Journal of Applied Ecology 2007
44, 875–884

Diet reconstruction and historic population dynamics in a threatened seabird

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Summary

1. For the overwhelming majority of species, we lack long-term information on the dynamics of populations. As a consequence, we face considerable uncertainty about how to discriminate among competing hypotheses of population decline and design conservation plans.

2. The marbled murrelet *Brachyramphus marmoratus* is a small seabird that nests in coastal old-growth forest but feeds year-round in near-shore waters of the north-eastern Pacific. Although a decline in nesting habitat is the primary reason why marbled murrelets are listed as threatened in Canada, nest predation and food availability may also influence population abundance. To examine the hypothesis that murrelet populations are influenced by variation in diet quality, we analysed stable-carbon and -nitrogen isotopes in feathers of museum specimens collected in the Georgia Basin, British Columbia.

3. Between 1889 and 1996, we found a decline in stable isotopic signatures that was approximately equal to a 62% drop in trophic feeding level. We also found that the estimated proportion of fish in murrelet diet was related closely to murrelet abundance over the past 40 years, as estimated from volunteer surveys. Using these isotopic data, we modelled population size as a function of variation in reproductive rate due to changes in diet quality and found that our model matched closely the 40-year field estimates. We then applied our 107-year isotopic record to the model to back-cast estimates of population growth rate to 1889.

4. Our results suggest that, up to the 1950s, murrelet populations in the Georgia Basin were capable of growing and were probably limited by factors other than diet quality. After this period, however, our results imply that murrelets were often, but not solely, limited by diet quality.

5. *Synthesis and applications*. Protecting nesting habitat may not be sufficient to rebuild populations of this highly secretive and threatened seabird and recovery might also require the restoration of marine habitat quality, as well as a better understanding of how ocean climate affects prey abundance and reproductive rate. Combined with contemporary demographic data, stable isotope analysis of historic samples provides a unique opportunity to reconstruct population histories for species where we lack long-term information.

Key-words: back-cast, *Brachyramphus marmoratus*, Pacific coast, population decline, seabirds, stable isotopes, trophic level

Journal of Applied Ecology (2007) **44**, 875–884
doi: 10.1111/j.1365-2664.2007.01329.x

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Introduction

Identifying factors that limit the abundance of animals is a critical step towards diagnosing the causes of population decline. For the overwhelming majority of species, however, we have little information about the historic dynamics of populations. As a consequence, we face considerable uncertainty about how to discriminate among competing hypotheses of population trend and how to design reliable conservation plans (Caughley 1994; Jackson *et al.* 2001; Baker & Clapham 2004). Here, we reconstruct a 107-year record of variation in diet for the marbled murrelet *Brachyramphus marmoratus* Gmelin 1789, a threatened seabird that nests in coastal old-growth forest but feeds year-round in near-shore waters of the north-eastern Pacific from California to Alaska (Nelson 1987), to test if diet quality influenced population growth.

Murrelets are highly secretive birds that forage individually or in small groups and nest on the limbs of large trees up to 100 km inland (Nelson 1987; Hull *et al.* 2001). The first nest was discovered in 1974 (Binford, Elliot & Singer 1975), and only about 200 have been described to date (Zharikov *et al.* 2006). Despite these impediments to research, evidence suggests that the availability of suitable nesting habitat in old-growth forest is a key factor limiting murrelet populations over much of their range, and recovery efforts have therefore focused mainly on conserving nesting habitat to promote population persistence (Ralph *et al.* 1995; Burger 2002). Although a decline in nesting habitat is the primary reason why marbled murrelets are listed as threatened in Canada (Burger 2002), nest predation and food availability probably also influence their population growth (Ralph *et al.* 1995; Burger 2002; Peery *et al.* 2004). So far, comprehensive tests of these potentially competing hypotheses have proved technically challenging and hard to sustain financially. Thus, it is possible that while the conservation of nesting habitat is necessary to conserve murrelet populations in future, it may not be sufficient to promote population growth.

We explored the hypothesis that murrelets are limited by feeding conditions at sea (Peery *et al.* 2004), specifically by the availability of forage fish relative to macro-zooplankton. Although macro-zooplankton are not necessarily of higher caloric value than fish (Vermeer & Cullen 1982; Hedd *et al.* 2002), forage fish are expected to be higher-quality prey for seabirds because they are much larger, which results in more energy gained per unit effort. For example, Becker & Beissinger (2006) estimated that a seabird such as the marbled murrelet would have to consume between 45 and 80 euphausiids to equal the energetic value of small forage fish such as a Pacific sardine *Sardinops sadax* or northern anchovy *Engraulis mordax*. Evidence suggests that murrelets are flexible foragers across their breeding range, taking a variety of forage fish and marine invertebrates (primarily macro-zooplankton; Burkett 1995).

To estimate diet, we analysed stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) in feathers of museum specimens collected in the Georgia Basin, a highly exploited marine ecosystem in southern British Columbia, Canada (Pauly *et al.* 1998, 2001; Beamish *et al.* 2004). Both isotopes can be used to trace the structure of marine food webs (Hobson & Welch 1992; Kline & Pauly 1998), with $\delta^{15}N$ showing a stepwise enrichment between trophic levels (DeNiro & Epstein 1981; Post 2002) and $\delta^{13}C$ distinguishing between pelagic and benthic prey (Fry & Shear 1989). Feathers are metabolically inert after growth, and so provide an isotopic signature of diet during the period in which they were grown (Hobson & Wassenaar 1997). Little is known about the diets of murrelets in the Georgia Basin. Munro & Clemens (1931) reported that the stomach contents of four marbled murrelets in Departure Bay contained surfperch spp. (*Cymatogaster*), larval fish, euphausiids spp. and other small invertebrates. Northwest of the Georgia Basin in the Queen Charlotte Islands, Sealy (1975) found that subadult murrelet stomach contents contained 67% sandlance (*Ammodytes* spp.) and 27% euphausiids spp. Sealy (1975) also found that euphausiids spp. were more abundant earlier in the breeding season and presented some evidence that higher trophic level prey were taken preferentially in relation to their relative abundance, leading to the hypothesis that breeding could be influenced by the abundance of forage fish.

We then examined the relationship between predicted diet and murrelet abundance, as estimated from volunteer surveys between 1958 and 2000. Next, we tested whether reproductive rate, driven by variation in diet quality, was sufficient to explain trends in murrelet abundance by comparing a model to estimates of abundance from field observations. Finally, by applying pre-1958 stable isotope values to the model, we back-cast population growth rates to 1889 to ask what effect variation in diet quality might have had on historic population growth rate.

Methods

FEATHER SAMPLING AND STABLE ISOTOPE ANALYSIS

We sampled feathers from adult marbled murrelet specimens in alternate (breeding) plumage ($n = 102$) from nine museums across Canada and the United States. We analysed brown-tipped breast feathers, which are grown during the prebasic moult from March to April (Nelson 1987). Because murrelets begin breeding in late April to early May (Nelson 1987; McFarlane Tranquilla, Williams & Cooke 2003), isotope values from these feathers provide a signature of diet during the late prebreeding or the early breeding period. In the field, we have observed some murrelets that were captured in mid-April in Desolation Sound, south-western British Columbia, growing new breast feathers at the same time as they were developing a brood patch (i.e. suggesting that they are beginning to breed; D. R. Norris and P. Arcese, unpublished data). All museum samples originated from the Georgia Basin (range: 50°43′–47°15′ N, 121°58′–125°29′ W) between 1889 and 1996. Stable isotope analysis was conducted at the Queen's Facility for Isotope Research, Kingston, Ontario. Isotope ratios (R) are expressed in δ units where $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$. δ^{15}N is the ratio of ^{15}N/^{14}N relative to air, and δ^{13}C is the ratio of ^{13}C/^{12}C relative to Pee Dee Belemnite. Before analysis, feathers were washed in 2 : 1 chloroform : methanol solution for 24 h, rinsed in distilled water, and left to air-dry for 48 h. Between 0·10 and 0·15 mg of each feather (including material from the vane and rachis) was weighed in a tin capsule, then combusted and oxidized in a TC Elemental Analyser and introduced online into a Finnegan MAT Delta Plus XL isotope ratio mass spectrometer. During analysis, we ran four standards (reported here as mean ± SD). For carbon, these were the international standard NBS 21 graphite (–27·97‰ ± 0·13, $n = 35$) and an in-house standard UC-1 graphite (–5·77‰ ± 0·22, $n = 28$). For nitrogen, we used the international standard RM 8548 ammonium sulphate (19·86‰ ± 0·40, $n = 43$). For both elements, we also used an in-house keratin-based standard: domestic chicken *Gallus gallus* feathers (δ^{13}C: –19·46‰ ± 0·19; δ^{15}N: 7·7‰ ± 0·34, $n = 25$), which were prepared in the same fashion as murrelet feathers (cut up into small pieces totalling 0·10 and 0·15 mg). All four standards showed very low variability and matched values run previously in our laboratory. We also ran duplicate feather samples from the same murrelet ($n = 51$), which produced a mean (± SE) difference or repeatability of ±0·25‰ (± 0·04) for δ^{15}N and ±0·18‰ (± 0·03) for δ^{13}C.

Some evidence suggests that individuals replace breast feathers sequentially from anterior to posterior (Nelson 1987). Using a subset of birds ($n = 13$), we found no difference between δ^{15}N or δ^{13}C values of breast feathers sampled from the anterior vs. posterior areas of the breast (two-tailed paired t-test, δ^{15}N: $t = 1{\cdot}28$, $P = 0{\cdot}23$; δ^{13}C: $t = -0{\cdot}17$, $P = 0{\cdot}87$), suggesting either that murrelets have similar diets over the prebreeding period or that they moult their breast feathers at similar times. We proceeded to use posterior breast feathers in subsequent analyses. Similar to previous work on this species (Becker & Beissinger 2006; Becker *et al.* 2007), we found no difference in isotopic compositions between males (δ^{15}N mean ± SD: 14·7 ± 1·3; δ^{13}C mean ± SD: –16·2 ± 1·1) and females (δ^{15}N: 14·8 ± 1·3; δ^{13}C: –16·4 ± 1·2; two-tailed t-test, δ^{15}N: $t_{88} = 0{\cdot}60$, $P = 0{\cdot}55$; δ^{13}C: $t_{88} = -0{\cdot}78$, $P = 0{\cdot}44$), so sexes were pooled.

DIETARY MIXING MODEL

We used IsoError (Phillips & Gregg 2001), a dual-isotope (δ^{15}N, δ^{13}C), three-source mixing model, to estimate the relative proportion of prey groups in murrelet diet for each year between 1889 and 1996. Potential prey items (with published or unpublished source) included euphausiid spp. sandlance (Hobson, Piatt & Potocchelli 1994; E. Davies, M. Hifpner, R. C. Ydenberg, unpublished data), Pacific herring *Clupea harengus*, eulachon *Thaleichtys pacificus*, black prickleback *Xiphister atropurpureus*, blackbelly eelpout *Lycodopsis pacifica*, shiner surfperch *Cymatogaster aggregata* (Hobson *et al.* 1994) and amphipod spp. (Hobson, Drever & Kaiser 1999). All prey samples were from coastal British Columbia: Barkley Sound, south-western Vancouver Island (Hobson *et al.* 1994), Triangle Island, northern Vancouver Island (E. Davies, M. Hifpner, R. C. Ydenberg, unpublished data) and Queen Charlotte Islands (Hobson *et al.* 1999). Although there may be some seasonal variation in isotopic signatures in marine food webs (Kline 1999), most prey samples were collected in May or June, just after murrelets moulted feathers. Based on their separation along the two isotopic gradients, prey samples were grouped into three diet sources: forage fish, euphausiids and amphipods. We used a diet-tissue (– feather) fractionation factor of +3·7‰ for δ^{15}N and +1‰ δ^{13}C, the same values used for recent isotope-dietary studies on marbled murrelets (Becker & Beissinger 2006; Becker *et al.* 2007), which are based on diet-tissue isotopic experiments of a closely related species (common murre *Uria aalge*). Minor adjustments (± 2‰) to the diet-tissue fractionation factor value shifted the proportion estimated for each diet group simultaneously and did not affect rankings of prey items in the murrelet diet (as in Becker & Beissinger 2006) nor the relationship between diet and murrelet abundance.

MURRELET ABUNDANCE AND STATISTICAL ANALYSIS

As an index of abundance between 1958 and 2000, we used the number of marbled murrelets reported per hour from the National Audubon Society Christmas Bird Count (CBC; www.audubon.org). Counts were summed annually over 11 areas in the Georgia Basin: Campbell River, Comox, Lasqueti Island, Nanaimo, Nanoose Bay, Parksville/Qualicum Beach, Pender Harbour, Squamish, Sunshine coast, Vancouver and Victoria. CBC counts do not distinguish between age classes. Because the number of observers varied each year, we divided annual estimates by the number of observer hours. Annual estimates were smoothed using LOESS with a second-degree polynomial and 20-year smoothing window. The 20-year smoothing window was chosen because gaps in our isotope data ranged from 1 to 11 years over the 107 years time-series; thus larger windows risked underestimating temporal variation in annual estimates, and narrower windows introduced potential bias due to uneven sampling. Nevertheless, modest adjustments (10–30 years) to the smoothing window had little influence on the results we report here. We first examined changes in isotopic compositions of feathers over time using linear mixed-model regression, with year as both a random factor and fixed trend effect, because there were different numbers of birds sampled in each year. Using Akaike's information criterion (AIC) (Burnham & Anderson 2002), we compared this model with one that had year as a random factor only. Differences between the models were assessed with ΔAICc and Akaike weights (w_i).

Because linear mixed models explained a relatively small portion of the variance, we fitted the isotopic time-series (δ^{15}N and δ^{13}C) using a cubic spline ($\alpha = 1$), allowing us to assess more accurately annual and decadal variation in the data. From this fit, we used predicted isotopic values for each year to estimate the proportion of prey items consumed by murrelets, as calculated by a dual-isotope, three-source mixing model (see above). We explored the relationship between isotope values (as well as predicted diet) and murrelet abundance with linear or quadratic regression.

POPULATION MODEL

We tested if variation in female reproductive rate expressed as a function of diet quality (estimated with stable isotopes) could account for annual variation in CBC estimates between 1958 and 2000. To do so, we followed the method of stock reconstruction for single species assessment using a time-series of abundance estimates outlined by Walters (1986) and Walters & Martell (2004). We modified a simple deterministic model of Beissinger & Nur (1997) by assuming that juvenile ($s_j = 0{\cdot}74$), subadult ($s_s = 0{\cdot}79$) and adult ($s_a = 0{\cdot}88$) survival rates were constant and equal to rates estimated for the Georgia Basin (Cam *et al.* 2003; Steventon, Sutherland & Arcese 2003, 2006). Following these authors, we also assumed that only adult females are able to breed. Thus, with N_a and N_s representing the number of adult and subadult females alive at time t, respectively, we can estimate the total number of females alive prior to breeding at time $t + 1$ (N_{t+1}) as:

$$N_{t+1} = s_a N_a + s_s N_s + s_j b_t N_a \qquad \text{eqn 1}$$

where b_t is the annual fraction of adult females that produce a female juvenile (murrelets produce one egg per year; Nelson 1987). If we assume further that CBC counts estimate N_t, and that adults (N_a) comprise 66% of N_t (expected percentage calculated from an age-structured model with S_a, S_s, S_j as above and assuming $b_t = 0{\cdot}31$, which is the mean value based on δ^{15}N values during the period before the CBC counts), we can estimate a time-series of b_t sufficient to reproduce the CBC counts by rearranging eqn 1 as:

$$b_t = (N_{t+1} - s_a N_a - s_s N_s)/s_j N_a \qquad \text{eqn 2}$$

We used estimates of b_t from eqn 1 to test our prediction that b_t and δ^{15}N (at time t) were related positively (Fig. 1). After fitting this relationship, we next compared estimates of population trend from our model to CBC counts from 1958 to 2000, under the assumption that b_t varied as a function of estimated diet quality. With survival rates constant, our model population therefore grew or declined only as a function of variation in reproductive rate due to diet quality. Thus, starting population size had no influence on population growth or our comparison with CBC counts. Finally, we used isotope values from the entire time-series (including pre-1958) to estimate population growth rate (λ) from 1889 to 1996.

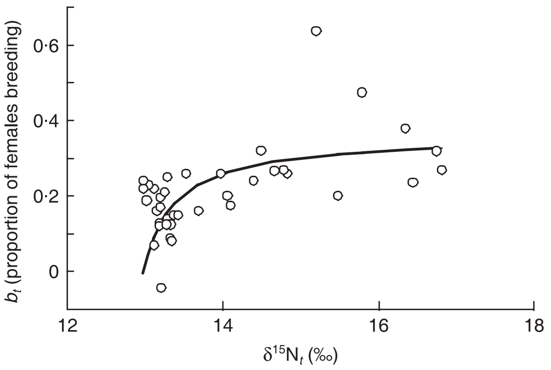

Fig. 1. Estimated variation in the fraction of adult females producing a female fledgling (b_t; from eqn 2) in 38 years from 1958 to 1995 vs. δ^{15}N (at time t) in the breast feathers of marbled murrelets in the Georgia Basin. The solid line represents the predicted fraction of females breeding annually (RS), modelled as a saturating function of δ^{15}N, where $\text{RS} = [(\delta^{15}\text{N} + 12{\cdot}99) \times \text{RS}_{\text{max}}]/(\delta^{15}\text{N} + 12{\cdot}99 + \text{Half Saturation Constant})$. The line is fitted by maximum likelihood, uses a value of $\text{RS}_{\text{max}} = 1{\cdot}05$, a Half Saturation Constant = 0·13, subtracts a constant value of 12·99 from δ^{15}N values, and scales the relationship on the x-axis. Other functions we explored such as the relationship between δ^{15}N and survival fit the data less well and modest variation in scaling had no marked effect on our final model fit to abundance estimated in the field.

Results

From 1889 to 1996, we observed a decline of δ^{15}N values in marbled murrelet breast feathers (fixed effect $b = -0{\cdot}019$, SE = 0·005, $P < 0{\cdot}001$, $r = 0{\cdot}28$, $n = 102$; mixed-model regression; Fig. 2a), suggesting that the mean trophic level of the prebreeding diet has declined over the past century. Evidence also suggested that this model was a better fit compared to a model with random effects only (mixed model: – log L = –165·45, AIC = 323·96, $w_i = 0{\cdot}989$; random effects model: – log L = –159·98, AIC = 332·91, ΔAIC = 8·946, $w_i = 0{\cdot}011$; $G = 5{\cdot}47$, d.f. = 1, $P < 0{\cdot}01$). δ^{15}N values from pre-1900 were 15·6‰ compared to 13·3‰ between 1988 and 1996, implying a 62% drop in trophic level between these time-periods (assuming a mean difference of 3·7‰ between trophic levels). A non-significant trend over time was found in δ^{13}C values from the same feathers (fixed effect $b = -0{\cdot}01$, SE = 0·005, $P = 0{\cdot}06$, $n = 102$; Fig. 2b).

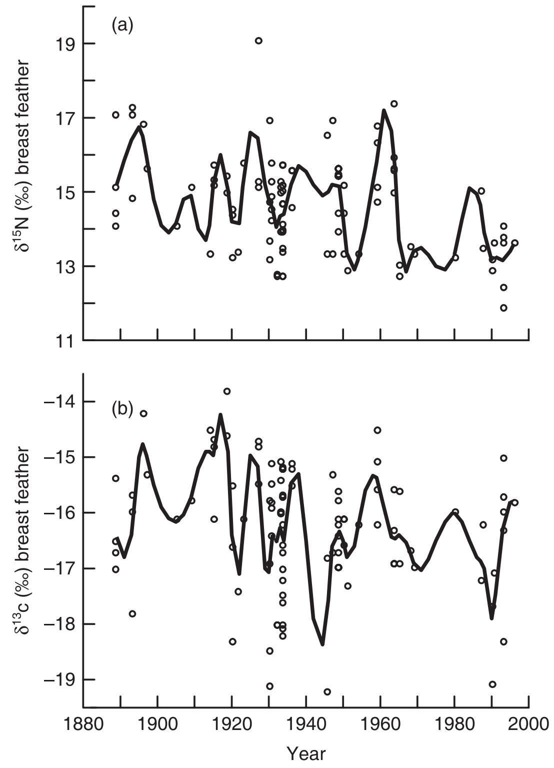

Fig. 2. Variation in the isotopic composition and diet of marbled murrelets in the Georgia Basin from 1889 to 1996. Smoothed cubic spline fit (dark line) of (a) stable-nitrogen isotopes (δ^{15}N) and (b) stable-carbon isotopes (δ^{13}C) in breast feathers (open circles). Using mixed models, we found a significant decline in δ^{15}N (fixed effect $b = -0\cdot019$, SE = 0·005, $P < 0\cdot001$, $r = 0\cdot28$, $n = 102$) and a non-significant trend in δ^{13}C ($b = -0\cdot01$, SE = 0·005, $P = 0\cdot06$, $n = 102$).

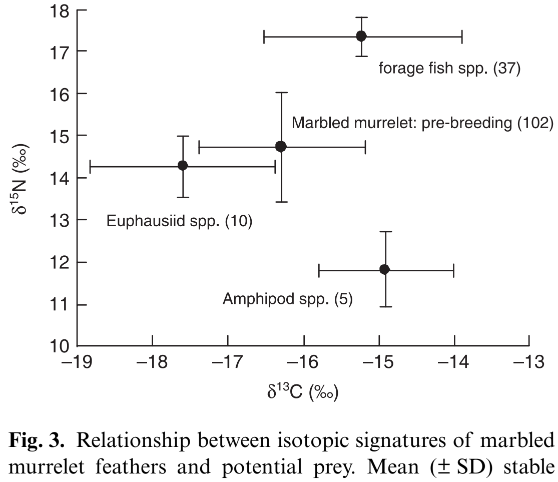

Fig. 3. Relationship between isotopic signatures of marbled murrelet feathers and potential prey. Mean (± SD) stable carbon (δ^{13}C) and stable-nitrogen (δ^{15}N) isotope values of marbled murrelet breast feathers sampled over a 107-year period in the Georgia Basin (subtracting an assumed diet-tissue discrimination factor of 3·7‰ for δ^{15}N and 1·0‰ for δ^{13}C), forage fish, euphausiids and amphipods (sample sizes in brackets).

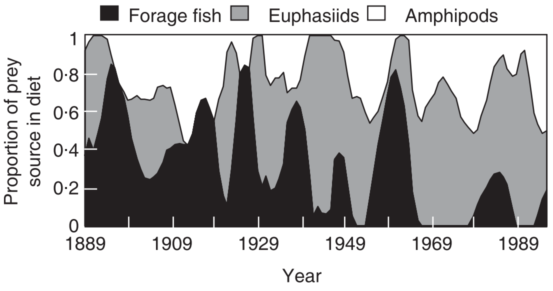

Fig. 4. Diet reconstruction of marbled murrelets over 107 years. The proportion of fish, euphuasiids and amphipods in murrelet diet predicted from a dual isotope (δ^{15}N, δ^{13}C) mixing model (see Methods). Over time, the proportion of fish showed a linear decline ($R^2 = 0\cdot33$, $P < 0\cdot0001$), euphuasiids increased ($R^2 = 0\cdot20$, $P < 0\cdot0001$) and amphipods remained relatively constant ($R^2 = 0\cdot02$, $P = 0\cdot11$).

After adjusting for diet-tissue discrimination, the mean prebreeding diet of all murrelets fell between the isotopic values expected if birds fed exclusively on fish or on euphausiids (Fig. 3). We used a two-isotope, three-source mixing model to reconstruct the proportion of forage fish and zooplankton (euphausiids or amphipods) in murrelet diet over the 107-year period. We found a decline in the proportion of fish, an increase in the proportion of euphausiids, and no change in amphipods (Fig. 4). Fish comprised a mean (± SE) of 61% (± 4·4, $n = 11$) of the diet before 1900, but only 9% (± 6·3, $n = 26$) after 1970. In contrast, euphausiids comprised 27% (± 8·5) of the diet pre-1900, but rose to 61% (± 11·2) post-1970.

To explore the hypothesis that diet influenced murrelet population dynamics, we tested if isotope values and predicted diet composition were related to murrelet abundance in the Georgia Basin, as estimated from surveys conducted between 1958 and 2000 (see Methods). We found that both prebreeding δ^{15}N values and the proportion of fish in the murrelet diet were related closely and positively to CBC counts, with the highest variance explained in abundance when both isotopes (Fig. 5a) and predicted diet (Fig. 5b) were measured 3–4 years previous to murrelet abundance. These striking results suggest that when murrelets fed at higher trophic levels, breeding success increased due to a positive effect of diet on prebreeding condition (Peery *et al.* 2004). A lagged effect of diet on population size is not surprising, because juveniles do not breed until 3–5 years of age (Ralph *et al.* 1995); thus, annual variation in the production of juveniles should influence population size in the postbreeding period directly, but also indirectly via its effect on the total number of females that breed 3–5 years hence (e.g. Lande, Engen & Sæther 2006). Although the highest variance in murrelet abundance was explained by diet measured 3–4 years previously, it is likely that there are also smaller, more immediate effects of changes in diet on population size (as shown by R^2 values in the inset of Fig. 5).

We next compared our estimates of the annual fraction of females producing a juvenile (b_t) from eqn 2 (see Methods) to δ^{15}N in the prebreeding diet. As predicted, this relationship was positive, rising rapidly from values of $b \sim 0$ at δ^{15}N values below 13·5, then rising to an asymptote near $b \sim 0\cdot35$ at δ^{15}N values over

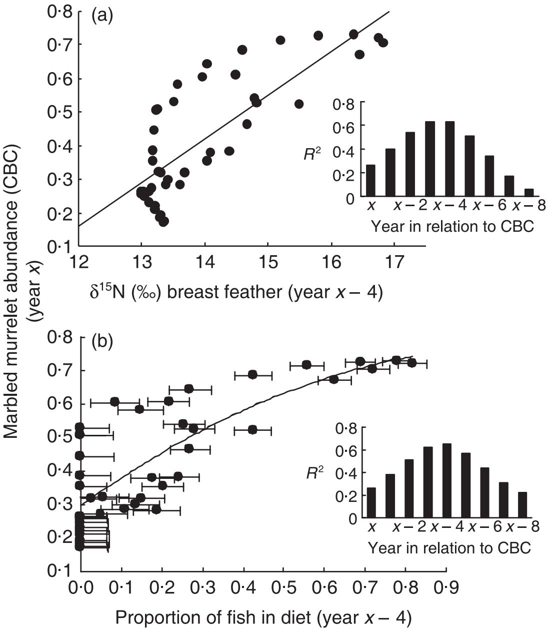

Fig. 5. Relationship between diet and marbled murrelet abundance over the past 43 years. Both (a) δ^{15}N values in breast feathers (R^2 = 0·63, P < 0·0001) and (b) the proportion of fish (± SE) predicted in the diet; (R^2 = 0·65, P < 0·0001) of murrelets (in year x) are significant predictors of abundance 4 years later (year x + 4), as estimated from the National Audubon Society Christmas Bird Count. Insets: in both δ^{15}N (top) and the proportion of fish (bottom), most of the variation (R^2) in murrelet abundance (CBC counts in year x) was explained when variables were measured between 3 and 4 years prior to abundance estimates.

14·5 (Fig. 1). We then fitted this relationship to a saturating curve (Fig. 1). Predicted values of female reproductive rate from this fitted relationship in the last 5 years of our δ^{15}N time-series (1992–96) reached a high of 23% of females breeding successfully with δ^{15}N = 13·61, to a low of 15% with δ^{15}N = 13·17 (Fig. 1). These values closely matched empirical estimates of reproductive rates from radio-tracked murrelets in the Georgia Basin between 1998 and 2001 (0·19–0·23 female offspring/female; Bradley *et al.* 2004).

We then asked if our model, using the fitted relationship between reproductive rate and δ^{15}N, predicted murrelet abundance similar to CBC estimates from the field between 1958 and 1996. We modified a simple, three age-class deterministic model of Beissinger & Nur (1997) and assumed constant rates of adult, subadult and juvenile survival as estimated in the Georgia Basin by Cam *et al.* (2003), such that variation in λ occurred only as a consequence of variation in female reproductive rate. We found that model predictions and CBC estimates of variation in abundance were correlated closely and positively (Spearman's correlation, r_s = 0·74, P < 0·0001, n = 39; Fig. 6a), consistent with the hypothesis that murrelet abundance is influenced by the effects of prebreeding diet quality on reproductive rate.

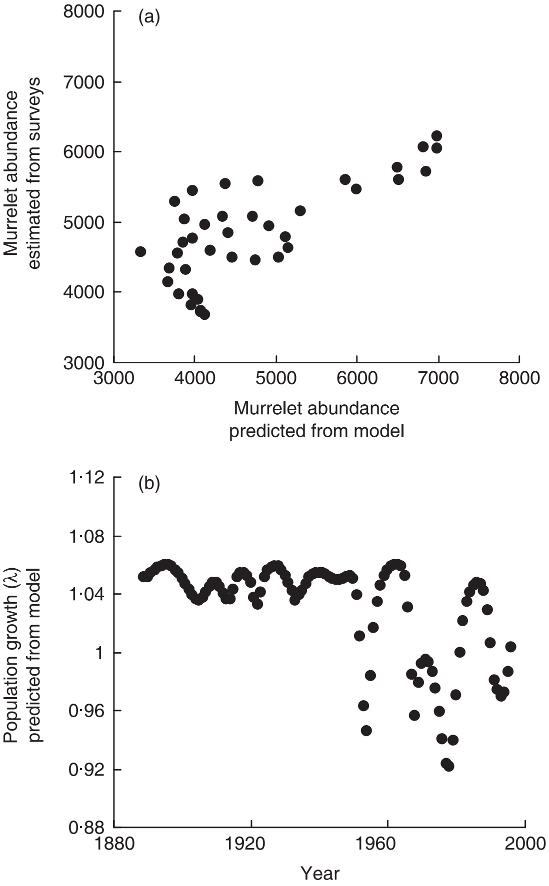

Fig. 6. Historical population dynamics of marbled murrelets. (a) Murrelet abundance estimates from field surveys (as in Fig. 5 but scaled) was correlated highly with abundance predicted from a population model, which is based on the assumption that the proportion of females breeding is a saturating function of δ^{15}N (Fig. 1). (b) Back-cast time-series of population growth (λ) derived from the population model.

To explore the potential population consequences of long-term declines of δ^{15}N values in the murrelet diet, we used our model to back-cast estimated population growth rates (λ) to 1889, when field surveys of abundance were unavailable. Our results suggest that population growth was relatively constant prior to 1950 but fluctuated greatly thereafter (Fig. 6b). These results also imply that murrelet populations in the Georgia Basin were limited by feeding conditions at sea more often after 1950, perhaps as a consequence of over-fishing or regional changes in climate (Pauly *et al.* 1998). In contrast, the relatively high and invariant growth rates prior to 1950 suggest that marine conditions probably played a smaller role in limiting population growth during this period.

Discussion

Our results demonstrate that stable isotopes can be a powerful tool for identifying the effect of trophic feeding level on population dynamics in a species that is both difficult to study and threatened. In the absence of historic data on population trend, there is likely to be considerable uncertainty about the key mechanisms driving population change (Jackson *et al.* 2001). Failing to identify these mechanisms increases the possibility that current conservation actions will be insufficient to prevent future population declines (Baker & Clapham 2004).

The decline in δ^{15}N values in murrelets reported here are even larger than declines recorded in California. In Monterey Bay, δ^{15}N values in murrelet breast feathers sampled from 1895 to 1911 were 1·4‰ higher (38% higher trophic level) during cold conditions and 0·5‰ higher (14% higher trophic level) during warm conditions compared to feathers sampled during equivalent conditions between 1998 and 2002 (Becker & Beissinger 2006). From 1889 to 1996, we estimated that δ^{15}N values declined by 2·3‰ in the Georgia Basin, BC, implying a 62% drop in trophic level. High variation in isotopic signatures over this period (Fig. 2) also led us to ask if diet might influence murrelet numbers via its effect on the annual fraction of females that reproduce successfully. We found a strong correlation between diet and the abundance of murrelets 3–4 years later (Fig. 5). Interestingly, our simple model, which assumed constant survival rates and variation in reproduction linked to isotopic signatures, produced a lag similar to that observed between isotopic signatures in museum specimens and an independent index of abundance from field surveys (Fig. 6a). Overall, our results suggest that variation in diet quality may influence the dynamics of murrelet populations in the Georgia Basin, as has already been shown for colonial breeding alcids in British Columbia (Gjerdrum *et al.* 2003; Hedd *et al.* 2006) and marbled murrelets breeding in California (Peery *et al.* 2004; Becker *et al.* 2007).

Isotopic signatures of archived museum specimens can provide a unique wealth of information for reconstructing historical diets and habitat use (Dalerum & Angerbjörn 2005; Hilton *et al.* 2006). For example, δ^{15}N and δ^{13}C signatures in feathers of northern fulmars *Fulmarus glacialis* in the north-east Atlantic were higher before 1940 compared to 1993, suggesting that this species was feeding on whale offal in the early half of the 20th century (Thompson, Furness & Lewis 1995). Although δ^{15}N values of North Pacific pinnipeds have shown little change over the last half of the 20th century, δ^{13}C values have declined over the same time-period, suggesting a shift in foraging locations or a change in isotopic signatures at the base of the food web (Hirons, Schell & Finney 2001; Hobson *et al.* 2004). Over a longer time-period, changes in δ^{15}N and δ^{13}C signatures in feathers and bone collagen of California condors *Gymnogyps californianus* demonstrated a diet switch from a heavy reliance of marine-derived nutrients during the Pleistocene to exclusively terrestrial-derived nutrients over the past century (Chamberlain *et al.* 2005).

Our results demonstrate a new approach to understanding the dynamics of a little-known species where traditional demographic studies are technically too difficult or costly to advance. Potentially, our method can be applied to a wide range of species in different ecosystems. For example, Levin *et al.* (2006) showed recently that variation in stable-oxygen isotopes (δ^{18}O) in the tooth enamel of east African mammals tracked long-term variation in environmental aridity, suggesting that one might use such data to reconstruct population histories for species limited in their abundance by rainfall (Mduma, Sinclair & Hilborn 1999). In the Chesapeake Bay (USA) an increase in δ^{13}C values in striped bass *Morone saxatillis*, related to shifts in diet or foraging location, have occurred with declines in physical condition (Pruell, Taplin & Cicchelli 2003), raising the possibility that archived tissues, such as scales, might help reconstruct estimates of stock size and population dynamics in this species.

It is possible that long-term isotopic signatures are also influenced by factors unrelated to changes in the diet of marbled murrelets. For example, anthropogenic inputs of atmospheric CO_2 may lower δ^{13}C values in marine food webs (the 'Suess effect'; Gruber *et al.* 1999; Hilton *et al.* 2006). However, we found little (non-significant) trend in δ^{13}C values in breast feathers over time, consistent with our assumption that variation in isotopic ratios was driven mainly by temporal changes in diet. Adjusting δ^{13}C values to account for the Suess effect (estimated as 0·16‰ decline per decade; Quay *et al.* 2003) had the effect of decreasing the predicted proportion of fish estimated in the murrelet diet (Figs 3 and 4), supporting further our conclusion that the trophic feeding level of murrelets has declined over the last century.

The prevalence of nitrates or the degree of vertical or horizontal advection might also cause variation in δ^{15}N values at the base of the food web. However, Rau, Ohman & Pierrot-Bults (2003) showed that δ^{15}N values of zooplankton sampled off the California coast varied only ± 1–2‰ over a 50-year period with no significant trend over time. Schell, Barnett & Vinette (1998) also found that δ^{15}N (and δ^{13}C) values of zooplankton in high-latitude Pacific waters did not vary significantly over 10 years. Despite low variation of isotopic signatures, Rau *et al.* (2003) also provided evidence that zooplankton were enriched in ^{15}N during El Niño years. In contrast, we have found no evidence that δ^{15}N values were correlated with large-scale ocean climate variables, such as the Pacific Decadal Oscillation or Southern Oscillation Index (D. R. Norris, P. Arcese, unpublished data), suggesting either that climatic events had little impact on isotopic signatures at the base of the food web, or that annual variation in δ^{15}N values of zooplankton due to climate was small compared to annual variation in the murrelet diet.

Our interpretation of the positive correlation between murrelet abundance estimated by the CBC and our model assumes that individuals counted each winter in the Georgia Basin represent mainly birds that also breed in the region. Although it is possible that some murrelets wintering in the Georgia Basin breed in northern British Columbia or Alaska, Becker & Beissinger (2006) and Peery *et al.* (2004) found that most marked birds in northern California over-wintered within

300 km of their breeding areas. Although our model suggests that murrelets are influenced by marine conditions our results should be interpreted with caution, given our assumptions of limited movements between the breeding and non-breeding seasons. A priority for future research is to obtain an independent validation of our general model by comparison with other trend estimators, such as more recent radar and at sea surveys. We are also working to test whether the fraction of birds nesting varies annually with diet quality.

It is also possible that our isotopic 'landscape' of prey was not representative of actual murrelet diets as our prey samples were from only three locations. However, the $\delta^{13}C$ and $\delta^{15}N$ values of euphasiid and forage fish did not differ significantly between these locations or between these locations and areas further north (see values in Hobson *et al.* 1994; Kline 1999). This suggests that the isotopic signatures of the prey items that we utilized show relatively low variation along the northwest Pacific coast. Nevertheless, we recognize that additional prey sampling is needed to confirm these relationships, including sampling other fish species and over multiple years and seasons.

Our results emphasize the potential importance of conserving multiple habitats throughout the annual cycle in highly vagile species that are difficult to track year-round (Janzen 1986; Marra, Hobson & Holmes 1998; Cherel *et al.* 2006; Norris & Taylor 2006). For murrelets, our work is consistent with Peery *et al.*'s (2004) conclusion that protecting nesting habitat may be insufficient to promote population recovery. In this case, population recovery might require the restoration of marine habitat quality, as well as a better understanding of how long-term trends in ocean climate affect prey abundance and reproductive rate (Becker *et al.* 2007). Quantifying long-term changes in the amount and quality of habitats used over the entire life history of species is likely to be critical for correctly diagnosing the causes of population decline and designing reliable recovery plans in many species.

Acknowledgements

We thank the Burke Museum (University of Washington), Slater Museum (University of Puget Sound), Royal BC Museum, Cowan Museum (University of British Columbia), Canadian Museum Nature, Field Museum, Conner Museum (University of Washington State), Carnegie Museum, Royal Ontario Museum and the Academy of Natural Sciences–Philadelphia for their generous donation of feather samples. The study was supported generously by H. and W. Hesse, Endangered Species Recovery Fund (World Wildlife Fund Canada and Environment Canada), the Natural Sciences and Engineering Research Council and the Izaak Walton Killam Memorial Trust. M. Longstaffe and K. Klassen kindly assisted with stable isotope analysis. Gary Shugart and Carl Walters provided essential advice on sampling protocol and parameter estimation. Jennifer Gill, Amy Newman and two anonymous reviewers provided excellent comments.

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Received 6 November 2006; final copy received 12 March 2007
Editor: Morten Frederiksen