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Regimes of chlorophyll-a in the Coral Sea: implications for evaluating adequacy of marine protected areas

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Spatial management of the highly dynamic pelagic realm, and the highly mobile species it supports, requires dynamic processes to be incorporated into reserve design. To achieve this, planners need information on how these processes vary across space and time, and how this variation relates to species of conservation interest. This study presents a new method of quantifying variability that captures both between- and within-year changes in variables of interest. We applied this method to remotely-sensed chlorophyll-a in the Coral Sea to find five distinct regimes of variation that serve as surrogates for assemblages of species of conservation interest. We performed a gap analysis to determine protection of the regimes both internationally and nationally within Australia's network of marine reserves in the Coral Sea. We also identified key areas for protection within each regime, in terms of chlorophyll-a variability and species associations, and examined their protection status. Depending on conservation objectives, reserve systems that span multiple national jurisdictions and a rezoning of Australian national waters might be necessary to meet protection requirements for the regimes and for key areas within them. The current suspension and review of the Coral Sea Commonwealth Marine Reserve management plans and the recent proclamation of New Caledonia's as yet unzoned Coral Sea Nature Park offer planners an opportunity to incorporate dynamic processes into conservation planning for the Coral Sea. The method we present can be applied at other locations for time-series of any variable/s of interest, aiding the spatial management of dynamic features in both marine and terrestrial contexts.

Spatial planning is an important tool for managing and mitigating human impacts on the environment (Douve 2008, O'Leary et al. 2012). Most current methods for planning terrestrial and marine protected areas are based on static depictions of the physical and biological characteristics of regions (Pressey et al. 2007). However, a range of features relevant to conservation planning are dynamic (Grantham et al. 2011, Hobday et al. 2011). Here, we use 'dynamic' to refer to features that are variable in space and/or time. Further, we refer to dynamic features as a subset of processes – sequences of changes in the physical or biological properties of the environment – that operate over spatial and/or temporal scales relevant and amenable to management (Pressey et al. 2007). Examples of such processes are adjustment of species' ranges to climate change (Hannah et al. 2007), larval connectivity (Blowes and Connolly 2012), aggregations of megafauna (Zainuddin et al. 2006), diversification of lineages (Rouget et al. 2003), and the spatio-temporal dynamics of disturbance (Leroux et al. 2007) and resources (Hobday and Hartmann 2006).

Dynamic features are not necessarily protected by reserve systems designed to protect static features (Pressey et al.

2007). If features are dynamic over spatial extents that are small in relation to reserve size, they might be protected by happenstance. Examples might be the oxbows formed by small rivers, or treefall gaps and associated successional processes. If features are dynamic at temporal scales that are long in relation to the temporal scale of reserve design, they might be protected because reserve planners have ample time to respond (e.g. shifts of vegetation classes towards the poles in response to climate change). However, features that are dynamic across large spatial scales and over short timeframes, relative to reserve design, are less likely to be protected adequately unless such features are specifically incorporated into the design of protected areas (Pressey et al. 2007).

Planning directly for dynamic features both guarantees their protection, and increases the likelihood that patterns of biodiversity within protected areas will not become outdated. For example, a reserve system designed to accommodate species' movements in response to climate change is more likely to protect species long-term than a reserve system designed around species occurrences at one point in time (Rouget et al. 2003, Ban et al. 2012). The need to incorporate dynamic features explicitly into conservation planning

is widely recognized (Groves et al. 2012), but there are few examples (Pressey et al. 2007), and these are spread thinly across diverse geographies and types of dynamics.

There is an apparent paradox in conservation planning being inherently spatial, while needing to address the persistence of features that are dynamic in both space and time. However, spatial surrogates – the physical or biological features with which processes of interest are associated (Rouget et al. 2003) – can help planners understand the spatial dimensions of processes of interest and requirements for management to promote their persistence. For example, permanent bathymetric features such as seamounts and shelf breaks are static surrogates for upwellings (Hyrenbach et al. 2000). Chlorophyll-*a* and sea-surface temperature can be of ecological and conservation interest in their own right, but are also dynamic surrogates (Weeks et al. 2006, Alpine and Hobday 2007, Lombard et al. 2007) and static surrogates (Peñaflor et al. 2009, Hobday et al. 2011) for water-mass boundary fronts and other hydrological processes.

In this context, spatial surrogates are features that mediate processes (seamounts are a static example) or are consequences of processes (concentrations of chlorophyll-*a* are dynamic examples). Planning with spatial surrogates requires identification of a remotely detectable feature that accurately reflects the spatial and temporal variability of processes of interest (Lombard et al. 2007, Groves et al. 2012).

The effectiveness of protected areas can depend on how long dynamic features remain within reserve boundaries (Woinarski et al. 1992, Alpine and Hobday 2007). This is particularly challenging in marine conservation planning, where features can vary with frequencies, magnitudes, and scales unseen in most terrestrial environments (Carr et al. 2003). An important aspect of dynamic features in the ocean is their persistence, or how long they remain in any particular area (Hyrenbach et al. 2000). A feature's persistence is related to its ability to concentrate biodiversity: long-lasting features will aggregate more species than short-term features (Grantham et al. 2011, Ban et al. 2014). We use the term 'variability' to refer to variation of a dynamic feature of interest in both space and time, thereby including the idea of persistence. Since the short-term variability of dynamic marine features can change through time, for example with El Niño Southern Oscillation cycles or gradual climate change, it is necessary to review historical behavior and/or to forecast future behavior to effectively incorporate dynamic features into the design of protected areas.

The variability of dynamic features can be described with historical time-series based on satellite imagery. Time-series data provide information on the past variation of features, from which inferences can be drawn about variation in the near future (Ban et al. 2012). Temporal and/or spatial averaging are frequently applied to reduce the temporal resolution (resulting in fewer images in the time-series) and/or the spatial resolution (resulting in fewer pixels in each image). This reduces the volume of data and can allow characteristics of variability to emerge.

Temporal averaging can be applied across the entire time-series to produce a sole image depicting overall average conditions for each pixel (Grantham et al. 2011, Redondo-Rodriguez et al. 2012). This can involve a significant loss of information by accepting one value as representative for a

location. If a feature displays little variability, this method might be appropriate. However, if a feature varies greatly in space and/or time (e.g. the Northern Pacific chlorophyll front migrates 1000 km seasonally; Polovina et al. 2001), the average value of associated variables in many pixels will poorly represent the full spatial extent of the feature of interest at any point in time. More information on variability can be preserved by averaging temporally within multiple subdivisions of the time-series (Bograd et al. 2004, Heron et al. 2006, Peñaflor et al. 2009, Weeks et al. 2010, Thomas et al. 2012). However, temporal averaging across the entire or subdivided time-series does not preserve information on the spread of data around average values, which is a potentially important measure of the magnitude of change over time at any given location.

In this study, we sought to characterize the variability of chlorophyll-*a* – a proxy for phytoplankton biomass (Weeks et al. 2006) – in the Coral Sea, and to interpret this variability in terms of conservation planning. Methods for remotely detecting marine chlorophyll-*a* are well developed, and a long time-series of satellite images is available. Sharp gradients in chlorophyll-*a* mark the boundaries of processes such as upwellings, fronts, and eddies. The hydrological dynamics of these processes cause high levels of chlorophyll-*a* by increasing the availability of nutrients for primary production compounded by concentrating primary producers at high densities (Polovina et al. 2001, Yen et al. 2004). Primary consumers exploit these productive areas, in turn attracting species in higher trophic levels (Weimerskirch 2007). Many pelagic species of conservation interest have been observed aggregating within these highly productive areas, including tuna (Polovina et al. 2001, Zainuddin et al. 2006), turtles (Polovina et al. 2000, 2001, 2004), seals (Lombard et al. 2007), seabirds (Russell et al. 1999, Weimerskirch 2007, Grémillet et al. 2008), and cetaceans (Hyrenbach et al. 2000, Ardron et al. 2008). To promote the persistence of these species, which are highly mobile and widely dispersed, high-concentration patches of chlorophyll-*a* provide a surrogate for areas of likely aggregation, and are therefore high priorities for protection.

The Coral Sea provides an opportunity to explore conservation planning in the pelagic realm. Currently, the pelagic realm – oceanic waters non-adjacent to land where species and processes have minimal interaction with the substratum – has less than 2% of its waters under protection (Spalding et al. 2013). Calls for a paradigm shift in pelagic protection and management (Worm et al. 2003, Ban et al. 2014) have been motivated by increasing awareness of both overexploitation of pelagic resources and the sensitivity of the realm to human activities such as shipping, waste dumping, and climate change (Ardron et al. 2008, Halpern et al. 2008, Game et al. 2009). The nature of the environment – highly dynamic with highly mobile species – necessitates that protected areas in the pelagic realm are designed to incorporate dynamic features.

In this context, our study has four aims. The first is to introduce a new method of quantifying variability that captures both between- and within-year changes in variables of interest. Second, we set out to characterize chlorophyll-*a* in the Coral Sea using ten years of remote-sensing data to find distinct regimes of variability. Third, we wanted to

identify key areas for conservation within each regime, both in terms of values of chlorophyll-a and localized biological features. Fourth, we aimed to examine the protection of regimes at the international level, and nationally within Australia's network of protected areas in the Coral Sea. This study serves to better link studies of remote sensing of dynamic features and conservation planning. Both research areas are well represented individually in the marine literature but, with few exceptions (Alpine and Hobday 2007, Lombard et al. 2007, Grantham et al. 2011), have not been applied concurrently. Our paper adds to this small body of research by demonstrating a novel approach to incorporating regimes of dynamic, remotely-sensed features into spatial planning.

Methods

Study area

The Coral Sea (Fig. 1) lies between the eastern Australian continental shelf to the west, New Caledonia and Vanuatu to the east, and is bordered to the north by the Torres Strait, Papua New Guinea, and the Solomon Sea. To the south, the Tasman Front separates the Coral Sea from the Tasman Sea. Our study covered the waters between 142.5°–165.2°E and 6.1°–24.5°S, a total area of 4 938 784 km². This region includes parts of the Exclusive Economic Zones (EEZs) of

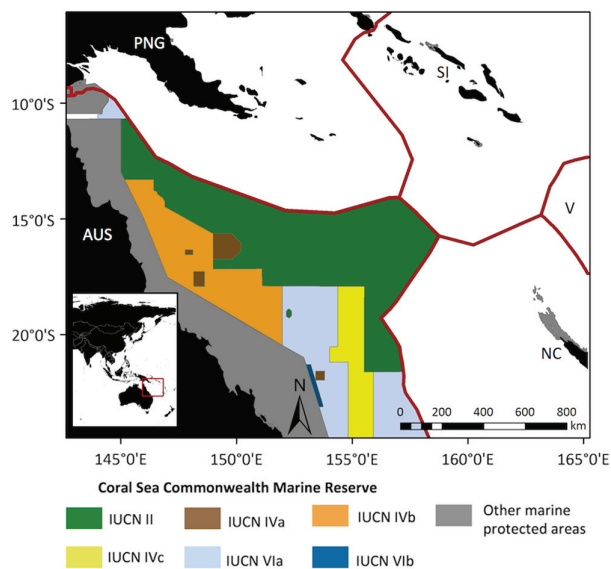


Figure 1. The study area. Red rectangle in inset map delimits study area. Main map shows marine reserves and Exclusive Economic Zones (EEZs) within the study area. Red lines in main map indicate boundaries of EEZs. Countries with EEZs in the study area (clockwise from left) are: Australia (AUS); Papua New Guinea (PNG); Solomon Islands (SI); Vanuatu (V – land not visible); and New Caledonia (NC). International Union for Conservation of Nature (IUCN) categories in the Australian Coral Sea Commonwealth Marine Reserve are shown. IV and VI categories are subdivided to reflect differences in allowed activities in sub-categories (Table 1). We hereafter refer to the IUCN categories and sub-categories as zones. For information on the objectives of the IUCN categories see Dudley (2008).

Table 1. Class probability analysis for regime success. Class probability is a pixel-by-pixel analysis based on the probability of pixel membership to each regime. Values in column 2 were calculated across the pixels allocated to each regime. Columns 3–6 are the percentages of each regime within different classes of probability of membership.

	Average probability across regime	Percentage of regime within probability intervals			
		100–95%	95–90%	90–50%	50–0%
Regime 1	92.41%	85.03%	2.29%	6.31%	6.38%
Regime 2	87.62%	77.48%	3.78%	7.75%	11.00%
Regime 3	83.57%	71.74%	3.98%	9.42%	14.86%
Regime 4	92.68%	86.63%	2.87%	4.97%	5.54%
Regime 5	90.17%	83.63%	2.70%	5.14%	8.53%

five countries: Australia, Papua New Guinea, the Solomon Islands, Vanuatu, and New Caledonia. Waters within EEZs are under national jurisdictions, and include the ocean to 200 nm offshore. Where there is less than 400 nm of ocean between the coasts of two countries, the EEZ boundaries are pulled back (UNCLOS 1982), following an agreement between countries; e.g. treaty between Australia and the Independent State of Papua New Guinea (CoA 1995).

Australia's portion of the Coral Sea is almost entirely covered by the Great Barrier Reef Marine Park, the Torres Strait Protected Zone Joint Authority, and the Coral Sea Commonwealth Marine Reserve (CSCMR). The CSCMR is divided into protected-area categories recognized by the International Union for Conservation of Nature (IUCN) (Fig. 1, Supplementary material Appendix 1, Table A1). Those parts of the EEZs of Papua New Guinea, the Solomon Islands, and New Caledonia within the study area also contain reserves. All marine reserves in the study area lie within the Exclusive Economic Zones of their governing countries, with the exception of the Torres Strait Protected Zone Joint Authority, which spans the EEZs of Australia and Papua New Guinea (Fig. 1). Adjustments of the study area for the purposes of analysis are discussed in section Data preparation.

Satellite data

We acquired MODIS Aqua chlorophyll-a L3 standard mapped images from January 2003 (the first full year of coverage) to December 2012 (most recent full year at time of analysis). This data set was chosen over those from other ocean colour sensors for its currency and quality of data (Franz et al. 2005). We used a Data Products tool within the Marine Geospatial Ecology Tools package (Roberts et al. 2010) to download the images into ArcGIS 10 from the NASA OceanColor website (< <http://oceancolor.gsfc.nasa.gov/> >). Balancing the potential loss of data variation through spatio-temporal compositing against the improvement in data density, we chose to use 9-km, monthly composites, resulting in 120 composites across the 10-yr period. Each composite contained 48 953 ocean pixels with values representing chlorophyll-a concentration in mg m⁻³, or no data (Supplementary material Appendix 2, Table A2). All image preparation and analyses were completed in ArcGIS 10.

Data preparation

To focus the analysis on dynamic pelagic processes, the following areas were excluded from consideration: pixels within the Great Barrier Reef Marine Park and the Torres Strait Protected Zone Joint Authority (largely covering continental shelf), and all remaining pixels within 30 nm of land (Supplementary material Appendix 2, Fig. A1; Table A2). Pixels in the Gulf of Papua were found to have extremely high chlorophyll-a values, possibly caused by the outflow of the Fly River. Although this region contains processes of ecological significance, our study sought to highlight differences in chlorophyll-a within oligotrophic pelagic waters, and so pixels in the Gulf of Papua were removed. The exclusion of near-coastal regions has an added benefit of reducing the potential for erroneous data values due to bottom reflectance in optically-shallow conditions (Weeks et al. 2010).

Even using monthly 9-km composite images, there were substantial numbers of pixels missing data. We filled missing pixels spatially using the Del2a fill within the Marine Geospatial Ecology Tools package (Roberts et al. 2010). For the few cases where the Del2a fill resulted in non-physical negative values, we revalued pixels to zero. The fill process reduced the amount of missing data from 9.0% of all pixels across the time-series to 5.8%.

Analysis of the mean concentration and variability for each month and pixel (section Analyses) required a minimum data density to ensure consistency. Where a pixel was missing data for more than half of the time-series for any month, we excluded the pixel from the analysis. After these exclusions, a total of 38 553 pixels remained in the analysis (Supplementary material Appendix 2, Table A2).

Analyses

We characterized each pixel by two parameters for each month of the year: climatological average concentration and predictability. These values captured the variation in concentration within- and between-years, both of which are important in describing variation in chlorophyll-a (Condal et al. 2013) and differentiating between types of oceanographic processes (e.g. static, persistent, ephemeral) relevant to conservation planning. Climatological average concentration indicated the magnitude of chlorophyll-a concentration over the time-series in any given pixel in each month of the year. Predictability referred to the consistency in values of monthly concentration over the time-series. It is thus the ability, for any month of the year, to forecast the monthly concentration from one year to another, for example to predict the January 2013 concentration from that in previous years. Within-year variation, or the range in monthly values of climatological average concentration and predictability, carried information on seasonality.

Concentration and predictability analyses

We averaged the monthly composites for each month of the year across the 10-yr time-series to produce 12 monthly climatologies representing overall average concentration for each pixel. We defined predictability as one minus the

normalized coefficient of variation (CV) in monthly concentration values across the time series for each month of the year. We chose this statistic over others, such as standard deviation or variance, for two reasons: it removes the inherent correlation between large numbers and large variances by standardizing values with respect to the mean; and use of the square root of the variance makes the differences between small values become proportionally larger. The latter was desirable because chlorophyll-a concentration is commonly low in tropical pelagic waters, yet small differences can be important ecologically and represent different oceanographic processes.

To facilitate comparisons across months, we normalized the 12 monthly images of coefficient of variation to the scale 0–1, based on the lowest and highest values, respectively, of any pixel in any of the 12 monthly images. Finally, we subtracted normalized values from one, such that highest and lowest predictability values were one and zero, respectively:

$$CV_{(i)} = \frac{\sigma_{(i)}}{\mu_{(i)}} \quad (1)$$

$$Predictability_{(i)} = 1 - \left(\frac{CV_{(i)} - CV_{(min)}}{CV_{(max)} - CV_{(min)}} \right) \quad (2)$$

where $CV_{(i)}$ is the coefficient of variation of pixel(i) for a given climatological month calculated as the ratio of climatological standard deviation $\sigma_{(i)}$ to the climatological mean $\mu_{(i)}$, and $CV_{(min)}$ and $CV_{(max)}$ are the lowest and highest coefficient of variation values for any pixel in any month of the year, respectively.

Classifying regimes of chlorophyll-a

With every pixel in the study area characterized by 24 values (values of climatological average concentration and predictability for each month of the year), we sought to understand distinctive regimes of variation with a cluster analysis of pixels. We defined regimes as groups of pixels with similar within-year variation in climatological concentration and predictability. To find regimes, we used the hierarchical Iso Cluster Unsupervised Classification tool in ArcGIS, which has been previously applied to time-series data (Erkkilä and Kalliola 2004). We input the 12 monthly climatologies of average concentration and the 12 monthly images of predictability as variables and set the initial number of clusters (regimes) to 10, which we considered a conservatively high number. We used default settings for all other parameters.

Validation of regimes

We demonstrated the validity of regimes using two methods, one qualitative and one quantitative. In the first, we explored interactions between large-scale processes known to influence chlorophyll-a to determine if the patterns found by the cluster analysis were supported by conditions on the ground. Second, we quantified cluster success using the Class Probability tool in ArcGIS. This tool uses variable means and variance-covariance matrices for each regime, and the original 24 variables (monthly images of climatological concentration and predictability) to calculate the probability of each pixel's membership to each regime. We then

calculated average probability of membership across all pixels within each regime, and the percentage of each regime's pixels within different probability intervals.

Regimes of chlorophyll-a in relation to the Australian EEZ and the Coral Sea Commonwealth Marine Reserve (CSCMR)

We measured the coverage of regimes by EEZs in terms of percentage of each regime's total extent in the study area and coverage of regimes by CSCMR zones in terms of percentage of each regime's extent in Australian waters. These analyses correspond to the common assumption that, like other environmental surrogates (Pressey 2004), regimes convey information about physical and biological patterns and processes of conservation interest.

Distinctive parts of regimes

We identified areas within regimes that could be considered as having particularly high conservation significance. These analyses correspond to the common assumption that broad environmental surrogates, due to their heterogeneity, are not sufficient as a sole guide for conservation planning (Pressey 2004). We recognized heterogeneity within regimes in two ways. First, we used one regime as an example to illustrate spatial variation in climatological concentration and predictability by identifying two categories of pixels within each month of the year: pixels with above-average concentration and predictability (potentially high priority for management), and pixels with below-average concentration and above-average predictability (potentially low priority for management). To capture within-year persistence of these characteristics, we selected pixels contained in either category for at least eight months of the year.

Second, we compiled information on pelagic species associated with each regime to highlight areas with particular biological significance. No prior systematically collected data on key species and their habitats exists for this region.

We used Web of Science literature search for 'Coral Sea' and 'Western Pacific' and followed this with an exhaustive search for all documents cited within the first round of literature found. This included sourcing hard copies of older papers and reports. A database of documented Coral Sea research with explicit species occurrences was compiled before the identification of the five regimes (Supplementary material Appendix 3, Table A3). We limited our review to the pelagic waters and species of the regimes, omitting benthic observations of the deep seabed, submerged seamounts, and emergent reefs.

Results

Overview of concentration and predictability

An overview of the spatial variability in chlorophyll-a across the Coral Sea can be gained from temporally averaging climatological concentration and (separately) predictability across all months of the year (Fig. 2). Generally, gradients in concentration were apparent from high values adjacent to the 30 nm buffers (maximum 0.62 mg m^{-3}) to low values in the open ocean (minimum 0.06 mg m^{-3}) (Fig. 2A). The highest concentrations of chlorophyll-a are in the northernmost and southernmost sections of the study area, with a band of generally lower concentration between these. There were several isolated, distinct high-concentration patches within the Australian and New Caledonian EEZs. The predictability image showed a general gradient from high values in the southwest (maximum 0.95), to low values in the northeast (minimum 0.66) (Fig. 2B).

Regimes of chlorophyll-a

The results of the cluster analysis (Fig. 3) were consistent with the observed latitudinal variation in the annual climatological average concentration and the SW-NE variation in predictability. The initial setting for the number of clusters was, as expected, excessive; the resultant dendrogram

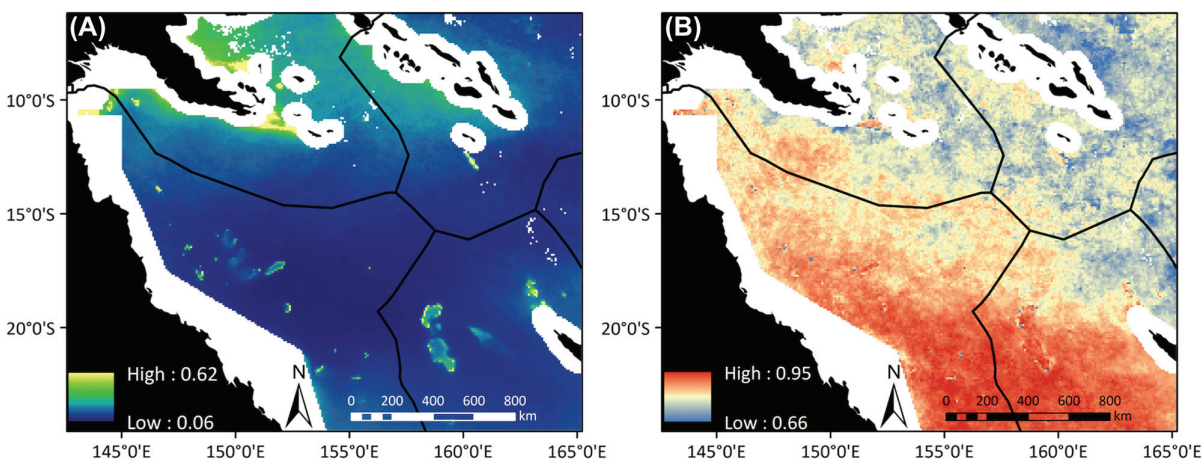


Figure 2. Spatial variation in chlorophyll-a patterns across the Coral Sea. Averages calculated across all months of the year for (A) monthly climatological average concentration (mg m^{-3}); and (B) monthly predictability (unit-less). Black lines indicate the boundaries of Exclusive Economic Zones (see Fig. 1 for countries associated with each EEZ).

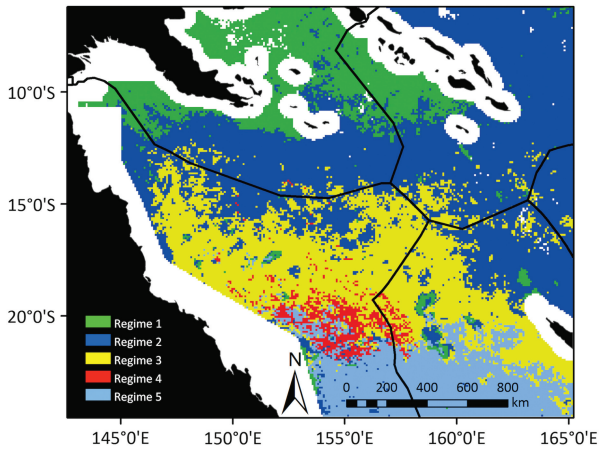


Figure 3. The five regimes of chlorophyll-a within the study area. Regimes are groups of pixels with similar between- and within-year variability in chlorophyll-a, characterized by climatological average concentration and predictability. Black lines indicate the boundaries of Exclusive Economic Zones (see Fig. 1 for countries associated with each EEZ).

(Fig. 4A) led us to reduce the number of clusters (regimes) to five (Fig. 4B), based on the reduction in inter-cluster distance and supported by an interpretation of oceanography and bathymetry. For ease of reference and due to the latitudinal pattern, the regimes are numbered from north (1) to

south (5) across the study region (Fig. 3). The dendrogram (Fig. 4B) showed regime 1 to be the most distinct, followed by regimes 5 and 4. Regimes 2 and 3 were the most similar.

Regime 1 included waters between Cape York and the Solomon Islands, and several isolated patches throughout the study area (Fig. 3). Mean concentration reached a peak in July of 0.17 mg m^{-3} , and highest mean predictability values were from May through July (>0.87) (Fig. 5A). Regime 2 covered the eastern extent of the study area from north of New Caledonia, and extended west below the Solomon Islands and Papua New Guinea (Fig. 3). In this part of the study area, mean concentration reached a winter peak of 0.11 mg m^{-3} from June to August, and highest mean predictability values were in June and July (>0.87) (Fig. 5B). Regime 3 was adjacent to the central portion of the Great Barrier Reef Marine Park and extended east and south through the study area to the southwestern side of New Caledonia (Fig. 3). There was a winter peak in mean concentration during July and August of 0.10 mg m^{-3} , and highest mean predictability was in November (0.91) (Fig. 5C). Regime 4 was largely located within the Australian EEZ (Fig. 3). There was a winter peak in mean concentration of 0.11 mg m^{-3} in July and August, and mean predictability was uniformly high, remaining between 0.9 and 1.0 across all months (Fig. 5D). Regime 5 was along the southern edge of the study area stretching from Australia towards New Caledonia (Fig. 3). This regime had the most distinctive winter peak in mean concentration, with highs of 0.14

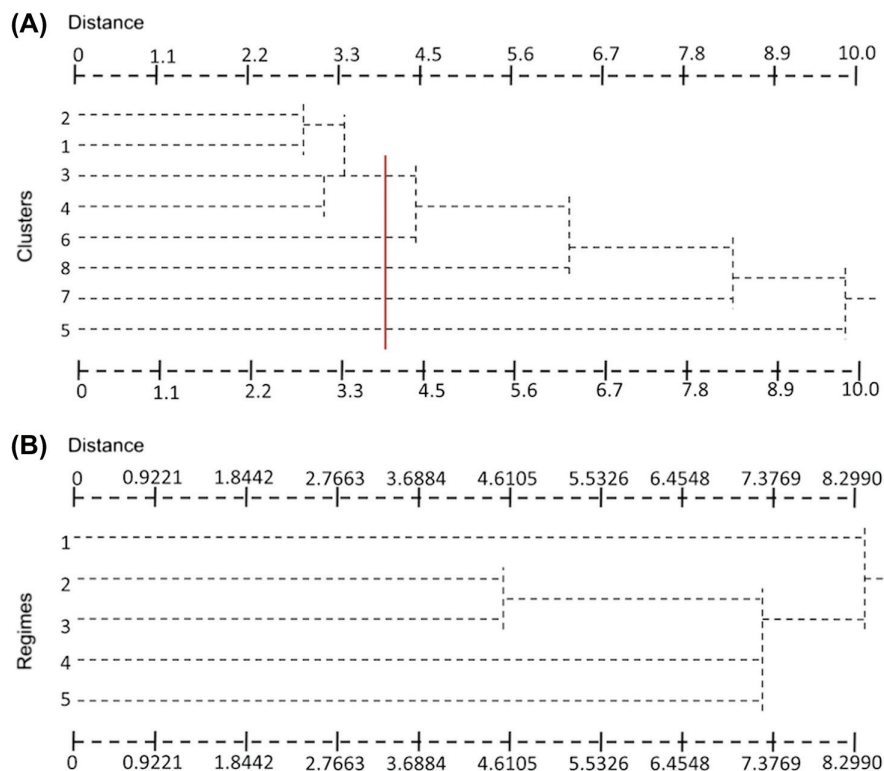


Figure 4. Dendrograms showing the Euclidean distance between chlorophyll-a clusters. Shorter distance of separation (horizontal axis) indicates higher degree of similarity between regimes. (A) The dendrogram from the initial setting of 10 clusters depicts only eight groupings, because neighboring clusters that were statistically similar were merged during the iterative process. (B) The final dendrogram after the number of clusters was reduced to five, corresponding to the red vertical line in (A). In (B), regimes 5 and 4 have similar but distinct separation points; 7.33 and 7.29, respectively.

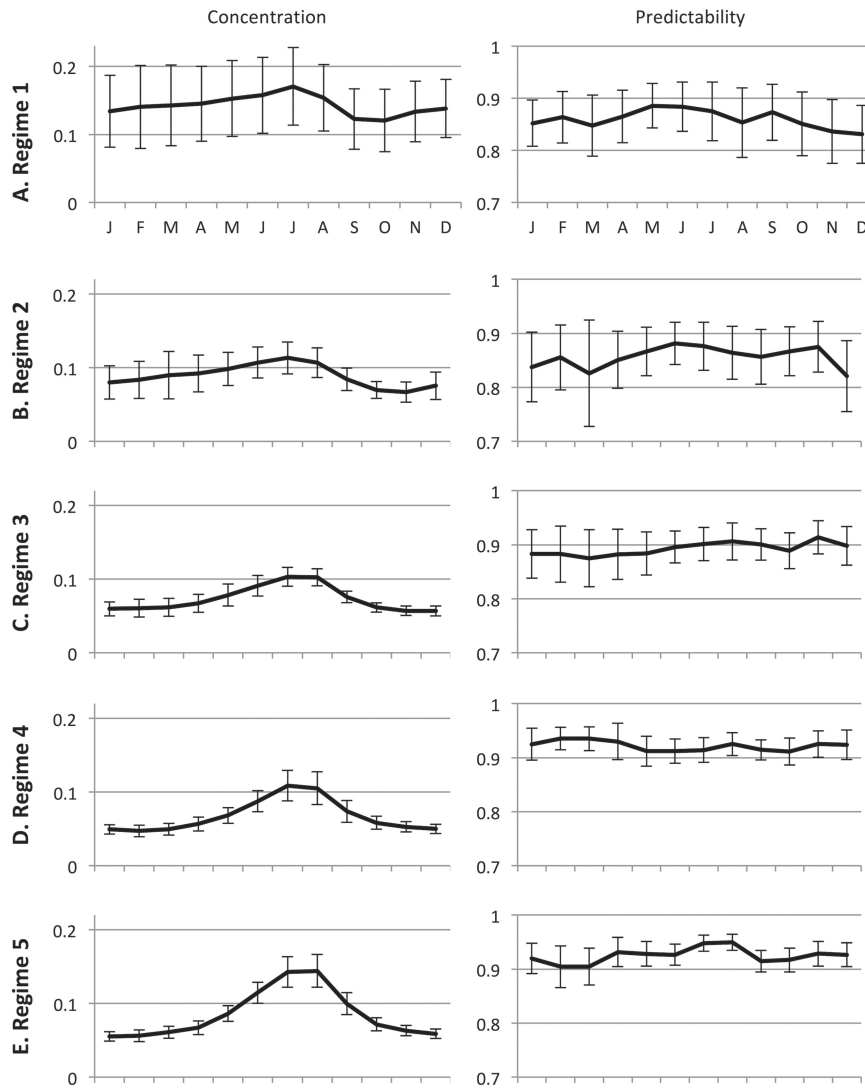


Figure 5. The seasonal characteristics of the five Coral Sea chlorophyll-a regimes. For each regime, graphs show the spatial mean of: (left panel) monthly climatologies of average concentration (mg m^{-3}); and (right panel) monthly predictability (unit-less) for each regime. Whiskers indicate one standard deviation.

mg m^{-3} in July and August, coinciding with a similar winter peak in mean predictability (0.95) (Fig. 5E).

The relationship between regimes, based on their signatures of chlorophyll-a concentration and predictability, changed from month to month (Fig. 6). Regime 1 had the highest concentration across all months, and had the lowest predictability in six of the months. Regime 2 had the second highest concentration, except during winter months (Fig. 6 – August), and had the lowest predictability in six of the months (Fig. 6 – March, December). Generally, regimes 3 and 4 had low concentrations and high predictabilities. For much of the year, regime 5 was similar to 3 and 4 in terms of concentration and predictability, but had a distinct peak in concentration and predictability during winter (Fig. 6 – August).

Regime validation – qualitative

Interactions between oceanography (Fig. 7A, B), bathymetry (Fig. 7C, D), and adjacent landmasses supported the distinct

chlorophyll-a signatures of the five regimes. Regime 1 is dominant on the Papua New Guinean shelf and in the Solomon Sea, but is also scattered across topographic high points in the Coral Sea, including oceanic coral reefs and emergent seamounts. It is well known that, in oligotrophic seas, reefs and seamounts are associated with patches of higher productivity; the causes include benthic communities attached to the structures, particles entrained by water movements, and upwellings of deep nutrient-rich waters (Couvelard et al. 2008). The margins of the Coral Sea have previously been found to have higher chlorophyll-a concentrations than the interior (Furnas and Mitchell 1996). Regime 1 waters in the Gulf of Papua are influenced by the Gulf of Papua Current, also known as the Hiri Gyre. This gyre plays a role in the biological oceanography of the area, entraining and distributing larvae of commercially important species (e.g. rock lobsters, freshwater eels) and potentially retaining relatively high nutrient concentrations generated by discharge from the Fly River (Ceccarelli et al. 2013). Furnas and Mitchell (1996) found that the Solomon Sea had

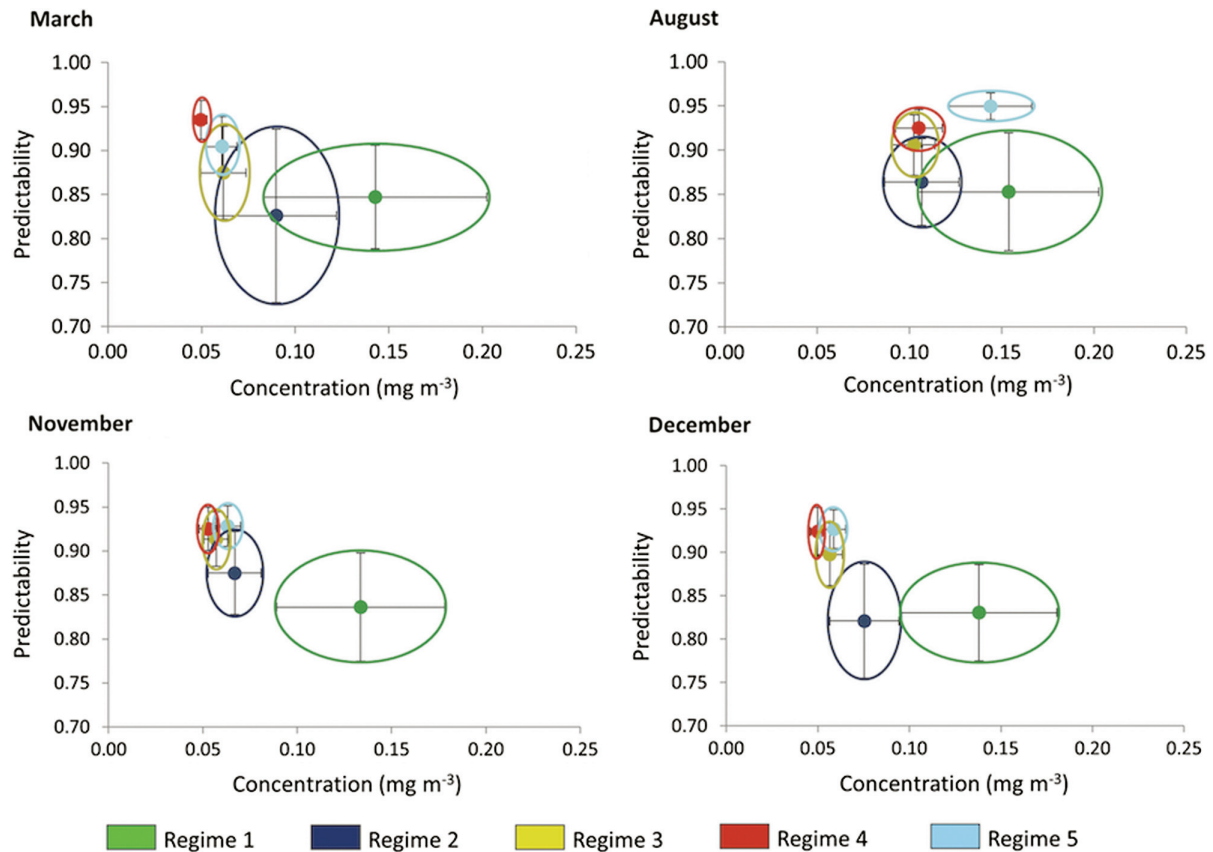


Figure 6. Examples of monthly signatures of chlorophyll-a regimes. For four selected months, plots show the spatial means (filled dots) and standard deviations (whiskers) of monthly climatologies of average concentration (horizontal) and monthly predictability (vertical) for each regime. Ellipses are shown to identify overlaps between regimes.

higher rates of primary production than the Coral Sea to the south. Flooding from seasonal summer rainfall (Smith et al. 2008) probably contributes to elevated concentrations during months outside of the typical winter chlorophyll-a peak. Regime 1 also has relatively low and spatially variable predictability, perhaps reflecting the influence of variability in the Gulf of Papua Current, the New Guinea Coastal Current, and outflows from the Fly River.

Regime 2 is to the north of the main east-to-west jets of the South Equatorial Current and is most closely associated with the North Vanuatu Jet (Gourdeau et al. 2008). These jets turn northward against the Australian continental shelf, influencing the oceanography of the Gulf of Papua and the Solomon Sea (SPICE Community 2012). The strength of the jets varies seasonally and their seasonality is highly variable between years (Steinberg 2007), which might explain the relatively low, and spatially variable, predictability of regime 2. The South Equatorial Current is strongest from September to December (Condie and Dunn 2006), suggesting that the influx of oligotrophic Pacific Ocean water might be causing the low chlorophyll-a concentration of regime 2 over these months. Regime 2 might also be affected seasonally by the Gulf of Papua Current, bringing seasonal influxes of higher-concentration water from the north.

Regimes 3 and 4 lie within the central area of east-west flow, and chlorophyll-a might be somewhat influenced by eddies

cleaving from the East Australian Current. Topographically, these two regimes coincide with the Townsville Trough, the southern Queensland Plateau, the Marion Plateau, and the northern Chesterfield Plateau. Both regimes have relatively low concentrations and high predictabilities, probably in part because they are both far from shore and so beyond the influence of run-off or upwelling. Regime 4 has a stronger seasonal signal of concentration and a higher predictability than regime 3, which might be caused by a combination of cooler temperatures – which can increase vertical mixing of the water column as surface layers cool and sink (Racault et al. 2012) – and interactions between currents and bathymetry.

Regime 5 is likely influenced by the East Australian Current and associated eddies, cooler waters from the Tasman Sea, and a more pronounced seasonality in current strength. It coincides with the Marion Plateau, the Kenn Plateau, the Chesterfield Plateau, and the Tasmantid Seamount Chain. Increased chlorophyll-a concentrations in winter might coincide with the raised topography of the Kenn Plateau because this regime ends abruptly at the edge of this plateau and gives way to regime 3 with lower concentrations. The South Caledonia Jet, off the southern margin of Fig. 7A, B, is highly episodic (Kessler and Cravatte 2013), but is unlikely to significantly affect the predictability of this regime.

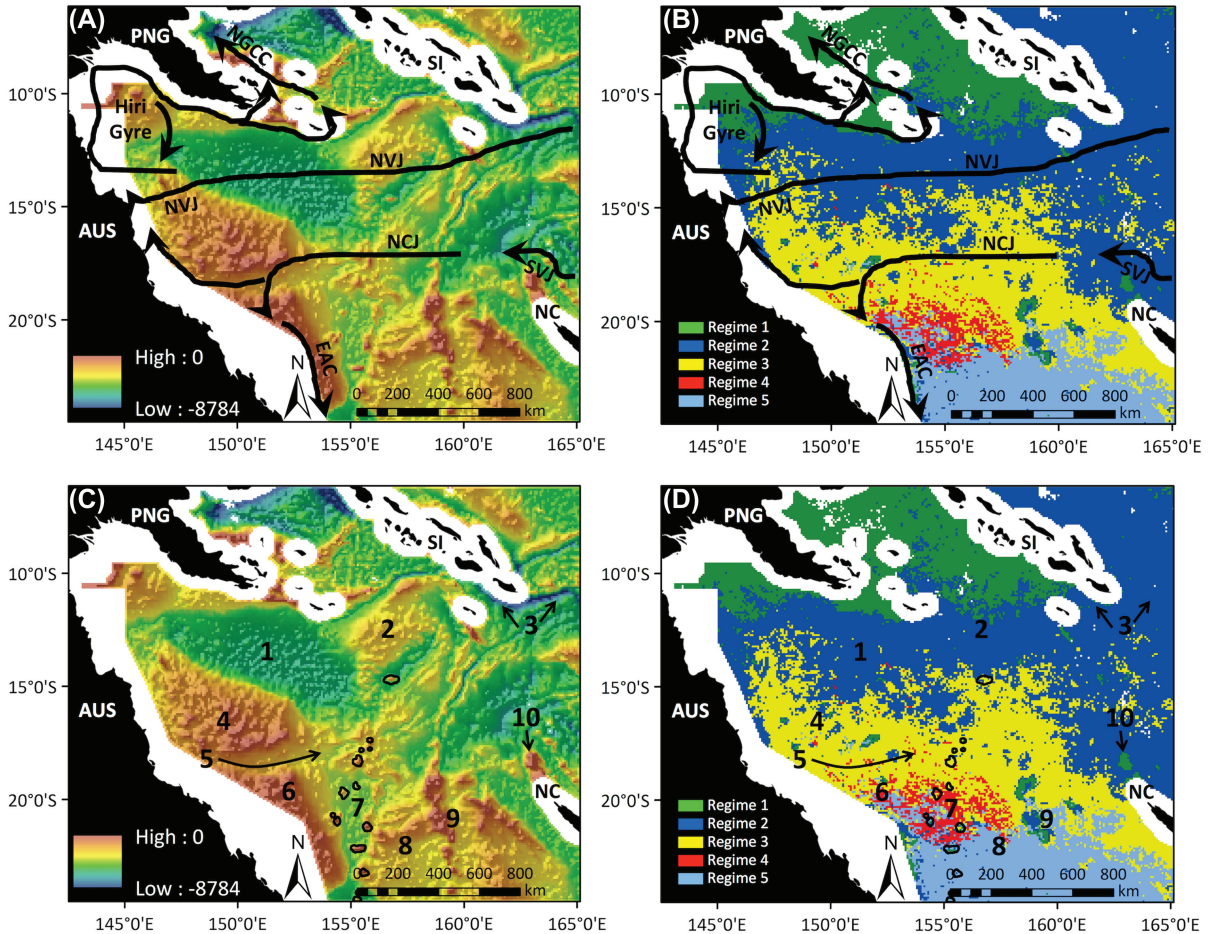


Figure 7. Bathymetry and oceanography of the study area in relation to chlorophyll-a regimes. (A) Oceanography. The South Equatorial Current enters the Coral Sea in four jets: the North Vanuatu Jet (NVJ), the South Vanuatu Jet (SVJ), the North Caledonia Jet (NCJ), and the South Caledonia Jet which flows just to the south of the study area. Also shown are the East Australian Current (EAC), the New Guinea Coastal Current (NGCC), and the Hiri Gyre. (B) Regimes in relation to oceanography. (C) Major bathymetric features: 1. Coral Sea Basin; 2. Louisiade Plateau; 3. New Hebrides Trench; 4. Queensland Plateau; 5. Townsville Trough; 6. Marion Plateau; 7. Tasmanid Seamounts; 8. Kenn Plateau; 9. Chesterfield Plateau; 10. D'Entrecasteaux Zone. (D) Regimes in relation to bathymetric features. Bathymetric grids acquired from < www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html# >.

Regime validation – quantitative

Regimes 1 and 4 were the most successfully defined: average probability of membership across each regime's pixels was 92.41 and 92.68%, respectively (Table 1). Regime 3 was the least successfully defined (average probability of membership of 83.57%), with 14.86% of pixels having probabilities of membership $\leq 50\%$.

Regimes in relation to EEZs and zones within the CSCMR

Countries with the largest percentages of each regime (Fig. 8A) will have primary responsibility for conservation management of that regime. Countries having large responsibilities for regimes (with an arbitrary threshold of 30% of extent in the study area) were: Papua New Guinea (regime 1); Solomon Islands (regime 2); Australia (regimes 3, 4 and 5); and New Caledonia (regimes 3 and 5).

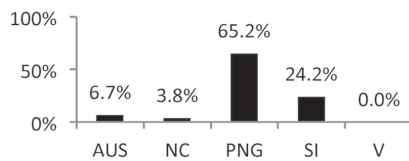
Zones within the CSCMR will need to be managed with a view to their representation of regimes (Fig. 8B). Zones with particular importance for each regime (with an arbitrary threshold of 30% of extent in Australian waters) were: zone II (regimes 1, 2 and 3); zone IVc (regime 4); and zone VIa (regimes 4 and 5). Percentages of total regime extents in Australian waters (Fig. 8A) highlight the international importance of zone II for regime 3, zones IVc and VIa for regime 4, and zone VIa for regime 5.

Distinctive parts of regimes

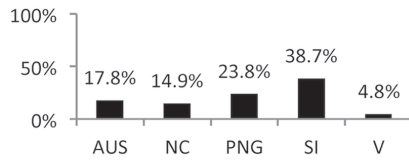
We chose regime 2 to demonstrate within-regime heterogeneity with respect to concentration and predictability. Regime 2's persistent high-concentration, high-predictability pixels (potentially higher priority for management) were located in several distinct patches associated with the Hiri Gyre and isolated bathymetric elevations such as the Chesterfield Islands and the northern New Caledonian lagoon (Fig. 9,

(A) Regimes within EEZs

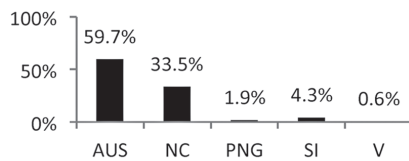
Regime 1 - 5470 pixels



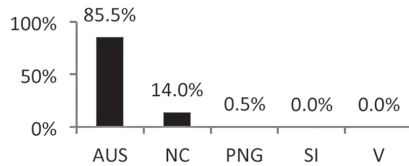
Regime 2 - 17271 pixels



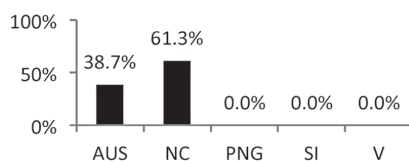
Regime 3 - 9877 pixels



Regime 4 - 1047 pixels

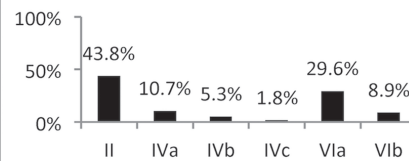


Regime 5 - 4888 pixels

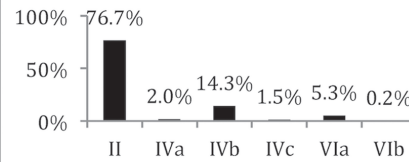


(B) Regimes within the CSCMR

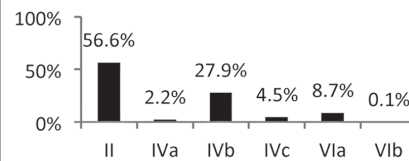
Regime 1 - 338 pixels



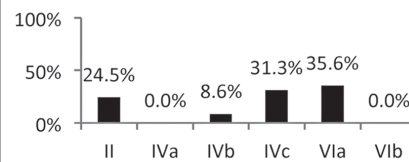
Regime 2 - 3093 pixels



Regime 3 - 5915 pixels



Regime 4 - 898 pixels



Regime 5 - 1907 pixels

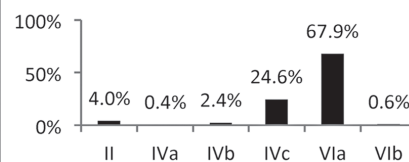


Figure 8. The spatial overlap between chlorophyll-a regimes and management boundaries within the study area. (A) The percentage of each regime's total extent in the Coral Sea study area within each of the five EEZs: Australia (AUS), New Caledonia (NC), Papua New Guinea (PNG), Solomon Islands (SI), and Vanuatu (V). (B) The percentage of each regime's total extent in Australia's Coral Sea Commonwealth Marine Reserve within each of the Reserve's IUCN categories and sub-categories.

refer Fig. 7A, B). Management will largely fall to Papua New Guinea, which contains the majority of these pixels (Supplementary material Appendix 4, Fig. A2A). Persistent low-concentration, high-predictability pixels in regime 2 (potentially low priority for management) were located within a linear band along the path taken by the South Equatorial Current (Fig. 9, refer Fig. 7A, B).

Our review of pelagic species associations revealed unique assemblages within each regime (Table 2). Differences between regimes in pelagic species associations were indicated by opportunistic observations and, more reliably, datasets collected relatively consistently across the study area. The review also identified isolated biological features that appear to have particular conservation significance.

Discussion

Our classification of regimes offers insights into the spatial and temporal variability of an important environmental proxy – chlorophyll-a – in the Coral Sea, although the method is applicable more widely. The regimes serve as static surrogates for dynamic features, representing both within- and between-year variability over 10 yr of remote sensing data. The distinct chlorophyll-a signatures of the regimes are supported by existing knowledge of the interactions between local bathymetry and oceanographic processes (section Regime validation – qualitative), and the class probability analysis for each regime (Table 1). The relatively lower success of regimes 2 and 3 is expected – these regimes are the

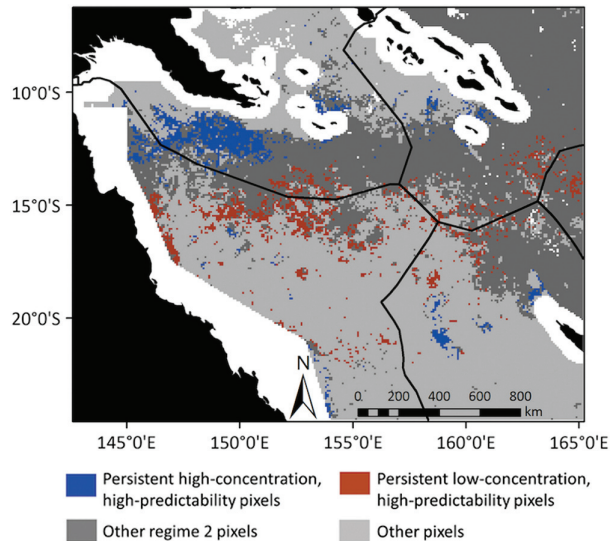


Figure 9. Spatial heterogeneity within regime 2. Persistent high-concentration, high-predictability pixels are those with above-average monthly values of climatological concentration and predictability across 8 or more months of the year; persistent low-concentration, high-predictability pixels are those with below-average monthly values of climatological concentration and above-average predictability across 8 or more months of the year. Black lines indicate Exclusive Economic Zones.

most similar (Fig. 4B) and it is likely that there is a degree of interchangeability between their pixels. The utility of the regimes as surrogates for planning is supported by indications of distinctiveness in some associated species (Table 2). This kind of information can assist spatial management of the pelagic ocean, where knowledge of species distributions is often unknown or incomplete and must be inferred from surrogates (Last et al. 2010, Hobday et al. 2011).

Spatial heterogeneity within regimes

Internal heterogeneity in both climatological concentration and predictability is considerable for some regimes, especially for regimes 1 and 2, as indicated by the spatial standard deviations of values (Fig. 5A, B). While this heterogeneity can lead to overlap in values of climatological concentration and predictability between the regimes, the overlap varies seasonally (Fig. 6), helping to explain why, for example, regimes 1 and 2 are distinct, despite overlapping in characteristics in some months of the year.

Conservation of chlorophyll-a regimes and associated pelagic species

The spatial management of regimes will be dictated by planners' conservation goals and objectives. Each regime serves as a surrogate for assemblages of species of conservation interest (Table 2); ideally then, each regime should be represented within zones of marine protected areas that provide the appropriate protection for associated species. Given finite conservation resources, planners should prioritize high-concentration regimes, such as 1 and 2, and regime

5 during winter months. The heterogeneity of regimes – both in terms of climatological concentration and predictability, and species associations (Table 2) – should be used to guide decisions about which parts of regimes are protected.

Conservation implications of pixel values

Within regimes, high-concentration pixels are of conservation interest for two reasons. First, they aggregate pelagic predators in the open ocean that are otherwise widely dispersed. Second, pelagic fisheries operations are concentrated over areas of high concentrations of chlorophyll-a (Polovina et al. 2001), making marine biodiversity in these areas more vulnerable (see Margules and Pressey 2000 and Allison et al. 2003 for examples of conservation planning exercises that incorporate the likelihood of exposure to threatening processes into prioritization). Furthermore, high-concentration pixels that have high predictability are also important, lending confidence that features of conservation interest will remain under protection in the near future. In this regard, low-concentration, high-predictability pixels are candidate areas for exclusion from conservation attention. Patches of low chlorophyll concentration are unlikely to concentrate pelagic predators or fisheries, and high predictability indicates these conditions persist between years. Planners will need to decide what values represent high and low categories of concentration and predictability, and the answers should, ideally, be informed ecologically. Our criteria (Fig. 9) are starting points for discussion.

Conservation implications of species assemblages

Despite data limitations (section Critiques and caveats), certain features of the Coral Sea can be delineated with reasonable accuracy and can be expected to remain distinctive even after additional data are collected. Fisheries and larval distribution data for billfish, seabirds, sharks, and tunas were collected relatively consistently across the study area (blue shading in Table 2), so the intra- and inter-regime differences in occurrences for these species are reasonably reliable. These data can help guide decisions about which regimes to protect for each species. For example, management can be directed with confidence toward the highest concentrations of bigeye, yellowfin and skipjack tunas within the study area in regime 1, and likewise for concentrations of albacore tuna in regime 2. Management can also focus on localized biological features (green shading in Table 2, Fig. 10) that are discrete locations with persistent or predictable occurrences of species of conservation interest. These data can help guide decisions about which parts of regimes to protect for each species. Examples include the aggregations of lanternfish and the breeding grounds for black marlin near the edge of the Great Barrier Reef Marine Park around 15°S in regime 2 (Fig. 10).

Towards explicit conservation objectives for regimes

Specific, quantitative objectives are a basic requirement of systematic conservation planning (Margules and Pressey 2000). Appropriate objectives for dynamic, and particularly pelagic, features are a significant gap in the conservation literature (Groves et al. 2012), but there are ways forward, even with limited information (Ban et al. 2012). Objectives for conservation management of the pelagic Coral Sea should

Table 2. Summary of species associated with the five chlorophyll-a regimes. Small filled circles indicate species presence; large filled circles indicate regimes with highest concentrations of species, if known. Blue-shaded cells indicate datasets collected relatively consistently across the study area. Green-shaded cells indicate isolated biologic features of particular significance to conservation planning. Literature sources correspond to Supplementary material Appendix 3, Table A3.

Species	Regime 1	Regime 2	Regime 3	Regime 4	Regime 5
Billfish					
Broadbill swordfish	•	•	•	●	●
Striped marlin		•	•	•	●
Black marlin (adult)		•	•	•	•
Cetaceans					
Bryde's whale	•				
Minke whale		•			
Toothed and beaked whales spp.					•
Spinner dolphin	•				
Bottlenose dolphin	•				
Sperm whale	•				
Seabirds					
Albatross spp.		•			
Petrel spp.		•			
Sharks					
Tiger shark			•		
Blue shark	•	•	•	•	●
Oceanic whitetip shark	•	●	●	•	•
Mako shark		•	•	•	●
Thresher shark	•	•	•	•	•
Silky shark	•	●	•	•	•
Tunas					
Albacore tuna	•	●	•	•	•
Bigeye tuna	●	•	•	•	•
Yellowfin tuna	●	•	•	•	•
Skipjack tuna	●	•			
Turtles					
Green turtle	•	•	•	•	•
Hawksbill turtle	•	•			
Loggerhead turtle	•	•	•	•	•
Leatherback turtle	•	•	•		•
Other					
Concentration of gelatinous zooplankton	●				
Spawning/breeding grounds					
Lanternfish		•			
Black marlin		•			
Humpback whale	•	•			
Striped marlin		•			•
Tuna (multiple species)	●	●	•	•	•

be based on how much of each regime should be managed, which specific parts of regimes should or should not be managed, and the kinds of management needed. Seasonal variations in chlorophyll-a characteristics and localized biological features can guide decisions about when conservation management is needed. As far as possible, objectives for regimes in the Coral Sea should be based on biological insights, as for pelagic habitats elsewhere (Hobday et al. 2011).

Chlorophyll-a regimes in relation to EEZs

Australia's is the only EEZ in the study area lying almost completely within marine parks (Fig. 1). However, regimes 1 and 2 occurred only minimally within Australian waters, with most of their areas unprotected in other EEZs (Fig. 8A). A large percentage of regime 5 was within Australian waters, but whether this – and the Australian protection of regimes 1 and 2 – is sufficient to meet management targets will depend on specific objectives for protection. If objectives for regimes cannot be met within Australian waters, multi-national management of regimes will be necessary. This would involve

additional reserves in the EEZs of Papua New Guinea and/or Solomon Islands for regime 1, (Fig. 8A): in the the EEZs of New Caledonia, Papua New Guinea, and/or Solomon Islands for regime 2: and within the New Caledonian EEZ for regime 5. The selection of new reserves should be guided by information on spatial heterogeneity within regimes and localized biological features. Planners should first consider areas of overlap. For example, persistent high-concentration, high-predictability pixels in regime 2 overlap with both breeding grounds for humpback whales and the concentration of gelatinous zooplankton in the Papua New Guinean EEZ (Fig. 9, 10).

Of particular interest here is the recent (April 2014) proclamation of the Coral Sea Natural Park covering the entire EEZ of New Caledonia. The zoning of this park will be a valuable opportunity to secure the protection of the many ecologically significant pelagic features present within New Caledonian waters. This EEZ contains roughly 15% of regime 2 – a high-concentration regime with minimal current protection across the Coral Sea – and over 60% of

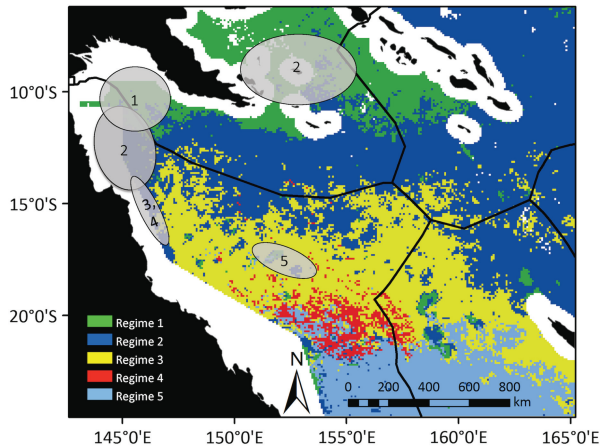


Figure 10. Localized biological features within the study area. More detail and sources of information are in Supplementary material Appendix 3, Table A3. 1. Concentrations of gelatinous zooplankton (Dhugal Lindsay pers. comm.). 2. Breeding grounds for humpback whales (Vang 2002). 3. Spawning aggregation of lanternfish (McPherson 1988, Flynn and Paxton 2012). 4. Spawning grounds for black marlin (Leis et al. 1987). 5. Nesting areas for green turtles (Miller et al. 2001, Harvey et al. 2005). Black lines indicate Exclusive Economic Zones. Note: humpback whales have distinct feeding and breeding grounds (Rock et al. 2006) that are not directly associated with the chlorophyll-a characteristics of the regimes. However this information can help direct the management of the regimes, and is included on the map.

regime 5 – a seasonally high-concentration regime containing a spawning ground for striped marlin. The Lord Howe Seamount chain runs north-south through this EEZ. If this chain is categorized as a National Park (IUCN II), a migration route for humpback whales and important habitats for sperm whales, spinner dolphins, and bottlenose dolphins would be protected from commercial fishing. The bycatch of marine mammals has significant biodiversity and economic ramifications for fishery operations within Australian waters (McPherson 2011) and elsewhere. The proclamation of this park has great potential to benefit the biodiversity of the Coral Sea. However, this potential will not be fully realized if protected area design prioritizes minimal spatial overlap with pre-existing extractive activities; e.g. oil and gas extraction, fishing, and seafloor mining (Devillers et al. 2014).

Chlorophyll-a regimes in relation to zoning of Australia's Coral Sea Commonwealth Marine Reserve

Within the CSCMR, zone II – the Marine National Park Zone – is the most strictly managed and offers the highest level of protection to features within its boundaries (Supplementary material Appendix 1, Table A1). As with the international evaluation, high-concentration regimes (1, 2, and 5) and the aggregations of top predators they support should be considered highest priority for protection. Within the CSCMR, large portions of regimes 1 and 2 within Australian waters were within zone II, and it is possible that overall objectives for their protection could be met under current management (Fig. 8B). However, regime 5 – a seasonally high-concentration, high-predictability regime – is poorly represented within zone II (4.0%). Most of regime 5 in Australian waters was within zones IVc and VIa, leaving

waters containing a striped marlin spawning ground and a migration route for humpback whales exposed to impacts from longlining and other forms of commercial fishing (Hanamoto 1977, Vang 2002). As part of future research, specific conservation objectives should be applied to quantitatively evaluate the zoning of the CSCMR in terms of the dynamics of chlorophyll-a and localized biological features.

Importantly, with the change of Federal Government in 2013, all management plans for the CSCMR have been suspended pending a new review process. Any new zoning determined by this review should seek to maintain and extend strict protection in zone II of regimes for which Australia has a large responsibility, especially regime 5, parts of regimes with persistent high-concentration, high-predictability pixels, and localized biological features.

Within Australian national waters, planners might consider regimes in conjunction with the Provincial Bioregions (CoA 2006). The regimes supplement the Provincial Bioregions by adding information on chlorophyll-a, which was not included directly in the pelagic regionalisation (Lyne et al. 2005). Chlorophyll-a and primary productivity were previously used to create chlorophyll regions within Australian national waters to compare with the classes found by the pelagic regionalization. However, this coarse-resolution analysis placed the entirety of Australia's portion of the Coral Sea within the same chlorophyll region (Lyne et al. 2005, see also Hobday et al. 2011), while our analysis found five distinct regimes within this same area. This suggests that the spatial variation of chlorophyll-a in oligotrophic tropical waters was obscured by the much greater latitudinal variation in the nation-wide classification.

Wider applicability

There is a current trend of establishing large pelagic protected areas. Recent examples are the expansion of the Pacific Remote Islands Marine National Monument in the central Pacific and the proclamation of the Coral Sea Natural Park. Our method for defining regimes of variation can help direct the selection and zoning of these reserves to accommodate the dynamics of chlorophyll-a and other variables that affect species distributions, including sea surface temperature (Peñaflores et al. 2009, Ban et al. 2012), sea level anomaly (Alpine and Hobday 2007), or cyclones (Allison et al. 2003). Furthermore, the definition of regimes for terrestrial dynamics can aid the spatial management of processes on land; e.g. drought refugia (Klein et al. 2009), fire (Leroux et al. 2007), and climate warming (Carvalho et al. 2011).

Critiques and caveats

To the best of our knowledge, our literature compilation was exhaustive; however, it might be incomplete. Furthermore, the remoteness of the Coral Sea and the sparse sampling of this very large region mean that many of its important ecological features are yet to be described (McKinnon et al. 2014). As new data become available, apparent absences of species in some regimes might prove false, so Table 2 cannot be a complete representation of compositional differences between regimes.

While using time-series data to describe the past behavior of dynamic features allows for inferences to be drawn about their behavior in the near future, models will be needed to predict long-term conditions, especially with impending climate change. Conservation planning is about the future, so it will be important for this line of research to focus more on modeling future dynamics. Studies have used models to predict the future trends of dynamic features, but only a few have incorporated model predictions into conservation planning (see Game et al. 2008, Carvalho et al. 2011, for examples).

The accuracy of using remotely-sensed chlorophyll-a to predict aggregations of higher trophic level species has been debated, due to the time lag of trophic transfer (Grémillet et al. 2008). Ideally, then, the implications for spatial management should be interpreted with ecological insights in addition to remote-sensing analyses. Where possible, information on lower trophic levels species should be included to address ecological protection. This could present a problem for the application of this method in data-poor regions, although the results from well-studied regions might be applicable more widely.

While it is simple to conceptualize reserve systems that span multiple EEZs, it is more complicated to put these reserves into practice. Only a handful of multi-national systems of reserves exist, in part due to the challenges of international governance and enforcement for reserves that span multiple national jurisdictions (Game et al. 2009). Additionally, certain assumptions must be met for dynamic reserves (including temporary reserves) to be successful, including: cost-effectiveness, long-term, recurring implementation, and sufficient understanding of dynamics (Moilanen et al. 2014). Assumptions should be evaluated on a case-by-case basis, and therefore the suitability of dynamic management will vary by location.

Conclusions

The remote nature of pelagic reserves means that many of the features they can protect will be associated with dynamic processes. Reserves designed for static features do not necessarily accommodate dynamic processes, so dynamics need to be incorporated directly into reserve design. To this end, traditional static reserve designs might need to be updated to designs that better achieve objectives for dynamic features, including seasonal reserves, dynamic reserves, and real-time management (Hobday and Hartmann 2006). While these alternative designs have yet to be widely implemented, they have already been applied in several locations (Beacham et al. 2004, Chassot et al. 2011). Uncertainty around data, methodology, and outcome will always be present in management of the pelagic ocean, and cannot be cited as a reason to forestall conservation action (Avery 2003). In the face of mounting pressures, both exploitative and climate-related, stakeholders should be concerned not with the cost of action, but with the cost of inaction.

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Supplementary material (Appendix ECOG-01450 at <www.ecography.org/readers/appendix>). Appendix 1–4.