INTRODUCTION

Successful conservation of threatened species requires proper identification of the demographic vital rates that drive population trends and the extrinsic factors that influence those vital rates (Green 1995, Norris 2004). Accomplishing these objectives can be chal-

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). Murrelets 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 murrelets 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 murrelets. 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 (δ^{15}N) in juvenile breast feathers col-lected from museum specimens and contemporary at-sea captures from the Georgia Basin. In marine ecosystems, δ^{15}N values in predators predictably reflect the isotopic composition of their prey, because δ^{15}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 murrelets 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) murrelets 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°eya to the we ic fS1ay-the last ceyL.3(own-tipped brc)-d Brecorfromf 2 oldtr 0lry W, b5ne0.

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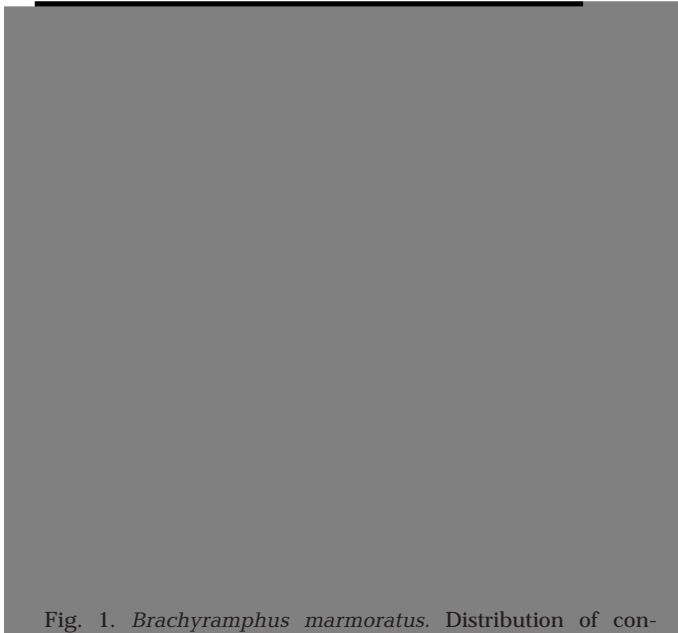
Fig. 1. *Brachyramphus marmoratus.* Distribution of contemporary (1994–2001) marbled murrelet productivity (number of offspring per adult or subadult; *R*) estimates generated from random subsampling of at-sea survey observations in Desolation Sound, British Columbia (repeated 10 000 times; subsample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

Fig. 2. *Brachyramphus marmoratus.* Stable-nitrogen isotope (δ^{15}N) values in hatch-year marbled murrelet breast feathers

Nestling diet

Our GLMM with year as a fixed effect and site as a random effect found a strong negative trend in δ^{15}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, 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 δ^{15}N values between the highest and lowest trophic level prey species was 2.1‰ (Table 1). Pacific sand lance had the lowest δ^{15}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 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

Prey species	Mean δ^{15}N difference	Energy content (kJ fish^{-1})	Sand lance delivery equivalent	Source δ^{15}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]

[a]

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, δ^{15}N increases between trophic levels (Hobson et al. 1994). Thus, the negative trend in δ^{15}N indicates a decline in nestling trophic feeding level. The magnitude of this estimated decline (2.6‰) corresponds to the full range of δ^{15}N values estimated across potential prey species, where the difference between the lowest and the highest δ^{15}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 δ^{15}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

(Norris et al. 2007, present study). δ