Diet reconstruction and historic population dynamics in a threatened seabird

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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 fi.2(ari-upts and(nes ion the libes of)]TJ T* 0.12 Tw [l ar)27.1(ge tr)12.9(sesuep ta 10 r)10(kmr fl and (Nelson

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as they were developing a brood patch (i.e. suggesting that they are beginning to breed; D. R. Norris and P. Arcese, unpublished data).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 $\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$. $\delta^{15}N$ is the ratio of $^{15}N/^{14}N$ relative to air, and $\delta^{13}C$ 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

878

D. Ryan Norris
et al.

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}
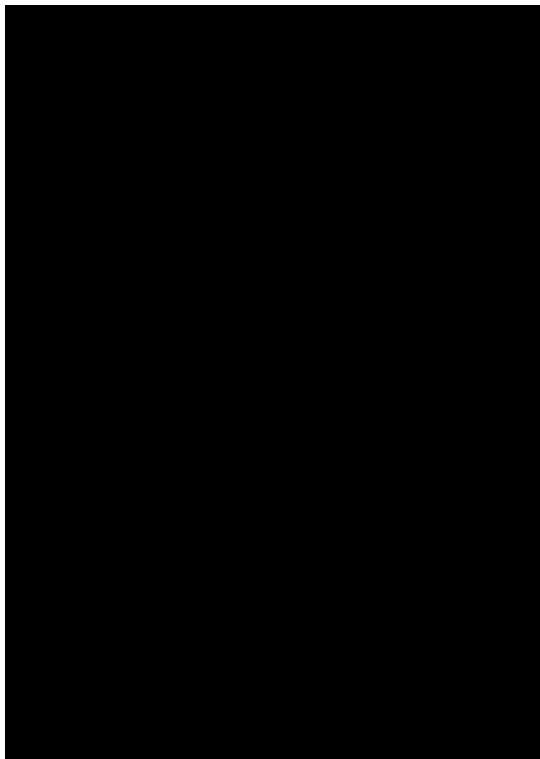
of forage fish and zooplankton (euphausiids or amphipods) in murrelet diet over the 107-year period. We found a decline in the proportion of fish, an increase in the proportion of euphausiids, and no change in amphipods (Fig. 4). Fish comprised a mean ($\pm$ SE) of 61% ($\pm$ 4·4, $n = 11$) of the diet before 1900, but only 9% ($\pm$ 6·3, $n = 26$) after 1970. In contrast, euphausiids comprised 27% ($\pm$ 8·5) of the diet pre-1900, but rose to 61% ($\pm$ 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 $\delta^{15}N$ 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 $\delta^{15}N$ in the prebreeding diet. As predicted, this relationship was positive, rising rapidly from values of $b \sim 0$ at $\delta^{15}N$ values below 13·5, then rising to an asymptote near $b \sim 0.35$ at $\delta^{15}N$ values over

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

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100

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