Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing models

Patrick G.R. Jodice and Michael W. Collopy

Abstract: The diving behavior of Marbled Murrelets (*Brachyramphus marmoratus*) was studied using telemetry along the Oregon coast during the 1995 and 1996 breeding seasons and examined in relation to predictions from optimal-breathing models. Duration of dives, pauses, dive bouts, time spent under water during dive bouts, and nondiving intervals between successive dive bouts were recorded. Most diving metrics differed between years but not with oceanographic conditions or shore type. There was no effect of water depth on mean dive time or percent time spent under water even though dive bouts occurred in depths from 3 to 36 m. There was a significant, positive relationship between mean dive time and mean pause time at the dive-bout scale each year. At the dive-cycle scale, there was a significant positive relationship between dive time and preceding pause time in each year and a significant positive relationship between dive time and ensuing pause time in 1996. Although it appears that aerobic diving was the norm, there appeared to be an increase in anaerobic diving in 1996. The diving performance of Marbled Murrelets in this study appeared to be affected by annual changes in environmental conditions and prey resources but did not consistently fit predictions from optimal-breathing models.

Résumé : Nous avons étudié le comportement de plongée de Guillemots marbrés (*Brachyramphus marmoratus*) par télémétrie le long de la côte d'Oregon au cours des saisons de reproduction 1995 et 1996; les résultats ont été examinés à la lumière des prédictions des modèles de respiration optimale. La durée des plongées, des pauses, des épisodes de plongée, du temps passé sous l'eau au cours des épisodes et des intervalles en surface entre les épisodes a été enregistrée. La plupart des mesures reliées aux plongées variaient d'une année à l'autre mais ne variaient pas en fonction des conditions océanographique ou en fonction du type de rive. La profondeur de l'eau n'avait pas d'effet sur la durée des plongées ou sur le pourcentage de temps passé sous l'eau, même si les plongées se faisaient entre 3 et 36 m. Nous avons constaté l'existence d'une relation positive significative entre la durée moyenne des plongées et la durée moyenne des pauses à l'échelle des épisodes de plongée, chaque année. À l'échelle d'un cycle de plongée, nous avons noté une relation positive significative entre la durée des plongées et la durée des pauses précédant les plongées chaque année, de même qu'une relation positive significative entre la durée des plongées et la durée des pauses suivant les plongées en 1996. Les plongées aérobies paraissaient représenter la norme, mais, en 1996, les oiseaux semblent avoir eu davantage recours aux plongées anaérobies. La performance de plongée des Guillemots marbrés semble être affectée par les changements annuels des conditions du milieu et de la ressource proies, mais ne correspond pas de façon constante aux prédictions des modèles de respiration optimale.

[Traduit par la Rédaction]

Introduction

Foraging and diving behavior of pursuit-diving seabirds is ultimately restricted by physiology: maximum dive time is limited by the need to surface and replenish oxygen stores. Limits to diving performance (i.e., maximum dive depth or dive duration) among species and taxa can often be explained as an allometric relationship with body mass (e.g., Burger 1991; Boyd and Croxall 1996; Schreer and Kovacs 1997). However, for pursuit-diving seabirds, duration and depth of dives are each typically less than the maximum attainable and there is often a large degree of variability in dive duration and depth within and among individuals of a species (Burger 1991). This suggests that factors other than large-scale physiological processes also affect diving behavior. Optimization-based models have been used to examine the interacting effects of foraging and physiology on breath-hold divers, with particular emphases on the relationships between dive and surface duration and between diving behavior and prey-capture effort (e.g., Kramer 1988; Houston and Carbone 1992). We examine the fit of predictions from two optimization models to empirical diving data from Marbled Murrelets (*Brachyramphus marmoratus*).

Kramer (1988) developed an optimal-breathing model (OBM) based upon the marginal-value theorem (Charnov 1976) and central place foraging theory (Orians and Pearson

Received January 15, 1999. Accepted May 13, 1999.

P.G.R. Jodice.[1] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, U.S.A.
M.W. Collopy. USGS Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, U.S.A.

[1] Author to whom all correspondence should be sent at the following address: Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331, U.S.A. (e-mail: jodicep@ucs.orst.edu).

1979; Houston and McNamara 1985) that attempted to explain the diving, and thus foraging, patterns of aerobically breathing divers. Kramer (1988) and Lea et al. (1996) provided thorough reviews of these predictions and what follows is condensed from them. The basic premise of the OBM is that divers minimize time spent away from the food source. The major predictions were that (1) dive time will increase with water depth (or other factors affecting capture effort); (2) as dive time increases with depth or capture effort, surface time will also increase; (3) the oxygen content of the blood will be constant following all dives regardless of depth to prey or capture effort; (4) divers will not load oxygen stores to maximum capacity prior to a dive; and (5) diving efficiency (dive time / surface time; sensu Dewar 1924) decreases as dive time increases.

Predictions 1 and 2, which have received attention since early studies on diving were conducted (e.g., Dewar 1924; Stonehouse 1967), imply that dive time should be positively related to depth to prey. Maximizing dive duration when prey are shallow would deplete oxygen stores unnecessarily and thus lengthen time spent at the surface and lengthen time spent away from the food source. Therefore, if divers are benthic foragers, a positive relationship should develop between water depth and both dive time and surface time. The quantitative relationship between dive time and water depth can thus be used to determine foraging habits.

Lea et al. (1996) state that predictions 2 and 3, when considered together, imply that there should be a strong relationship between dive duration and the preceding surface interval and note that this critical prediction had not been tested with field data prior to their analysis. Lea et al. (1996) refer to this relationship as "anticipatory breathing" and note that the term does not "imply expectation or any other cognitive process on the animal's part." Anticipatory breathing should occur because the basic premise of the OBM would be satisfied only when time spent at the surface was limited to what was necessary to store sufficient oxygen for the upcoming dive. Such a diving pattern is in contrast to "reactive breathing," which occurs when the diver remains on the surface long enough to fully recover from the previous dive and thus completely replenish oxygen stores. Reactive breathing results in a positive relationship between dive duration and the ensuing surface duration (Lea et al. 1996) and would not necessarily minimize time spent away from the food source.

Ydenberg and Clark (1989) extended the scope of inference of Kramer's OBM by specifically addressing the role of anaerobic metabolism during diving and foraging. Their model predicts that anaerobic metabolism will occur infrequently during diving. Two situations where anaerobiosis should occur are (1) when the probability of prey capture is high enough to outweigh the high cost and low ATP gain of anaerobiosis or (2) when the probability of losing contact with the current prey source during the surface interval is high, especially if location of a new prey source is unlikely.

Based on the predictions from the two models discussed, we posed the following questions regarding Marbled Murrelet diving behavior: (*i*) What is the quantitative relationship between dive durations and surface intervals at different temporal scales (i.e., within and among diving bouts)? Do these data support the prediction of "anticipatory" breathing? (*ii*) What is the effect of water depth and other environmental variables on diving behavior? Do these data support the prediction of a positive relationship between water depth and dive duration? (*iii*) What is the predicted frequency of anaerobic metabolism during Marbled Murrelet diving bouts? We quantified diving patterns of Marbled Murrelets by using radiotelemetry signals to measure duration of dives, duration of pauses (i.e., surface intervals), duration of dive bouts (i.e., a series of dives and surface intervals assumed to constitute a distinct foraging session), percent time spent under water during dive bouts, and duration of intervals between dive bouts. This study generates data that are directly comparable to those from recently published studies on diving behavior of alcids and other pursuit-diving seabirds and provides the first field test of anticipatory breathing in an alcid. Furthermore, since Marbled Murrelets, like all alcids, dive almost exclusively to forage (Gaston and Jones 1998), an examination of their diving patterns also leads to direct inferences about their foraging behavior.

Methods

Field techniques

Marbled Murrelets, considered threatened throughout much of their range, forage near shore on schooling fish and typically nest in coastal old-growth forests. We captured individuals at sea along the central Oregon coast (43°50′–44°50′) between 1 May and 1 August in 1995 and 1996. A three-missiled net gun, fired from a 5-m Zodiac boat equipped with a 45-hp outboard engine, was used to capture birds while in flight (Quinlan and Hughes 1992; D. Varoujean II, personal communication). Captured birds were weighed and examined for injuries post capture; however, it was not possible to determine sex, age or age-class, or reproductive status. While at sea, radio tags (mass 2.0 g, ca. 1% of body mass, 18 × 5 × 5 mm; Holohill, Ltd., Carp, Ont.) were attached along the midline of the back with polypropylene surgical sutures and quick-setting marine epoxy (Titan Corp., Lakewood, Wash.). All birds were released as near to the capture site as possible within 30 min of capture and were monitored immediately via telemetry to ensure that they recovered from the procedure.

A randomization process was used to choose which telemetered individual would be observed during specific time periods within and among days. Diving behavior was recorded remotely (i.e., without visual contact) by monitoring telemetry signals from shore with three- or four-element Yagi antennas. Transmitted signals were inaudible when birds dived and audible when birds were at the surface (Wanless et al. 1993; Monoghan et al. 1994). This enabled us to record dive time, surface time, dive-bout length, and intervals between dive bouts to ±1 s. A dive was defined as any signal loss lasting >4 s; signal losses lasting ≤4 s occurred when waves lapped over the birds, when preening activities resulted in the antenna dipping under water, or when murrelets made very short foraging dives. However, since it was not possible to remotely distinguish among these events, this lower dive limit was set. The 4-s limit was based on published dive times of Marbled Murrelets (Strachan et al. 1995) and personal observations of Marbled Murrelets and other alcids preening and foraging in the wild and in captivity. Signal losses of ≤4 s accounted for 3.3% of all recorded signal losses (i.e., potential dives), so we likely discarded <3% of all recorded dives by adopting this rule.

Surface intervals (also referred to as pause times) were defined as the time elapsed between two successive dives. Maximum pause time was defined as 180 s (as long as the birds did not change location; see the definition of dive-bout interval below). A dive cycle was defined as a dive and either a previous or an ensuing pause. A dive (i.e., foraging) bout was defined as three or more consecutive dive cycles. Intervals between diving bouts were recorded whenever successive diving bouts were observed for the same bird. A dive-bout interval was differentiated from a dive-cycle pause (i.e., a maximum of 180 s) on the basis of time and movement. If the surface interval was >3 min, or <3 min with a change in location, the event was defined as an interval between dive bouts. Choice of this time frame was based on frequency distributions of Marbled Murrelet pauses and on personal observations of Marbled Murrelets foraging. Only diurnal dive-bout intervals were considered in these analyses, since diving was never recorded at night. We calculated diving efficiency as dive time / ensuing surface time (Dewar 1924), although there was little difference if preceding surface times were used in the equation. Percent time spent under water during dive bouts was calculated as total dive time / duration of dive bout.

Statistical analyses

We considered data on dive bouts and bout intervals for an individual bird to be independent if bouts or intervals did not occur during the same tide stage on a given day. When two or more dive bouts or intervals were observed for one bird within a tide stage on a given day, we randomly selected bouts or intervals for analysis. Only diurnal dive bout interval data and data gathered from completely observed dive bouts (i.e., the initial, terminal, and all interim dives were recorded) were used in analyses; however, all dive-cycle data were used in calculations of overall means of dive and pause times and diving efficiency. When possible, successive dive bouts were observed if they met independence criteria and did not interfere with recording data on other birds.

Analysis of covariance (ANCOVA) was used to seek evidence for either anticipatory or reactive breathing at the dive-cycle scale. Separate models were run for each year and included dive time as the response variable, individual bird and dive bouts nested within bird as factors, and the residuals of duration for both the preceding and ensuing pause time as covariates. Using residuals eliminated autocorrelation between surface times (absolute value of correlation coefficient for lags 1–5 < 0.26 for 1995 and 1996) and resulted in a very weak correlation between previous and ensuing pause times (r = 0.06 for 1995, r = 0.25 for 1996).

The relationships between diving metrics and environmental variables were determined using general linear models (GLMs). The response variables were dive-bout duration (minutes), mean dive time within bout (seconds), total percent time spent under water during a dive bout, and duration of intervals between dive bouts (minutes). A multivariate approach was not chosen because Spearman's correlation coefficient (r_s) among the response variables, after the effects of the explanatory variables were accounted for, was low (Ramsey and Schafer 1997; $-0.21 < r_s < 0.16$). To meet GLM assumptions, duration of dive bouts and duration of bout intervals were transformed with a square root function, while percent time spent under water was transformed with the arcsine square root function; mean dive time within bouts did not require transformation. Back-transformed means and confidence intervals are presented for all data except mean dive time within bouts.

GLMs were constructed using a forward, single-best-predictor process with an F-to-enter value of 4.0. Independent variables considered for use included year, individual bird nested within year, time of day, tide stage, sea state, sea-surface temperature, upwelling index, date in summer, and shore type (water depth is considered separately below). Year and bird nested within year were forced into each model. Time of day included five categories: time period 1 occurred from sunrise ±90 min, time period 5 extended from 31 min after sunset until 91 min before sunrise, and time periods 2, 3, and 4 were partitioned equally among the remaining time between time periods 1 and 5. However, analyses were restricted to time periods 1–4, since too few diving bouts were recorded during daylight hours in time period 5 and no diving bouts were recorded after dark (n = 30 nocturnal tracking sessions). Tide stage was obtained from local tide tables and assigned to one of four categories: high and low tides were defined as ±1 h from the peak and low height, respectively, while falling and rising tides comprised the time between high and low. Sea state was determined using a modified Beaufort scale; beaufort 1 and 2 = mild seas, beaufort 3 and 4 = moderate seas, and beaufort ≥5 = rough seas. Shore type was classified as rock or sand and was included to account for potential effects of shore type on prey availability (Varoujean and Williams 1995). Interaction terms were created on the basis of final main effects but were kept in the model only when significant ($P \leq 0.10$).

We also used GLMs to examine the relationship between diving performance and water depth when the latter could be obtained for diving bouts. This occurred when a telemetered bird's location could be accurately established immediately before and after a diving bout. Since we had no idea when dive bouts would begin, these data were obtained opportunistically. Locations of telemetered birds were estimated by obtaining bearings from 2 or 3 shore locations, each at least 1.5 km apart, and all were taken within 10 min of each other. Furthermore, bearings were also recorded every 20 min during the diving bout in order to track the bird's movements. If a location was estimated within 10 min of the initiation and completion of a dive bout and birds remained relatively stationary during the dive bout we considered the location suitable for estimating water depth. This resulted in a subset of dive bouts (n = 59) for analyzing the effects of water depth on diving. Estimated locations were plotted on National Oceanic and Atmospheric Administration (NOAA) charts. Based on adjustments for tide stage and height, water depth was estimated to the nearest metre and then grouped into four categories to account for deviations in location estimates, charted depths, and tide heights: class 1 = 0–10.0 m, class 2 = 10.1–20.0 m, class 3 = 20.1–30.0 m, and class 4 >30.1 m. Water depth was then included in GLMs as an independent variable with year and bird nested within year; dependent variables were mean dive time within bout and percent time spent under water within bout.

Statistical analyses were performed using SAS. Values shown in the text are means ± SD unless otherwise noted.

Results

Dive and surface intervals and interrelationships

Fourteen Marbled Murrelets were captured and radio-tagged during 1995 (n = 9) and 1996 (n = 5), with no recaptures occurring within or between years. Mean body masses of captured birds were similar between years (1995: 216.0 ± 6.4 g, n = 9; 1996: 216.0 ± 14.7 g, n = 5). Dive data were recorded from 11 birds (too few complete diving records were obtained from two of the other birds and one died soon after capture) with which contact was maintained for 10–30 days each. This resulted in remote audio observations of 2324 (n = 7 birds) and 3855 (n = 4 birds) dive cycles in 1995 and 1996, respectively. Although all birds had brood patches at varying stages of development when captured, none were tracked to nesting sites; therefore, these data represent the diving behavior of non-nesting birds.

Dive duration varied less within each year than either surface duration or diving efficiency (Table 1). Mean dive time, pause time, and diving efficiency each differed between years (P = 0.017, 0.0001, and 0.002, respectively; two-tailed randomization tests). The relationship between dive time and pause time varied according to the scale at which it was examined. At the dive-bout scale, mean pause time was strongly related to mean dive time (Table 2, Fig. 1). Although the slope of this relationship did not differ between years (the

Table 1. Summary statistics (mean and coefficient of variation; CV) for diving performance of 11 telemetered Marbled Murrelets observed along the central Oregon coast in May–August of 1995 and 1996.

	1995			1996		
	n	Mean	CV (%)	*n*	Mean	CV (%)
Dive duration (s)	2443	26.84	35.36	3952	24.75	40.15
Surface interval (s)	2326	21.27	76.16	3855	13.13	69.88
Diving efficiency	2326	1.99	135.08	3855	3.05	122.70
Dive-bout duration (min)	68	27.80	57.72	59	33.26	51.47
Percent time spent under water during dive bout	68	49.53	25.16	59	62.17	16.43
Duration of nondiving intervals between bouts (min)	39	49.63	59.93	44	75.67	56.00

Table 2. Relationships among mean surface intervals within dive bouts and mean dive times within bouts, year, and individual effects nested within years, determined from an ANCOVA model[a] for telemetered Marbled Murrelets along the central Oregon coast in May–August of 1995 and 1996.

Independent variable	df	*F*	*P*
Mean dive duration (s)	1112	89.1	0.0001
Year	1112	30.3	0.0001
Bird (year)	7112	4.7	0.0001

[a] $F_{[9,112]} = 30.1$, $P < 0.0001$, $r^2 = 0.71$.

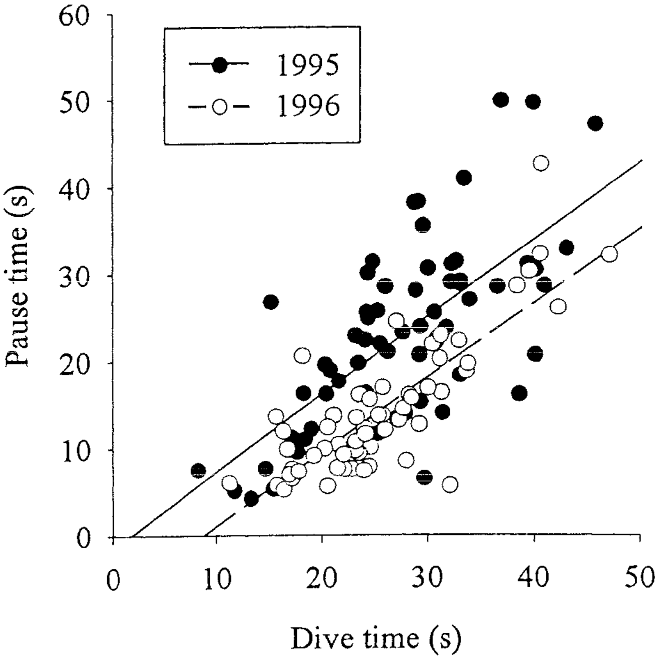
interaction term of mean dive time and year was not significant ($F_{[1,111]} = 0.2$, $P = 0.63$) and was thus removed from the ANCOVA model), the intercepts differed by about 9 s, indicating that mean pause time became shorter in 1996 (Fig. 1, Table 1). Individual bird effects, although significant, contributed little to this model, based on the magnitude of the *F* statistics (Table 2).

At the shorter temporal scale of the dive cycle, the relationship between dive time and pause time varied between years (Table 3), although in each year the ANCOVA model was highly significant (1995: $F_{[65,1650]} = 45.7$, $P < 0.0001$, $r^2 = 0.64$; 1996: $F_{[59,2861]}$ 52.3, $P < 0.0001$, $r^2 = 0.52$). Despite a strong bird and bout effect on mean dive time each year ($P < 0.0001$ for each variable each year), there was still a positive relationship between dive time and preceding pause time in 1995 and a positive relationship between dive time and both preceding and ensuing pause times in 1996. Furthermore, the strength of the relationship between dive time and both preceding and ensuing pause times was stronger in 1996 than in 1995, as determined by differences in coefficient estimates (Table 3).

Dive bouts, bout intervals, and relationships with environmental variables

Duration of dive bouts and the number of dives in a bout (range 3–204) varied greatly within and among individuals (Table 1). The duration of successive dive bouts from the same bird were only moderately correlated ($r_s = 0.32$, $n = 90$ successive dive bouts; data pooled among years). Duration of dive-bout intervals also varied greatly (Table 1), although there was a moderate correlation between the duration of successive dive-bout intervals ($r_s = 0.53$, $n = 47$; data pooled among years). The duration of dive-bout intervals was not correlated with either the duration of the previous or the ensuing diving bout in 1995 or 1996 ($r_s = 0.08$ ($n = 80$) and 0.12 ($n = 81$), respectively; data pooled among years). The duration of dive-bout intervals was not correlated with mean dive time ($r_s = -0.09$), mean pause time ($r_s = -0.09$), or percent time spent under water ($r_s = -0.07$) from preceding bouts in 1995. However, an increase in correlative strength among the same three variables occurred in 1996 ($r_s = -0.35$, -0.37, and 0.26, respectively).

Fig. 1. Regression of mean pause times on mean dive times from dive bouts of telemetered Marbled Murrelets along the central Oregon coast in May–August of 1995 and 1996 (also see Table 2).



The four dive GLMs accounted for 19–35% of the variation in the dive data with one or two significant explanatory variables in each model (Table 4). Of the explanatory variables available for inclusion in the dive GLMs, few were significant in any model. Sea state had a significant effect on

Table 4. Relationships among environmental variables and diving performance of telemetered Marbled Murrelets along the central Oregon coast in May–August of 1995 and 1996.

Explanatory variable	Source df	Duration of dive bout, min (error df = 116, r^2 = 0.19)		Mean dive time within dive bouts, s (error df = 111, r^2 = 0.30)		Percent time spent under water during dive bouts (error df = 112, r^2 = 0.35)		Duration of interval between bouts, min (error df = 89, r^2 = 0.25)	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Year	1	1.3	0.257	2.1	0.147	35.0	<0.001	7.0	0.010
Bird (year)	7	2.4	0.023	5.1	0.001	2.9	0.008	1.4	0.218
Sea state	2	4.4	0.014	2.5	0.086	ns		ns	

Note: Results were obtained by means of forward, single-best-predictor, nested (bird within year) GLMs; "ns" indicates that the variable was not selected for that specific model.

Table 3. Significance of anticipatory (predive surface interval) and reactive (postdive surface interval) breathing patterns of telemetered Marbled Murrelets along the central Oregon coast in May–August of 1995 and 1996, as determined by nested (dive bout within bird) ANCOVA models.

	P	Coefficient estimate	95% CI
1995			
Preceding pause	0.0004	0.037	0.017, 0.057
Ensuing pause	0.9790	0.001	0, 0.021
1996			
Preceding pause	0.0001	0.209	0.169, 0.249
Ensuing pause	0.0001	0.159	0.119, 0.199

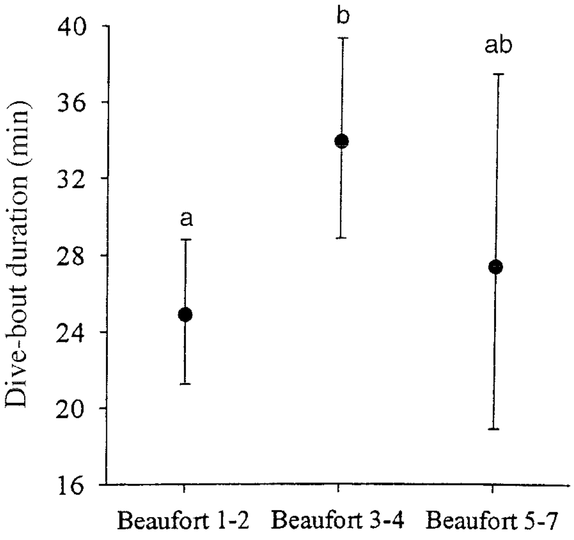


Fig. 2. Mean duration (±95% CI) of dive bouts of telemetered Marbled Murrelets along the central Oregon coast during three sea-state categories in May–August of 1995 and 1996. Categories with the same letter were determined to be not significantly different using GLMs and a post-hoc Tukey–Kramer test with $\alpha = 0.10$. Means and confidence intervals for bout duration are back-transformed from square-root functions.

bout duration and a marginal effect on mean dive time (Table 4, Fig. 2). Year strongly affected the duration of intervals between bouts and percent time spent under water within bouts (Table 4, also see Table 1). Individual bird effects were significant in three of four models.

Most dive bouts occurred in water <10 m (Fig. 3), despite the fact that Marbled Murrelets can probably dive to >25 m (Burger 1991). We did not observe a significant effect of water depth on mean dive time or percent time spent under water within a bout when water depth in each model was regarded as either a continuous variable ($F_{[1,49]} < 1.3$, $P > 0.25$ for each model) or a categorical variable ($F_{[3,48]} < 0.7$, $P > 0.50$ for each model). There was also no significant relationship between dive time and water depth, even when just the five maximum recorded dive times each year were used in a simple linear regression (dive time (s) = 52.95 + 0.0311 water depth (m); $F_{[1,9]} < 1.0$, $P = 0.96$).

Aerobic and anaerobic diving

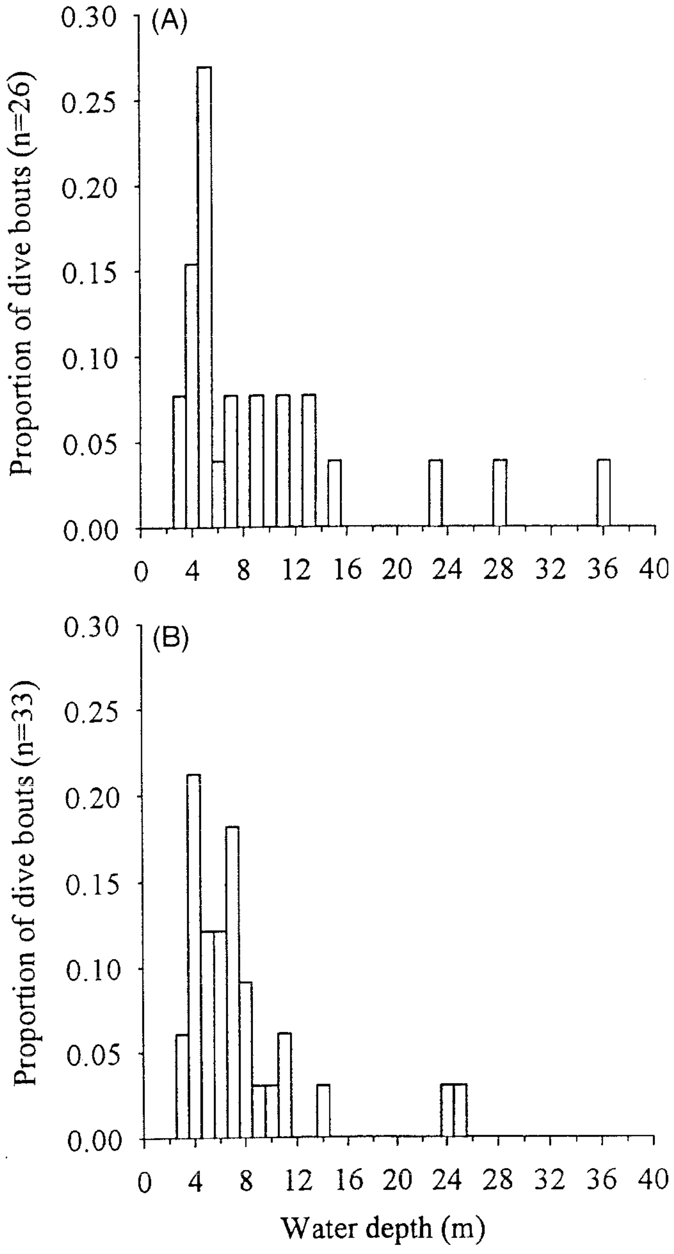
We used models presented in Burger (1991) and Schreer and Kovacs (1997) to determine the proportion of observed Marbled Murrelet dives that exceeded the estimated aerobic diving limit (ADL; in seconds) for this species. However, since the results presented in Table 5 are not based upon direct measurements of the energetic cost of diving in this species, a range of potential values is included. Croll et al. (1992) and Burger (1991) each suggested that the metabolic rate likely increased over SMR approximately three times during diving. Using this estimate indicated that a very low percentage of Marbled Murrelet dives would have exceeded ADL based on the models used (Table 5). Diving predominantly within aerobic limits is further suggested for both years by the lack of either a strong negative correlation between individual dive times and elapsed dive-bout time (1995: $r_s = -0.14$, 1996 $r_s = -0.32$) or a strong positive correlation between individual pause times and elapsed dive-bout time (1995: $r_s = -0.10$, 1996 $r_s = -0.19$; Wanless et al. 1988, 1993).

Discussion

Diving performance

Dive times reported in this study appeared to be similar to those reported elsewhere for Marbled Murrelets both with and without transmitters (for review see Strachan et al. 1995)

Fig. 3. Water depths for dive bouts of telemetered Marbled Murrelets along the central Oregon coast in May–August of 1995 (A) and 1996 (B).



and similar to those for other piscivirous alcids, given differences in body mass (Clowater and Burger 1994; Schreer and Kovacs 1997). Reports of pause times for this species are scarce, however, so it is difficult to make comparisons for that metric. The mean dive-bout duration recorded in this study (27–33 min) appears to be greater than the only other reported value for Marbled Murrelets (18 ± 10.2 min, $n = 20$ bouts; Varoujean and Williams 1995), which was obtained from birds in southern Oregon and northern California carrying larger and heavier transmitters. Varoujean and Williams (1995) also estimated a mean percent time spent under water during dive bouts of 67.6 ± 4% ($n = 20$ bouts) from the same telemetered birds, a value slightly higher than those reported in this study (49–62%). Therefore, our data indicate that there appeared to be no negative effect of transmitters on diving performance. The potential effect of transmitters on breeding performance is less clear. For example, all captured birds in this study had brood patches in some stage of development, but only one was ever known to fly inland. However, telemetry studies in Alaska, British Columbia, and California have all reported a higher than expected incidence of captured birds with brood patches, suggesting that the presence of a brood patch may not be a good indicator of current breeding effort (E.E. Burkett, personal communication; L.W. Lougheed, personal communication; S.K. Nelson, personal communication).

Mean dive duration and maximum dive depth for alcids each appear to be related to body mass (Wanless et al. 1988; Burger 1991; Schreer and Kovacs 1997). If diving performance is related to body mass, then increases in foraging effort may not be achieved strictly through increases in dive duration, since body mass would limit the range of the potential increase in effort. However, body-mass limitations may have less of an effect on surface interval or bout duration and therefore these metrics may be more flexible. This may explain why Marbled Murrelets displayed less variability in dive time than in either pause time or duration of dive bouts during each year of this study.

The dive–pause relationship

The relationship between dive and pause duration at the dive-cycle scale varied within and between individuals for the Marbled Murrelets we studied. Despite this strong individual bird effect, however, interannual differences in the dive–pause relationship were still evident. Reactive- and anticipatory-diving patterns were evident in 1996, while only weaker anticipatory-diving patterns were evident in 1995. While the coefficient estimates for preceding surface intervals we obtained from ANCOVA models of dive time were similar to those reported by Lea et al. (1996; range 0.09–0.38), our coefficients for ensuing pause times were much less than theirs (range 0.42–1.42). This indicates that much stronger reactive-breathing patterns are possible, at least for other species. Three factors that may affect the dive–pause relationship within the dive cycle, and thus its consistency with predictions from the OBM, are prey-handling behavior, depth of foraging within the water column, and capture effort. Each is discussed in turn.

Lea et al. (1996) observed anticipatory diving in species of shags and cormorants (Phalocrocoracidae) that swallowed prey beneath the surface and reactive diving more often in species that swallowed prey on and sometimes beneath the surface. Lea et al. (1996) suggest that subsurface prey handling minimizes disruption of the diving pattern. This would then allow birds to develop a more consistent diving pattern, storing only as much oxygen during surface intervals as was used on previous dives. Marbled Murrelets exhibited both of these prey-handling behaviors during this study (personal observation); this flexibility in prey handling may contribute to the inconsistent relationship between observed dive and pause times.

Anticipatory and reactive diving both tend to occur more frequently as birds forage in the benthic zone and not through-

Table 5. Estimates of aerobic diving limit (ADL) and percentage of observed dives exceeding ADL for a range of potential diving metabolic rates (DMR) shown as a multiple of standard metabolic rate (SMR) for telemetered Marbled Murrelets along the central Oregon coast in May–August of 1995–1996.

DMR as a multiple of SMR	ADL (s) based upon 44.5 mL[a] $O_2 \cdot kg^{-1}$	% of observed dives > ADL	ADL (s) based upon 58.0 mL[b] $O_2 \cdot kg^{-1}$	% of observed dives > ADL
1.5	95.70	<0.001	124.73	0.00
2.0	71.77	<0.001	93.55	0.01
3.0[c]	47.85	0.93	62.37	0.01
4.0	35.89	14.99	46.77	1.17
5.0	28.71	38.68	37.42	10.58
6.0	23.92	59.10	31.18	27.33
7.0	20.51	69.70	26.73	46.72
8.0	17.94	78.44	23.39	59.10
9.0	15.95	83.29	20.79	69.70

[a] Mass-specific oxygen-storage capacity used in ADL models by Burger (1991).
[b] Mass-specific oxygen-storage capacity used in ADL models by Schreer and Kovacs (1997).
[c] DMR estimated for Thick-billed Murres by Croll et al. (1992).

out the water column. While Lea et al. (1996) observed anticipatory-diving patterns more often in species of shags and cormorants that foraged in the benthic zone, Watanuki et al. (1996) and Cairns (1992) observed weak reactive-diving patterns in Japanese Cormorants (*Phalacrocorax capillatus*) and Black Guillemots (*Cepphus grylle*), respectively, both of which foraged throughout the water column. The lack of a significant relationship between dive time and water depth for the Marbled Murrelets we studied suggests that they foraged throughout the entire water column. This may contribute to the range of dive patterns observed within and between years.

Variations in dive-cycle patterns may also be related to prey-capture effort. Anticipatory diving appears to occur when maximum capture effort is required; there appears to be a weaker or nonobservable relationship between dive and pause times when less effort is required (Lea et al. 1996). Ydenberg and Clark's (1989) model also predicted that diving effort would increase when prey were difficult to relocate or capture, and Chappell et al. (1993) observed that Adélie Penguins (*Pygoscelis adeliae*) decreased pause times when prey were patchy. The stronger reactive- and anticipatory-breathing patterns displayed by Marbled Murrelets in 1996 may thus reflect an increase in capture, and thus diving, effort. For example, Monoghan et al. (1994) observed a stronger relationship between dive and pause times of Common Murres (*Uria aalgae*) during years of reduced prey availability in Scotland, and Wanless et al. (1993) observed an increase in diving effort in European Shags (*Phalacrocorax aristotelis*) and attributed it to a change in prey availability. There is evidence that some change in prey conditions occurred in our study area between 1995 and 1996. A colony of Common Murres in the study area experienced near total abandonment early in the 1996 breeding season, and a die-off of adults occurred throughout the summer (R.W. Lowe, personal communication); each was attributed to decreases or differences in local forage-fish availability and not to colony-specific mortality events. Therefore, a change in prey availability could have contributed to the change we observed in the dive–pause relationship and such an observation would be consistent with observations from other alcids and seabirds.

Although the dive–pause relationship observed during this study varied within and between years at the dive-cycle scale, there was a significant and more consistent relationship between mean dive time and mean pause time at the bout scale. Such a relationship is common among diving birds (e.g., Cairns 1992; Clowater and Burger 1994; Lea et al. 1996) and represents a longer term physiological need to balance diving (energy expended) with recovery (replenishing oxygen; Ydenberg 1988; Lea et al. 1996; de Leeuw 1996). This relationship demonstrates that compensation for greater time spent under water can occur at a time scale greater than each individual dive cycle and therefore examination of only dive-cycle data may be misleading. As with the dive–pause relationship observed at the shorter dive-cycle scale, this pattern was evident despite individual-bird effects.

Effects of environmental variables on diving

A significant positive relationship between water depth and dive time has often been observed for pursuit-diving seabirds and this relationship has been attributed to birds foraging in the benthic zone (e.g., Dewar 1924; Croll et al. 1992; Clowater and Burger 1994). Such a relationship is consistent with Kramer's prediction that dive time will be positively and linearly related to distance to prey. However, not all pursuit-divers demonstrate a significant relationship between water depth and dive time. Cairns (1992) and Watanuki et al. (1996) observed a weak relationship between water depth and dive time in Black Guillemots and Japanese Cormorants, respectively, and, based on Kramer's predictions, suggested that these birds foraged throughout the water column and not just at the sea floor. We did not observe a significant relationship between dive time and water depth in this study and therefore suggest that these Marbled Murrelets also foraged throughout the water column. This observation is consistent with the habits of their primary prey, the Pacific sand lance (*Ammodytes hexapterus*), which occurs throughout the water column, undergoes daily vertical migrations, and thus probably causes foraging conditions to vary significantly across relatively short time scales (Wanless et al. 1993; Burkett 1995).

In studies of diving, dive parameters other than dive time or environmental variables other than water depth have rarely been discussed. While explanatory variables other than water depth may not be as universally important in determining general trends in diving behavior across species, they certainly contribute to the variability observed in diving and foraging behavior within and among species, and could likely elucidate ecological mechanisms that may affect diving behavior. For example, the increase in bout duration that we observed during moderate seas may reflect the increased effort required to locate, pursue, and capture prey, possibly because of increases in turbidity and associated decreases in light levels. Cannell and Cullen (1998) demonstrated experimentally that Little Penguins (*Eudyptula minor*) increased dive duration during periods of low light. More variable bout durations in heavy seas may be due to either early termination of diving or the need for more time to obtain prey.

The increase we observed in percent time spent under water during a bout and duration of intervals between bouts, and the decrease we observed in mean pause time within bouts, in 1996 likely represent an increase in foraging effort in that year. As with previous analyses, these differences were observed despite significant individual effects in some of the dive parameters. These types of changes in diving behavior (e.g., increases in diving effort) have been associated with decreases in prey availability in other pursuit-diving seabirds, as previously mentioned (e.g., Wanless et al. 1993; Monoghan et al. 1994). For these Marbled Murrelets, diving effort may have been affected by changes in prey availability due to annual differences in regional oceanographic conditions. For example, between January 1994 and May 1996, the average monthly sea-surface temperature (SST) along the central Oregon coast was at least 1.5°C above normal in 19 months and at least 2.5°C above normal in 12 months (National Buoy Data Center 1997; Pacific Fisheries Environmental Group 1997). Such increases in SST have previously been linked to reduced nesting success and seabird mortality and likely occur when upwelling decreases and primary productivity decreases, and hence conditions unsuitable for growth and development of fish stocks are created (Duffy 1989; Wilson 1991). For example, decreases in alcid productivity have previously been attributed to inadequate prey resources (Uttley 1994). Therefore, prey resources in the study area may have been poorer in 1996 than in 1995, possibly as a result of the cumulative effect of >2 years of above-average SSTs, and may have contributed to the observed changes in Marbled Murrelet dive patterns. This type of change in local prey resources is supported by the previously discussed Common Murre die-off and colony abandonment.

Aerobic and anaerobic diving

Typically, the duration of surface intervals is reduced during anaerobic diving, rather than the duration of dives being increased. Furthermore, anaerobic metabolism during diving may be demonstrated by a significant negative relationship between dive time and elapsed bout time, or a significant positive relationship between pause time and elapsed bout time (Wanless et al. 1993; Watanuki et al. 1996). Weak relationships among these diving parameters for the Marbled Murrelets we studied suggest that frequent anaerobic metabolism did not occur during diving. It appears unlikely that murrelets exceeded ADL in more than 20% of their dives, based on recent estimates of increases in metabolic rate required for diving in alcids (2–3 × SMR; Croll et al. 1992), penguins (<2 × SMR; Bethge et al. 1997), and Tufted Ducks (*Aythya fuligula*, <4 × SMR; de Leeuw 1996). It is more likely that Marbled Murrelets exceeded ADL in fewer than 10% of their dives (SMR × 3). The latter estimate appears accurate in light of the weak-to-moderate correlation between dive time and elapsed bout time.

The frequency of anaerobic diving may be affected in part by body mass. In penguins, for example, the frequency of anaerobic diving tends to be positively related to body mass (Bethge et al. 1997). The relatively low body mass of Marbled Murrelets, therefore, may explain their low incidence of anaerobic diving compared with larger alcids (e.g., Croll et al. 1992).

Foraging behavior also has a strong influence on diving metabolism. Divers that forage on ephemeral schools of prey are more likely to exhibit anaerobic metabolism, especially when the probability of contacting new schools of fish is low, the probability of recontacting schools is intermediate, or the probability of capture once a school is located is high (Ydenberg and Clark 1989). In contrast, for species that pursue solitary prey, longer surface intervals brought about by longer dives do not hamper an individual from maintaining contact with prey and hence surface time can be lengthened without detriment to foraging success (e.g., Clowater and Burger 1994). Therefore, the low frequency of anaerobic metabolism observed in our Marbled Murrelets is not surprising, given that their primary prey are various species of schooling fish (e.g., Pacific sand lance, Pacific herring (*Clupea harengus*); Burkett 1995).

Nevertheless, changes in the frequency of anaerobic metabolism may occur. In this study, for example, the stronger correlation between dive time and elapsed dive-bout time in 1996 than in 1995 and the decrease in mean pause time that occurred between 1995 and 1996 both suggest a shift in diving behavior with a likely increase in the frequency of anaerobiosis. These observations of increased foraging effort in 1996 coincide with indications of changes in hunting behavior brought about by changes in prey availability and are in agreement with predictions of Ydenberg and Clark's (1989) model.

Diving behavior of Marbled Murrelets in this study did not conform strictly to the predictions of anticipatory diving or depth-related diving noted in Kramer's (1988) OBM. We speculate that the observed variability in dive patterns in these individuals were due to annual changes in environmental conditions and prey resources. Therefore, factors such as these must be considered when interpreting dive data or the results of tests of theoretical breathing models. Despite improvements in remote data-recording devices such as telemetry and time–depth recorders, however, few studies have been able to consistently monitor dive patterns of individuals over long periods of time or focus directly on physiological aspects of pursuit-diving seabirds in field situations. Therefore, models such as the two discussed herein provide valuable hypotheses that may be used to direct diving-related studies. The results of this study confirm the important influence of environmental variables on diving behavior, along with the relevance of physiological constraints. The results also suggest common factors that might limit diving performance among species.

Finally, a word of caution pertaining to sample size and scope of inference is necessary. Our study, like most telemetry studies, was observational as opposed to manipulative (i.e., experimental) in nature, and as such is limited in its scope of inference to the individuals studied and the spatial and temporal frame of the study (Ramsey and Schafer 1997). Furthermore, the number of individuals we observed was small relative to the number of observations recorded per individual. This is often the case with telemetry studies and, while not invalidating the results, should lead to caution in interpreting and applying them. Nevertheless, our sample sizes, both for numbers of individuals and numbers of observations per individual, were often similar to or higher than those in other published telemetry and nontelemetry studies of pursuit-diving seabirds.

Acknowledgements

This research was funded by the Oregon State Office of the Bureau of Land Management, U.S. Geological Survey (USGS), and the USGS Forest and Rangeland Ecosystem Science Center. This manuscript benefited from reviews by S.E.G. Lea, S.L. Garman, R.L. Jarvis, F.L. Ramsey, L.W. Jodice, and an anonymous reviewer. L. Ganio and M. Huso provided statistical advice. B. Arden, K. Brennan, K. Carlsen, S. Fife, N. Freir, L. Irvine, M. Kneeland, J. Niger, and M. Stafford assisted with data collection. D. Varoujean II trained the senior author in capture and transmitter-attachment techniques and provided valuable advice on all aspects of the fieldwork. All field protocols were approved by the Oregon State University Animal Care and Use Committee, Oregon Department of Fish and Wildlife, and U.S. Fish and Wildlife Service.

References

Bethge, P., Nicol, S., Culik, B.M., and Wilson, R.P. 1997. Diving behaviour and energetics in breeding little penguins (*Eudyptula minor*). J. Zool. (Lond.), **242**: 483–502.

Boyd, I.L., and Croxall, J.P. 1996. Dive durations in pinnipeds and seabirds. Can. J. Zool. **74**: 1696–1705.

Burger, A.E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. Can. Wildl. Serv. Occas. Paper No. 68. pp. 9–15.

Burkett, E.E. 1995. Marbled Murrelet food habits and prey ecology. U.S. Dep. Agric. Gen. Tech. Rep. PSW-GTR-152. pp. 223–246.

Cairns, D.K. 1992. Diving behavior of Black Guillemots in northeastern Hudson Bay. Colon. Waterbirds, **15**: 245–248.

Cannell, B.L., and Cullen, J.M. 1998. The foraging behaviour of Little Penguins *Eudyptula minor* at different light levels. Ibis, **140**: 467–471.

Chappell, M. A., Shoemaker, V.H., Janes, D.N., Bucher, T.L., and Maloney, S.K. 1993. Diving behavior during foraging in breeding Adelie Penguins. Ecology, **74**: 1204–1215.

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Biol. **9**: 129–136.

Clowater, J.S., and Burger, A.E. 1994. The diving behaviour of Pigeon Guillemots (*Cepphus columba*) off southern Vancouver Island. Can. J. Zool. **72**: 863–872.

Croll, D.A., Gaston, A.J., Burger, A.E., and Konnoff, D. 1992. Foraging behavior and physiological adaptation for diving in Thick-Billed Murres. Ecology, **73**: 344–356.

de Leeuw, J.J. 1996. Diving costs as a component of daily energy budgets of aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks. Can. J. Zool. **74**: 2131–2142.

Dewar, J.M. 1924. The bird as a diver. Witherby and Co., London.

Duffy, D.C. 1989. Seabirds and the 1982–1984 El Niño – Southern Oscillation. *In* Global ecological consequences of the 1982–83 El Niño – Southern Oscillation. *Edited by* P.W. Glynn. Elsevier, New York. pp. 395–415.

Gaston, A.J., and Jones, I.L. 1998. The auks: Alcidae. Oxford University Press, Oxford.

Houston, A.I., and Carbone, C. 1992. The optimal allocation of time during the diving cycle. Behav. Ecol. **3**: 255–265.

Houston, A.I., and McNamara, J.M. 1985. A general theory of central place foraging for single prey-loaders. J. Theor. Biol. **28**: 233–262.

Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. Can. J. Zool. **66**: 89–94.

Lea, S.E.G., Daley, C., Boddington, P.J.C., and Morison, V. 1996. Diving patterns in shags and cormorants (*Phalacrocorax*): tests of an optimal breathing model. Ibis, **138**: 391–398.

Monoghan, P., Walton, P., Wanless, S., Uttley, J.D., and Burns, M.D. 1994. Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding guillemots (*Uria aalge*). Ibis, **136**: 214–222.

National Buoy Data Center. 1997. Sea surface temperatures. Available via http://nimbo.wrh.noaa.gov/portland/marine.html.

Orians, G.H., and Pearson, N.E. 1979. On the theory of central place foraging. *In* Analysis of ecological systems. *Edited by* D.J. Horn, D.R. Mitchell, and G.R. Stairs. Ohio State University Press, Columbus. pp. 155–177.

Pacific Fisheries Environmental Group. 1997. Upwelling indices and sea surface temperatures. Available via http://www.pfeg.noaa.gov.

Quinlan, S.E., and Hughes, J.H. 1992. Techniques for capture and radio-tagging of Marbled Murrelets. Proc. West. Found. Vertebr. Zool. **5**: 117–121.

Ramsey, F.L., and Schafer, D.W. 1997. The statistical sleuth: a course in methods of data analysis. Duxbury Press, Belmont, Calif.

Schreer, J.F., and Kovacs, K.M. 1997. Allometry of diving capacity in air-breathing vertebrates. Can. J. Zool. **75**: 339–358.

Stonehouse, B. 1967. Feeding behaviour and diving rhythms of some New Zealand shags, Phalacrocoracidae. Ibis, **109**: 600–605.

Strachan, G., McAllister, M., and Ralph, C.J. 1995. Marbled Murrelet at-sea and foraging behavior. U.S. Dep. Agric. Gen. Tech. Rep. PSW-GTR-152. pp. 247–254.

Uttley, J.D., Walton, P., Monoghan, P., and Austin, G. 1994. The effects of food abundance on breeding performance and adult time budgets of guillemots (*Uria aalge*). Ibis, **136**: 205–213.

Varoujean, D.H., and Williams, W.A. 1995. Abundance and distribution of Marbled Murrelets in Oregon and Washington based on aerial surveys. *In* Ecology and conservation of the Marbled Murrelet. U.S. Dep. Agric. Gen. Tech. Rep. PSW-GTR-152. pp. 327–338.

Wanless, S., Morris, J.A., and Harris, M.P. 1988. Diving behaviour of guillemot (*Uria aalgae*), puffin (*Fratercula arctica*) and razorbill (*Alca torda*) as shown by radio-telemetry. J. Zool. (Lond.), **216**: 73–81.

Wanless, S., Corfiled, T., Harris, M.P., Buckland, S.T., and Morris, J.A. 1993. Diving behavior of the shag (*Phalacrocorax aristotelis*) in relation to water depth and prey size. J. Zool. (Lond.), **231**: 11–25.

Watanuki, Y., Kato, A., and Naito, Y. 1996. Diving performance of male and female Japanese Cormorants. Can. J. Zool. **74**: 1098–1109.

Wilson, U.W. 1991. Responses of three seabird species to El Niño events and other warm episodes on the Washington coast, 1979–1990. Condor, **93**: 853–858.

Ydenberg, R.C. 1988. Foraging by diving birds. Proc. Int. Ornithol. Congr. **19**: 1832–1841.

Ydenberg, R.C., and Clark, C.W. 1989. Aerobiosis and anaerobiosis during diving by Western Grebes: an optimal foraging approach. J. Theor. Biol. **139**: 437–449.