

Modeling to aid management of marine top predators in a changing climate

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Marine top predators can include species that occupy a high trophic level (e.g., predatory sharks), have few predators (e.g., marine turtles), or can exert top-down control on food webs due to their large energetic demands (e.g., whales). While many species in the open ocean are widely distributed (e.g., Read et al. 2013; Reygondeau et al. 2012), the higher trophic levels are noteworthy as they are also wide-ranging (e.g., tuna (Itoh et al. 2003; Block et al. 2011; Hobday et al. 2015), seabirds (Shaffer et al. 2006), turtles (Shillinger et al. 2008; Briscoe et al. 2016)). These wide-ranging species can serve as ecological linkages within and across ocean basins, through both ontogenetic (larvae to adult) and seasonal migrations (Boustany et al. 2010; Hobday et al. 2015; Briscoe et al. 2016). Many wide-ranging marine animals show site fidelity at particular times during their lives or have relatively small and well-defined areas of critical habitat, which facilitates both exploitation (e.g., Hobday et al. 2015) and protection (e.g., Ban et al. 2014). This fidelity can be related to the temporal and spatial predictability of their physical habitats, as evidenced by

predictable seasonal aggregations of high-trophic fishes, birds, turtles, and mammals (Scales et al. 2014), which is aided by sensory capabilities that permit them to locate specific physical and biological features.

These species are also of interest, as they are often charismatic, providing commercial, cultural, or ecological value (e.g., Weng et al. 2015). Top predators in marine ecosystems are supported by the productivity of primary and secondary consumers; thus they integrate a range of processes across these lower levels in the trophic food web. Their relatively long life spans and wide-ranging movements mean that many marine predator populations integrate variability across larger spatial and temporal scales than many lower-trophic-level populations (Shaffer et al. 2006). Top predators also have movement and sensory capabilities that permit active targeting of biophysical features (Scales et al. 2014). These characteristics make assessments of top predator populations particularly valuable for investigations of large-scale ecosystem variability and change.

For example, in the California Current System (CCS), plankton (Fisher et al. 2015; Lluch-Belda et al. 2005) and nekton (Lynn 2003; Phillips et al. 2007; Lluch-Belda et al. 2005) exhibit distributional shifts associated with El Niño-Southern Oscillation (ENSO) events, which are echoed by changes in the distribution of top predators. While the distribution of planktonic organisms is indicative of changes in circulation and habitat suitability, shifts in the distributions of top predators and other nekton are often the result of changes in migration patterns based on the availability of prey. Historical observations of the distributions of top predators indicate that along the West Coast of North America, populations are typically displaced poleward during El Niño events. Also, distributions of species with ranges that are typically offshore (e.g., highly migratory fishes) are contracted towards the West Coast, and the catch-per-unit-effort of tunas and yellowtail are often increased in response to the increased availability to nearshore fishers (Sydeman and Allen 1999; Benson et al. 2002; Henderson et al. 2014). Shifts in species distributions attributed to El Niño are often documented in local newspapers and fishing reports as well as in scientific publications (Lluch-Belda et al. 2005; Cavole et al. 2016). However, many predator populations resident to the CCS (e.g., common murre, Cassin's auklet, and splitnose rockfishes) exhibit extreme negative productivity anomalies during El Niño (Black et al. 2014), and these events are the most prominent anomalies in time-series spanning multiple decades. Mass strandings of pinnipeds (e.g., sea lions) and die-offs of seabirds have also been associated with El Niño events. These unusual mortality events have been attributed to reduced availability of forage fishes and the exacerbated effects of harmful algal blooms that accompanied past El Niño events (McCabe et al. 2016).

This nearshore compression of viable habitat can also expose these species to a range of relatively concentrated anthropogenic threats, including fishing, oil and gas exploration, transport, and pollution (e.g., Ban et al. 2014). For example, Maxwell et al. (2013) combined electronic tracking from eight top predator species in the CCS with data on 24 anthropogenic stressors to develop a metric

of cumulative utilization and impact. The distribution of these stressors and species showed that comprehensive management approaches are required, as no single approach was likely to be successful. Predicting the time-varying distribution and abundance of these and other high-trophic-level species may offer additional management insight, and allow a dynamic approach to management and conservation (e.g., Hobday et al. 2014; Scales et al. 2014; Lewison et al. 2015; Maxwell et al. 2015; Hazen et al. 2016).

Using top predators to monitor ocean changes

There is a suite of tools available for monitoring the response of top predator populations and distributions to variation in environmental conditions. At-sea surveys record the presence and abundance of air-breathing marine predators, such as seabirds, whales, sea turtles, and pinnipeds, which can be reliably sighted at the ocean surface or detected using acoustic methods. Standardized, repeat surveys such as the California Cooperative Oceanic Fisheries Investigations (CalCOFI; Bograd et al. 2003) and NOAA's Cetacean Ship Surveys (e.g., CalCurCEAS 2014; Rankin et al. 2016) provide longitudinal datasets informative for understanding population trends and regional habitat preferences (Forney et al. 2015; Sydeman et al. 2014). When combined with *in situ* measurements of physical conditions and prey distributions, survey datasets generate insight into the finer-scale biophysical mechanisms that underlie the dynamics of predator-prey interactions (Benoit-Bird et al. 2013; Embling et al. 2012). Over broader scales, aerial surveys are useful for mapping distributions of air-breathers (Barlow & Forney 2007), and as new technologies become more widely available—such as autonomous underwater vehicles (AUVs), unmanned aerial vehicles (UAVs) (Christiansen et al. 2016; White et al. 2016), and passive acoustics (Morano et al. 2012)—they are increasingly used to survey and study predator populations.

Animal tracking and telemetry allow for remote acquisition of data describing movements and behaviors of marine predators as they move freely through their

natural environment. Tracking individuals of known age, sex, body condition, and breeding status has revealed previously cryptic at-sea behaviors (Block et al. 2011; Hazen et al. 2012; Hussey et al. 2015). For example, satellite telemetry has revealed the complexities of ocean-basin scale migrations in several populations (e.g., seabirds (Clay et al. 2016; Shaffer et al. 2006), sea turtles (Briscoe et al. 2016), and pinnipeds (Robinson et al. 2012)). Understanding migratory behaviors improves our knowledge of phenology (timing) and increases chances of detecting climate change responses. Telemetry datasets have also proven particularly powerful in identifying important foraging habitats (e.g., Block et al. 2011; Grecian et al. 2016; Raymond et al. 2015). When linked with measures of body condition or population-level metrics, such as breeding success, tracking datasets provide novel insights into population status and responses to physical variability (e.g., Biuw et al. 2007). Together, these technologies have revolutionized understanding of at-sea habitat use by marine predator populations across the global ocean and hold promise for the use of top predators themselves as monitors of ecosystem change.

Additional statistical tools are necessary to relate predator distribution data to their prey and the environment. Species Distribution Models (SDMs) quantify predator habitat preferences by combining movement or distribution datasets with physical data from in situ measurements, satellite remote sensing, or ocean models (Robinson et al. 2011). A variety of techniques are used for modeling habitat preferences, such as Resource Selection Functions (e.g., generalized linear or additive models), machine learning (e.g., regression or classification trees; Elith & Leathwick 2009), and ensemble predictions from multiple algorithms (Scales et al. 2015). SDMs can enhance the value of tracking data in identifying foraging habitats and provide insight into how predictability in the locations of at-sea habitats links to persistence in the physical environment historically, in real-time, or for future projections (Hobday and Hartmann 2006; Hazen et al. 2013; Becker et al. 2014; Hazen et al. 2016). Individual-based or agent-based models link biological responses to

heterogeneity and variability in the physical environment using sets of mechanistic rules that underlie biophysical interactions. To date, individual-based models have been used most extensively for lower trophic-level marine predators, such as small pelagic fish (e.g., Pethybridge et al. 2013), as the mechanisms that link the distributions of these organisms to biophysical conditions are generally better understood than for top predators. However, this approach has distinct advantages for modeling top predator habitat use as it explicitly includes prey-field dynamics, an aspect often missing from SDMs owing to the lack of empirical data describing broad-scale prey distributions. Recent advances using regional ocean models with an individual-based model framework have proven effective in modeling predator habitat selection (e.g., California sea lions (Fiechter et al. 2016)) and hold promise for forecasting top predator distributions in changing oceanic seascapes. In particular, a combination of statistical and mechanistic models can identify non-stationarity in predator-environment relationships and can use energetic and movement rules to incorporate prey into predictive models (Muhling et al. 2016).

Managing for a changing climate

Marine top predators are actively managed in many regions to provide social (e.g., tourism), economic (e.g., harvesting), or ecological benefits (e.g., healthy reefs). Traditional management approaches remain an important tool for managing top predators exploited in marine fisheries and addressing conservation objectives. However, in regions with both short-term and long-term change, static spatial management may not represent the best solution when there are competing goals for ocean use (protection or exploitation), as oceanic habitats are mobile and static protection often requires large areas to cover all of the critical habitat for a particular time period (Hobday et al. 2014; Maxwell et al. 2015). Instead, dynamic spatial management may be a suitable alternative, provided that species movements are predictable and suitable incentives exist (Hobday et al. 2014; Maxwell et al. 2015; Lewison et al. 2015). Several approaches, using data and models described in the previous section, can

be used to develop a dynamic management approach in response to variable species distributions, including those based on historical patterns (e.g., past responses to ENSO), real-time, and forecasted prediction of species occurrence. Real-time approaches can use observed data (e.g., satellite data or assimilated ocean model output), while seasonal and decadal approaches require validated models and forecasts of ocean state (Figure 1).

The longest standing real-time example comes from the Australian Eastern Tuna and Billfish Fishery (ETBF; Hobday and Hartmann 2006). Fishers in this multi-species longline fishery often target different species—yellowfin, bigeye, and southern bluefin tunas; marlin; and swordfish—depending on seasonal availability and prevailing ocean conditions, and are themselves subjected to management decisions that alter their fishing behavior. In this region, dynamic ocean management was first used in 2003 to reduce unwanted bycatch of quota-limited southern bluefin tuna (SBT). The distribution of likely SBT habitat, which can change rapidly with the movement of the East Australian Current, was used to dynamically regulate fisher access to east coast fishing areas. A habitat preference

model was used to provide near real-time advice to management about the likely SBT habitat (Hobday et al. 2010). Managers use these habitat preference reports to frequently update spatial restrictions to fishing grounds, which involve dividing the ocean into a series of zones based on expected distribution of SBT. These restrictions limit unwanted interactions by fishers that do not hold SBT quota (SBT cannot be landed without quota and in that situation must be discarded) and allow access to those that do have SBT quota to operate efficiently (Hobday et al. 2010). The underlying habitat model has evolved from a surface temperature-based model to an integrated surface and sub-surface model, and currently includes a seasonal forecasting element to aid managers and fishers planning for future changes in the location of the habitat zones (Hobday et al. 2011). This ongoing improvement and adaptation of the system has seen new oceanographic products tested and included in the operational model. This dynamic approach has reduced the need for large area closures while still meeting the management goal but does require more flexible fishing strategies to be developed, including planning vessel movements, home port selection, and quota purchase.



Figure 1. Decisions relevant to fisheries, aquaculture, and conservation sectors at forecasting timescales are noted above the time line. Seasonal forecasting is considered most useful for proactive marine management at this time, with decadal forecasting in its infancy. Modified from Hobday et al. 2016.

In parallel with improved biological data, numerical climate forecast systems have greatly improved over the last 30 years and now have the capability to provide useful seasonal forecasts (National Research Council, 2010). Dynamic forecast systems include i) global climate models (GCMs), which consist of atmosphere, ocean, land, and ice components; ii) observations from multiple sources (e.g., satellites, ships buoys); iii) an assimilation system to merge the observations with the model's "first guess" to initialize forecasts; and iv) post-processing software to display and disseminate the model output. Such systems are currently used to make forecasts at scales on the order of 100 km on seasonal and even decadal timescales (e.g., Kirtman et al. 2014; Meehl et al. 2014; Stock et al. 2015). In addition, output from the GCMs is being used to drive much higher-resolution forecasts from regional ocean models (Siedlecki et al. 2016). Model skill on seasonal timescales is a function of persistence,

multi-year climate modes (e.g., ENSO, IOD), and its teleconnections and transport by ocean currents. Model skill on decadal timescales arises due to anthropogenic climate change and slowly evolving ocean circulation features such as the Atlantic Meridional Overturning Circulation (AMOC; Salinger et al. 2016). GCM-based forecast systems are currently being used to predict sea surface temperature, sub-surface temperatures, and other ocean conditions that are subsequently used in marine resource applications described above (Hobday et al. 2011; Eveson et al. 2015, Figure 2). However, skill from statistical methods is currently on par with those from much more complex and computer-intensive numerical models (Newman 2013; Jacox et al. 2017), and forecast skill will always be limited regardless of the quality of both models and observations due to the chaotic elements of the climate system.

Ecosystem Prediction

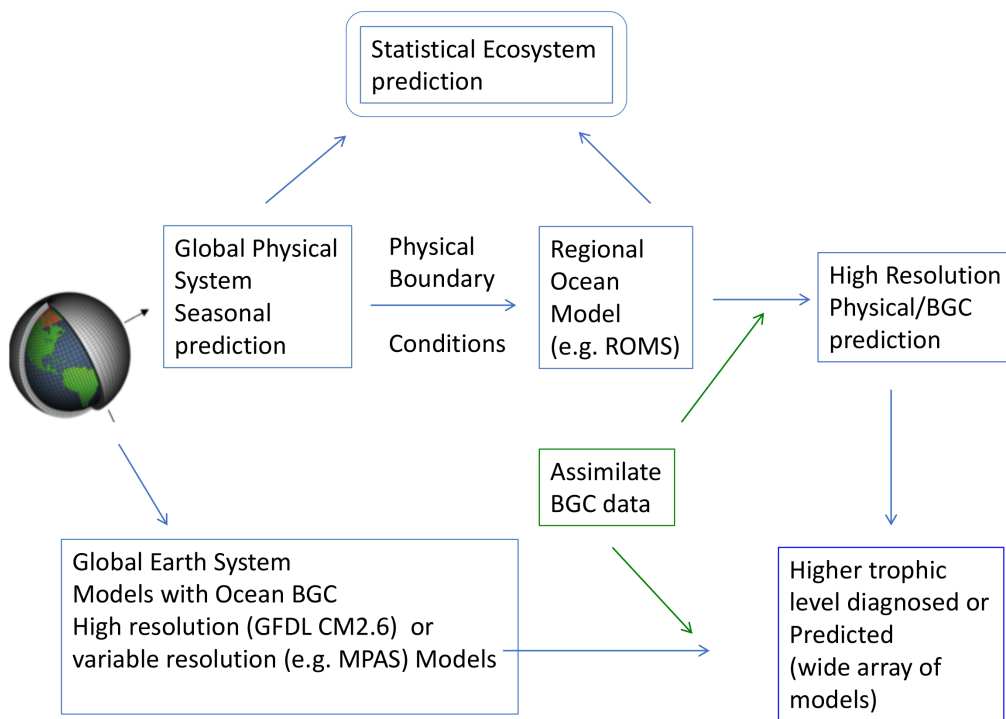


Figure 2. Ecosystem predictions require a suite of inputs and modeling steps to ensure both physical and biological components in the ecosystem are adequately represented. Physical models (from 1 degree to 1/10 degree downscaled models) can be used to predict higher trophic level distributions directly or can be used to drive individual based movement models of prey and predator to incorporate trophic dynamics in ecosystem predictions.

Where do we go from here?

As described above, ocean forecast systems and biological data are being linked to advance top predator management. Three priorities to strengthen this link and better inform management efforts include: (i) gather and share data, (ii) identify effective measures and improve mechanistic understanding of prey availability, and (iii) understand the spatial and temporal overlap between humans and particular focal species.

First, while the capacity to monitor marine top predators has made considerable strides in recent years (Hussey et al. 2015), juvenile portions of many top predator populations can be under-represented and need particular attention (Hazen et al. 2012). Tagging efforts provide detailed data on animal movement and can provide finer-scale data than traditional shipboard surveys. However, there are only a few examples of broad-scale tagging efforts that allow for measurement of diversity and multi-species habitat use, such as the Tagging of Pacific Predators and the Ocean Tracking Network (Block et al. 2011, Hussey et al. 2015). There is a growing trend for these data to be made widely available in repositories (e.g., Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebate Populations (OBIS-SEAMAP), Seabird Tracking Database) that allow for greater synthesis than individual datasets alone (Halpin et al. 2006; Lascelles et al. 2016). This should be encouraged as standard practice, as in the oceanographic community (e.g., Global Ocean Ship-Based Hydrographic Investigations Program (GO-SHIP) database). Data collection must continue, as climate variability and change influence the relationship between top predators and their environment, and additional data are necessary to both test and refine predictive models.

Second, while the movements of many highly migratory predators are tied closely to prey availability, most models of marine top predator habitat use remotely sensed or in situ oceanographic measurements as proxies for prey distribution, which is rarely available. The difficulty is in measuring prey distribution at the scales appropriate for predators (e.g., Torres et al. 2008). We can measure

fine-scale foraging behavior using archival tag data and associated prey measurements (e.g., Goñi et al. 2009; Hazen et al. 2009), but these ship-based approaches cannot provide data at the scales used in management-focused habitat models (see Lawson et al. 2015). We can model prey distributions mechanistically to inform models of top predator movements (Fiechter et al. 2016), but these approaches have not yet been coupled with real-time prediction. Prey data at migration-wide scales would greatly improve both statistical and mechanistic models by offering insight to where residence times are highest, yet these data remain difficult beyond fine-spatial scales (Benoit-Bird et al. 2013; Boyd et al. 2015).

Finally, both animals and humans use the marine environment at multiple spatial and temporal scales. For example in the Pacific, blue whales migrate from high-latitude foraging grounds to tropical breeding grounds seasonally and travel to discrete foraging hotspots based on prey availability (Bailey et al. 2009), and container vessels are making decisions such as ship speed, choice of shipping lanes, and port of call on multiple time scales as well (Hazen et al. 2016). This requires information on long-term habitat pathways and high-use areas (e.g., for static protection), as well as the shorter-term (e.g., seasonal) triggers of migration and identification of ocean features that result in high prey aggregations and increased residence times. Comparably, a fisher may change her long-term investment decisions (e.g., quota purchase, hiring crew) based on projections of long-term stock dynamics, or may decide when to start fishing seasonally based on weather and proximity to port, or when to set a net based on when fish schools are plentiful (Figure 1). Thus, management approaches could also be nested to include real-time predictions, seasonal forecasts, and decadal projections to inform multiple management processes (Hobday and Hartmann 2006; Hobday et al. 2011; Salinger et al. 2016). This suite of dynamic spatial management tools would represent an adaptive strategy robust to shifting habitats and species in response to climate variability and change.

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