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Modeling baseline conditions of ecological indicators: Marine renewable energy environmental monitoring

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ABSTRACT

Ecological indicators are often collected to detect and monitor environmental change. Statistical models are used to estimate natural variability, pre-existing trends, and environmental predictors of baseline indicator conditions. Establishing standard models for baseline characterization is critical to the effective design and implementation of environmental monitoring programs. An anthropogenic activity that requires monitoring is the development of Marine Renewable Energy sites. Currently, there are no standards for the analysis of environmental monitoring data for these development sites. Marine Renewable Energy monitoring data are used as a case study to develop and apply a model evaluation to establish best practices for characterizing baseline ecological indicator data. We examined a range of models, including six generalized regression models, four time series models, and three nonparametric models. Because monitoring data are not always normally distributed, we evaluated model ability to characterize normal and non-normal data using hydroacoustic metrics that serve as proxies for ecological indicator data. The nonparametric support vector regression and random forest models, and parametric state-space time series models generally were the most accurate in interpolating the normal metric data. Support vector regression and state-space models best interpolated the non-normally distributed data. If parametric results are preferred, then state-space models are the most robust for baseline characterization. Evaluation of a wide range of models provides a comprehensive characterization of the case study data, and highlights advantages of models rarely used in Marine Renewable Energy environmental monitoring. Our model findings are relevant for any ecological indicator data with similar properties, and the evaluation approach is applicable to any monitoring program.

1. Introduction

Statistical models are commonly fit to ecological indicator data to detect and measure change in environmental monitoring programs, but observed patterns are potentially affected by the choice of model used to analyze data (e.g., Jones-Farrand et al., 2011; Olden and Jackson, 2002; Thomas, 1996). Ecological indicators characterize ecosystem attributes such as structure, composition, and function (Niemi and McDonald, 2004; Noss, 1990) that vary over time or location. An indicator can be measured directly or derived from metrics to serve as proxies for indicators (e.g., counts, concentrations, rates). Statistical models can then be applied to indicator or metric data to characterize baseline conditions, which includes estimation of pre-disturbance variability, data trends, and relationships between biotic and abiotic components of the environment (Treweek, 1996, 2009). Quantifying baseline conditions enables the design of operational monitoring programs that measure change caused by known disturbances (Schmitt and Osenberg, 1996; Treweek, 2009). By standardizing indicators and models used to analyze ecological baseline data, uncertainty in assessment of environmental change is reduced and sites can be compared across time and locations.

In terrestrial and aquatic ecosystems, ecological indicators are used to quantify ecosystem change in response to disturbances. Examples include climate change (Ainsworth et al., 2011), resource harvest (e.g. commercial fisheries; Large et al., 2013), and human activity − ranging from population growth to acoustic disturbances (Andrews et al., 2015). For monitoring programs, indicators need to be evaluated with models to develop standards for quantifying anthropogenic effects on the environment. Anthropogenic disturbances to ecosystems result from the addition or cessation of human activity with positive or negative effects. One example of an anthropogenic activity that may impact aquatic ecosystems is marine renewable energy (MRE; see Table A1 for the list of defined abbreviations) technologies, including offshore wind turbines, surface wave energy convertors, and tidal stream turbines.

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With the exception of offshore wind operations, current MRE development is largely demonstration scale (e.g., 1–2 devices installed for testing and validation), rather than commercial enterprises that are grid connected. In the United States, the lack of commercial scale MRE projects is partially attributed to the uncertainty associated with environmental effects of MRE development. At this time, there are no standard monitoring requirements for baseline or operational monitoring of MRE sites within the United States and other nations (Copping et al., 2016).

In an effort to ensure efficient, comparable, and informative monitoring programs, initial guidelines have been developed for MRE monitoring study design and data collection. These guidelines emphasize the use of ecological indicators to assess change caused by MRE development (Boehlert et al., 2013; Klure et al., 2012). Indicators recommended for measuring change include abundance, distribution, diversity, and behavior (Niemi and McDonald, 2004; Noss, 1990) of ecosystem components that may be affected by development, including marine mammals, birds, fish, and habitat (Boehlert et al., 2013; Klure et al., 2012; McCann, 2012). Common methods to collect metrics that serve as proxies for indicators, such as abundance counts, diversity indexes, location measurements, include trawl, acoustic, and optical surveys (Klure et al., 2012; McCann, 2012; Polagye et al., 2014). Despite recommendations of indicator use, current guidelines lack best practices for analyzing indicator or metric data. Previous efforts to analyze MRE monitoring data have been narrow in scope, usually restricted to generalized regression models. We define generalized regression models to include linear regressions (e.g., Hammar et al., 2013; ORPC, 2014), semi- or parametric generalized linear (mixed) models (GLMMs) (e.g., Bergström et al., 2013; Embling et al., 2013; Stenberg et al., 2015), and generalized additive (mixed) models (GAMMs) (e.g., Benjamins et al., 2016; Mackenzie et al., 2013). These models have been used to characterize baseline conditions and to predict effects of MRE development on those conditions (e.g., Duck et al., 2006; Tollit and Redden, 2013; Viehman et al., 2015). The use of semi- and full parametric models for monitoring is constrained due to the limited range of error distribution assumptions, and a required parametric relationship between predictors and response variable.

An evaluation of a wider range of model classes is needed to establish best practices when analyzing environmental data to establish baselines for ecological indicators. Time-series and nonparametric models differ from generalized regression models, and yet are equally capable of fitting indicator data, predicting environmental effects, and measuring change. Evaluating the ability of generalized, time series, and nonparametric regression models to characterize ecological time series data is necessary to recommend best practices. We use data from a proposed MRE site as a case study for model evaluation, but because this framework is general, the models and methods presented here are applicable to a wide range of monitoring programs and indicators. Establishing best practices for characterizing baseline conditions decreases site characterization and operational monitoring costs, enables comparison among sites, and reduces uncertainty in environmental assessments.

2. Methods

2.1. MRE baseline case study

The case study baseline data was collected at a tidal turbine pilot project site proposed by the Snohomish County Public Utility District No. 1 from May 11 to June 8, 2011 (Horne et al., 2013). The site is located ~1 kilometer off Admiralty Head, Puget Sound Washington (48.18° N, −122.73° W), at a depth of ~60 m (Public Utility District No. 1 of Snohomish County, 2012). The project would deploy two, 6 m Open Hydro turbines (http://www.openhydro.com/). Active acoustic backscatter data recorded using a 120 kHz BioSonics DTX echosounder mounted on a Sea Spider platform is assumed representative of a primary monitoring method that would be deployed throughout the life of an MRE project. Acoustic backscatter is representative of nekton (i.e., macro-invertebrates and fish that move independently of fluid motion) density within the water column (Maclennan et al., 2002). The echosounder sampled at 5 Hz for 12 min every 2 h, and a -75 dB re $1 m^{-1}$ threshold was applied to the data to remove noise (Horne et al., 2013). Data values were constrained to 25 m from the bottom, a height corresponding to twice that of the proposed OpenHydro tidal turbine.

A suite of metrics derived from the acoustic backscatter data are available to quantify nekton density and vertical distribution in the water column (cf. Burgos and Horne, 2007; Urmy et al., 2012). Two metrics were chosen to represent MRE monitoring data: mean volume backscattering strength (Sv) (dB re $1 m^{-1}$) and an aggregation index (AI) (m^{-1}). Both metrics are continuous, display periodic autocorrelation (Jacques, 2014), and are trend-stationary (i.e., statistical data properties are constant over time, assuming that the periodicity and trend in the data are associated with deterministic environmental variables). These two metrics serve as proxies of abundance and behavior, which are indicators of nekton structure and function (cf., Niemi and McDonald, 2004; Noss, 1990; Wiesebron et al., 2016). Sv data serves as a proxy for nekton density and are normally distributed. The AI data measures animal patchiness, are non-normal, right-skewed, and composed primarily of low aggregation values with spikes of high aggregation (Fig. 1). The terms *low state* and *high state* will be used to refer to the two magnitudes of AI values. These metrics are considered representative of MRE baseline data, because MRE monitoring guidelines consider fish a primary receptor (i.e., ecosystem component that responds to change) of MRE environmental stressors (i.e., external events or features associated with MRE development) (e.g., Boehlert et al., 2013; Klure et al., 2012; McCann, 2012).

Ancillary environmental measurements collected during Admiralty Inlet surveys (cf. Jacques, 2014) were used as potential covariates in the candidate models. Daily tidal range (m), tidal speed (m/s), and Julian day of year were matched to each time stamp from May 11th through June 8, 2011. Tidal range was calculated as integrated tidal speed through the day (Jacques, 2014). A Fourier series defined by a 24 h period was also included as an environmental variable to represent time-of-day.

2.2. Evaluation approach

We developed an evaluation to assess the ability of statistical models to characterize baseline environmental conditions that identify potential effects of MRE development and to accurately measure effects during operations. The approach is intended to evaluate data variability, trends, and relationships between components of the environment. We used cross-validation as a model selection tool to quantify interpolation accuracy (i.e., ability to predict data within the range of the empirical data) (Hastie et al., 2009). This approach ensured an equal assessment of model accuracy across all statistical model classes (parametric v. non-parametric), while at the same time, parameterized all candidate models to have the greatest probability of success in accurately characterizing the data. Residual diagnostics were used to assess the validity of model error distribution and autocorrelation structure assumptions. The 10-fold cross validation model selection and residual diagnostics provide estimates of model fit accuracy and residual variability. Patterns in selected covariates among models were interpreted as trends and important predictor variables of the indicator data. Results from the evaluation were then used to recommend model (s) most capable of characterizing normally and non-normally distributed monitoring data. All analyses were conducted using the R v.3.1.2 statistical software environment (R Core Development Team, 2014).

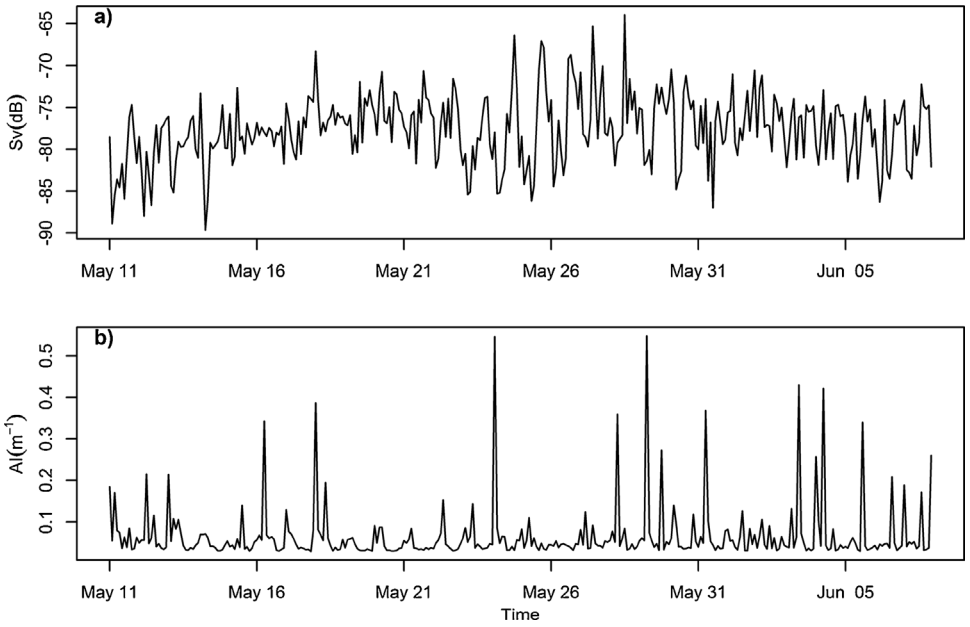

Fig. 1. Acoustic-based metric values derived from data collected from May 11th to June 8, 2011 in 2 h intervals. (a) Normally distributed nekton density (Sv dB re 1 m^{-1}) and (b) non-normal aggregation index values (AI m^{-1}) ranging from 0 to 1 that consisted of low index values with higher value spikes through the series.

2.3. Candidate model classes

Statistical models evaluated include: generalized regression models, time series regression models, and non-parametric regression models (Table 1). Unlike generalized regression models used in MRE monitoring studies (c.f., ORPC, 2014; Tollit and Redden, 2013; Viehman et al., 2015), time series models are structured to potentially estimate autocorrelation, stationary properties, and process error variance (i.e., natural variability in the true state of the population), and/or observation error (Pattengill-Semmens et al., 2011). Time series models may be deterministic or stochastic (i.e., do not assume a fixed trend and include lagged dependent variables to model the process) (Chandler and Scott, 2011). Unlike parametric models, nonparametric models do not have predetermined functional forms, they do not require a theoretical data distribution or assume linearity, and instead use the data to develop the variable relationships in the model. Nonparametric models have been recommended when little is known *a priori* about the data, and when accurate predictions of response variables are needed (Gitzen, 2012). All equations and parameter definitions are detailed in Appendix B. A summary of specific model parameterizations can be found in Table B1. Sample data and model fitting code are provided in Appendices C and D in Supplementary material.

Linear regression and Generalized-Least-Squares (GLS) regression are traditional methods used to detect change in Before-After Control-Impact (BACI) monitoring studies (Stewart-Oaten and Bence, 2001; Wagner et al., 2002). Specifically, an analysis of variance (i.e., ANOVA) is considered a special case of a linear regression often used to estimate the statistical significance of BACI factor variables and their interactions (Hewitt et al., 2001). A GLS model can account for autocorrelation (Pinheiro, 2000), while linear regression models typically do not. Therefore, both a linear regression and a GLS model were included in the generalized regression class of candidate models. Generalized Linear Models (GLMs) were also included within the generalized regression class of candidate models because they are an extension of linear regressions that are not constrained to assume normally distributed data. A GLM can be extended to a Generalized Linear Mixed Model (GLMM) to additionally account for autocorrelation within the structure of a mixed-effects model (Pinheiro, 2000). We only considered GLMs and GLMMs for non-normal (i.e., AI) data. Generalized Additive (Mixed) Models (GA(M)Ms) were the most complex candidate models evaluated as members of the generalized regression model class. GAMs and GAMMs are semi-parametric extensions of GLMs (Wood, 2006). In addition to parametric covariates, GAMs and GAMMS include nonparametric smoother functions of predictor variables to model nonlinear relationships (Wood, 2006).

Within the class of time series models, a Regression-Autoregressive-Moving-Average (Reg-ARMA) model was included, because an ARMA model is a traditional time series model that is commonly used for modeling stochastic trends (Chandler and Scott, 2011; Chatfield, 1989). To date, an ARMA model has not been used in MRE biological monitoring studies. The ARMA model was formatted as a Reg-ARMA to model dependent data using environmental predictors in addition to lagged, dependent values (Hyndman, 2015). A Regression-Autoregressive-Moving-Average-Generalized-Autoregressive-Conditional-Heteroskedasticity (Reg-ARMA-GARCH) model was also included as a candidate time series model. GARCH models can be viewed as extensions of ARMA models that are applicable for modeling time series with heteroskedastic variance, such as the AI data. GARCH models have been previously identified as a possible analytic tool for tracking MRE monitoring data over time (Horne et al., 2013). The GARCH model used in the evaluation was formatted as a Reg-ARMA-GARCH model to include environmental predictors. When independent predictor variables are included in an ARMA-GARCH model, the model becomes a linear regression with errors estimated using an ARMA model, and the variance of the residuals estimated using the GARCH model (Ruppert, 2011). Lastly, a univariate autoregressive state-space model (SSM) was included as a candidate model within the time series model class. An ARMA process may be structured as a SSM, but a SSM can also be extended to directly estimate more complicated time series elements such as: multivariate data, nonstationary trends, missing observations, and it explicitly partitions the total variance into process (i.e., stochastic) and observation (i.e., measurement) errors (See and Holmes, 2015). A SSM is a dynamic time series model that has been widely used (e.g., economics, engineering, and ecology; Holmes et al., 2012), including characterization of the acoustic baseline data from Admiralty Inlet (Jacques, 2014).

Two forms of SSMs were used in the evaluation, one with fixed low observation error and estimated high process error (SSM-P) and the other with fixed low process error and estimated high observation error (SSM-M). We assumed that sources of observation error are due to calibration and hydrographic conditions based on the case study data collection methods (Simmonds and MacLennan, 2005), and both sources have been suggested to equate to a maximum of 5% of the total error. Therefore, the SSM-P was structured with fixed observation error

Table 1
Characteristics of candidate regression models including model class, linear or nonlinear form, parametric or nonparametric structure, error components (observation and/or process error), error distribution, and autocorrelation structure.

Model	Class	Form	Parametric/Nonparametric	Error Components	Error Distribution	Auto-correlation Structure
Linear	GR	Linear	Parametric	Observation error	Normal	None
Generalized least squares (GLS)	GR	Linear	Parametric	Observation error	Normal	Residual correlation
Generalized linear model (GLM)	GR	Linear	Parametric	Observation error	Exponential family	None
Generalized linear mixed model (GLMM)	GR	Linear	Parametric	Observation error	Exponential family	Residual correlation
Generalized additive model (GAM)	GR	Nonlinear	Semi-parametric	Observation error	Exponential family	None
Generalized additive mixed model (GAMM)	GR	Nonlinear	Semi-parametric	Observation error	Exponential family	Residual correlation
State-space model (SSM)	Time series	Linear	Parametric	Process and Observation error	Normal	AR-1 lagged variable
Regression–autoregressive moving average model (Reg-ARMA)	Time series	Linear	Parametric	Observation error	Normal	ARMA error
Regression– autoregressive moving average –generalized autoregressive conditional heteroscedasticity model (Reg-ARMA-GARCH)	Time series	Linear	Parametric	Observation error	Generalized normal	ARMA error; GARCH residual variance
Random forest (RF)	NP	Nonlinear	Nonparametric	N/A	None	Lagged variables
Support vector regression (SVR)	NP	Nonlinear	Nonparametric	N/A	None	Lagged variables

Note: The column *Class* refers to the included model classes: generalized regression (GR), time series, or nonparametric (NP) models.

of 10% of the total error for the normal and non-normal data set, while the SSM-M was structured with fixed process error that equated to 10% of the total error.

A Random Forest (RF) and Support Vector Regression (SVR) are machine learning algorithms (i.e., models that are structured to predict data patterns given a training set of data) that were included in the model evaluation as candidate nonparametric models. The regression forms of these candidate models originally stem from a RF classification model (Brieman, 2001) and Support Vector Machine (SVM) classification model (Vapnik et al., 1997). A Random Forest is a collection of statistical decision trees applied to random bootstrap samples of data that are averaged to produce predicted values (Liaw and Wiener, 2002). In comparison, a SVR uses a specified kernel function to map data into a higher dimensional space to produce a linearly separable regression (Cortes and Vapnik, 1995; Hsu et al., 2010). A Linear kernel SVR (SVR-L) and a Radial-Basis-Function kernel (SVR-RBF) were used as candidate models in the evaluation. RF models have previously been used to characterize the importance of environmental factors and forecast species distribution in wind renewable energy biological monitoring studies (e.g., Belaire et al., 2014; Hayes et al., 2015). Unlike RF models, SVR models have not previously been used in MRE biological monitoring studies, but they are commonly used for species distribution modeling (e.g., Drake et al., 2006; Lorena et al., 2011).

2.4. Model selection

10-fold Cross-validation (CV) model selection was used to select the optimal structure of each model, and to compare the accuracy of parameterized candidate models. In 10-fold CV, 10 equally-sized, random subsets of data are used repeatedly such that 9 subsets compose a training-set and a single subset is used as the test-set to produce a total of 10 training and test datasets. Predicted values from the model applied to the test-sets are used to calculate an average Root-Mean-Squared-Error (RMSE). RMSE is a measure of model accuracy based on the average deviance of model predicted values ($\hat{y}_i$) from observed values (y_i):

$$\sqrt{\frac{1}{n}*\sum_{i=1}^{n}(y_i-\hat{y}_i)^2} \quad (1)$$

where i is the observed i^{th} value, and n is the sample size. A RMSE value closer to 0 indicates a more accurate data interpolation. CV has been recommended when there is not high *a priori* knowledge of model structure, and the goal is to interpolate within the data range (Gitzen et al., 2012). The use of 10 subsets in a cross validation has been suggested as the most effective number of training/test sets for model selection (Arlot and Celisse, 2010; Hastie et al., 2009), providing a balance between bias (i.e., a model that underfits data), and variability (i.e., a model that overfits data) (James et al., 2015).

We performed model selection on 24 versions of each candidate model to identify the optimal structure, before comparing the performance across models. Rather than including all possible interactions of model covariates, a set of models based on *a priori* knowledge of the biological system (Burnham and Anderson, 2002) were selected. Covariates used in each model included Julian day, tidal range, tidal speed, and a Fourier series defined by a 24 h period. All covariates were demeaned (i.e., sample mean subtracted from covariate values) before analysis. We considered two-way interactions: Julian day-tidal speed, Julian day-tidal range, tidal speed-tidal range, and tidal speed- 24 h period, but three-way interactions were not considered. All possible combinations of the covariates and specified two-way interactions produced 24 versions of each candidate model. All combinations of the 24 covariates were evaluated (576 model versions) within the two-part state-space and reg-ARMA-GARCH models because combinations of covariates may equally affect both the process and observation of the response in a SSM, and the reg-ARMA-GARCH model allows for

Table 2
Average Root-Mean-Squared-Error (RMSE) and corresponding percent relative RMSE (% rRMSE) ranked order accuracy of each parameterized candidate model from the 10-fold Cross-Validation model selection for the Sv data, including environmental predictors, autocorrelation structure, and presence of autocorrelation in the residual ACF plots.

Model	Average RMSE	% rRMSE	Environmental Predictors	Auto-correlation Structure (AR,MA)	Residual Auto-correlation
SVR-RBF	3.05 (0.147)	0	Day, Fourier Series, Tidal Range, Tidal Speed	(1,0)	Yes
RF	3.16 (0.274)	3.48	All Environmental Predictors	(14,0)	No
SVR-L	3.22 (0.313)	5.54	Fourier Series	(13,0)	No
SSM-P	3.30 (0.238)	8.12	Process Equation: Day, Fourier Series, Tidal Range Observation Equation: Day, Tidal Range, Day-Tidal Range	(1,0)	Yes
SSM-M	3.34 (0.239)	9.49	Process Equation: Tidal Range, Tidal Speed, Tidal Speed-Tidal Range Observation Equation: Day, Fourier Series, Tidal Speed	(1,0)	Yes
GAM	3.43 (0.190)	12.36	Day, Fourier Series, Tidal Range†, Day:Tidal Range†	NA	Yes
GAMM	3.45 (0.190)	13.08	Day, Fourier Series, Tidal Range†	(1,0)	Yes
Reg-ARMA-GARCH	3.53 (0.169)	15.69	Mean Equation: Day, Fourier Series, Tidal Range, Day: Tidal Range Variance Equation: Day, Fourier Series, Tidal Range,	ARMA:(1,0) GARCH:(2,3)	Yes
Reg-ARIMA	3.54 (0.168)	15.94	Day, Fourier Series, Tidal Range, Day: Tidal Range	(1,0)	Yes
GLS	3.54 (0.161)	16.03	Day, Fourier Series, Tidal Range, Day: Tidal Range	(1,0)	Yes
LM	3.54 (0.163)	16.09	Day, Fourier Series, Tidal Range, Day: Tidal Range	NA	Yes

Notes: Models are ranked in descending order of average RMSE and associated variances of average RMSE are shown in parenthesis. The number of autoregressive (AR) and moving-average (MA) variables in model autocorrelation structures is shown in parenthesis as (AR, MA). The specified (AR, MA) structure of the nonparametric models indicates the number of lagged dependent variables included in the parameterized models. The environmental predictors are listed in alphabetical order of main effects followed by interactions. The Tidal Range† predictor is parametric in the GA(M)Ms.

covariates in both the conditional mean and variance equation.

The model selection protocol in this study is based on the strategy developed by Diggle et al. (1994) and Wolfinger (1993), and used in Zuur et al. (2009). The residual variance structure was determined prior to selecting predictor variables during model selection (Diggle et al., 1994; Wolfinger, 1993). Initially, the optimal autocorrelation structure was deduced using the 10-fold CV method and the full version of each candidate model (i.e., all main effects and interactions, Zuur et al., 2009). Then, 10-fold CV was used to select the optimal structure of predictor variables. The Autoregressive Moving Average (ARMA) correlation structure selection included all combinations of autoregressive (AR) and moving average (MA) lagged variable values ranging from 0 to 3. ARMA error structures with an AR or MA lag value larger than 3 tend not to converge and may not be necessary to model autocorrelation (Schabenberger and Pierce, 2002; Zuur et al., 2009). The number of lagged variables in the nonparametric models was selected prior to the covariate structure. Autocorrelation Function (ACF) plots of the detrended data indicated that autocorrelation was no longer present after 50 data points for the normal data and after 62 data points for the non-normal data. To be consistent in the selection process, 0 to a maximum of 62 lags were included in the non-parametric model selection for both normal and non-normal datasets.

Nonparametric models included an additional model selection for tuning parameters (i.e., parameters that control the training algorithm). The Random Forest regression has three tuning parameters: node size, number of trees, and number of predictor variables (mtry) (Breiman, 2001). The nodesize was set to 5 data points, as it has little effect on the fit of a Random Forest model (Gutiérrez et al., 2011; Ishwaran and Malley, 2014). The number of trees and value of mtry were selected using 10-fold CV. The default value of number of trees, 500, was increased by steps of 500 until the RMSE value stabilized. The mtry parameter was stepped from the default value of $p/3$, where p is the number of predictor variables, $+/-$ 2 units until the RMSE value no longer decreased (Liaw and Wiener, 2002). The Support Vector Regression included kernel tuning parameters. The SVR-L and SVR-RBF models include a cost tuning parameter, and SVR-RBF also includes a gamma tuning parameter (see Appendix B). Both parameters affect bias-variance tradeoffs within the SVR (Hastie et al., 2009). An iterative 10-fold CV grid search of cost values ranging from 2^{-5} to 2^{15} by a factor of 2^2 and gamma values ranging from 2^{-15} to 2^3 by a factor of 2^2 was used (cf. Berk, 2008; Hsu et al., 2010). At each iteration a finer grid search, ranging from the optimal parameter value from the previous iteration $+/-$ a factor of 2^2, was repeated until the RMSE value reached a minimum.

2.5. Model evaluation

The ability of selected models to characterize baseline data was evaluated by examining model fit, covariate selection, and residual diagnostics. RMSE metrics were ranked from smallest to largest to assess model ability to accurately interpolate baseline data. Percent relative RMSE (% rRMSE) values were calculated as the percent difference in a model's average RMSE relative to the minimum average RMSE value to provide an interpretable scaling of results. Consistency of environmental covariates across candidate models was used to identify potentially important predictor variables of nekton density and aggregation, and to indicate a model's ability to identify these variables. Residual diagnostics, including an inspection for homogeneity and independence using residual and ACF plots, were conducted by refitting the final version of each candidate model to the entire dataset.

3. Results

3.1. Model accuracy

The more complex and flexible nonparametric and stochastic time-series models more accurately interpolated baseline nekton density (i.e. Sv) data, based on average RMSE, than the more simplistic deterministic parametric models (Table 2). The SVR-RBF model produced the most accurate interpolation of the data based on its average RMSE value of 3.05. The other non-parametric models, RF and SVR-L, produced the successive best interpolations of the data with corresponding average RMSE values that were 3.48% and 5.54% higher than SVR-RBF. The most flexible linear parametric models, SSM-P and SSM-M, were the next most accurate candidate models. The semi-parametric GA(M)Ms produced better interpolation of the data than all other deterministic parametric models, consistent with ranked order from most to least flexible candidate models. The simplest candidate models, GLS and linear regression, had the worst interpolative accuracy (~16% rRMSE).

Unlike the model selection results for nekton density, the candidate models' ability to accurately interpolate nekton aggregation index (i.e.

Table 3
Average Root-Mean-Squared-Error (RMSE) and corresponding percent relative RMSE (% rRMSE) ranked order accuracy of each parameterized candidate model from the 10-fold Cross-Validation model selection for the AI data, including environmental predictors, autocorrelation structure, and error distribution.

Model	Average RMSE	% rRMSE	Environmental Predictors	Auto-correlation Structure (AR,MA)	Error Distribution
SVR- RBF	0.0667 (0.000920)	0	Day, Fourier Series, Tidal Speed, Day: Tidal Speed, Tidal Speed: Fourier Series	(13,0)	NA
SSM-P	0.0673 (0.000869)	0.897	Observation Equation: Fourier Series	(1,0)	Normal
GLM	0.0674 (0.000847)	1.06	Day, Fourier Series	NA	Gamma (identity)
GLMM	0.0674 (0.000855)	1.06	Day, Tidal Range	(1,0)	Gamma (identity)
GLS	0.0675 (0.000859)	1.11	Fourier Series	(1,0)	Normal
LM	0.0675 (0.000858)	1.12	Fourier Series	NA	Normal
Reg-ARIMA	0.0675 (0.000865)	1.15	Fourier Series	(1,2)	Normal
Reg-ARMA-GARCH	0.0675 (0.000953)	1.19	Mean Equation: Day, Fourier Series, Tidal Range Variance Equation: Fourier Series	ARMA: (1,0); GARCH: (2,0)	Skewed-student-t
GAM	0.0677 (0.000874)	1.47	Fourier Series, Tidal Speed	NA	Gamma (identity)
GAMM	0.0677 (0.000877)	1.52	Fourier Series	(2,0)	Gamma (identity)
SSM-M	0.0677 (0.000880)	1.53	Process Equation: Day Observation Equation: Day, Fourier Series	(1,0)	Normal
RF	0.0681 (0.000888)	2.06	Fourier Series, Tidal Speed	(2,0)	NA
SVR-L	0.0689 (0.000858)	3.35	Day, Fourier Series, Tidal Range, Day: Tidal Range, Tidal Range: Fourier Series	(1,0)	NA

Notes: Models are ranked in descending order of average RMSE and associated variances of average RMSE are shown in parenthesis. The number of autoregressive (AR) and moving-average (MA) variables in model autocorrelation structures is shown in parenthesis as (AR, MA). The specified (AR, MA) structure of the nonparametric models indicates the number of lagged dependent variables included in the parameterized models. The environmental predictors are listed in alphabetical order of main effects followed by interactions.

AI) data was not ranked in a consistent descending order of model complexity, and relative difference in interpolation accuracy was more similar among models (Table 3). Again the SVR-RBF model produced the lowest average RMSE value (0.0667). The other two non-parametric models, RF and SVR-L, produced the highest average RMSE values, but they were only 2.06% and 3.35% higher than the SVR-RBF average RMSE value. The SSM-P was the second most accurate interpolative model (~0.9% rRMSE), while SSM-M was the third least accurate interpolative model (1.53% rRMSE). The GL(M)Ms were the third and fourth most accurate models, with the most simplistic models, GLS and linear regression, ranked directly below the GL(M)Ms in interpolation accuracy.

3.2. Model fit comparison

All candidate models included the 24 h Fourier series as an environmental predictor of nekton density (Table 2). SVR-L is the only candidate model that did not also include day and tidal range as environmental predictor variables. Smoothing parameters in the GA(M)Ms do not exhibit strong nonlinear patterns, which is indicated by their estimated degrees of freedom (EDF). If a GA(M)Ms EDF is close to 1, the smoothing parameters can be replaced by a linear term (Wood, 2001). The only nonlinear smoothing parameter in the parameterized GA(M)Ms, besides the cyclic time-of-day, is the day covariate (i.e., GAM EDF = 2.74, GAMM EDF = 2.69) (Fig. 2). All parametric and semi-parametric regression models also contained the day-tidal range interaction predictor variable, except for SSM-M and GAMM. SSM-M and SVR-RBF are the only candidate models that included tidal speed as a relevant environmental predictor, except for RF, which included all environmental predictors and their interactions. The SVR-L and RF models included up to 26 and 28 h lags in the dependent variable as model covariates, whereas SVR-RBF only included a 2 h lag.

Final versions of each model included residuals with slight autocorrelation when fit to the nekton density data except for SVR-L and RF

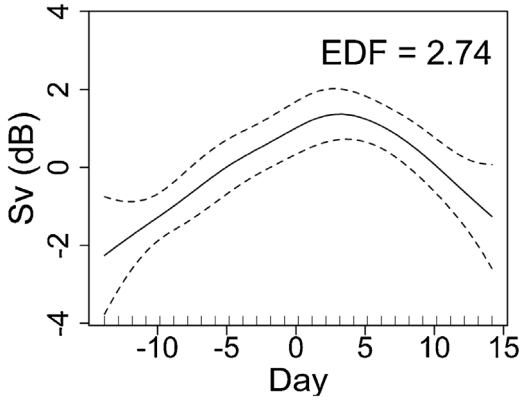

Fig. 2. Parameterized nonlinear relationship between the demeaned day covariate and nekton density (Sv). The corresponding EDF was estimated from the GAM. The dashed line represents 2 standard error bounds on the estimated values (cf. Wood, 2006). Note: Tidal range is a parametric variable in the parameterized GAM. The day covariate smoother spline in the GAMM is similarly parameterized (not shown).

(Table 2). Candidate models that did not account for autocorrelation (i.e., linear regression and GAM) included 2 and 24 h correlations in the residuals. All other generalized regression models and time-series models included a lag-1 correlation in their autocorrelation structures, and only exhibited 24 h correlation in the residuals. SVR-RBF had autocorrelated residuals at an 18 h lag, which differed from all other candidate models. All residuals were homogenous for all candidate models, indicating that the normality assumption was appropriate for modeling the distribution of nekton density data.

For the AI data the majority of candidate models included few environmental predictors (≤ 3 per parameterized model), and no interaction effects. All models included the 24 h Fourier series as an environmental predictor, except for the GLMM, which only included day and tidal range as predictor variables (Table 3). RF and GAM only

included tidal speed as a predictor variable in addition to the 24 h Fourier series. The GLM and SSM-M only included the day predictor variable in addition to the 24 h Fourier series. The SVR-RBF and SVR-L models included the highest number of environmental predictors (7 variables), and are the only candidate models that included interaction effects. Although there are similarities in the parameterization of SVR-L and SVR-RBF, they differ in their choice of tide covariate and lagged dependent variable structure (cf. Table 3). The SVR-L and RF models included fewer lagged dependent variables than SVR-RBF. SVR-L and RF included 2 and 4 h lags in the dependent variable, whereas SVR-RBF included up to a 26 h lag in the model.

No parameterized candidate model had autocorrelated residuals when fit to the nekton AI data. All model residuals were heteroskedastic, indicating that no model was able to capture the highly right-skewed distribution of AI data.

4. Discussion

4.1. Model efficacy

Evaluation of models used to monitor change in ecological indicators have been previously conducted (e.g., Bell and Schlaepfer, 2016; Thomas, 1996; Ward et al., 2014), but results of the evaluations have not been widely used in management settings, such as recommending models for monitoring Marine Renewable Energy programs. This study illustrates that the choice of model alters data characterization (e.g., Jones-Farrand et al., 2011; Thomas, 1996). Specifically, state-space models provide a thorough characterization of baseline monitoring data by accurately interpolating normal and non-normal data relative to all other candidate models, quantifying parametric estimates of environmental predictors, and separating process from observation error. Nonparametric (i.e., RF, SVR-L, and SVR-RBF) models also excel in interpolating data, but their predictor variables are not as interpretable or consistent as SSMs, making them unsuitable for data characterization. Interpolation accuracy of deterministic parametric and semi-parametric models (i.e., Reg-ARMA, reg-GARCH, GLS, Lin, GL(M)M, and GA(M)M) was lower than SSMs. State-space models have previously been recommended to characterize renewable energy monitoring data due to their incorporation of process and observation error, inclusion of environmental predictors in the model structure, and predictive abilities (Diffendorfer et al., 2015; Jacques, 2014)

4.1.1. Interpolation accuracy

All nonparametric models excel in interpolating nekton density data, but SVR-RBF is the only nonparametric model that also accurately interpolates nekton aggregation data relative to all other candidate models. RF and SVR models are known for their predictive accuracy due to their lack of structural assumptions (James et al., 2015). Among support vector regressions, SVR-RBF models tend to have greater interpolation accuracy than SVR-L models because of their more flexible nonlinear kernel (e.g., Crone et al., 2006; Kordon, 2009).

State-space models also accurately interpolate nekton density and aggregation data relative to other candidate models. SSM estimates of process and observation error, and the lag-1 structure of the process equation provide flexibility to accurately fit the stochastic nature of time series data (Dornelas et al., 2013; Hampton et al., 2013). SSM-P produced a more accurate interpolation of both datasets compared to SSM-M, because the fixed low measurement error was a more appropriate assumption of the variability of linear backscatter values produced by a stationary echosounder. The more accurate interpolation of both datasets by the SSM-P compared to the SSM-M can be used to ensure the most accurate parameterization of a SSM for any baseline monitoring study that uses a similar sampling method and design as applied in the case study.

Interpolation accuracy of deterministic parametric and semi-parametric models (i.e., Reg-ARMA, reg-GARCH, GLS, Lin, GL(M)M, and GA(M)M) were generally lower than those of nonparametric and state-space models. Predicted results from the time-series models, Reg-ARMA and Reg-ARMA-GARCH, were similar to those from the linear regression, GLS, GLM, and GLMMs, which is not surprising as these time-series models are also linear, parametric, and produce deterministic predictions regardless of their inclusion of autocorrelated error (Hyndman and Athanasopoulos, 2014). The inability of deterministic parametric models to accurately estimate complex data patterns relative to more flexible models (see Barry and Elith, 2006; Shmueli, 2010) was validated in the current study based on the average RMSE results.

4.1.2. Environmental predictors

Even though nonparametric models are flexible and excellent predictive models, they do not consistently identify the same environmental predictors, and are difficult to interpret relative to all other evaluated models. The SVR model is known to be highly sensitive to choice of kernel and tuning parameters, and can be difficult to interpret (Berk, 2008; Lorena et al., 2011). SVR-L and SVR-RBF models differed in their environmental predictors, number of lagged dependent variables, and interpolation accuracy for both nekton density and aggregation data. These differences illustrate the influence of kernel choice and tuning on model consistency and characterization of data. Unlike the SVR models, the RF model produces estimates of variable importance, which enables the RF model to be used in exploratory analyses to identify relevant predictors of a dataset (Gitzen et al., 2012; Strobl et al., 2008).

The remaining candidate models provide parametric estimates of predictor variables, which is an advantage over nonparametric models for making inferences (James et al., 2015). Parametric models are often used in MRE monitoring to provide quantitative measures of the amplitude and shape of predictor variables, along with uncertainty around those estimates (Maclean et al., 2014). Selection of predictor variables by these models was generally consistent for the nekton density data, with the exception of the SSM-M and GAMM. Differences in proportions of observation and process error relative to total variability has been shown to alter parameter estimates of SSM variables (e.g., Dennis et al., 2006; Ives et al., 2003), and is illustrated by the difference in the SSM-P and SSM-M 10-fold CV model selection results. Model selection in GAMs can be affected by autocorrelated data. GAMs are known to overfit nonlinear smoother splines in the presence of autocorrelation, while GAMMs have difficulty converging when estimating both autocorrelation and smoother splines (Wood, 2006, 2015). No model fully characterized the nekton aggregation data, based on the lack of consistent predictor variables and heteroskedastic residual diagnostics in all models. Differences in the selection of environmental covariates for the aggregation index data among candidate models further illustrates effects of model assumptions and structure on baseline characterization (cf. Barry and Elith, 2006). For instance, Gamma distributed GL(M)Ms both include day as a covariate, whereas linear regression and GLS only include the 24 h Fourier series. Differences in distributional assumptions between these models consistently impacted the inclusion of day as a covariate, regardless of other differences in model structure.

4.1.3. Partitioning of residual error

Explicit parametric estimates of both process and observation error in the state-space models provides a more biologically accurate and complete representation of nekton characteristics relative to all other candidate models. In this study, SSMs are the only evaluated models that include both process and observation error parameters. Given that nekton density and behavior are known to vary at MRE monitoring sites (e.g. Jacques, 2014; Wiesebron et al., 2016), the SSM-P is an appropriate choice as it can quantify variability when using high process error estimates. All deterministic parametric and semi-parametric candidate models do not partition error, and implicitly assume all error is attributed to observation. The SSM-P has the most accurate

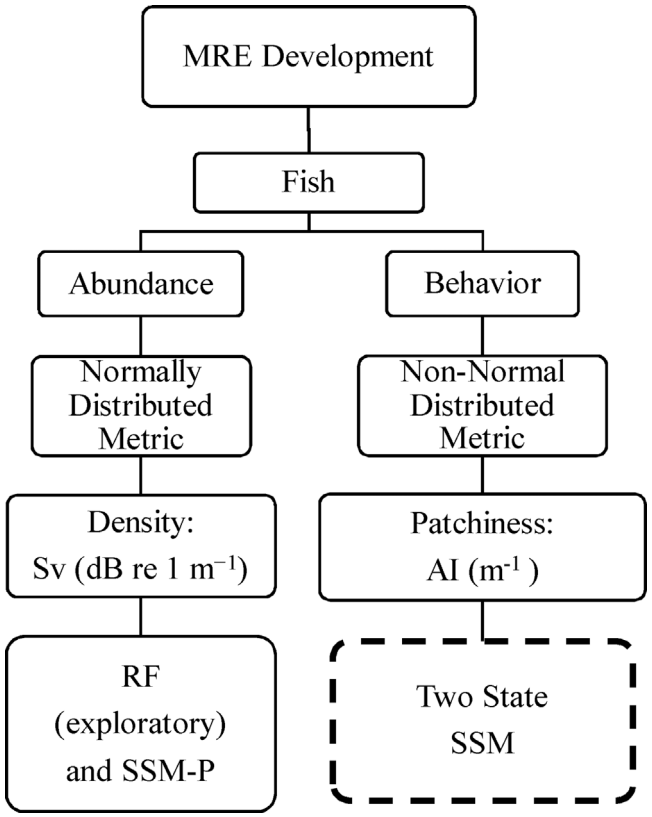

Fig. 3. Schematic of recommended models to characterize environmental receptor indicators. An example framework for MRE monitoring consists of an environmental stressor (i.e., MRE development), a monitored receptor (i.e., fish), indicators of the state of fish (i.e., abundance and behavior), and demonstrative normal and non-normally distributed metrics representative of indicators (i.e., density (Sv) and patchiness (Aggregation Index)). The dashed box indicates the need for further evaluation to identify a two state, state-space model for characterization of aggregation index data.

interpolation of nekton density and aggregation compared to all other parametric candidate models. Partitioning of total error into process and observation components in state-space models has been shown to reduce bias and improve accuracy when estimating population abundances (e.g., de Valpine and Hastings, 2002; Lindley, 2003; Ward et al., 2010). The SSM-P characterized spikes in AI values as natural variability (i.e. process error), which is a more accurate representation of nekton behavior than the assumption by all deterministic parametric models that spikes in aggregation data are observation error, as supported by a previous study attributing spikes in AI data to a periodic pattern driven by diel vertical migration (Urmy et al., 2012). Although nonparametric models produced a more accurate interpolation of nekton data than SSM-P, nonparametric models provide a less complete and interpretable characterization of nekton as they do not explicitly quantify residual model error.

4.2. MRE monitoring model recommendations

Recommendations for characterizing baseline MRE data (Fig. 3) are derived from the synthesis of model efficacy. Criteria used to recommend models include results from the 10-fold CV and residual diagnostics.

4.2.1. Normally distributed data

A Random Forest model is recommended to initially identify important predictor variable(s), coupled with SSM-P to characterize baseline predictor variables, trends, and variability in normally distributed data (Fig. 3). CV results and residual diagnostics of the RF model indicate that it provides an accurate and complete assessment of autocorrelation and relevant environmental predictors of nekton density. The RF model may be used for initial exploratory analysis, because it quantifies the importance of all environmental predictors, but it does not provide explicit estimates of model parameters or partition observation and process error in the data.

The SSM-P was the best interpolator of data among parametric and semi-parametric models. Parametric estimates of process error, measurement error, density-dependence, and predictor variables provide an interpretable assessment of components needed for baseline characterization. The SSM structure is flexible and adjustable, and may be altered to include a 24 h lag to remove the observed residual autocorrelation (Hampton et al., 2013) in the data.

4.2.2. Non-normally distributed data

No model fully characterized the AI data, based on residual diagnostics and 10-fold CV results. The model evaluation may not have identified a model that accurately captured all properties of the non-normal baseline data, but it did highlight advantages of using a state-space model to characterize the data. SSM-P was the most accurate parametric model and characterized spikes in the AI data as process error, which is more biologically accurate than the assumption of spikes as observation error (as inferred in all deterministic parametric/semi-parametric models). For the non-normal, spikey data, a Box-Cox power transformation (Box and Cox, 1964) may be necessary to fit the normal distribution assumption of a SSM. Alternatively, a non-normal, state-space model may be used to provide an accurate interpolation of data, and to reduce heteroskedasticity in the residuals. To fully model spikes in the AI data, it may also be necessary to fit a state-space model that characterizes spikes as more than process error. As an example, a Markovian switching, state-space model is capable of modeling AI data as a two-state structure, with the probability of being in the low or high state dependent on the state at the previous time-step (Ghahramani and Hinton, 2000).

4.3. Implications of model evaluation for ecological monitoring programs

Model evaluation enables direct assessment of model behavior, advantages, and constraints used to identify the most appropriate model(s) for meeting ecological objectives (e.g., Elith and Graham, 2009; Olden and Jackson, 2002). This evaluation demonstrated the effect of model choice and parameterization on the characterization of baseline data, and identified state-space models as most applicable for characterizing baseline MRE monitoring data. State-space models consistently produced the most accurate parametric interpolation of nekton data. The evaluation of a range of models provides a thorough and complete characterization of ecological data (Jones-Farrand et al., 2011) that can be used to identify best practices for efficient and accurate baseline ecological characterization, and can be used in the design of operational MRE monitoring programs.

Accurate estimates of baseline variability is critical to designing a monitoring program that has the power to detect change outside the natural range of variability (Klure et al., 2012; McCann, 2012). Baseline estimates of variability can be used in power analyses to calculate the sample size needed detect a predetermined magnitude of change in operational monitoring (Carey and Keough, 2002). In this study, the evaluation assessed baseline nekton variability with the cross-validation results highlighting the ability of nonparametric and SSM-P models to accurately interpolate baseline data relative to all candidate models. This result suggests that the data have a highly variable range around the mean, because flexible models and the assumption of high natural variability (i.e., process error) were required to accurately predict the structure of the data. Partitioning residual variability as process and observation error in a state-space model provides an additional assessment of variability that can be used to formulate sampling designs for MRE monitoring programs. If estimated process error in a state-space model is greater than observation error, then the number of

samples must be increased, relative to baseline sampling, to improve precision of model fit (e.g., See and Holmes, 2015). If the estimate of process error is less than observation error, then fewer samples are needed to reach the same target precision of model fit, which reduces monitoring costs. Reducing monitoring costs through fewer samples is especially valuable when using traditional sampling techniques (e.g., trawl surveys) that are associated with higher costs per sample than remote sensing data such as active acoustics used in the case study.

The pattern and structure of environmental variables included in the final version of each candidate model provides insight into important predictors of nekton density and aggregation. Consistent selection of day, 24-h Fourier series, and tidal range as covariates among almost all candidate models reduces the uncertainty of the importance of these variables as environmental predictors of nekton density (Burnham and Anderson, 2002; Johnson and Omland, 2004). The inclusion of day as a predictor of nekton density infers a trend over time. The GA(M)M results suggest that this trend is slightly concave, but the greater interpolation accuracy of the SSMs suggest that the data are not strongly nonlinear, and that a linear trend within a stochastic model is a more appropriate representation of the data. The synthesis of these results is vital given that environmental predictors in baseline models and their relationship (i.e., size and shape) to the dependent variable are used to identify and understand potential effects of development on the ecosystem (Treweek, 1996), and in the design of sampling resolutions and data collection methods in monitoring programs (Boehlert et al., 2013; Klure et al., 2012; McCann, 2012).

The model evaluation provides a baseline characterization of ecological indicators for MRE environmental monitoring, with the approach and results being applicable for reducing uncertainty in the analysis of ecological indicator data used for any environmental management program. For example, metric data derived from acoustic monitoring enable an effective assessment of fish health indicators (Trenkel et al., 2011) for population assessments (Jennings, 2005) within Ecosystem Based Fishery Management (EBFM) (Large et al., 2013; Trenkel et al., 2011). Recommended models are also applicable for the characterization of any ecological indicators that use metrics with similar data properties as the case study. For example, the RF and SSM combination recommended for characterizing nekton density is applicable for any temporally continuous, normally distributed metric data. The development of best practices for the characterization of ecological indicator data is invaluable for any monitoring program, because standardizing monitoring methods reduces uncertainty in the assessment of environmental change, and provides comparable data across time and monitoring sites to produce the most efficient environmental monitoring programs (Froján et al., 2016).

5. Conclusion

This study was motivated by the absence of model evaluations capable of characterizing MRE baseline monitoring data. Including all primary classes of regression models provided a palette of candidate models that could be used to characterize normal and non-normal data. The recommended Random Forest and SSMs have not been commonly used in MRE monitoring studies. The standardization of MRE monitoring, including the choice of analytic model, is predicted to reduce cost and uncertainty in MRE permitting in the United States (Dubbs et al., 2013) and consenting in the United Kingdom.

Assumptions were required to ensure a comprehensive and generalizable model evaluation, and best practice recommendations for analyzing baseline MRE ecological indicator data. The data used in the case study was assumed representative of MRE site baseline data. Models used in the evaluation were assumed to be representative of regression models commonly used in ecological monitoring studies. Mechanistic or Bayesian models were not used to characterize baseline data, but could be evaluated using the same approach. A quantitative comparison of parameter estimates and statistical significance values in top performing parametric models may advance the understanding of model accuracy and baseline characterization.

This study used an evaluation to recommend statistical models capable of characterizing baseline conditions of ecological indicators in environmental monitoring programs. There is an additional need to accurately detect change relative to baseline conditions during MRE operations. To guarantee consistent and comparable results in baseline and operational monitoring, the same techniques should be used during both phases of MRE site development. Therefore, models used for baseline characterization must also be able to detect and forecast change in monitoring variables. An additional evaluation of model ability to detect change is needed to complete a best practice procedure for analyzing Marine Renewable Energy environmental monitoring data.

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Appendix A. Glossary of defined abbreviations

Table A1
Abbreviated terms and the associated definitions listed by order of occurrence.

Order of Occurrence	Abbreviation	Defined Term
1	MRE	Marine Renewable Energy Company
2	ORPC	Ocean Renewable Power Company
3	GL(M)Ms	Genearlized Linear (Mixed) Models
4	GA(M)Ms	Generalized Additive (Mixed) Models
5	Sv	mean volume backscattering strength
6	AI	aggregation index
7	GLS	Generalized Least Squares
8	BACI	Before-After Control-Impact
9	ANOVA	analysis of variance
10	Reg-(AR)(MA)	Regression-(Autoregressive) (Moving Average)
11	Reg-ARMA-GARCH	Regression-Autoregressive Moving Average-Generalized Autoregressive Conditional Heteroskedasticity
12	SSM	State-Space Model
13	SSM-P	State-Space Model-Process (version of SSM with estimated high process error)
14	SSM-M	State-Space Model-Measurement (version of SSM with estimated high measurement error)
15	RF	Random Forest
16	SVR	Support Vector Regression
17	SVM	Support Vector Machine
18	SVR-L	Support Vector Regression-Linear (version of SVR that uses a linear kernel)
19	SVR-RBF	Support Vector Regression-Radial Basis Function (version of SVR that uses a radial basis function kernel)
20	CV	cross-validation
21	RMSE	Root Mean Squared Error
22	GR	Generalized Regression
23	NP	Nonparametric
24	ACF	Autocorrelation Function
25	mtry	Number of predictor variables in a Random Forest regression
26	rRMSE	relative Root Mean Squared Error
27	EDF	Estimated Degrees of Freedom
28	EBFM	Ecosystem Based Fishery Management

Appendix B. : Detailed model methods

Table B1
Summary of candidate model parameterization.

Model	Parameterization	R function/package	References
Linear	–	lm/stats (v.3.1.2)	–
GLS	–	gls/nlme (3.1.118)	–
GLM	Gamma response with identity link function	glm/stats (v.3.1.2)	Polgreen and Brooks (2012)
GLMM	Random intercept = 24 h count index	glmmPQL/MASS (v.7.3.35)	Pinheiro (2000)
GAM	24 h count index = cyclic cubic spline All other environmental covariates = thin-plate splines with shrinkage* All interaction terms = tensor product interaction	gam/mgcv (v.1.8.3)	Wood (2006, 2015)
GAMM	Identical to GAM Maximum iterations of optimization = 1000†	gamm/mgcv (v.1.8.3)	Wood (2006, 2015)
Reg-ARMA	Fitting method = Maximum Likelihood	Arima/forecast (v.6.2)	Hyndman (2015)
Reg-ARMA-GARCH	Model = 'sGarch' (standard GARCH) Skewed-student-t response (non-normal data) Parameter estimation solver = "hybrid"	ugarchfit/rugarch (v.1.3.6)	Hu and Kercheval (2008), Ghalanos (2015)
SSM-M	B = "unconstrained" u = "unconstrained" Q = 0.1658484 (normal), 4.893103e-05 (non-normal) Initial state set at time t = 1 Maximum iterations of optimization = 10000	MARSS/MARSS (v.3.9)	Holmes et al. (2014)
SSM-P	B = "unconstrained" u = "unconstrained" R = 0.1658484 (normal), 4.893103e-05 (non-normal) Initial state set at time t = 1 Maximum iterations of optimization = 10000	MARSS/MARSS (v.3.9)	Holmes et al. (2014)
RF	Ntree = 2500 (normal), 500 (non-normal)	randomForest/randomForest (v.4.6.10)	Liaw and Wiener (2002)
SVR-L	C = 0.0104 (normal), 2.56 (non-normal)	svm/e1071 (v.1.6.4)	Berk (2008); Hsu et al. (2010)
SVR-RBF	C = 1.25 (normal), 2.11 (non-normal) Gamma = 0.402 (normal), 0.0957 (non-normal)	svm/e1071 (v.1.6.4)	Berk (2008); Hsu et al. (2010)

Note: The parameterization of the error distribution in the GLM model was applied to the GLMM, GAM, and GAMM model for the non-normal Aggregation Index data.

* If the estimated degrees of freedom of smoother terms was near 1 then the smooth was replaced with a parametric term and the results from the 10-fold CV model selection process were re-calculated.

† See supplemental code for exact specification of GAMM iterations. If model parameterization is not specified the defaults in each R package were used to fit models.

1. Candidate model equations and definition of terms

1. Linear Regression

$$y = a + bx + \varepsilon,\ \varepsilon \sim Normal(0, \sigma^2) \quad \text{(eq.B.1)}$$

The intercept term is α, b is the estimated parameter term, x is the predictor variable, ε is the error term, and σ^2 is the variance of the error distribution.

2. Generalized Least Squares (GLS)

$$y = a + bx + \varepsilon,\ \varepsilon \sim Normal(0, \sigma^2 V) \quad \text{(eq.B.2)}$$

The GLS model is similar to the linear regression model, but the V term represents a matrix that accounts for autocorrelation in the residual correlation structure.

3. Generalized Linear Model (GLM)

$$g(\mu) = a + bx + \varepsilon,\ \mu = \mathrm{E}(y) \quad \text{(eq.B.3)}$$

$g()$ is the link function, which relates the linear predictor to the expected value (μ) of the exponential family distribution function.

4. Generalized Linear Mixed Model (GLMM)

$$g(\mu) = a + X_i B + Z_i b_i + a_i + e_i,\ \mu = \mathrm{E}(yi) \quad \text{(eq.B.4)}$$

$X_i B$ represents the main effects in the GLM equation. X_i is the design matrix for the predictor variables, and B is the matrix of predictor variables. $Z_i b_i$ represents the random effects component of a GLMM. Z_i is the design matrix for the random effects, and b_i is the subject, i, specific effect (or random effect). a_i is the random intercept.

5. Generalized Additive (Mixed) Model GA(M)M

$$g(\mu) = a + bx + f(x) + \varepsilon,\ \mu = E(y) \quad \text{(eq.B.5)}$$

$f()$ is a smooth function. The GAMM can be written similarly to the GLMM with the inclusion of smooth functions (cf. Lin and Zhang, 1999; Wood 2006).

6. Regression-Autoregressive-Moving-Average (Reg-ARMA) Model

$$y_t = a + b_1 x_{1t} + \ldots b_p x_{pt} + n_t \quad \text{(eq.B.6)}$$

$$n_t = b_1 n_{t-1} + \ldots b_p n_{t-p} + e_t + \theta_1 e_{t-1} + \ldots + \theta_q e_{t-q};\ e_t \sim Normal(0, \sigma)$$

n_t is the error remaining from the linear regression model. b_1-b_p are parameters multiplied to the lagged error terms. $\theta_1 - \theta_q$ are parameters multiplied to the moving-average components of the ARMA model.

7. Reg-ARMA-Generalized-Autoregressive-Conditional-Heteroskedasticity- Autoregressive-Moving-Average (Reg-ARMA-GARCH) Model

A Reg-ARMA-GARCH model is similar to a Reg-ARMA model with the addition of modeled residual variance:

$$\sigma_t^2 = w + \alpha_1 \varepsilon_{t-1}^2 + \ldots + \alpha_q \varepsilon_{t-q}^2 + \beta_1 \sigma_{t-1}^2 + \ldots + \beta_p \sigma_{t-p}^2 \quad \text{(eq.B.7)}$$

σ_t^2 denotes the conditional variance, w is the intercept, α_1-α_q and β_1-β_p are parameters multiplied to the lagged residuals and conditional variance terms.

8. Multivariate-Autoregressive-State-Space (MARSS) Model

$$\text{Process equation: } x_t = B_t x_{t-1} + u_t + C_t c_t + w_t,\ w_t \sim MVN(0, Q_t) \quad \text{(eq.B.8)}$$

$$\text{Observation equation: } y_t = x_t + D_t d_t + v_t,\ v_t \sim MVN(0, R_t)$$

The process model contains a density-dependent parameter (B_t), a mean level parameter (u_t), independent parameters (C_t) multiplied to predictor variables (c_t), and error (w_t) that is normally distributed with variance Q_t. The observation model also includes independent covariates (D_t), predictor variables (d_t), and error (v_t) that is normally distributed with variance R_t (cf. Holmes et al., 2014).

9. Random Forest (RF) Algorithm

The Random Forest is a collection of n_{trees} that are random bootstrap subsamples of the training data. Samples not selected for model training are used as out-of-sample data to calculate error of the model. Within each tree, a randomly chosen subsample of the predictor variables (m_{try}) are used to fit the data. The predictor variable and split of the data based on the predictor variable that produce the best estimate of the dependent variable based on Mean-Squared-Error (MSE) are calculated. This process is repeated until 5 data points remain in each node of the tree. The final predicted values are based on the average of the individual tree predictions.

10. Support Vector Regression (SVR)

If the linear regression function is denoted as$y_i = wx_i + b$, in which b is the intercept term, w is the estimated parameter term, x_i is the predictor variable, then the minimization attempted by an SVR is denoted as:

$$Q = \frac{1}{2}||w||^2 + C\sum_{i=1}^{l}(\varepsilon_i + \varepsilon_i^*) \quad \text{(eq.B.9)}$$

Subject to $\{y_i - wx_i - b \le \varepsilon + E_i;\ wx_i + b - y_i \le \varepsilon + E_i^*;\ E_i, E_i^* \ge 0\}$ (Vapnik, 1995)

In this equation C is the "cost" constant that represents the value up to which deviations from Ɛ, a predefined value of residual error, are acceptable. E and E^* are error values above (E) and below (E^*) Ɛ that allow for the optimization problem to be feasible (Smola and Schölkopf, 2004; Thissen et al., 2003).

The linear kernel is calculated as:

$$K(x_i, x_j) = (x_i^T x_j) \quad \text{(eq.B.10)}$$

The Radial Basis Function kernel is calculated as

$$K(x_i, x_j) = \exp(-\gamma||x_i - x_j||^2),\ \gamma > 0 \quad \text{(eq.B.11)}$$

x_i and x_j are two input vectors, and the gamma value (γ) controls the width of the kernel (Thissen et al., 2003).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.07.015.

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