Chapter 9

Molts and Plumages in the Annual Cycle of the Marbled Murrelet

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Abstract: Marbled Murrelets have distinct basic, alternate and juvenal plumages. In after-hatching-year (adult) birds, the incomplete pre-alternate molt occurs rapidly over a period of about one month per individual between late February and mid-May. The complete pre-basic molt occurs between mid-July and December. At this time, individuals are flightless for about two months. In late summer, it is difficult to distinguish adult birds undergoing pre-basic molt from juveniles at sea. Field methods for separating these age categories at sea at this time of the year are presented. By early fall, older juveniles are not distinguishable in the field from after-hatching-year birds in basic plumage. The timing of pre-basic and pre-alternate molts were closely related to the timing of breeding, movements and other aspects of the annual cycle of Marbled Murrelets in Barkley Sound, British Columbia.

Little has been published on the plumages and molts of the Marbled Murrelet (*Brachyramphus marmoratus*). Although the general pattern of molt and plumages has been documented, many details that are important for interpreting aspects of the biology of this enigmatic species have remained undescribed. Adults, also referred to as after-hatching-year birds (i.e., breeding adults and subadults, including first-year birds in their second calendar year), have distinct alternate versus basic plumages that they wear during summer and winter periods, respectively. Subadults have not attained full maturity and have not yet bred. The mottled-brown alternate plumage is certainly responsible for the English name "Marbled" Murrelet. In addition, juveniles less than 6 months old, also known as hatching-year birds, wear a distinct juvenal plumage during late summer. Murrelets replace their alternate plumage with a basic plumage during a complete pre-basic molt (involving flight and body feathers) in the late summer and fall. Similarly, during an incomplete pre-alternate molt (involving only body feathers), they replace their basic plumage with the alternate plumage in spring. These general plumage stages and molts are similar for many other seabirds and birds in general (Welty and Baptista 1988). The juvenal, alternate, and basic plumages of the Marbled Murrelet are illustrated in many reputable bird identification field guides (e.g., Harrison 1983, National Geographic Society 1983).

Many past studies of Marbled Murrelets have not required a detailed knowledge of the stages of molts and plumages. Workers quantifying distribution and abundance of murrelets at sea have usually lumped all murrelets together regardless of plumage, or they conducted their studies in summer or winter when most or all birds were in the same plumage. Plumages of birds observed at inland nesting areas have not been distinguished because individuals fly high overhead under low light conditions or darkness during censuses. Interest in the relationship of plumage and molt to other aspects of the murrelet's life history has grown rapidly since 1992. Researchers in Alaska, British Columbia, Washington, Oregon, and California have recently attempted to census juveniles at sea in the late summer and early fall to indirectly determine breeding success. These efforts were prompted by concerns that the very low numbers of juveniles compared to adults (1-5 percent) observed during recent surveys in Oregon and California represent very low breeding success (Nelson, pers. comm.; Hardin, pers. comm.; Ralph and others, this volume; Strong and others 1993). Such low levels of breeding success could indicate that murrelet populations in Washington, Oregon and California can no longer maintain themselves. However, surveys at this time of the year have difficulties that can lead to undercounting or overcounting juveniles in relation to adult birds from the same breeding population, including: (1) the degree that researchers can accurately separate the plumages of juveniles and adult birds in the field, even under adequate viewing conditions; (2) possible post-breeding season movements of adults, juveniles, or both into or out of the area studied; (3) differential use of at-sea habitats by various age classes and during different stages in the annual cycle; and (4) the timing and degree of natural and anthropogenic mortality of juveniles and adult birds. Thus, the adult:juvenile ratio is complex and must be interpreted with caution.

To address these difficulties, especially the first, we reviewed available information on plumages and molt from published and unpublished sources with three main objectives in mind. First, we summarized information on plumages and molt and identified gaps. Second, we summarized some other aspects of murrelet biology during the molt period that may be important for assessing the adult:juvenile ratio. Third, we developed field criteria for separating juveniles from adult birds at sea during the late summer and early fall. This method, based on current knowledge, will require modification as new results are obtained. Our goal has been to provide workers with sufficient information to gather more data to confirm and expand on known patterns. This summary is not complete and we refer the reader to other chapters in this volume for additional information on murrelet biology during the breeding and non-breeding seasons.

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Methods

We relied heavily on studies involving collected birds that allowed a close examination of plumages and molt condition. Sealy (1972; 1974; 1975a,b) studied breeding phenology, diet and body condition of murrelets at Langara Island, British Columbia, March–July 1970–1971. Carter (Carter 1984, Carter and Sealy 1990, Rodway and others 1992) studied at-sea distribution and foraging behavior of murrelets, as well as breeding phenology, diet and body condition, in Barkley Sound, British Columbia, May-October and December 1979-1980. Carter (unpubl. data) collected a complete series of birds undergoing pre-basic molt, as well as some juveniles, from July to October. These birds were preserved as study skins by Sealy and are housed at the University of Manitoba Zoology Museum, Winnipeg, Manitoba. In addition, Carter (unpubl. data) observed Marbled Murrelets off Victoria, British Columbia, during November-March 1978-1980 (see Gaston and others 1993). These studies were collated to present a general picture of murrelet plumages and molts throughout the year for southern Vancouver Island, British Columbia.

To confirm plumage and molt patterns identified from other studies, we examined a total of 106 specimens from the late summer and fall periods in the Royal British Columbia Museum (Victoria, British Columbia) and in the California Academy of Sciences (San Francisco, California). We examined total length, the ratio of dark:light coloration, ventral coloration and patterning, dorsal coloration, and primary wing molt. Total length was measured from 46 adult and 30 juvenile (including recently-fledged and older juvenal plumages) specimens that had been collected during June through September. The ratio of dark:light coloration was determined by placing a grid marked with 0.5 inch x 0.5 inch quadrats over the dorsal, left and right sides of museum specimens and tallying the number of quadrats filled with mainly dark or mainly light plumage. Only the dorsal surface and sides of the specimens were examined in order to determine the dark:light ratio for the area of the bird most often seen when they are sitting on the water. Notes on the ventral coloration and patterning and dorsal coloration were also recorded for 67 adult and 35 juvenile specimens.

Plumages

Basic and Alternate Plumages

Kozlova (1957) provides good general descriptions of the basic and alternate plumages of the Marbled Murrelet. The following is a summary of Kozlova (1957) with a few added comments. In basic plumage, adults are dark brownish above, with bluish grey margins to the back feathers and largely white scapulars. The sides of the head and band around the neck, extending almost to the nape, are white. The underparts are white with some brown feathers still sprinkled on the flanks (*figs. 1* and *2*). In alternate plumage, the upper body parts are brownish black with rusty-buff margins to the back feathers. The sides of the head, front and

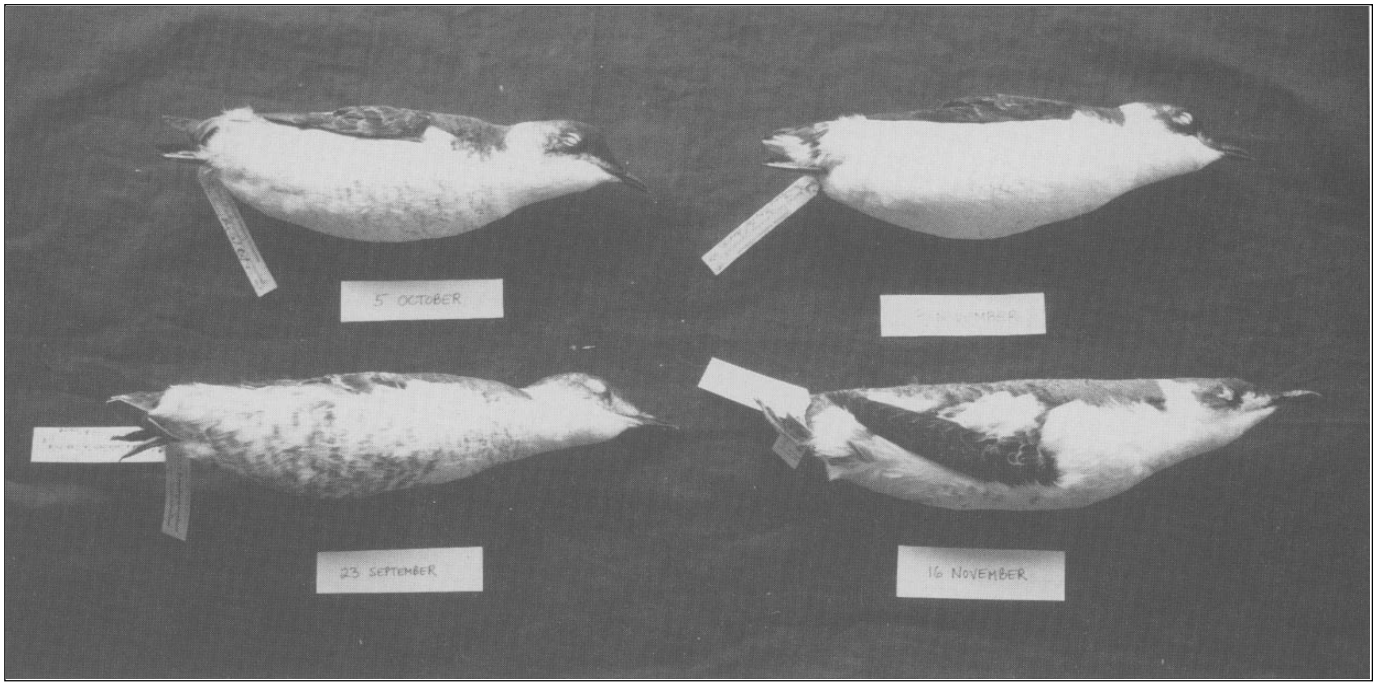

Figure 1—Plumage similarities during fall between older juvenile Marbled Murrelets (top) and adult birds (bottom). Collection dates of juveniles: 5 October 1907 (left), 8 November 1907 (right). Collection dates of adult birds: 23 September 1895 (left), 16 November 1895 (right). Specimens are housed at the California Academy of Sciences, San Francisco, California. Photo taken by H.R. Carter.

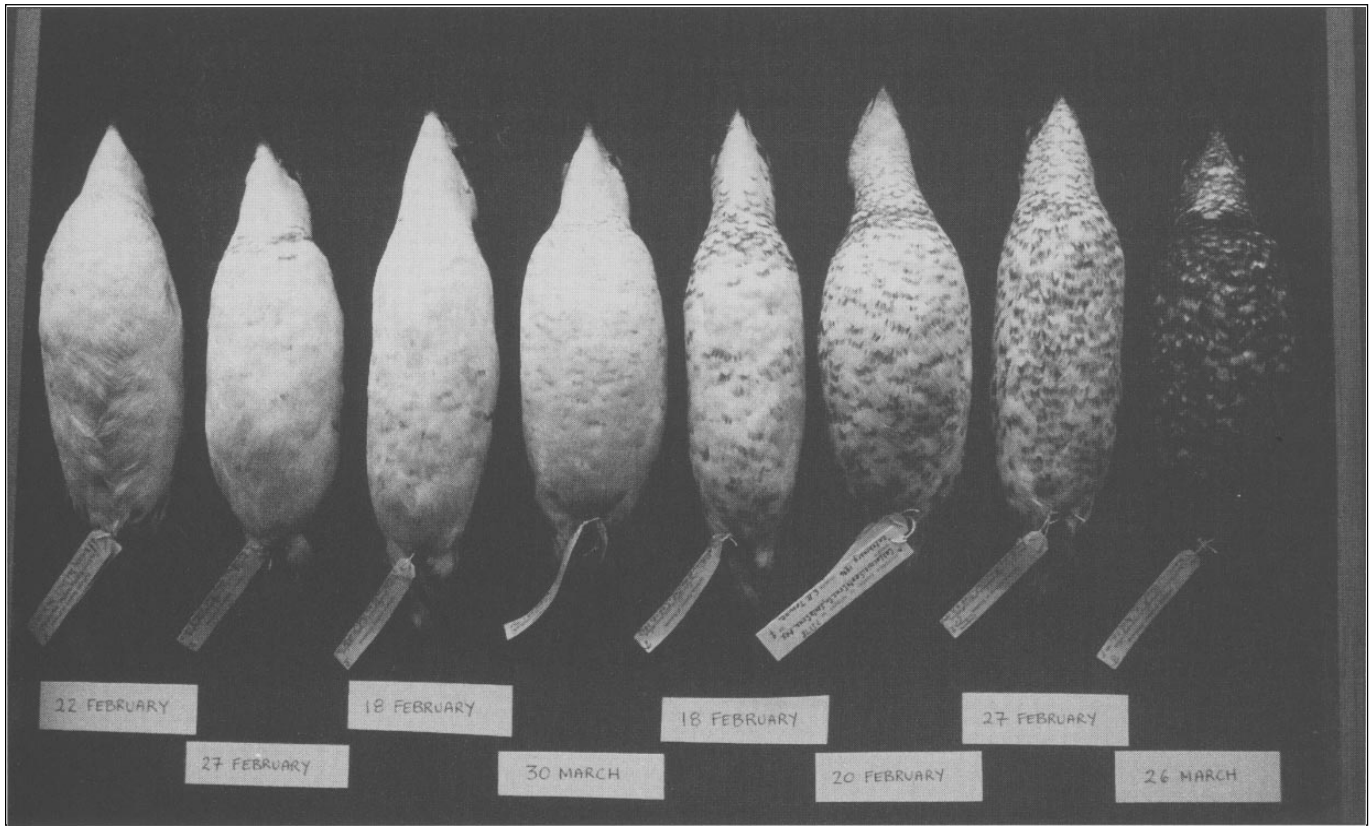

Figure 2—Pre-alternate molt sequence in Marbled Murrelets. Museum specimens are ordered to reflect changes in ventral plumage during pre-alternate molt. The far left specimen is in basic plumage and the far right specimen is in alternate plumage. Collection dates of specimens from left to right: 22 February 1900, 27 February 1907, 18 February 1907, 30 March 1907, 18 February 1907, 20 February 1896, 27 February 1907, 26 March 1907. Specimens are housed at the California Academy of Sciences, San Francisco, California. Photo taken by H.R. Carter.

sides of the neck, and underparts are covered with white feathers that are edged with broad dark-brown margins (*fig. 2*). These dark margins take up about half of each feather. The flanks are almost entirely dark brown, the upper wing coverts are dark brown with occasional narrow white edges, and the under wing coverts and axillaries are brownish grey. The rectrices are brownish black, occasionally with narrow white margins and brownish dots on the outer rectrices. There are no known differences in plumage appearance between sexes or ages of adult birds. However, in some European alcids, first-year birds may retain certain upperwing coverts, leading to a visible contrast between older, retained feathers against newer, replaced feathers (Pyle, pers. comm.). Such detailed examinations are required for the Marbled Murrelet to unveil such possible distinctions when examining birds in the hand.

Murrelets in basic plumage closely resemble the plumage of several other alcids, being "dark above" and "light below." The basic plumage is often considered closer to an older, ancestral plumage. The evolution of the cryptic alternate plumage is an obvious adaptation for nesting solitarily in old-growth forests (Binford and others 1975). It is likely that the Marbled Murrelet originally evolved its cryptic plumage by using similar nesting habitats as the closely-related Kittlitz's Murrelet (*B. brevirostris*). The latter species also attains a very cryptic alternate plumage for nesting solitarily on mountain scree slopes in Alaska and Russia up to 100 km inland from the ocean (Day and others 1983). However, the alternate plumage of the Marbled Murrelet is darker overall and, unlike the Kittlitz's Murrelet, the rust-tipped back feathers of Marbled Murrelets closely match the bark of typical nest trees. While about 3 percent of the Alaskan population of Marbled Murrelets nests solitarily on the ground (Day and others 1983, Mendenhall 1992, Piatt and Ford 1993), it is unclear whether they represent remnant, ancestral ground-nesting behavior or a more recent redevelopment of such behavior. In any case, the cryptic alternate plumage was one preadaption that may have allowed Marbled Murrelets to originally colonize and nest in old-growth forests.

Distinctions between the plumages and other characteristics of the American Marbled Murrelet (*B. m. marmoratus*) and the Asian Marbled Murrelet (*B. m. perdix*) can be found in several papers (Erickson and others 1994; Kozlova 1957; Sealy and others 1982, 1991; Sibley 1993). Recent evidence indicates that the Asian Marbled Murrelet

should be considered to be a separate species (Friesen and others 1994a, Piatt and others 1994).

Nestling Plumage

Binford and others (1975) described the downy chick in detail. Newly-hatched chicks are covered by a thick layer of natal down. Generally, the yellowish down is interspersed with irregular dark spots that cover the upper parts and are more prevalent on the head. A paler grey down covers the belly (Simons 1980). The down covers the developing juvenal plumage and is retained for a relatively long period of time, until just prior to fledging. At this time, the down appears to be preened or scratched off and may be ingested by the chick (Simons 1980). At fledging, juvenile birds fly to the ocean (Carter and Sealy 1987b, Hamer and Cummins 1991). Most juveniles arrive at sea in juvenal plumage, although some individuals may still retain some down, especially on the neck and crown (Sealy 1975a).

The cryptic downy nestling plumage of the Marbled Murrelet is also an obvious adaptation for nesting in old-growth forests (Binford and others 1975) or on mountainous scree slopes. Chicks of precocial alcids have more dense down coverings and resemble the adult plumage in pattern and coloration. Other semi-precocial alcid nestlings (like the Marbled Murrelet) have unmarked grey down. The late retention of this downy nestling plumage, in association with nest placement, tree bark or rock color, adult activities, and chick behavior, is probably important for reducing predation at the nest site.

Juvenal Plumage

Recently-fledged juveniles are uniformly dark brownish above with white scapulars. The underparts and sides of the head are white and speckled with blackish brown which does not fully conceal the white ground color of the feathers (*fig. 3*). The under wing coverts are brownish grey with some white. White bars are present on the outer rectrices and the inner vanes are pale brownish. Recently-fledged juveniles also retain the egg tooth for some time after fledging (Sealy 1970), although it is almost impossible to see the egg tooth in the field. The late retention of the egg tooth is probably related to the late retention of nestling down, early fledging (i.e. when less than fully grown), or both.

The juvenal plumage of recently-fledged juveniles differs from older juveniles that have been at sea for a longer period of time. Recently-fledged juveniles appear darker overall with most feathers on the sides of the head, neck, breast and abdomen edged with thin dark margins (*fig. 3*). This pattern gives juveniles a "speckled" appearance, especially on the breast and upper abdomen. Thicker dark margins occur on the side and flank feathers (similar to adults). Recently-fledged juveniles often exhibit a neckband formed by a greater density of feathers with dark margins in the upper breast region. The plumage of recently-fledged juveniles is often referred to as the "juvenal plumage" in such field identification guides as the National Geographic Society guide (1983). Older juveniles appear to become whiter and lose any neck band and most or all of the dark margins that characterize typical juvenal plumage (*fig. 1*). This transition may occur as early as a few weeks after fledging. In addition, the uniform dark brown to black feathers on the upperparts of recently-fledged juveniles are replaced with feathers edged with thick grey margins in older juveniles (similar to adult birds). It is unclear how these plumage changes occur during this period (see below). Once older juveniles have completed this plumage transition, they are impossible to separate from adult birds in full basic plumage in the field (*fig. 1*). However, in the hand, remnant speckling of the juvenal plumage can be seen on the ventral parts of some birds as late as February.

One hypothesis that explains the plumage transition between recently-fledged and older juveniles is that murrelets have not achieved their full juvenal plumage at fledging. Chicks fledge at 70 percent adult weight (Sealy 1975a) and grow to attain full adult size at sea. For instance, recently-fledged juveniles often still have sheathed outer primaries. The dark margins on recently-fledged juveniles may represent a stage of feather growth between the shedding of natal down and the full attainment of juvenal plumage when full adult size is reached. The dark-margined ventral feathers and/or the grey back feathers may be replaced near the end of the "nestling" growth period that occurs at sea. Alternatively, the thin and fragile dark margins of the ventral feathers may wear off quickly when exposed to salt water and swimming and diving activities. A second explanation for the plumage transition between recently-fledged and older juveniles is that a separate partial body molt occurs, causing loss and replacement of dark-margined ventral feathers and dark back feathers with completely white and grey-margined feathers, respectively. Kozlova (1957) stated that the juvenal plumage is exchanged for the first winter plumage in the fall. She did not provide the basis for this statement, and it is unclear if actively molting feather tracts were observed on specimens examined. If such a molt did occur, it would probably occur some time well after fledging. We cannot currently determine which mechanism best explains this transition because the actual fledging dates of specimens examined is not known and could vary by several months due to protracted breeding. Some form of feather replacement could be supported by finding actively molting feather tracts on juveniles collected in late summer and early fall.

Annual Cycle of Molts and Plumages

Pre-alternate and pre-basic molts are controlled by levels of sex and other hormones, which change throughout the year. The pre-alternate molt precedes breeding and is associated with egg-laying and/or associated nesting behaviors. However, the onset and progression of molt probably also is modified by several environmental factors. Molt imposes high energetic demands within the annual cycle of the Marbled Murrelet. In particular, the replacement of flight and body feathers during the pre-basic molt requires significant changes

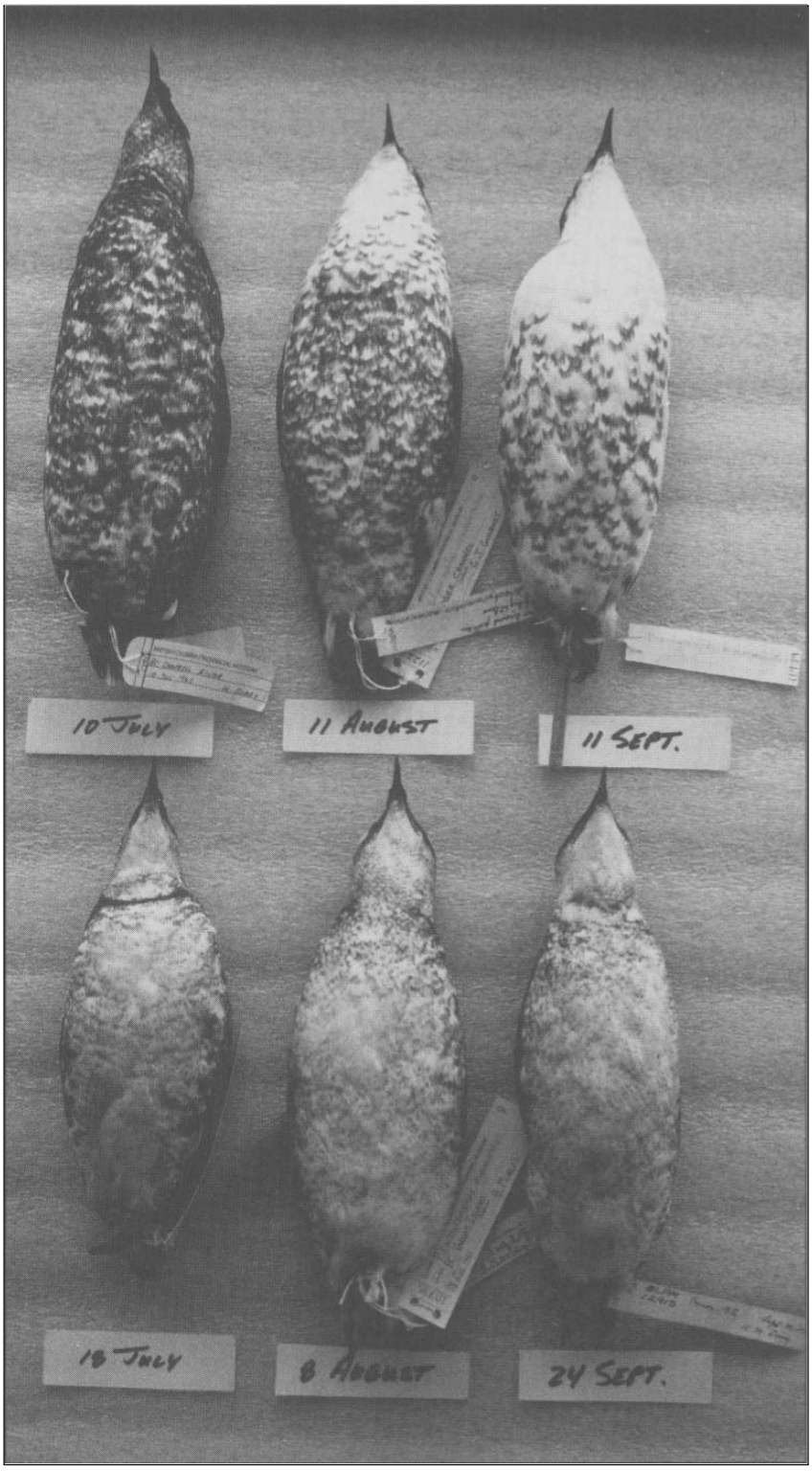

Figure 3—Ventral plumage differences between adult Marbled Murrelets undergoing pre-basic molt (top) and recently-fledged juveniles (bottom). Note the "blotchy" appearance of adult birds versus the "speckled" appearance of juveniles. Collection dates of adult specimens: 10 July 1965, 11 August 1964, 11 September 1969. Collection dates of juvenile specimens: 18 July 1920, 8 August 1961, 24 September 1924. Specimens are housed at the Royal British Columbia Museum, Victoria, British Columbia. Photo taken by J.L. Stein.

in behavior and biology. Flightless murrelets must select molting areas which provide adequate prey resources within swimming distance for about two months. Clearly, it is impossible for Marbled Murrelets to overlap breeding with the flightless pre-basic molt because they would be unable to fly to nests. In contrast, the gradually molting auklets retain flight during the pre-basic molt and do overlap pre-basic molt with breeding (Bédard and Sealy 1984, Emslie and others 1990, Payne 1965).

It is likely that the timing of molt varies between years and between different parts of the breeding range, in concert with variation in the timing of breeding and variation in local prey resources (Ewins 1988, Emslie and others 1990). It is clear that the hormonal integration of molt, breeding and other aspects of the annual cycle of the Marbled Murrelet is complex and our understanding of these processes is limited. In southern parts of the breeding range in North America where murrelets are largely resident, visitation of nesting areas does not occur during the flightless pre-basic molt, does occur during the winter period (when birds are in basic plumage), is reduced during pre-alternate molt (prior to egglaying), and then occurs throughout the breeding season by birds in alternate plumage (Carter and Sealy 1986, Naslund 1993b). Some birds that nest farther north in parts of British Columbia and Alaska appear to winter in different areas or habitats than where they breed. While a portion of the population may visit nesting areas for most of the year, a significant portion or the majority may visit nesting areas only during the breeding season (Rodway and others 1992). Such major differences in the annual cycles of differing populations undoubtedly results in complex patterns of molts and plumages in different geographic areas.

Timing of Breeding and Pre-Basic Molt

In Barkley Sound, British Columbia, Carter (1984) found that the asynchronous or protracted timing of breeding within this population of Marbled Murrelets appeared to lead to a protracted pre-basic molt period (*fig. 4*). Breeding occurred mainly from early April to the end of July, although it extended as late as mid-September. The first fledglings were observed on 4 July 1979 and 28 June 1980 and the last fledgling (a recently-fledged juvenile with an egg tooth) was collected on 5 October 1980. The last bird in alternate plumage was observed flying and carrying a fish on 17 September 1980.

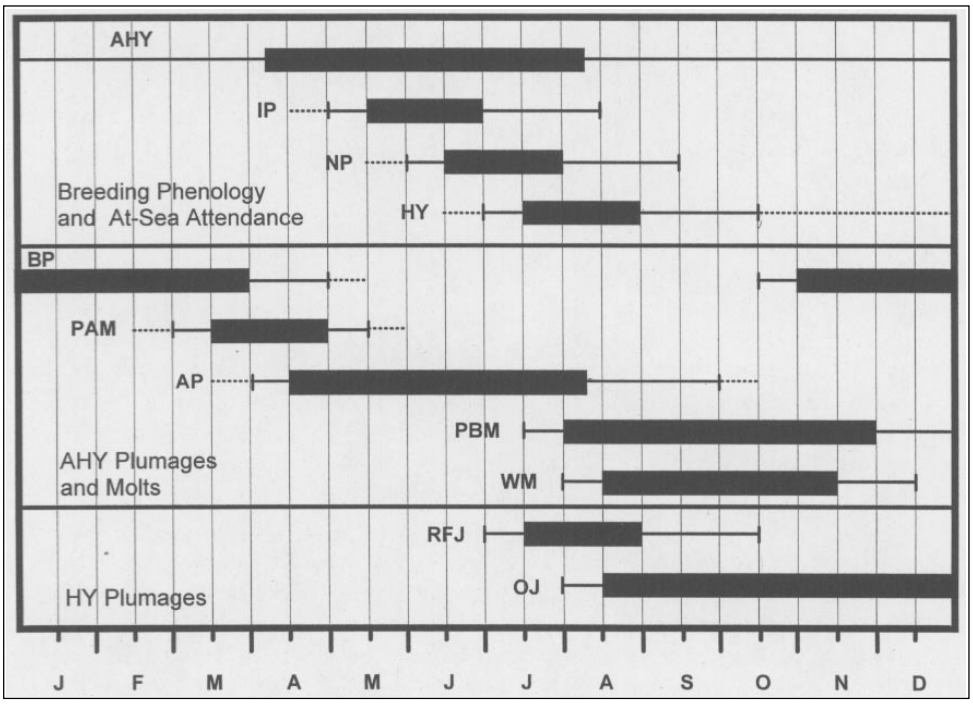

Figure 4—Annual cycle of molts, plumages, breeding phenology and attendance of at-sea feeding areas for Marbled Murrelets in southern Vancouver Island, British Columbia, in 1979-1980 (Carter 1984; Carter, unpubl. data; Sealy 1975b). Codes are: AHY (attendance by adult, after-hatching-year birds); IP (incubation period); NP (nestling period); HY (attendance by juvenile, hatching-year birds); BP (basic plumage); PAM (pre-alternate molt); AP (alternate plumage); PBM (pre-basic molt); WM (wing primary molt); RFJ (recently-fledged juvenile); and OJ (older juvenile). Thick portions of ranges indicate timing for a large proportion of the population. Thin lines indicate usual range. Dots indicate extremes.

Most recently-fledged juveniles occurred at sea in July and August in Barkley Sound (Carter 1984, Guiguet 1971), although recently-fledged and older juveniles occurred there into early October when observations ceased (*fig. 4*).

To project possible timing of molt for other populations in relation to Barkley Sound, we have summarized the earliest and latest possible fledging dates for Marbled Murrelets in different areas from British Columbia to California. Less is known about the average and latest fledging dates (but see Hamer and Nelson, this volume a). At Langara Island, British Columbia, Sealy (1974, 1975a) reported the first young on the water on 6 and 7 July in 1970 and 1971, respectively. In all of British Columbia, juveniles have been observed at sea between 28 May and 5 October (Rodway and others 1992). In Washington, the earliest known nest fledging date is 22 June 1993 (Ritchie, pers. comm.). A juvenile collected on 3 August 1950 in the San Juan Islands, Washington, still had an egg tooth (Leschner and Cummins 1992a). In Oregon, juveniles have been observed at sea as early as 15 June (Hardin, pers. comm; Nelson, pers. comm.; Strong and others 1993). Inland records of fledglings in California occur from 12 June to late September whereas recently-fledged juveniles have been found at sea as early as 1 June (Carter and Erickson 1988, 1992; Carter and Sealy 1987b). In general, nesting appears to occur slightly earlier, but over the same general period from late April to September, in the southern part of its range. Thus, the timing of molt would not be expected to vary much throughout this area in relation to the timing observed at Barkley Sound, British Columbia, in 1979-1980 (*fig. 4*).

In Barkley Sound, British Columbia, pre-basic molt extended over a long period from mid-July to at least late November (*fig. 4*). The first bird undergoing pre-basic wing molt was collected on 24 July 1980 (Carter 1984). Whereas some collected birds had almost completed wing molt by mid-September, others that were still molting in early October would not have completed remigial molt until November (Carter, unpubl. data). Murrelets examined by Sealy (1975a) on 20 July at Langara Island had begun body molt on their capital and spinal tracts, but the remiges and rectrices had not begun to molt when observations ceased on 12 August. Kozlova (1957) stated that the complete molt of adult American Marbled Murrelets occurs in September and October and may extend into November, but she did not give the geographic locations of the specimens examined. She also noted that an Asian Marbled Murrelet collected in the Sea of Okhotsk on 31 August had already shed its flight and tail feathers but that other birds obtained in late August on the east coast of Kamchatka showed no traces of molt. Stresemann and Stresemann (1966) noted a rapid molt of the flight feathers that occurred between early August and late October, after examining specimens mainly from California. The closely related Kittlitz's Murrelet also undergoes a flightless pre-basic molt in Alaska between August and October (Sealy 1977). Only a few other references to molting Marbled Murrelets have been made. Smith (1959) noted a bird "in changing plumage" drowned in a fisherman's net at Cohoe Beach, Alaska, on 22 August 1959. DeBenedictis and Chase (1963) noted one bird "in molt" on 27 July 1963 between Santa Cruz and Pigeon Point, California. Gill and others (1981) noted two flightless adults in Nelson Lagoon, Alaska, on 3 September 1977. On 1 September 1992, eight murrelets were collected in Mitrofania Bay, Alaska (Piatt, pers. comm.; Pitocchelli, pers. comm.): four birds were in alternate plumage (three with bare brood patches and one with a regressing brood patch), two birds were well into pre-basic molt and two birds were recently-fledged juveniles (with neck bands and egg teeth). In general, it appears that the timing of pre-basic molt follows breeding phenology throughout their range in North America. Large numbers of molting birds occur in museum collections which still need to be summarized to confirm this generalization (Carter, unpubl. data; Becking, pers. comm.).

Failed breeders or stressed adult birds may initiate an unusually rapid body molt much earlier than the rest of the population. At Langara Island, British Columbia, Sealy (1975a) collected an adult female on 9 July 1971 with a fully developed brood patch and a flaccid ovary. This bird had already undergone a nearly complete body molt into basic plumage, without having yet started wing molt.

Timing of Pre-Alternate Molt

The timing of pre-alternate molt is more poorly known than for pre-basic molt and appears to vary between breeding adults and subadults. For the American Marbled Murrelet, Kozlova (1957) stated that the incomplete pre-alternate molt began in April and is completed by late May. Molt may be delayed until June in first-year birds. One male, collected on 31 May in the Diomede Islands, had many growing alternate plumage feathers (evident through active blood-filled papillae) on the upper parts, whereas most of the rest of the body was in basic plumage. This bird was collected north of the current breeding range for the species (Sealy and others 1982). It is possible that this bird was not molting in the usual pattern. Sealy (1975a) noted a slight delay in the pre-alternate molt in subadult murrelets at Langara Island, British Columbia. Both adults and subadults returned to Langara Island in late April. Most adults were in alternate plumage whereas subadults were still in basic plumage, although actively molting on their capital and spinal tracts. All subadults eventually achieved alternate plumage by late May (Sealy, pers. comm.). In Barkley Sound, British Columbia, two of 45 birds in alternate plumage were considered to be subadult non-breeders because they lacked brood patches and had small gonads in June and July (Carter 1984). No birds in basic plumage were observed in Barkley Sound from early May to late July (Carter, unpubl. data). Occasional summer sightings of murrelets in basic plumage have been reported to Carter from various areas along the west coast of North America but none have been confirmed with specimens or photographs. Museum specimens must be examined to further confirm that all adult birds (including first-year birds) attain the full alternate plumage during the breeding season.

Pre-Basic Molt Duration and Sequence

The length of time required to complete the pre-basic molt is not well known because individuals have not been followed in captivity or in the wild throughout this period. In Barkley Sound, British Columbia, Carter (unpubl. data) determined that the relatively synchronous molt of the primaries, secondaries and rectrices in each individual required about 65 days but ranged between 45 and 75 days, based on a regression of molt scores and date (Pimm 1976). The entire pre-basic molt (body and remiges) probably requires about 2–3 months per individual. In adult birds, pre-basic molt occurs almost simultaneously in all body tracts. Body molt begins slightly before and ends slightly after remigial molt. In the field, body molt is visible first in the throat area, as the dark feathers are lost and replaced with white feathers. The completion of body molt proceeds from anterior to posterior in ventral feather tracts from the breast to the vent area. In some ventral areas, thick dark-margined feathers are not all lost simultaneously and some are retained for a period of time. Remnant feathers from the alternate plumage were visible mainly in abdominal areas on museum specimens we examined as late as December. The grey-edged, dark back feathers (typical of the basic plumage) gradually replace the rust-edged feathers as the molt progresses. Certain museum specimens that had not yet shed their primaries already showed some grey-edged back feathers, suggesting that molt starts earlier in this region.

During pre-basic molt, murrelets are flightless (Carter 1984), as is expected during a synchronous wing molt. Such molts are considered to be adaptive by shortening the period of feather replacement in birds with aerodynamically inefficient wings such as loons (Savile 1957, Woolfenden 1967), alcids, and diving petrels (Storer 1971, Stresemann and Stresemann 1966, Watson 1968). Stresemann and Stresemann (1966) considered the Marbled Murrelet to have an "accelerated" pre-basic molt where they incorrectly assumed that birds could barely fly during molt. Whereas murrelets are in fact flightless, they do have a less than synchronous pattern of primary replacement. Carter (unpubl. data) found that the first six primaries are lost in order and almost simultaneously; the outer four primaries are lost later. The order of feather loss and replacement is similar to gradual molting auklets and to most birds. The delay in the molt of the outer primaries also was evident in birds examined by Stresemann and Stresemann (1966). Eventually, all primaries are shed and growing at the same time. However, due to the delay in the shedding of the outer primaries, the growth of the inner primaries are completed first, leading to a rounded wing tip in birds later in the molt (*fig. 5*). Regardless of the delay in the outer primaries, pre-basic molt still occurs relatively rapidly. Molt duration is similar to Common Murres, *Uria aalge* (mean = 63 days in nine captive birds; Birkhead and Taylor 1977) but takes longer than for ducks (e.g., 18-29 days; Bailey 1980, Balat 1970).

Pre-Alternate Molt Duration and Sequence

The duration and sequence of pre-alternate molt is even less well known. It is likely that this molt occurs more rapidly than the pre-basic molt. Carter and Erickson (1988, 1992) noted that museum specimens from California collected

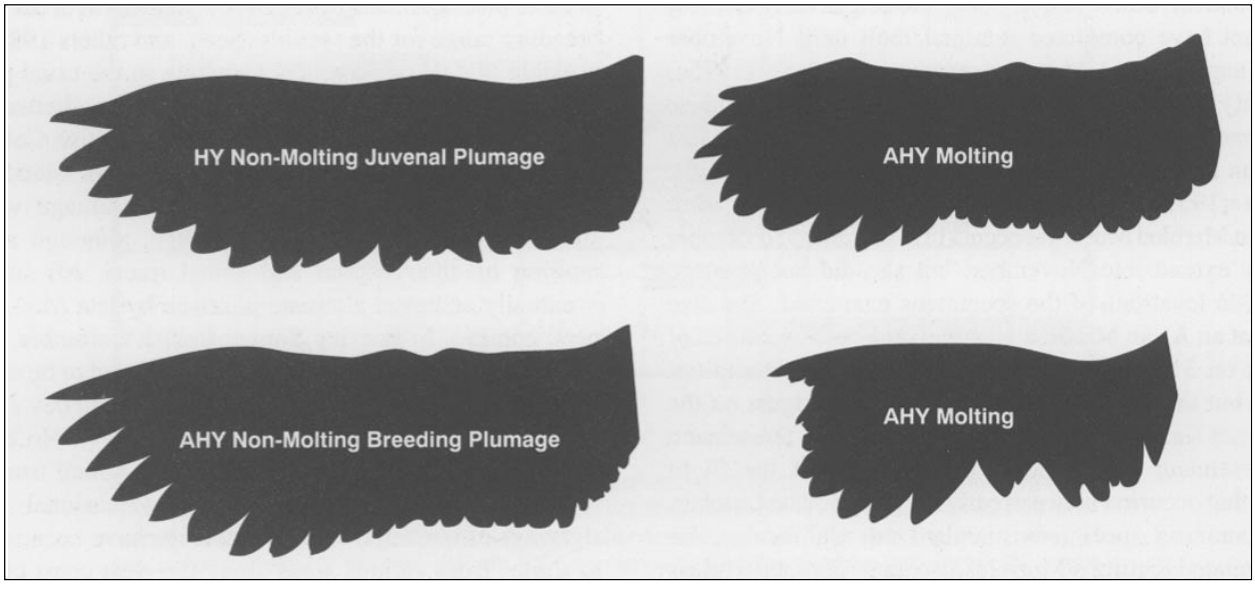

Figure 5—Wing tracings of juvenile, hatching-year (HY) and adult, after-hatching-year (AHY) Marbled Murrelets, illustrating differences between non-molting and molting birds. Molting adult birds have "stubby" wings (bottom right) if all primaries have been recently lost, or "paddle-shaped" wings (top right) as the new inner primaries grow out before the outer primaries. All birds were collected on 1 September 1992 in Mitrofania Bay, Alaska by J. Pitocchelli. Tracings by H.R. Carter.

as early as 18 February already had some white body feathers with broad dark margins on their underparts (*fig. 2*). It is not likely that these represent remnant feathers that were not replaced during pre-basic molt because several specimens exhibited a similar pattern in late February. By March, many specimens were well into alternate plumage. The first bird in full alternate plumage was collected on 26 March, as were several birds on the same date. Without further information, pre-alternate molt appears to occur rapidly and requires about one month. Additional field work and examination of more specimens will better establish the full sequence of the pre-alternate body molt. However, the highest density of dark, thick-margined feathers were seen in the neck area on several spring specimens, suggesting that molt proceeds from anterior to posterior in the ventral tracts.

Behavior and Diet of Murrelets During Pre-Basic Molt

In Barkley Sound, British Columbia, Carter (1984) noted that most adult birds departed from the Sound after breeding in early August (*fig. 4*) and presumably underwent the pre-basic molt elsewhere. However, the smaller numbers of adult birds that remained, moved into nearshore areas and underwent molt from late July to November. During this period, they occurred with juvenile birds which also did not appear to leave the Sound until at least early October. Even the smaller numbers of remaining adult and juvenile birds were mostly gone by late December 1979 (Carter, unpubl. data). Stresemann and Stresemann (1966) asserted that Marbled Murrelets molt after reaching their wintering areas. We presume that they reached this conclusion after examining molting birds from California where, at that time, murrelets were not known to breed. Undoubtedly, the proportion of birds that remain to molt near breeding areas rather than molt at wintering areas will depend on a variety of factors, including the timing of breeding, degree of winter residency, the timing of winter dispersal or migration, and other environmental parameters. McAllister (pers. comm.) reported that most adult birds remained in the general vicinity of summer feeding areas in southeastern Alaska but tended to occur in somewhat different areas and closer to shore during molt in September.

In Barkley Sound, flock sizes of adult birds during pre-basic molt were difficult to obtain since few birds were present and it was difficult to separate molting and juvenile birds from a distance (Carter, unpubl. data). There were 30 flocks from which molting birds were collected in 1979–1980. Of these flocks, 10, 15, 2, 2 and 1 contained 1, 2, 3, 5 and 6 birds, respectively. The larger flocks also contained juveniles. McAllister (pers. comm.) noted the tendency for juveniles to occur very close to shore in southeastern Alaska, although he found juveniles in different areas than molting adults. Most molting and juvenile birds were observed very close to shore, usually within 200 m, in Barkley Sound (Carter, unpubl. data). Most birds were observed in the Deer Group islands (south of Fleming Island, mainly in Satellite Passage and near Seppings Island) and in the Broken Group islands (Sechart Channel, Coaster Channel and between Gibraltar and Nettle islands) (Carter, unpubl. data). In contrast, birds were found both in nearshore, inshore and offshore habitats in many parts of the Sound during the breeding season (Carter 1984, Sealy and Carter 1984). One adult bird that was collected on 24 July 1980 about 1.5 km SE of Cree Island was just beginning primary molt. Birds must swim into nearshore areas if they become flightless farther offshore.

Carter (unpubl. data) collected five pairs of molting Marbled Murrelets in Barkley Sound in the pre-basic molt period. All were male-female pairs and were probably mated. One pair had started body molt but not wing molt and the rest were all actively undergoing wing molt. All mates were almost synchronized and had very similar molt scores, despite the generally asynchronous timing of molt within the population.

During molt in Barkley Sound, adult and juvenile murrelets fed primarily on small fish of size classes II and III (fish length classes: I, <30 mm; II, 30–60 mm; and III, 60–90 mm), primarily Pacific Herring (*Clupea harengus*), Pacific Sand lance (*Ammodytes hexapterus*) and Northern Anchovy (*Engraulis mordax*) (Carter 1984). On average, similar size classes (II and III) were eaten by wintering birds in December, but smaller size classes (I and II) of the same species were eaten by adults during the main breeding season.

Guide for Differentiating Juvenile Murrelets from Adult Birds at Sea in Late Summer and Early Fall

It is not difficult to differentiate a recently-fledged juvenile from an adult bird at sea in alternate or basic plumage, given adequate viewing conditions. Due to the protracted breeding season, however, many complete or partial plumages of both juveniles and adult murrelets may be encountered at sea during the late breeding and early post-breeding seasons. As mentioned previously, many factors affect counts of juveniles at sea during this time, including timing of fledging, at-sea mortality after fledging, timing of post-breeding dispersal and ocean habitats used. Highest counts will occur in suitable habitats in the post-breeding season when most or all juveniles have fledged but have not yet dispersed. However, during this period, confusion in identification occurs because adult birds undergoing pre-basic molt become difficult to separate from juveniles. In addition, older juveniles attain a first-winter plumage that is inseparable in the field from adult birds in basic plumage. Despite the difficulties of determining breeding success indirectly from surveys of juveniles at sea, such surveys are still one of the only measures of breeding success, unless larger numbers of nests can be located and monitored.

To help prevent misidentification of juveniles at sea, Stein and Carter (1994) examined museum specimens and reviewed literature and unpublished data from British Columbia, Washington, and California in order to evaluate

five main criteria for use as an efficient, standardized method in identifying juveniles versus adult murrelets in the late breeding and early post-breeding season from June to November. The criteria examined included: (1) relative size; (2) dark:light coloration ratio; (3) ventral coloration and patterning; (4) dorsal coloration; and (5) primary molt and wing shape.

Recently-fledged juveniles are smaller than adult birds (70 percent adult mass at fledging) but become more similar to adult birds in size after foraging at sea during the first few months after fledging. Total length differed significantly between adult and juvenile birds ($t = 7.52$, $P < 0.001$) but some juveniles collected in August and September were as long as adults collected during these months. In the field, size may be a useful criterion for differentiating juveniles from adults when mixed flocks are encountered early in the post-breeding season, but will be less useful during August and September when many juveniles have already grown at sea for at least a month.

Recently-fledged juveniles are lighter in color than adults in alternate plumage. In alternate plumage, a murrelet was estimated to have a 90:10 dark:light (D:L) ratio. In basic plumage, the ratio changed to 55:45 D:L. One molting adult collected on 19 June 1985 was 75:25 D:L. By August, more molting adults were found in the collections. Flightless adults collected on 11, 22, and 31 August measured 70:30, 65:35, and 79:21 D:L, respectively. By September, there was a larger range of color ratios. Some birds were close to completing the pre-basic molt while others were still in alternate plumage. Birds collected on 11, 16 (two specimens), 20, and 30 September varied from 53:47, 99:1, 47:53, 85:15, and 52:48 D:L, respectively. Juvenile specimens were also examined. Generally, older juveniles appeared to be lighter overall than recently-fledged juveniles. The coloration ratio for juveniles with egg teeth averaged 65:35 D:L ($n = 15$), whereas juveniles without egg teeth averaged 58:42 D:L ($n = 14$). Due to protracted breeding, juveniles varying in age by 2-3 months may be present on the water in August and September and be easily confused with molting adults that may have similar color ratios.

Recently-fledged juveniles possess a "speckled" appearance, resulting from many of the feathers on the sides of the head, neck, breast and abdomen being edged with thin dark margins (*fig. 3*). However, older juveniles without egg teeth appear lighter overall as many of the dark margins are lost. In contrast to the thin dark margins of juvenal feathers, the dark margins of the feathers of adult birds are much wider and have a "blotchy" appearance (*fig. 3*). As adult pre-basic molt progresses from anterior to posterior in ventral tracts, the density of blotchy feathers decreases. During boat survey work in Washington, "blotchy" feathers were often visible on the posterior ventral surface of molting adults as they dove in front of the boat (Stein, unpubl. data). This criterion was often helpful in separating adult birds that were more advanced in their pre-basic molt from juveniles. Remnant blotches or "speckled" feathers were noted on some specimens as late as November and December, but they probably would not have been noticeable in the field (*fig. 1*).

As pre-basic molt progresses in adult birds, the rust-edged back feathers are gradually replaced by the grey-edged, dark back feathers, typical of basic plumage. Some grey-tipped back feathers were observed on adult specimens collected as early as June although specimens in which all orange-tipped feathers had been replaced had not been collected until July. Although recently-fledged juveniles are uniformly dark brown to almost black above, the upperparts of older juveniles possess grey margins similar to adult birds. Grey-tipped feathers were not noted on juvenile specimens collected earlier than September, but were more common after this time. Dorsal surface coloration appears to be an unreliable criterion for separating older juveniles from adult birds during the pre-basic molt.

About 35 percent ($n = 20$) and 78 percent ($n = 9$) of adult birds collected in August and September, respectively, appeared flightless. Except for their flightless condition, these specimens were similar in appearance to juveniles. During August 1993 boat surveys in Washington, the condition of the molted primaries was the most reliable criterion for differentiating confusing birds (Stein, unpubl. data). Many adult birds were advanced in their pre-basic body molt by this time and could not be differentiated from older juveniles on the basis of the other four criteria mentioned above.

In summary, the number of criteria useful for differentiating juveniles from adult murrelets decreases as the post-breeding season progresses. Of the five criteria evaluated, the first four would be useful in June and July. Recently-fledged juveniles are smaller than adults (70 percent body weight at fledging), lighter overall, appear speckled on the throat, breast, abdomen, and are uniformly dark brown to black on the upper body parts. In comparison, most adults in June and July are still in their alternate plumage and are much darker overall with rust-edged back feathers still apparent. By August and September, most adult birds are undergoing pre-basic molt, have lost the dorsal rust coloration, have replaced many of the dark-edged ventral body feathers with totally white feathers, and appear much lighter overall. Many juveniles, which have grown at sea for at least a month by this time, lose many of the characteristic speckled feathers, either by wear or replacement. During these months, the most reliable criterion for differentiating juvenile from adult birds is the condition of the molted primaries that can be best assessed when birds flap their wings while sitting on the water. Molting adults have "stubby" wings, if all primaries have recently been lost. Later, wings appear more rounded and have a "paddle-shaped" appearance when the new inner primaries become fully grown before the outer primaries (*fig. 5*). Juveniles lack gaps and have more pointed wing tips than molting birds at all times. In October and November, it is not practical to separate juveniles from adult birds in the field (*fig. 1*), although some late breeders, late molters and late fledglings may still be encountered and differentiated on the basis of all criteria.

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PART III

Terrestrial Environment