Spatial and temporal variability in the diet of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska. *Can J Zool* 77:697–706

Green RE (1995) Diagnosing causes in bird population declines. *Ibis* 137:S47–S55

Harfenist A (1995) Effects of growth rate variation on fledging of rhinoceros auklets *Cerorhinca monocerata*. *Auk* 112: 60–66

Hedd A, Bertram DF, Ryder JL, Jones IL (2006) Effects of interdecadal climate variability on marine trophic interactions: rhinoceros auklets and their fish prey. *Mar Ecol Prog Ser* 309:263–278

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 84:9–18

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798

Hull CL, Kaiser GW, Lougheed C, Lougheed L, Boyd S, Cooke F (2001) Intraspecific variation in commuting distance of marbled murrelets (*Brachyramphus marmoratus*): ecological and energetic consequences of nesting further inland. *Auk* 118:1036–1046

Janssen MH (2009) Diet composition and breeding success in a threatened Pacific seabird, the marbled murrelet (*Brachyramphus marmoratus*). MSc thesis, University of Guelph, ON

Janssen MH, Arcese P, Kyser TK, Bertram DF, McFarlane- Tranquilla L, Williams TD, Norris DR (2009) Pre-breeding

diet, condition, and timing of breeding in a threatened seabird, the marbled murrelet *Brachyramphus marmoratus*. *Mar Ornithol* 37:33–40

Kline TC Jr (1999) Temporal and spatial variability of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ in pelagic biota of Prince William Sound, Alaska. *Can J Fish Aquat Sci* 56:94–117

Kuletz KJ (2005) Foraging behaviour and productivity of a non-colonial seabird, the marbled murrelet (*Brachyramphus marmoratus*), relative to prey and habitat. PhD thesis, University of Victoria, BC

Litzow MA, Piatt JF, Prichard AK, Roby DD (2002) Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* 132:286–295

Lougeed C, Lougeed LW, Cooke F, Boyd S (2002) Local survival of adult and juvenile marbled murrelets and their importance for estimating reproductive success. *Condor* 104:309–318

McFarlane Tranquilla L, Williams T, Cooke F (2003) Using vitellogenin to identify interannual variation in breeding chronology of marbled murrelets (*Brachyramphus marmoratus*). *Auk* 120:512–521

Miller TW (2006) Trophic dynamics of zooplankton and nekton in the Northern California current ecosystem: an integrated approach to using diet and stable isotope analysis. MS thesis, Oregon State University, Corvallis, OR

Morley YM, Ydenberg RC (1997) Intra-specific variability in nestling growth and fledging behavior of Cassin's auklets *Ptychoramphus aleuticus* at Triangle Island, British Columbia. *Condor* 99:361–371

Nelson SK (1997) The marbled murrelet (*Brachyramphus marmoratus*). In: Poole A, Gill F (eds) *The birds of North America*. Academy of Natural Sciences and American Ornithologist's Union, Washington, DC

Nelson SK, Hamer TE (1995) Nest success and the effects of predation on marbled murrelets. In: Ralph CJ, Hunt GL, Raphael MG, Piatt JF (eds) *Ecology and conservation of the marbled murrelet*. US Dep Agric For Serv Gen Tech Rep PSW-152, p 89–97

Norris K (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *J Appl Ecol* 41:413–426

Norris DR, Arcese P, Preikshot D, Bertram DF, Kyser TK (2007) Diet reconstruction and historic population dynamics in a threatened seabird. *J Appl Ecol* 44:875–884

Peery MZ, Beissinger SR, Newman SH, Burkett EB, Williams TD (2004) Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. *Conserv Biol* 18:1088–1098

Peery MZ, Becker BH, Beissinger SR (2006) Combining demographic and count-based approaches to identify source–sink dynamics of a threatened seabird. *Ecol Appl* 16:1516–1528

Peery MZ, Becker BH, Beissinger SR (2007) Age ratios as estimators of productivity: testing assumptions on a threatened seabird, the marbled murrelet (*Brachyramphus marmoratus*). *Auk* 124:224–240

Piatt JF, Kuletz KJ, Burger AE, Hatch SA and others (2007) Status review of the marbled murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia. US Geological Survey Open-File Rep 2006-1387

Ralph CJ, Hunt GL, Raphael MG, Piatt JF (1995) Ecology and conservation of the marbled murrelet. US Dep Agric For Serv Gen Tech Rep PSW-152

Rau GH, Ohman MD, Pierrot-Bults A (2003) Linking climate variability to nitrogen dynamics off central California: a 50 year record of $^{15}\text{N}/^{14}\text{N}$ in CalCOFI zooplankton. *Deep-Sea Res II* 50:2431–2447

Ricklefs RE (1997) Comparative demography of new world populations of thrushes (*Turdus* spp.). *Ecol Monogr* 67: 23–24

Romano MD, Piatt JF, Roby DD (2006) Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. *Waterbirds* 29:407–414

Sears J, Hatch SA, O'Brien DM (2008) Disentangling effects of growth and nutritional status on seabird stable isotope ratios. *Oecologia* 159:41–48

Sørensen JE, Tamelander T, Hop H, Hobson KA, Johansen I (2006) Sample preparation effects on stable C and N isotope values: a comparison of methods in Arctic marine food web studies. *Mar Ecol Prog Ser* 328:17–28

Stearns SC (1992) *The evolution of life histories*. Oxford University Press, New York

Suryan RM, Irons DB, Brown ED, Jodice PGR, Roby DD (2006) Site-specific effects on reproductive success of an upper trophic-level marine predator: bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. *Prog Oceanogr* 68:303–328

Theriault TW, Hay DE, Schweigert JF (in press) Biological overview and trends in pelagic forage fish abundance in the Salish Sea (Strait of Georgia, British Columbia). *Mar Ornithol* 37

Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294:1–8

Williams CT, Buck CL, Sears J, Kitaysky AS (2007) Effects of nutritional restriction on nitrogen and carbon stable isotopes in growing seabirds. *Oecologia* 153:11–18

Ydenberg RC, Clark CW, Harfenist A (1995) Intraspecific fledgling mass variation in the Alcidae, with special reference to the seasonal fledgling mass decline. *Am Nat* 145:412–433

*Editorial responsibility: Jeffrey Seminoff,
La Jolla, California, USA*

*Submitted: April 14, 2009; Accepted: August 11, 2009
Proofs received from author(s): September 10, 2009*