

## **MARBLED MURRELET (*BRACHYRAMPHUS MARMORATUS*) POPULATION TRENDS AND THE CALIFORNIA CURRENT**

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## MARbled MURRELET (*BRACHYRAMPHUS MARMORATUS*) POPULATION TRENDS AND THE CALIFORNIA CURRENT

### ABSTRACT

Population trend is a key metric used in wildlife management and conservation. Trend can be estimated by regression, but there are various models that can be fit. It is important to explore different regressions to ensure the most appropriate model is used to support management actions or ecological understanding. The marbled murrelet (*Brachyramphus marmoratus*) is a federally protected seabird species that occurs in the Pacific Northwest of North America. To better understand population trends of this declining species, multiple trend models were fit to 2001-2020 at-sea survey data for marbled murrelet in California, Oregon, and Washington. The statistical properties and plausibility of each model were compared. Linear, exponential, and Monte Carlo exponential models all indicated that a flat trend ( $\lambda$  close to zero) existed. A quadratic model had a plausible fit which may reflect the pattern of fluctuating ocean conditions. A segmented model had a good fit but had issues of biological plausibility. The best model overall was a sinusoidal model with a linear term, which also may correlate with ocean conditions. We show that conditions in the California Current are likely related to murrelet productivity. The linear and exponential models have utility for regulatory purposes, whereas the other models may suggest mechanisms regulating the population. We concluded that trend can be summarized in multiple ways, but a thorough analysis, perhaps using multiple distributions, is necessary to avoid incorrect conclusions.

### KEY WORDS

*Brachyramphus marmoratus*, conservation, demography, endangered species, marbled murrelet, California Current, Oregon, population trend, Washington, California

## Table of Contents

1.0	INTRODUCTION .....	5
2.0	METHODS .....	6
3.0	RESULTS .....	8
4.0	DISCUSSION.....	11
5.0	CONCLUSIONS.....	13
	REFERENCES .....	13

## 1.0 INTRODUCTION

For species of concern, commercial species (e.g., ocean fisheries), and recreational or subsistence harvests (e.g., game species), an estimate of population trend is a key management index (Wagner et al. 2013). A strong upward trend might enable a species to be removed from regulatory protection, or for a recreational or commercial harvest to resume, continue, or intensify. A stable population might indicate that extinction risk for a species is low or that current levels of take are sustainable. Trends might be related to underlying processes (e.g., harvest level, rate of habitat loss, habitat change, climate, natural population cycles).

When a population change is suspected, statistical trend models are often used to verify a trend, or monitor results of management activities, and indicate that a change in management is warranted. For example, the dramatic decline of some bat species in the eastern US due to white-nose syndrome (Frick et al. 2010) is apparent with annual raw counts in hibernacula and with observations of reduced capture rates and detections via acoustic detectors. This trend is evident due to dramatic declines (>90%) in some species over a relatively short period of time. Likewise, the California condor (*Gymnogyps californianus*) (Roach and Patel 2019) recently has had a strongly positive trend, clearly having increased from historic lows.

A population trend is a somewhat abstract summary statistic that reflects useful information about a species' abundance trajectory. One of the difficulties with assessing trend is that over long periods, populations are likely to fluctuate a great deal, with detectable "trends" increasing (up and down) with shorter time segments (Loehle and Arghami 2017). Populations might even cycle on decadal, or longer, time scales, leading to a high likelihood of spurious trend estimates derived from shorter time periods. For short periods, lack of statistical power can also make trend detection difficult (Wagner et al. 2013).

Because trend is not a physical metric, but rather is a summary statistic, there are multiple ways to conceptualize it, each of which leads to a different statistical approach. To better understand this, we present several trend metrics and explore their assumptions and complications. The example data set is for marbled murrelet (*Brachyramphus marmoratus*) in the US Pacific Northwest.

The marbled murrelet is a small seabird found along the western coast of North America, ranging from Northern California to Alaska. It has been suffering long-term declines over most of its range (Huff et al. 2006), including Canada (Bertram et al. 2015), leading to its listing by the US Fish and Wildlife Service as federally Threatened, and state endangered listing status in California, Oregon, and Washington (Huff et al. 2006; Desimone 2016). The reasons for population decline appear to be the loss of old-growth forest for nesting, low reproductive rates, and declining diet quality and/or quantity at sea (Peery et al. 2004; Becker and Beissinger 2006; Huff et al. 2006; Becker et al. 2007; Norris et al. 2007; Gutowsky et al. 2009). The Northwest Forest Plan (USDA Forest Service and BLM 1994a and 1994b) should, in theory, help the marbled murrelet over time (McIver et al. 2022), so the detection of trend for this species may provide an indication of success or failure of the Plan.

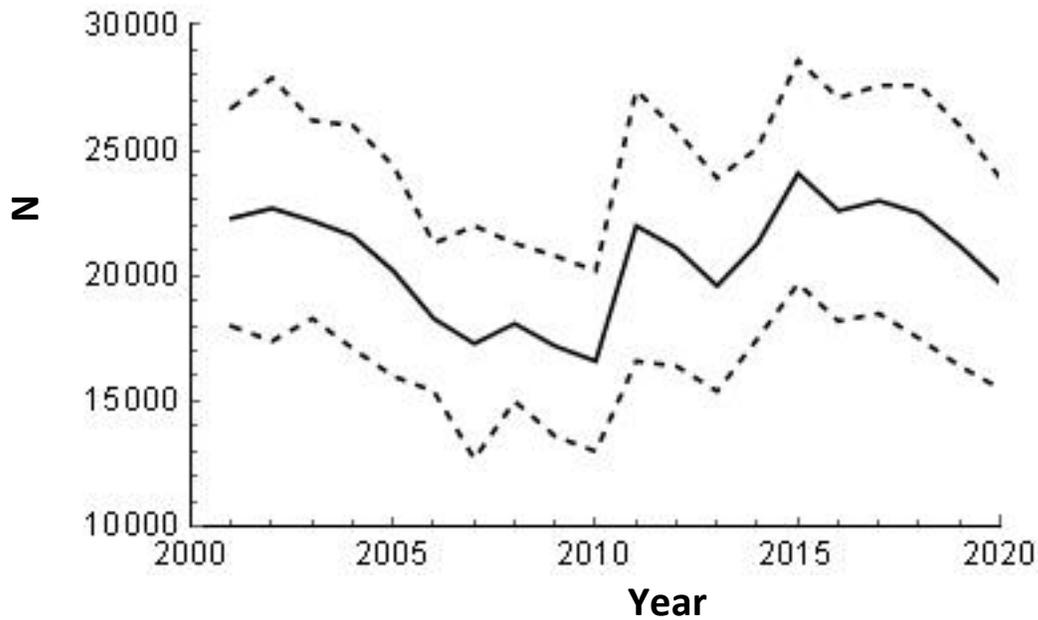
Due to the marbled murrelet's small size and habit of nesting on large limbs in old trees, the species' demography has been difficult to study (Huff et al. 2006; Raphael 2006). More specifically, marbled murrelets are extremely difficult to survey in the forest due to their cryptic nests and behavior. Therefore, at-sea surveys remain the best method to estimate regional population size (Madsen et al. 1999), and the most widely used method for long-term monitoring (Miller et al. 2006).

## 2.0 METHODS

Population estimates and 95% confidence limits for 2001 through 2020 (Table 1, Figure 1) from Mclver et al. (2022, p.10, Table 2) were used to evaluate population trends across the range of marbled murrelets from California through Washington, USA. The at-sea monitoring data were based on counts from ocean transects in the breeding season. No attempt was made by Mclver et al. to estimate total population. Given the constant methods and sampling effort with lack of extrapolation, detectability is not an issue unless detectability changes over time. However, there is no evidence of a change in detectability. To compare possible trend estimates from the at-sea relative abundance data, six methods were compared. Models were evaluated using tools in [Wolfram Mathematica](#).

**Table 1.** *Marbled murrelet population estimates for Washington, Oregon, and California. Data from Mclver et al. (2022). Rounded to nearest 100.*

Year	Birds	Birds lower 95% confidence limit	Birds upper 95% confidence limit
2001	22,300	18,000	26,700
2002	22,700	17,400	27,900
2003	22,200	18,300	26,200
2004	21,600	17,100	26,000
2005	20,200	16,000	24,400
2006	18,300	15,300	21,300
2007	17,300	12,700	22,000
2008	18,100	15,000	21,300
2009	17,200	13,700	20,800
2010	16,600	13,000	20,200
2011	22,000	16,600	27,400
2012	21,100	16,400	25,800
2013	19,700	15,400	23,900
2014	21,300	17,492	25,100
2015	24,100	19,700	28,600
2016	22,600	18,200	27,100
2017	23,000	18,500	27,600
2018	22,500	17,500	27,600
2019	21,200	16,400	26,000
2020	19,700	15,500	23,900



**Figure 1.** Marbled murrelet time-series for the three-state region (black line) and 95% confidence intervals (dashed lines) for each date (see Table 1).

**Table 2.** Trend models with goodness-of-fit statistics. Slope from linear component of models relative to 2001 level.

Model	Slope	$R^2_{adj}$	$AIC_c$
Linear	0.27%	-0.0028	370.54
Exponential	0.3%	-0.03	370.52
Quadratic	0.145%	0.14	369.25
Segmented	-0.05%*	0.70	
Sinusoidal	0.15%	0.74	352.08

A linear model is the simplest way of describing how the population has changed over time (Wagner et al. 2013). Simple linear regressions of the population trend were performed to evaluate trend on the arithmetic and log scales. It is possible with these data to use weighted regression, but the results remained consistent due to fairly constant confidence intervals (Figure 1), and thus weighting was left out for simplicity. A linear model with log-transformed data was based on an assumption of proportional population change. This approach is common with population data (McIver et al. 2022; Wagner et al. 2013). The shape of the data suggested that a quadratic model might be descriptive, so one was developed. It is possible that a piecewise linear model could fit the data, so we also demonstrated that approach. Finally, a sinusoidal model with a linear term was fit.

A novel approach was also developed based on the 95% confidence intervals of the at-sea relative abundance data. Consider a simple population model:

$$N_{t+1} = \lambda N_t \tag{1}$$

where  $\lambda$  is the population growth rate and  $N_t$  is the population at  $t$ . To be consistent with the data, projections using hypothetical  $\lambda$  need to stay within the 95% confidence intervals at each  $t$ . The initial  $N_0$  also has uncertainty. We can randomly generate  $\{N_0, \lambda\}$  pairs, solve for the time trajectory using eq. 1, and keep only the parameter sets that satisfy the bounding constraints. This Monte Carlo method generates a set of feasible parameter pairs that do not contradict the known data. Each  $\{N_0, \lambda\}$  pair defines a population trajectory for the species with a possible constant  $\lambda$  over time consistent with the data. Note that this is simply a summary of one way of looking at the data, not a “true” trend or a statistical model.

### 3.0 RESULTS

The best-fit linear trend for the 3-state region had a slope of +59.4 birds/y or +0.27% annually based on the first year (Table 2, Figure 2). The slope of the trend line was not significant ( $P=0.5$ , confidence intervals overlapped zero), indicating that there was no trend in this series, which is consistent with McIver et al. (2022). The fit to the exponential model (Figure 2) had  $\lambda=1.003$  (0.3%)/yr., identical to the linear model and visually indistinguishable from it. For this model,  $P=0.5$  and confidence intervals included zero. For  $\lambda$  close to 1, the exponential model approximated a straight line. For both the linear and exponential models,  $R^2_{adj}$  was  $<0$  because the model was less informative than the mean. The quadratic model (Figure 3) appeared to capture these data and had  $R^2_{adj}=0.14$ . The segmented model (Figure 4) had a better fit, with  $R^2_{adj}=0.70$ . The sinusoidal model (Figure 5) had a slope coefficient of 0.15% and  $R^2_{adj}$  of 0.74. The period was about 14.6y. For the Monte Carlo-consistent modeled marbled murrelet population trajectories, only eight trajectories (defined by  $N_0$  and  $\lambda$ ) were found that satisfied the constraints based on the confidence interval data out of 10,000 random trials (Figure 6). Mean population growth rate ( $\lambda$ ) of these eight feasible values was found to be 1.004, with all slopes positive. The best  $AIC_c$  and  $R^2_{adj}$  values were for the sinusoidal model, though no  $AIC_c$  value could be computed for the segmented model.

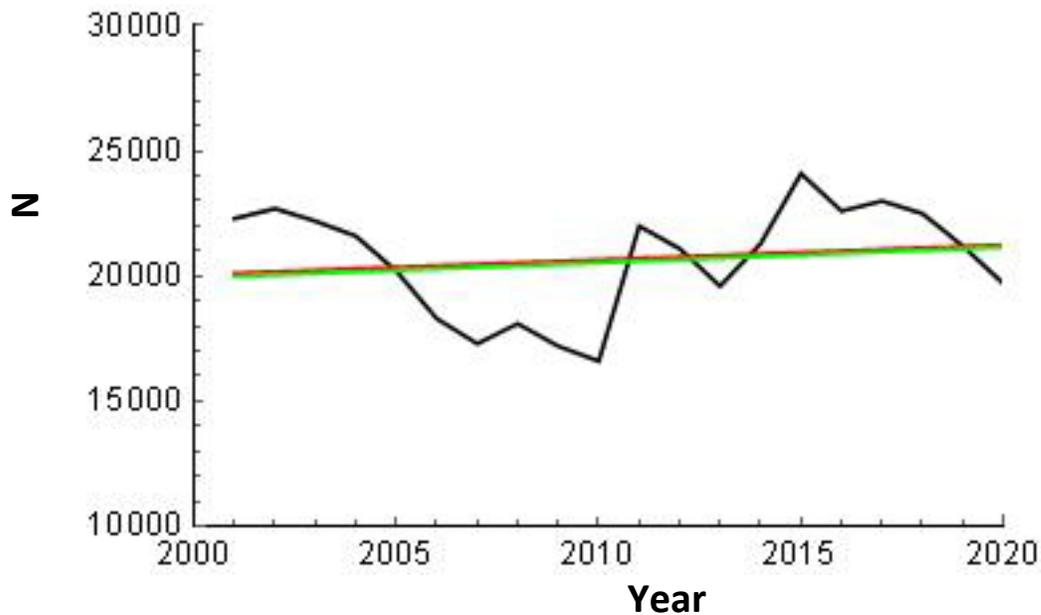


Figure 2. Marbled murrelet population with linear fit (red line) and exponential fit (green line).

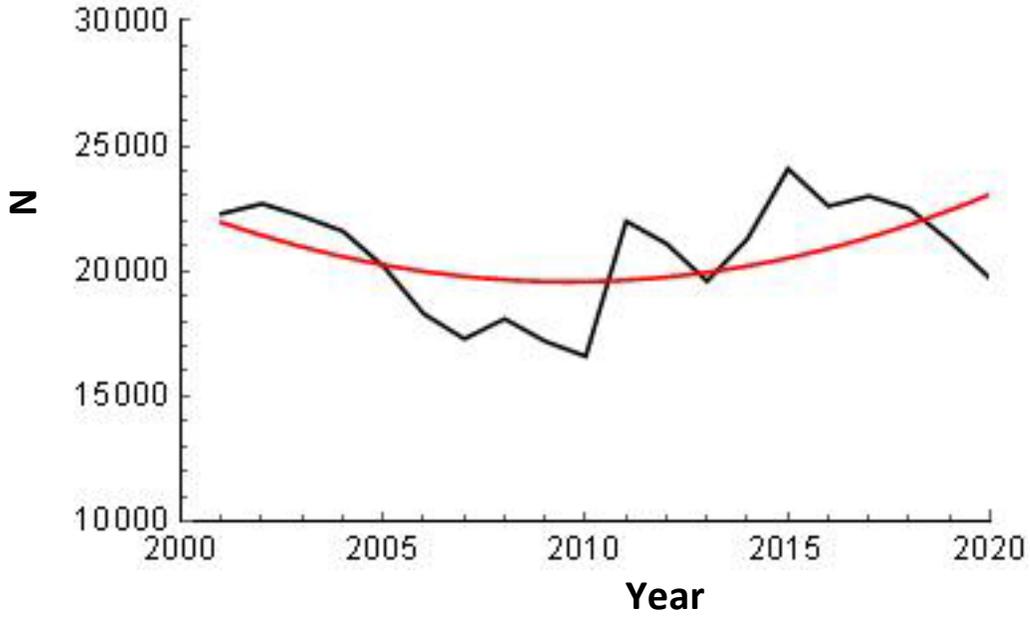


Figure 3. Quadratic model fit to marbled murrelet data.

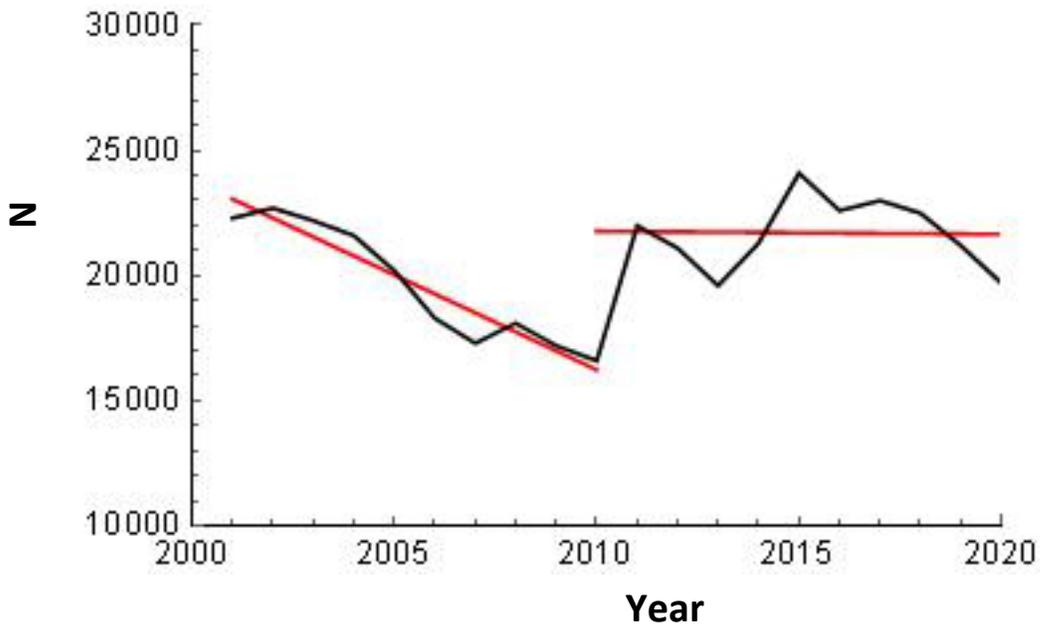


Figure 4. Segmented linear fit to marbled murrelet data.

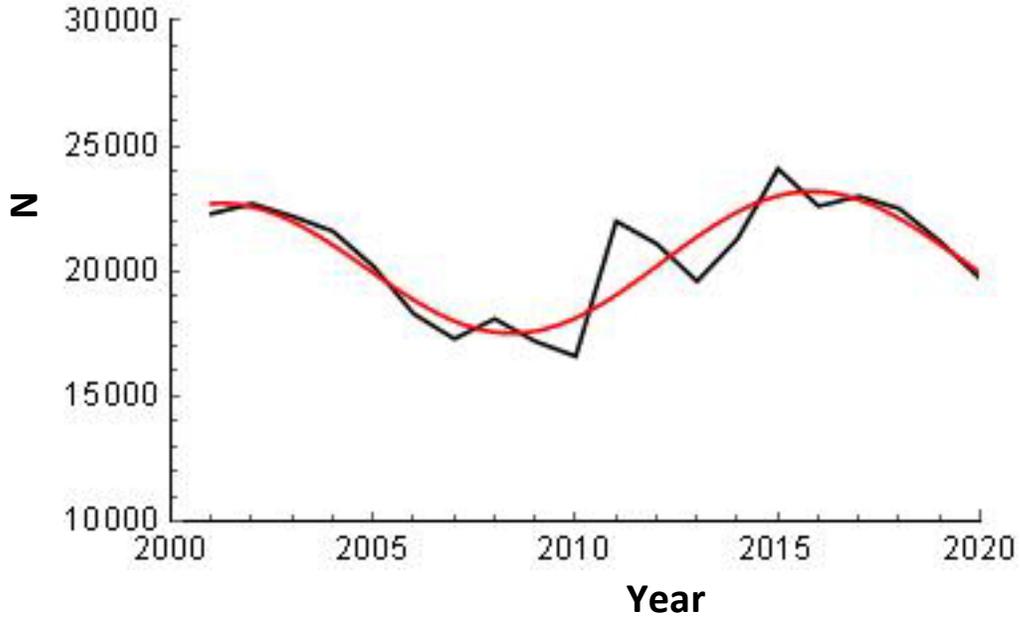


Figure 5. Sinusoidal fit to marbled murrelet data.

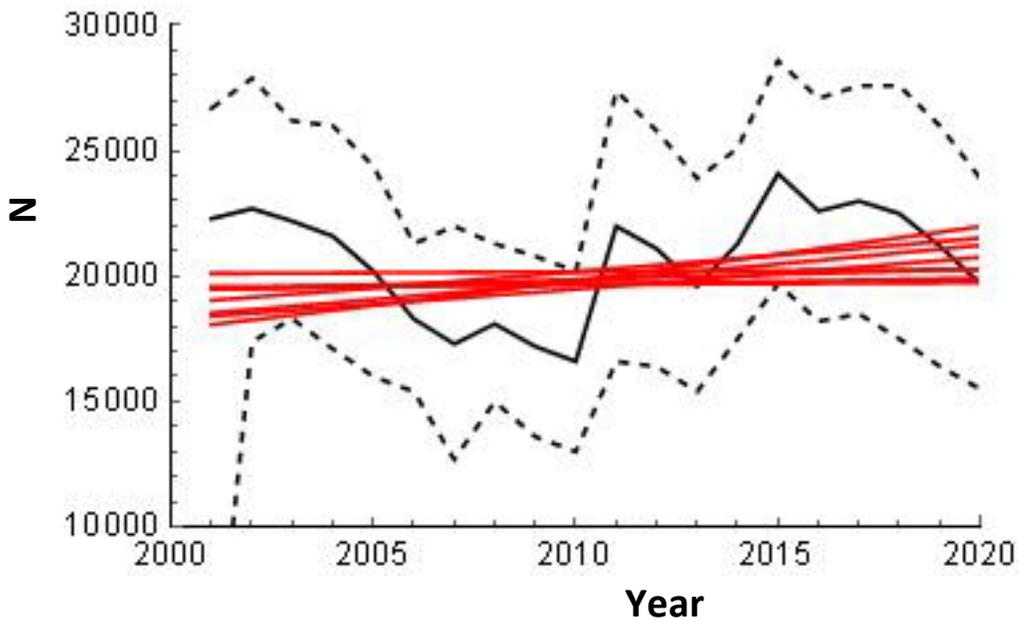


Figure 6. Marbled murrelet population (black line), Monte Carlo consistent population trajectories (red), upper and lower 95% population confidence limits (black dashed lines).

## 4.0 DISCUSSION

The linear and exponential models (Figure 2) were essentially equivalent and visually congruent, with  $R_{adj}^2$  essentially zero. Because regression analysis uses the mean as the null, we typically can only say that a fitted slope close to zero does not differ significantly from zero, but we cannot ascertain that it is zero. One metric that can represent significance of a low slope is the confidence intervals on the slope. In this case, we can estimate that  $0.994 \leq \lambda \leq 1.012$  for the exponential model. For the linear model, the estimated percent change for the years 2001 to 2022 is between -0.61% and +1.2%, essentially the same. The Monte Carlo resampling approach was consistent with these results.

The quadratic model (Figure 3) had a better fit ( $R_{adj}^2=0.14$ ) than the linear and exponential models, though 0.14 does not represent a particularly high explanatory level. The  $AIC_c$  of 369.25 was marginally better (lower) than that for the linear model of 370.54. It is not clear if this model performed better and if we can use it to make statements about population trends. If we could relate this model to ocean conditions as this affects food quantity and quality (Becker and Beissinger 2006; Becker et al. 2007; Huff et al. 2006; Gutowsky et al. 2009), or some other driver, then this model could be useful. Without such a relationship, however, it would be risky to extrapolate the ending upturn. In addition, this curve cannot be converted to a “trend” per se. Population fluctuations over periods of 20 years are also not unusual (Loehle and Arghami 2017).

The segmented linear model (Figure 4) explained more of the variation in the data, with  $R_{adj}^2=0.70$ . However, the discontinuity between 2010 and 2011 represented a 32.5% increase, an impossible increase for this species, given the low breeding propensity (Lorenz et al. 2017) and single egg per season (Beissinger 1995). The slope changed from -758 birds/y to -11.5 birds/y in a single year. This change in slope coincided with the numerical discontinuity from 2010-2011. The discontinuity could result from a change in sampling or other artifact, but we are not aware of any such issue, especially that could change the slope so radically (Loehle et al. 2022). Before using this model, these issues would need to be explored.

The sinusoidal model had the largest  $R_{adj}^2$ , best fit visually, and the lowest  $AIC_c$ . If the modeled trend could be related to some cyclical driver, it could potentially be extrapolated by at least a few years. As an example of a potentially cyclical driver for trend in marbled murrelet population, we explore some correlations with ocean conditions for this model below.

The linear, exponential, sinusoidal, and Monte Carlo exponential provided similar results for slope (Table 2) which would be unlikely if the true trend was negative. For a flat “true” trend, this makes sense. For management purposes, these estimates of slope (trend) answer the basic question about the status of the population, though of course a longer series would be more informative. The quadratic model seems supported by the data and unlikely to be due to chance but cannot be extrapolated per se. While the segmented model has good statistical support, it lacks biological plausibility without further investigation. The sinusoidal model seems the best supported by fit statistics and visual inspection. This would be a good model to try to relate to demographic drivers like ocean conditions. Thus, the different models serve fundamentally different purposes.

While it is assumed that nesting habitat losses could account for part of the long-term decline in murrelet abundance (e.g., Huff et al. 2006; Raphael 2006), area of inland nesting habitat, defined mainly by large trees, does not change in a pattern or speed consistent with fluctuations found in these data. It is plausible that modest population decline and recovery over the study period were due, at least in part, to ocean conditions that affected prey abundance. A long-term decline in prey quality for this bird has been documented (Becker and Beissinger 2006; Becker et al. 2007; Gutowsky et al. 2009; Norris et al. 2007). Multiple indicators exist for oceanic conditions,

such as sea surface temperature (SST) magnitude and spatial pattern, and copepod abundance (NOAA 2021), but it is not clear how these indicators relate directly to forage fish availability and quality (Rivers et al. 2022). Betts et al. (2020) developed an index based on indicators of conditions favorable to juvenile salmon survival and were able to develop plausible models for nest site occupancy. However, juvenile salmon do not forage in the same areas or eat the same foods as murrelets, so it remains unclear whether this correlation has biological relevance.

We offer additional evidence for linkages to ocean conditions. It is well-documented that the northern Pacific has oscillatory climatic modes. Both the Pacific Decadal Oscillation and El Niño-Southern Oscillation (ENSO) have been shown to be relatively consistent, long-term systems of fluctuating ocean SST patterns, winds, and currents (Amaya et al. 2019; Jiménez-Estevé and Domelsen 2019; McGregor et al. 2010; Verdon and Franks 2006) with interactions and modulations of the two dynamic systems over time. The consistency of these phenomena over time does not mean that an exact periodicity is ever present. The patterns repeat over time with rough periodicity, but patterns are complex across space and time. There are eddies and turbulence at all scales in the ocean which make local periods not necessarily identical to the global or Pacific-wide cycles. Multiple historical studies have found relationships between these two cycles and Pacific fish stocks (Hollowed et al. 2001; Lehodey et al. 2021; Mantua 2015; Sydeman et al. 2013).

Given that murrelets forage close to shore, it is useful to examine patterns in the near-shore environment (Betts et al. 2020). Hollowed et al. (2001) noted that ENSO is particularly strong along the North American West Coast. The West Coast near-shore environment is dominated by the California Current, which is strongly affected by ENSO (Fiedler and Mantua 2017; Jacox et al. 2015; Lehodey et al. 2021), with up to 2°C temperature swings and changes in salinity, current strength and distance to shore, and mixed layer depth. Multiple changes in the California Current have been documented in recent decades, including some that affect upwelling (Hyrenbach and Veit 2003; Oedekoven et al. 2001). These changes have major effects on the biota (Ainley et al. 2005; Fiedler and Mantua 2017; Jacox et al. 2015; Sydeman et al. 2013). Stronger winter upwelling has been shown to lead to earlier nesting in several species, likely due to increased prey abundance early in the breeding season (Black et al. 2010; Shroeder et al. 2009). Overall bird abundance spatial patterns have a coherent relationship to krill abundance (Santora et al. 2011).

Responses by the bird community to ocean conditions are complex (Ainley et al. 2005; Ainley and Hyrenbach 2010; Nur et al. 2011). Different bird species forage at different depths in different locations to obtain their preferred prey (Oedekoven et al. 2001; Ainley and Hyrenbach 2010). There is even potential competition with whales (Ainley and Hyrenbach 2010). In response to changing conditions, species are affected differently (Ainley and Hyrenbach 2010). Behavioral flexibility leads species to change migration routes, where they forage, and prey taken (Oedekoven et al. 2001). Despite some degree of nest site fidelity, it is possible that murrelets at both regional and local levels also respond to prey by changing where and when they forage, especially for unpaired or young birds, or when conditions preclude nesting.

To understand the ocean mechanisms driving murrelet demography, we would need detailed information on diet, where and when murrelets forage, how their prey varies over time, and demographic response to diet. Most of this information is not readily available. Rivers et al. (2022) proposed a detailed research agenda to gather the needed information. However, there are some historical patterns in the California Current that may point to mechanisms worth exploring now. There is, on average, a five-fold increase in chlorophyll concentrations from Northern California to southern Vancouver Island (Hickey and Banas 2008), a trend that corresponds roughly to murrelet density along this zone. Sydeman et al. (2013) found a large decline in seabird productivity off California during 2001-2007, the same period that saw a decline in murrelets. In the 1980s and 1990s, there was roughly a 14-15 yr. interval between January-March temperature peaks along the coasts of Washington and Oregon (Figure 3 in Hollowed et al. 2001) compared to the estimated 14.6 y cycle found here for murrelet. Fiedler and Mantua

(2017) found a pattern of high California Current SST values in the 1990s and 2014-2016 (the end of their data, their Figure 1) with a local minimum between these peaks in 2008, the same year as the minimum value for the fitted murrelet sine function. These relationships are in no way offered as explanatory. Rather, they suggest that the behavior of the California Current may be a good place to look for murrelet demographic drivers, as also noted by Rivers et al. (2022).

The modeling exercise undertaken here illustrates the difficulties of determining and using trend information. For this and other applications, such as fitting a habitat model, a true best model that is flat might be rejected because  $P > 0.05$  and another model (e.g., segmented) accepted despite biological implausibility. Thus, caution is warranted when conducting multi-model comparisons or screening.

## 5.0 CONCLUSIONS

Trend is an important metric for evaluating population status and determining management objectives. Different modeling approaches may lead to different conclusions, and legitimacy for extrapolating trend beyond the temporal window of the data it was derived from. It may be useful to explore possible trend models rather than just using the most obvious one to avoid incorrect inference. In the case of marbled murrelet, the simple trends do not indicate that recovery is happening but do seem to rule out significant declines. The quadratic and segmented models appear to have better fit but lack underlying justification. The best-fit model is sinusoidal with period =14.6y. This might relate to ocean conditions, particularly in the California Current, that affect food supply.

## REFERENCES

- Ainley, D.G., Spear, L.B., Tynan, C.T., Barth, J.A., Pierce, S.D., Ford, R.G., and Cowles, T.J. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep-Sea Research* 11:123-143.
- Ainley, D.G., and Hyrenbach, K.D. 2010. Top-down and bottom-up factors affecting seabird population trends in the California Current system (1985-2006). *Progress in Oceanography* 84:242-254.
- Amaya, D.J., Kosaka, Y., Zhou, W., Zhang, Y., Xie, S.-P., and Miller, A.J. 2019. The North Pacific pacemaker effect on historical ENSO and its mechanisms. *Journal of Climate* 32:7643-7661.
- Becker, B.H., and Beissinger, S.R. 2006. Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology* 20:470-479.
- Becker, B.H., Peery, M.Z., and Beissinger, S.R. 2007. Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. *Marine Ecology Progress Series* 329:267-279.
- Beissinger, S.R. 1995. Population trends of the marbled murrelet projected from demographic analyses. 385-394 in Ralph, C.J., Hunt, G.L., Jr., Raphael, M.G., and Piatt, J.F., technical editors. *Ecology and conservation of the marbled murrelet*. General Technical Report PSW-152. USDA Forest Service, Albany, California, USA.
- Bertram, D.F., Drever, M.C., McAllister, M.K., Schroeder, B.K., Lindsay, D.J., and Faust, D.A. 2015. Estimation of coast-wide population trends of marbled murrelets in Canada using a Bayesian hierarchical model. *PLoS ONE* 10:e0134891.
- Betts, M.G., Northrup, J.M., Bailey Guerrero, J.A., Andread, L.J., Nelson, S.K., Fisher, J.L., Gerber, B.D., Garcia-Heras, M.-S., Yang, Z., Roby, D.D., and Rivers, J.W. 2020. Squeezed by a habitat split: warm ocean conditions and old-forest loss interact to reduce long-term occupancy of a threatened seabird. *Conservation Letters* 2020:e12745.

- Black, B.A., Schroeder, I.D., Sydeman, W.J., Bograd, S.J., and Lawson, P.W. 2010. Wintertime ocean conditions synchronize rockfish growth and seabird reproduction in the central California Current ecosystem. *Canadian J. Fisheries and Aquatic Sciences* 67:1149-1158.
- Desimone, S.M. 2016. *Periodic status review for the marbled murrelet*. Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- Fiedler, P.C., and Mantua, N.J. 2017. How are warm and cool years in the California Current related to ENSO? *Journal of Geophysical Research* 122:5936-5951.
- Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G., Butchkoski, C.M., and Kunz, T.H. 2010. An emerging disease causes regional population collapse of a common North American bat species. *Science* 329:679–682.
- Gutowksy, S., Janssen, M.H., Arcese, P., Kyser, T.K., Ethier, D., Wunder, M.B., Bertram, D.F., McFarlane Tranquilla, L., Loughheed, C., and Norris, D.R. 2009. Concurrent declines in nestling diet quality and reproductive success of a threatened seabird over 150 years. *Endangered Species Research* 9:247–254.
- Hickey, B.M., and Banas, N.S. 2008. Why is the northern end of the California Current system so productive? *Oceanography* 21:90-107.
- Hollowed, A.B., Hare, S.R., and Wooster, W.S. 2001. Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. *Progress in Oceanography* 49:257-282.
- Huff, M.H., Raphael, M.G., Miller, S.L., Nelson, S.K., and Baldwin, J., technical coordinators. 2006. *Northwest Forest Plan—the first 10 years (1994-2003): status and trends of populations and nesting habitat for the marbled murrelet*. General Technical Report PNW-GTR-650. USDA Forest Service, Portland, Oregon, USA.
- Hyrenbach, K.D., and Veit, R.R. 2003. Ocean warming and seabird communities of the southern California Current System (1987-98): response at multiple temporal scales. *Deep-Sea Research II* 50:2537-2565.
- Jacox, M.G., Fiechter, J., Moore, A.M., and Edwards, C.A. 2015. ENSO and the California Current coastal upwelling response. *Journal of Geophysical Research: Oceans* 120:1691-1702.
- Jiménez-Esteve, B., and Domelsen, D.I.V. 2019. Nonlinearity in the North Pacific atmospheric response to a linear ENSO forcing. *Geophysical Research Letters* 46:2271-2281.
- Lehodey, P., Bertrand, A., Hobday, A.J., Kiyofuji, H., McClatchie, S., Menkès, C.E., Pilling, G., Polovina, J., and Tommasi, D. 2021. ENSO impact on marine fisheries and ecosystems. P. 429-451 In: McPhaden, M.J., Santoso, A., and Cai, W. (eds). *El Niño Southern Oscillation in a Changing Climate, Geophysical Monograph* 253.
- Loehle, C., and Arghami, N. 2017. Bounded random walks as a null model for evaluating population trends. *Population Ecology* 59:109–117.
- Loehle, C., Verschuyl, J., and Solarik, K.A. 2022. Population trends for marbled murrelet (*Brachyramphus marmoratus*) in the Pacific Northwest, USA. *Northwestern Naturalist* 103:20-29.
- Lorenz, T. J., Raphael, M.G., Bloxton, T.D., and Cunningham, P.G. 2017. Low breeding propensity and wide-ranging movements by marbled murrelets in Washington. *Journal of Wildlife Management* 81:306–321.
- Madsen, S., Evans, D., Hamer, T., Henson, P., Miller, S., Nelson, S.K., Roby, D., and Stapanian, M. 1999. *Marbled murrelet effectiveness monitoring plan for the Northwest Forest Plan*. General Technical Report PNW-GTR-439. USDA Forest Service, Portland, Oregon, USA.
- Mantua, N.J. 2015. Shifting patterns in Pacific climate, West Coast salmon survival rates, and increased volatility in ecosystem services. *PNAS* 112:10823-10824.
- McGregor, S., Timmermann, A., and Timm, O. 2010. A unified proxy for ENSO and PDO variability since 1650. *Climate of the Past* 6:1-17.
- McIver, W.R., Baldwin, J., Lance, M.M., Pearson, S.F., Strong, C., Raphael, M.G., Duarte, A., and Fitzgerald, K. 2022. *Marbled murrelet effectiveness monitoring, Northwest Forest Plan: At-sea Monitoring - 2021 summary report*. 25 p.
- Miller, S.L., Ralph, C.J., Raphael, M. G., Strong, C., Thompson, C.W., Baldwin, J., Huff, M.H., and Falxa, G.A. 2006. At-sea monitoring of marbled murrelet population status and trend in the Northwest Forest Plan area. 31–

- 60 in Huff, M.H., Raphael, M.G., Miller, S.L., Nelson, S.K., and Baldwin, J., technical coordinators. *Northwest Forest Plan—the first 10 years (1994–2003): status and trends of populations and nesting habitat for the marbled murrelet*. General Technical Report PNW-GTR-650. USDA Forest Service, Portland, Oregon, USA.
- NOAA. "Ocean Indicators Summary for 2019." NOAA Fisheries. NOAA, 2021. <https://www.fisheries.noaa.gov/west-coast/science-data/ocean-indicators-summary-2019>.
- Norris, D.R., Arcese, P., Preikshot, D., Bertram, D.F., and Kyser, T.K. 2007. Diet reconstruction and historic population dynamics in a threatened seabird. *Journal of Applied Ecology* 44:875–884.
- Nur, N., Jahncke, J., Herzog, M.P., Howar, J., Hyrenbach, K.D., Zamon, J.E., Ainley, D.G., Wiens, J.A., Morgan, K., Balance, L.T., and Stralberg, D. 2011. Where the wild things are: predicting hotspots of seabird aggregations in the California Current System. *Ecological Applications* 21:2241-2257.
- Oedekoven, C.S., Ainley, D.G., and Spear, L.B. 2001. Variable response of seabirds to change in marine climate: California Current, 1985-1994. *Marine Ecology Progress Series* 212:265-281.
- Peery, M.Z., Beissinger, S.R., Newman, S.H., Burkett, E.B., and Williams, T.D. 2004. Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. *Conservation Biology* 18:1088–1098.
- Raphael, M.G. 2006. Conservation of the marbled murrelet under the Northwest Forest Plan. *Conservation Biology* 20:297–305.
- Rivers, J.W., Guerrero, J.B., Brodeur, R.D., Krutzikowsky, G.K., Adrean, L.J., Heppell, S.A., Jacobson, K.C., Milligan, K., Nelson, S.K., Roby, D.D., Sydeman, W.J., Torres, L.G., and Barth, J.A. 2022. Critical Research Needs for Forage Fish within Inner Shelf Marine Ecosystems. *Fisheries* 47:213-221.
- Roach, R., and PATEL, M.V. 2019. *California condor: a literature synthesis of primary threats and population recovery efforts*. Undergraduate thesis. Dominican University, San Raphael, California, USA.
- Santora, J.A., Ralston, S., and Sydeman, W.J. 2011. Spatial organization of krill and seabirds in the central California Current. *ICES Journal of Marine Science* 68:1391-1402.
- Schroeder, I.D., Sydeman, W.J., Sarkar, N., Thompson, S.A., Bograd, S.J., and Schwing, F.B. 2009. Winter pre-conditioning of seabird phenology in the California Current. *Marine Ecology Progress Series* 393:211-223.
- Sydeman, W.J., Santora, J.A., Thompson, S.A., Marinovic, B., and Di Lorenzo, E. 2013. Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. *Global Change Biology* 19:1662-1675.
- USDA (U.S. Department of Agriculture) Forest Service and BLM (Bureau of Land Management). 1994a. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. USDA Forest Service, Portland, Oregon, and BLM, Moscow, Idaho.
- USDA (US Department of Agriculture) Forest Service and BLM (Bureau of Land Management). 1994b. Record of Decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the Northern Spotted Owl and standards and guidelines for management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. USDA Forest Service, Portland, Oregon, and BLM, Moscow, Idaho.
- Verdon, D.C., and Franks, S.W. 2006. Long-term behaviour of ENSO: interactions with the PDO over the past 400 years inferred from paleoclimate records. *Geophysical Research Letters* 33:L06712.
- Wagner, T., Irwin, B.J., Bence, J.R., and Hayes, D.B. 2013. Detecting temporal trends in freshwater fisheries surveys: Statistical power and the important linkages between management questions and monitoring objectives. *Fisheries* 38:309-319.