



Pelagic bioregionalisation using open-access data for better planning of marine protected area networks



Leslie A. Roberson^{a,*}, Erwann Lagabriele^{a,b}, Amanda T. Lombard^a, Kerry Sink^c,
Tamsyn Livingstone^d, Hedley Grantham^e, Jean M. Harris^d

^a Faculty of Science, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth, 6031, South Africa

^b UMR 228 ESPACE-DEV, Université de la Réunion, IRD, France

^c South African National Biodiversity Institute, Centre for Biodiversity Conservation, Kirstenbosch, South Africa

^d Scientific Services, Ezemvelo KZN Wildlife, Queen Elizabeth Park, Pietermaritzburg, South Africa

^e The Ecology Centre and Centre for Applied Environmental Decision Analysis, University of Queensland, St. Lucia, Australia

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ABSTRACT

Systematic conservation planning (SCP) to design marine protected areas (MPAs) has traditionally focused on species distributions or benthic habitat features that drive the determination of conservation priorities. Pelagic ecosystem protection is usually incidental because these ecosystems are often data-poor and are difficult to visualize in a planning context. Pelagic ecosystems, however, face increasing and cumulative impacts from threats such as overfishing and climate change, and a precautionary approach is required to protect both known and unknown biodiversity patterns and ecosystem processes. Data-driven pelagic habitat classifications are important when planning for habitat protection in the absence of sufficient in-situ data. In this study, we describe a method for creating a bioregional map of the upper-mixed layer of South Africa's pelagic realm. We selected relevant variables and parameters that best reflect key ecosystem properties at broad, meso, and local scales. We conducted a hierarchical cluster analysis using open-access sea surface temperature (SST), chlorophyll-*a* (chl-*a*), net primary productivity (NPP), mean sea level anomalies (MSLA), and seabed slope and depth data. The resulting map delineates three bioregions subdivided into seven biozones and sixteen pelagic habitats within South Africa's continental Exclusive Economic Zone (EEZ). This habitat map was incorporated into SCP of a proposed expanded MPA network that includes offshore protected areas and meets National objectives. The proposed network will increase protection of the pelagic realm (>30 m depth) of the EEZ from 0.002% to 6.0%. We contend that bioregional analyses based on publicly available remote-sensing data are useful for identification of offshore habitats, especially when robust biological data are unavailable, as a framework for ecosystem reporting, and for inclusion in a systematic design for a representative offshore MPA network. Further research should focus on modelling and mapping the permanence of pelagic habitats and different spatio-temporal scales of variability, validating habitat boundaries with biological data, and understanding the threats and efficacy of achieving pelagic protection through management mechanisms like MPAs.

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1. Introduction

Protection of offshore and pelagic ecosystems has been highlighted as a major gap in the global marine protected area (MPA) network, which is heavily biased towards coastal and benthic habitats (Devillers et al., 2014; Game et al., 2009). Exactly how

biased depends on the definition of pelagic or offshore environments, but Spalding et al. (2013) estimate that some level of protection is afforded to less than 2% of the pelagic realm, defined as oceanic waters non-adjacent to land where species and processes have minimal interaction with the substratum. An analysis of representation of fish, mammal, and invertebrate distributions in the global MPA network indicates that a majority of gap species – those with ranges entirely outside any protection – do not occur near the coast (Klein et al., 2015), which further emphasizes the importance

* Corresponding author.

E-mail address: leslie.roberson@gmail.com (L.A. Roberson).

of offshore MPAs. Several challenges have impeded the implementation of offshore MPAs, including the relative shortage of biological and physical data for offshore areas (Leathwick et al., 2008), the dynamic nature of pelagic environments (Grantham et al., 2011), and the legislative and logistic difficulties of managing areas that span multiple jurisdictions or are far from the coast (Gregg et al., 2012; Kaplan et al., 2010).

Global pelagic protection has increased with the recent proliferation of very large MPAs (IUCN and UNEP-WCMC, 2016), which often include protection of certain pelagic (and usually highly mobile) species as a conservation objective (Davies et al., 2012). Still, the existing spatial coverage of the world's oceans is far from global conservation targets such as the Convention on Biological Diversity's (CBD) Target 11, which calls for formal protection of 10% of marine and coastal areas considering a multitude of factors (e.g. connectivity, ecological representation) by 2020 (Devillers et al., 2014). The area of "effective" protection is much lower because many MPAs are poorly enforced or offer only partial protection (Lester and Halpern, 2008).

As more States extend protection into large or offshore areas of their EEZs, a systematic approach to MPA planning will help to maximise benefits, minimize conflicts, and meet conservation objectives (Devillers et al., 2014). Systematic conservation planning (SCP) can improve MPA design by providing a framework to develop plans that address specific and explicit conservation objectives and examine whether existing mechanisms meet conservation requirements (Margules and Pressey, 2000). MPA effectiveness, however, depends on successful implementation and appropriate management.

SCP in deep or open ocean habitats requires ecological knowledge and data, which are often difficult and expensive to obtain (Rice et al., 2011). Bioregionalisations or surrogate approaches have provided practical solutions to problems of data paucity, and have often been used to facilitate systematic planning for the protection of marine habitat diversity (Spalding et al., 2012). Bioregionalisation can be defined as the process of delineating a continuous spatial coverage of contiguous spatial units that support distinct biological assemblages (Costello, 2009; Koubbi et al., 2011). Those spatial units can be delineated (and their biological surrogacy assessed) using geophysical and biological observation data, modelled data or expertise, or a combination of both (Grantham et al., 2010). The spatial units can be used for monitoring and reporting the state of the environment, risk and threat assessment, ecosystem-based management (EBM) of human activities, identification of priority areas for protection, modelling and prediction of impacts and climate-induced changes, and allocation of research effort (Hobday et al., 2011; Rice et al., 2011; Spalding et al., 2007).

1.1. Review of pelagic bioregionalisations

Mapping and categorising oceanic features is not a new concept. Oceanographers have long produced characterizations of physical ocean dynamics, while biological approaches have focused on mapping taxonomic distributions in the ocean, particularly fish species (e.g., Briggs, 1974; Briggs and Bowen, 2012). More recent biogeographic classification schemes have been utilised in various ways by management (e.g., Large Marine Ecosystems, EUNIS marine habitat classification, NOAA's marine and estuarine classification scheme) but they differ from bioregionalisations because they lack spatially explicit habitat boundaries or contiguous spatial units (Allee, 2000; Davies et al., 2012; Gregg et al., 2012; Sherman and Hempel, 2008).

Many regional and global bioregionalisations have been developed for pelagic environments (Table 1). A pelagic bioregionalisation classifies water masses at a given spatial scale as

habitats with spatially explicit boundaries. Spatial scale refers to the spatial characteristic of an object or process, including its spatial resolution and geographic extent (Gustafson, 1998). Scale is increasingly considered explicitly in habitat mapping studies (Lecours et al., 2015). A multi-level conceptualisation of the spatio-temporal organization of the ocean can provide the underlying structure for the bioregionalisation (Koubbi et al., 2011). To this purpose, understanding and integrating the operational scale of oceanographic features and processes is an important aspect of a bioregionalisation endeavour. Operational scale refers to the appropriate scale at which objects and their interactions are to be examined (Whittaker et al., 2001). For instance, distinct local-scale patterns (such as pockets of warm water within a large cold water mass) result from mesoscale oceanographic features (such as eddies) which alter global patterns and processes observed at the broadest scale (such as latitudinal temperature gradients).

For a bioregionalisation to be useful to SCP, the spatial scale must have biophysical significance, yet be specifically suited to management so that the bioregionalisation can be integrated into administrative boundaries and align with the management of fisheries and other key activities (Fraschetti et al., 2008; Trembl and Halpin, 2012). If the spatial units are too large, important details are overlooked; if too small, the result is an unmanageable number of decision-making groups (Norse, 2010). The identification of habitat boundaries is difficult in dynamic pelagic environments but a focus on ecological or functional boundaries is an improvement over purely political divisions, even if those boundaries are fuzzy (Bridge et al., 2015; Lourie and Vincent, 2004).

Surrogates that are fixed in space, such as seamounts or other permanent bathymetric features, have been used to predict pelagic assemblages with some consistency (Hobday et al., 2011; Hyrenbach et al., 2000). Remotely detectable factors, such as chlorophyll fronts, can be equally useful as dynamic surrogates for biological assemblages (Weeks et al., 2006; Welch et al., 2016). Publicly available satellite data, either as a singular source or supplemented with additional datasets, has become an important resource for pelagic bioregionalisation exercises. The quality of satellite data products has improved dramatically, and validation exercises have inspired confidence in their utility even in highly variable regions of the ocean (Allee et al., 2014; McClain, 2009). The predictive power of different satellite-derived parameters varies depending on the geographic area described, but factors such as primary productivity and sea-surface temperature (SST) derived parameters have been shown to be particularly good predictors of species diversity and distributions of a wide variety of taxa, including seabirds (Weimerskirch et al., 2004), highly migratory fish (Sequeira et al., 2012) and mammal species (Bost et al., 2009), and even benthic species assemblages (Kachelriess et al., 2014; Tittensor et al., 2010).

Still, there remains some discomfort with the concept of treating temporally and spatially dynamic water masses as persistent and spatially distinct habitats (Koubbi et al., 2011). Most bioregionalisations focus on biological surrogates (e.g., Commonwealth of Australia, 2005; Hao et al., 2015; Powles et al., 2004) or static benthic features (e.g., Connor et al., 2006; Harris and Whiteway, 2009; Howell, 2010). Others, such as the Seascapes for the Scotian Shelf of Atlantic Canada (Roff et al., 2003) or the Marine Ecoregions of the World (Spalding et al., 2007), define a horizontal layer of the water column assumed to be coupled with the benthos but are based on measurements of the seafloor or inshore coastal habitat features. The linkages between benthic and pelagic ecosystems are complex (Navarrete et al., 2005), and analyses that specifically describe pelagic environments are important for attaining representative habitat diversity in offshore protected area networks (Game et al., 2009).

Table 1
 Details of medium to broad-scale pelagic bioregionalisations based on satellite-derived or biophysical parameters, and their implementation in systematic conservation planning (SCP). Studies not specifying a vertical limit are labelled “Pelagic” extent. “Epipelagic” is the top 200 m of the water column. SST = sea surface temperature, NPP = net primary production, SSH = sea surface height.

Reference	Name	Area	Extent	Structure	Key parameters and features	Objectives
Chollett et al. (2012)	Physical environments of the Caribbean Sea	Caribbean	Pelagic	Hierarchical, nested	SST, turbidity, salinity, mechanical disturbance (wind-driven wave exposure and hurricane incidence)	Potential use in SCP
Condie and Dunn (2006)	Seasonal characteristics of the surface mixed layer in the Australasian region	Australasia	Epipelagic	One level, proposed subregions	Seasonal chl- <i>a</i> , NPP, nutrients, temperature, salinity, mixed layer depth	Potential use in SCP
Connor et al. (2006)	UK SeaMap	United Kingdom EEZ	Pelagic; separate benthic analysis	One level, seasonal	Surface salinity, surface and bottom temperatures, frontal probability	Potential use in SCP
Delavenne et al. (2013)	Seasonal water column typology of the Eastern English Channel	Eastern English Channel	Pelagic	One level, seasonal	Depth, seabed shear stress, annual temperature contrast	Potential use in SCP
Devred et al. (2007)	NW Atlantic ecological provinces	NW Atlantic	Pelagic	Hierarchical, nested	SST, NPP, bathymetry, geographic location (latitude and longitude)	Potential use in SCP
Dinter (2001)	OSPAR Maritime Area	NE Atlantic and Arctic	Epi/meso-pelagic (<1000 m depth)	Hierarchical, nested	Depth strata, water temperature, fronts, nutrients	Intended for SCP (OSPAR MPAs)
Gonzalez-Silvera et al. (2004)	Biogeographical regions of the tropical and subtropical Atlantic Ocean off South America	Tropical/subtropical Atlantic off South America	Pelagic	One level	Monthly variability in SST, chl- <i>a</i> , pigment	Potential use in SCP
Grant et al. (2006)	CCAMLR	Southern Ocean	Pelagic; separate benthic analysis	One level	Bathymetry, SST, nitrate concentration, silicate concentration	SCP (CCAMLR MPAs)
Gregg and Bodtker (2007)	Marine Regions in the North Pacific	North Pacific	Pelagic	One level	Wind stress, surface current velocity, SSH, sea surface salinity, SST	Potential use in SCP
Hardman-Mountford et al. (2008)	Biomes and provinces of the pelagic ocean	Global	Pelagic	Hierarchical, nested	Chl- <i>a</i>	Potential use in SCP
Hobday et al. (2011)	Defining dynamic pelagic habitats in oceanic waters off eastern Australia	Eastern Tuna and Billfish Fishery area	Pelagic	One level	Bathymetry, SST, temperature at 250 m, chl- <i>a</i> , nutrient climatology	Potential use in SCP
Longhurst (2007)	Ecological geography of the sea	Global	Pelagic	One level	Chl- <i>a</i> , NPP, surface currents, mixing depth, upwelling, depth strata	Potential use in SCP
Lyne and Hayes (2005)	National Marine Bioregionalisation Integration Project	Australian waters	Pelagic	Hierarchical, not nested	Salinity, nutrients, SST, eddies and fronts, surface and subsurface currents, chl- <i>a</i> , phytoplankton distribution map, pelagic fish provinces	SCP (Australia EEZ)
Raymond (2011)	A circumpolar pelagic regionalisation of the Southern Ocean	Southern Ocean	Pelagic	One level	SST, depth, sea ice information	SCP (CCAMLR MPAs)
Sharp et al. (2010)	Bioregionalisation and spatial ecosystem processes in the Ross Sea region	Ross Sea	Pelagic; separate benthic analysis	Hierarchical, nested	Water temperature, salinity, depth, sea ice information	SCP (CCAMLR MPAs)
Snelder et al. (2006)	New Zealand Marine Environment Classification	New Zealand EEZ	Benthic-pelagic; finer scales based on benthic info	One level	Depth, seabed slope, orbital velocity, mean annual solar radiation, SST amplitude, SST gradient, winter SST, tidal gradient	Potential use in SCP
Spalding et al. (2012)	Pelagic Provinces of the World	Global	Epipelagic	Hierarchical, nested	Oceanographic drivers (e.g., boundary currents, upwelling) and taxonomic patterns	Potential use in SCP
UNESCO (2009)	Global Open Oceans and Deep Seabed (GOODS)	Global	Pelagic; separate benthic analysis	One level	Bathymetry, NPP, SST, salinity, O ₂ , organic matter flux, substrate type, depth strata	Potential use in SCP
Welch et al. (2016)	Regimes of chlorophyll- <i>a</i> in the Coral Sea	Coral Sea	Epipelagic	One level	Seasonal and annual variability in chl- <i>a</i>	Potential use in SCP

Despite the advent of new pelagic bioregionalisations and validation techniques, the majority are academic exercises independent of SCP (Table 1). Large-scale MPA planning remains focused on benthic classifications or target species data even when a pelagic bioregionalisation is available, such as the rezoning of the Great Barrier Reef Marine Park (GBRMP) and the Convention for the Protection of the Marine Environment of the North-east Atlantic (OSPAR) (see Foley et al., 2010; Leslie, 2005; Lourie and Vincent, 2004; Rice et al., 2011). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) developed pelagic bioregion units for utilisation in several objectives, including MPA planning, threat assessment, monitoring and prediction of broad-scale changes, allocation of research effort, and fisheries assessments (Grant et al., 2013). To date the bioregion units have been used primarily for MPA planning. Although the management context differs, our pelagic bioregionalisation methodology for South Africa's EEZ is similar to the CCAMLR example.

1.2. Background to the pelagic bioregionalisation of the South African EEZ

Bioregional maps of marine habitats either map the benthos, the water column, or they incorporate both benthic and pelagic ecosystems. They can be based on physical or biological data, or both. Many analyses have investigated biogeographical patterns in South African waters, with little consensus on the names of biologically distinct areas, levels of dissimilarity between areas, locations of biogeographic breaks, and the areas of overlap zones (Lombard et al., 2004; Sink et al., 2011b). Sampling is heavily biased towards certain taxa and areas, with very limited biogeographic data for most deep and offshore areas (Appendix A).

Scientists and managers in South Africa recognize the lack of data for offshore and pelagic habitats and their underrepresentation in the national protected area network, which currently covers 0.16% of the continental EEZ (Sink and Attwood, 2008) and only 0.002% of areas beyond the 30 m depth contour. There has been increasing concern about the potential impacts of certain activities (e.g. trawling and mining) on benthic habitats in South Africa, particularly in vulnerable marine ecosystems (VMEs) such as cold-water coral reefs. An Offshore Marine Protected Area (OMPA) initiative was developed in South Africa to address the lack of offshore protection of both benthic and pelagic ecosystems and species in the national MPA network (Sink et al., 2011a).

1.3. Objectives of this study

No data-driven pelagic habitat map existed at an appropriate scale for SCP in the South African EEZ. This map was needed to achieve key objectives of the OMPA initiative, such as including relevant stakeholders (e.g. pelagic fishing sectors), maximising biodiversity targets (e.g. protecting important pelagic habitats and processes), minimising cumulative impacts to industries, and implementing MPAs and other management measures simultaneously (Sink et al., 2011a). The OMPA initiative developed both a pelagic bioregionalisation map, which served as a surrogate for pelagic habitats in the upper mixed layer, and a benthic habitat map, which used available in-situ biophysical data and expert knowledge. Both products were used in OMPA, and the subsequent development of the expanded MPA network, but here we report only on the pelagic bioregionalisation component. The aim of this study is to summarise the process undertaken to develop a pelagic bioregionalisation for inclusion in a systematic design for a representative offshore MPA network. This pelagic bioregionalisation uses depth and seabed slope and the satellite-derived parameters chlorophyll-*a*, net primary productivity, sea-surface temperature,

and mean sea level anomalies to delineate pelagic habitats. The classification method and outputs and the resulting protection plan for the pelagic habitats is described below.

2. Methods

2.1. Study area

The planning area for the offshore MPA network is the continental South African EEZ (henceforth referred to as the South African EEZ), which excludes the Prince Edward Islands. A larger study area was selected for the bioregionalisation classification in order to account for the connectivity among pelagic habitats within the greater Agulhas and Benguela current systems (Fig. 1).

South Africa's pelagic environment is dominated by two major current systems: the colder Benguela current along the West Coast and the warmer Agulhas current along the East Coast. The Benguela current in the South Atlantic is unique among the four major global eastern boundary currents because of its interactions with the Agulhas current, the western boundary current of the Indian Ocean (Longhurst, 2007). The inshore component of the Benguela is characterised by pulsed, seasonal, wind-driven upwelling cells, and long-term trends in the system are difficult to distinguish because of strong inter-annual and decadal signals (Hutchings et al., 2009). Variability on the east coast is driven primarily by mesoscale eddy activity related to connectivity between the South East Madagascar and Agulhas currents, although the dynamics of this system are not well understood (Beal et al., 2011; Halo et al., 2014). On the South Coast, the Agulhas current injects warm, nutrient poor water into the Benguela in the form of anticyclonic rings, with another component retroflecting eastward, dividing, and moving towards the Southern Indian Ocean Gyre and the Antarctic circumpolar current (Spalding et al., 2012). This warm water link between the Atlantic and Indian oceans fuels dynamic and variable ecological processes (Grantham et al., 2011), and is known to support coastal and shelf assemblages with large numbers of endemic species (Griffiths et al., 2010).

2.2. Model framework

The bioregionalisation uses surrogate variables and related parameters extracted from remote sensing data and integrated in a cluster analysis. Our method is a synthesis of the approaches developed by Grant et al. (2006), Lyne and Hayes (2005), and Post (2008). The pelagic bioregionalisation involved the following steps, described in subsequent sections: 2.2.1 Model assumptions; 2.2.2 Identification of key bio-physical patterns and processes; 2.2.3 Identification of relevant variables and parameters; 2.2.4 Collation and preparation of data sets; 2.2.5 Application of clustering procedures; 2.2.6 Post-analysis, assessment and validation.

2.2.1. Model assumptions

For this study we assumed pelagic assemblages to be distinct from benthic and demersal assemblages based on both ecological and management objectives, as well as the spatial scale over which these ecosystems function (Harris and Whiteway, 2009; Lyne and Hayes, 2005). We analysed the pelagic environment separately from the benthos and did not explicitly include benthic related geophysical features such as seamounts or canyons in the pelagic habitats model even though they are often associated with distinct pelagic communities (Vetter et al., 2010). The slope parameter provides some indication of major bathymetric features. These features were explicitly included in the benthic bioregionalisation component of the offshore MPA plan, and all associated biological assemblages were implicitly included in any

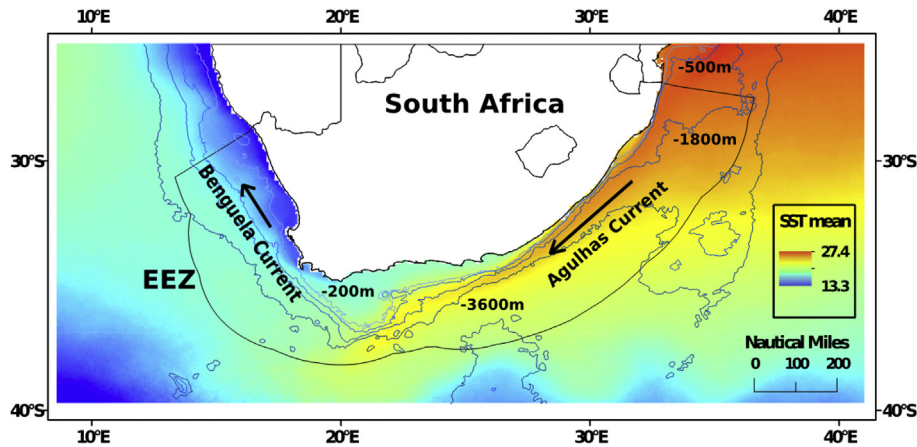


Fig. 1. Ocean depth (m) and 2009 mean sea surface temperature ($^{\circ}\text{C}$) in the pelagic bioregionalisation study area, the approximate location and direction of the primary components of the Benguela and Agulhas currents, and the South African EEZ (the planning area for the offshore MPA network). The Agulhas bank is the area on the continental shelf off the southern coast of South Africa (approximately 0–200 m depth).

Table 2
Ecosystem properties, variables and parameters identified for the classification of pelagic bioregions, biozones and habitats (max = maximum, CV = coefficient of variation).

Level	Important ecosystem properties, variables and parameters	Parameters
Bioregion	Broad scale oceanic patterns and circulation regimes Distribution of pelagic communities is globally driven by the physical structure of the ocean e.g., latitude and broad scale bathymetry reflecting continental shelves and ocean basin circulation patterns Key variables are depth ($\log \text{Depth} + 1$), mean SST and chl- <i>a</i> NPP, partially linked to SST and chl- <i>a</i> , also affects the distribution of biota at this scale	SST mean SST max Chl- <i>a</i> mean NPP mean Depth and slope
Biozone	Mesoscale variability of broader oceanic patterns and circulation regimes Distribution of pelagic biota driven by permanent or semi-permanent mesoscale variations Key drivers of these variations are changes in the distribution of broad scale structure and circulation patterns caused by mesoscale features such as upwelling and eddies This variability can be detected by deriving a CV for SST, chl- <i>a</i> and NPP time series Eddy distribution is calculated from MSLA	SST CV Chl- <i>a</i> CV NPP CV MSLA
Habitat	Local scale processes Finer-scale variability also affects the distribution of biota These variations are associated with the occurrence of SST and chlorophyll fronts (often induced by currents or eddies)	SST fronts frequency Chl- <i>a</i> fronts frequency

habitat classified as a VME (Sink et al., 2011a).

We assumed that variables measured at the ocean surface reflect the properties of the water column because they are strongly correlated with processes at depth, although they do not explicitly address vertical variability (Longhurst, 2007; Oliver and Irwin, 2008). At the time of the analysis, superficial satellite measurements were the only data available that allowed a full horizontal assessment of the EEZ. We assumed that the final pelagic classification was most accurate in the upper mixed layer of the water column, or to about 200 m depth, although the vertical dynamics of the system were not explicitly included in the model.

We recognised that temporal variability in pelagic environments occurs at many different scales, and the effectiveness of protected areas depends greatly on the persistence of dynamic features within reserve boundaries (Alpine and Hobday, 2007; Hyrenbach et al., 2000). Other bioregional analyses have focused on seasonal variability (Table 1). At this point, the proposed MPA network in South Africa is only feasible with static spatial boundaries and therefore we did not integrate seasonality explicitly. We consider the oceanic system to be stable across time – particularly in the Agulhas Current zone – and used averaging over a multi-years interval to delineate pelagic habitats (Beal et al., 2011). This inter-annual averaging does result in information loss, particularly of processes that are predictable over time but occur over short time scales.

2.2.2. Identification of key bio-physical patterns and processes

In order to integrate oceanographic features and processes operating at multiple spatio-temporal scales into a single relevant integrative spatial scheme, we conceptually organized the classification into three hierarchical spatial scales (bioregions, biozones, and habitats), thus accounting for broad, meso, and fine-scale oceanographic features and processes. Variables depicting habitats (and associated parameters) were selected based on this multi-scale scheme (Table 2).

2.2.3. Identification of relevant variables and parameters

We selected relevant variables and parameters that best reflect the key ecosystem properties at each scale. The selection was made based on the multi-scale organization scheme of the ocean and builds on interviews with key experts from the University of Cape Town including J. Lutjeharms, B. Bakeberg, and M. Rouault, and M. Roberts from the Department of Environmental Affairs (DEA). The selected variables are sea surface temperature (SST), chlorophyll-*a* (chl-*a*), SST and chl-*a* fronts, net primary productivity (NPP), semi-permanent eddies frequency derived from mean sea level anomalies (MSLA), and seabed slope (Table 2). We tested turbidity (K490) but excluded it from the final analysis owing to its close correlation with chl-*a*. The chosen parameters indicate the average state of the variables (mean value across time series) or their variability (minimum, maximum and coefficient of variation). Multi-sensor

satellite-based measurement data coupled with in-situ measurement (fixed buoys, drifting buoys, boat-based measures) were used to describe the meso-scale structures and the variability of oceanic water. Synthetic studies were developed to describe the study area in the Agulhas current (Lutjeharms, 2007; Lutjeharms and Anson, 2001) and in the Benguela current (Hagen et al., 2001; Weeks et al., 2006).

Overall, when averaged over a large domain at low spatial resolution, validation endeavors have found that satellite-based oceanographic products that measure quantities like chl-*a* concentration or the seawater inherent optical properties (e.g. absorption) are correlated with in-situ measurements (Zibordi et al., 2006). Several studies have tested the accuracy of satellite data products with in-situ sampling in our study region. In the Benguela Current ecosystem, Demarcq et al. (2007) found general agreement of satellite-derived chl-*a* and SST with the location of chl-*a* fronts sampled from 1971 to 1989. The Benguela Calibration cruise found the sensors operating in the region to be sufficiently accurate for phytoplankton functional types and photosynthetic parameters, as long as samples were taken within a few minutes of satellite measurements (Aiken et al., 2007). Backeberg et al. (2008) validated a high-resolution ocean model of the greater Agulhas Current system with both satellite and in-situ samples, and found good consistency between the measurements and the predicted spatio-temporal distribution of SST values. However, the Benguela and Agulhas Current systems are both highly variable and exhibit different dynamics that complicate satellite data products (e.g., large river plumes on the East Coast and seasonal upwelling and phytoplankton decomposition on the West Coast). Fine-scale and very near-shore processes remain a challenge to resolve with low resolution satellite data (Smit et al., 2013).

2.2.4. Collation and preparation of data sets

We acquired open-source satellite time series (monthly and 8 days means) over the 2002–2007 period. Considering the spatial scale and variety of water types in our study area, we selected Aqua MODIS Level 3 (4 km resolution) SST (11 μm night time) and chl-*a* (OCI algorithm) data sets from the NASA ocean colour website (<https://oceancolor.gsfc.nasa.gov/data/aqua/>), MODIS-based (9 km resolution) NPP data from the Oregon University website (<http://www.science.oregonstate.edu/ocean.productivity/>), and MSLA data from the AVISO website (<http://www.aviso.oceanobs.com/>) (Table 3). A comparison of SeaWiFS and MODIS normalized water-leaving radiances with in-situ values (chl-*a*) showed relatively low differences in clearer oceanic (Case 1) and more turbid coastal (Case 2) waters (Folkestad et al., 2007; Zibordi et al., 2006). Higher differences were observed for the MERIS data in the equivalent spectral range (e.g., 443–560 nm) (Zibordi et al., 2006). MODIS-based products (including NPP, SST and chl-*a*) have the advantage of being provided at a similar spatial resolution of 9 km.

Data processing and analysis were performed using ArcGIS Desktop Release 10 and extensions (Institute, 2011). Chl-*a* values

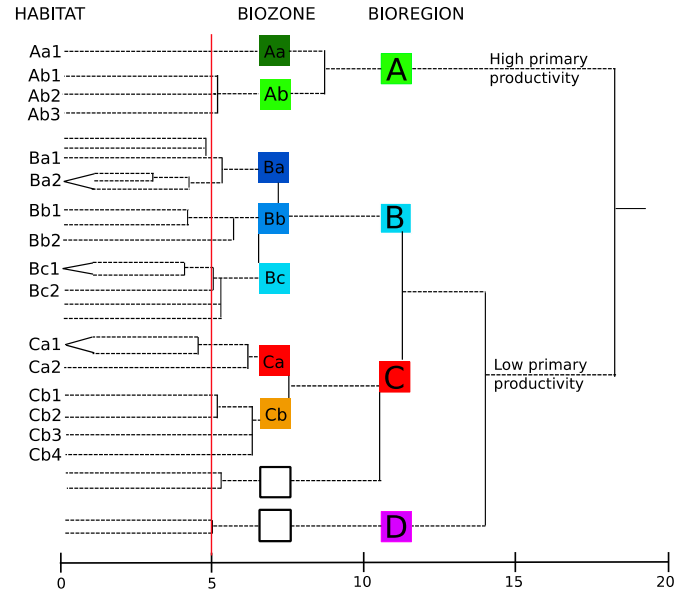


Fig. 2. Dendrogram showing the inter-cluster distances (from 0 to 20), and their membership to the three cut-off levels (habitats, biozones, and bioregions). The inter-cluster distance cut-off (5) for the habitats is indicated in red. The identified bioregions are the West and South Coasts (A), Offshore (B), East Coast (C), and Southern Ocean (D). Biozones and habitats falling outside the EEZ are not labelled. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were capped at 10 mg m⁻³ to remove potentially inaccurate values. SST and chl-*a* fronts were mapped on 8-days images using the Cayula and Cornillon (1992) algorithm implemented in the Marine Geospatial Ecology Toolbox (MGET) (Roberts et al., 2010) in ArcGIS 10. Eddies features were detected on MSLA data using the Okubo-Weiss algorithm in MGET with default algorithm parameters, and extracted by applying a +10 cm threshold.

All data were clipped to a similar rectangular extent, snapped (strictly aligned without pixel overlap), then all data sets were re-sampled to 9 km. The depth-related parameter (slope) was derived from the DEM SRTM 30 PLUS Version 5 (Becker et al., 2009). Depth values were log (|X|+1) transformed to flatten the deeper values. The slope layer was generalized using a L-pass mean filter (3 × 3 pixels) to remove noise. The spatial resolution of the eddy maps was increased to 9 km based on the demonstration by Backeberg et al. (2008) that sea surface height (SSH) patterns derived from the 10 km resolution HYCOM model are consistent with SSH patterns derived from satellite observation at the 30 km resolution. All statistical parameters were calculated per pixel across time series (mean, min, max and CV). Finally, we applied a land-sea mask and normalized all parameters values from 0 to 1 using the fuzzy linear function in ArcGIS.

Table 3
Spatial data sets collated for the pelagic bioregionalisation.

Dataset	Source/provider	Initial spatial resolution	Parameter used
SST	MODIS 2002–2007 L3 mapped Monthly	4 km	Mean and Max (°C), CV,
	MODIS 2002–2007 L3 mapped 8 days		Fronts frequency (%)
Chl- <i>a</i>	MODIS 2002–2007 L3 mapped Monthly	4 km	Mean (mg m ⁻³), CV,
	MODIS 2002–2007 L3 mapped 8 days		Fronts frequency (%)
NPP	MODIS 2002–2007 Monthly – Oregon University	9 km	Mean (mgC m ⁻² day ⁻¹), CV
MSLA	AVISO Delayed Time MSLA computed with respect to a 2001-07 mean, 8 days	30 km	Eddies frequency (%)
DEM	DEM SRTM V5 Plus (seamless land-sea)	0.9 km	Depth (log Depth + 1)) Slope (degrees)

2.2.5. Application of clustering procedures

Groups of pixels exhibiting similar biophysical profiles were identified using the clustering method “iso-cluster” in the ArcGIS 10 Spatial Analyst Extension. The iterative algorithm assigns each pixel to a cluster according to its profile of variables and parameters listed in Table 3, and aims to minimize the Euclidean distance among pixels within each cluster. The initial number of clusters was limited to 60 (estimated to be a manageable number of units) and the algorithm was run with 10,000 iterations and a sampling value of 1 to produce robust groupings. A dendrogram (or classification tree) was derived to visually analyse the distance among clusters. Some clusters that split at low inter-cluster distance cut-offs were combined into “pelagic habitats,” the spatial unit used for the offshore MPA planning. This cluster tree was then cut to a distance threshold of five, based on the visual analysis of the dendrogram and a judgment of the number and size of units that would be most useful for management.

The final tree was recalculated with the merged clusters (Fig. 2). The clusters were generalized in ArcGIS to create a map of spatial units with contiguous areas applicable to management. Patches with an area less than 1000 km² were identified and removed, then these gaps were re-classified by expanding the remaining patches and applying and reapplying a boundary clean function (expand-shrink). Finally, a raster to vector transformation was applied to convert pixel clusters to polygons for better visualization of the habitats.

2.2.6. Post-analysis, assessments and validation

2.2.6.1. Quality assessment of cluster classification. We performed a maximum likelihood classification (MLC) in ArcInfo to provide a quality assessment indicator for the cluster mapping. The MLC calculates the probability that each pixel in the image belongs to a given cluster, and produces a map showing the degree of uncertainty associated with the classification grid across the planning domain (Lagabrielle, 2009; Post, 2008).

We then calculated the overlap of the uncertainty map and the pelagic habitat map in ArcGIS. We converted the continuous

uncertainty scale to a binned scale with classes 1–14, then overlaid the uncertainty map with the pelagic habitats map. We used the biophysical boundaries of the pelagic habitats in the overlap calculation (including areas extending outside the EEZ). We calculated the area of each pelagic habitat falling in each uncertainty class, then combined the classes into low (1–5), medium (6–9) and high (10–14) uncertainty. These breaks were selected from the natural breaks that emerged from a histogram (not shown) of the percent area of each habitat falling in each of the 14 classes.

2.2.6.2. Comparison to a finer-scale bioregionalisation of KwaZulu-Natal. We compared the habitat boundaries to a bioregionalisation of an area covering 130,000 km² (one-tenth the area of the EEZ) off the coast of KwaZulu-Natal (KZN) that falls mostly within the East Coast bioregion (Livingstone et al., In Press). The KZN analysis is a two-level hierarchical benthic-pelagic bioregionalisation that incorporates benthic sediment and biotic data where it was available in the shallower (usually < 200 m) areas (on the continental shelf), but the offshore component is similar to our bioregionalisation as it uses only depth and satellite-derived parameters. Both bioregionalisations use satellite-derived SST and chl-*a* and depth and slope data. The KZN analysis uses turbidity whereas our bioregionalisation incorporates MSLA and NPP. The KZN analysis uses satellite data from 2001 to 2004.

Although the source data and methods are somewhat similar, the spatial scales of the hierarchical levels of the two models are not the same, which prevents a robust, direct comparison of the overlap of the classification polygons. Still, we used ArcGIS to calculate the percent overlap of our fine and meso-scale levels (habitats and biozones, respectively) and the KZN fine and broader-scale levels (biozones and bioregions, respectively) to see if any patterns emerged.

2.2.6.3. Expert workshop. Expert opinion, as can be obtained from workshops or informal evaluations, is an important part of the development and validation of many bioregionalisations (Caldow et al., 2015). A workshop was held in South Africa in July 2010

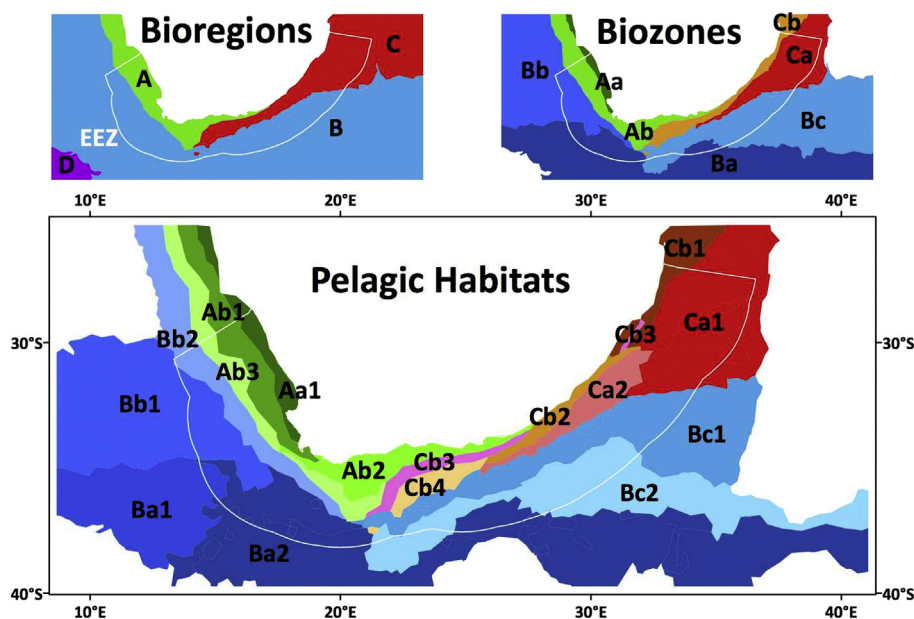


Fig. 3. Bioregions, biozones, and pelagic habitats identified in the cluster analysis. Only biozones and pelagic habitats falling within the continental South African EEZ are shown.

Table 4

Description of defining features of the pelagic habitats (pelagic realm defined from the 30 m depth contour). Pelagic habitat area is calculated only within the EEZ (the MPA planning domain), but % area of Low and High uncertainty refers to the entire pelagic habitat including any area falling outside the EEZ. Hab = habitat.

Bioregion	Hab	Key characteristics	Area		Uncertainty (% area)	
			km ²	Rank	Low	High
West and South Coasts	Aa1	Very high mean NPP and chl- <i>a</i> with high variability in mean NPP; very cold water (SST mean = 15.2 °C); very low eddy and SST front frequency over the shallow, gradually sloping shelf of the centre of the Benguela upwelling regime in the south Atlantic Ocean	31,552	11	10.3	14.8
	Ab1	Very high mean chl- <i>a</i> and NPP both with high variability; very high occurrence of chl- <i>a</i> fronts and very low eddy frequency; cold water (SST mean = 16.6 °C) due to upwelling over the shallow, gradually sloping Benguela shelf area of the south Atlantic Ocean	53,805	10	13.2	15.8
	Ab2	Very high mean chl- <i>a</i> and NPP both with very high variability over the shallow, gently sloping Agulhas bank; moderate Indian Ocean temperatures that are highly variable (SST mean = 19.1 °C)	67,704	6	15.2	10.5
Offshore	Ab3	High mean NPP, High and variable mean chl- <i>a</i> with high frequency of chl- <i>a</i> fronts related to the eastern limit of the Benguela upwelling on the outer shelf; Cold Atlantic temperatures (SST mean = 18.3 °C); Very low eddy frequency	54,797	9	7.8	17.8
	Ba1	Consistently low chl- <i>a</i> ; cold (SST mean = 17.8 °C) but highly variable water over the deep, gradually sloping Atlantic Ocean abyss; High frequency of eddies	97,877	4	7.3	13.7
	Ba2	Cool (SST mean = 19.4 °C) water over steeply-sloping Indian and Atlantic Ocean abyss; Very high frequency of eddies; Agulhas retroflection transition to the Southern Ocean	143,760	2	5.1	17.7
	Bb1	Cold (SST mean 18.7°C) Atlantic Ocean abyss; Consistently low NPP; SST fronts are very rare	71,584	5	9.5	13.0
	Bb2	Cold (SST mean = 18.5 °C) Atlantic open ocean transition toward the Benguela upwelling region; Consistently low NPP and chl- <i>a</i> ; Low frequency of eddies	63,646	7	9.6	20.5
	Bc1	Moderate temperature (SST mean = 21.8 °C); Consistently low NPP; Low chl- <i>a</i> mean and front frequency; High frequency of SST fronts in the open Indian Ocean	9553	16	12.8	13.6
	Bc2	Moderate and consistent temperature (SST mean = 20.5 °C); Consistently low chl- <i>a</i> in the Indian Ocean abyss and Agulhas retroflection and transition toward the Southern Ocean	125,394	3	5.7	14.1
East Coast	Ca1	Very warm (SST mean = 24.1 °C) Indian Ocean abyss; Very low NPP and chl- <i>a</i> with very low frequency of chl- <i>a</i> fronts	169,574	1	8.5	16.9
	Ca2	Consistently warm (SST mean = 23.5 °C) Indian Ocean water; Very low frequency of chl- <i>a</i> fronts but high frequency of SST fronts	59,190	8	17.1	15.2
	Cb1	Very warm (SST mean = 24.9 °C) shallow Indian Ocean shelf; Low frequencies of eddies and SST fronts	21,524	15	30.6	14.8
	Cb2	Very consistent warm (SST mean = 23.5 °C) water with low SST front frequency at the core of the Agulhas current along the eastern continental shelf; High mean chl- <i>a</i> and NPP with high variability	27,247	14	13.2	24.8
	Cb3	Consistently cool (SST mean = 21.2 °C) water over shallow, steeply sloping Indian Ocean shelf; Very high but variable chl- <i>a</i> ; Very frequent chl- <i>a</i> and SST fronts; Low eddy frequency	31,399	12	17.0	28.1
	Cb4	Consistently moderate (SST mean = 22.2 °C) Indian Ocean water; Very frequent SST and chl- <i>a</i> fronts associated with the very steep outer shelf	30,738	13	12.2	25.2
Total			1,059,344	16	9.2	15.9

with eight oceanographers, marine biologists, and fisheries scientists with expertise in South African waters (see Appendix B), in addition to three of the authors of this paper (AL, EL, KS). The experts reviewed the results of the pelagic bioregionalisation and discussed how the spatial units could best be used in SCP. Additional comments were provided by Prof. J. Lutjeharms (Oceanography Department, University of Cape Town).

2.3. Assessing threats to pelagic habitats

The bioregionalisation provides a spatial framework to assess the level and types of threats to the pelagic environment. We undertook a preliminary assessment of one threat using cost data related to fishing sectors. These fishing data were collated and used as one of the industry costs considered in the planning of the offshore MPA network (Sink et al., 2011a). The cost calculation is a proxy for the intensity of the combined fishing sectors. In ArcGIS, we overlaid the costs map with the pelagic habitats and calculated the overlap for each habitat in the EEZ. Costs were divided into three categories (zero, zero – 1000, and >1000) and used as a proxy for the intensity of threats to the pelagic environment from fishing activity. Fishing cost data was only available within the EEZ.

3. Results and discussion

3.1. Habitat classification and characterisation

The final pelagic bioregions map delineates 3 bioregions, 7 biozones, and 16 habitats occurring in the South African EEZ (Fig. 3). The parameter values for each cluster were assigned to rank based categories to help characterise each pelagic habitat relative to the study area. The three lowest ranking values for each parameter (0–10 percentile) were categorised as “Very Low,” ranks 23–26 (10–25%) were categorised as “Low,” ranks 4–7 (75–90%) were “High,” and the top 3 ranks (90–100%) were “Very High” (Table 4). All clusters were included in the ranking, although only clusters with overlap in the EEZ were assigned to pelagic habitats. See Appendix C for the complete results for each cluster and parameter.

The first hierarchical level (the bioregions) shows broad-scale differences in mean productivity, temperature and depth. The West and South Coasts bioregion is characterised by cold, high primary productivity water over the continental shelf; the East Coast bioregion is warm, lower primary productivity water mostly over the continental shelf; and the Offshore bioregion has

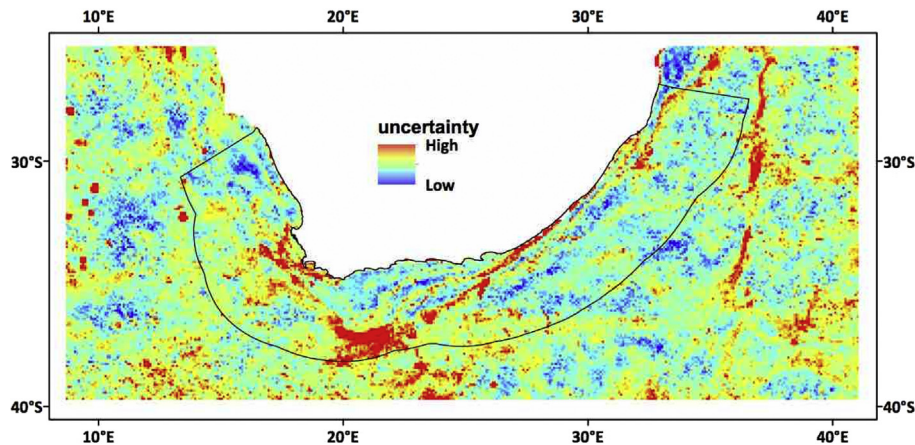


Fig. 4. The Maximum Likelihood Classification of the pelagic bioregionalisation showing the uncertainty that a pixel belongs to its allocated cluster.

moderate temperatures, low primary productivity, and deep water beyond the continental shelf (Table 4).

The second level (the biozones) captures mesoscale features within the bioregions, particularly upwelling and eddies. The boundaries of the seven biozones are based primarily on eddy distribution calculated from MSLA, and variability in SST, chl-*a*, and NPP. The two biozones in the high primary production West and South Coasts bioregion indicate a distinction between the centre of the upwelling regime on the West Coast (Biozone Aa), and the South West Coast and deeper West Coast waters (Biozone Ab) that exhibit slightly higher frequency of eddies and more variable SST. The Offshore bioregion contains three biozones, all with consistently low primary productivity. Biozone Ba is located in an area of Agulhas retroflection towards the Southern Ocean, and has high eddy frequency and variable SST. Biozone Bb in the Atlantic open ocean has less variable SST and fewer eddies. Biozone Bc in the Agulhas retroflection area has the most consistent SST in the Offshore bioregion. The two biozones in the East Coast bioregion are roughly divided inshore and offshore of the continental shelf. Biozone Ca is off the shelf over the Indian Ocean abyss and is characterised by moderate eddy frequency and moderate SST variability. Biozone Cb has lower eddy frequency and represents the core of the Agulhas current along the steeply-sloping Indian Ocean shelf.

The highest resolution level (the pelagic habitats) indicate local-scale variations often associated with SST and chl-*a* fronts (Table 4). Seven clusters within the EEZ had relatively small inter-cluster distances and were combined into three pelagic habitats (Ba2, Bc1, and Ca1). Interestingly, all but two habitats (Cb3 and Cb4) are spatially continuous (e.g., not made of more than one polygon) although no explicit distance criterion was set in the clustering process.

3.2. Quality assessment of cluster classification

The MLC calculation produced a map showing the degree of uncertainty associated with the classification grid across the study area (Fig. 4). The uncertainty map is not a measure of the variability or permanence of the pelagic habitats (which are incorporated into the model as the CVs of the parameters), but it does provide additional information about the habitat by indicating the degree of confidence in the spatial boundaries (Table 4). The MLC shows that most of the high uncertainty areas fall within the EEZ. High uncertainty values correlate with benthic features, specifically the sharp depth contrasts around the west coast submarine canyons and at the continental shelf – abyssal transition on the south and east coasts. The most striking area of uncertainty extends from the

southern tip of the Agulhas Bank at about 37° S, an area where 7 of the 16 habitats converge. The frequency distribution (not shown) of uncertainty classes is approximately normal; most of the pelagic habitat areas overlap with medium uncertainty (classes 6–9) of cluster membership, but a spike in the highest uncertainty class (14) correlates with the size of the red area at the tip of the Agulhas Bank. The three habitats with the largest proportions of area classified as high uncertainty (28.1, 25.2 and 24.8%) are all in Biozone Cb in the East Coast bioregion (Table 4). Interestingly, the remaining habitat in Biozone Cb (Cb1) has only 14.8% area classified as H uncertainty, and the largest proportion (30.6%) of low uncertainty area of the 16 pelagic habitats falling in the EEZ.

3.3. Validation of biogeographic boundaries

3.3.1. Overlap with KZN bioregionalisation

The overlap calculation indicates the importance of spatial scale, relative size of study area, and selection of variables and parameters. As expected, the shape and size of the polygons produced by the two bioregionalisations do not match closely. Our bioregionalisation includes eddies calculated from MSLA, and NPP instead of turbidity. Some of the difference in boundaries can therefore be attributed to the different source data, especially since mesoscale eddy activity is an important driver of variability in the East Coast bioregion area (Halo et al., 2014). However, most of the discrepancy is likely due to the different spatial scales of the hierarchical levels and the extent of the study areas. Since the habitat characterizations are based on relative means, the EEZ units will necessarily differ from those in the comparatively small and heterogeneous KZN study area. The scale of the KZN bioregionalisation is appropriate for SCP and research planning in that area, as many projects and initiatives are focused on the Agulhas Current. Similarly, there are several spatial classifications produced specifically for the Benguela Current. If representative pelagic habitat protection is an objective for the South African EEZ, then those habitat units should be based on the full extent of South African waters. Then, large-scale bioregionalisations can be compared to higher resolution maps to explore interesting or important local-scale processes in more detail.

3.3.2. Expert workshop

There was general consensus among the experts on the selected variables and datasets, the spatial scales of the three levels, and the hierarchical clustering method used to produce the pelagic bioregionalisation. There was concern that the nature of the spatial

and temporal averaging masks certain important processes, particularly, the short-lived, high productivity events in the subtropical convergence of nutrient-rich subantarctic waters and nutrient-poor Southwest Indian Ocean waters occurring in the Offshore bioregion. The bioregional map does not indicate which habitats are more or less ephemeral. Analysis of patterns of variability and the spatial and temporal permanence of pelagic features is important for ecosystem monitoring and assessment and protected area planning, and should be a focus of future analyses (Hardman-Mountford et al., 2008; Welch et al., 2016).

The experts also agreed that the habitat units should be considered valid for the upper mixed layer only, as the vertical dynamics of the system (e.g., thermocline depth) are not included in the model. The accuracy of the biogeographic boundaries could be improved with three-dimensional oceanographic models and validation data sets, which would allow the distinction of depth layers and the production of bioregional maps in different depth zones. Such products are more complex to analyse but a similar approach has been implemented for the bioregionalisation of the Australian EEZ (Lyne and Hayes, 2005).

A main consensus of the expert workshop was that scientists and planners would have more faith in the habitat boundaries if they were validated with biological datasets. Analyses of various teleost families, phytoplankton, or zooplankton communities have provided useful inputs to improve the precision of pelagic habitat boundaries (Condie and Dunn, 2006; Koubbi et al., 2011; Ward et al., 2012). Increasingly, bioregionalisation endeavours are exploring the correlation between satellite-derived habitat classifications and pelagic fish or top predator assemblages, which are often closely coupled with surface-derived parameters (Hobday et al., 2011; McClellan et al., 2014; Revill et al., 2009; Reygondeau et al., 2012). Isotopic analysis of tuna and billfish species have also been shown to offer more precise characterizations of pelagic habitats (Hobday et al., 2011). Other studies have devised qualitative approaches to judge the accuracy of pelagic habitats (Ardron, 2008; Welch et al., 2016).

For South Africa, Grantham et al. (2011) designed a theoretical MPA network for the West and South Coasts that would maximise target species representation. Kirkman et al. (2016) provide a broad-scale spatial characterisation of the same area based on an expert workshop and existing data on physical and biological processes. These two studies are not strictly bioregionalisation exercises, but they do integrate data on physical processes with biological datasets for species across a range of trophic levels, and provide preliminary examples for future validation exercises. Some relevant biological data is now available for the full extent of South Africa's EEZ but the data quality and resolution are patchy. Therefore, a rigorous comparison of our pelagic bioregionalisation with biological datasets is beyond the scope of this study. Efforts are currently underway to identify and collate additional datasets to adequately cover the EEZ.

The expert workshop identified two main applications for the pelagic bioregionalisation. The first application is reporting on ecosystem status. Based on their broad spatial characterisation of the Benguela Current Large Marine Ecosystem, Kirkman et al. (2016) suggest locations for transects to monitor physics, chemistry and biology. The spatial units identified in the KZN bioregionalisation (Livingstone et al., *In Press*) have been used to plan sampling locations for two large research collaborations focused on this area (the Bioregion Surrogacy and Spatial Solutions projects of the African Coelacanth Ecosystem Programme). Similarly, the EEZ bioregionalisation could be used as a spatial framework for allocating limited resources for future offshore sampling. Of particular interest are habitats characterised by highly variable SST or primary production or H eddy frequency, the areas of high uncertainty of

cluster membership indicated on the MLC map, and habitats with large overlap with high fishing costs. These areas are likely to represent interesting or poorly understood biophysical processes, highly dynamic and variable environments, and ecosystem functions most threatened by direct human exploitation.

The second application of the bioregional map is for SCP with the objective of protecting representative pelagic habitats and important processes. However, there was disagreement about the effectiveness of temporal versus spatial conservation measures. Most of the experts favoured temporal or dynamic closures over static MPAs because of the highly dynamic nature of pelagic megavertebrate species. There is debate in the literature about if and how static MPAs can be effective at protecting different highly mobile pelagic species (see Game et al., 2009; Hooker et al., 2011; Miller and Christodoulou, 2014). However, the experts agreed that given the lack of in situ data and the importance of surrogates for pelagic biodiversity, the bioregionalisation is an important complement to species data.

3.4. Pelagic habitat protection

3.4.1. Representation in the proposed MPA network

The pelagic bioregionalisation was used in SCP of a proposal to expand South Africa's MPA network. The MPA proposal was altered constantly as new information was considered, but here we discuss three iterations of the MPA map: priority areas for protection, the draft proposal network, and the proposed network. First, priority areas for protection were identified but with approximate spatial boundaries. This map was created by collating the pelagic bioregionalisation with the benthic habitat map as well as data on VMEs, Ecologically and Biologically Significant Areas (EBSAs), and distributions of priority species and fisheries catches (Sink et al., 2011a). These biodiversity data were combined with spatial data on the intensity of industry activities such as fishing, mining and petroleum. Marxan conservation planning software (Ball et al., 2009) was used to identify candidate areas for offshore protection with the least cost to existing industries, and subsequent iterations of planning scenarios were discussed with stakeholders to identify priority areas according to the constraints of a range of objectives.

The second version we discuss is the draft proposal of the MPA network, which included 21 new MPAs and expansions of existing MPAs that would protect 10.2% of the pelagic (>30 m depth) area of the EEZ ("Draft," Table 5). This proposal underwent a six-month consultation process with stakeholders such as oil and gas, aquaculture, and fisheries, as well as a series of workshops around the country with additional experts, stakeholders, and area-specific data. This proposed MPA network encompasses 6.0% of the pelagic area of the EEZ ("Proposed," Table 5). It was gazetted for further comment from the public and is currently being adjusted accordingly.

The proposed MPA network does not provide equal representative protection at the pelagic habitat or bioregion levels (Table 5). The East Coast bioregion has the greatest proposed representation (8.8%), followed by the West and South Coasts (7.0%) and Offshore (4.0%) bioregions. Under the proposed MPA network, the median area protected across the pelagic habitats is 7.4% and the average is 11.5%. All habitats have less than 15% of their area proposed for protection, except for Cb1, a small area of the Indian Ocean shelf with 53.6% MPA coverage (this habitat also had the best score for certainty of cluster membership). This area was selected for many objectives, including potential VMEs (known canyon and cold water coral locations), benthic and pelagic habitats and processes important for threatened species (leatherback turtle foraging and coelacanth habitat), bycatch management (crustacean trawl), and integrated enforcement opportunities. The three habitats with the least representation (0, 0, and 0.3%) under the gazetted MPA

Table 5
Pelagic habitat area within the EEZ, % area within the existing MPA network, a draft network, and the proposed network, and % area overlap with three categories of costs to fishing: Zero, Medium (>0 > 1000) and High (>1000).

Bioregion	Habitat	Area (km ²)	Area within MPA network (%)			Overlap with fishing costs (%)		
			Existing	Draft	Proposed	Zero	Medium	High
West and South Coasts	Aa1	31,552	0.2	2.8	5.1	37	43	20
	Ab1	53,805	1.3	4.8	6.0	42	28	30
	Ab2	67,704	0.5	10.6	8.6	24	60	16
	Ab3	54,797	0	10.4	7.4	8	44	47
Offshore	Ba1	97,877	0	0	0	65	35	0
	Ba2	143,760	0	18.8	11.3	55	45	0
	Bb1	71,584	0	0	0	24	76	0
	Bb2	63,646	0	3.0	0.3	4	91	5
	Bc1	9553	0	3.8	3.2	71	28	1
East Coast	Bc2	125,394	0	4.8	1.5	83	17	0
	Ca1	169,574	0	17.5	3.6	16	84	0
	Ca2	59,190	0	0.8	2.9	44	56	0
	Cb1	21,524	1.3	60.1	53.5	69	28	2
	Cb2	27,247	3.9	25.3	18.5	34	62	4
	Cb3	31,399	0	13.4	13.8	18	45	37
	Cb4	30,738	0	14.4	6.4	21	77	3
Total	1,059,344	0.002	10.2	6.0	40	53	7	

network are all in the Offshore bioregion, and have consistently low NPP in common.

The proposed MPAs are zoned for complete protection from trawling and oil and gas exploration. Shipping and some pelagic commercial fishing and recreational fishing are permitted. We explored broad patterns in the costs data developed for fishing sectors (Table 5). Seabed impacts (e.g. mining) were ignored, given that they were incorporated into the separate benthic analysis. Fishing costs ranged from 0 to 145,083, with an average of 365. As expected, most of the high threat area is in the West and South Coasts bioregion, and the least is in the Offshore bioregion. The habitats in the Offshore bioregion have a large overlap with the medium fishing class (e.g., 91% overlap with habitat Bb2), which could still signal a significant threat to pelagic assemblages. The area of high fishing costs is concentrated in certain pelagic habitats, particularly Ab3 (47% overlap), Cb3 (37% overlap) and Ab1 (30% overlap).

Future analyses should consider benthic-pelagic connectivity and cumulative threats to pelagic habitats, such as acoustic disturbance from shipping and seismic exploration, and land-based pollution. We assumed that the cost data act as a proxy for cumulative threats to pelagic environments from that industry (e.g. fishing). However, cost is not the same as threat, and some activities will disproportionately affect certain habitats. Vulnerable areas were considered in the benthic analysis, and a similar metric of vulnerability of pelagic habitats to both individual and cumulative threats would be a valuable extension of this pelagic habitat map. Importantly, this analysis considered the pelagic habitats to be stable across time, and did not account for changing spatial patterns in exploitation of marine resources, or for climate change impacts such as ocean warming and acidification. Modelling techniques for predicting dynamic processes and climate change impacts on marine environments have advanced. Recent analyses have explored methods for incorporating spatial shifts in pelagic habitats (Della Penna et al., 2017) and predictions of susceptibility and resilience to climate change into SCP (Davies et al., 2016; Levy and Ban, 2013).

The pelagic bioregionalisation provides a measure of the current status of protection of South Africa's pelagic ecosystems. Initially, 10% coverage of both benthic and pelagic habitats was a guideline for the design of the proposed MPA network, based on the CBD target. Pressure from stakeholders shrunk the total protected area from 10 to 6.0% of pelagic waters within the EEZ. Only one habitat has more than the 30% coverage recommended by the World Parks Congress, and three of the 16 habitats have zero or less than 1% coverage (Table 5). Policy-driven conservation targets have been criticized for their

ecological irrelevance (Rondinini and Chiozza, 2010), but these targets provide a framework that is communicable in a management context and they have been useful in mobilizing marine conservation actions at both local and international levels (Wood et al., 2008). Evaluations of global conservation targets indicate that even the 10% target is likely far too limited to accomplish the goals of protecting biodiversity, maintaining ecosystem services, setting areas aside for precautionary protection, and achieving socioeconomic priorities; subsequent recommendations have called for at least 30% coverage (O'Leary et al., 2016). The conservation targets should serve as a reminder that the proposed MPA network, while moving towards increasing protection, is still too limited to achieve certain objectives, such as effective protection of many highly mobile species (O'Leary et al., 2016).

The proposed MPA network still increases pelagic protection from 2478 km² to 63,387 km² (from 0.002% to 6.0%). Following the assumption that different pelagic habitats support different biological assemblages, every effort was made to retain coverage of as many pelagic habitats as possible when the proposed MPA boundaries were adjusted to compromise with stakeholders. The hope is that the gazetted MPA network in South Africa might still provide some incidental protection of unknown pelagic processes and biodiversity (Bridge et al., 2015). Although the debate about the efficacy of static MPAs for pelagic assemblages is still relevant, precautionary data-poor protection was assumed to be better than no protection (O'Leary et al., 2012). Furthermore, marine conservation has shifted away from single species objectives towards a more holistic framework of protecting biodiversity composition, structure and functions, including ecosystem services (Norse, 2010). Given the overrepresentation of megavertebrates in existing pelagic species data for South Africa, a data-driven habitat map was an important element of a data-driven SCP process.

At this point, static MPA boundaries are the most feasible option for effective implementation and enforcement. The proposed MPA network is an important step forward, but important pelagic features, such as eddies and upwelling zones, will change in location and intensity over time. Future management practices could be adapted to better match the dynamic nature of pelagic habitats, and the different processes in the upper mixed layer, the deeper strata of the water column, and the benthos. Large-scale or dynamic MPAs – or a combination of static and dynamic management schemes – are more likely to protect these critical ecosystems (Game et al., 2009; Toonen et al., 2013).

4. Conclusions

Previous marine habitat maps for South Africa are based on benthic or species data with substantial species and area sampling biases. Existing biophysical analyses do not cover the full extent of the EEZ, which is important for planning representative MPA networks in a geographical setting like South Africa, where a long coastline straddles two ocean current systems with substantial differences in SST means, primary production, and drivers of variability. The use of publicly available satellite data allows for a rigorous, cost-effective, and relatively quick bioregional classification of the entire planning area. This classification provides complete spatial coverage and units at a scale relevant to management. There remains some discomfort amongst scientists and planners regarding the inclusion of conservation targets for dynamic pelagic habitats within a static spatial scheme. Uncertainty in the habitat boundaries, persistence, and association with unique biological assemblages resulted in less emphasis on pelagic habitats in the identification of priority areas for protection. The representation of pelagic environments in the proposed MPA network was also limited by the constraints placed by marine industry stakeholders on the areas and boundaries of protected areas. The final network proposal thus had a smaller area than was recommended by the SCP approach to achieve conservation objectives related to pelagic ecosystems. However, the process of selecting the areas was systematic, rigorous and data-driven. If the proposed MPA network is well-monitored and enforced, these MPAs will provide protection for 6% of South Africa's marine environment, compared with the current 0.002%, thus providing a major improvement in South Africa's marine conservation estate.

Authors and contributions

Leslie A. Roberson: Conducted literature review, wrote article, created Table 1 and Appendix A, prepared Tables 2–5, Figs. 1 and 2, and the appendices revised article (multiple versions).

Dr. Erwann Lagabrielle: Conceptualized and executed the

modelling procedure; wrote the report (2009, unpublished) on the model which guided this article (particularly the Methods section), produced the original versions of Figs. 1–4, revised article (multiple versions).

Prof. Amanda T. (Mandy) Lombard: Conceptualized the original study and the article, created final versions of Figs. 1, 3 and 4, did the GIS analyses and calculations for Tables 4 and 5, revised article (multiple versions).

Dr. Kerry Sink: Provided motivation for the study as part of the MPA expansion project, conceptualized original study, advised on interpretation of results, revised content.

Tamsyn Livingstone: Conducted the first pelagic bioregionalisation in South Africa which guided this study, revised article.

Dr. Hedley Grantham: Advised on interpretation of results, revised article.

Dr. Jean M. Harris: Helped to conceptualize the first pelagic bioregionalisation in South Africa which guided this study, revised article.

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Appendix

Appendix A

Overview of marine and coastal biogeographic studies of South Africa using biological and physical datasets at various scales.

Reference	Study
Anderson et al., 2009	Distribution of seaweed species in the warm-temperate Agulhas Province
Bolton and Anderson, 1997	Marine vegetation of southern Africa
Bolton, 1986	A temperature dependent approach to marine phytogeography of the Benguela upwelling region
Bolton et al., 2004	Intertidal seaweed biogeography on the east coast of South Africa
Brown and Jarman, 1978	Coastal Marine Habitats
Brown et al., 1991	Phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems
Bustamante et al., 1997	The influences of physical factors on the distribution and zonation patterns of South African rocky-shore communities
Bustamante et al., 1995	Consumer biomass and gradients of intertidal primary productivity around the coast of South Africa
Dingle et al., 1987	Deep-sea sedimentary environments around Southern Africa
Emanuel et al., 1992	A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa
Harris et al., 2013	Intertidal habitats along the Benguela coast
Harrison, 2002	Biogeography of fishes in South African estuaries
Hommersand, 1986	Biogeography of the South African marine red algae
Jackelman et al., 1991	Marine benthic flora of the Cape Hangklip area and its phytogeographic affinities
Jackson, 1976	Intertidal ecology of the east coast of South Africa
Kirkman et al., 2016	Spatial characterisation of the Benguela ecosystem
Livingstone et al., In Press	Benthic-pelagic habitat classification of KZN on the East Coast of South Africa
Penrith and Kensley, 1970	Constitution of the fauna of rocky shores of South West Africa
Primo and Vazquez, 2004	Zoogeography of the southern African ascidian fauna
Riegl et al., 1995	Africa's southernmost coral communities
Schumann, 1998	The coastal ocean off south-east Africa, including Madagascar
Shannon, 1985	Evolution of the Benguela: physical features and processes
Sink et al., 2005	Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal
Stegenga and Bolton, 1992	Distribution of rhodophyta in the Cape Province relation to marine provinces
Stephenson and Stephenson, 1972	Intertidal life on rocky shores
Turpie et al., 2000	Biogeography of South African coastal fishes

Appendix B

Name and affiliation of the 11 attendees of the 2010 workshop to review the pelagic bioregionalisation (eight experts in addition to three of the authors of this study). Affiliation is at the time of the workshop.

Name	Affiliation
Dr. Amanda Lombard	Nelson Mandela Metropolitan University
Dr. Carl Van der Lingen	Department of Environmental Affairs
Mr. Craig Smith	Department of Agriculture Forestry and Fisheries
Ms. Cloverley Lawrence	South African National Biodiversity Institute
Dr. Erwann Lagabrielle	Nelson Mandela Metropolitan University
Dr. Juliette Hermes	South African Environmental Observation Network
Dr. Kerry Sink	South African National Biodiversity Institute
Dr. Mike Roberts	Department of Environmental Affairs
Ms. Natasha Karenyi	South African National Biodiversity Institute
Dr. Robin Leslie	Department of Agriculture Forestry and Fisheries
Dr. Steve Kirkman	Department of Environmental Affairs

Appendix C

Mean parameter values per cluster for parameters derived from datasets listed in Table 3. Cluster values are assigned to rank-based categories: "VL" (Very Low), the 3 lowest ranking values or the 0–10 percentile, "L" (Low), ranks 23–26 or 10–25%, "H" (High), ranks 4–7 or 75–90%, and "VH" (Very High), the top 3 ranks or 90–100%. Highest mean values for each parameter are shown in bold and Lowest are italicized. Rank is from Highest (absolute value) to Lowest. Clusters not assigned to a habitat are outside the continental South African EEZ.

Bioregion	Habitat	Cluster	SST mean (°C)			SST CV			SST max (°C)			SST fronts (%)		
			Mean	Rank	Cat	Mean	Rank	Cat	Mean	Rank	Cat	Mean	Rank	Cat
West and South Coasts	Aa1	48	15.2	28	VL	0.09	19	–	18.3	28	VL	2.5	27	VL
	Ab1	47	16.7	26	L	0.09	18	–	19.8	26	L	5.4	14	–
	Ab2	1	19.1	18	–	0.11	4	H	22.8	16	–	2.3	29	VL
Offshore	Ab3	9	18.3	22	–	0.09	17	–	21.5	25	L	5.5	12	–
	Ba1	7	17.8	24	L	0.11	6	H	21.5	24	L	4.7	17	–
	Ba2	24	19.6	16	–	0.09	8	–	23.1	17	–	4.5	9	–
	Ba2	23	19.2	15	–	0.1	16	–	22.8	15	–	5.6	18	–
	Ba2	34	18.4	21	–	0.1	12	–	22.4	19	–	5.4	13	–
	Bb1	13	18.7	19	–	0.1	10	–	22.3	20	–	2.4	28	VL
	Bb2	10	18.5	20	–	0.1	11	–	21.9	21	–	3.9	21	–
	Bc1	2	21.8	11	–	0.09	15	–	25.4	10	–	6.1	7	H
	Bc1	20	21.8	10	–	0.08	26	L	25.2	11	–	8.2	3	VH
	Bc2	11	20.5	13	–	0.08	27	VL	23.8	14	–	4	20	–
East Coast	Ca1	41	23.5	7	H	0.09	13	–	27.2	5	H	5.5	11	–
	Ca1	43	24.7	3	VH	0.08	22	–	28.3	3	VH	4.3	19	–
	Ca2	21	23.5	6	H	0.08	24	L	26.8	6	H	6.3	6	H
	Cb1	40	24.9	1	VH	0.08	20	–	28.4	1	VH	2.8	26	L
Outside SA EEZ	Cb2	38	23.5	5	H	0.07	28	VL	26.7	7	H	3.7	24	L
	Cb3	45	21.2	12	–	0.07	29	VL	24.3	12	–	15.5	1	VH
	Cb4	39	22.2	9	–	0.08	25	L	25.5	9	–	10.4	2	VH
		27	22.3	29	–	0.09	3	–	26.2	29	–	5.9	15	–
		29	24	27	H	0.08	2	L	27.6	27	H	3.8	10	–
		42	24.8	25	VH	0.08	1	–	28.4	22	VH	3.8	5	L
		14	20.4	17	–	0.1	9	H	24.2	18	–	4.9	25	–
		3	14.3	14	VL	0.12	7	VH	17.9	13	VL	5.1	16	–
		4	15.9	23	VL	0.12	5	VH	19.6	23	VL	5.6	4	–
		6	17.5	8	L	0.13	14	VH	21.8	8	–	6.4	8	H
	22	17.8	4	L	0.11	23	H	21.6	4	L	7.4	22	H	
	12	19.1	2	–	0.1	21	–	22.7	2	–	3.2	23	L	

Bioregion	Habitat	Cluster	Depth (m)			Slope (Degrees)			Eddies (%)			Chl- <i>a</i> fronts (%)		
			Mean	Rank	Cat	Mean	Rank	Cat	Mean	Rank	Cat	Mean	Rank	Cat
West and South Coasts	Aa1	48	–127	28	VL	0.19	29	VL	1.5	28	VL	3.5	13	–
	Ab1	47	–255	27	VL	0.3	27	VL	1.2	29	VL	6.9	1	VH
	Ab2	1	–114	29	VL	0.23	28	VL	6.4	26	L	2.9	19	–
Offshore	Ab3	9	–749	24	L	1.2	12	–	3.5	27	VL	4.6	5	H
	Ba1	7	–4910	5	H	0.68	23	L	64.2	6	H	3.9	10	–
	Ba2	24	–3851	7	–	1.49	14	H	68.6	2	H	3.4	12	–
	Ba2	23	–4675	14	H	1.14	5	–	83.2	4	VH	3.6	15	–
	Ba2	34	–3585	15	–	4.69	1	VH	77.2	3	VH	3.9	9	–
	Bb1	13	–4395	11	–	0.52	24	L	44.7	16	–	3.5	14	–
	Bb2	10	–2580	20	–	1.3	9	–	17	24	L	3.7	11	–
	Bc1	2	–2853	18	–	1.38	8	–	45.3	15	–	2.3	23	L
	Bc1	20	–4137	13	–	1.45	6	H	38.6	18	–	2.5	21	–
	Bc2	11	–4595	8	–	0.95	19	–	57.1	9	–	2.8	20	–
East Coast	Ca1	41	–2845	19	–	1.22	11	–	53.6	11	–	1.8	28	VL
	Ca1	43	–1795	22	–	0.96	17	–	51	12	–	2	27	VL

Appendix C (continued)

Bioregion	Habitat	Cluster	Depth (m)			Slope (Degrees)			Eddies (%)			Chl-a fronts (%)		
			Mean	Rank	Cat	Mean	Rank	Cat	Mean	Rank	Cat	Mean	Rank	Cat
Outside SA EEZ	Ca2	21	-3165	16	–	1.28	10	–	33.3	20	–	1.7	29	VL
	Cb1	40	-619	25	L	1.03	16	–	16.3	25	L	2.9	18	–
	Cb2	38	-1550	23	L	3.55	2	VH	24.4	21	–	3	16	–
	Cb3	45	-365	26	L	1.42	7	H	20.5	23	L	6.5	2	VH
	Cb4	39	-1966	21	–	2.46	3	VH	58.5	8	–	6.2	3	VH
		27	-4963	3	H	0.78	21	–	5.9	15	–	2.1	17	L
		29	-4823	2	H	0.31	18	L	3.8	10	–	2.1	8	L
		42	-4278	10	–	1.08	4	–	3.8	5	L	2.2	7	L
		14	-5195	9	VH	0.92	25	–	4.9	25	–	2.4	4	–
		3	-5058	1	VH	0.87	20	–	5.1	16	–	2.9	22	–
		4	-5083	17	VH	0.95	13	–	5.6	4	–	4.1	6	–
		6	-4527	4	–	1.66	22	H	6.4	8	H	4.1	25	H
		22	-2924	6	–	1.18	26	–	7.4	22	H	4.3	26	H
		12	-4537	12	–	0.5	15	L	3.2	23	L	5.5	24	H
Bioregion	Habitat	Cluster	Chl-a mean (mg m ⁻³)			Chl-a CV			NPP mean (mgC m ⁻²)			NPP CV		
			Mean	Rank	Cat	Mean	Rank	Cat	Mean	Rank	Cat	Mean	Rank	Cat
West and South Coasts	Aa1	48	5.99	1	VH	0.47	17	–	4320	1	VH	0.41	7	H
	Ab1	47	1.76	2	VH	0.69	3	VH	2073	2	VH	0.48	1	VH
	Ab2	1	1.29	3	VH	0.99	1	VH	1583	3	VH	0.48	2	VH
	Ab3	9	0.5	6	H	0.55	7	H	1004	5	H	0.35	13	–
Offshore	Ba1	7	0.24	17	–	0.41	26	L	589	15	–	0.33	16	–
	Ba2	24	0.29	15	–	0.44	10	–	692	13	–	0.31	9	–
	Ba2	23	0.28	14	–	0.51	21	–	650	10	–	0.38	21	–
	Ba2	34	0.32	10	–	0.49	14	–	692	11	–	0.38	8	–
	Bb1	13	0.19	22	–	0.44	22	–	519	21	–	0.27	28	VL
	Bb2	10	0.31	12	–	0.43	23	L	739	8	–	0.28	25	L
	Bc1	2	0.18	23	L	0.48	16	–	484	23	L	0.31	23	L
	Bc1	20	0.22	18	–	0.46	19	–	556	18	–	0.3	24	L
East Coast	Bc2	11	0.2	21	–	0.43	24	L	539	20	–	0.31	22	–
	Ca1	41	0.16	25	L	0.51	12	–	434	25	L	0.33	18	–
	Ca1	43	0.14	27	VL	0.47	18	–	390	27	VL	0.32	20	–
	Ca2	21	0.21	19	–	0.54	9	–	512	22	–	0.34	15	–
Outside SA EEZ	Cb1	40	0.34	9	–	0.54	8	–	621	14	–	0.35	14	–
	Cb2	38	0.56	5	H	0.95	2	VH	855	6	H	0.47	3	VH
	Cb3	45	0.8	4	H	0.6	4	H	1268	4	H	0.37	10	–
	Cb4	39	0.36	8	–	0.6	5	H	737	9	–	0.37	12	–
		27	0.15	13	L	0.51	27	–	426	19	L	0.32	4	–
		29	0.13	16	VL	0.43	28	L	384	16	VL	0.28	6	VL
		42	0.13	11	VL	0.38	6	VL	360	12	VL	0.26	5	VL
		14	0.16	20	L	0.51	20	–	460	17	L	0.33	26	–
		3	0.29	24	–	0.39	11	VL	552	24	–	0.47	17	H
		4	0.27	7	–	0.38	15	VL	575	7	–	0.43	11	H
	6	0.31	26	–	0.6	13	H	665	26	–	0.45	19	H	
	22	0.39	28	H	0.48	25	–	803	28	H	0.37	27	–	
	12	0.21	29	–	0.46	29	–	568	29	–	0.28	29	L	

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