

CHAPTER 1

DIVING AND FORAGING PATTERNS OF MARBLED MURRELETS: TESTING PREDICTIONS FROM OPTIMAL BREATHING MODELS

ABSTRACT

Diving behavior of Marbled Murrelets (*Brachyramphus marmoratus*) was studied using radio telemetry along the central Oregon Coast during the 1995 and 1996 breeding season and diving performance was compared to predictions from optimal breathing models. Duration of dives, pauses, dive bouts, time underwater during dive bouts, and non-diving intervals between successive dive bouts were recorded. All diving metrics differed between years; other explanatory variables representing short-term sea conditions and location had less consistent effects on diving performance. There was no effect of water depth on mean dive time or percent time underwater. There was a significant, positive relationship between mean dive time and mean pause time at the dive bout scale each year. At the shorter temporal scale of the dive cycle, there was no significant relationship between dive time and pause time in 1995 but a positive significant relationship between dive time and both preceding and ensuing pause times in 1996. This indicates that both anticipatory and reactive breathing patterns were common in 1996 but not in 1995. Although it appears that aerobic diving was the norm, there was likely an increase in anaerobic diving in 1996. Diving performance of Marbled Murrelets in this study appeared to be affected by annual changes in environmental conditions and prey resources and but did not consistently fit with predictions from optimal breathing models.

INTRODUCTION

Foraging behavior of pursuit-diving seabirds is a function of diving performance, which is ultimately restricted by physiology; an individual can dive for only so long before it must return to the surface to breathe and replenish oxygen stores. Limits to diving performance (i.e., 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 most 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 (e.g., body mass) affect diving behavior. Since diving in these species is tied directly to foraging, one avenue of exploration has been to consider the relationship between the physiology of diving and the ecology of foraging. Optimization-based models that consider both general principles of foraging theory and diving physiology have been developed for this purpose (e.g., Kramer 1988, Houston and Carbone 1992). These models attempt to predict how breath-hold divers will partition their time between the surface and the foraging zone (i.e., subsurface) and how diving behavior will vary with effort required for prey capture. We examine two such optimization models and compare empirical field data from diving patterns of a threatened alcid, the Marbled Murrelet (*Brachyramphus marmoratus*), with predictions about diving behavior. Ecological factors that might affect the fit of the field data to the model predictions also are discussed.

Kramer (1988) developed an optimal breathing model (OBM) that attempted to explain the diving, and thus foraging, patterns of aerobically breathing divers. The model drew upon concepts from marginal value theorem (Charnov 1976) and central place foraging theory (Orians and Pearson 1979, Houston and McNamara 1985). Its basic

premise is that aerobic divers will attempt to minimize their time away from the food source by minimizing surface intervals, which are necessary to replenish oxygen stores. Given that oxygen is replenished at a decreasing rate over time, longer dives may lead to substantially longer surface intervals. Therefore, time away from the food source would be minimized: 1) when divers stored the minimum amount of oxygen necessary for each dive, i.e., spent as little time on the surface as necessary replenishing oxygen, and; 2) when divers surfaced when a set amount of oxygen was used as opposed to depleting all oxygen stores (Kramer 1988).

Kramer's OBM includes five predictions regarding dive duration, surface duration, and their interrelationships. Kramer (1988) and Lea et al. (1996) provided thorough reviews of these predictions and what follows is condensed from them. First, the OBM predicts that dive time will increase with water depth (or other factors affecting capture effort). Second, as dive time increases with depth or capture effort, surface time will also increase. Third, the oxygen content of the blood will be constant following all dives regardless of depth to prey or capture effort. Fourth, divers will not load oxygen stores to maximum capacity previous to a dive. Fifth, the ratio of dive to pause duration will decrease as dive time increases (i.e., the relationship between dive and surface intervals is not consistently linear). Here, we consider the implications of predictions 1 – 3 and develop two questions of interest to examine.

Predictions one and two have received attention since early studies on diving were conducted (e.g., Dewar 1924, Stonehouse 1967). These two predictions imply that dive time should be positively related to depth of prey. This is implied because the duration of a dive should not be maximized when prey are closer to the surface. Maximizing dive duration when prey are shallow would deplete oxygen stores unnecessarily and thus lengthen time at the surface and lengthen time away from the food source. Therefore, if divers are benthic foragers, a positive relationship should develop between water depth and both dive and surface times. The quantitative relationship between dive time and

water depth can thus be used to determine foraging habits.

Lea et al. (1996) state that predictions two and three, when considered together, imply that there should be a strong relationship between dive duration and the preceding surface interval. This would occur because the basic premise of the OBM would be satisfied if time at the surface was limited to what was necessary to store sufficient oxygen for the upcoming dive. Lea et al. (1996) refer to this relationship as “anticipatory breathing” (and they note the term does not “imply expectation or any other cognitive process on the animal’s part”). 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. Completely replenishing oxygen stores requires more time than simply storing sufficient oxygen for the upcoming dive. Therefore, reactive breathing results in a positive relationship between dive duration and the ensuing surface duration (Lea et al. 1996). Reactive breathing would not necessarily minimize time away from the food patch and therefore is not the predicted diving pattern based on optimization assumptions. Lea et al. (1996) note that the prediction of anticipatory breathing had not been tested prior to their analysis.

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 should 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 locating a new prey source is unlikely.

We used the predictions from both of the above models to examine diving behavior of Marbled Murrelets. Diving data for this species, as for most alcids, are scarce (Gaston and Jones 1998). Furthermore, since Marbled Murrelets, like all alcids, dive almost exclusively to forage, an examination of their diving patterns leads to direct inferences

about their foraging behavior. The following questions were posed regarding Marbled Murrelet diving behavior: 1) How do diving patterns of Marbled Murrelets observed in this study compare with those of other alcids, as well as with those previously reported for this species? 2) What is the quantitative relationship between duration of dives and surface intervals at different temporal scales (i.e., within and among diving bouts)? Do these data support the prediction of 'anticipatory' breathing? 3) What affect do water depth and other environmental variables have on diving behavior? Do these data support the prediction of a positive relationship between water depth and dive duration? 4) What is the predicted frequency of anaerobic metabolism during Marbled Murrelet diving bouts? We quantified diving patterns of telemetered Marbled Murrelets during the 1995 and 1996 breeding season along the central Oregon coast. We measured 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 underwater during dive bouts; and duration of intervals between dive bouts. This study generates data that are directly comparable to recently published studies on diving behavior of alcids and other pursuit-diving seabirds.

METHODS

Field Techniques

Marbled Murrelets were captured at sea along the central Oregon Coast ($43^{\circ} 50'$ - $44^{\circ} 50'$) between 1 May and 1 August, 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. This technique has previously been used with this species (Quinlan and Hughes

1992, Varoujean pers. comm.). Captured birds were processed while at sea and radio tags (mass ~ 2.0 g; Holohill, Ltd., Ontario) were attached along the midline of the back with sutures and quick-setting marine epoxy (Titan Corp., Lakewood, WA). All birds were released as near to the capture site as possible within 30 minutes of capture and were monitored immediately via telemetry to ensure they recovered from the procedure.

Since Marbled Murrelets dive almost exclusively to forage, diving patterns can be used to infer foraging activity. A randomization process was used to choose which telemetered individual would be observed during specific time periods within and among days. Diving behavior of telemetered Marbled Murrelets was recorded remotely (i.e., without visual contact) by monitoring telemetry signals which were inaudible when birds dove and audible when birds were at the surface (Wanless et al. 1993, Monaghan et al. 1994). Duration of dive time, surface time, dive bout length, and intervals between dive bouts were recorded to +1 s. A dive was defined as any signal loss >4 s; signal losses <4 s occurred when waves lapped over the birds, when preening activities resulted in the antenna dipping underwater (personal observation), or when Murrelets took short foraging dives. However, since it was not possible to remotely distinguish among these events, a lower dive limit was. The 4 s time limit was chosen 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 captivity. Signal losses of <4 s only accounted for 3.3% of recorded signal losses.

Pause times (i.e., surface intervals) were defined as the time between two successive dives. Maximum pause time was defined as 180 s (as long as the birds did not change location; see definition of dive bout interval below). A dive cycle was defined as a dive and either a previous or 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 based on time and movement. A non-diving period of

<3 minutes was considered a dive cycle pause as long as the individual did not change location; if the interval was >3 minutes or if a change in location occurred, the event was defined as an interval between dive bouts. This time frame was chosen based on frequency distributions of Marbled Murrelet pauses and on personal observations of foraging Marbled Murrelets. Only diurnal dive bout intervals were considered in these analyses since diving was never recorded at night. We calculated the dive:pause ratio using dive time and ensuing pause time (versus preceding pause time) to maintain consistency with other studies. Percent time underwater during dive bouts was calculated as total dive time/duration of dive bout.

Statistical Analyses

We considered dive bout and bout interval data for an individual bird to be independent if bouts or intervals did not occur during the same tide stage on a given day. We randomly selected bouts or intervals for analysis when two or more dive bouts or intervals were observed for one bird within a tide stage on a given day. 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 for overall means of dive and pause times and dive:pause ratios.

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 one record for each dive within a bout. Dive time was the response variable, bout identity was a factor, and duration of both the preceding and ensuing pause time were each covariates. A resampling procedure was used to obtain coefficient estimates and confidence intervals from each ANCOVA model instead of relying on significance probabilities estimated directly from the models. This procedure reduced the risk of

obtaining misleading probability values (i.e., low P values) due to either small standard error values associated with large sample sizes (i.e., 1,683 dive cycles in 1995, 2,910 dive cycles in 1996) or serial correlation of sequential pause times (Spearman $r(r_s) = 0.754$; Noreen 1989). We ran 1,000 ANCOVA models for each year's data and randomly selected 500 dive cycles without replacement to be used in each iteration (we chose 500 dive cycles based on a biological justification suggested in Lea et al., 1996). The mean of the coefficient estimates from the 1,000 iterations was calculated and presented as the estimated coefficient along with a 95% confidence interval; the latter was determined by obtaining the 5th and 95th percentiles from the estimates. Significance was indicated if confidence intervals did not contain zero.

General linear models (GLMs) were used to explore the relationship between diving characteristics and environmental variables. The response variables were; dive bout duration (minutes), mean dive time within bout (seconds), total percent time underwater during a dive bout, and duration of intervals between dive bouts (minutes). A multivariate approach was not chosen because the correlation among the response variables, after accounting for the effects of the explanatory variables, were low (Ramsey and Schafer 1997; $-0.205 < r_s < 0.161$). Duration of dive bouts and duration of bout intervals were transformed with a square root function while percent time underwater was transformed with the arcsin 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. These models are hereafter referred to as diving GLMs.

Independent variables considered for use in the diving GLMs included; time of day, tide stage, sea state, sea surface temperature, upwelling index, week within the summer (week 1 starts with 1 May each year), coastal region, water depth, and year. A term for individual identity was not included for three reasons: 1) we expected to observe variability in diving behavior among individuals based on previous diving studies with other pursuit-diving species; 2) we were not able to determine sex, age, or reproductive status

of any individuals and therefore would not be able to attribute any differences in diving behavior to known biological factors, and; 3) we were more interested in examining general patterns in diving behavior within the species and comparing it to model predictions than attempting to record and explain individual variation in diving behavior.

Plots of explanatory variables and correlation analyses were used to determine multicollinearity among the explanatory variables; week and sea surface temperature were excluded. Akaike's information criterion (AIC) was used to develop optimal and parsimonious models with the remaining independent variables. This resulted in the upwelling index being dropped from the models for each response variable. Time of day included five categories; time period one occurred from sunrise + 90 minutes, time period five extended from 31 minutes after sunset until 91 minutes before sunrise, and time periods two, three, and four were partitioned equally among the remaining time between time periods one and five. However, analyses were restricted to time periods 1, 2, 3, and 4 since so few diving bouts were recorded in time period 5. Tide stage was obtained from local tide tables and assigned to one of four categories; high and low tides were defined as +1 hr from the peak and low heights, 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.

Six broad-scale coastal areas were defined for use as explanatory variables in GLMs (Fig. 1.1). These areas were designated based on similarity in coastal features and were included to account for effects of shore type (e.g., sandy beach, cliffs) on prey availability or behavior which might then affect diving behavior (see Varoujean and Williams 1995). The areas were: Siuslaw, a sandy shore area; Newport, a sandy shore area; Foulweather, a cliff dominated shore with offshore rocks and small islands; Depoe Bay, an area of rocky bays and inlets; Lincoln City, sandy beaches; and the Northern area, a mix of rocky and sandy shores with bluffs and offshore rocks. The Siuslaw, Newport, Lincoln City, and

Northern areas all contain bays and major river mouths.

Water depth was obtained only for diving bouts with precise locations of telemetered birds. This required recording a triangulated location immediately before and after a diving bout. Since we had no idea when dive bouts would begin, these data were obtained opportunistically. Furthermore, bearings were recorded every 20 minutes during the diving bout in order to track the birds movements. If birds remained relatively stationary during the dive bout we considered the location estimate sufficiently precise to estimate water depth. This resulted in a subset of dive bouts ($n = 59$ dive bouts) for analysis of 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 and grouped into four categories to account for deviations in location estimates, charted depths, and tide heights; Class 1 = 0 - 10 m, Class 2 = 10.1 - 20 m, Class 3 = 20.1 - 30 F, and Class 4 > 30 m.

We modeled the relationship between water depth and diving parameters with GLMs and simple linear regression (SLR) models. These are referred to as depth GLMs and depth SLRs. Response variables were; dive bout duration, mean dive time from each bout, and percent time underwater during each bout. Dive bout interval was excluded since birds were typically not associated with one location or water depth during an interval. Water depth was included as the only explanatory variable in the depth GLMs and SLRs. We also ran additional GLMs to investigate the effect of water depth on diving while considering additional environmental factors as explanatory variables. For each response variable, we modeled water depth as a categorical explanatory variable and also included as explanatory variables any environmental variable determined to be significant in the diving GLMs (i.e., from analysis of the data set without water depth as a variable). This final approach was undertaken because the significance of the other environmental variables had already been established with the larger data set used in the diving GLMs and it seemed appropriate to make use of that information. The simple

linear regression approach was undertaken to provide results that were comparable to other diving studies.

RESULTS

Dive and Surface Intervals and Interrelationships

Fourteen Marbled Murrelets were captured and radio-tagged during 1995 ($n = 9$) and 1996 ($n = 5$). Mean body mass of Marbled Murrelets captured during this study was similar between years (1995 mean = 216.0 g, $sd = 6.4$ g, $n = 9$; 1996 mean = 216.0 g, $sd = 14.7$ g, $n = 5$). Diving data were recorded from 11 of these birds resulting in remote audio observations of 2,324 ($n = 7$ birds) and 3,855 ($n = 4$ 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 diving behavior of non-nesting birds.

Mean dive time within each year varied less than either mean pause time or mean dive:pause (Fig. 1.2). Mean dive time, mean pause time, and mean dive:pause ratio each differed between years ($P = 0.017, 0.0001, 0.002$, respectively; 2-tailed randomization tests).

The relationship between dive time and pause time varied based upon the scale at which it was examined. At the dive bout scale, there was a significant, positive relationship between mean dive time and mean pause time each year (Fig. 1.3). The percent of variation explained by these regression models was moderate each year but increased 17% in 1996. However, at the shorter temporal scale of the dive cycle, the relationship between dive and pause time varied substantially between years (Table 1.1). There was no significant relationship between dive time and preceding or ensuing pause time or

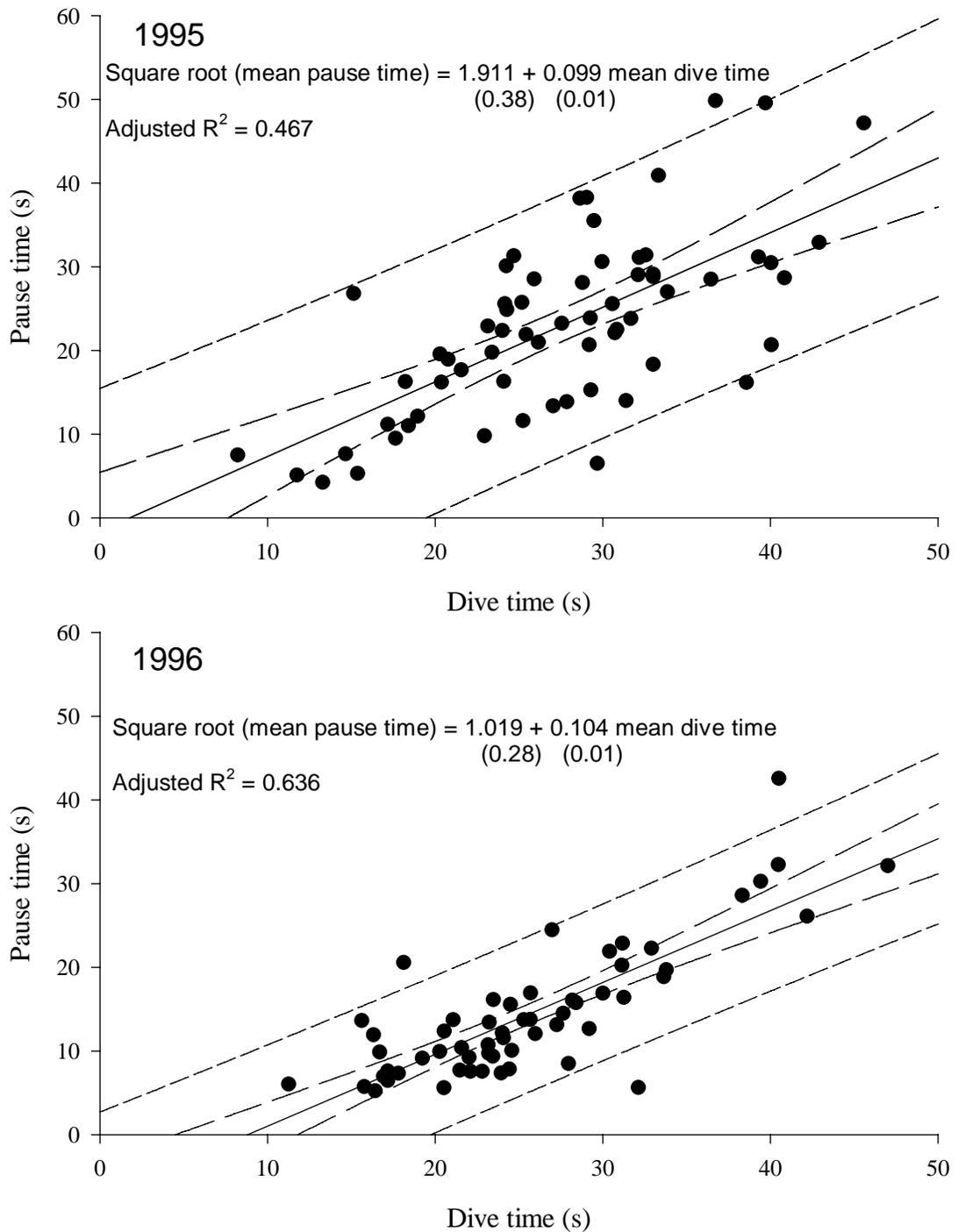


Figure 1.3. Regression of mean pause time on mean dive time from diving bouts of telemetered Marbled Murrelets along the central Oregon Coast, May - August 1995 and 1996. Short-dashed outer lines = 95% prediction intervals; long-dashed inner lines = 95% confidence intervals. Values in parentheses beneath equations are standard errors.

Table 1.1. Determination of breathing patterns in telemetered Marbled Murrelets along the central Oregon Coast, May - August, 1995 and 1996. Significance determined from mean coefficient estimates and 95% confidence intervals of 1000 resampled ANCOVA models, 500 samples of dive cycles drawn without replacement per iteration. Models 1 and 2 contain 1st order terms for pause times for 1995 and 1996, respectively; models 3 and 4 contain 1st and 2nd order terms for pause times for 1995 and 1996, respectively.

Parameter'	Lower CI	Mean coefficient estimate	Upper CI	Significant?
Model 1 - 1995				
Intercept	17.51	23.09	28.24	
Preceding pause time (s)	-0.016	0.039	0.111	No
Ensuing pause time (s)	-0.051	0.009	0.103	No
Model 2 - 1996				
Intercept	27.68	33.99	39.82	
Preceding pause time (s)	0.077	0.211	0.371	Yes (+)
Ensuing pause time (s)	0.036	0.158	0.291	Yes (+)
Model 3 - 1995				
Intercept	23.03	17.34	11.57	
Preceding pause time	-0.011	0.243	0.596	No
Ensuing pause time	-0.092	0.125	0.411	No
Preceding pause time ²	-0.008	-0.002	0.001	No
Ensuing pause time ²	-0.006	-0.001	0.001	No
Model 4 - 1996				
Intercept	15.80	21.57	27.65	
Preceding pause time	0.254	0.529	0.851	Yes (+)
Ensuing pause time	0.103	0.394	0.703	Yes (+)
Preceding pause time ²	-0.017	-0.008	-0.002	Yes (-)
Ensuing pause time ²	-0.014	-0.006	-0.003	Yes (-)

¹ Preceding pause times test for reactive diving, ensuing pause times test for anticipatory diving.

² Significance of a positive relationship occurs if the mean estimate and lower CI are both > 0; significance of a negative relationship occurs if the mean estimate and upper CI are both < 0.

pause time² in 1995. However, a positive relationship between dive time and both preceding and ensuing pause times and pause times² was evident in 1996, indicating that reactive and anticipatory diving patterns each were more frequent during that year.

Diving Bouts, Bout Intervals, and Relationships with Environmental Variables

Duration of dive bouts (Fig. 1.2; $n = 68$ bouts from 7 birds in 1995, 59 bouts from 4 birds in 1996) and the number of dives in a bout (range = 3 - 204) varied greatly within and among individuals. The duration of successive diving bouts from the same bird were only moderately correlated ($r_s = 0.317$, $n = 90$ successive dive bouts, data pooled among years). Duration of dive bout intervals also varied greatly (Fig. 1.2; $n = 39$ intervals from 7 birds in 1995, 44 intervals from 4 birds in 1996). However, the duration of dive bout intervals was not correlated with either the duration of the previous or ensuing diving bout ($r_s = 0.078$ ($n=80$) and 0.120 ($n=81$), respectively, data pooled among years). There was, however, a moderate correlation between the duration of successive dive bout intervals ($r_s = 0.529$, $n=47$, data pooled among years). Duration of dive bout intervals was not correlated with mean dive time, mean pause time, or percent time underwater from preceding bouts in 1995 ($r_s = -0.090$, -0.088 , and -0.071 , respectively). However, an increase in correlative strength among these same variables appeared to occur in 1996 ($r_s = -0.349$, -0.369 , and 0.257 , respectively).

The four diving GLMs accounted for 27% to 39% of the variation in the diving data with two to four significant explanatory variables in each model (Table 1.2). Short-term sea conditions during diving bouts included tide stage and sea state; the former was not significant in any models while the latter had a significant effect only on bout duration (Table 1.2, Fig 1.4a). Temporal factors included time of day and year (Table 1.2); time of day moderately affected dive time (Fig. 1.4b). Year, however, strongly affected the

Table 1.2. Effects of environmental variables (determined by general linear models with Type 4 sums of squares) on diving performance of telemetered Marbled Murrelets along the central Oregon Coast, May - August 1995 & 1996¹.

Explanatory Variable	Num. DF	Duration of diving bout (min) (error df = 105) ($r^2 = 0.2729$)		Mean dive time w/in diving bouts (s) (error df = 100) ($r^2 = 0.3472$)		% time underwater during diving bouts (error df = 99) ($r^2 = 0.3867$)		Duration of interval between bouts (min) (error df = 58) ($r^2 = 0.3268$)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Area	5	1.89	0.102	3.30	<i>0.008</i>	3.55	<i>0.005</i>	0.31	0.906
Sea state	2	3.97	<i>0.022</i>	1.83	0.166	1.13	0.327	2.21	0.119
Tide	3	0.26	0.854	0.35	0.792	0.12	0.946	1.23	0.309
Time of day	3	1.14	0.335	2.26	<i>0.086</i>	0.78	0.509	1.54	0.213
Year	1	0.43	0.514	8.21	<i>0.005</i>	35.43	<i>0.001</i>	9.66	<i>0.003</i>
Area * year	2	1.61	0.204	3.55	<i>0.032</i>	5.43	<i>0.006</i>	3.68	<i>0.031</i>
Sea state * time	5	1.91	<i>0.099</i>	1.15	0.341	0.35	0.879	0.66	0.579

¹ Italicized bold values < 0.05; bold values > 0.05 and < 0.10.

Figure 1.4. Mean (\pm 95% CI) dive bout duration (A and C) and dive time (B) recorded during diving bouts of telemetered Marbled Murrelets along the central Oregon Coast, May – August, 1995 & 1996, during three sea state categories (A), four time of day categories (B), and their interactions (C). Categories sharing any identical letter were determined not to be significantly different using GLMs and a post-hoc Tukey-Kramer test with $\alpha = 0.10$. Italicized values beneath time of day * beaufort categories in C are sample sizes. Means and confidence intervals for bout duration are back-transformed from square root functions.

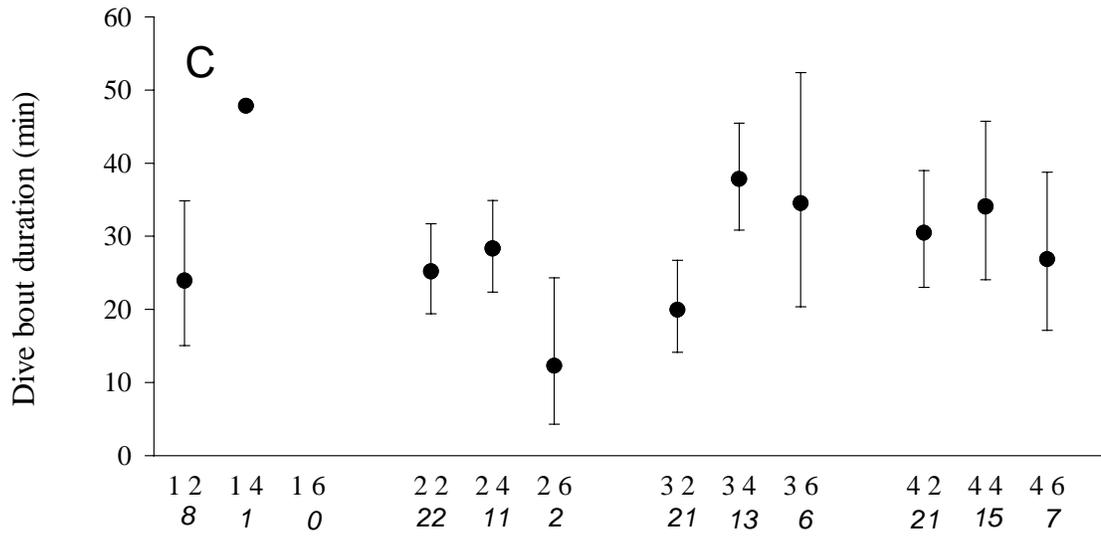
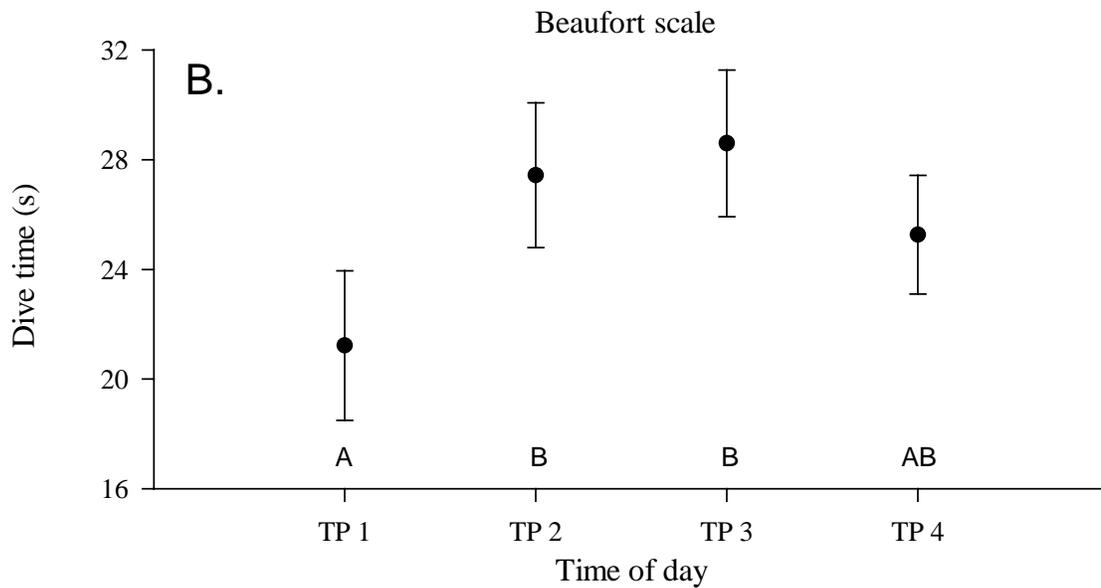
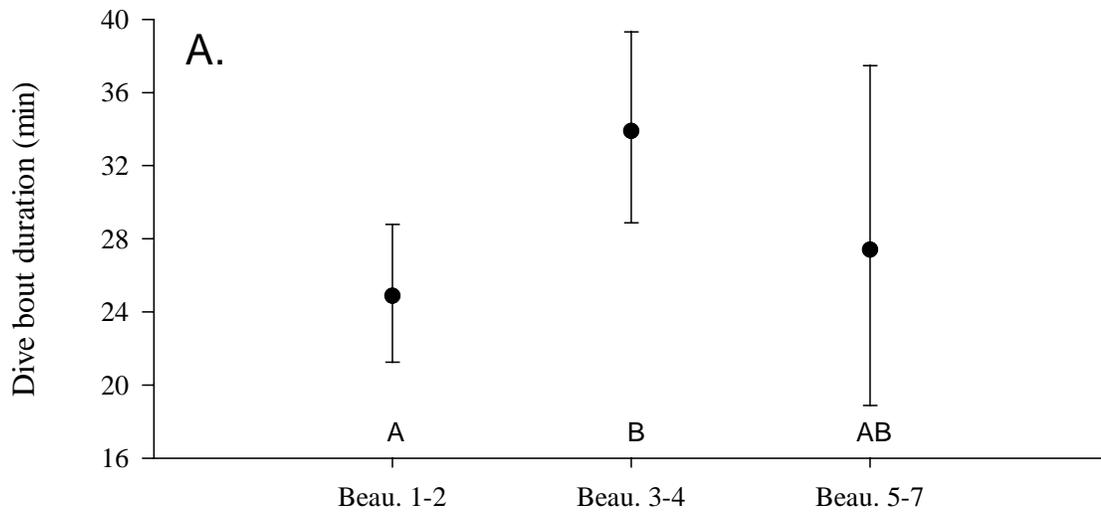


Figure 1.4 Time * beaufort category

duration of intervals between bouts, the percent time underwater within bouts (Fig. 1.2) and the mean dive time within bouts (1995 mean dive time = 27.48 s (95% CI 25.49, 29.47), 1996 mean dive time = 25.61 s (95% CI 23.66, 27.56)). The interaction of sea state and time of day moderately affected bout duration. Each diving response variable except bout duration was affected by the coastal region as either a main effect or as an interaction with year (Table 1.2). Pairwise differences among coastal regions were few and in two cases significance of the overall effect may have been due to either small sample size or unbalanced data (Fig. 1.5a, Fig. 1.6c, respectively).

Most dive bouts occurred in water <10 m (Fig. 1.7) despite the fact that Marbled Murrelets can likely dive to >25 m (Burger 1991). We did not observe a significant effect of water depth on mean dive time or percent time underwater within a bout when water depth in each model was considered as either a continuous variable (depth SLRs; $F_{1,56} < 0.109$, $P > 0.742$ for each model) or as a categorical variable (Table 1.3). There also was 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); $F = 0.002$ df=1,9, $P = 0.961$).

Aerobic and Anaerobic Diving

The proportion of observed Marbled Murrelet dives exceeding their aerobic diving limit (ADL; in seconds) was estimated using models presented in Burger (1991) and Schreer and Kovacs (1997). Since ADLs are based on estimates of the increase in standard metabolic rate (SMR) necessary to endure diving, and because those figures are difficult to obtain for every species, a range of predicted ADLs and the resultant percentage of observed Murrelet dives exceeding predicted ADLs are presented (Table 1.4). The proportion of Murrelet dives expected to exceed ADL varied widely, depending upon the

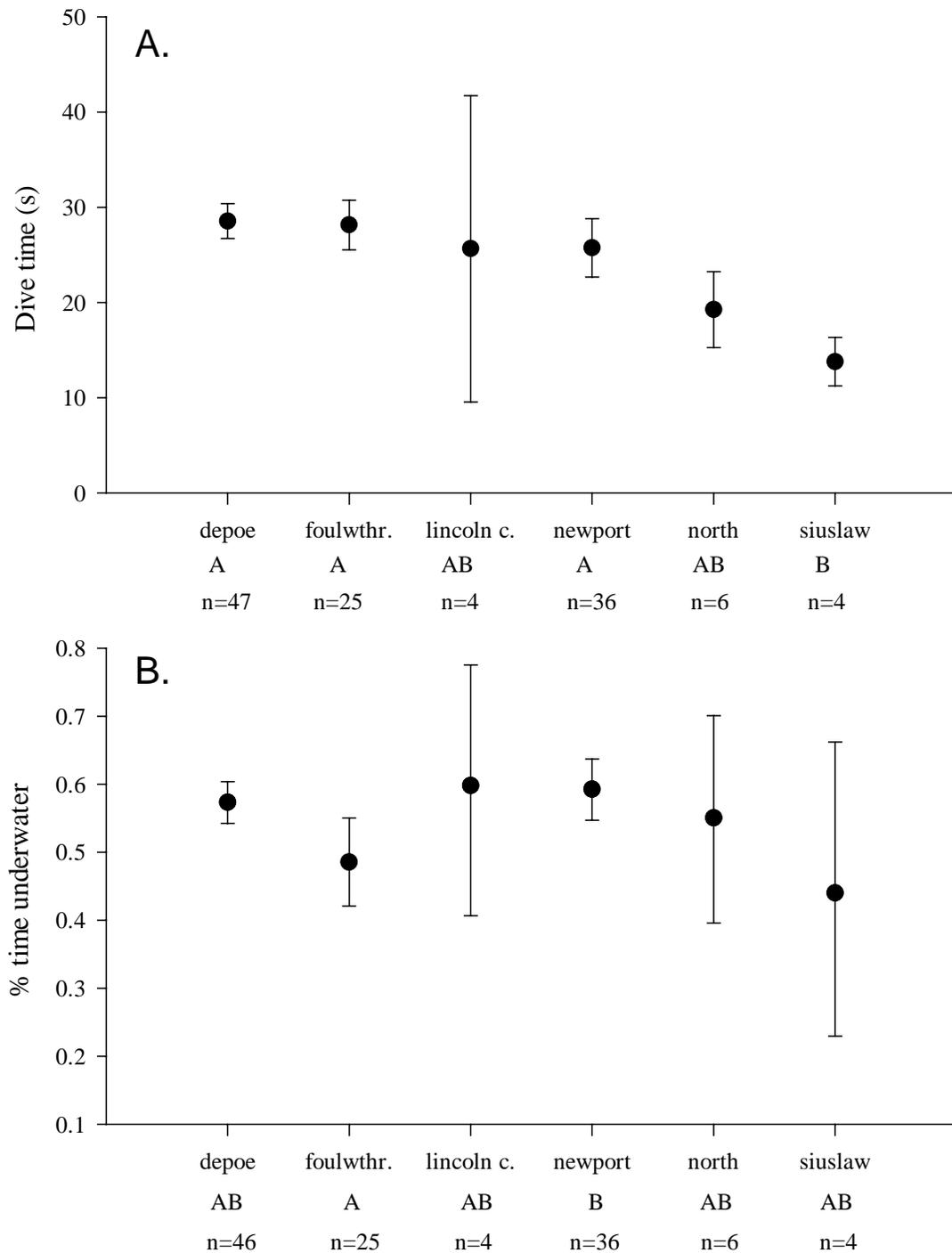


Figure 1.5. Mean (\pm 95% CI) dive time (A) and percent time underwater (B) recorded during diving bouts of telemetered Marbled Murrelets in six areas along the central Oregon Coast, May - August 1995 and 1996. Categories sharing any identical letter were determined not to be significantly different (GLMs with Tukey-Kramer tests with $\alpha = 0.10$). Sample sizes for each category appear beneath tick labels. Values for percent time underwater are back-transformed from arcsin root functions.

Figure 1.6. Mean (\pm 95% CI) dive time (A), percent time underwater (B), duration of intervals between dive bouts (C) of telemetered Marbled Murrelets in three areas of the central Oregon Coast, May – August, 1995 & 1996. Only data from locations with observations each of the two years are displayed. Abbreviations for areas are: de = Depoe Bay, fw = Cape Foulweather, and nw = Newport; the number following the abbreviation corresponds to the year. Means and confidence intervals for percent time underwater are back-transformed from arcsin root functions and means and confidence intervals for dive bout intervals are back-transformed from square root functions. Sample sizes for each category appear beneath tick labels.

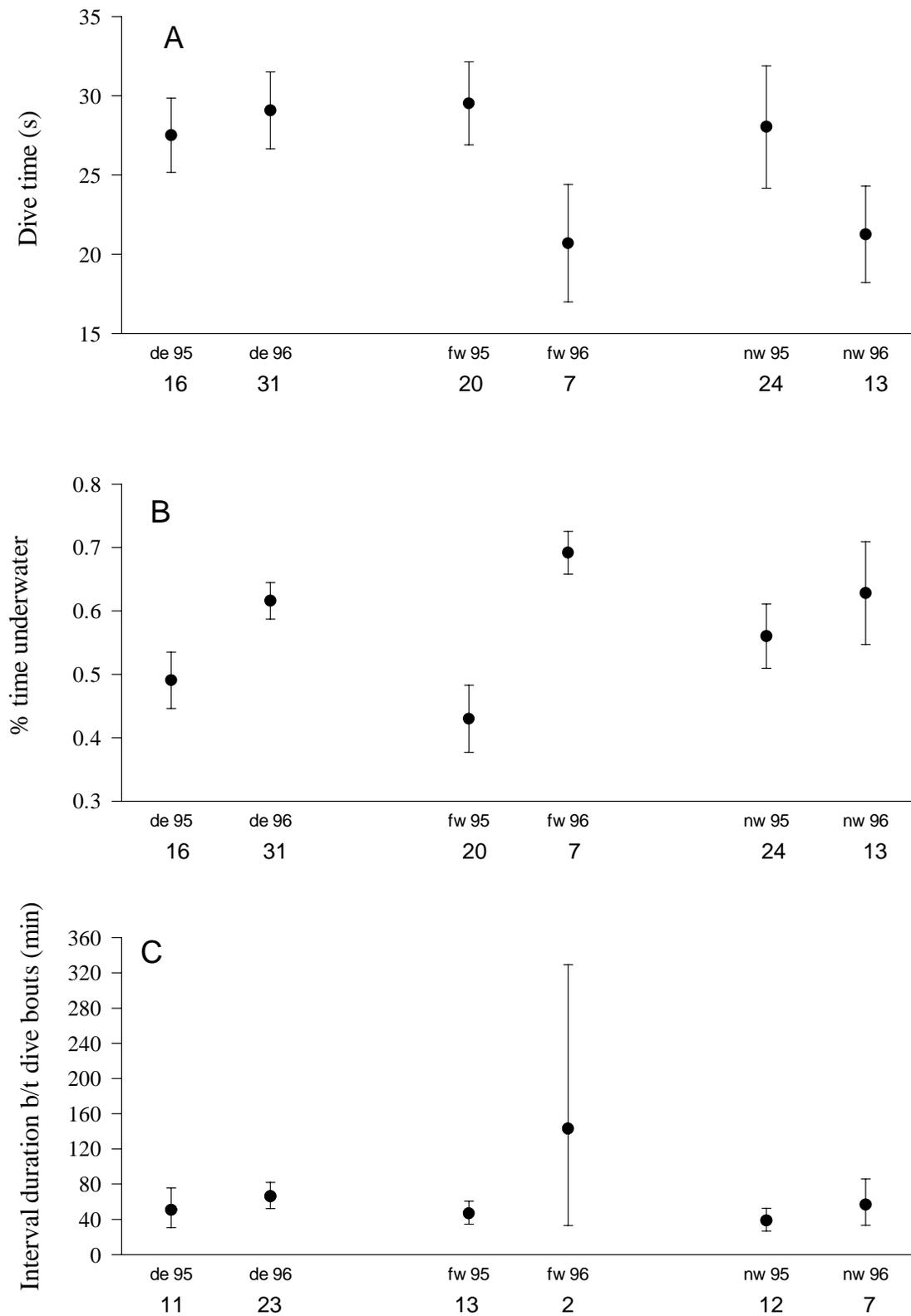


Figure 1.6.

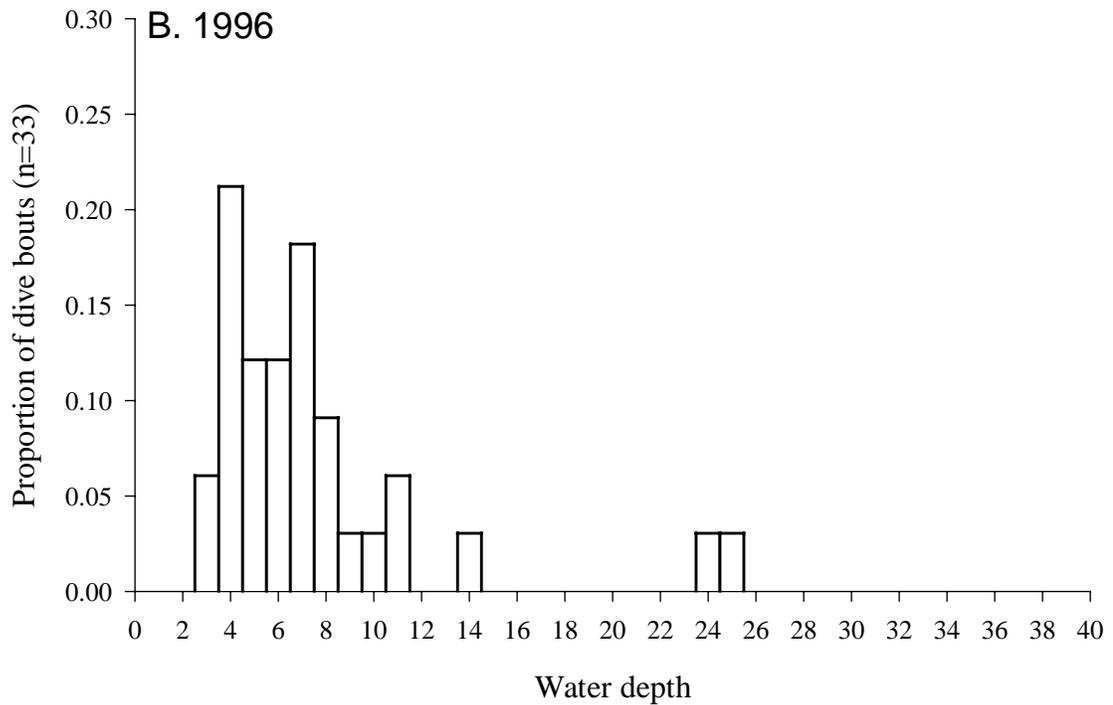
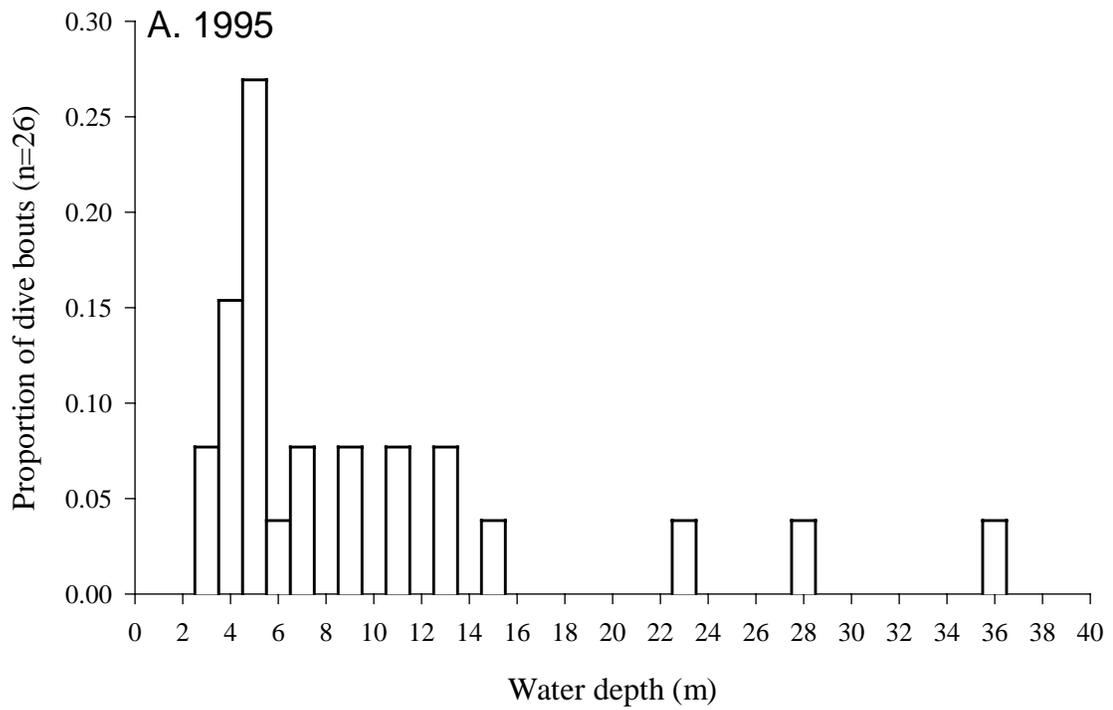


Figure 1.7. Proportion of dive bouts recorded by water depth from telemetered Marbled Murrelets along the central Oregon Coast, May - August 1995 (A) and 1996 (B).

Table 1.3. Effects of water depth (determined by general linear models with Type 4 sums of squares) on diving performance of telemetered Marbled Murrelets along the central Oregon Coast, May - August 1995 - 1996.

Response variable	Explanatory variable	DF	<i>F</i>	<i>P</i>
Mean dive time within bouts (s)	depth	3,36	0.27	0.845
Mean dive time within bouts (s)	depth*area	6,36	0.64	0.698
Mean dive time within bouts (s)	depth*year	3,36	0.85	0.475
% time underwater during bouts	depth	3,38	0.47	0.707
% time underwater during bouts	depth*year	3,38	0.48	0.695
% time underwater during bouts	depth*area	6,38	0.83	0.554

Table 1.4. Estimates of aerobic diving limit (ADL) and percentage of observed dives exceeding ADL for telemetered Marbled Murrelets along the central Oregon Coast, May – August, 1995 and 1996. ADL based upon mass specific O₂ stores and mass specific standard metabolic rate (SMR) and diving metabolic rate (DMR) presented in models and equations from Burger (1991) and Schreer and Kovacs (1997).

DMR as a multiple of SMR	Predicted ADL (s) based upon 44.5 ml ¹ O ₂ kg ⁻¹	% observed dives > ADL	Predicted ADL (s) based upon 58.0 ml ² O ₂ kg ⁻¹	% 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 ³	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

¹ used by Burger (1991).

² used by Schreer and Kovacs (1997)

³ DMR determined for Thick-billed Murres by Croll et al. (1992)

increase in SMR chosen. However, Croll et al. (1992) and Burger (1991) each suggested that metabolic rate during diving likely increased over SMR approximately three times; using this estimate resulted in a very low percentage of Murrelet dives exceeding ADL. Diving predominantly within aerobic limits is further suggested for each year by the lack of either a strong negative correlation between individual dive times and elapsed dive bout time (1995 $r_s = -0.1403$, 1996 $r_s = -0.3157$) or a strong positive correlation between individual pause times and elapsed dive bout time (1995 $r_s = -0.1027$, 1996 $r_s = -0.1945$; Wanless et al. 1988, Wanless et al. 1993).

DISCUSSION

Diving Performance

Using radio-telemetry to investigate diving behavior has benefits and drawbacks. For example, entire dive bouts can be recorded with telemetry while it is difficult to do so with visual observations. Additionally, multiple observations of diving bouts from the same individual can be recorded over days or weeks with telemetry. On the other hand, transmitter attachment may have negative effects on diving or breeding performance (e.g., Wanless et al. 1988). However, it may be difficult to assess negative effects of the telemetry process if all aspects of an individual's condition are unknown. For example, although all captured birds in this study had brood patches in some stage of development, only one was ever known to fly inland. While this may suggest a negative effect on breeding, telemetry studies of this species in Alaska, British Columbia, and California have each noted that most of the birds captured had brood patches and few have been tracked inland (Burkett pers. comm., Lougheed pers. comm., Nelson pers. comm.).

Additionally, Marbled Murrelets captured with the same technique we used and fitted with larger radio tags than those we deployed have been tracked to nest sites (Quinlan and Hughes 1992, Varoujean pers. comm.).

Despite transmitter attachment, however, dive and pause times reported in this study appeared similar to those reported elsewhere for Marbled Murrelets both with and without transmitters (see Strachan et al. 1995 for review). However, the mean duration of dive bouts recorded in this study (27 min - 33 min) appears greater than the only other reported value for Marbled Murrelets (mean = 20 min, s.e. = 0.04, n = 20 bouts; Varoujean and Williams 1995), which was obtained from telemetered birds in southern Oregon and northern California. Varoujean and Williams (1995) estimated a mean percent time underwater during dive bouts of 67.6% (s.e. = 1.0) from the same telemetered birds, a value slightly higher than those reported in this study (49% - 62%).

Diving performance among alcids appears to be related to some extent to body mass. Wanless et al. (1988) reported a significant relationship between mean dive duration and body mass for Common Murres (*Uria aalga*), Atlantic Puffins (*Fratercula arctica*), and Razorbills (*Alca torda*). Burger (1991) reported a significant allometric relationship between maximum dive depth and body mass among alcids. If dive duration is related to body mass then increases in foraging effort may not be achieved strictly by increases in dive duration since body mass would limit the range of the potential increase in effort. However, decreases in surface interval duration or increases in bout duration may be limited less by body mass and therefore may be more flexible. This may explain why Marbled Murrelets displayed less variability in dive times than either pause times or duration of dive bouts during each year of this study.

The Dive-Pause Relationship

The dive-pause relationship observed in this study varied within and between years

and at different time scales. Reactive and anticipatory diving patterns were evident in 1996 as both linear and quadratic effects, but no significant relationships were evident in 1995. Occurrence of both linear and quadratic effects in the dive cycle have been reported previously (R.P. Wilson 1991); linear relationships occur when dive duration is near its mean while power relationships occur when dive duration approaches maximum limits. 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 are discussed in turn.

Lea et al. (1996) observed different diving patterns in species of shags and cormorants (*Phalacrocoracidae*) that exhibited different prey handling behavior. Anticipatory diving occurred in species that swallowed prey beneath the surface while reactive breathing occurred more often with species that swallowed prey while on and sometimes beneath the surface. Lea et al. (1996) suggest sub-surface prey handling minimizes disruption to the diving pattern. This would then allow birds to develop a more consistent diving pattern whereby they store 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 each tend to occur more frequently as birds forage in the benthic zone and not throughout the water column. Lea et al. (1996) observed anticipatory diving patterns more often in 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, respectively, each of which foraged throughout the water column. The lack of a significant relationship between dive time and water depth for these Marbled Murrelets suggests they foraged throughout the entire water column. This may contribute to the range of diving patterns observed within and between years.

Variations in dive cycle patterns also may be related to prey capture effort. Anticipatory diving appears to occur when maximum capture effort is required; there appears to be a weaker or non-observable relationship between dive and pause times when less effort is required (Lea et al. 1996). Ydenberg and Clark's (1989) model also predicted diving effort would increase when prey were difficult to find, relocate, or capture, and Chappell et al. (1993) observed that Adelie Penguins (*Pygoscelis adeliae*) decreased pause times when prey were patchy. The reactive and anticipatory breathing patterns displayed by Marbled Murrelets in 1996, but not 1995, may thus reflect an increase in capture, and thus diving, effort. For example, increases in diving effort with decreases in prey availability have been observed in other seabirds. Wanless et al. (1993) observed an increase in diving effort in shags and attributed it to a change in prey availability. Similarly, Monaghan et al. (1994) observed a stronger relationship between dive and pause times of Common Murres during years of reduced prey availability in Scotland. Additionally, there is evidence that some change in prey conditions occurred in the study area between 1995 and 1996. For example, a colony of Common Murres in the study area experienced near total abandonment early in the breeding season and a die off of adults occurred throughout the summer (Lowe, pers. comm.); each were attributed to changes in local forage fish availability and not 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.

Although the dive-pause relationship during this study was inconsistent within and between years at the dive cycle scale, there was a significant and more consistent relationship between mean dive 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 underwater can occur at a time scale greater than each individual dive cycle and therefore examination of dive cycle data only may be misleading.

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 significant relationship between water depth and dive time. For example, Cairns (1992) and Watanuki et al. (1996) observed weak relationships 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 these Marbled Murrelets also foraged throughout the water column. This observation is consistent with the habits of their primary prey, sand lance (*Ammodytes hexapterus*), which occur throughout the water column, undergo daily vertical migrations, and thus likely cause foraging conditions to vary significantly across relatively short time scales (Wanless et al. 1993, Burkett 1995).

Diving studies have rarely discussed diving parameters other than dive time or environmental variables other than water depth. While explanatory variables other than water depth may not be as universally important to 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. Of the five main and two interaction effects used

in the diving GLMs in this study, the variables representing short term effects (time of day, tide stage, sea state, and sea state * time) were not significant as often nor as strongly as those variables representing longer term effects (coastal area, year, area*year).

Changes in diving characteristics due to short-term variables likely reflect the effects of local conditions on foraging behavior. For example, the observed increase in bout duration during moderate seas may reflect increased effort required to locate, pursue and capture prey, possibly due to increases in turbidity and decreasing light levels. However, more variable bouts in heavy seas may be due to either early termination of diving or greater time requirements to acquire prey. For example, Cannell and Cullen (1998) demonstrated experimentally that Little Penguins (*Eudyptula minor*) increased dive duration during periods of low light. The differing effect of sea state by time of day on diving may be due to birds attempting to maximize prey intake before foraging opportunities cease at night (there were no observations of telemetered Marbled Murrelets diving after dark during, n = 30 nocturnal tracking sessions). Ydenberg and Clark (1989) suggest divers are more likely to dive anaerobically late in the day when post bout recovery time is relatively unlimited. Foraging in heavy seas may require more energy and thus may be avoided early in the day when the price for overextending the energy budget is higher.

The larger spatial and temporal scale effects of coastal area and year tended to interact in this study. Discounting this interaction for bout intervals (where the significance of the interaction may be due entirely to data from the Cape Foulweather area where sample size was very low in 1996; Fig. 1.6c), an underlying pattern was observed: mean pause time during bouts (i.e., time between dives) decreased from 1995 to 1996 at each area. This may be inferred by examining directional changes in dive time and percent time underwater within an area. For example, mean dive time decreased in 1996 in the Newport area while percent time underwater did not change; therefore a decrease in mean pause time proportional to the decrease in mean dive time also must have occurred.

Proportion of time spent underwater during a dive bout increased during 1996 in the Cape Foulweather and Depoe Bay areas. This was accompanied by no change in dive time in Depoe Bay (and thus a decrease in mean pause time in 1996) and a decrease in dive time at Cape Foulweather (and thus a proportional decrease in mean pause time in 1996). Decreases in mean pause time are consistent with the decrease observed in individual pause times and the increase observed in the dive:pause ratio data in 1996.

The year effects observed in the diving GLMs likely represented an increase in foraging effort in 1996 and it appeared all diving parameters were affected. For example, pause time within dive cycles decreased in 1996; a stronger relationship developed between mean dive and mean pause times within and among bouts in 1996; duration of intervals between dive bouts increased and showed a stronger, positive correlation with mean dive time, mean pause time, and percent time underwater in 1996; the strength of the negative correlation between elapsed bout time and dive time (a measure of aerobic versus anaerobic metabolism; Wanless et al. 1988) increased in 1996; and mean dive time decreased while percent time underwater increased in 1996. These types of changes in diving behavior (e.g., increases in diving effort) have been attributed to decreases in prey availability in other pursuit-diving seabirds as previously mentioned (e.g., Wanless et al. 1993, Monaghan et al. 1994). Regional oceanographic conditions may have affected prey availability and hence diving effort for these Marbled Murrelets. For example, by May 1996, the Oregon Coast had experienced a prolonged increase in average monthly sea surface temperatures (SST). Since January 1994, average monthly SST was at least 1.5° C greater than normal in 19 of the previous 28 months, with 12 of those months greater than 2.5° C above normal (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, primary productivity decreases, and hence conditions unsuitable for growth and development of fish stocks are created (Duffy 1989, U.W. Wilson 1991). For example, decreases in alcid

chick 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 due to the cumulative effect of >2 years of above average SST and may have contributed to the observed changes in Marbled Murrelet diving 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 are reduced during anaerobic diving as opposed to the duration of dives being increased; hence the dive:pause ratio departs from unity during anaerobic metabolism. Furthermore, anaerobic metabolism during diving may be evidenced 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 frequent anaerobic metabolism did not occur while diving. It appeared unlikely that Marbled Murrelets exceeded ADL in more than 20% of their dives based on recent estimates of increases in metabolic rate required for diving in alcids (2-3x SMR; Croll et al. 1992), penguins (<2x SMR, Bethge et al. 1997) and Tufted Ducks (*Aythya fuligula*; <4x SMR, de Leeuw 1996). It is more likely that murrelets exceeded ADL in fewer than 10% of their dives (SMR x 3). The latter estimate appears accurate in light of the weak-to-moderate correlation between dive time and elapsed bout time.

Body mass, ecological factors, and general foraging behavior have all been suggested as mechanisms affecting the frequency of anaerobic diving. For example, frequency of anaerobic diving in penguins tends to increase with an increase in body mass (Bethge et al. 1997); therefore, the relatively low body mass of Marbled Murrelets may explain their

apparent low frequency of anaerobic diving when compared to larger alcids (e.g., Croll et al. 1992). Furthermore, a change in the frequency of anaerobic diving has been attributed to changes in hunting behavior brought about by changes in prey availability. In this study, the stronger correlation between dive time and elapsed dive bout time in 1996 than 1995 suggests a shift in diving behavior, with a likely increase in the frequency of anaerobiosis. This would not necessarily be caused by an increase in the number of dives exceeding ADL, but could be due to decreases in pause times and thus shorter recovery periods between dives, each of which occurred in 1996.

General foraging behavior is likely to also have a strong influence on diving metabolism. Ydenberg and Clark's (1989) model predicted that, for birds that forage on ephemeral schools of prey, anaerobic metabolism is more likely to occur when the probability of contacting new schools of fish is low, when the probability of re-contacting schools is intermediate, or when the probability of capture once a school is located is high. Generally, they argue, this will lead to relatively low levels of anaerobic metabolism in birds that forage on schooling fish. Similarly, Clowater and Burger (1994) suggested that the longer dives of Pigeon Guillemots in their study, when compared to dive times of other alcids of similar body mass were likely due to pursuit of solitary prey. Longer dives do not hamper an individual from maintaining contact with solitary prey as with ephemeral schools and hence recovery times can be lengthened without detriment to foraging success. Given that the primary prey of Marbled Murrelets are various species of schooling fish that occur throughout the water column, such as sand lance and Pacific herring (*Clupea harengus*; Burkett 1995), it suggests that a low frequency of anaerobic metabolism should be expected, and that the change in the degree of anaerobic metabolism between years may be due to a change in prey availability.

Marbled Murrelets in this study appeared to conform to the model predictions that anaerobic metabolism should not be the norm in pursuit-diving birds. However, their diving behavior did not conform to the predictions of anticipatory diving or depth-related

diving noted in Kramer's (1988) optimal breathing model. We speculate that the observed variability in diving 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 field tests of or developing applications of theoretical breathing models.

Despite improvements in remote data recording devices such as telemetry and time-depth recorders, few studies have been able to consistently monitor diving patterns of individuals over long periods of time or to focus directly on physiological aspects of diving 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. Compared to diving data for other alcid, the results of this study confirm the important influence of prey availability and environmental variables on diving behavior. 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, as are most telemetry studies, was purely observational. Results from such studies are limited in their scope of inference to the individuals studied and the spatial and temporal frame of the study (Ramsey and Schafer 1997). Furthermore, the numbers of individuals we observed was relatively small compared to the number of observations recorded per individual. This is often the case with telemetry studies and, while not invalidating results, should lead to caution in interpreting and applying results. However, our sample sizes, both for numbers of individuals and numbers of observations per individual, were often similar or higher when compared to other published telemetry and non-telemetry studies of pursuit-diving seabirds.