

Temporal resolutions in species distribution models of highly mobile marine animals: recommendations for ecologists and managers

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Abstract

While ecologists have long recognized the influence of spatial resolution on species distribution models (SDMs), they have given relatively little attention to the influence of temporal resolution. Considering temporal resolutions is critical in distribution modelling of highly mobile marine animals, as they interact with dynamic oceanographic processes that vary at time scales from seconds to decades. We guide ecologists in selecting temporal resolutions that best match ecological questions and ecosystems, and managers in applying these models. We group the temporal resolutions of environmental variables used in SDMs into three classes: instantaneous, contemporaneous and climatological. We posit that animal associations with fine-scale and ephemeral features are best modelled with instantaneous covariates. Associations with large-scale and persistent oceanographic features are best modelled with climatological covariates. Associations with mesoscale features are best modelled with instantaneous or contemporaneous covariates if ephemeral processes are present or inter-annual variability occurs, and climatological covariates if seasonal processes dominate and inter-annual variability is weak.

Introduction

Highly mobile marine animals such as marine mammals, seabirds, sea turtles and fish are unevenly distributed in the ocean. Ecologists have long sought to understand and predict their patterns of distributions, particularly for commercially valuable species subject to exploitation (Lehodey, Bertignac, Hampton, Lewis, & Picaut, 1997) and for protected species vulnerable to incidental harm (Reilly, 1990). They often employ species distribution models (SDMs) that statistically relate distribution patterns to environmental conditions by linking animal observations to environmental variables. SDMs have been successfully used to examine many ecological, management and conservation questions (Elith & Leathwick, 2009). In particular, they have been widely used to explain and predict distribution patterns of highly mobile marine animals in a variety of ecosystems (Benson et al., 2011; Forney, Becker, Foley, Barlow, & Oleson, 2015; Gregr, Baumgartner, Laidre, & Palacios, 2013; Hartog, Hobday, Matear, & Feng, 2011; Mannocci et al., 2014).

It has become apparent that the hierarchical structure of processes in the marine environment drives the distribution and movement patterns of marine animals at multiple spatiotemporal scales (Benoit-Bird, Battaile, Nordstrom, & Trites, 2013; Fauchald, Erikstad, & Skarsfjord, 2000; Fauchald & Tveraa, 2006; Fritz, Said, & Weimerskirch, 2003; Pinaud & Weimerskirch, 2005) (Figure 1). At fine scales, animals track ephemeral prey patches that extend over tens of meters to satisfy their energy requirements (Goldbogen et al., 2008; Heaslip, Iverson, Bowen, & James, 2012). At intermediate scales, animals associate with ephemeral and seasonally-occurring oceanographic features such as eddies and fronts that extend over tens to hundreds of kilometres and represent suitable foraging habitats (Benson et al., 2011; Hobday & Hartog, 2014; Tew Kai & Marsac, 2010). At broad scales, animals associate with persistent water masses and current systems that extend over thousands of kilometres and delimit their geographic ranges or migration routes (Jaquet, Whitehead, & Lewis, 1996; Reygondeau et al., 2012; Shillinger et al., 2008). Thus, the distributions of highly mobile marine animals appear determined by both short-term ocean variability and persistent patterns of longer-term ocean climate.

Researchers use a variety of methods to obtain synoptic data on marine animal distributions and the marine environment at a wide range of spatial and temporal extents (Panel 1, Figure 2). Data collected over large extents are often characterized by coarser resolutions or “grain sizes”

(e.g., global grids of aggregated fisheries catch records or of *in situ* oceanographic observations) than data collected over small extents (e.g., echosounder backscatter swaths of potential prey biomass). An underlying assumption of SDMs is that environmental covariates are proxies for mechanistic drivers of animal distributions (Palacios, Baumgartner, Laidre, & Gregr, 2013). Fine-scale drivers of animal distributions, e.g., the spatial distribution of prey patches, are best elucidated with SDMs that incorporate environmental covariates at fine temporal and spatial resolutions (Torres, Read, & Halpin, 2008). SDMs are also increasingly used to inform management and enhance conservation, often by creating gridded maps of predicted species distributions (Forney et al., 2015; Hartog et al., 2011; Torres et al., 2013). This process relies on gridded environmental products available for use in the models (e.g., Tyberghein et al., 2012), and their resolutions can influence the specification of temporal and spatial resolution in the models. Effective models require data at adequate resolutions to reveal patterns at the scale of the ecological or management question without imposing unnecessary complexity.

Ecological modellers have long recognized the influence of spatial scale on marine animal interactions with the environment, and have explicitly studied the effects of spatial resolution on the outcomes of SDMs (Becker et al., 2010; Jaquet et al., 1996; Redfern, Barlow, Ballance, Gerrodette, & Becker, 2008). However, relatively few modellers have studied the influence of temporal resolution on SDMs (Becker et al., 2010; Mannocci et al., 2014; Roberts et al., 2016; Scales et al., 2017). To do so, modellers must evaluate complex tradeoffs. For example, is it better to obtain a desired environmental covariate from daily satellite images that show dynamic features in detail but suffer substantial data gaps due to clouds, or to use multi-day composite images that “fill in” the missing data but “blur out” dynamic features? Investigating the consequences of these decisions is often tedious, time-consuming, and usually secondary to the modeller’s main research objective. Faced with this difficulty, many modellers simply select a coarse temporal resolution that is convenient, without thoroughly considering whether it can reveal patterns at the temporal scale of the ecological question. Others have attempted to sidestep the problem by using the highest resolution available without considering whether the complexity and processing cost is necessary to answer the ecological question. In fact, even when high temporal resolution data are available and processing cost is not a factor, coarse temporal resolutions may be preferred to answer certain ecological questions. Mismatches in either direction can yield sub-optimal results.

We propose that the best models—those that effectively describe or predict marine animal distribution patterns at a desired temporal scale without utilizing unnecessarily high resolution data—are obtained when the temporal characteristics of the animals’ distribution and environmental data sufficiently match the scale of the ecological question and the variability of the ecosystem. First, we identify three classes of temporal resolutions of dynamic environmental data that are commonly used for covariates in marine animal SDMs. Next, we examine how the scale of the ecological question informs the selection of temporal resolutions of environmental and animal distribution data. We then investigate the implications of ecosystem variability on the choice of contemporaneous or climatological covariates in SDMs. We conclude with practical recommendations for the modelling community and discuss the relevance for the management of highly mobile marine animals.

Temporal resolutions of environmental covariates

We propose to group the temporal resolutions of environmental covariates used in SDMs into three classes, which we term *instantaneous*, *contemporaneous* and *climatological*. Although the specification of these classes is primarily a matter of convenience (rather than a systematic and consistent attempt to fully capture the scale of all relevant processes), in our collective experience they represent the most practical approach for incorporating environmental covariates into SDMs while preserving meaningful ecological scales. We define the three classes below and illustrate them by analysing a time series (1985-2014) of sea surface temperature (SST) data collected at a stationary buoy (Figure 3).

Instantaneous covariates represent the state of the environment in close proximity to the animal (i.e., within its direct perceptual range) at the moment it was observed. They are often collected at high frequency (typically seconds to hours) and in tight synchrony with the animal’s observation via *in situ* devices. For example, echosounders are used to obtain information on instantaneous prey distribution in the vicinity of foraging individuals (Goldbogen et al., 2008). In Figure 3a, the instantaneous resolution is illustrated by SST observed hourly across a focal year.

Contemporaneous covariates represent the state of the environment in a time window (typically days to months) around the animal’s observation that smooths out, to some degree, the conditions experienced by the animal during this window. Contemporaneous covariates are often

extracted from time series of satellite images, ocean model outputs, or *in situ* measurements. In Figure 3a, the contemporaneous resolution is illustrated by 5-day averages of the hourly SST observations from the focal year.

Climatological covariates represent the long-term (i.e., typical) state of the environment at the animal's location during the part of the year it was observed. Climatological datasets divide the calendar year into shorter time slices such as days, weeks, months or seasons, and for each slice, apply a summary statistic (e.g., mean, variance, frequency or probability) to many (often at least 10) years of observations made during that slice to estimate the long-term state (Figure 3b). As a result, climatologies smooth out inter-annual variability while maintaining intra-annual (e.g., seasonal) variability and preserving spatial gradients. Climatologies are often derived from satellite images (Tyberghein et al., 2012) or summarizations of *in situ* databases (e.g., the World Ocean Atlas (Levitus et al., 2013) and the CSIRO Atlas of Regional Seas (Ridgway, Dunn, & Wilkin, 2002)). In Figure 3a, the climatological resolution is illustrated by 5-day averages from 30 years of the hourly SST observations.

Scale of the ecological question

We examine how the scale of the ecological question informs the selection of temporal resolutions of environmental and animal distribution data for incorporation into SDMs from a practical standpoint. An exhaustive description of oceanographic processes influencing animal distributions at all scales from a theoretical standpoint is beyond the scope of the present paper. Readers interested in a more extensive treatment are referred to papers including those by Ballance, Pitman, & Fiedler (2006), Haury, McGowan, & Wiebe (1978), Hazen, Suryan, et al. (2013), and Hunt & Schneider (1987).

Fine-scale ecological questions

Fine-scale ecological studies seek to describe the associations of individuals with oceanographic processes extending up to a few kilometres and a few hours, and to understand the mechanisms underpinning them. Within the hierarchy of spatial scales (Figure 1), at the finest scales, highly mobile marine animals are thought to search and select prey within patches (Fauchald et al., 2000). Fine-scale ecological questions include examining the distributions of marine animals in relation to aggregations of prey (Benoit-Bird & Au, 2003; Josse, Bach, &

Dagorn, 1998; Tremblay, Thiebault, Mullers, & Pistorius, 2014), distribution of predators indicating the presence of prey (Tremblay et al., 2014), and fine-scale hydrodynamic features such as tidally-driven island wakes (Bailey & Thompson, 2010; Johnston & Read, 2007) and Langmuir circulation cells (Ladd, Jahncke, Hunt, Coyle, & Stabeno, 2005). Because these associations are ephemeral, involving short-duration behaviours such as feeding events, they are best elucidated with instantaneous covariates collected concomitantly with individuals' observations (Figure 4). Instantaneous covariates are expected to describe phenomena directly sensed by individuals (e.g., prey aggregations detected by vision). High-resolution telemetry tracks coupled with covariates simultaneously recorded from animal-borne instruments, autonomous underwater vehicles, echosounders and other *in situ* devices are well suited to address fine-scale ecological questions. For example, Goldbogen et al. (2008) shed light on predator-prey mechanisms underpinning the fine-scale distribution of humpback whales (*Megaptera novaeangliae*) by examining dive profiles of individuals equipped with high-resolution digital tags in relation to the instantaneous density of krill in the water column measured by a boat-borne echosounder.

While fine-scale correlative and process-based studies have helped identify animal associations with instantaneous hydrodynamic features and prey aggregations (see previous references), fine-scale distribution modelling studies remain rare. Generally, high-resolution data are better suited to derive functional relationships valuable for validating a theory or mechanism, rather than for the purpose of distribution modelling. For example, Palacios et al. (2013) proposed an approach that relies on fine-scale process studies to identify key ecological relationships that can inform SDMs at coarser scales. The practical difficulty of obtaining sufficient instantaneous data on both individual distributions and hydrodynamic or biological features constitutes a great challenge when developing fine-scale SDMs. A fine-scale distribution modelling study was conducted for bottlenose dolphin (*Tursiops truncatus*) in Florida Bay, U.S.A. (Torres et al., 2008). The authors found that a model based on environmental covariates indirectly related to dolphin distribution (e.g., chlorophyll-*a* concentration) achieved a higher predictive capacity than a model based on prey data, probably due to the insufficient intensity of prey sampling in this heterogeneous coastal environment.

Mesoscale ecological questions

Mesoscale ecological studies seek to understand associations of individuals or populations with processes extending over tens to hundreds of kilometres and persisting hours to months. Mesoscale ecological questions include elucidating movements and distributions of marine animals in relation to eddies, fronts and current meanders (Becker et al., 2010; Benson et al., 2011; Hobday & Hartog, 2014; Tew Kai & Marsac, 2010). These mesoscale features are presumably used by migratory animals to find biologically rich areas in the open ocean within which to concentrate their foraging explorations. For example, Benson et al. (2011) related the movements of Indo-Pacific leatherback sea turtles (*Dermochelys coriacea*) equipped with satellite tags to contemporaneous chlorophyll-*a* concentration and sea surface height variation derived from remote sensing. Area-restricted search behaviour exhibited by individuals near mesoscale eddies, meanders, and frontal zones indicated active foraging. The authors suggested that management strategies prioritize bycatch reduction in these important foraging areas.

Mesoscale associations may be modelled using instantaneous, contemporaneous or climatological covariates (Figure 4). If animals associate with ephemeral mesoscale features such as tidal mixing fronts and plume fronts that persist up to a few hours (Bailey & Thompson, 2010; Ladd et al., 2005; Zamon, Phillips, & Guy, 2014), instantaneous covariates may be used. In practice, instantaneous environmental data (i.e., representing the state of the environment within the animal's perceptual range) rarely span the full spatial extent of mesoscale features. Indeed, synoptic sampling of animal distributions and the environment can either span the full habitat at the expense of not resolving finer-scale processes, or be conducted at a high resolution at the expense of not encompassing the full habitat. Mesoscale associations are most commonly modelled with contemporaneous covariates (Becker et al., 2010; Hartog et al., 2011; Murray & Orphanides, 2013; Weimerskirch, Corre, Jaquemet, Potier, & Marsac, 2004) or climatological covariates (Humphries, Huettmann, Nevitt, Deal, & Atkinson, 2012; Mannocci et al., 2014; Roberts et al., 2016). If the associations are seasonal and not subject to inter-annual variability—e.g., associations with an oceanographic feature that forms at the same time and location every year—they may be adequately captured by seasonal climatologies. Contemporaneous covariates may also be used but sometimes offer no added benefit for their substantial added cost. For example, Roberts et al. (2016) found that daily contemporaneous covariates did not perform better

than 8-day climatological covariates for modelling the density of pilot whales off the United States' east coast. The climatological model utilized 46 satellite images, vs. over 8000 for the contemporaneous model. Even when processing cost is not a factor, there are still situations where climatological covariates may be preferred. For example, animals migrating to and from specific locations at specific times likely base their “decisions” on migration (e.g., on migration timing) on data they integrate across long periods of time. However, if animals associate with ephemeral phenomena, or the associations are subject to inter-annual variability—e.g., sensitive to the El Niño Southern Oscillation (ENSO)—they are best modelled with contemporaneous covariates. We discuss the implications of ecosystem variability on the choice of climatological or contemporaneous covariates in SDMs below.

Macroscale ecological questions

Macroscale ecological studies seek to understand associations of individuals, populations or species with oceanographic processes and features spanning thousands of kilometres and persisting for many years. Macroscale ecological questions include investigating migration routes and geographic ranges of marine animals in relation to oceanic gyres, boundary currents and biogeographic provinces (Hyrenbach, Veit, Weimerskirch, Metzl, & Hunt, 2007; Jaquet et al., 1996; Reygondeau et al., 2012; Shillinger et al., 2008). Macroscale questions may be framed in the context of macroecology, a branch of ecology that seeks to elucidate natural laws and principles which underlie the nature, structure and functioning of ecological systems (Kent, 2005). Macroscale studies are concerned with associations reflecting processes that have taken place over evolutionary time scales and climatological covariates serve well for this purpose. They usually draw on databases of animal sightings, fisheries or whaling catches, or other sources that span long periods of time (Gregg, 2011; Hann, Smith, & Torres, 2016; Monsarrat et al., 2015; Reygondeau et al., 2012; Torres et al., 2013).

Macroscale associations are best modelled with climatological covariates (Figure 4). For example, Torres et al. (2013) modelled the seasonal distribution of southern right whales (*Eubalaena australis*) derived from historical catches in relation to climatological oceanographic covariates extracted from the CSIRO Atlas of Regional Seas and from remote sensing (Ridgway et al., 2002) to characterize the whales' range in the Australasian region. By comparing the

predicted habitat suitability maps with maps of shipping traffic, the authors were able to identify areas of increased risk of collision where mitigation measures could be implemented.

Variability of the study ecosystem

A well-posed ecological question—whether it is asked by modellers or resource managers—should take ecosystem variability into account. A recurring problem, particularly for studies of mesoscale associations, is whether contemporaneous covariates are necessary or climatological covariates are sufficient to model these associations. Failing to choose contemporaneous covariates when they are necessary risks missing important patterns. Choosing contemporaneous covariates when climatological covariates better match the ecological question incurs unnecessary complexity. To illustrate these situations, we explored the temporal variability of SST in two ecosystems. We applied wavelet analysis—a frequency decomposition technique (Torrence & Compo, 1998)—to SST measurements recorded hourly at stationary buoys in each ecosystem to produce three-dimensional diagrams (Year x Period x Power) that highlight the periods at which dominant variability occurred (see Appendix S1 in Supporting Information for methodological details). We discuss the implications of ecosystem variability on the choice of contemporaneous or climatological covariates.

The California Current: an inter-annually variable ecosystem

The California Current is an eastern boundary current that flows southward along the west coast of North America. Productivity in this ecosystem is largely driven by coastal upwelling that varies seasonally and inter-annually, and by localized wind events occurring irregularly at approximately a weekly time scale (Bograd et al., 2009). Wavelet analyses of SST measurements collected by a buoy near Point Arena (39.235°N 123.974°W), California, from 1985-2014 revealed these patterns of variability (Figure 5). During the years examined, significant periodicities were observed at daily, annual, and multi-annual scales (Figure 5d). At the annual scale, SST showed a moderate seasonal cycle with a minimum in the spring and a maximum in the fall (Figure 5b), but considerable variation among years (Figure 5a). At the multi-annual scale, SST varied at periods of 4-8 years in synchrony with ENSO (Figure 5c, 5d). Although weekly-scale episodic events were occasionally observed, this time scale did not exhibit statistically-significant periodicity when aggregated across the study years (Figure 5d).

The strong inter-annual variations in the physical environment of this ecosystem drive corresponding inter-annual variations in biological activity. In years of strong El Niño, coastal upwelling is delayed and weaker, leading to anomalously warm water and depressed primary production (Bograd et al., 2009). Altered primary production in turn affects the distribution, abundance and demographics of zooplankton (Sydeman et al., 2006), pelagic nekton (e.g., sardines, anchovies, hake, and jack mackerel) (Brodeur et al., 2006) and top predators (Adams, Takekawa, Carter, & Yee, 2010; Boustany, Matteson, Castleton, Farwell, & Block, 2010; Forney, Ferguson, Becker, & Fiedler, 2012; Weise, Costa, & Kudela, 2006). For example, Dall's porpoise (*Phocoenoides dalli*) were found in large numbers off central California in years of strong upwelling and cold waters but shifted their distribution farther north in years of weak upwelling and warm waters (Forney et al., 2012). Similarly, Pacific bluefin tuna (*Thunnus orientalis*) exhibited contrasting latitudinal movements in different years that were correlated with peaks in upwelling-induced primary productivity (Boustany et al., 2010). Pinnipeds and seabirds, which forage from a central place during the breeding season, extended their foraging movements farther offshore in years of warmer waters (Adams et al., 2010; Weise et al., 2006). For other seabird species (e.g., Cassin's auklet, *Ptychoramphus aleuticus*), anomalous oceanographic conditions resulted in the abandonment of breeding colonies and severe reproductive failures (Sydeman et al 2006).

When inter-annual variability is significant, as in the California Current, models built with climatological covariates will reflect the intra-annual (e.g., seasonal) variability but smooth out the inter-annual variations. To capture inter-annual variations in the distributions and movements of marine animals inhabiting eastern boundary current ecosystems such as the California Current, contemporaneous covariates should be used.

The Gulf of Maine: a seasonally variable and changing ecosystem

The Gulf of Maine is a highly-productive, temperate marginal sea situated on the North American continental shelf. Although inter-annual variability occurs in physical processes such as surface winds, river runoff, and hydrodynamics (Li, He, & McGillicuddy, 2014), seasonal variations are larger than inter-annual variations in this ecosystem. Wavelet analyses of SST measurements collected by a buoy 16 nautical miles east of Boston (42.346°N 70.651°W), Massachusetts, from 1985-2014 indicated significant periodicities at daily (Figure 6d) and annual

(Figures 6c, 6d) scales. At the annual scale, SST showed a pronounced seasonal cycle and little variation among years (Figures 6a, 6b). The analysis indicated no significant variations at the multi-annual scales over the studied years.

The North American continental shelf north of Cape Hatteras is part of a large-scale coastal current system that originates in the Arctic Ocean (Shearman & Lentz, 2010). This recurrently productive system provides consistent summer foraging habitat for many migratory marine animals, including Atlantic bluefin tuna (*Thunnus thynnus*) (Walli et al., 2009), leatherback sea turtles (James, Eckert, & Myers, 2005), humpback whales (Clapham et al., 1993) and striped bass (*Morone saxatilis*) (Mather, Finn, Ferry, Deegan, & Nelson, 2009). When seasonal variability in ecosystem processes dominates inter-annual variability, as in the Gulf of Maine, climatological covariates are often sufficient for modelling animal distributions, provided that climatologies partition the year into sufficiently small slices (e.g., days, weeks or months) that reflect the ecologically relevant intra-annual variability. Contemporaneous covariates are also suitable but will often increase complexity and processing cost for little added benefit (Roberts et al., 2016).

These guidelines may not hold if the ecosystem is subject to long-term disruptive trends, such as those induced by climate change. During 1875-2007, the Gulf of Maine warmed at an average rate of $0.01^{\circ}\text{C yr}^{-1}$ (Shearman & Lentz, 2010). The warming rate accelerated in recent decades, to $0.03^{\circ}\text{C yr}^{-1}$ for 1982-2013 and then to $0.23^{\circ}\text{C yr}^{-1}$ for 2004-2013, a rate faster than 99% of the global ocean in the last decade (Pershing *et al.* 2015) (the wavelet analysis we presented is designed to characterize periodic phenomena and does not detect these long-term trends). It has been proposed that this rapid warming may be why the region's spawning stock biomass of Atlantic cod (*Gadus morhua*), an overfished species, has failed to recover following a large reduction in fishing pressure (Pershing et al., 2015). These findings stress the need to consider long-term variability induced by multi-decadal oscillations or climate change, which may not be apparent in relatively short-duration time series. To account for the long-term effects of climate change on marine animal distributions, contemporaneous covariates should be used in combination with sufficiently long time series of animal occurrence.

Practical recommendations for ecologists and managers

Oceanographic processes are extremely complex and dynamic, and while fully elucidating their influence on animal distributions is a desirable goal, for the practical purpose of SDMs we acknowledge that current sampling abilities and requirements lead to imperfect models and potentially biased predictions. Nevertheless, practical recommendations are critically needed for ecologists and managers who increasingly rely on these models. These recommendations should result in improved SDMs in the future.

We posit that the temporal resolutions of covariates in SDMs should be informed by a clearly defined ecological question taking the dynamics of relevant oceanographic processes and the variability of the study ecosystem into account. When modelling ephemeral associations of individuals with fine-scale hydrodynamic features or prey aggregations that pertain to behavioural processes, instantaneous covariates should be used. When modelling persistent associations of individuals, populations or species with macroscale features and biogeographic provinces (reflecting processes that have taken place over evolutionary time scales), climatological covariates should be used. Climatological variables can be particularly valuable for modelling annual migrations of long-lived marine taxa that rely on memory and cultural processes to find predictably-productive foraging grounds (Clapham et al., 1993; Weimerskirch, Mougey, & Hindermeier, 1997). When modelling associations of individuals or populations with mesoscale features, instantaneous or contemporaneous covariates should be used when ephemeral processes are present or inter-annual variability occurs in the study ecosystem, and climatological covariates should be used when seasonal processes dominate and inter-annual variability is weak.

These recommendations notwithstanding, the reality is that many covariates are only available in climatological form (e.g., nutrient concentrations at depth). Climatologies offer practical advantages including a reduced processing cost and less missing data—the latter is especially useful when spatial predictions are needed because climatological grids offer complete coverage of the desired prediction area.

The successful management of highly mobile marine animals is grounded in SDMs that effectively predict their distributions by relating them to underlying ecological processes. SDMs developed from contemporaneous covariates are particularly relevant for adaptive or near-real time

ocean management of dynamic ecosystems (Maxwell et al., 2015). They have been used in the context of dynamic fisheries management to predict areas and time periods subject to captures of unwanted species and make recommendations (e.g., displacement of fishing effort) for their reduction (Hartog et al., 2011; Howell, Kobayashi, Parker, Balazs, & Polovina, 2008). For example in Hawai'i, a voluntary bycatch reduction measure is based on associations of loggerhead sea turtles (*Caretta caretta*) with a spatiotemporally-variable ocean current modelled with contemporaneous thermal ranges (Howell et al., 2008). SDMs developed from contemporaneous covariates are also increasingly applied to reduce the spatiotemporal overlap of human activities with protected species (e.g., shipping traffic and blue whale (*Balaenoptera musculus*) in the California Current) (Hazen et al., 2016).

SDMs developed from instantaneous covariates have a comparatively limited value for management because such models typically cover small spatial extents. In addition, the ephemeral nature of fine-scale ecological processes combined with the practical difficulty of obtaining instantaneous data confer a low predictive ability to these models. However, analyses of fine-resolution data can be applied for deriving functional relationships and for gaining insights into mechanistic parameters that can inform SDMs at coarser scales (Palacios et al., 2013).

SDMs developed from climatological covariates are relevant for static management. They have been used to predict important species habitats with a high potential for delineation of marine protected areas and implementation of mitigation measures (Mannocci, Roberts, Miller, & Halpin, 2017; Redfern et al., 2017; Torres et al., 2013). These SDMs are most appropriate in the context of area-based planning processes launched globally by intergovernmental processes such as the description of Ecologically or Biologically Significant Areas by the Convention on Biological Diversity (Bax et al., 2016).

As marine ecosystems undergo global climate change, there is an increasing need to incorporate potential shifts in the distribution of marine taxa into management plans (Cuddington et al., 2013; Silber, Lettrich, & Thomas, 2016). SDMs developed from contemporaneous covariates and sufficiently long time series of animal occurrence may be used along with global climate change scenarios to project species distributions into the future (Hartog et al., 2011; Hazen, Jorgensen, et al., 2013; Péron, Weimerskirch, & Bost, 2012). SDMs developed from climatological covariates may also be suitable for this purpose, but projections from such models should be

interpreted with great caution in ecosystems that are sensitive to long-term disruptive trends. In particular, the physiology and behaviour underlying the modelled species-habitat relationships may change under different climate regimes (Lefevre, McKenzie, & Nilsson, 2017; Myers, 1998), reducing the validity of the projections.

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Figure captions

Figure 1: Conceptual representation of the hierarchical structure of the marine environment influencing the distribution of mobile animals at multiple scales. According to the hierarchical patch theory, prey patches are nested within features of enhanced prey availability, which are themselves nested within broader systems. Figure inspired from Kotliar & Wiens (1990).

Figure 2: Conceptual space-time diagrams illustrating the synoptic sampling of (a) mobile marine animal distributions and (b) the marine environment. HRDTs: high-resolution digital tags. ABIs: animal-borne instruments. AUVs: autonomous underwater vehicles. Examples of important biological and oceanographic features with respect to marine animal distributions are superimposed on Figure 2b (the “Stommel Diagram”). 1: Prey patches and fine-scale turbulence; 2: tidal fronts and plume fronts; 3: fronts, eddies and meanders; 4: coastal upwelling; 5: gyres, boundary currents and other basin-scale features. Figure 2b was adapted from Haury et al. (1978) and Dickey, Lewis, & Chang (2006).

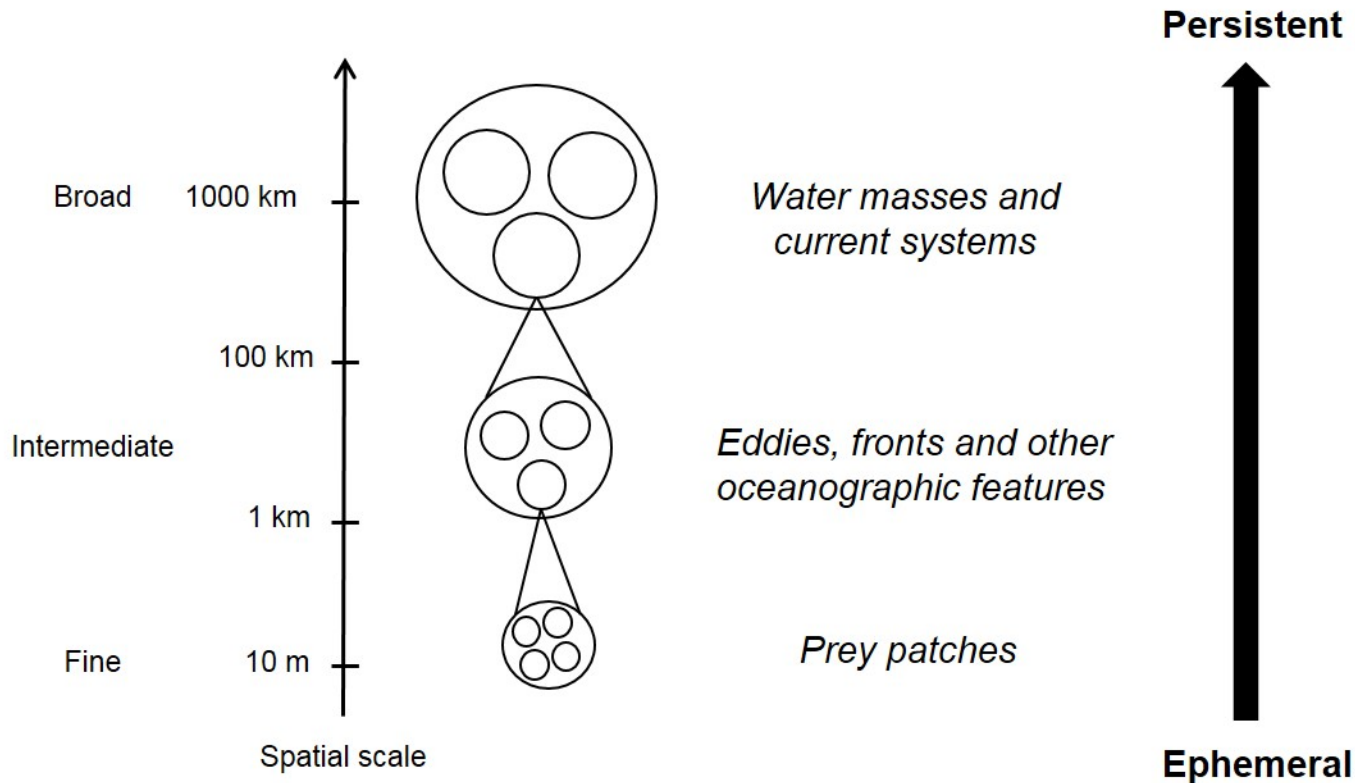
Figure 3: The three classes of temporal resolution illustrated with a time series (1985-2014) of SST data collected at a stationary buoy located 16 nautical miles off Boston (National Data Buoy Center <http://www.ndbc.noaa.gov/>, station 44013, 42.346°N 70.651°W). (a) Diagram showing SST at the instantaneous resolution (hourly data across year 2003), the contemporaneous resolution (hourly data averaged on successive 5-day windows for year 2003) and the climatological resolution (hourly data averaged on a 5-day moving window from 1985-2014). (b) Three-dimensional diagram illustrating how the climatology was derived by averaging SST on a 5-day moving window from 1985-2014 (to minimize spikes in SST).

Figure 4: Influence of the scale of the ecological question on the temporal resolution of covariates used in SDMs of highly mobile marine animals.

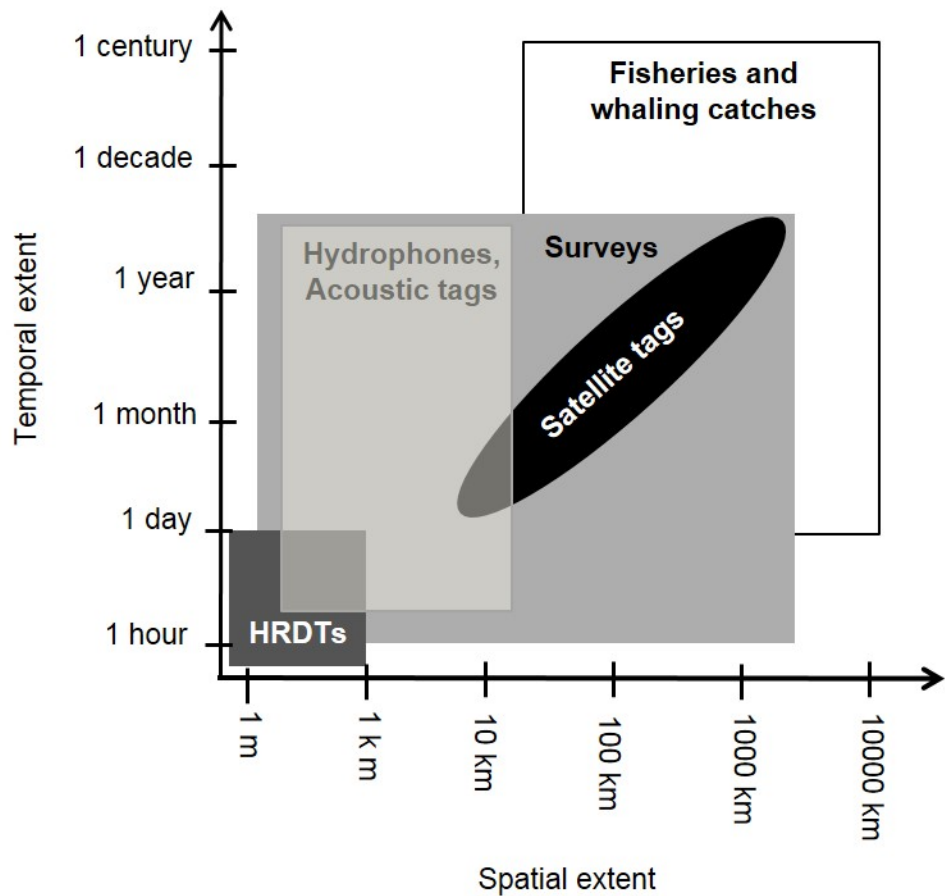
Figure 5: (a) Hourly SST recorded at the Point Arena buoy from 1985-2014 (<http://www.ndbc.noaa.gov/>, station 46014, 39.235°N 123.974°W). (b) Contemporaneous SST (hourly data averaged on successive 5-day windows for year 1991; red line) and climatological SST (hourly data averaged on a 5-day moving window from 1985-2014; black line) (c) Results of wavelet analyses displayed on a two-dimensional time-period diagram. Power has been log-transformed for visualization. Data below the cone of influence (black line) should be ignored (see

Appendix S1). (d) Results of wavelet analyses integrated over 1985-2014. The continuous black line shows power by period integrated over 1985-2014. The dashed line shows significance limit at the 95% confidence level (black line situated to the right of the blue line indicates significantly powerful periods) (see Appendix S1).

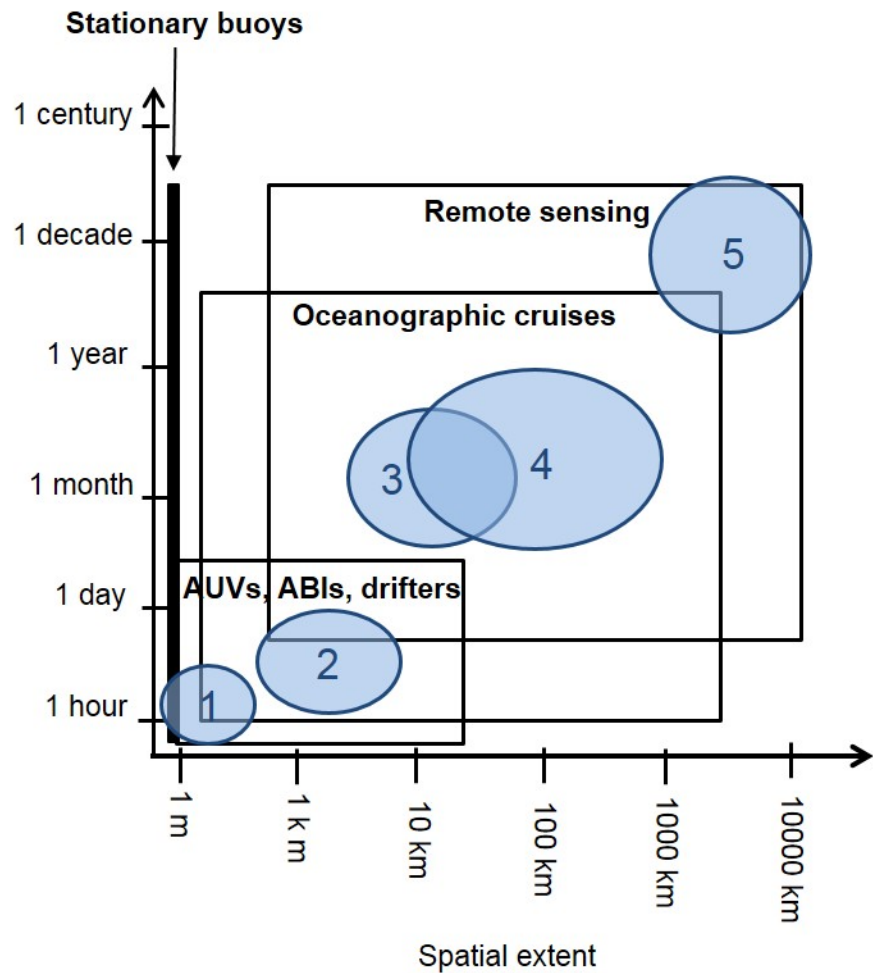
Figure 6: (a) Hourly SST recorded at the Boston buoy from 1985-2014 (<http://www.ndbc.noaa.gov/>, station 44013, 42.346°N 70.651°W). (b) Contemporaneous SST (hourly data averaged on successive 5-day windows for year 1991; red line) and climatological SST (hourly data averaged on a 5-day moving window from 1985-2014; black line). (c) Results of wavelet analyses displayed on a two-dimensional time-period diagram. Power has been log-transformed for visualization. Data below the cone of influence (black line) should be ignored (see Appendix S1). (d) Results of wavelet analyses integrated over 1985-2014. The continuous black line shows power by period integrated over 1985-2014. The dashed line shows significance limit at the 95% confidence level (black line situated to the right of the blue line indicates significantly powerful periods) (see Appendix S1).



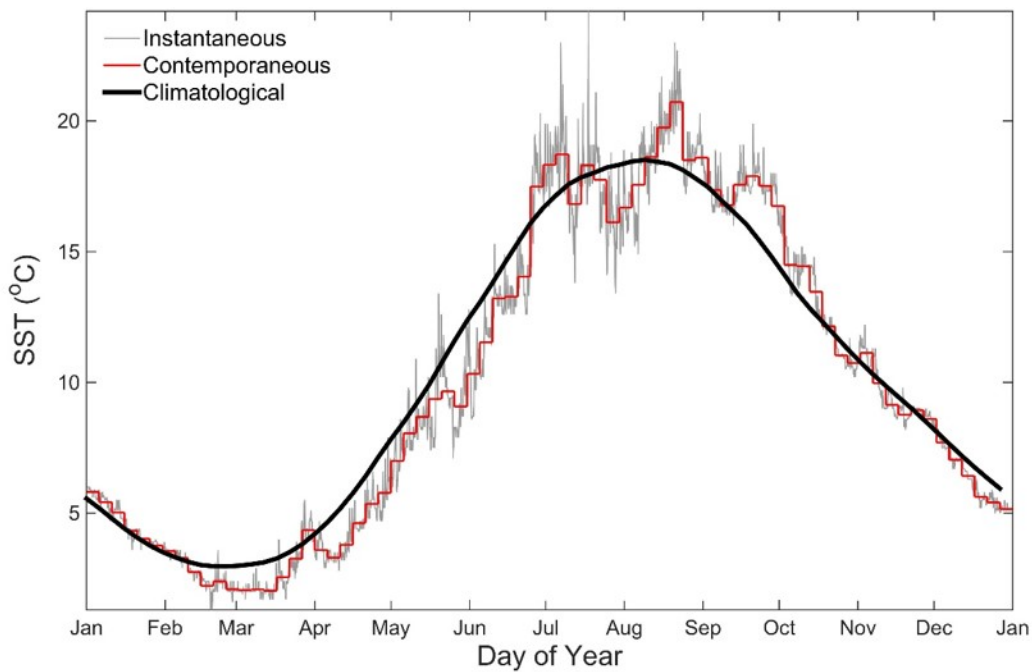
(a)



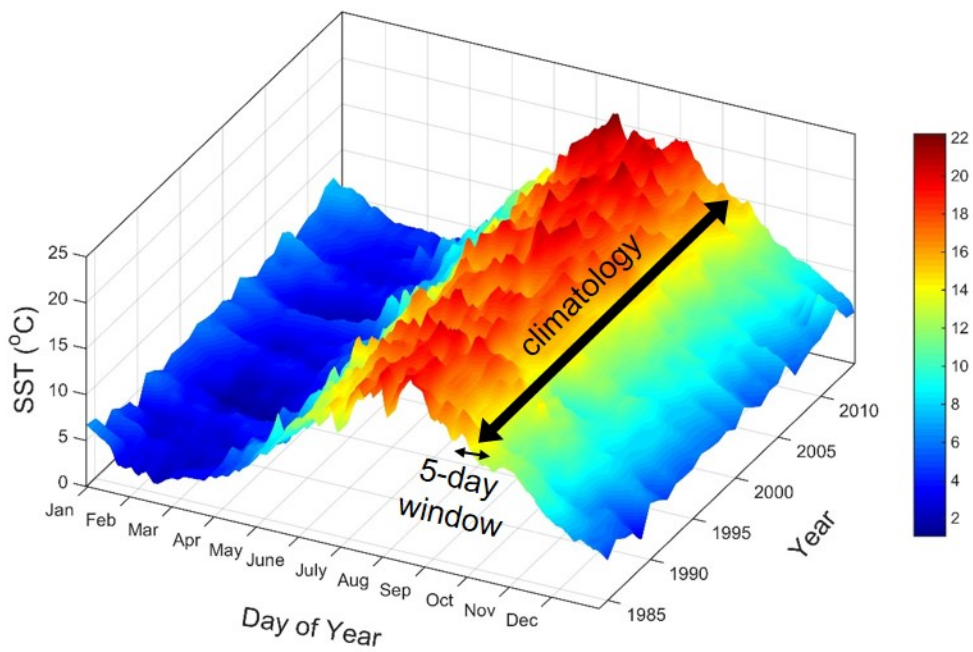
(b)



(a)



(b)



Scale of the ecological question

Behavioral
processes

Fine scale

Mesoscale

Macroscale

Evolutionary
processes

Examples of
animal distribution
data

High-resolution digital
tags, focal follows

At-sea surveys,
satellite tags

Fisheries and whaling
catches

Examples of
environmental data

Echosounders,
animal-borne instruments,
gliders

Remote sensing,
oceanographic cruises,
ocean model outputs

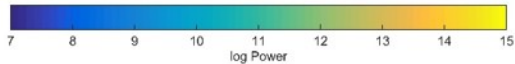
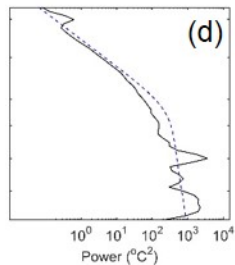
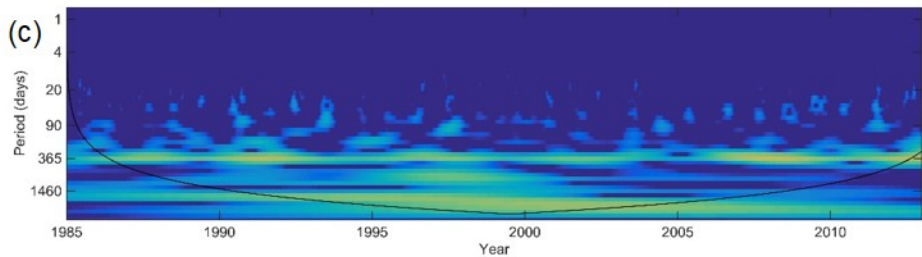
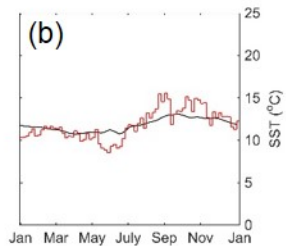
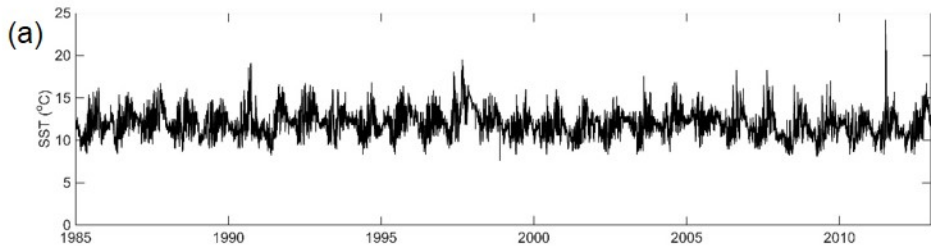
Remote sensing,
summarization of *in situ*
databases

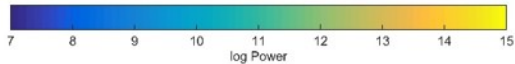
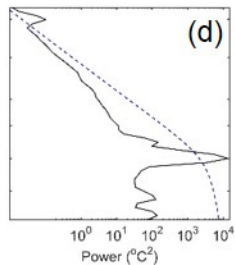
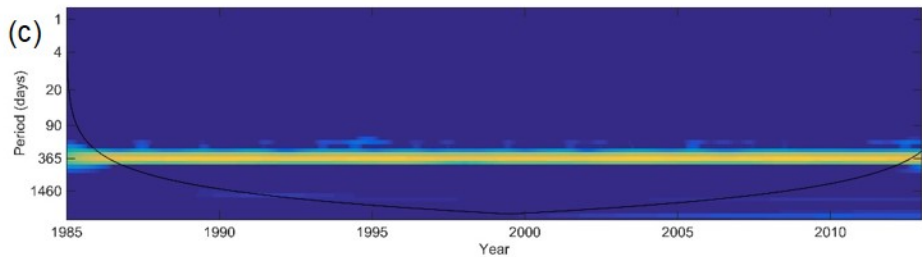
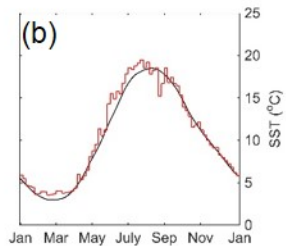
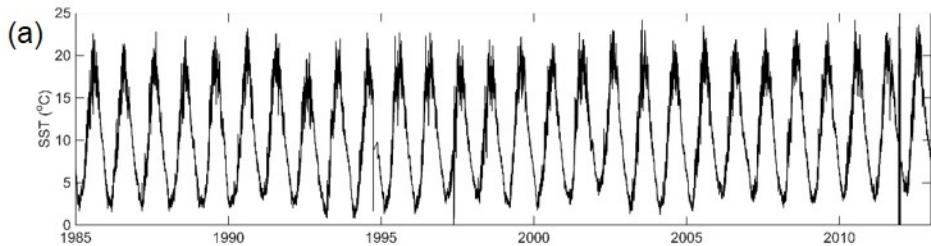
Temporal resolution of
covariates

Instantaneous

Instantaneous,
contemporaneous or
climatological

Climatological





Panel 1: Synoptic sampling of mobile marine animal distributions and their environment

Distribution data on highly mobile marine animals (e.g., marine mammals, seabirds, sea turtles and fish) are obtained at a variety of spatiotemporal extents (Figure 2a). Recoverable high-resolution digital tags (HRDTs) such as those that record motion and attitude, and focal follows (e.g., surface observations) describe the distributions of individuals over meters and hours. Hydrophones and acoustic tags describe the distributions of individuals over meters to tens of kilometers and hours to years. Satellite-monitored tags describe the distributions of individuals over tens to thousands of kilometers and days to years. At-sea surveys describe the distributions of populations and species over several meters to thousands of kilometers and hours to years. Fisheries and whaling catches describe the distributions of populations and species over tens to thousands of kilometers and days to decades.

Data on the marine environment are obtained at a variety of spatiotemporal extents (Figure 2b). Autonomous underwater vehicles (AUVs) (e.g., gliders), animal-borne instruments (ABIs) and drifters describe biological and hydrodynamic processes spanning less than one meter to tens of kilometers and less than one hour to days (e.g., thin layers, prey patches, plume fronts). Oceanographic cruises describe ocean processes spanning less than one kilometer and one day (e.g., prey patches) to thousands of kilometers and several years (e.g., oceanic gyres). Remote sensing describes near-surface oceanographic processes extending several hundreds of meters and days (e.g., eddies and fronts) to thousands of kilometers and decades (basin-scale features). Stationary buoys can be used to monitor oceanographic processes over many years at discrete locations with a high sampling frequency (seconds or hours) (see Figures 3, 5 and 6).

Supporting information

Appendix S1: Methodological details of the wavelet analyses

Hourly buoy sea surface temperature data were downloaded from the National Data Buoy Center (<http://www.ndbc.noaa.gov>) (stations 46013 and 44014). The start and end of the data were trimmed so that datasets for both buoys covered the same time period (1985-2014), and leap days were removed. Datasets had missing data due to periodic sensor malfunction or buoy maintenance. If missing periods were less than 12 hours, temperature data were interpolated between the last and subsequent temperature values. If missing periods were greater than 12 hours, data from the same time periods for the following year were used to fill the gaps. The temperature time series was then re-plotted as a standardized hourly variance from the mean temperature over the entire record. For standardization, temperature variations for each buoy were adjusted to a mean variance of 1 to control for differences in the overall temperature range between regions. The purpose of this was to ensure strength of periodicities in the wavelet analysis was driven by regularity of the period and not influenced by the amplitude of the period. As we were mainly interested in creating a visualization for illustration purposes, we were not concerned with the potential bias towards strengthening an annual periodicity that could be introduced by filling in data gaps from adjacent years. However, as a precaution we also ran subsequent analyses after filling in gaps with zero variance values. Significant periods were the same between the two analyses, but using data from adjacent years produced “cleaner” figures and we only present the results from those analyses.

The wavelet analysis was run using the program Wavetest (http://paos.colorado.edu/research/wavelets/wave_matlab/wavetest.m) in Matlab version R2014b. The minimum scale for the analysis was 12 hours with 4 sub-octaves per octave and a lag-1 autocorrelation value that was calculated from the hourly temperature data. Power was plotted on a log scale to account for the large range in values within either region. The “cone of influence” was calculated based on the methodology outlined in (Torrence & Compo, 1998). This is done by padding the beginning and end of the time series with zeros to correct for edge effects introduced by the Fourier transform as it assumes cyclicity in data that actually exists as a finite time series. These zeros are removed after the wavelet transform but this methodology introduces the possibility of edge effects in the data, resulting in lower confidence in results at the beginning and

end of the data series. The results underneath the cone of influence outline the regions for which little confidence exists in the outputs from the wavelet analyses.

Significance at the 95% confidence level was calculated by comparing the theoretical red-noise power spectra to Monte Carlo results based on the lag-1 autocorrelation calculated from each temperature time series. This red-noise background spectrum calculated using the variance of the temperature data was then multiplied by the 95th percentile value the Chi-squared distribution to identify the power spectra above the significance level. Global power and significance values were calculated by taking the average over all periods for the full data series.

Biosketch

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