Risso's and Pacific white-sided dolphin habitat modeling from passive acoustic monitoring

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ABSTRACT: Habitat characterization allows prediction of dolphin distributions in response to oceanographic processes and can be used to understand and predict effects of anthropogenic disturbances. Many habitat models focus on contemporary dolphin occurrence and environmental predictor data, but time-lagged oceanographic data may increase a model's predictive power due to ecological successional processes. Using hourly occurrence of Risso's dolphin *Grampus griseus* clicks and 2 types of Pacific white-sided dolphin *Lagenorhynchus obliquidens* clicks in autonomous passive acoustic recordings, we investigate the importance of time-lagged predictor variables with generalized additive models. These models relate dolphin acoustic activity from recordings at 6 sites in the Southern California Bight between August 2005 and December 2007 to oceanographic variables including sea surface temperature (SST), SST coefficient of variation (CV), sea surface chlorophyll concentration (chl), chl CV, upwelling indices, and solar and lunar temporal indices. The most consistently selected variables among the trial models evaluated during cross-validation were SST (100% of models) and SST CV (80%) for Risso's dolphin clicks; solar indices (100%) and SST and SST CV (60% each) for Pacific white-sided type A (PWS A) clicks; and SST CV (100%), solar indices (100%) and SST (80%) for Pacific white-sided type B (PWS B) clicks. Best predictive models for Risso's dolphins and PWS A clicks included time-lagged variables, suggesting the importance of ecological succession between abiotic variables and dolphin occurrence, while best models of PWS B clicks were for current conditions, suggesting association with prey-aggregating features such as fronts and eddies.

KEY WORDS: Risso's dolphin · *Grampus griseus* · Pacific white-sided dolphin · *Lagenorhynchus obliquidens* · Habitat model · Generalized additive model · Passive acoustic monitoring · Southern California Bight

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INTRODUCTION

Conservation scientists and resource managers may be able to improve delphinid distribution and abundance estimates by developing quantitative predictive habitat models that relate the abundance or distribution of these marine predators to the distribution of their prey and the underlying physical oceanography (Redfern et al. 2006). Most quantitative cetacean habitat models have been built from ship-based and aerial-based visual survey data (Forney 2000, Ferguson et al. 2006, Becker 2007). These visual surveys are capable of covering large spatial areas, but are limited in their temporal coverage due to survey platform, personnel

and cost constraints. The inability to sample during night and rough weather conditions may affect the accuracy or precision of resulting models. Additionally, visual survey data are limited to times when cetaceans are conspicuous at the surface. Models based on these data may not represent 'prime' habitat (i.e. habitat that is important to feeding or breeding, and hence the animals' overall fitness) if the animals are more easily observed when resting or transiting to such key areas (Hamazaki 2002). Alternate sampling methods, such as passive acoustic monitoring, may provide a better representation of cetacean presence and activity in prime habitats and thereby improve model accuracy and precision.

The accuracy and precision of habitat models is also dependent on the environmental data upon which they are built. Habitat models developed for predictive purposes should include environmental variables that are easily accessible and available across regions and times of interest (Hamazaki 2002, Becker 2007), such as remotely sensed sea surface temperature, chlorophyll, and altimetry data, upwelling indices, and bathymetric descriptors. While increased delphinid occurrence may result from increased prey abundance related to biological and physical oceanographic conditions (Jaquet & Whitehead 1996, Fiedler et al. 1998), measures of prey abundance are not readily attainable and oceanographic conditions are often used as proxies. The relationship between delphinid occurrence and oceanographic variables, such as sea surface temperature, upwelling and phytoplankton abundance, may include a time lag depending on whether zooplankton blooms are created by successional or aggregational mechanisms (Jaquet 1996, Gregr & Trites 2001, Croll et al. 2005). For successional zooplankton blooms, a lag time may be as great as 4 mo between initial physical oceanographic conditions, phytoplankton bloom development, zooplankton bloom development and the aggregation of fish, squid and dolphins (Vinogradov 1981). Conversely, aggregational zooplankton blooms, such as those found at convergence zones where downwelling aggregates buoyant organisms, are related to current oceanographic conditions (Gregr & Trites 2001). This mechanistic difference in zooplankton bloom development may bias the successful dolphin habitat models based on contemporaneous (zero-lagged) remotely sensed data toward those that describe or quantify aggregational systems.

The development of habitat models that include acoustic delphinid survey data and time-lagged environmental variables may improve their predictive power. Autonomous, fixed-sensor, passive acoustic-based surveys offer a technique to assess dolphin occurrence over long periods, in remote locations, during adverse weather conditions and during nighttime periods. Recent spectral analysis of Risso's dolphin (*Grampus griseus*) and Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) echolocation clicks off southern California revealed the existence of species and possibly sub-species click types (Soldevilla et al. 2008) that can be used to examine their occurrence in autonomous acoustic data. Sampling delphinid echolocation clicks, which are produced most frequently during foraging activities (Norris et al. 1994, Barrett-Lennard et al. 1996, Van Parijs & Corkeron 2001, Nowacek 2005), also increases the likelihood that models represent prime foraging habitat. While these methods excel at temporal coverage, fixed-sensors placed at multiple sites can be sampled to increase spatial coverage. Finally, the inclusion of temporal lags to environmental data in habitat models may improve predictive power and lead to hypotheses about the mechanisms causing prey aggregation.

This study investigates the utility of incorporating time-lagged oceanographic data into predictive habitat models of dolphin acoustic occurrence. Habitat models are built within a generalized additive model (GAM) framework and incorporate autonomously recorded echolocation click occurrence with remotely sensed oceanographic variables, upwelling indices, and solar and lunar temporal indices. GAMs offer a flexible regression technique for modeling the importance of environmental correlates for habitat prediction (Hastie & Tibshirani 1990) and are commonly utilized in studies of marine habitat. Forward-backward selection and cross-validation methods are employed to select models with the best predictive power. We investigate the hypotheses that (1) the inclusion of readily available oceanographic predictor variables results in models with better ability to predict dolphin occurrence than the null model in which predictor variables are absent and (2) the inclusion of time-lagged predictor variables results in models with better predictive abilities than those built on zero-lagged data.

MATERIALS AND METHODS

Study area and animals. The Southern California Bight (SCB) (Fig. 1) is a highly productive upwelling region characterized by 3 environmental features: (1) the California Current, an equatorward flowing eastern boundary current (Reid et al. 1958, Wooster & Jones 1970); (2) the Southern California Eddy, a large counterclockwise gyre within the bight (Reid et al. 1958, Hickey 1979); and (3) complex bathymetry including high islands and banks, and low troughs and basins (Shepard & Emery 1941, Emery 1960) that lead
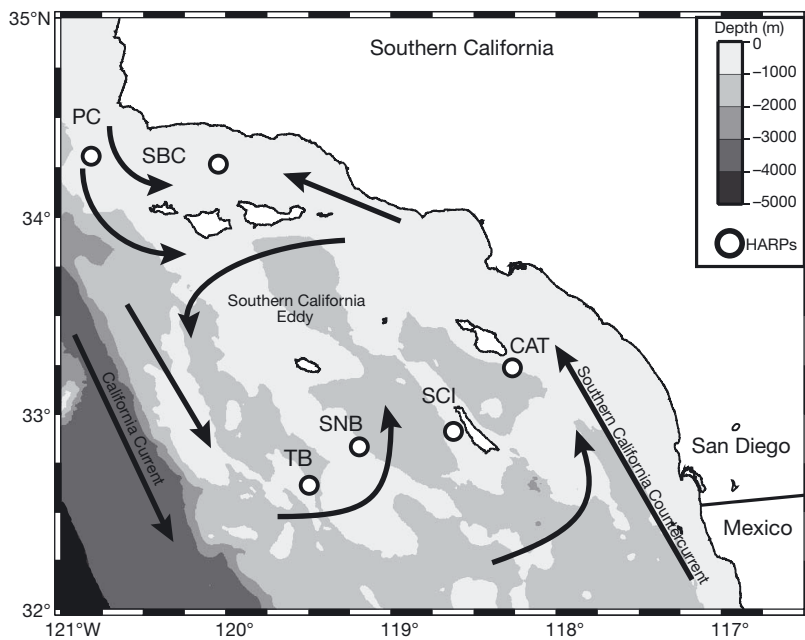
Fig. 1. Study area including the current circulation patterns and locations of High-frequency Acoustic Recording Package (HARP) deployment sites. Depths are indicated by grayscale bar. Sites: PC = Point Conception; SBC = Santa Barbara Channel; TB = Tanner Basin; SNB = San Nicholas Basin; SCI = San Clemente Island; CAT = Santa Catalina Island. Current circulation map adapted from Hickey (1992)

to formation of mesoscale (50 to 200 km) and sub-mesoscale (1 to 50 km) eddies throughout the bight (Kolpack 1971, Brink & Muench 1986, DiGiacomo & Holt 2001, Caldeira et al. 2005).

Risso's dolphins are relatively large, tropical to temperate odontocetes that feed nearly exclusively on cephalopods (Leatherwood et al. 1980, Clarke & Pascoe 1985, Clarke 1996). Pacific white-sided dolphins, a cold-temperate pelagic species endemic to the North Pacific Ocean (Leatherwood et al. 1984, Barlow & Forney 2007), forage opportunistically on epipelagic and mesopelagic schooling fishes and cephalopods (Brown & Norris 1956, Fitch & Brownell 1968, Stroud et al. 1981, Walker et al. 1986). Both Risso's and Pacific white-sided dolphins exhibit high seasonal and inter-annual variability in occurrence and distribution off southern California (Green et al. 1992, Shane 1994, Forney & Barlow 1998, Kruse et al. 1999, Benson et al. 2002, Barlow & Forney 2007). Risso's dolphin habitat around the world is characterized by steep bathymetry and warm waters (Dohl et al. 1983, Green et al. 1992, Baumgartner 1997, Baumgartner et al. 2001), whereas Pacific white-sided dolphin habitat is characterized by cool waters near the shelf-break (Benson et al. 2002, Yen et al. 2004, Becker 2007). Off southern California, Risso's dolphins produce one species-specific click type with distinct spectral patterns, while Pacific

white-sided dolphins produce 2 spectrally distinct click types, denoted types PWS A and PWS B (Soldevilla et al. 2008, 2010a,b). Spatial and temporal trends in PWS A and PWS B click occurrence support the hypothesis that these click types respectively represent the morphologically and genetically distinct northern and southern populations that overlap in the SCB (Walker et al. 1986, Lux et al. 1997, Soldevilla et al. 2010b).

Acoustic data. Acoustic data collection and click detection methods have been described previously (Soldevilla et al. 2008, 2010a,b). Briefly, echolocation clicks of 3 types (Risso's, PWS A and PWS B) were detected in time series of 1 to 4 mo duration from 30 autonomous High-frequency Acoustic Recording Package (HARP) deployments at 6 SCB locations between August 2005 and December 2007 (Fig. 1). To quantify important dolphin habitat while reducing the autocorrelation inherent in time-series data, the duration that dolphins spend echolocating at each site per week is used as a dependant variable in habitat models. For each click type, hourly click bout occurrence was summed to obtain the total hours per week with acoustic detections. Echolocation clicks of medium-sized odontocetes may be detectable up to 9 km for on-axis orientations (Ward et al. 2009), though 4 to 5 km may be a more reasonable detection estimate given variability in animal orientations (Marques et al. 2009). Therefore, the temporal and spatial resolutions of the dependant variable are 1 wk and approximately a 5 km radius, respectively.

Temporal coverage at the 6 sites is variable due to instrument servicing ship time constraints, occasional instrument failures, and recording sampling schedules (Fig. 2). Two-thirds of the available acoustic data were sampled continuously, while the remaining data were recorded on a sampling schedule of 5 min 'on' and either 5, 10, or 15 min 'off' for a given deployment. Scheduled recording may decrease the probability of detecting calling bouts. Therefore, the detection probabilities were estimated for the 3 sampling schedules by subsampling continuous data as follows. For each hour of 23609 h of continuous data, 60 permutations, starting at each minute of the hour, were conducted with 5 min sampled followed by X min omitted (where $X = 5$, 10 or 15 min). For each subsampled hour, click type presence or absence was determined for each of the 60 permutations and the hourly probability of detection was calculated as the mean of the 60 permu-
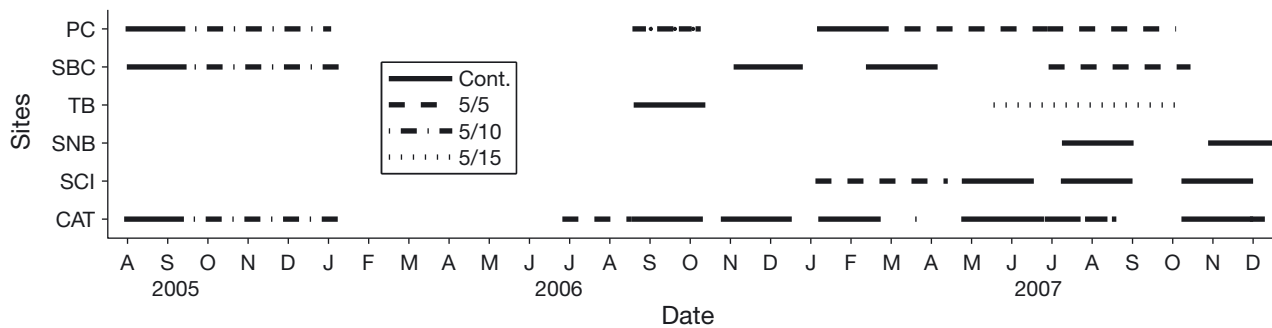
Fig. 2. High-frequency Acoustic Recording Package (HARP) data availability and sampling schedule at each of 6 sites in the Southern California Bight (SCB). Data availability is indicated by presence of a line at each site while sampling schedule (continuous, 5 min on/5 min off, 5 min on/10 min off, an 5 min on/15 min off) is indicated by line type. See Fig. 1 for abbreviations

tations. Hourly probabilities were averaged across all hours and sites to obtain a single detection probability for each click type at each sample level. Site-specific detection probabilities were not utilized due to low sample sizes at some sites; detection probabilities did not differ significantly between sites.

Environmental data. Lunar cycles (US Naval Observatory, http://aa.usno.navy.mil), upwelling indices (Pacific Fisheries Environmental Laboratory, www.pfeg. noaa.gov/products/PFEL/modeled/indices/upwelling/ upwelling.html), and remotely sensed satellite data (M. Kahru, Scripps Institution of Oceanography, http:// spg.ucsd.edu/Satellite_Data/California_Current/) were readily accessible from internet databases for use as predictor variables. A weekly solar index, included to account for seasonal effects, numbered weeks sequentially from 1 to 52 starting with the first day of the year. Nighttime lunar duration, a continuous proxy for lunar phase, was calculated as the duration that the moon was above the horizon while the sun was below the horizon each week. The daily coastal upwelling index, an index of the strength of the wind forcing on the ocean, was available as a single value for the entire SCB, representing the average upwelling over a $3° \times 3°$ (333×333 km) region centered at 33° N and 119° W. Daily upwelling indices were averaged over 7 d periods. Seven day composites of sea surface temperature (SST) and chlorophyll concentration (chl) at 1 km^2 resolution provide fine spatial and temporal resolution of oceanographic variation while minimizing missing data caused by cloud coverage (e.g. Becker 2007). Using WIM & WAM software (www.wimsoft.com), spatially averaged mean SST and chl time series were obtained for an area defined by a 20 km radius centered around each of the 6 HARP sites. Output statistics from wam_statist for each area included total number of 1 km^2 pixels, number of pixels with valid data, mean value of pixels, and standard deviation of pixel values. Weekly samples with less than 5% valid data due to cloud cover were omitted to prevent use of

non-representative data. Coefficients of variation (CVs) in the spatial domain were calculated from the WAM output statistics for both SST and chl as proxies for temperature and productivity fronts (e.g. Becker 2007). Mean SST and chl are highly correlated as a result of increased productivity associated with cold, nutrient-rich upwelled waters. Predictor variables in a GAM model should be independent and orthogonal (Hastie & Tibshirani 1990). To prevent the model from fitting correlated predictor variables, log$_{10}$chl was regressed against SST and residual log$_{10}$chl values were included in the model terms instead.

Habitat model analysis. The relationships between dolphin acoustic activity and environmental variables were investigated within a GAM framework (Hastie & Tibshirani 1990). The GAM, a nonparametric extension of the generalized linear model, may be represented as

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j(X_j) \qquad (1)$$

in which $g(\mu)$, the link function, relates functions of the additive predictor variables, $\alpha + \sum_{j=1}^{p} f_j(X_j)$, to the mean of the response variable, μ. The link function allows specification of alternative distributions for non-normally distributed response data. Errors of discrete count data are often well approximated with a Poisson error distribution, but the typical clumping of behavioral data leads to over-dispersion of errors (McCullagh & Nelder 1999). In this study, the response variable, number of hours per week with click type present, was modeled as an over-dispersed Poisson distribution. The right side of the equation is the additive predictor, which can incorporate nonparametric forms $f_j(X_j)$ (such as smoothing splines) in GAMs, allowing greater flexibility in fitting relationships of the predictor variables. The predictor variables included in this model are: mean SST, residual chl, SST CV, chl CV, upwelling index, lunar duration, and the

interaction of week and region (week × region). This last term was included with a factorial interaction for region (i.e. north vs. south) due to known differences in seasonal occupation within the SCB (Soldevilla et al. 2010a,b). To account for decreased probability of detection due to incomplete weekly coverage and sampling schedule, an offset term (α) was included for each sample to account for (1) number of hours per week with recordings and (2) the appropriate reciprocal of detection probability.

S-Plus 6.0 (Insightful) was used to build and compare GAM models for each of the 3 click types. Multiple models were built to compare hypotheses of the effect of temporal lag in environmental data on the occurrence of dolphin clicks. Depending on the mechanisms of prey aggregation, lag times between environmental data and the occurrence of dolphins may range from 0 to 16 wk. While it is likely that lag times differ between environmental variables, inclusion of all possible lag times for each variable would make the model selection process unnecessarily complex. Therefore, we explored a wide breadth of individual models that were created from environmental data at only 0, 1, 2, 4, 8, and 16 wk time lags. To approximate an over-dispersed Poisson distribution for the response variable, the S-Plus quasi-likelihood distribution was modeled with a logarithmic link function and variance proportional to the mean. Models were constructed with options for linear terms and smoothing splines with less than 3 degrees of freedom. This allowed the flexibility of incorporating non-linear effects while restricting unrealistic complexity that might be difficult to interpret ecologically (Forney 2000, Ferguson et al. 2006). S-Plus does not accommodate factorial spline interaction terms, therefore week was modeled as a polynomial fit.

To ensure the models contained only significant terms, model development incorporated the forward/backward stepwise selection of variables using the S-Plus function step.gam. Akaike's Information Criterion (AIC) was used to determine the best model at each step of the forward/backward selection process. To improve estimation of the dispersion parameter and allow selection of higher order spline fits when appropriate, stepwise selection of variables occurred twice for each model, following Ferguson et al. (2006). The first call to the stepwise selection process started with the null model and included only higher order terms, while the second call to the selection process began with the best model from the first call and included functions with 1 degree of freedom.

Use of AIC can over-fit a model to the data, leading to lower predictive ability. Therefore, a cross-validation approach was used to assess the predictive power of a number of models. Studies that incorporate spatially rich surveys over several years typically assess predictive power through a cross validation approach in which survey data from a single year is omitted and the model is tested on this novel dataset (e.g. Forney 2000, Hastie et al. 2005, Ferguson et al. 2006, Becker 2007). In contrast, this study is temporally rich at several sites, so a cross-validation approach was used in which contiguous blocks of time from individual sites comprised the out-set for model testing. Removal of a large block of related data (e.g. from 1 year or 1 site) would result in stronger tests than removal of randomly selected samples. However, Soldevilla et al. (2010a,b) found site-specific and seasonal differences in dolphin occurrences. Given the uneven sampling effort across sites, exclusion of seasons or years of data at a single site from the model-building process may result in low predictive power of these tests. A compromise was developed in which 20% of the data were removed as a series of 4 randomly selected smaller blocks of time from individual sites, ensuring that no more than 13 consecutive wk at a single site were removed at a time. In this manner, a cross-validation approach that used 80% of the data to develop models and removed 20% of the data for use in evaluation was implemented. Therefore, for each click type, the stepwise building procedure was performed on 5 datasets, i.e. combinations of data with a different 20% of the data left out, which resulted in 5 best models. The best of these 5 models was selected by comparing cross-validation performance using predict.gam and selecting the model with the lowest average squared prediction errors (ASPEs) on its novel evaluation data.

Time series of delphinid occurrence and environmental data included in the habitat models are available online; see supplement at www.int-res.com/articles/suppl/m423p247_supp.pdf.

RESULTS

HARP recordings contained 251 week-long samples from deployments at 6 sites in the SCB. Of these 251 samples, Risso's dolphin, PWS A and PWS B clicks were detected in 101, 71, and 30 wk, respectively. Over 80% of the weeks contained complete recordings with 168 h, and all weeks contained at least 6 full days (144 h) of recorded time. The maximum hours per week containing Risso's dolphin and PWS A and PWS B clicks were 84, 54, and 98 h, respectively, while mean hours per week with click detections were 12.4, 4.4 and 2.1 h, respectively. Detection probabilities ranged between 0.830 and 0.972 for the 3 click types and 3 sampling schedules (Table 1).

Of the best Risso's dolphin models for the 5 cross-validation datasets, 2 and 4 wk lagged models were

selected for 2 and 3 datasets, respectively (Table 2). The consistency of predictor variable selection across models can indicate their importance as habitat predic-

Table 1. *Grampus griseus* and *Lagenorhynchus obliquidens.* Mean detection probabilities (± SD) and correction factors for 3 click types and 3 sub-sampling scenarios based on sub-sampling of continuous High-frequency Acoustic Recording Package (HARP) data. Correction factors (i.e. the inverse of detection probability) are included as an offset in habitat models. The sub-sampling duration indicates the non-recording duration between 5 min recordings for 5, 10, and 15 min 'off' sampling schedules. PWS = Pacific white-sided

Duration off (min)	Risso's	PWS A	PWS B
Detection probability			
5	0.968 (0.002)	0.945 (0.003)	0.972 (0.005)
10	0.927 (0.003)	0.888 (0.005)	0.930 (0.007)
15	0.882 (0.003)	0.830 (0.006)	0.883 (0.008)
Correction factor			
5	1.033	1.058	1.028
10	1.079	1.126	1.075
15	1.134	1.205	1.133

tors. The most important predictors were mean SST (100% of models) and SST CV (80%). Chl variables (40%) and the week × region interaction (40%) were moderately important, while moon duration (20%) and upwelling (0%) were rarely included. The model with the best predictive power on the novel evaluation data included the 4 wk lagged oceanographic data with 3 df spline fits to residual chl and mean SST and 1 df linear fits to the CVs of both chl and SST (Table 2, Fig. 3). Positive relationships exist between the number of hours with clicks present per week and mean SST, log chl residual and chl CV, while a negative relationship is present for SST CV. The spline fit for log chl residual exhibits a slight dip around –2, while the spline fit for mean SST reaches a maximum around 20°C before leveling out. The final model explained 47% of the deviance (a likelihood-based goodness-of-fit measure). A comparison of the observed and predicted hours with detections illustrates the goodness of fit and predictive power (Fig. 4A). The correlation between observed and predicted hours is positive (Fig. 4D) indicating the model goodness of fit, though a lot of variability remains to be explained.

Table 2. Terms included in best models. The best models are presented for each of the 5 cross-validation datasets of each click type. Null and final Akaike's Information Criterion (AIC) values are presented from the training data and average squared prediction error (ASPE) values are presented from the test data. The dataset with the best predictive model for each click type is represented by **bold** typeset. Lag times indicate which week model was chosen as the best for each cross-validation model. Environmental variables that were included in the model are indicated and represent the best fit that was chosen followed by the selected degrees of freedom (L = linear, p = polynomial, s = spline). The inclusion of the interaction term of region (north or south) by week is indicated by N. No interaction term was included for Pacific white-sided type (PWS) B as they were only detected at the southern sites. Terms that were not included in the best models are indicated by a dash. The percent of models that included each environmental variable is presented to indicate the importance of that variable across different cross-validation datasets. Variables included in more models are likely to be important indicators of dolphin occurrence. SST = sea surface temperature; chl = chlorophyll; resid = residual; CV = coefficient of variation

|	Null AIC	Final AIC	ASPE	Lag	Upwelling	Moon duration	Chl resid	Chl CV	SST mean	SST CV	Region × week
Risso's dolphin											
Dataset 1	3640.2	2563.7	190.1	4	–	–	–	–	s3	L	–
Dataset 2	**4131.1**	**2470.9**	**169.4**	**4**	**–**	**–**	**s3**	**L**	**s3**	**L**	**–**
Dataset 3	3623.2	2464.9	393.0	4	–	s2	–	–	s3	–	Np3
Dataset 4	3848.5	2776.5	414.5	2	–	–	s3	s2	L	s2	NL
Dataset 5	4132.8	2706.1	208.9	2	–	–	L	–	s2	s2	–
Models including term (%)			0	20	60	40	100	80	40		
PWS A											
Dataset 1	2302.3	1682.1	187.0	2	s3	–	–	–	–	s3	Np2
Dataset 2	2265.6	1743.9	130.4	4	–	–	L	L	L	s3	Np3
Dataset 3	2571.0	2004.6	51.6	16	s3	–	–	–	–	–	Np2
Dataset 4	**2510.7**	**2109.0**	**18.8**	**4**	**–**	**–**	**–**	**–**	**L**	**s3**	**Np2**
Dataset 5	2230.4	1285.1	174.3	16	–	s3	L	–	L	–	Np2
Models including term (%)			40	20	40	20	60	60	100		
PWS B											
Dataset 1	942.9	367.1	500.3	8	s3	–	–	–	–	s3	p2
Dataset 2	**2479.0**	**563.1**	**5.4**	**0**	**s3**	**–**	**–**	**–**	**s3**	**s3**	**p2**
Dataset 3	2427.9	695.8	5.6	1	s3	s2	–	–	s3	s3	p2
Dataset 4	2493.9	529.5	111.0	16	–	L	L	–	L	s3	L
Dataset 5	2294.6	507.2	30.6	16	–	L	s3	–	L	s3	p2
Models including term (%)			60	60	40	0	80	100	100		
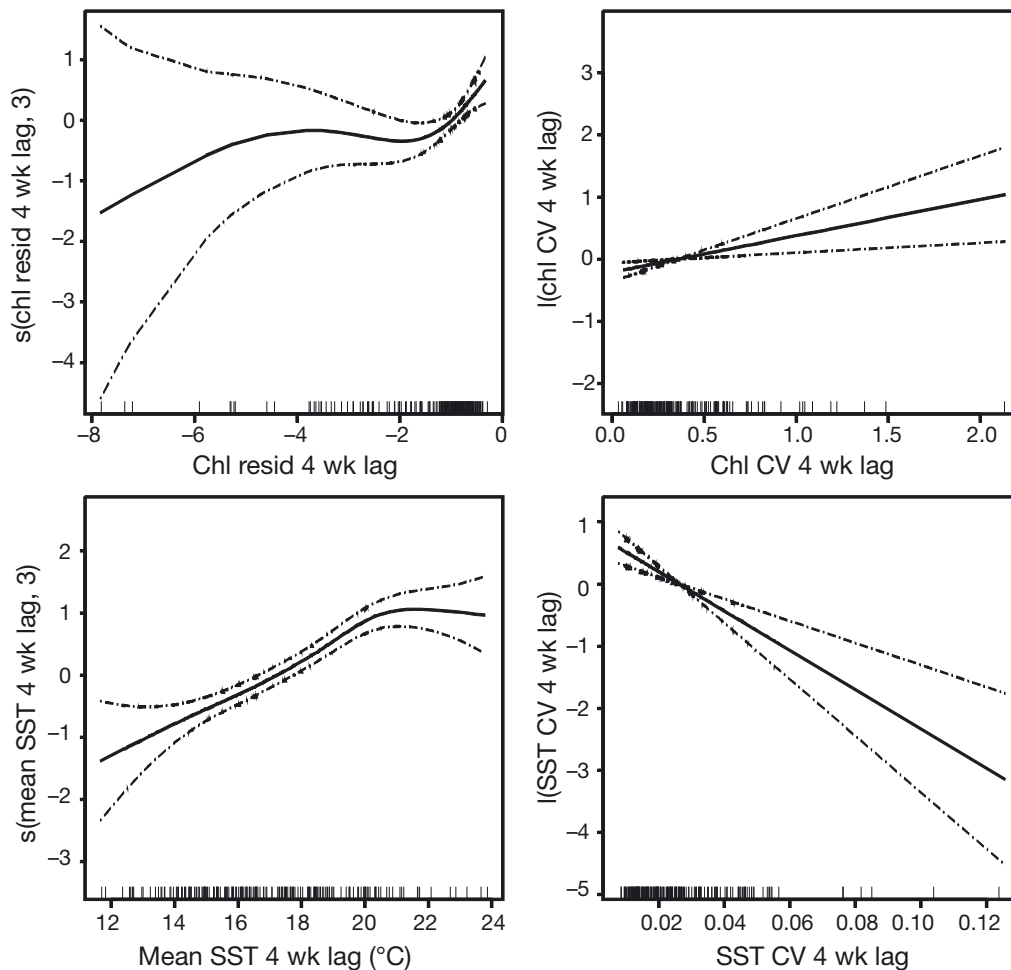
Fig. 3. *Grampus griseus.* Modeled partial fits of oceanographic variables to Risso's dolphin hours detected per week. The solid line represents the best fit while dotted lines represent the confidence intervals. All plots are at the same vertical scale so that the strength of the slope indicates the importance of the variable in the model. The *y*-axis label indicates the fit type (l = linear, s = spline) and the degrees of freedom. Rugplot at the bottom indicates location of sample values. SST = sea surface temperature; chl = chlorophyll; resid = residual; CV = coefficient of variation

Of the 5 best PWS A click models, the 2, 4 and 16 wk lagged models were selected for 1, 2, and 2 datasets, respectively (Table 2). The week × region interaction (100%) and both SST variables (60%) were selected more often than chl residual (40%), upwelling (40%), moon duration (20%) and chl CV (20%). The model with the best predictive power on the novel evaluation data incorporated the 4 wk lagged data with a 1 df linear term for mean SST, a 3 df spline fit for SST CV and a 2 df polynomial fit to the week × region interaction (Table 2, Fig. 5). The relationships between number of hours with PWS A clicks and SST variables were generally negative, and the SST CV relationship exhibited wide confidence intervals due to low sample size at higher values. Hours per week with detections peaked during the summer in northern regions and during the fall through winter in the southern regions.

The final model had a relatively poor fit to the data the model was built upon, explaining 24% of the model deviance (Fig. 4B). A slight positive correlation between observed and predicted hours was evident and suggests that most of the variability remains to be explained (Fig. 4E).

PWS B models had the least consistency in temporal lag selection: 0 (current conditions), 1, 8, and 16 wk lag models were selected for 1, 1, 1 and 2 datasets respectively (Table 2). There was greater consistency in variable selection across models. The most important variables were SST CV (100%) and week × region interaction (100%), and mean SST (80%) while upwelling (60%), moon duration (60%), chl residual (40%), and chl CV (0%) were selected less often. The model with the best predictive power on novel data incorporated the 0 wk lagged oceanographic data with
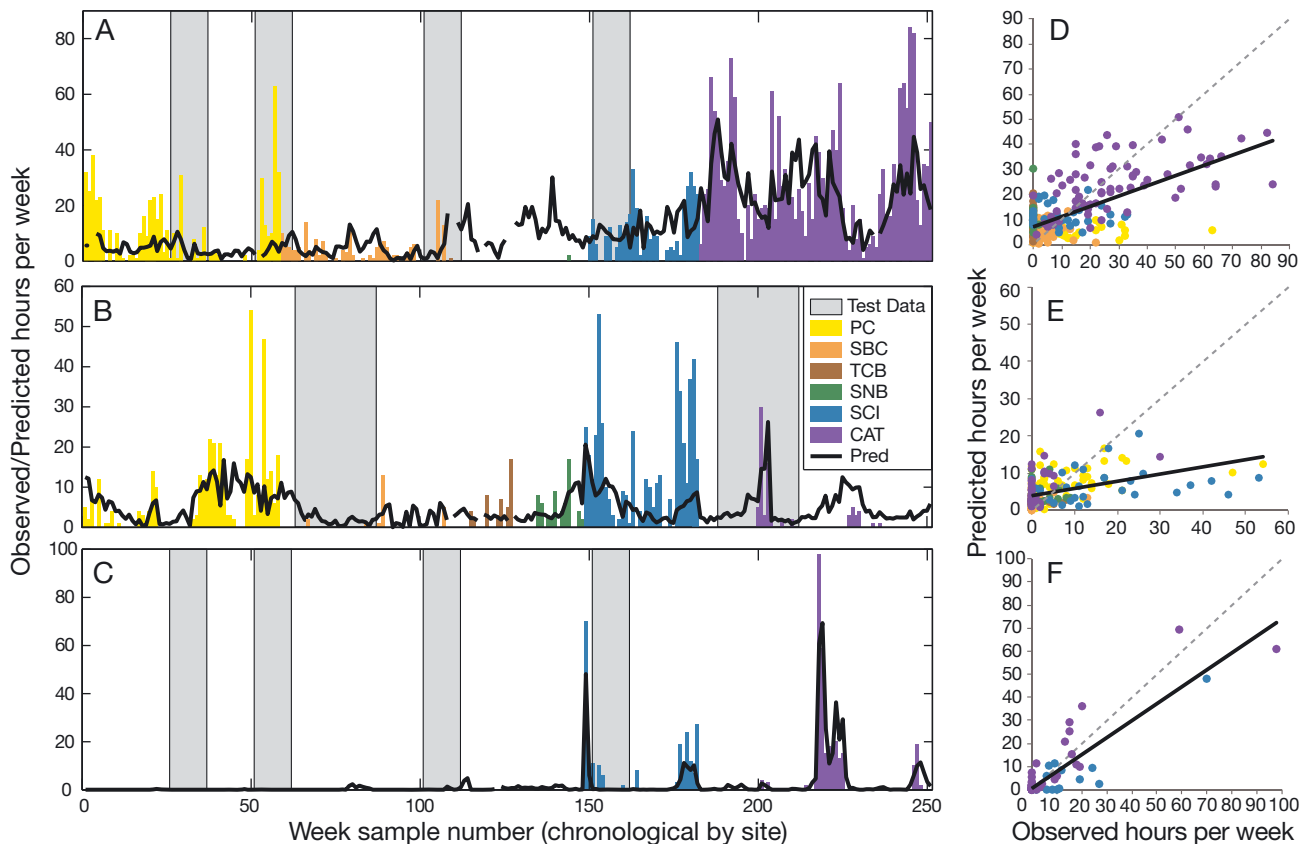
Fig. 4. *Grampus griseus* and *Lagenorhynchus obliquidens.* Observed and predicted values from the best models for (A,D) Risso's dolphin, (B,E) Pacific white-sided dolphin type (PWS) A, and (C,F) PWS B. Observed values are plotted by sample number chronologically by site in A, B and C, and sample observations and predictions are compared in D, E, and F. Observed values are represented by colored bars where the color indicates the site. See Fig. 1 for site abbreviations. The black line represents predicted values from the model. Breaks in the prediction line indicate the absence of environmental data which were not included in models. In the chronological plots, data that were removed during model building but used to test predictive power are highlighted by light gray boxes. In the scatter plots, the best fit line is indicated by the black line and a one-to-one correspondence (perfect prediction) is indicated by the thin gray dashed line.

3 df spline fits for upwelling, mean SST, and SST CV and a 2 df polynomial fit to the week × region interaction (Table 2, Fig. 6). Number of hours with PWS B clicks peaked at a mean SST of 18°C and fell off rapidly at lower temperatures. A positive relationship between click hours and upwelling is suggested, with a leveling off at high values (>150 m³ s⁻¹). The relationship between hours with PWS B detections and SST CV was generally negative and exhibited wide confidence intervals due to low sample size at higher values, suggesting it should be interpreted with caution. PWS B clicks were only heard at southern sites where there are low detections during summer and a seasonal peak in late fall to early winter. The final model explained 82% of the deviance (Fig. 4C). The positive correlation between observed and predicted hours approaches 1:1 (Fig. 4F), illustrating the high predictive power of this model.

DISCUSSION

The present study is one of the first to use passive acoustic monitoring data to model delphinid habitat (e.g. Hastie et al. 2005, Skov & Thomsen 2008). Strong relationships are found between delphinid acoustic activity and dynamic environmental features on a long-term and fine-scale temporal resolution that is not feasible with visual monitoring. In particular, mean SST and low SST spatial variability (SST CV) were important predictors of acoustic activity for all 3 delphinid groups, seasonal variability proved to be an important predictor for both Pacific white-sided dolphin groups, and chlorophyll abundance and variability were important for Risso's dolphins. Defining the response variable as a function of echolocation clicks, which are produced most often during foraging (Norris et al. 1994), increases the likelihood that models incorporating these

environmental features represent foraging habitat. By understanding the relationship to dynamic features, models can provide better predictive power and allow investigation into the mechanisms causing changes in delphinid distribution and abundance.

The incorporation of time-lagged environmental data in acoustic-based habitat models can provide insight into the oceanographic aggregating mechanisms of different dolphin prey types. Dolphin response to current conditions at a fixed location would indicate an advanced ecosystem containing aggregations of higher trophic levels that attract dolphin prey, as found in downwelling convergence zones or eddies that are moving past the location. Conversely, a time lag between environmental conditions and dolphin occurrence would indicate time for successional processes, as

higher trophic levels develop and support delphinid prey, as found in coastal upwelling and eddy formation. The best model of PWS B clicks included environmental data at the current time, suggesting foraging on prey that aggregate at fronts or convergence zones, while the best models of Risso's dolphin and PWS A clicks included environmental data at a 4 wk time lag, suggesting foraging on prey that respond to successional processes following events such as upwelling. The combination of a 4 wk lag in low spatial variability in temperature (SST CV) and high chl seems counterintuitive, but may represent the need for calm relaxation periods following upwelling for water stratification and phytoplankton bloom development (Huntsman & Barber 1977, Jones & Halpern 1981) that lead to abundant food for the higher trophic level prey (Lasker
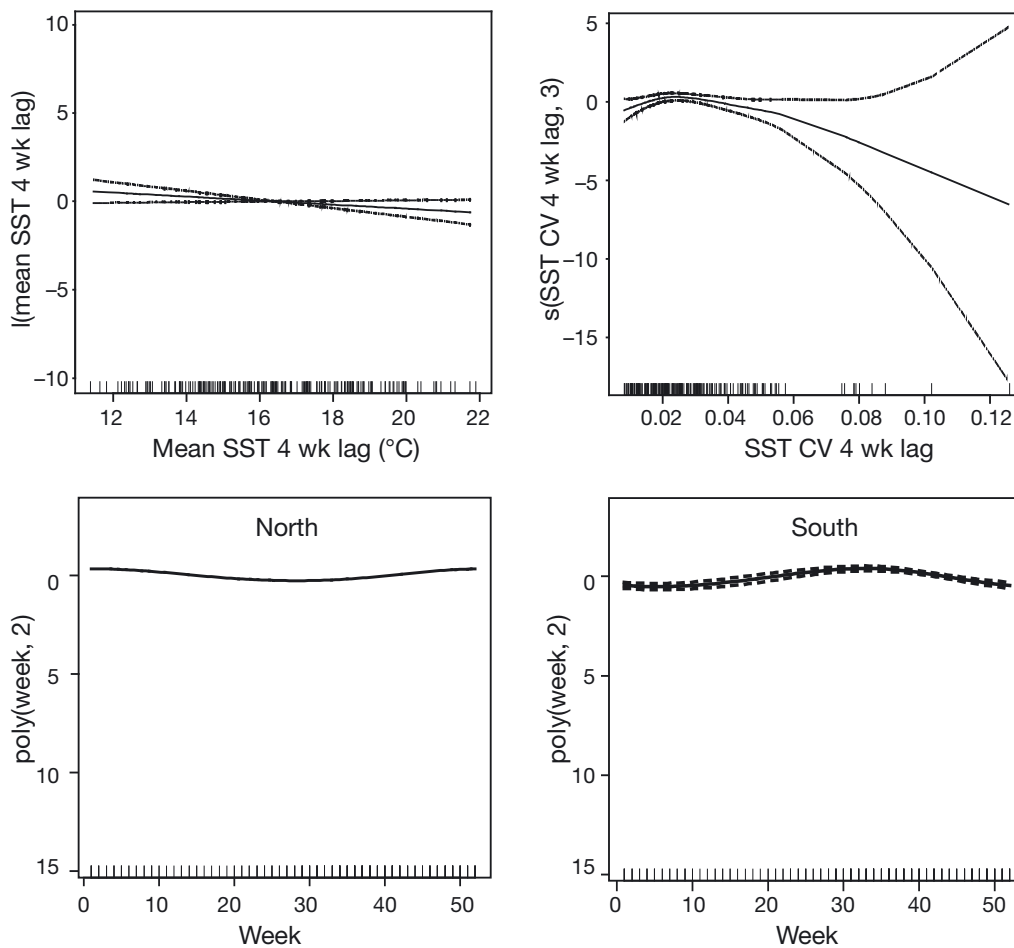

Fig. 5. *Lagenorhynchus obliquidens.* Modeled partial fits of oceanographic variables to Pacific white-sided dolphin click type A hours detected per week. The solid line represents the best fit while dotted lines represent the confidence intervals. Plots are at the same vertical scale so that the strength of the slope indicates the importance of the variable in the model. The *y*-axis label indicates the fit type (l = linear, poly = polynomial, s = spline) and the degrees of freedom. Rugplot at the bottom indicates location of sample values. The lower 2 plots represent the interaction between region and week such that the left and right plots are for the northern and southern regions, respectively. The interaction plots were created with R using mgcv because S-Plus was not able to plot interactions terms. The 2 algorithms produced similar model fits for sea surface temperature (SST) and SST coefficient of variation (CV), which suggests that these interaction plots are valid for the S-Plus algorithm

1975, 1978) of Risso's and Pacific white-sided dolphins. This hypothesis requires that these productive waters remain in a fixed location over time (e.g. Vinogradov 1981), and it is unknown if this is a reasonable assumption in this region. An alternative hypothesis for the 4 wk time lag is that prey aggregations may be moving with periodic features found in the SCB. For example, high amplitude current fluctuations, which may be attributable to eddy advection or coastally trapped waves, exhibit 20 to 30 d periodicity at SCB basins (Hendricks 1977, Hickey 1992).

The modeled relationships between dolphin acoustic activity and environmental variables are reasonable when compared with what is known about the ecology of each group. The models suggest Risso's dolphins prefer warmer waters, peaking at 20°C and above, while PWS B peak in moderate waters around 18°C and PWS A prefer cooler waters. Similarly, Risso's dol-

phins have been observed inhabiting warm-temperate waters (Kruse 1989, Tynan 1997, Benson et al. 2002) and expanding their range north during extended warm periods (Leatherwood et al. 1980), while studies of northern Pacific white-sided dolphins indicate preference for cooler waters (Benson et al. 2002, Becker 2007). The temperature difference between the 2 Pacific white-sided dolphin types reflects the southerly and northerly distribution of their echolocation activity and possibly population ranges (Soldevilla et al. 2010b). Additionally, the seasonal variability described by Soldevilla et al. (2010b) was incorporated into the models. A positive relationship to the upwelling index was an important predictor for PWS B click detections, which seems counter-intuitive given the negative relationship to SST CV. This discrepancy may be a result of the use of local data for SST CV compared to regional values general to the entire SCB for the upwelling index,
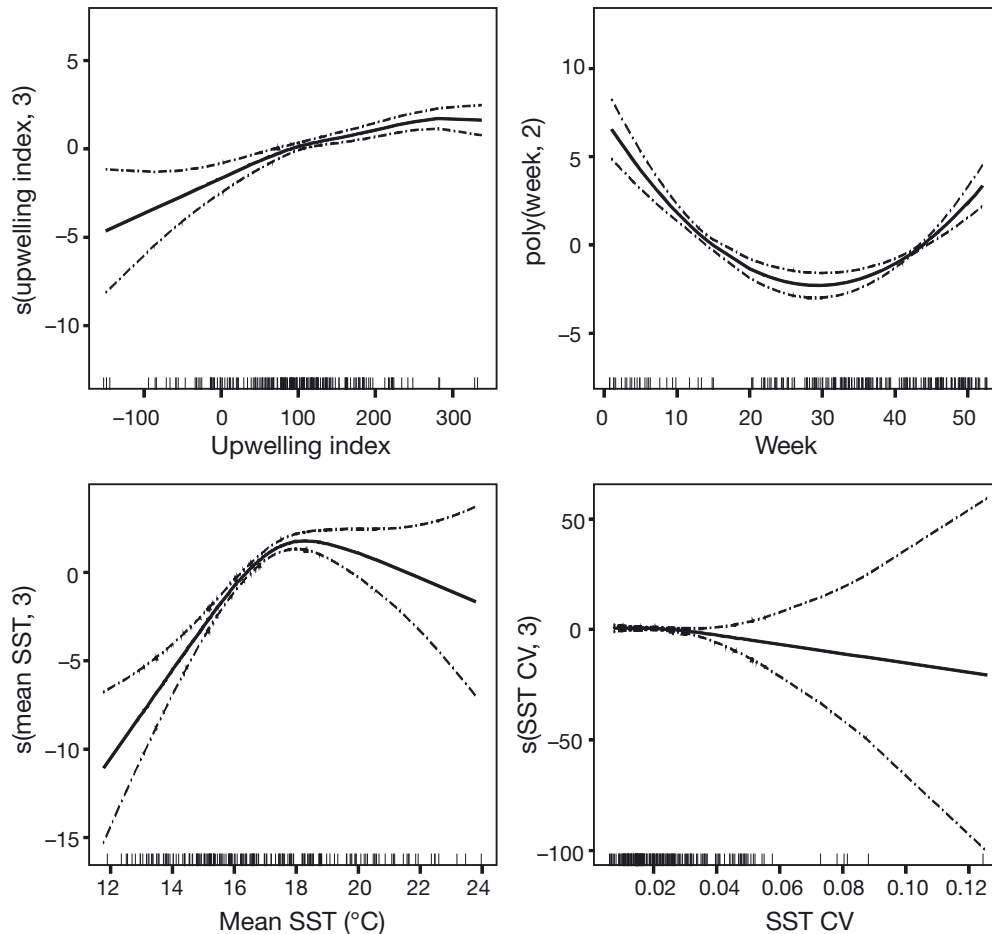

Fig. 6. *Lagenorhynchus obliquidens.* Modeled partial fits of oceanographic variables to Pacific white-sided dolphin click type B hours detected per week. The solid line represents the best fit while dotted lines represent the confidence intervals. Plots are at the same vertical scale so that the strength of the slope indicates the importance of the variable in the model, with the exception of SST CV which had large confidence intervals. The *y*-axis label indicates the fit type (poly = polynomial, s = spline) and the degrees of freedom. Rugplot at the bottom indicates location of sample values. SST = sea surface temperature; CV = coefficient of variation

or it may be a result of the high uncertainty in the relationship to SST CV at higher values. The regional upwelling index may reflect basin-wide oceanographic changes that support movements up from Baja California, Mexico. Local upwelling indices, which can provide important information about prey aggregating mechanisms, may be important for all dolphins and should be considered in future models.

The explained deviance for the best models of the 3 dolphin groups spanned a wide range, with values of 24, 47, and 82% for PWS A, Risso's, and PWS B, respectively. These explained deviances are generally an improvement over those found in visual survey habitat studies of a variety of species, which range between 1 and 43% (Ferguson 2005, Becker 2007). The moderate to high explained deviances found in this study may indicate that the models include some of the most important variables needed to explain dolphin echolocation activity, while lower fits indicate that other data, such as measures of prey abundance, or different time lags may be important. Additionally, the better fit of these spatio-temporal models compared to spatial visual survey models may indicate that temporal variation, such as seasonality, is inherently more predictable than spatial variability. It is interesting to note that quality of fit appears to be site-specific for Risso's and PWS A models (Fig. 4). An examination of additional explanatory variables including bathymetric differences or additional oceanographic differences between the sites that affect prey distribution or the occurrence of predators or competitors as well as increased site coverage in the region may improve explanatory power of models in this region.

While explained deviances of these models are moderate to high, the variability among the 3 groups may reflect differences in the portion of the dolphins' range that is covered by this study, in the life history of the animals, or in the quantity or quality of data compared to the complexity of habitat to be modeled. The study area includes the northern extent of the PWS B group range, and the high fit may reflect the incorporation of both prime habitat and non-habitat into the model, while PWS A is heard throughout and beyond the study area so that the entire area represents viable habitat only which may be more difficult to precisely model. Similarly, dolphins may not occur in the study area when environmental conditions are good because they are inhabiting areas outside the study area where conditions are better, resulting in lower observed occurrences than predicted. For these reasons, future studies should extend the spatial range of the study area to include more of, and extend beyond, the dolphins' known ranges. Differences in model explanatory power may reflect differences in prey preferences, as suggested by Soldevilla et al. (2010b) for

Pacific white-sided dolphin types based on differences in diel activity and spatial occurrence. Pacific white-sided dolphins are opportunistic foragers on variable prey types. It is possible that PWS B represents a population adapted toward a specialist approach to foraging while PWS A represents a generalist approach and therefore multiple habitat preferences to model. Complex habitat models require larger sample sizes (Becker 2007), so more data may be needed to improve PWS A models. Finally, it is possible that the especially high explained deviance for PWS B is a byproduct of the generally low number of observed detections for this dolphin group such that the model could always predict low values. In the case of the best PWS B model, the training data included high and low observed detections, while the test set had only low observed detections. However, the remaining models which included test sets with more variability in observed detections include similar variables supporting the validity of the best model.

An important caveat to predictive modeling is that the statistical significance of terms included in models does not necessarily imply the ecological significance of those variables to the dolphins (Hamazaki 2002). The predictive models presented in this study provide insight into ecological relationships that can be used to develop and test appropriate hypotheses about the mechanisms behind dolphin occurrence. Gaps in our mechanistic understanding include knowledge of both dolphin prey type and prey response to the environment. Risso's dolphins are known to feed primarily on cephalopods (Clarke 1996), and many species of squid are found off California (Okutani & McGowan 1969, Roper & Young 1975), though stomach content analyses are available for only 1 Risso's dolphin stranded off California almost 50 yr ago (Orr 1966). On the other hand, Pacific white-sided dolphins are opportunistic foragers and feed on the most abundant, appropriately sized prey (Brown & Norris 1956, Fitch & Brownell 1968, Stroud et al. 1981, Walker et al. 1986), so their prey types likely change over time. Concurrent sampling of dolphins and their prey and comparison of habitat models of potential prey species (e.g. Schismenou et al. 2008) with dolphin habitat models could help determine which prey species are most important in dolphins' diets during the study period.

Remotely sensed SST and chl data can indicate the presence of fronts and areas of high productivity; however, the ecological structure of the regions, including the specific composition of phytoplankton, zooplankton and fish assemblages, can only be determined through *in situ* oceanographic sampling, including water samples, net tows and multi-frequency acoustic backscatter. *In situ* sampling of some properties could be incorporated into moorings at the HARP location,

including temperature, salinity, current meters, fluorescence and multi-frequency active acoustics. However, automated technologies to determine prey species identity from active acoustics are still under development, so concurrent ship-based marine mammal surveys and oceanographic sampling may be a better venue for exploring mechanisms affecting prey and dolphin abundance. Concurrent dolphin acoustic and environmental sampling of this sort would allow finer resolution of prey field and water properties resulting in a better indication of water mass and frontal structure, and allowing mechanistic questions to be asked when using autonomous acoustic data. Models based on remotely sensed data remain important for resource managers who do not have access to *in situ* oceanographic data in real-time.

This study indicates the importance of temporal variability in predicting dolphin occurrence. While this study was limited to incorporating a consistent lag time for all oceanographic variables in each model, it seems likely that multiple lag times are important, both because succession processes might result in abiotic and biotic variables having different lags, and also because these dolphin species feed on a variety of prey, each of which may be responding to features at different time lags. While this could be examined using GAM models, inclusion of so many hypothesis tests can result in Type 1 errors. Numerous methods for analyzing time series are available and these could be used to identify a greater variety of temporal correlations and phase shifts (i.e. lag times) than the regression models in this study could. Temporal cross-correlation techniques can incorporate multiple variables and relate both frequency of occurrence and phase shifts more easily than the time-lagged GAM models described here. Unfortunately these techniques were not feasible due to the gaps present in our time series. Future studies should minimize large time-series gaps; data with small gaps may be analyzed using techniques such as ARIMA or Kalman filtering.

Modeling the occurrence of echolocating dolphins depends on the ability to detect their click production. Factors which may affect the likelihood of detecting calling animals include sound propagation conditions and acoustic masking. Sound propagation conditions may vary across sites and seasons leading to spatial and temporal variability in detection probability; however, conditions are typically downward refracting in the SCB across seasons and sites. Examination of click detection of all species does not indicate a strong bias for any site or season. Additionally, at the frequencies used for echolocation, attenuation severely limits detection range, and therefore the potential for significant variation owing to seasonal variations in propaga-

tion conditions is reduced. Vessels, sonars, other animals, rain, wind and waves may produce sounds that mask the echolocation clicks of our chosen species so it is important to consider spatial and temporal variability in these sources. Preliminary analyses indicate that vessel noise is consistent throughout the year at all sites except Santa Catalina Island where there is an increase in occurrence during the summer (May to September), while wind and rain noise within the frequency band of clicks occurs minimally throughout the year. Future studies should explicitly incorporate metrics of ambient noise into habitat models.

The models presented here are based on presence/absence modeling from fixed passive acoustic sensors at multiple sites, providing unique insight into the amount of time animals spend in a given habitat. This is an important indicator of habitat quality and spatio-temporal usage patterns that is necessary for managers and planners to determine when and where cetaceans are likely to be found and how anthropogenic events may impact them. However, to determine the long-term impacts of events on a population, predicting the numbers of individuals is also critical, yet cetacean abundance estimation from passive acoustic monitoring remains a work in progress (e.g. Barlow & Taylor 2005, Marques et al. 2009, Whitehead 2009) and behavioral variability in sound production remains a challenge. At this point, incorporating the strengths of both visual and acoustic survey methods offers the best chance for realizing all features of habitat importance.

CONCLUSION

Temporal predictive models of cetacean habitat provide researchers and managers with the ability to examine how dynamic ocean processes affect the occurrence of cetaceans in a specific area of interest. The combination of remotely sensed oceanographic data and long-term acoustic sampling of acoustically classifiable cetaceans such as Risso's and Pacific white-sided dolphins offer the potential to examine these temporally changing patterns and understand the time scales of importance. The models presented here for Risso's and Pacific white-sided dolphins indicate that processes occurring as much as 16 wk prior may explain or predict dolphin occurrence, although the models with best predictive power were based on 0 wk and 4 wk lagged oceanographic data. The ability to predict dolphin occurrence with time-lagged data is especially pertinent for managers who wish to minimize the impact of anthropogenic events by enabling them to plan events several weeks in advance.

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