Population studies of Marbled Murrelets (Brachyramphus marmoratus) in British Columbia

Fred Cooke

Abstract

We describe a novel approach to the study of a population of forest nesting seabirds (Marbled Murrelets *Brachyramphus marmoratus*) which are thought to be declining as a result of various potential threats to their environment. This is the first research on this species which makes wide use of individually marked birds. It was made possible through the development of two capture techniques; (1) a floating mist net system which can be used in narrow coastal inlets close to where the birds breed and (2) using dip nets at night. These techniques not only led to the marking of more than 1000 birds for a population based study, but allowed the collection of blood samples for physiological examination of breeding status in the absence of a large sample of birds at nests. We provide the first evidence of breeding area philopatry in this species. We also document the first longevity record for the species. Using a newly developed sexing technique based on DNA technology, which could have wide application for other seabird studies, we found a large excess of males in our marked population. This probably reflects a differential tendency of males to be captured, and may reflect a greater tendency of males to fly into the woods.

Résumé

Nous décrivons une nouvelle approche pour l'étude d'une population d'oiseaux de mer (Alque marbré, Brachyramphus marmoratus) nichant en forêt et que l'on croit en déclin, à cause de plusieurs menaces potentielles sur leur environnement. C'est la première étude sur cette espèce qui utilise des oiseaux marqués individuellement. Ceci fut rendu possible grâce au développement de deux techniques de capture ; (1) un système de filets japonais flottants qui peut être utilisé dans les fjords étroits près des sites de nidification et (2) la capture nocturne sur l'eau à l'aide d'épuisettes. Ces techniques ont permis non seulement de marquer plus de 1,000 oiseaux pour une étude de population, mais ont aussi permis la récolte d'échantillons sanguins pour des études physiologiques du statut de nidification étant donné l'absence d'échantillons d'oiseaux au nid. Nous présentons la première évidence de philopatrie aux sites de nidification chez cette espèce. Nous documentons aussi le premier record de longévité pour l'espèce. Nous avons démontré un excès de mâles dans notre population marquée en utilisant une technique nouvellement développée, basée sur les analyses d'ADN, technique qui pourrait avoir une application plus large pour l'étude d'autres populations d'oiseaux de mer. Ce biais en faveur des mâles reflète probablement un taux de capture plus élevé pour les mâles et peut aussi refléter une tendance plus forte des mâles à fréquenter la forét.

Fred Cooke, Chair of Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 186. (*fcooke@sfu.ca*)

Introduction

Much avian research associated with Canadian forests has emphasized a multi-species approach. By contrast, the work which we describe focuses on a single species, the Marbled Murrelet (*Brachyramphus* marmoratus), that is thought to be vulnerable to the changes in forest ecosystems which result from forestry practices. The research program was planned as a cooperative one among several agencies, the Canadian Wildlife Service/National Science and Engineering Research Council Chair of Wildlife Ecology at Simon Fraser University, the British Columbia Ministry of Forests (MOF) and the Canadian Wildlife Service (CWS). The work has been directed by Andrew Derocher and Louise Waterhouse (MOF), Gary Kaiser, Sean Boyd and Kathy Martin (CWS), and Tony Williams and Fred Cooke of the CWS/NSERC Chair of Wildlife Ecology at Simon Fraser University. Many graduate and summer students have been involved in the data collection and this paper represents an overview of the work.

The Marbled Murrelet is a small alcid which is widely distributed along the Pacific coast of North America, and in British Columbia has been found nesting only in coastal old-growth forests. There are several reasons for concern for the conservation of these birds. Firstly, they are unique among alcids in that they nest solitarily or in loose associations in large trees, usually within 60 kilometers of the sea (Harner and Nelson 1995a). These areas are susceptible to logging and development. Secondly, they have an apparent dependence for nest sites located atop large side branches of old-growth coniferous trees (Hamer and Nelson 1995a). Trees are usually at least 100 years old before such side branches develop which are large enough to accommodate a nest and these trees are in great demand by the lumber industry. Thirdly, throughout the year they require marine habitat for their food supply, mainly small fishes such as Sand Lance (Ammodytes hexapterus) and tend to be found close to the shore (Carter and Sealy 1990). This habitat is increasingly used by human populations on the Pacific coast. Potential threats include gill-netting, oyster leases, oil spills, increased recreational usage and urban development with its production of toxic waste (Fry 1995). Fourthly, the murrelet is a species with low fecundity (Nelson and Hamer 1995) and is suspected of having a late age of sexual maturity (Sealy 1995), as are other members of the Alcidae (Nettleship 1996). It lays only one egg per clutch, and there is no evidence of more than one nesting attempt per year. It is assumed to be long lived but there is no evidence on this point. In such species increases in adult mortality could affect population viability. Fifthly, fragmentation of forests may make their nests more vulnerable to predation, particularly by Common Ravens (Corvus corax), Northern Flying Squirrels (Glaucomys sabrinus) and Steller's Jay (Cyanocitta stellerí). Low nest success has been recorded in areas where there has already been much destruction of old growth forests (Nelson and Hamer 1995).

Research on the Marbled Murrelet in British Columbia is a major challenge to biologists and conservationists because of its secretive habits. The first active nest in the province was found only in 1993. (Jones 1993). The species is classified as threatened or endangered by the U.S. Fish and Wildlife Service in Washington, Oregon and California, as well as by the State of California and is red-listed in the Province of British Columbia. In Canada, it is a nationally threatened species and there is a Marbled Murrelet Recovery Team, chaired by Anne Harfenist of the Canadian Wildlife Service. There is a widespread public belief that the population is under threat from logging practices, but very little solid information exists about either population changes or the requirements needed to maintain healthy populations. Provincial government guidelines through the British Columbia Forest Practices Code are planned to provide provisions for setting aside areas where old growth forest will be maintained when there is evidence of activity (preferably nesting) of this species. These guidelines arose partly as a result of concern for habitat protection and the Marbled Murrelet came to represent a symbol in some quarters of the need for protection of biodiversity. The areas which may be set aside represent large reductions in the profitability of the forests to the logging companies, and so naturally there is concern that the right areas are chosen from the perspective of the needs of the species. From the point of view of both

the public and the companies, it was important to be sure that this protection of this species is based on solid science and that the measures taken will in fact help the species.

Much research to date has concentrated on determining standardized methods for assessing numbers of birds both in the marine and forest habitats with a view to monitoring distribution, population changes and habitat requirements. Although recent work has concentrated on studying the demographic processes necessary to understand the population dynamics of the species, the elusiveness of the nesting behaviour and lack of marked populations has made progress slow. A population model of the species by Beissinger (1995) had to rely on limited data for some of the parameters and inference from other species of alcids for others.

We adopted a demographic approach in our studies which concentrates on two questions: (1) Is there evidence for declines in the British Columbia populations? and (2) If so, what are the important components of the life cycle which are responsible for these changes?

Trends in murrelet populations are not easy to detect and often depend on reports from naturalists.

Perhaps the best evidence of decline comes from historical data from California, where the only locations where birds can still be found at sea are those areas adjacent to residual areas of old growth Redwood (Sequoia sempervirens) in the northern and central parts of the State (Ralph 1994).

Most information on population levels is based on two sorts of counts (i.e. at sea and in the forest) and for both, teams of biologists have established standard protocols (Ralph et al. 1994; Paton, 1995; Strong et al. 1995). These are, however, subject to considerable sampling variance and environmentally induced fluctuations and have been of limited utility to date in documenting long-term trends (Becker et al. 1997). Moreover given the presumed high annual survival rates of this species, even if there had been marked changes in demographic patterns of fecundity, it might be difficult to detect declines from counting. Another approach involves finding and observing nests (Hamer and Nelson 1995b), but sample sizes are still extremely small despite much effort. This tells us something of the breeding biology, but little about demographic changes or evidence for anthropogenic effects on the population.

We felt that a new approach was necessary, beyond counts and nest observations. To carry out a demographic study, it is essential, first, to catch and individually mark a large population, and second, to follow the breeding success of individuals within and between seasons. Even though this is a daunting task for a species as difficult to study as Marbled Murrelets, because of the potential conservation threats, we thought it to be of sufficient importance to try.

This seemingly impossible task for Marbled Murrelets may seem a foolhardy research project except for three recent innovations: (1) Development of a capture method. We use a floating mist-net technique (Kaiser et al. 1995) which allowed us to catch large numbers in the Desolation Sound Area, where many birds occur during the breeding season. More recently we have used a dip-netting technique whereby birds are collected from the open water at night using small boats. (2) In addition to studying the breeding biology by finding nests, we decided to concentrate on monitoring the physiological state of the birds in the nesting area during the breeding season by catching them in the inlets. Physiological and morphological changes would give us some indications of nesting phenology and should also enable us to determine breeding versus non-breeding status in the population. (We do not report on the

physiological aspects of the work here). (3) Recent developments in molecular methods for sexing birds from blood samples (Griffiths et al. 1996) allowed us to sex individuals, since in common with all seabirds, it is almost impossible to do this by morphological methods alone. The ability to know the sex of the individual birds allows many more demographic questions to be asked.

The objectives of this paper are to: (1) describe the approach we have taken to establish a demographic study of the Marbled Murrelet in British Columbia; (2) report on some of our early findings; and (3) to place these findings within the context of the many other research studies on this species.

Methods

We chose the Desolation Sound area located in the Northern part of the Strait of Georgia, British Columbia, as the major study site because large numbers of Marbled Murrelets were known to be in the area during the breeding season and because of a history of studies on this species in this area (Kaiser et al. 1991; Mahon et al. 1992). Theodosia Inlet ($50^{\circ} 05^{\circ}$ N, $124^{\circ}40^{\circ}$ W) was chosen as our banding site because large numbers fly through this narrow (<200m) inlet during the dawn and dusk periods. We also chose an area of potential nesting habitat in the Bunster Range (within 30 km of the banding site) for a detailed nesting area study.

We used a series of floating mist nets comprising up to two arrays of three 18 m nets, which could be strung out across a large part of the inlet. The poles are inserted into a flotation device which is attached by rope to the shore and to an anchored buoy located beyond the nets from the shore line. A pulley system between the shore and the buoy allows the nets to be put in place from the shoreline. Nets are attended using small boats. This system is described in more detail in Kaiser et al. (1995). Nets were in place most evenings from 2100h to about 2315h (PDT) and most mornings from 0400h to 0630h from late May until mid August. In addition to processing all birds caught, we make a count of those birds seen flying over and around the nets, and record direction of flight of all birds.

Birds caught were weighed and measured for tarsus, culmen and wing chord. The presence or absence, and condition of a brood patch were recorded. Some birds received supplemental markers such as nasal disks, wing-tags and radios (Cooke et al. 1998). A small blood sample was taken for two major reasons. It provided samples of: (a) DNA to determine the sex of the birds using a modification of the method described by Griffiths et al. (1996); and (b) blood proteins, enzymes and hormones, which might be useful in assisting us in determining the stage in the breeding cycle of the birds.

Nest finding was an essential, though not dominant focus of the research; it was required to provide a temporal framework for interpreting the information gathered from the birds in the inlet. We used two approaches for finding nests: (1) by attaching radio transmitters to birds caught on the inlet, we hoped to follow them to nest sites, thus not biasing the sample of nesting birds to locations and habitats where we suspected breeding; (2) by placing a field crew in the Bunster Range during and after the nesting period, we located birds as they visited specific nesting trees, which we later climbed to find actual nest sites.

The study began in 1994, though exploratory banding was carried out in 1991 and 1993. We document our findings from the banding data for the years 1994 through 1997. Other results are in the process of being reported elsewhere.

Results Surveys

The only published documentation of population changes in British Columbia comes from at-sea surveys repeated several years apart (Kelson et al. 1995) They documented a decrease in numbers during the period. We have carried out at-sea surveys in the Desolation Sound area using standard techniques, but

Table 1. Comparisons of average numbers of all waterbirds ('All') and Marbled Murrelet ('MAMU') counts at Boundary Bay, British Columbia, 1980-81 (Savard 1988) and 1994-95 (Cooke 1996).

	19	80/81	1994/95		
Month	Ail	MAMU	All	MAMU	
Nov	6355	4	4010	0	
Dec	5401	2	3142	0	
Jan	3255	2	3354	0	
Feb	2173	0	1370	0	
May	675	11	2430	0	
Jun	702	42	417	0	
July	899	3	725	I.	
Aug	751	2	644	<u> </u>	
Total	20211	66	16092	2	

have not yet enough years of data for useful comparisons. Thus our only evidence for population change comes from a different British Columbia population in the Strait of Georgia, that in Boundary Bay. Casual observations in this area showed Marbled Murrelet as a common bird in the region particularly during the summer.

We compared a published survey (Savard 1988), which documents all waterbirds seen along a 6 km stretch of shoreline between Crescent Beach and White Rock, British Columbia, in the winter of 1980-81, with a survey using similar methods carried out by volunteers from the White Rock and Surrey Naturalists in 1994-95 (Cooke 1996). Table 1 documents the average number of Marbled Murrelets relative to other water birds in the months when surveys were made in the respective years. There has been a highly significant decline in murrelets numbers between 1980 and 1995 relative to other waterbird species numbers in this region ($\chi^2 = 78.9$; p<0.001). Subsequent counts in 1996 and 1997 showed that Marbled Murrelets continued to be very rare throughout the year in this area; in fact, no birds of this species were seen in either year. These findings are consistent with more casual observations made by naturalists in the area.

Captures and recaptures

Table 2 documents the number of birds caught and recaptured in mist nets for each season up to 1997. Within season recaptures are not included. Years 1991 and 1993 were essentially experimental seasons when we developed the banding and capture techniques. Since 1994, we have been operating the station throughout the summer season, from late May until early August, coinciding with the period when Marbled Murrelets flew along the inlet. A full banding crew was present during this time and nets were operating whenever tide and weather permitted. Both evening and early morning banding sessions were carried out where possible. Roughly equal numbers were caught in each time period (Derocher et al. 1996). Of the birds caught, 84% (416 / 494) were captured as they flew out of the inlet in both morning and evening banding sessions; the rest were flying into the inlet. A slightly higher proportion of birds (90%, 2454/2852) detected by radar in 1996 and 1997 were flying out of the inlet. This difference is significant (χ^2 = [0.06, p<0.01). All birds caught were adults and all had brood patches, although late in the season most birds were showing signs of re-feathering.

Year banded		Year recaptured				No. and (%) of		
	Number banded	1993	1994	1995	1996	1997	cobort recaptured	
1991	21	0	0	1	Q	2	3 (14)	
1993	15		1	1	0	0	2 (13)	
1994	173			7	4	9	20 (13)	
1995	189				6	22	30 (15)	
1996	95					5	5 (6)	
1997	172							
Total	665		1	9	10	38	58 (12)*	

Table 2. Numbers of Marbled Murrelets banded and recaptured by mist net in Theodosia Inlet, British Columbia, 1991-97. Within-year recaptures excluded.

Percentage excludes birds first banded in 1997.

Sex ratios

One of the surprising features of the study was the finding of a highly skewed sex ratio among the birds which we caught (Table 3). There was no significant variation in this ratio throughout the banding period, nor any difference in the ratios in the morning and evening sessions (Vanderkist et al. 1999).

Table 3. Numbers of Marbled Murrelets of each sex in the samples of birds caught in mist nets at Theodosia Inlet, British Columbia, 1994-1997.

Үевг	Males	Females	Total	Sex ratio	
1994	48	19	67	2.5:1	
1995	80	42	122	1.9:1	
1996	66	38	105	L7:1	
1997	121	69	190	1.8:1	
Total	275	153	428	1.8:1	

Nests

One nest tree was found in 1994, 8 in 1995, 23 in 1996 and 30 in 1997, for a total of 62 nest trees, mostly in our main study area in the Bunster Range. Only the nest found in 1994 was located by attaching radio transmitters to the birds, although in 1998 we had great success with this approach. The others were found by visual detection during the season or by tree climbing later. Of these, 25% of the trees contained more than one nest, which suggests that they had been used for more than one breeding attempt, though not necessarily in the same breeding season (Manley 1999).

Discussion

This paper presents a few highlights of a systematic long-term study of a seabird species that has proven difficult for biologists to study. Our documentation of population declines in the Strait of Georgia is the only quantitative data available to our knowledge and emphasizes the conservation concern which has been expressed for this species. Although this count was made a considerable distance from the study site, it may be symptomatic of the Strait of Georgia as a whole. A bird banded at Desolation Sound in June 1995 was recaptured alive in the southern Georgia Basin in September 1996 (Beauchamp et al. 1999).

The development of a reliable capture technique has allowed us to examine a live sample of nesting birds. During the course of the study, 774 individuals have been captured and banded through the 1997 breeding season. Most of these (n=655) were in mist nets but 109 birds were caught by dip netting. This demonstrates that we are able to sample large numbers of murrelets for study purposes without resorting to the collection of dead specimens, a procedure formerly used widely (e.g., Sealy 1974) but no longer acceptable considering the threatened status of the species.

Assuming brood patches are an indication of breeding status (Sealy 1974), then all the birds caught were breeders. It seems unlikely that all the birds occurring in a region during the summer would be breeding birds, given the fact that all known species of

Alcidae have delayed sexual maturity (Nettleship (1996) and Sealy (1974) reported non-breeders in his sample. Since our nets intercept mainly birds flying between forest and inlet, this strongly suggests that only breeding birds enter and leave the forests during the summer. Most birds were caught while leaving the forest rather than entering it, since most were caught flying in a seaward direction. Since as many birds must enter the forest as leave it, this would again suggest that we are catching birds non-randomly. Birds detected flying over and around the nets, either by sound, sight or radar showed a similar strong bias towards flying in a seaward direction, which suggests that different routes may be used on the inward and outward trips. An alternative suggestion is that birds fly at different heights in the two directions. The dynamics of flight may cause the birds entering the forest to fly at a higher flight altitude than those leaving. A lower altitude would allow greater opportunity for us to catch them. This explanation however is inconsistent with our finding that a significantly higher proportion of birds in our radar sample, which includes many birds which flew over the net, were flying out of the inlet compared to our mist net sample.

Around 12% of the Marbled Murrelets caught in the years 1994 through 1997 were birds banded in a previous year. This demonstrates for the first time that known individuals use the same area of inlet over a period of years. Although capture-mark-recapture (CMR) methods are typically the means used to determine patterns of fidelity to specific sites, difficulties associated with catching Marbled Murrelets and locating their nests have hitherto precluded using this approach. This fidelity to the region of Theodosia Inlet supports the idea that Marbled Murrelets are philopatric to their breeding areas and the high local survival estimate calculated (see below) also supports that. Divoky and Horton (1995) summarized what is known about breeding philopatry (i.e. the return of individual birds to locations used in a previous season) in Marbled Murrelets. Evidence came solely from the occasional re-use of nest sites in subsequent years. However, identities of the individuals were not ascertained and although re-use suggests that the same birds are using their nest sites of a previous year, there was no direct evidence. Indeed, if nest sites are limiting, as several authors have argued (e.g., Burger 1995; Hamer and Nelson 1995), perhaps prime nest sites are always in demand and are likely to be re-occupied not necessarily by the same birds as in previous seasons.

Despite the lack of direct evidence, Divoky and Horton (1995) argued that nest-site tenacity may be lower in Marbled Murrelets than in most other alcids. The habit of nesting in trees would liberate this species from the need to have high nest-site fidelity (in contrast to other alcids) unless the number of suitable trees and platforms becomes very limited, as likely has happened in some parts of its range.

The frequency of recaptured birds is high enough to calculate at least a preliminary local survival rate. A value of 85% was calculated (Cooke et al. 1998; S. Lougheed, unpublished data), but there are wide confidence limits on this value. Nevertheless it is close to that assumed by Beissinger (1995) based solely on a comparison with the body masses of other alcids. More years of data are necessary before more reliable survival estimates can be calculated.

The recapture data also provide us with a longevity record for Marbled Murrelets of at least 7 years. Two birds caught in 1991 as adults were recaptured in 1997. If we assume delayed breeding in this species, then these birds must be at least 8 years old. As banding continues it is likely that these records will soon be broken.

Despite the presence of recaptured birds in our banding samples of 1994-1997, the number of recaptures is relatively low, about 12% of those banded prior to 1997. We can think of at least two possible non-exclusive explanations for this. We may be sampling from a relatively large population; or birds may learn to avoid the area where the mist-netting occurs if they have some long-term memory of the initial capture (trap shyness). At present it is impossible to differentiate between these possibilities.

The almost 2:1 sex ratio in favour of males was a complete surprise to us. It seems unlikely that the population sex ratio would be so heavily skewed towards males, but this cannot be niled out. We have every confidence in the method for assigning sex so it seems more realistic to imagine that some form of capture bias explains the unusual result. The pattern was the same in all four seasons and there was no evidence of changes in sex ratio at different parts of the breeding sequence. Nets were placed across the inlet only in late May, at a time which coincided with the first observations of murrelets flying into the inlets. This also coincides with the onset of the nestling stage of the life cycle (Hamer and Nelson 1995b), and so we assume that most of the birds caught are actively feeding young at the nest. Several birds were carrying fish on capture. One possible explanation for the sex ratio bias is that males feed the chicks more than the

females. Observations at the nest (Nelson and Harner 1995) show that birds differ individually in plumage, but there has been no indication as to the sex of the visiting birds. There is also no evidence that one parent feeds more than another. At present this finding is a puzzle for which we have no explanation. We are continuing to examine this question, using other methods of sampling.

The information on the nesting birds was presented elsewhere (Manley1999) but is included here briefly to provide an overview of all aspects of the project. Ultimately, we need to relate our knowledge of birds in the forests to what we can discover from their behaviour at sea. By piecing together information on different aspects of the behaviour of the birds during the summer months, we can slowly learn more about this elusive species.

Overview and future directions

The above findings show the value of long term studies of individually marked birds. Such studies provide the essential framework for detailed demographic data collection. This is fundamental to an understanding of the demographic and environmental causes of population changes, and is the most effective. way of pointing to conservation solutions. There are still many gaps in our knowledge however. Most of the birds caught in the mist nets are well advanced in their nesting cycle. Incubation probably begins in British Columbia in April, and we do not catch birds until late in May. The recently developed technique of dipnetting birds can be carried out at all times of year and will allow a more thorough understanding of the egglaying and incubation period. It will also allow the capture of juvenile birds which could then provide insight into the crucial recruitment stage of the life cycle. Radio telemetry provides an additional tool for tracking incubating birds back to the nest locations, and any nests found in this way will not be subject to the biases due to expectations of where the observer thinks the nests ought to be. Radios will also allow juvenile birds to be followed after first arrival on the inlets from the nests, and will allow a more reliable estimate of nesting success. To date, one of the problems in estimating fledging success is that late fledging juveniles are easily confused with adults which undergo their pre-alternate body moult soon after nesting is finished.

Physiological approaches are valuable additions to the standard ecological approaches to studying the breeding biology. The use of blood sampling to measure hormonal state and the existence of egg proteins should be useful not only to discover the timing of nesting events from birds captured away from the nesting sites, but also may give an indication of the frequency of non-breeding and the age of first breeding. These demographic parameters are currently unknown in Marbled Murrelets and indeed in most alcids.

A long-term, capture-mark-recapture (CMR) data set is essential for determining survival, longevity and recruitment. The data we have collected to date provides a solid beginning for the calculation of these, but more years are needed before we can obtain reasonably precise measures of these fundamental life history parameters as well as provide evidence for their annual variation. Only with many more years of data can we hope to understand the factors which influence the murrelets, information which is necessary for wise conservation action.

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References

- Beauchamp, W.D., F. Cooke, C. Lougheed and L.W. Lougheed. 1999. Seasonal movements of Marbled Murrelets: evidence from banded birds. Condor 101: 671-674.
- Becker, B.H., S.R. Beissinger and H.R. Carter. 1997. At-sea density monitoring of Marbled Murrelets in central California: methodological considerations. Condor 99: 743-755.
- Beissinger, S.R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. Pages 385-393 in Ecology and conservation of the Marbled Murrelet (C.J. Raiph, G.L. Hunt, Jr., M.G. Raphaei and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.
- Burger, A.E. 1995. Inland habitat associations of Marbled Murrelets in British Columbia. Pages 151-161 in Ecology and conservation of the Marbled Murrelet (C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.
- Carter, H.R and S.G. Sealy. 1990. Daily foraging behaviour of Marbled Murrelets. Pages 93-102 in Auks at Sea (S.G. Sealy, ed.). Studies in Avian Biology 14, Cooper Ornithological Society, Lawrence, Kansas.
- Cooke, F. 1996. Waterbird surveys of Boundary Bay-Crescent Beach to White Rock, 1994-1995. Discovery 25: 30-34, 53-58.
- Cooke, F, I.A. Manley, L. Lougheed, C.B. Lougheed and B. Vanderkist. 1998. Nesting habitats, abundance and ecology of Marbled Murrelets on the British Columbia coast. Unpublished manuscript report to the Forest Renewal British Columbia Research Program of the Science Council of British Columbia. Department of Biological Sciences, Simon Fraser University. Burnaby, British Columbia. 22 pp.
- Derocher, A.E., G.W. Kaiser, F. Cooke, I.A. Manley and M.J. Gill. 1996. Research on Marbled Murrelets in the Desolation Sound area during the 1994 breeding season. Technical Report Series No. 257, Canadian Wildlife Service - Pacific and Yukon Region, Delta, British Columbia.
- Divoky, G.J. and M. Horton. 1995. Breeding and natal dispersal, nest habitat loss and implications for Marbled Murrelet populations. Pages 83-87 in

Ecology and conservation of the Marbled Murrelet (C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.

- Fry, D.M. 1995. Pollution and fishing threats to Marbled Murrelets. Pages 257-260 in Ecology and conservation of the Marbled Murrelet (C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California..
- Griffiths, R., S. Daan and C. Dijkstra. 1996. Sex identification in birds using two CHD genes. Proceedings of the Royal Society of London B, 263: 1251-1256.
- Hamer, T.E. and S.K. Nelson. 1995a. Nesting Chronology of the Marbled Murrelet. Pages 49-56 in Ecology and conservation of the Marbled Murrelet (C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.
- Hamer, T.E. and S.K. Nelson. 1995b. Characteristics of Marbled Murrelet nest trees and nesting stands.
 Pages 69-82 in Ecology and conservation of the Marbled Murrelet (C.J. Ralph, G.L. Hunt, Jr., M.G. Raphae) and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.
- Jones, P.H. 1993. Canada's first active Marbled Murrelet nest discovered and observations. British Columbia Naturalist 31: 8.
- Kaiser, G.W., T.E. Mahon and M.D. Fawcett. 1991. Studies of Marbled Murrelets in marine habitats during 1970. Canadian Wildlife Service Technical Report Series No. 131: 1-52.
- Kaiser, G.W., A.E. Derocher, S. Crawford, M.J. Gill and I.A. Manley. 1995. A capture technique for Marbled Murrelets in coastal inlets. Journal of Field Ornithology 66: 321-333.
- Kelson, J.D., I.A. Manley and H.R. Carter. 1995. Decline of the Marbled Murrelet in Clayoquot Sound, British Columbia. Northwest Naturalist 76: 90-98.
- Mahon, T.E., G.W. Kaiser and A.E. Burger. 1992. The role of Marbled Murrelets in mixed-species feeding flocks in British Columbia. Wilson

Bulletin 104: 738-743.

- Manley, I.A. 1999. Behaviour and habitat selection of Marbled Murrelets nesting on the Sunshine Coast. M.Sc. thesis, Simon Fraser University, Burnaby, British Columbia.
- Nelson, S.K. and T.E. Harner. 1995. Nest success and the effects of predation on Marbled Murrelets. Pages 89-97 in Ecology and conservation of the Marbled Murrelet (C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.
- Nettleship, D.N. 1996. Family Alcidae (Auks). Pages 678-722 in Handbook of the birds of the world, Volume 3: Hoatzin to Auks (J. del Hoyo, A. Elliot and J. Surgatal, eds.). Lynx Edicions, Barcelona, Spain.
- Paton, P.W.C. 1995. Marbled Murrelet inland patterns of activity: Defining detections and behavior.
 Pages 113-116 in Ecology and conservation of the Marbled Murrelet (C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.
- Ralph, C.J. 1994. Evidence of changes in populations of the Marbled murrelet in the Pacific Northwest. Pages 286-292 in A century of Avifaunal Changes in western North America (J.R. Jehl, Jr. and N.K. Johnson, eds.). Studies in Avian Biology 15, Cooper Ornithological Society, Lawrence, Kansas.
- Ralph, C.J., S.K. Nelson, M.M. Shaughnessy, S.L. Miller and T.E. Hamer. 1994. Methods of surveying Marbled Murrelets in forests. Technical Paper No.1, Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, Oregon. 48 pp.
- Savard, J-P.L. 1988. A summary of current knowledge on the distribution and abundance of moulting seaducks in the coastal waters of British Columbia. Technical Report Series No. 45, Canadian Wildlife Service - Pacific and Yukon Region, Delta, British Columbia.
- Sealy, S.G. 1974. Breeding phenology and clutch size in the Marbled Murrelet. Auk 91: 10-23.
- Strong, C.S., B.S. Keitt, W.R. McIvor, C.J. Palmer and I. Gaffney. 1995. Distribution and population estimates of Marbled Murrelets at sea in Oregon during the summers of 1992 and 1993. Pages 339-352 in Ecology and conservation of the Marbled

Murrelet (C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, eds.). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.

Vanderkist, B.A., X.-H. Xue, R. Griffiths, K. Martin, W. Beauchamp and T. D. Williams. 1999. Evidence of male bias in capture samples of Marbled Murrelets from genetic studies in British Columbia. Condor 101: 398-402.