THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

CITATION

Hobday, A.J., and J.R. Hartog. 2014. Derived ocean features for dynamic ocean management. *Oceanography* 27(4):134–145, http://dx.doi.org/10.5670/ oceanog.2014.92.

DOI

http://dx.doi.org/10.5670/oceanog.2014.92

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Derived Ocean Features for Dynamic Ocean Management

By Alistair J. Hobday and Jason R. Hartog



ABSTRACT. Primary environmental variables, such as sea surface temperature, wind speed, and chlorophyll, have been used widely in a variety of studies by biological oceanographers to explore the relationship between "physics" and, say, distribution and abundance of marine organisms. Fisheries scientists in particular have explored a range of relationships between physics and catch data to understand fish distribution and fishing impacts. The explanatory power of models based on such primary variables is typically limited and may not lead to insight into mechanisms behind the environmental associations. Variables that are more direct measures of habitat, such as thermal fronts, upwelling zones, eddies, and water column descriptors (e.g., mixed layer depth), may yield additional explanatory power. We have developed a suite of these derived variables and demonstrate their utility using examples from Australian fisheries and marine spatial planning. Refinement and access to derived variables may be useful in a range of applications, including catch standardization, habitat prediction, ecosystem models, spatial management, and harvest strategies, and will play an important role in the emerging area of dynamic ocean management.

INTRODUCTION

With increasing pressure on ocean resources from a range of extractive and nonextractive uses (e.g., Worm et al. 2006; Merrie et al., 2014), the need for more effective management policies and options is only growing stronger (Gjerde et al., 2013; Maury et al., 2013; Ban et al., 2014). One branch of open ocean management, loosely defined here as concerned with noncoastal waters (> 3 nm offshore, or > 200 m deep), is focused on the sustainable management and conservation of often wide-ranging marine species impacted by activities associated with fishing, transport, and pollution (Ban et al., 2014). Pelagic species of concern include exploited fishes (e.g., tunas), sharks, and associated bycatch as well as a range of iconic species that are impacted directly or indirectly by human activity, such as seabirds, marine mammals, and sea turtles.

Human activities are not randomly distributed in the ocean—nor are pelagic species—hence, interactions are spatially and temporally heterogeneous. Human activities are concentrated in shipping lanes, fishing grounds, and coastal regions. Pelagic species can be passively concentrated in the early stages of their life histories (e.g., eggs, larvae, juveniles), and they actively aggregate in particular ocean regions at other stages to feed, mate, or migrate (Bakun, 2006; Ritz et al., 2011). Even the most powerful swimming and widest-ranging pelagic species are still constrained by their physiology to particular temperatures and depths. Developing an understanding of the distribution of these species has thus been an important first step in resolving some of the conflicts between resource users and marine species (Hobday et al., in press). Thus, it is no surprise that a major research area in biological oceanography has been the search for relationships between abundance and distribution and environmental variables (Table 1), and, more recently, the use of these relationships to enhance sustainable management and conservation approaches. These relationships have also been used to justify inclusion of habitat proxies, or to develop species distribution models, for use in marine spatial planning (e.g., Alpine and Hobday, 2007; Grantham et al., 2011).

The search for environment-biology patterns in the ocean has a long history that is built on early work in fisheries oceanography in which recruitment of harvested species was related to a set of environmental variables (Hjort, 1914). A more recent common approach to understanding environment-biology relationships has been to match the known position of the species of interest (response variable) to a range of environmental variables (predictor variables), such as sea surface temperature (SST), salinity, oxygen concentration, and ocean currents, and then examine the relationship between the predictor and response variables (e.g., Bigelow et al., 1999). These relationships have a wide variety of applications, including to enhance understanding of patterns in abundance over time and to develop species distribution maps, and a range of statistical and modeling approaches have been used to infer the relationships.

Initially, the common environmental variables, here referred to as primary variables, were those that could be directly measured in situ from vessels or at coastal monitoring stations. Over time, as new technology emerges, a wider range of primary environmental variables with increasing spatial and temporal coverage has become available. Environmental data are now gathered using an array of electronic tags attached to individual animals; from a wide range of drifting (e.g., Argo) and moored scientific instruments; and perhaps most importantly, from satellites, which allow synoptic coverage of the global ocean. As a result, SST, sea surface height (SSH), chlorophyll (i.e., sea surface color; Figure 1), and wind speed are the most commonly used primary variables in the search for explanatory patterns. While in situ measurements are generally spatially and temporally limited, and satellite products cover only the surface ocean, three-dimensional ocean models (hindcasts) now also provide data layers (Oke et al., 2008) that can be used to generate derived products supporting even greater environmental characterization and matching to species occurrence data.

Primary environmental variables are used as covariates in a range of studies, and a typical approach in the analysis of environment-biology relationships is to assemble an environmental data set for each date and match the location of the species in the biological data. The available environmental variables are then used as predictor variables in a wide range of statistical and modeling approaches that over time have also increased in **TABLE 1**. Examples of links between primary (P) and external variables (E) and derived variables commonly used in analyses explaining the distribution and abundance of pelagic species. Several of these derived variables are discussed further in the text.

Primary or external variable	Derived variable	Explanation
SST (P)	Ocean temperature	Sea surface temperature (SST), measured right at the surface, is used as a proxy for upper ocean temperature and is often assumed to represent the mixed layer temperature.
SST gradient (P)	Frontal presence	Water masses meet at fronts, which can aggregate passive prey, making them important foraging grounds for a range of species.
Chlorophyll (P)	Productivity, prey availa <mark>bility</mark>	Chlorophyll can be a proxy for the density of prey organisms.
SSH (P)	Eddy typ <mark>e</mark> (upwelling or downwelling)	Sea surface height (SSH) indicates water motion, and thus the presence of upwelling or downwelling features such as eddies.
Wind speed (P)	MLD	Wind is related to the depth of mixing and hence the mixed layer depth (MLD). MLD is also influenced by surface heating and cooling. The mixed layer depth can constrain prey species to depths where they can be accessed by surface feeding animals or fisheries.
Currents (P)	EKE	Eddy Kinetic Energy (EKE). Energy in water motion can lead to enrichment and subsequent productivity increases.
Moon phase (E)	Depth of light penetration	The depth of light penetration at night influences both the visibility of the species and the depth at which prey occurs.
Latitude (E)	n/a	Some variables such as SST change with latitude, or fisher behavior might change with latitude, such that the response variable is also related to latitude. A range of derived variables may be suitable replacements.
Time (E)	n/a	Time variables (e.g., year, week, season) may be proxies for derived variables that better represent the ocean environment.

sophistication. In one of the most common methods, involving Generalized Linear Models (or Generalized Additive Models), the response variable is the abundance or presence of the species of interest, while the predictor variables are the matched (in time and space) primary environmental variables described earlier. Most analytical models also include external variables, such as latitude, longitude, month, and year, which have little relationship to the life of the fish. External variables are not expected to describe fish habitat but can account for variation due to missing variables or for human-derived biases in the data (such as temporal patterns in fisher behavior). In the case where the external variables (e.g., latitude) are significant, it has often been assumed that these external variables represent environmental variables that were not included in the model.

Despite the increase in availability of primary environmental data, and the sophistication of the analytical techniques, the explanatory power of many environment-biology models remains low or deteriorates over longer time

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periods, which limits their use in a predictive sense (e.g., Myers, 1998; Basson, 1999). This low power may be due to a true absence of a strong relationship (e.g., when animals are migrating, we might expect weaker environmental influences than when they are feeding or breeding). In such cases, a search for additional explanatory primary environmental variables will not be fruitful, and many environment-biology studies have ended with this unsatisfactory outcome. A second alternative, and the one we explore further here, is that the available primary environmental variables are really only proxies for other variables that better describe the habitat and hence improve the relationship between a species and its environment. We recognize that some primary variables, particularly those that define species' physiological tolerances (e.g., temperature), will always be important.

We define this second category of environmental variables as derived variables, as they are often derived from the primary variables. Derived variables can represent more realistic approximations of ocean habitats or mesoscale features such as fronts, upwelling zones, and eddies. The derived variables represent measures of these features, such as frontal presence and activity, upwelling intensity, and eddy characteristics (Table 1). These features also have "structure," "age," and "qualities" similar to terrestrial habitat forms, such as forests, meadows, and ecotones. Wider use of derived environmental products that better represent the habitats of marine species might lead to improvements in predictive models (e.g., Dell et al., 2014) or in process understanding (e.g., discerning the relative importance of different habitats for survival, growth, and reproduction). In using derived variables in statistical explanatory models, we expect that the importance of the external variables and even some of the primary variables would decrease after derived variables are considered. This hypothesis has not been widely tested, and may not apply in all

cases, but the greater availability and use of derived variables should allow a range of formal tests in the future. We provide a range of examples in the following sections. We also note that in using derived variables in some statistical models, it is important to check for (and remove) correlated primary variables. Some derived variables have been commonly used to date, particularly fronts (e.g., Herron et al., 1989; Podestá et al., 1993; Alpine and Hobday, 2007) and eddy kinetic energy (EKE; e.g., Zainuddin et al. 2006; Dell et al., 2011), but other derived products (e.g., eddies) have not been generally available for wider use (but see Chelton et al., 2011; http://cioss.coas. oregonstate.edu/eddies).

These derived measures represent ocean features and processes that can influence biology, such as via production at the base of the food web and distribution of predators. In combination with primary variables, identification and use of these derived measures of ocean habitat represent a new opportunity for more nuanced dynamic ocean management, as we demonstrate in the remainder of this paper. Derived ocean variables, while they require some additional processing, can also be made more widely available in real time; delivery of primary data is now faster and automated with regard to quality control, computer processing power allows desktop processing, and access to ocean model outputs can provide complete coverage and subsurface information (Hobday et al., 2014). Identification of relationships with derived ocean features may also support the development of dynamic ocean management (Hyrenbach et al., 2000; Palacios et al., 2006; Hobday et al., 2014), as heterogeneity in the distribution of these habitats may allow more sophisticated resolution of spatial conflicts with human activities (Dunn et al., 2011). Greater use of derived variables, as described in the following sections, may lead to improved understanding of ocean influences on marine species. Here, we provide examples for the Australian region, but global satellite coverage means that similar fields can be derived for any region.

DERIVED VARIABLES REPRESENT DYNAMIC OCEAN HABITATS

Some derived variables can be easily identified using existing maps of primary variables and just require some algorithm to define or encapsulate them (e.g., areas of upwelling or eddies). Once identified, these features can then be further processed into probability of occurrence maps, or treated as single layers. Other derived variables are based on calculations or processing to extract a more complicated data layer (fronts, EKE, mixed layer depth [MLD]). In the following sections, we explain the biological importance of selected derived variables and how they are defined and processed, and we illustrate their potential uses in dynamic ocean management (Hobday et al., 2014).

Upwelling Areas

Upwelling involves the movement of subsurface waters to shallower depths. In the case that the upwelled water moves from below the thermocline, nutrient-rich water may enter the euphotic zone, leading to increased production. Coastal upwelling may be wind driven (wind parallel to the coast can result in movement offshore of surface water, depending on the wind direction) or result from the movement of currents. Coastal upwelling in eastern boundary currents is responsible for extremely productive food chains, such as off Chile/Peru (Alheit and Niquen, 2004) and Namibia/South Africa (Cury et al., 2000). Coastal upwelling cells are common in many countries, and have a time scale of days to weeks following a wind event. In contrast, oceanic upwelling (e.g., equatorial upwelling) can be seasonally persistent (e.g., eastern tropical Pacific). If the upwelled cool, nutrientrich water reaches the surface, it may be visible in satellite imagery. Defining upwelling areas based on satellite or

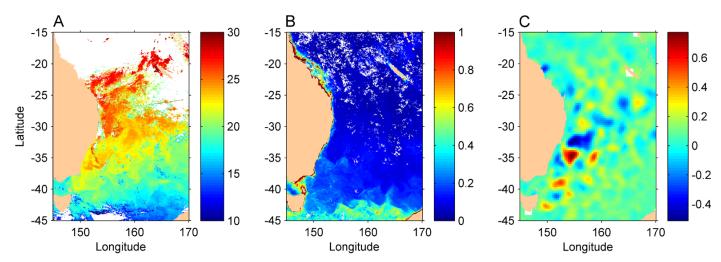


FIGURE 1. Examples of primary environmental variables for eastern Australia for March 15, 2012. (A) Sea surface temperature from an Advanced Very High Resolution Radiometer (AVHRR) three-day composite. (B) Monthly ocean color (chlorophyll) from the Moderate Resolution Imaging Spectroradiometer (MODIS). (C) Gridded mean sea level anomaly (MSLA) sea surface height from TOPEX/POSEIDON and ERS-1.

other ocean model data thus generates a description of a habitat that can be used as a derived variable in a range of analyses (e.g., Grantham et al., 2011) or to generate a time series that can become a predictor in the search for biological patterns (e.g., Cury and Roy, 1989).

Upwelling areas can be defined using thresholds that vary regionally and even seasonally within regions. In Southeast Australia, where small upwelling cells exist, upwelling regions are visible in satellite imagery and can be defined by areas where SSTs are below some threshold (e.g., T < 17°C; Figure 2) or chlorophyll exceeds a threshold (> 0.6 mg C m^{-3} ; Neiblas et al., 2009). A challenge is that thresholds that define upwelling areas need to be tuned regionally and seasonally, and so global upwelling products do not exist. Upwelling has been quantified based on wind-based estimates (Bakun index; Bakun, 1973; Hseih et al., 1995) for volumes of upwelled water, or with a combination of temperature, salinity, and chlorophyll values that can define biologically important upwelling areas.

Having defined an upwelling region, the extent and variation in that area can be used as an explanatory variable in the recruitment, abundance, production, or catchability of the species of interest. The extent of upwelling has been used in time series analyses to explain variation in recruitment of a diverse range of species, including barnacles (Roughgarden et al., 1988), urchins (Morgan et al., 2000), octopus (Faure et al., 2000), and salmon (Koslow et al., 2002). In a recent example, upwelling favorable winds and resultant upwelling have been used to forecast dangerous jellyfish blooms in Northeast Australia (Gershwin et al., 2014). A spatial delineation of upwelling areas has been less common (but see Palacios et al., 2006; Nieblas et al., 2009; Grantham et al., 2011), although probabilistic identification of upwelling regions has been an important input in spatial planning for Australian marine regions (Dambacher et al., 2012; Hayes et al., 2012; Hosack and Dambacher, 2012). By mapping the temporal dynamics of a derived variable such as upwelling area, and relating it to the distribution and movement patterns of species that seek or avoid upwelling areas, such as tuna (Willis and Hobday, 2007), sea turtles (Wingfield et al., 2011), jellyfish (Gershwin et al., 2014), and whales (Gill, 2002), management of activities that impact such species can be adjusted in time and space-a form of dynamic ocean management.

Eddies

Eddies are mesoscale ocean features that are found in all ocean basins (Chelton et al., 2011). They originate

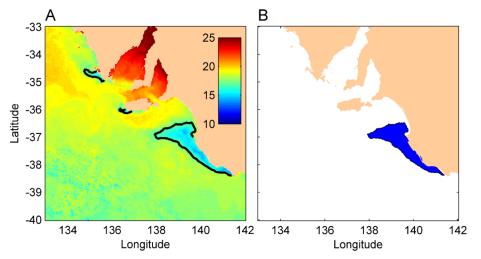


FIGURE 2. Upwelling in southern Australia. (A) Sea surface temperature on February 4, 2014, with three potential upwelling regions outlined. (B) Bonney upwelling area (blue), defined here as the contiguous region with SST < 17° C. Species associations with the habitat area can be determined.

from instability in ocean circulation, which is sometimes related to interactions with topographic features, and in other cases to meanders of ocean currents that can "pinch" off a self-contained body of water with physical-chemicalbiological properties that differ from surrounding waters. Eddies rotate either clockwise or anticlockwise and are variously known as cyclonic or anticyclonic, warm or cold core, and upwelling or downwelling (Bakun, 2006). They can be relatively stable and persistent in time and space or meander across the ocean (Chelton et al., 2011). Eddies that originate close to the coast can draw off high-chlorophyll water, increasing the productivity and transport of carbon (e.g., Henson and Thomas, 2008) and fish larvae (Gaughan, 2007; Condie et al., 2011) into offshore waters.

Eddies are easily seen in SSH images, and their enhanced or reduced productivity can be visualized in ocean color imagery. SSH anomalies have been used to locate eddies with a range of methods and thresholds (e.g., Hensen and Thomas, 2008; Chelton et al., 2011). Both cyclonic (low sea level anomaly) and anticyclonic (high sea level anomaly) eddies can be located, and once located, tracked through time based on pixel connectivity algorithms such that the age of each feature is also obtained (Hensen and Thomas, 2008; Chelton et al., 2011; Figure 3). Biological associations with these features can then be determined as described for upwelling regions.

An increase in phytoplankton concentration in eastern Australian cyclonic eddies has been documented (Everett et al., 2012), increased zooplankton and larval fish in eddies have been observed in a range of locations (Bakun, 2006; Condie et al., 2011), and eddies are known to be important foraging regions for a range of predators, including seabirds (Tew Kai et al., 2009), turtles (Luschi et al., 2003), and tuna (Young et al., 2001). Enhanced survival and growth of fish larvae in productive eddies have been reported (Loggerwell and Smith, 2001), while in low productivity eddies the opposite may occur (Gaughan, 2007). In the next section below entitled Habitat Use by Pelagic Species Can Inform Fisheries Management, we illustrate how eddy identification and association by different species may aid dynamic ocean management.

Fronts

Fronts occur as boundaries between water masses with different properties, and they can be defined based on rates of change in salinity, temperature, and even chlorophyll. As with eddies, fronts can be persistent in space and time or move with ocean currents (Sournia, 1994). Fronts are associated with convergence zones, which aggregate flotsam and passive or weakly swimming individuals from a range of lower trophic levels (Franks, 1992; Bakun, 2006). Thus, the distribution of food particles is concentrated at fronts, making them attractive foraging areas for a wide range of marine species. Many studies show that pelagic species are attracted to fronts, and measures of frontal activity are used in predictive habitat models and in explanations of fishing patterns (e.g., Dell et al., 2011).

A series of papers by Cayula and Cornillon (1990, 1992, 1995) describe a widely used method for identifying SST fronts using an edge detection algorithm. This is an intensive computational process, and it was historically applied to a small region of interest to generate a series of "edges" that define the temperature fronts in that region (e.g., Podestá et al., 1993), but with increased computing power, basin-wide front identification is possible. To develop products for Australia, we applied this algorithm to a time series of daily satellite SST images in order to identify the fronts in each image (Figure 4A) and then generated an index of frontal activity over that time series (Figure 4B). This derived variable is aggregated over an eight-day period to offset some of the issues that arise with cloud cover in single images (e.g., Miller, 2009), and its spatial scale matches the fishing and biological data that we typically use.

Frontal regions are important to a wide range of species, including seabirds (Bost et al., 2009), turtles (Polovina et al., 2000), swordfish (Podestá et al., 1993), and tuna (Royer et al., 2004). In these examples, fronts were specifically detected and included as a habitat variable, and in many more studies, SST gradients are commonly used as a proxy for frontal presence (e.g., Teo et al., 2007). With regard to marine spatial planning, the distribution of frontal regions has been important in the definition of ecologically or biologically significant areas (EBSA) in many of the oceans (e.g., Dunstan and Fuller, 2012; Dunn et al., 2014).

Eddy Kinetic Energy

Eddy kinetic energy is a representation of the mesoscale variability of the flow in a region and helps to identify regions where mesoscale eddies and current meanders are relatively common (Figure 4). EKE tends to be highest at the edge of currents and eddies, where the shear between water masses is greatest. As with eddies and upwelling features, these regions may be important feeding locations for a range of pelagic species due to enhanced production and aggregation of prey (Zainuddin et al., 2006).

EKE is simple to calculate from horizontal surface velocities by ignoring the vertical dimension, whose contribution is minor: EKE = $0.5 \cdot (u^2 + v^2)$, where *u* is the east-west component of the velocity of the surface ocean, and *v* is the north-south component. Typical units are cm² s⁻¹ (Zainuddin et al., 2006). These input layers can be based on SSH fields or on current velocities derived from ocean models (e.g., Oke et al., 2008; Figure 4C).

Along with fronts, EKE is one of the most widely used derived products. It is significantly associated with the distribution of tuna (Zainuddin et al., 2006; Dell et al., 2011), with intermediate values preferred by some species (Teo et al., 2007). As with the previous derived variables, EKE can be matched to biological data to determine its importance (e.g., for turtles; Shillinger et al., 2008).

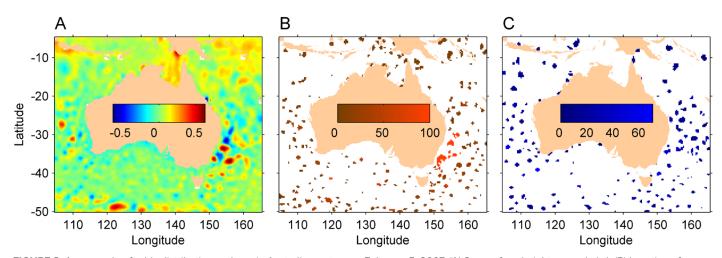


FIGURE 3. An example of eddy distribution and age in Australian waters on February 5, 2007. (A) Sea surface height anomaly (m). (B) Location of warm eddies (shaded by age, in weeks). (C) Location of cold eddies (shaded by age in weeks). The distribution of species can be mapped to these features, as described in the text.

Mixed Layer Depth

Mixed layer depth is a measure of the vertical structure of the water column and represents a region in the upper ocean where there is little variation in temperature or density with depth (Kara et al., 2000). The mixed layer can constrain the prey or the foraging range of pelagic species (e.g., Graham et al., 2007; Williams et al., 2014), and it is an important derived variable for explaining distribution, abundance, and catchability (Stramma et al., 2011; Campbell and Young, 2012). Information gathered from electronic tags can be particularly useful in understanding the physiological constraints of individuals foraging in cool waters below the mixed layer (Schaefer and Fuller, 2003) or where oxygen is limiting (Stramma et al., 2011). These constraints have been used in a range of fisheries applications to standardize catch rates (e.g., Bigelow and Maunder, 2007).

There are several ways to define the MLD, usually involving a difference method (e.g., depth at which the temperature or salinity changes by x units from the surface values) or with a derivative method (e.g., depth of the maximum rate of change in density) (Kara et al. 2000). Our MLD fields around Australia are derived from a modeled three-dimensional temperature and salinity

data product (synTS; Condie and Dunn, 2006). Unfortunately, ocean model data may not generate a realistic vertical profile (generally too smooth compared to observations; e.g., Condie and Dunn, 2006; Oke et al., 2008), so a derivative method cannot be accurately applied to generate MLD fields. In such cases, using a difference method is more appropriate, defining MLD as the minimum depth at which either temperature changes by 0.4°C from the temperature at 10 m or the salinity increases by 0.03 from the salinity at 10 m (Condie and Dunn, 2006). With such an approach, we generate consistent fields for use in our biological studies (e.g., Figure 4D).

HABITAT USE BY PELAGIC SPECIES CAN INFORM FISHERIES MANAGEMENT

To illustrate the utility of derived products for ocean management, we consider the association with eddies of species captured in the eastern Australia longline fishery. As described earlier, eddies are large, relatively stable, slow-moving features common to many coastal and open ocean regions (Chelton et al., 2011). If species preferentially associate with or avoid eddies, then mapping of eddies can be used to locate fishing activities dynamically (Hobday et al., 2014).

To illustrate this approach, we use catch data recorded from longline sets, which each consist of a single monofilament line that may be tens of kilometers in length and have some 1,200 hooks hanging to a depth of 10-300 m (Campbell and Young, 2012). A measure of fish abundance is the catch per unit effort (CPUE), typically expressed for longline fisheries as the number of individuals caught per 1,000 hooks. Using weekly fields of eddy distribution generated using the methods described in Hensen and Thomas (2008), we assigned each longline set for the 10-year period 2003 to 2012 in the area 25°-40°S and 145°-170°E as occurring outside eddies or inside either cyclonic (clockwise in the Southern Hemisphere) or anticyclonic (anticlockwise) eddies. The CPUE of each of 14 common pelagic species was then calculated and ranked by habitat preference (the ratio of the mean CPUE inside and outside eddies), which is a form of quotient analysis (Figure 5A). Confidence intervals of the null hypothesis of even distribution (ratio equal to 1) were computed by a resampling procedure (1,000 random draws of the CPUE data for each species) in order to test for the significance of quotient values larger or smaller than 1 (Bernal et al., 2007). Preference values can be defined as values of the covariates in which the CPUE

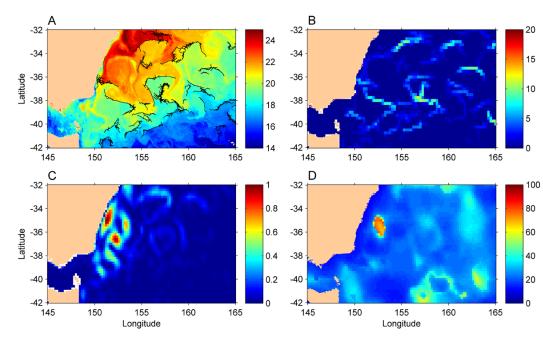


FIGURE 4. Examples of derived products for eastern Australia for January 2007. (A) Sea surface temperature image with fronts marked by black lines for January 5, 2007. (B) Frontal index at a coarser scale (eight-day) based on a count of frontal pixels in daily images (January 1-8, 2007). (C) Eddy kinetic energy derived from sea surface height imagery for January 5, 2007. (D) Mixed layer depth derived from a threedimensional ocean reanalysis product (synTS; Condie and Dunn, 2006) for January 5, 2007. All products are derived as described in the text.

quotient is larger than 1 (or greater than the upper confidence interval), avoidance values when the CPUE quotient is lower than 1 (and below the lower confidence interval), and tolerance as neither significant avoidance nor significant preference. This analysis shows that catch rates of some species in eastern Australia are lower and hence appear to avoid eddies (e.g., yellowfin tuna and tiger shark), while others are captured at higher rates inside eddies than outside (e.g., opah,

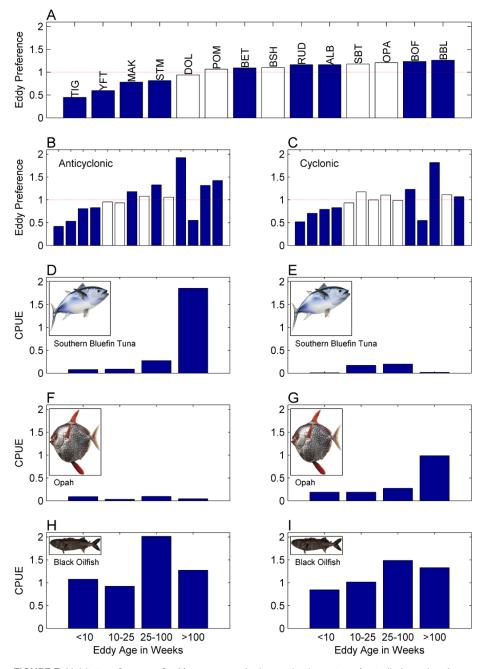


FIGURE 5. Habitat preferences for 14 common pelagic species in eastern Australia based on longline catch data. (A) Habitat preference for eddies (preference > 1) or non-eddies (preference < 1) by species. Codes represent tiger shark (TIG), yellowfin tuna (YFT), mako shark (MAK), striped marlin (STM), dolphinfish (DOL), pomfret (POM), bigeye tuna (BIG), blue shark (BSH), rudderfish (RUD), albacore tuna (ALB), southern bluefin tuna (SBT), opah (OPA), black oilfish (BOF), and broadbill swordfish (BBL). Solid bars indicate associations that were all significantly different from random association. The preference can also vary by eddy type (anticyclonic [B] and cylonic [C]). The order of species in B and C is the same as in panel A. The catch per unit effort (CPUE) also varies by age of the eddies, as shown for southern bluefin tuna in anticyclonic and cyclonic eddies (D,E), opah (F,G), and black oilfish (H,I). *Fish images ©CSIRO 2014*

black oilfish, and swordfish). In the cases with strong preferences (avoidance or association), these patterns were significant, with the observed ratio outside the 97.5% and 2.5% confidence intervals. When preferences are close to unity, the variation in the association leads to wider confidence intervals and nonsignificant results for some species. Species' preferences also differ between eddy type, with southern bluefin tuna strongly preferring anticyclonic eddies compared to cyclonic, and the converse for opah (Figure 5B,C). There are even more detailed habitat associations, for example, with eddy age. Our eddy tracking approach also allows each eddy to be aged, and shows how the habitat association might also change with age. Southern bluefin tuna, for example, show a dramatic increase in CPUE in older anticyclonic eddies (Figure 5D), while opah show a preference for older cyclonic eddies (Figure 5G). Other species, such as black oilfish, show no pattern with the age of the eddy (Figure 5H,I).

As eddies in this region are typically on the scale of 100 km wide and occupy less than 10% of the ocean at any one time, understanding habitat associations allows for some innovative voluntary fishing strategies or compulsory management approaches, such as avoiding or targeting eddies of a particular type or age. Such dynamic management approaches have been effective based on other habitat descriptions (Hobday and Hartmann, 2006; Howell et al., 2008; Hartog et al., 2011), and identifying key habitat associations is a critical aspect of extending these methods to a wider range of species (Hazen et al., 2013; Hobday et al., 2014).

COMBINING DYNAMIC OCEAN LAYERS TO INFORM SPATIAL PLANNING

Derived ocean variables can also be used in combination to define foraging hotspots (e.g., Palacios et al., 2006). To illustrate this concept, consider the importance of productivity in influencing the distribution of marine species. Satellite-based measures of ocean color can allow synoptic coverage of the ocean and be converted to an additional derived product-productivity (e.g., Behrenfeld and Falkowksi, 1997; see http://www.science.oregonstate.edu/ ocean.productivity/index.php), but they are generally limited to surface productivity. Not all ocean production has a surface productivity signal in chlorophyll (e.g., van Ruth et al., 2010). Thus, mapping of "productivity-generating" features such as upwelling eddies, EKE, and fronts may complement surface measures of productivity for identifying important ocean regions for marine planning purposes (Dunstan and Fuller, 2012), including dynamic ocean management. We illustrate such "productivity-feature maps" with a seasonally averaged combination of productive (cyclonic, upwelling) eddies identified from SSH data, EKE, and frontal density as described

above. A seasonal average (December-January-February, and so on) over a 10-year period for the presence of each feature in each derived product layer is scaled to the range [0 1] before calculating the mean value of all three layers (Figure 6). This method results in a map where the probability of these features is indicated at every pixel in the area of interest. These features are not always correlated with high values of surface chlorophyll (Figure 6). The relationship between chlorophyll and productivity is positive in some regions (upper envelope of pixel-pixel correlation), but there are regions with high chlorophyll and low productivity index values. Thus, this combination of derived features, even though it is associated with higher productivity and does attract a range of pelagic species (see earlier section Derived Variables Represent Dynamic Ocean Habitats),

would not be sufficiently represented in a spatial planning exercise that focused only on surface productivity as estimated from satellites (Dambacher et al., 2012). Thus, dynamic management that targets pelagic species attracted to high productivity areas should not be based just on identification of chlorophyll hotspots (Palacios et al., 2006).

HOW TO BETTER USE DERIVED PRODUCTS IN DYNAMIC OCEAN MANAGEMENT

Although the search for marine environment-biology relationships based on ocean variables has a long and sometimes frustrating history (Myers, 1998; Basson, 1999), improvement in understanding a range of relationships can be made by wider use of derived products. Overall, refinement and access to derived variables described here are likely to play

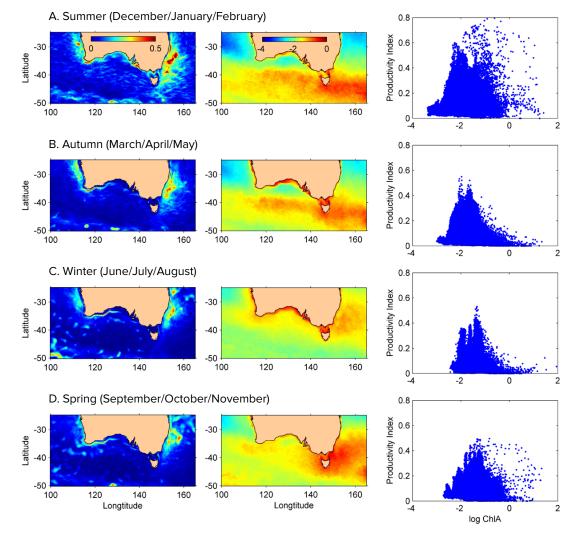


FIGURE 6. The seasonal productivity index derived based on the average of three derived productivitygenerating features for the period 1998-2007 (column 1) for southern Australia; the seasonal average chlorophyll (SeaWiFS) concentration (log-scale) (column 2): and the pixel-by-pixel correlation between the seasonal productivity index and chlorophyll (column 3).

an important role in the emerging area of dynamic ocean management, and they may be useful in a range of applications, including catch standardization, habitat prediction, ecosystem models, spatial management, bycatch reduction, marine spatial planning, and development of harvest strategies (Hobday et al., 2014). While several of these derived products are available at a global scale, we recommend development of regional products, as the critical values or thresholds of any given variable (primary or derived) will vary regionally, and even with regard to the species under study.

Here, we have illustrated derived products that describe physical processes or habitats, but note that many higher trophic level species are attuned to availability and distribution of prey. Prey fields are an additional derived variable that may offer increased explanatory power over primary variables in understanding the distribution and abundance of pelagic species (Schick and Lutcavage, 2009, Handegard et al., 2013). Basin-scale prey field data sets are now generated from some models (e.g., Lehodey et al., 2010), but they can differ from field-based observations by orders of magnitude (Kloser et al., 2009). Until improved prey observations are available to refine models (Handegard et al., 2013), it is unlikely that prey field data will be as commonplace as physical descriptions of ocean conditions. It is partly due to availability that the primary products we describe are so widely used, but the derived products based on them should be equally useful until products such as prey fields, which better describe the linkages between physics and high trophic level pelagic species, are available.

Just as biomes and habitats have become base layers in terrestrial spatial planning, both derived and primary ocean variables are important in a range of marine spatial planning applications. These derived products also lend themselves to application in dynamic management, as they implicitly represent features (e.g., eddies) that are nonstationary. Given that managing present-day activities and threats is important in many sectors, use of derived products and recognition of dynamic habitat features offer a range of benefits, not least of which is reducing areas in which activities are prohibited (Hobday et al., 2014). To date, most dynamic planning has been undertaken to manage the impacts of fishing and bycatch (Hobday and Hartmann, 2006; Howell et al., 2008; Hobday et al., 2014), but the growing need for more dynamic ocean management in response to increased pressures will see growth in other areas (Ban et al., 2014; Hobday et al., 2014; Merrie et al., 2014).

A focus on habitat representations in dynamic management also has advantages under climate change, as circulation changes will result in habitat shifts (e.g., Hartog et al., 2011; Hobday, 2011). Understanding the future distribution and abundance of fish species is a priority, and planning robust management relies on global climate model (GCM) forecasts, which do not represent mesoscale features (Stock et al., 2011). However, some of the derived products illustrated here can be calculated from the output of downscaled climate models (e.g., Sun et al., 2012; Dell et al., 2014), and access to such downscaled model data will become easier in the next few years, just as access to primary GCM data is now facilitated in central repositories (Stock et al., 2011).

It will be important to formally evaluate in a range of geographic locations whether the inclusion of derived variables leads to an improvement in model explanatory power over models using primary and "external" (e.g., latitude, month) variables, and, in particular, whether the use of derived variables leads to the removal of primary and external variables. If use of variables that are more related to the habitat as experienced by pelagic species (e.g., fronts, eddies) leads to better predictions of the response variables (e.g., abundance and distribution), then further study may be fruitful. If there is no improvement, then it is worth asking the question of biological/fisheries

oceanography in general: has the pursuit of environment-biology relationships reached a prediction barrier? If this is the case, we must consider including more difficult derived variables representing behavior and prey availability to better understand the drivers of distribution and abundance and to support effective ocean management of pelagic species.

ACKNOWLEDGEMENTS. We appreciate the past and ongoing funding support from the Fisheries Research and Development Corporation (FRDC), Australian Fisheries Management Authority (AFMA). and Commonwealth Scientific and Industrial Research Organisation (CSIRO), and assistance from many scientists involved in the Bluelink project, including David Griffin, Peter Oke, Scott Condie, and Richard Matear. Catch data were provided by AFMA and Rob Campbell, and we thank Dan Gledhill for species illustrations. We appreciate the collegiality of Dave Foley in the sharing of code to undertake eddy identification and tracking and Peter Cornillion for the SST front detection algorithm. Review by Scott Condie helped to tighten the language in an earlier draft, and the final version was improved by comments from Daniel Dunn, Elliott Hazen, and an anonymous reviewer.

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