

Dynamic partitioning of tropical Indian Ocean surface waters using ocean colour data - management and modelling applications

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Abstract

Over the past few decades, partitioning of the surface ocean into ecologically-meaningful spatial domains has been approached using a range of data types, with the aim of improving our understanding of open ocean processes, supporting marine management decisions and constraining coupled ocean-biogeochemical models. The simplest partitioning method, which could provide low-latency information for managers at low cost, remains a purely optical classification based on ocean colour remote sensing. The question is whether such a simple approach has value. Here, the efficacy of optical classifications in constraining physical variables that modulate the epipelagic environment is tested for the tropical Indian Ocean, with a focus on the Chagos marine protected area (MPA). Using remote sensing data, it was found that optical classes corresponded to distinctive ranges of wind speed, wind stress curl, sea surface temperature, sea surface slope, sea surface height anomaly and geostrophic currents (Kruskal-Wallis and post-hoc Tukey honestly significantly different

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tests, $\alpha = 0.01$). Between-class differences were significant for a set of sub-domains that resolved zonal and meridional gradients across the MPA and Seychelles-Chagos Thermocline Ridge, whereas between-domain differences were only significant for the north-south gradient (PERMANOVA, $\alpha = 0.01$). A preliminary test of between-class differences in surface CO₂ concentrations from the Orbiting Carbon Observatory-2 demonstrated a small decrease in mean pCO₂ with increasing chl, from 418 to 398 ppm. Simple optical class maps therefore provide an overview of growth conditions, the spatial distribution of resources – from which habitat fragmentation metrics can be calculated, and carbon sequestration potential. Within the 18 year study period, biotic variables were found to have decreased at up to 0.025%a⁻¹ for all optical classes, which is slower than reported elsewhere (Mann-Kendall-Sen regression, $\alpha = 0.01$). Within the MPA, positive Indian Ocean Dipole conditions and negative Southern Oscillation Indices were weakly associated with decreasing chl, fluorescence line height (FLH), eddy kinetic energy, easterly wind stress and wind stress curl, and with increasing FLH/chl, sea surface temperature, SSH gradients and northerly wind stress, consistent with reduced surface mixing and increased stratification. The optical partitioning scheme described here can be applied in Google Earth Engine to support management decisions at daily or monthly scales, and potential applications are discussed.

Keywords: Remote sensing, biogeography, habitat fragmentation, Orbiting Carbon Observatory-2 (OCO-2), Marine Protected Area, epipelagic

1. Introduction

Physical drivers such as light, temperature and dynamical mixing shape the epipelagic ecosystem, and the biota of deeper water layers is determined, at least in part, by the productivity of upper layers (Jerlov, 1976; Longhurst, 2007; Spalding et al., 2012; Kavanaugh et al., 2016; Proud et al., 2017). Dividing the oceans into geographical areas with common physical conditions has been approached using a range of methods and suites of data (reviewed by Krug et al., 2017; Kavanaugh et al., 2016), and referred to variously as ecological geography, partitioning, biogeography, biohydrography, biogeographical provinces and seascapes. Most schemes include nested spatial scales with slightly different nomenclature for different elements of hierarchical structure. Partitioning the oceans is similar to habitat mapping and species distribution modelling in the sense that a geographical representation of resources is produced. However, it does not relate to specific organisms, and no model of the relationships between predictor and response variables is produced (c.f. Blanco et al., 2015; Coelho et al., 2013; Scales et al., 2014; Zydalis et al., 2011). Partitioning schemes have found application to two key challenges. Firstly, they provide static and dynamical geographical boundaries to guide management planning (over the long term) and intervention (in the short term). Management tasks include monitoring ecosystem health, assessing risk and implementing control measures such as fishery closure, and information is required at multiple spatial scales and depth ranges to support these actions (Rice et al, 2011; Spalding et al., 2012; Caldow et al., 2015; Roberson et al, 2017). Short-term responses can only be supported when the frequency at which new data is available exceeds the rate of critical fluctuations occur-

ring within the ecosystem. The second use is to provide spatial context for the evaluation of climate model reliability (Vichi et al., 2011; Kavanaugh et al., 2014; Fay & McKinley, 2014). The focus here is on the exchange of climate-relevant gases across the air-sea interface and there is no requirement for low-latency information. Partitions serve as a proxy for ecosystem function with the inference that they constrain rates of CO₂ diffusion, biotic carbon uptake and the efficiency with which carbon is removed from the surface layer. Earth system models (ESM), in which the representation of biogeochemical cycles remains quite simplistic (Hense et al., 2017; Jung et al., 2019; Sreeush et al., 2018) and which are sensitive to feedback between biotic and abiotic components (Lim & Kug, 2017; Park & Kug, 2014; Romanou et al., 2014) can then be evaluated in the context of static or dynamic seascapes (Landschützer et al., 2019; Lovenduski et al., 2019).

Satellite remote sensing data, which currently provides the best compromise between area coverage and temporal resolution for surface ocean studies, has increasingly been used for partitioning, as the disparate worlds of marine management and oceanography converge on how this rich data source can best be used (Kachelriess et al., 2014; Maxwell et al., 2015; Miloslavich et al., 2018). Figure 1 illustrates some of the pelagic abiotic and biotic factors that can be derived from remote sensing data, and characteristics relevant for modelling and management decisions.

[FIGURE 1 HERE: SINGLE-COLUMN; COLOUR ONLY ONLINE]

Of the variables amenable to remote sensing, only ocean colour is directly affected by the pelagic ecosystem at short time-scales. Partitioning schemes mostly use an ocean-colour-derived variable, chlorophyll-a concen-

51 tration (hereafter chl), as a measure of biomass and combine it with other
52 key physical drivers such as temperature. However, being a function of the
53 concentrations of dissolved and particulate substances in the surface ocean,
54 ocean colour itself represents a response to the physical drivers. Using ocean
55 colour to derive chl incurs spatially-varying errors (Jackson et al., 2017) and
56 ignores other coloured variables of interest that may, or may not, covary with
57 chl (O'Reilly et al., 1998; Werdell et al., 2018).

58 Classifications based on water colour alone have shown that, whilst chl is
59 generally constrained by these classifications, information about other water
60 mass tracers is also present (Alvain et al., 2005, 2008; Vantrepotte et al., 2012;
61 Trochta et al., 2015; Krug et al., 2018; Monolisha et al., 2018; Dierssen, 2010).
62 Taken together with the knowledge that physical dynamics at all scales com-
63 bine to control the growth environment, this suggests an opportunity to use
64 pure optical classes as the smallest scale in a seascape heirarchy, with the
65 advantage that it is a low-latency product which could feed into decision-
66 making flows on a daily basis (e.g. using GoogleEarthEngine; Gorelick et al.,
67 2017) where coverage allows. This possibility is explored here, with a focus
68 on the Chagos marine protected area (MPA). If optical classes are found to
69 constrain abiotic drivers as well as biotic response, then a further question
70 arises of whether they can also be used to estimate carbon flows (extending
71 Kavanaugh et al., 2014) without the need to identify individual elements,
72 such as phytoplankton function type, as an intermediate step.

73 *1.1. The study area*

74 The Chagos marine protected area occupies 640,000 km² in the tropical
75 Indian Ocean, with the Chagos Archipelago system of islands and atolls at it

76 centre (Figure 2; UNEP-WCMC, 2016). The coastline of the Indian Ocean
77 is shared amongst over twenty countries, representing a substantial fraction
78 of the human population with variable socio-economic status and strong re-
79 liance on coastal and open-ocean fisheries (Hermes et al., 2019). The MPA
80 is of particular value because of its coral health, resilience and diversity,
81 extensive seagrass beds, potential support for the wider Indian Ocean fish-
82 eries and related benefits (Koldeway et al., 2010; Ateweberhan et al., 2018;
83 Gravestock & Sheppard, 2015; Esteban et al., 2018). In common with shallow
84 tropical corals around the world, reefs in the Chagos MPA are vulnerable to
85 temperature increases associated with climate change as well as to increases
86 in extreme high energy dynamics. Their relative resilience compared with
87 other reef systems is associated with protection from human disturbance as
88 well as to geographical location. Although extensive coral bleaching has oc-
89 curred (Sheppard et al., 2008), interactions between dynamical processes at
90 a range of scales and topographic diversity may alleviate temperature stress
91 (Sheppard, 2012; Hosegood et al., 2019). Understanding whether this nat-
92 ural protection will continue under ongoing climate change is important in
93 terms of economic as well as natural resource value.

94 The Chagos Archipelago lies at the edge of the South Indian tropical
95 gyre within the influence of the Indian Ocean monsoon. In austral summer,
96 northerly winds drive an anticyclonic cell and the gyre contracts, so that
97 the archipelago is at the northern edge. For the rest of the year, the MPA
98 lies at or near the southern edge of the gyre. The location and large-scale
99 circulation features are summarised in Figure 2. In the west, divergent winds
100 and negative wind stress curl lift the thermocline along 5-12°S creating the

101 Seychelles-Chagos Thermocline Ridge (SCTR), with a thermocline depth
102 around of 50 m and no surface signature, which extends around the MPA
103 throughout the year (Hermes & Reason, 2008, 2009; Aguiar-Gonzalez et al.,
104 2016; Xie et al., 2002).

105 [FIGURE 2 HERE: SINGLE or 1.5 COLUMN; COLOUR ONLY ON-
106 LINE]

107 The South Equatorial Current (SEC), flowing to the south of the MPA,
108 denotes the boundary between relatively nutrient replete but O₂-poor surface
109 waters to the north and southern sub-tropical gyre waters to the south which
110 are nutrient-depleted throughout the water column but represent a CO₂ sink
111 (Garcia et al., 2018; Landschützer et al., 2016). *In situ* biogeochemical data
112 are sparse across the tropical Indian Ocean and considerable deviations from
113 the mean conditions in the World Ocean Atlas have been reported (Subha
114 Anand et al., 2017; Chinni et al., 2019). Whilst the tropics are generally
115 considered to be oligotrophic, year-round elevated phytoplankton biomass
116 is observed close to the archipelago as well as over the Mascarene Plateau
117 to the west and broadly over the SCTR (Wilson & Qiu, 2008; Levy et al.,
118 2007). *In situ* measurements of net primary production in this region range
119 from close to zero up to 20 mgCm⁻²d⁻¹ and can be exceeded by bacterial
120 production (Subha Anand et al., 2017; Fernandes et al., 2008; Veldhuis et al.,
121 1997). A few high temporal resolution datasets from moored fluorometers
122 have shown high frequency, high magnitude fluctuations in phytoplankton
123 biomass (Hosegood et al., 2019; Strutton et al., 2015). Phytoplankton as-
124 semblages have been found to be dominated by Prochlorococcus and Syneco-
125 coccus as expected in the oligotrophic gyres, but substantial fractions of di-

126 atoms, dinoflagellates and prymnesiophytes have also been reported in the
127 TIO (Thorrington-Smith, 1971; Veldhuis et al., 1997; Soares et al., 2015).
128 To my knowledge, there are no long-term biogeochemical monitoring efforts
129 in the pelagic SCTR, despite detailed repeat monitoring in the shallow reef
130 waters of the MPA (e.g. Sheppard, 2012). Many studies have used cou-
131 pled ocean-biogeochemical models, together with available *in situ* or remote
132 sensing data, to elucidate biophysical coupling in the tropical Indian Ocean
133 (TIO) (e.g. Wiggert et al., 2006; Jin et al., 2012; Liu et al., 2013; Resplandy
134 et al., 2009; George et al., 2018). Of particular interest here are the results
135 of George et al. (2018), Dilmahamod et al. (2016) and Wiggert et al. (2006),
136 who explore meridional and zonal gradients in the SCTR.

137 The epipelagic growth environment is directly modulated by entrainment
138 and advection of nutrients and plankton, fluctuations in mixed layer tem-
139 perature and depth, the relative euphotic to mixed layer depths, turbulence
140 and varying illumination conditions. Conversely, feedback effects have been
141 demonstrated between chl and shortwave heating, SST, surface convergence
142 and basin-scale dynamical features (Back & Bretherton, 2009; Park & Kug,
143 2014). At the seasonal scale, the eastward extent of the SCTR and westward
144 extent of Indonesian Throughflow (ITF) respond to monsoon wind weakening
145 and reversal (Aguiar-Gonzalez et al., 2016). Two of the eight Madden-Julian
146 Oscillation (MJO) phases are centred in the TIO (Hendon & Salby, 2994),
147 with a westward-progagating Rossby wave (Seiki et al., 2013) impacting SST,
148 evaporation, precipitation, cloud cover, rainfall, salinity gradients (Guan et
149 al., 2014; Jin et al., 2013; McPhaden & Foltz, 2013) and wind-driven en-
150 trainment of nutrients into the mixed layer (Jin et al., 2012b). At the in-

151 terannual scale, El Nino and the Southern Oscillation (ENSO) and Indian
152 Ocean Dipole (IOD) events have been reported to affect surface conditions
153 and surface chlorophyll concentrations. Nino conditions affect mixed layer
154 temperatures through precipitation, downwelling (anticyclonic) winds and
155 westward propagating Rossby waves (Santoso et al., 2010; Dilmahamod et
156 al., 2016; Ma et al., 2014; Racault et al., 2017). Positive IOD phases coincide
157 with cooler surface temperatures in the eastern TIO and warmer conditions
158 to the west (SST anomalies of 0.1 to 0.3 °C or more; Currie et al., 2013;
159 Vialard et al., 2009). The impact of ENSO and IOD events is amplified when
160 they coincide, and both are expected to increase in frequency (IPCC, 2013;
161 Sheppard et al., 2008; Currie et al., 2013; Cai et al., 2014).

162 Despite the scarcity of data in the epipelagic in and around the Cha-
163 gos MPA, the importance of conditions in these waters has recently been
164 highlighted by electronic tagging of seabirds and high trophic level pelagic
165 feeders, which has been used to document foraging at considerable distances
166 (Pecoraro et al., 2017; Danckwerts et al., 2014; Le Corre et al., 2012), with
167 measurable positive impacts on reef health through nutrient redistribution
168 (Graham et al., 2018). The near-shore pelagic biome is also a critical food re-
169 source for corals (Houlbréque & Ferrier-Pagés, 2009) and the strength of this
170 relationship has now been demonstrated using remotely sensed ocean colour
171 data (Fox et al., 2019). Elevated chl related to the wind-driven circulation
172 around the Chagos MPA is therefore a potential resource both for the reef
173 and for pelagic organisms.

174 The underlying hypothesis for this study is that water colour represents
175 the evolving trophic status of the upper ocean and is characteristic of the suite

176 of physical drivers of ecosystem function as illustrated in Figure 1 (e.g. Jerlov,
177 1976), making it a candidate as a low-latency, fine-scale level in a seascape
178 heirarchy. This paper addresses how methodological choices affect optical
179 classifications, whether pure optical classes provide useful information about
180 the physical environment and potential applications of optical class maps.

181 **2. Methods**

182 *2.1. Remote sensing data*

183 This study spans August 2002 to October 2018. Remote sensing re-
184 flectance (Rrs), chlorophyll-a concentration (chl), normalised fluorescence
185 line height (nFLH) and sea surface temperature (SST) data from the NASA
186 Moderate Resolution Imaging Spectrometer aboard the Aqua satellite (MODIS-
187 Aqua), at Level 2 and Level 3, were acquired from the Ocean Biology Pro-
188 cessing Group (oceancolor.gsfc.nasa.gov). Rrs is the ocean colour product
189 with the least degree of processing and therefore the lowest uncertainty, with
190 errors on the order of 0.001 sr^{-1} but varying with waveband and water type
191 (Franz et al., 2007; IOCCG, 2019). Reflectances from the seven 1 km reso-
192 lution, 10 nm wavebands in the visible domain were augmented by band 1,
193 with 250 m resolution (50 nm waveband) and bands 3 and 4, with 500 m res-
194 olution (20 nm wavebands), and these three bands were spatially averaged to
195 match the 1 km wavebands. Globally, chl is the best-validated ocean colour
196 product, with mean errors of ca. $\pm 33 \text{ mgm}^{-3}$ (Hu, et al., 2012; O’Reilly et
197 al., 1998). Little product validation data is available for nFLH in the tropi-
198 cal Indian Ocean, but the MODIS-Aqua and MODIS-Terra products perform
199 well against *in situ* data in the Southern and Atlantic Oceans (Erickson et

200 al., 2019; Hoge et al., 2003).

201 Daily sea surface height (SSH), height anomalies (SSHA) and geostrophic
202 current velocities (denoted eastwards u and northwards v), from merged al-
203 timeter datasets, were acquired at ca. 30 km resolution from the Coper-
204 nicus Marine Environment Monitoring Service (CMEMS). Reported errors
205 on these products range from < 1 cm to 30 cm, with higher uncertainties
206 under more dynamic conditions (CMEMS, 2020). Eddy kinetic energy was
207 calculated as $EKE = 1/2(u^2 + v^2)$. Sea surface slope was calculated pixel-
208 wise as $\nabla SSH = \partial SSH/\partial x + \partial SSH/\partial y$, with no smoothing. Each product
209 was subsampled to 4 km resolution before applying the optical class masks
210 (section 2.7).

211 Daily surface wind fields from the SeaWinds and ASCAT scatterometer
212 sensors were acquired at 25 km resolution from the Jet Propulsion Labo-
213 ratory Physical Oceanography Distributed Archive Center (SeaPAC, 2006;
214 EUMETSAT/OSI SAF, 2018). Errors in these products are of order 0.1
215 ms^{-1} (Verhoef et al., 2017). Wind stress curl was calculated pixelwise as
216 $\nabla \times \tau = -\partial \tau_N/\partial x - \partial \tau_E/\partial y$, where τ_N and τ_E are the north-south and east-
217 west components of the wind stress and ∂x and ∂y are the pixel dimensions.
218 Monthly averages were calculated before subsampling to 4 km resolution and
219 applying the optical class masks (section 2.7)

220 Profiles of the partial pressure of CO_2 derived from Orbiting Carbon
221 Observatory 2 (OCO-2) data using the full physics model version 7.3 (O’Dell
222 et al., 2018) were acquired at native resolution (ca. 3 km^2) from the Goddard
223 Earth Sciences Data and Information Services Center (OCO-2 Science Team,
224 2016, GES DISC). Only estimates of pCO_2 from the lowest model altitude

225 were used and the ramifications of this are discussed in section 3.4. No spatial
226 or temporal compositing was applied.

227 Bathymetry data were acquired at 1 arc-second resolution from the Na-
228 tional Centers for Environmental Information (ETOPO1, 2019) and regrid-
229 ded using nearest-neighbour gridding to match the Level 3 Rrs data.

230 Data products, sources and abbreviations are summarised in table 1.

231 [TABLE 1 HERE]

232 2.2. *Dynamic partitioning based on ocean colour*

233 Fuzzy classification was applied to the Indian Ocean domain surrounding
234 the BIOT MPA (after Moore et al., 2001; Jackson et al., 2017). This method
235 was chosen for its potential to allow a single pixel to have multiple class
236 memberships, which is likely in natural phytoplankton populations, particu-
237 larly at the relatively coarse spatial scales of remote sensing data (1 to >30
238 km) in waters where mesoscale and submesoscale processes may be at play.
239 The study bounds were 40° to 100° E, -20° to 15° N, spanning the central
240 tropical Indian Ocean with the BIOT MPA roughly central to the domain
241 (Figure 3; UNEP-WCMC, 2016). In the absence of *in situ* data with which
242 to verify class memberships or interpret class composition, only the dominant
243 class assigned to each pixel at any given time was retained (multiple class
244 memberships were removed, to be considered in future work when validation
245 data are available). Biovolumes calculated from microscopy analysis on five
246 stations within the MPA were used as a preliminary test of whether differ-
247 ent classes represented different phytoplankton biomass (Kruskal-Wallis test;
248 Schwarz, 2020).

Variable	Abbreviation	Source
Remote sensing reflectance, Level 2	L2 Rrs	Ocean Biology Processing Group Level 2 data ocean-color.gsfc.nasa.gov
Remote sensing reflectance, Level 3	L3 Rrs	
Surface chlorophyll-a concentration	chl	
Surface normalised fluorescence line height	nfh	
Ratio of fluorescence line height to chlorophyll-a	fh:chl	MODIS-Aqua Level 3 monthly data, Giovanni data portal giovanni.gsfc.nasa.gov
Sea surface temperature	SST	
Metric for within-class spectral variability (chlorophyll-like pigments): ratio of residual reflectances (Rrs - class mean) at 555 nm to 443 nm	R555:443	
Metric for within-class spectral variability (accessory pigments): ratio of residual reflectances (Rrs - class mean) at 555 nm to 488 nm	R555:488	
Sea surface height (absolute dynamic topography)	SSH	AVISO Level 4 reprocessed gridded sea surface heights and derived variables (product suite SEALEVEL_GLO_PHY_L4
Sea surface slope	∇ SSH	REP-OBSERVATIONS_008_047),
Sea surface height anomaly	SLA	marine.copernicus.eu, $0.25^\circ \times 0.25^\circ$ regrided to 4 x 4 km
Eastward component of the geostrophic current	u	
Northward component of the geostrophic current	v	
Eddy kinetic energy	EKE	
Eastward component of the surface wind field	τ_E	Quikscat and ASCAT Level 3 gridded wind fields, podaac.jpl.nasa.gov, 25 x 25 km regrided to 4 x 4 km
Northward component of the surface wind field	τ_N	
Wind stress curl	$\nabla \times \tau$	
Water depth	z	ETOPO 1 arc-minute bathymetry regrided to 4 x 4 km (Amante & Eakins, 2009)
Indian Ocean Dipole index	IOD	Dipole mode index (Saji & Yamagata, 2003) esrl.noaa.gov/psd/gcos_wgsp/Timeseries/DMI
Madden Julian Oscillation index	MJO	Kilidas et al. (2014) esrl.noaa.gov/pas/mjo/mjoindex
Southern Oscillation Index	SOI	Ropelewski & Jones (1987) esrl.noaa.gov/psd/data/20thC_Rean/time-series/monthly/SOI
Surface partial pressure of CO ₂	pCO ₂	Level 2 OCO-2 physical model surface pCO ₂ , release 9, GES DISC (Boesch et al., 2019)

Table 1: Optical, biological and physical remote sensing products used to explore optical classes

249 [FIGURE 3 HERE: SINGLE-COLUMN or 1.5 COLUMN; PLEASE QUOTE
250 FOR COLOUR PRINTING COSTS]

251 *2.3. Impact of spatial and temporal compositing on optical classification*

252 As noted by Jackson et al. (2017, hereafter JSM), averaging of the re-
253 motely sensed reflectance spectra from instantaneous, Level 2 (ca. 1 x 1
254 km resolution) to Level 3 (ca. 4 x 4 km resolution, weekly or monthly)
255 data incurs a risk of smoothing out phytoplankton dynamics associated with
256 growth/decay/advection events that are short-lived, and it increases the dif-
257 ference between any available *in situ* reflectance data used in characterising or
258 evaluating optical classes from the already spatially-averaged remote sensing
259 pixel values. Daily data may also be most appropriate for some management
260 applications. However, cloud-cover and the reduced overpass rates at low
261 latitudes make the use of daily data for capturing spatial patterns challeng-
262 ing in this region. The impact of spectral aliasing (from averaging) on the
263 classification was tested by creating classes firstly from all the Level 2 (L2)
264 data for 2003, with no averaging or regridding. The resulting classes were
265 compared against the same suite of classification procedures applied to the
266 Level 3 (L3) monthly, 4 km gridded data for 2003 and against the hybrid
267 classification scheme produced by JSM and Moore et al. (2001) who used *in*
268 *situ* data.

269 Both the L2 and L3 data were classified in three forms: Remote sensing
270 reflectance (Rrs), Rrs with the mean 2003 Rrs subtracted ($Rrs - \overline{Rrs2003}$)
271 and Rrs normalized to 488 nm ($Rrs/Rrs488$). Training data were selected
272 randomly in space and time from the study domain. For comparability with
273 previous studies, three sizes of training dataset were used. The smallest

274 dataset contained 42,000 pixels, corresponding approximately to the volume
275 of data used by JSM for two of their study sites - they used two central
276 Indian Ocean sites referenced to Longhurst (2007) provinces. Additional
277 datasets of double and fifty times the original size were added to test for
278 sensitivity of the classification scheme to dataset size. Each dataset was
279 classified using the Matlab fcm function (Bezdek, 1981) with between 2 and 9
280 classes and the weighting exponent m was varied between 1.05 and 2.0. Class
281 separability and compactness were assessed using the partition coefficient
282 (F) and compactness and separation index (S) as in Moore et al. (2001);
283 Windham (1982); Xie & Beni (1991). In contrast to previous studies, all
284 ten available MODIS visible wavebands were used in the fuzzy classification
285 procedure.

286 *2.4. Interpretation of within-class spectral variability*

287 The use of ten wavebands for an optical classification allows limited explo-
288 ration of within-class spectral variability, which may be related to pigmen-
289 tation and size differences caused by change in phytoplankton community
290 composition or physiology, differences in backscatter related to the viral,
291 bacterial and phytoplankton communities, variability in the relative quanti-
292 ties of coloured, dissolved organic matter or inorganic particulate matter,
293 variability in the depth distributions of coloured materials and noise in the
294 satellite signal (Kirk, 1994; Brown et al., 2008; Defoin-Platel & Chami, 2007;
295 Alvain et al., 2005; Lain & Bernard, 2018; Brewin et al., 2011b). Having
296 excluded water depths shallower than 200 m and in the absence of *in situ*
297 validation data, the main focus here is on testing whether Rrs spectra varied
298 uniformly with optical class. Residual reflectance ratios $Rrs(555)/Rrs(443)$

299 and $Rrs(555)/Rrs(488)$ were calculated after subtracting the dominant class
300 mean reflectance spectrum (Table 4) at each pixel, as indicators of spectral
301 variability. In a full application of the fuzzy classification scheme (Moore et
302 al., 2001), this step could be pre-empted by allowing multiple class member-
303 ships at each pixel.

304

305 *2.5. Comparison against other classifications*

306 Class spectra produced in this study and by JSM were mapped to other
307 interpretations for comparison. Firstly, the standard NASA OC3M-CI algo-
308 rithms were applied to each central class spectrum to produce chl concentra-
309 tion (O'Reilly et al., 1998; Hu, et al., 2012). This was passed to abundance-
310 based algorithms for phytoplankton size class published by Brewin et al.
311 (2010, Atlantic Ocean), Brewin et al. (2011a, global *in situ* data), Brewin et
312 al. (2012, eastern Indian Ocean) and Devred et al. (2011) (North Atlantic
313 and global *in situ* data; IOCCG, 2014). Chl was also used to select the
314 closest stratified water trophic class from Uitz et al. (2006). For comparison
315 against Alvain et al. (2005, 2008), every 10th Level 2 MODIS Rrs file from
316 2003 was used to generate local PHYSAT-equivalent mean-chl spectra (39 chl
317 divisions from 0.01 to 4.00 mgm^{-3} in intervals of $\ln(0.15)$; between 67016 and
318 5488110 pixels per chl interval with a total of 64733448 pixels). These were
319 subtracted from each mean optical class spectrum and the residual compared
320 against the criteria provided by Alvain et al. (2008).

Name	Weighting coefficient m	Partition coefficient F	Separation index S	Source	
N5	1.05	10	0.986	0.211	This study
N8	1.05	10	0.982	0.342	This study
JSM	Unknown	6	Unknown	Unknown	Jackson et al. (2017)

Table 2: Classification schemes used for further analysis. See supplementary online material, Table S1, for full classification evaluation metrics.

321 *2.6. Classification of the 17 year Level 3 dataset*

322 Following evaluation of the L2 and L3 classifications, a suite of three
323 classification schemes was chosen and applied to 17 full years of MODIS-Aqua
324 Level 3 Rrs version 2018.0 (Table 2). Water depths shallower than 200 m were
325 excluded from analysis. This provided the framework for testing whether
326 other remotely sensed parameters were well constrained by the optical classes.

327 [TABLE 2 HERE]

328 *2.7. Relationship between colour class and biophysical parameters*

329 Summary statistics of remotely sensed biological and physical variables
330 were produced to characterize each class in each of seven geographical do-
331 mains (Figure 3): SCTR-W (10° to 5° S, 50° to 62° E), SCTR-E (10° to 5°
332 S, 63° to 75° E), SCTR-C (10° to 5° S, 76° to 88° E), Wiggert-N (7° to 2°
333 S, 60° to 85° E), Wiggert-S (12° to 7° S, 60° to 85° E), the MPA, z200 (the
334 whole study domain at depths greater than 200 m) and z1000 (the whole
335 study domain at depths greater than 1000 m).

336 The potential of purely optical classifications as indicators of the pelagic
337 growth environment was explored using within- and between-class statistics.
338 Non-parametric analysis of variance was used to test whether the optical
339 classifications reflected differences in each of the the biological and physical

340 variables (Kruskal-Wallis, applied to one variable at a time, assuming that
341 underlying distributions of each variable within each class subset of each geo-
342 graphical domain are the same, followed by post-hoc Tukey's honestly signifi-
343 cantly difference, HSD, tests between pairs of classes; Ruxton & Beauchamp,
344 2008) for each of the geographical domains. The distinctiveness of smaller
345 domains for which contrasting processes across zonal or meridional gradients
346 have been discussed in the literature (SCTR-W,E,C; Wiggert-N, S Wiggert
347 et al., 2006; George et al., 2018; Dilmahamod et al., 2016) was tested using
348 permuted multivariate analysis of variance (PERMANOVA; Anderson, 2001,
349 2017) on standardised variables (z-scores), with all fifteen biological and phys-
350 ical variables. Anomaly time-series were used in addition to simple z-scores
351 where clear seasonal cycles were present. Because of the large dataset sizes,
352 100 subsets of 1000 pixels were selected randomly through time within each
353 geographical domain for bootstrapped testing; pixels with missing data were
354 excluded at each iteration. Domain was taken as the first, fixed, factor and
355 class as the second, nested factor. Euclidean distance, correlation distance
356 and squared correlation distance gave similar PERMANOVA hypothesis test
357 results, whilst χ and χ^2 results varied; euclidean distance and 1000 permuta-
358 tions were used for all reported results (McCune & Grace, 2002; Anderson,
359 2017; Pillar, 2013). The fathom Matlab toolbox was used for PERMANOVA
360 tests (Jones, 2012). Mann-Kendall-Sen correlation coefficients (Sen, 1968;
361 Hamed & Rao, 1998) were used to identify which biological and physical
362 variables covaried within each class. Correlations were tested firstly using all
363 data and secondly using bootstrapping to insure against spatial and temporal
364 autocorrelation effects (100 random subsamples of 1000 pixels).

365 A full comparison of optical classes with OCO-2 pCO₂ data was beyond
366 the scope of this study - OCO-2 was launched in July, 2014, and the data
367 therefore do not span the study period considered here. OCO-2 data are also
368 lower in spatial and temporal coverage, although the recent launch of OCO-3
369 will mitigate this. As a proof of concept, a single month of OCO-2 surface
370 pCO₂ data were matched to MODIS Level 2 optical classes for January 2015
371 (same-day match-ups only), and between-class differences evaluated using
372 Kruskal-Wallis and post-hoc HSD tests, for the z1000 study domain.

373 Assuming that optical classifications do partition pixels dynamically in
374 space and time according to the physical and biological variables that can
375 be derived from remote sensing data, two additional tests were applied to
376 establish whether conditions within pixels assigned to each class changed
377 during the study period, and whether they are correlated with basin- and
378 global-scale circulation patterns. Mann-Kendall-Sen trend tests were ap-
379 plied in regressions of the class-averaged time-series of each remote sensing
380 variable against climate indices that characterize the Indian Ocean Dipole
381 (Dipole Mode Index, referred to hereafter as IOD; Saji & Yamagata, 2003),
382 Madden-Julian Oscillation (MJO; Kilidas et al., 2014) and El Nino-Southern
383 Oscillation, Southern Oscillation index (SOI; Ropelewski & Jones, 1987).
384 The SOI was chosen because it represents variability in the Walker circula-
385 tion, rather than directly in SST or combinations of variables. Habitat frag-
386 mentation metrics were used to characterise the distribution of lower trophic
387 level resources in the MPA, Wiggert-S and Wiggert-N domains to investigate
388 whether changes related to climate patterns can be detected in the pelagic
389 growth environment using available remote sensing data between 2002 and

390 2018. Patches of the same optical class were created using each month's
391 class map as a binary image, grouping adjacent pixels of like-class (Matlab
392 `bwconncomp`) and finding the perimeter, patch centre and number of pixels
393 contained within each class patch (Matlab `regionprops`). Average patch
394 area, distance between patches and patch density were calculated (Wang
395 et al., 2014) for each month for temporal regression and regression against
396 climate indices (Mann-Kendall-Sen test). Finally, correlations between the
397 total area occupied by each optical class within each subdomain and climate
398 indices were tested (Mann-Kendall-Sen trend test).

399 To test whether optical classifications could form a useful basis for fish-
400 eries management and enforcement, fishing catch and effort data from the
401 Indian Ocean Tuna Commission were acquired at monthly temporal resolu-
402 tion, in 1° and 5° grids (IOTC, 2020, 2014). The most common optical class
403 was assigned to each of these coarse fisheries grid cells, matched by year and
404 month, and between-class differences in catch, effort and catch per unit effort
405 (CPUE) were evaluated (Kruskal-Wallis and post-hoc HSD). This compari-
406 son was applied across the z1000 domain and within the IOTC data gridcells
407 that contain the MPA as well as $15^\circ \times 15^\circ$ and $25^\circ \times 25^\circ$ domains centred
408 on the MPA and the full z1000 area. Long-line fishing effort was reported in
409 hooks, whereas surface fishery effort was reported in hours; the two datasets
410 were analysed separately.

411 All data analysis and visualisation was carried out using Matlab 2018a
412 running under MacOS10.12.6.

413 **3. Results & Discussion**

414 *3.1. Comparison of classification results with Level 2 and Level 3 input data*

415 Classification results were similar for L2 and L3 data for the two smaller
416 datasets, but classes were less compact when the largest dataset was used.
417 Partition coefficients (F) remained above 0.9 for all three Rrs treatments
418 with weighting coefficients 1.05, 1.1 and 1.2, but separation coefficient S
419 increased from 0.15 to 0.3 as the number of classes, N, was increased
420 from two to nine, and the best separability was obtained for 2 classes with
421 all data treatments. Beyond N=8 classes, processing time increased signifi-
422 cantly and F and S values were unstable between repeat runs, therefore no
423 classification with 9 or more classes was pursued. Classification performance
424 metrics (F and S) for all L2 and L3 classifications are provided in full in the
425 Supplementary Online Material, Table S1, sheet ‘L2 L3 Classification F S’.
426 Rrs treatment made little difference to F and S for Rrs and $\overline{Rrs(2003)}$
427 ($<1\%$ variability in performance metrics for $m < 1.3$), but separation index
428 increased by a factor of 20 for Rrs/Rrs(488).

429 Figure 4 shows the JSM classes and the L2 and L3 class spectra produced
430 using Rrs with $m = 1.05$ and two to eight classes, and Table 3 shows the pro-
431 portions of pixels mapped to each class, with N=5 and N=8 class schemes
432 mapped to JSM classes using Euclidean distance between Rrs values at the
433 six common wavebands. Fewer of the JSM classes were reproduced in L3
434 classifications than in L2 classifications, with the extreme blue-water spectra
435 (highest and lowest Rrs(412) values) lost in an N=8-class scheme (Table 3).
436 Class spectra fell within or at the edges of the JSM classes, with most devi-
437 ation in spectral shape (relative to the closest JSM class) in the blue:green

438 wavebands. Only one of the three JSM coastal water classes was found in
439 the N=8 classifications produced here, and none with N=5.

440 [FIGURE 4 HERE, SINGLE-COLUMN; COLOUR ONLINE ONLY]

441 [TABLE 3 HERE]

442 As a compromise between F and S metrics and representation of the JSM
443 classes, and to enable direct comparison of results against similar studies,
444 the 5- and 8-class schemes (henceforth N5 and N8) produced using $m=1.05$,
445 42,000 training pixels and absolute Rrs spectra were used for further analy-
446 sis, together with the 6-waveband JSM classification. These Level 2 and 3
447 classifications for 2003 are summarized in Table 3 and the class spectra are
448 given in Table 4.

449 [TABLE 4 HERE]

450 Mapping of the N5 and N8 classifications from Level 2 and Level 3 data
451 to abundance-based and reflectance-based PFT algorithms is shown in Fig-
452 ure 5. PFT algorithms consistently interpreted the lower-OC3-CI chl classes
453 as being dominated by picoplankton, with the contribution of nano- and
454 microplankton fractions increasing with increasing chl. Eutrophic-type dis-
455 tributions, dominated by microplankton, were only produced in the N8 clas-
456 sification, but this was the only difference between 5- and 8-class schemes.
457 Since the proportion of pixels assigned to the 8th class was 0.3% (Table 3),
458 the abundance-based PFT algorithms generally classify these optical classes
459 as dominated by small cells. In contrast, switching from Level 2 to Level 3
460 data produced more PHYSAT-type spectra that fell into the pseudo-diatom
461 class (similar spectral shape to PHYSAT-diatom, but higher Rrs values).
462 The N5 and N8 schemes correspond to JSM classes between 1 and 9, and

Class	Level 2 % pixels assigned to each class			Level 3 % pixels assigned to each class		
	N5	N8	JSM	N5	N8	JSM
1		5.7	1.9			0.5
2	10.7		6.7	11.9	8.1	5.6
3		14.8	14.6		14.0	13.2
4	24.7	19.7	18.0	20.9	16.3	17.2
5	28.0	20.9	16.6	24.7	17.7	17.2
6		18.5	13.4		14.8	12.9
7	23.9		9.7	19.7	10.9	8.3
8		14.0	7.7			6.0
9	12.8		4.6	12.0	6.0	3.5
10		6.3	3.6			2.3
11			2.6			0.8
12			0.3			0.3
13		0.3	0.2		0.3	0.2
14			0.1			0.1

Table 3: Total number of Level 2 and Level 3 dominant classes mapped to each fuzzy cluster in the 10-waveband classifications (5 classes and 8 classes, N5, N8) and in the Jackson-Moore 6-waveband classification. The 10-waveband classes are mapped to the JSM classification by Euclidean distance (Figure 4).

Classification / class no.	Rrs(412) x1000	Rrs(443) x1000	Rrs(469) x1000	Rrs(488) x1000	Rrs(531) x1000	Rrs(547) x1000	Rrs(555) x1000	Rrs(645) x1000	Rrs(667) x1000	Rrs(678) x1000
N5: 1	15.032	11.065	9.366	7.298	2.621	1.929	1.535	0.009	0.204	0.256
N5:2	12.186	9.035	7.988	6.455	2.523	1.857	1.489	0.076	0.197	0.248
N5:3	9.620	7.332	6.782	5.672	2.447	1.814	1.458	0.059	0.191	0.247
N5:4	6.974	5.602	5.482	4.787	2.388	1.807	1.468	0.058	0.196	0.262
N5:5	3.961	3.476	3.748	3.480	2.215	1.768	1.474	0.085	0.224	0.324
N8:1	15.530	11.400	9.556	7.381	2.558	1.861	1.467	0.077	0.183	0.236
N8:2	13.131	9.683	8.426	6.718	2.519	1.842	1.469	0.070	0.189	0.241
N8:3	11.193	8.355	7.507	6.138	2.462	1.808	1.445	0.057	0.184	0.236
N8:4	9.375	7.166	6.656	5.583	2.418	1.787	1.433	0.048	0.183	0.241
N8:5	7.500	5.948	5.743	4.965	2.375	1.778	1.435	0.045	0.186	0.250
N8:6	5.514	4.593	4.680	4.196	2.313	1.779	1.457	0.054	0.195	0.271
N8:7	3.184	2.913	3.268	3.103	2.146	1.746	1.467	0.096	0.236	0.348
N8:8	7.662	9.253	11.578	12.541	14.101	14.027	13.220	4.781	3.947	3.880

Table 4: Class Rrs spectra for the N5 and N8 classifications produced in this study using Level 3 data.

463 with a finer gradation of Rrs spectra corresponding to 0.03 to 0.5 mgm^{-3} , the
464 JSM classes include more scope for identifying mixed size-class waters with
465 the PFT algorithms included here. The PHYSAT classification was designed
466 to identify cases in which a single PFT dominates water colour and, corre-
467 spondingly, not all classes could be mapped to a PHYSAT class (Figure 5).
468 Of those that did, *Synechococcus*-like cyanobacteria was the most common
469 designation (3 classes at Level 2, N5; 4 classes at Level 2, N8; 1 class at Level
470 3, N5 and JSM and 2 classes at Level 3, N8).

471 [FIGURE 5 HERE: SINGLE-COLUMN; ONLINE COLOUR ONLY]

472 Class maps for every second month of 2003 (Figure 6) show more frag-
473 mented spatial distribution of classes in the L2 data, corresponding to the
474 higher spatial resolution of the data and higher spectral separability. Broader
475 spatial patterns (O1000 km) are consistent between all classifications and in-
476 clude a limited seasonal north to south shift in class, distinction of coastal,
477 Somali Current and Arabian Sea waters from the central domain and coher-

478 ent and elongated patches of higher class (4-5 in the N5 classification) waters
479 in the central Indian Ocean, often enveloping the Chagos MPA. These zonal
480 bands are more evident in Figure 7, which summarises class diversity at each
481 pixel, as corresponding to the seasonally-varying SCTR, SEC and SECC
482 domains. Figure 8 shows a subset of the remote sensing climatologies, for
483 comparison.

484 [FIGURE 6, 7, 8 CLOSE TO HERE: SINGLE-COLUMN or 1.5 COL-
485 UMN; PLEASE QUOTE FOR COLOUR PRINTING]

486 Whether or not the smaller features correspond to ecologically meaning-
487 ful variations in the microbial biome or carbon cycling can only be answered
488 definitively with *in situ* data. The microscopy stations lay within classes 3
489 and 4, and a significant difference in phytoplankton biovolume was confirmed
490 (class 3 mean biovolume = $8.1 \times 10^5 \pm 2.6 \times 10^5 \mu m^3 l^{-1}$, N=3; class 4 mean
491 biovolume = $2.3 \times 10^6 \pm 8.4 \times 10^5 \mu m^3 l^{-1}$, N=9; Kruskal Wallis $p = 0.0126$).
492 There was also an order of magnitude difference in the ratio between phyto-
493 plankton and zooplankton biovolume (Schwarz, 2020). In the absence of a
494 larger *in situ* dataset with which to evaluate the full classification, comparison
495 between these classifications and previous studies is helpful. In spatial and
496 temporal variability, these optical classifications are most similar to previous
497 studies that use Rrs or radiance, as expected, and to some of the mesopelagic
498 biogeographies. The degree of patchiness is consistent with examples given
499 by JSM, and the classes assigned to the SCTR in their example of July 2004
500 are in direct agreement with the N5 classification produced here (JSM classes
501 7/8, based on 6 wavebands, correspond to N5 class 4, based on 10 wavebands;
502 Table 3). A similar degree of patchiness is reported by Oliver & Irwin (2008)

503 using nLw412, nLw551 and SST, and their approach, allowing the number
504 of classes to emerge from the data, assigned up to ten classes over the TIO,
505 which supports the richer N8 or JSM (N=14) classifications tested here in
506 terms of spectral separability. George et al. (2013) reported multiple patches
507 of elevated chl extending some 200 km along 67° E in the SCTR, as well as
508 suppression of surface chl by eddies further south. In contrast, classifications
509 that used chl as the only ocean colour variable, together with other physical
510 drivers, have been less spatially diverse (e.g. Longhurst, 2007; Spalding et
511 al., 2012; Reygondeau et al., 2013; Fay & McKinley, 2014; Sayre et al., 2017,
512 surface zone) and do not distinguish the SEC or SCTR domains clearly.

513 Mesopelagic classifications using a range of approaches including derived
514 ocean colour variables, acoustic data, World Ocean Atlas data and species
515 abundance mostly do distinguish the SCTR and SEC zones (Proud et al.,
516 2017; Sutton et al., 2017; Sutton & Beckley, 2017; Sayre et al., 2017, 200 to
517 800 m zones) although in some cases the distinction between coastal influ-
518 ences and SEC/SCTR features is unclear (Costello et al., 2017; Reygondeau
519 et al., 2018). Differences in the spatial richness of mixed-input epipelagic
520 classifications relate partly to the scales and methods used, but may also
521 reflect subtle changes in the growth environment that are related to phyto-
522 plankton community composition that are not detected in the chl algorithms,
523 or to chl variability being outweighed in a classification by the contribution
524 of SST, producing spatially coarser structures because of dynamics that have
525 no surface signature in SST (e.g. Santoso et al., 2010; Drushka et al., 2012;
526 Strutton et al., 2015), or both. Previous analysis of phytoplankton bloom
527 dynamics in the TIO, based on satellite-derived chl and biogeochemical mod-

528 elling, suggested a summer bloom spanning the full breadth of the basin at
529 SEC latitudes, but no winter bloom (Levy et al., 2007), and the modelled
530 emergent biogeography of Follows & Dutkiewicz (2011) predicted a band
531 of Prochlorococcus analogs and low species richness in this region which is
532 consistent with the PFT algorithm interpretation of classes 1 to 3 with N5.
533 However, Wiggert et al. (2006) predict larger phytoplankton cells between
534 January and May in the deep chlorophyll maximum in the SCTR and Jeffries
535 et al. (2015) found eukaryotes contributed >10% to relative cell abundance
536 at a deep water site within the Chagos MPA. Similarly, Thorrrington-Smith
537 (1971) found diatom and dinoflagellate communities in water samples from
538 100 m depth across the western TIO - a signal that is consistent with the
539 higher-chl PFT interpretations of classes 5 (N5) and 6-8 (N8) which could be
540 expected to be detected in satellite data in zones of strong vertical mixing,
541 such as the tropical gyre boundaries.

542 The loss, at L3, of classes representing high and very low chl values,
543 may be important for monitoring carbon export and ecosystem resources and
544 Duarte et al. (2013) suggested that a chlorophyll concentration of 0.44 mgm^{-3}
545 represents a transition between heterotrophic and autotrophic communities.
546 Application of the Duarte et al. (2013) threshold to L3 chl values in this area
547 is consistent with Fernandes et al. (2008), who reported net heterotrophic
548 production between 1° N and 5° S at 83° E , but the appearance of higher
549 ranges in L2 data, the prevalence of higher classes for most of the year and
550 the paucity of *in situ* data for the pelagic MPA domain area renders this
551 use of the classification results uncertain. Level 2 data classifications are
552 therefore potentially valuable for modelling and monitoring tasks (Tweddle

553 et al., 2018), despite the low daily spatial coverage. For the purposes of
554 exploring spatiotemporal variability over the MPA and wider TIO domain,
555 Level 3 classifications are explored further.

556 *3.2. Are biological and physical variables distinct for each optical class ?*

557 The class-specific ranges of remote sensing variables are summarised for
558 the MPA and z1000 domains in Figure 9 and Appendix 1. The N5 optical
559 classification constrained all variables most effectively. For the MPA, only sea
560 surface height (classes 4 and 5), eddy kinetic energy (classes 3 and 5) and the
561 R443:R555 reflectance ratio (classes 1 and 5) were ambiguous (Kruskal-Wallis
562 with post-hoc HSD tests, $p < 0.01$, $N > 10000$). Increasing class number in the
563 MPA was associated with increasing chl, FLH, ∇ SSH, u , τ_N and depth, and
564 with decreasing FLH:chl ratio, SST, SSH, v and τ_E . Westerly and northerly
565 currents, and westerly wind stress, associated with SWM wind reversals, were
566 associated with class 1 only (lowest chl).

567 [FIGURE 9 HERE; SINGLE-COLUMN; COLOUR ONLINE ONLY]

568 Greater between-class ambiguity in optical and physical variables was
569 found with N8 and JSM, both of which included sparse classes ($N < 10000$).
570 For N8, class 8, representing OC3M-CI chl = 2.39 mgm^{-3} , was always sparse
571 and class 7 (chl = 0.46 mgm^{-3}) was sparse in the SCTR-E and -C domains.
572 Similarly, JSM classes 10 to 14, representing chl $> 0.62 \text{ mgm}^{-3}$, were al-
573 ways sparse or empty, and class 9 (chl = 0.47 mgm^{-3}) was sparse in all the
574 sub-domains except z1000 and SCTR-W. Between-class variability was not
575 significant in the MPA for the majority of physical variables in N8 and JSM
576 (SSH, EKE, u , v , τ , $\nabla \times \tau$) or for FLH, but chl and the residual reflectance
577 ratios were significantly different in all 8 classes. This could be interpreted as

578 a smaller number of physically-distinct conditions hosting a larger number
579 of optically distinct conditions, consistent with growth, decay and succes-
580 sion occuring within each physical 'province' over the averaging period of 1
581 month. In JSM, only 8 classes were well-populated (No. pixels > 10000) and
582 all variables except $\nabla \times \tau$ were ambiguous for two or more classes. In the
583 wider z1000 domain, between-class variability was significant for most vari-
584 ables in each of the classifications (exceptions were N5: SST for classes 2 and
585 3; N8: ∇ SSH for classes 4 and 7, u for classes 6 and 7; JSM: SST for classes
586 1 and 8, v for classes 7 and 8 and τ_E for classes 1 and 2), reflecting the much
587 greater size of this dataset. In this wider domain, the tendency of windstress
588 variables with increasing class number was reversed so that increasing class
589 and chl were associated with increasing τ_E and decreasing τ_N .

590 All between-class test results are given in Supplementary Online Mate-
591 rial Table S1, sheet 'Variable Ranges by Class'. The optical classifications do
592 correspond to distinct ranges of biotic and abiotic variables, suggesting their
593 potential value in providing a useful diagnostic for management and mod-
594 elling applications. Five optical classes produces least ambiguity in physical
595 variables, although significant residual ocean colour differences are detected
596 in up to 7 classes. However, the biophysical relationships vary within the
597 wider domain, as may be expected from the known oceanographic processes
598 in the region, suggesting that the use of optical classes may be most appro-
599 priate within a heirarchical scheme (c.f. Kavanaugh et al., 2014; Oliver et al.,
600 2004; Oliver & Irwin, 2008). Exploration of between-class variability within
601 different sub-domains is addressed in the next section.

602 To test whether seasonal variability in winds and associated mixing and

603 entrainment (Halkides & Lee, 2011; Wiggert et al., 2006) produces between-
604 class ambiguity, Kruskal-Wallis tests were applied to the MPA data for each
605 month (Online Supplementary Figures S2, S3; Tables S2, S3). Seasonal wind
606 stress reversals were detected with the annual average conditions (negative
607 τ_E decreasing with increasing class number) found during austral winter and
608 the opposite trend (positive τ_E increasing with increasing class number) dur-
609 ing austral summer (Figure S2). The winter months were significantly differ-
610 ent at $\alpha=0.01$ for classes 3, 4 and 5 (higher chl), whereas austral summer
611 months were distinct in classes 2 and 4, and τ_N trends generally mirrored τ_E
612 trends. Less pronounced seasonal reversals were found for u, v and ∇SSH .
613 One hierarchical partitioning approach could therefore be to use the optical
614 classifications with a monthly or seasonal interpretation to constrain vari-
615 ability in the epipelagic growth environment, but a more objective approach
616 using the physical variables at higher levels of the hierarchy avoids the need
617 to assume a regular seasonal cycle. In either case, the correspondence be-
618 tween optical class and biotic environmental conditions needs to be explored
619 using *in situ* biogeochemical data if the optical classification is to be used to
620 deduce ecological function.

621 *3.3. Do optical classifications capture zonal or meridional differences around*
622 *the Chagos MPA?*

623 Between-class variability in remotely sensed variables for each of the sub-
624 domains is shown in Figure 10. Most remotely sensed variables tended to
625 increase or decrease monotonically with increasing optical class number, and
626 spatially segmenting the dataset had little effect on these tendencies. Of the
627 three SCTR domains, the westernmost area had the lowest SST values in

628 all classes, as well as lower SST and higher τ_N in the highest-chl class 5.
629 The central TIO domain, SCTR-C, which is the easternmost of the three,
630 had the highest SST and EKE values and much lower nFLH:chl values in
631 all classes. Stronger contrasts were evident between the Wiggert-N and -S
632 domains. nFLH, v , τ_N and nFLH:chl were lower in the northern than the
633 southern domain in some or all classes, whilst SST, ∇ SSH, EKE, u and
634 τ_E were higher. Whereas the depth-resolved modelling studies of George et
635 al. (2018) and Dilmahamod et al. (2016) suggested east-west gradients in
636 biophysical mechanisms operating across the SCTR, sub-domains SCTR-E,-
637 W and -C could not be distinguished in the surface remote sensing variables
638 studied here (PERMANOVA, $p > 0.1$, $N > 691 \times 100$; Table ??), although the
639 optical classes were significantly different in all domains and classifications
640 ($p < 0.005$, $N > 692 \times 100$). In contrast, differences were detected between
641 classes and domains for the north-south division discussed by Wiggert et al.
642 (2006) ($p < 0.037$, $N > 692$; Table 5). Excluding the shelf slope depths
643 between 200 and 1000 m had no impact on class ambiguities in any variable
644 (Figure 10).

645 [FIGURE 10 HERE; SINGLE-COLUMN; ONLINE COLOUR ONLY]

646 [TABLE 5 HERE]

647 Correlations between physical and biological variables within each class
648 and domain are shown in Figure 8. Chl was negatively correlated with SST in
649 all but the z200/z1000 domains. In the MPA, increasing SST was associated
650 with lower EKE and τ_N and with higher v , τ_E and $\nabla \times \tau$ in the lowest-chl
651 class (class 1) only, with the reverse relationships found in classes 2 to 5. The
652 lower chl class 1 is therefore associated with conditions in which τ_E and $\nabla \times \tau$

Table 5: Results of PERMANOVA tests for differences between regions. a) Fixed factor 1 is location in the western or eastern SCTR or adjacent central Indian Ocean domain; nested factor 2 is optical class. All 15 remotely sensed variables were included in the test as z-scores. Average values are from 100 random draws of 1000 data points from each domain, time-matched. Pixels with any missing data were excluded, yielding residual degrees of freedom between 600 and 800 (denoted 'Resid'). p-values were calculated using 999 permutations. b) Fixed factor 1 is location in the northern or southern central Indian Ocean sectors; other details as for a).

a) Seychelles-Chagos Thermocline Ridge W / E / C (George et al., 2018)					
	Factor	df	\bar{F}	\bar{p}	p range
N5	F1: Domain	2	1.096	0.406	0.104 to 0.847
	F2: Class	10.9 (10-12)	15.066	0.0012	0.001 to 0.006
	Resid:	[691-766]			
N8	F1: Domain	2	1.256	0.271	0.048 to 0.700
	F2: Class	15.8 (14-18)	13.785	0.001	0.001 to 0.003
	Resid:	[703-765]			
JSM	F1: Domain	2	1.515	0.142	0.015 to 0.424
	F2: Class	18.3 (16-22)	12.825	0.001	0.001 to 0.001
	Resid:	[688-771]			
b) Central tropical Indian Ocean N / S (Wiggert et al., 2006)					
	Factor	df	\bar{F}	\bar{p}	p range
N5	F1: Domain	1	3.420	0.0093	0.001 to 0.037
	F2: Class	7.4 (6-8)	20.871	0.0011	0.001 to 0.005
	Resid:	[692-755]			
N8	F1: Domain	1	4.030	0.003	0.001 to 0.014
	F2: Class	10.2 (9-11)	18.127	0.001	0.001 to 0.001
	Resid:	[708-775]			
JSM	F1: Domain	1	4.415	0.0023	0.001 to 0.013
	F2: Class	12.1 (10-15)	16.044	0.001	0.001 to 0.001
	Resid:	[692-755]			

653 do not correspond to surface cooling and the northward geostrophic current
654 component is positive. Chl and nFLH were positively correlated everywhere
655 except in class 1 (lowest chl) in the MPA, SCTR-C and Wiggert-N,S areas.
656 Higher nFLH:chl ratios were associated with lower τ_E , $\nabla \times \tau$, u, EKE, ∇ SSH,
657 SSH and SST in the MPA class 5, and to a lesser extent for classes 3 and 4,
658 suggesting the importance of the tropical gyre strength for surface chl. These
659 relationships are similar, but less pronounced, in the SCTR-W, Wiggert-N
660 and Wiggert-S domains, and in z1000 classes 3 and 4. Assuming relative
661 homogeneity of the phytoplankton community within a given optical class,
662 nFLH:chl can be interpreted as a proxy for relatively high iron limitation
663 (as opposed to other limiting factors, Behrenfeld et al., 2009). Although
664 Chinni et al. (2019) and Wiggert et al. (2006) suggest Fe-limitation in some
665 seasons within and north of the SCTR, George et al. (2013) reported that
666 the deep chlorophyll maximum (DCM) followed the nitricline and did not
667 measure iron concentrations, so the interpretation of nFLH:chl requires more
668 *in situ* data in this region. SLA, which is related to westward-propagating,
669 downwelling Rossby waves in the SCTR (George et al., 2018), decreased
670 with increasing optical class and was negatively correlated with chl in at
671 least 4 classes in all domains, including z1000 (Figure 11). The use of class-
672 specific correlations across different sub-domains captured other contrasts in
673 physical relationships, such as a switch from positive to negative coupling
674 between u and EKE in MPA class 1, SCTR-W classes 1,2,3 and 5; SCTR-C
675 classes 1 and 2; Wiggert-N class 1, whilst the relationship was negative for
676 all classes in Wiggert-S, suggesting dominance of the westward SEC in the
677 southern domain and more varied interactions in the northern SCTR (e.g.

678 mesoscale and fine-scale processes, George et al., 2013; Hosegood et al., 2019).
679 For all domains, the greatest between-class differences were found between
680 classes [1,2] and classes [3,4,5], suggesting that the different physical processes
681 driving the growth environment can be distinguished by the chl 0.08 mgm^3
682 isoline (Figure 5). Biophysical coupling in the Chagos MPA was most similar
683 to that in the Wiggert-S domain (Figure 10; Supplementary Material Table
684 1, sheet ‘Variable Ranges by Class’).

685 [FIGURE 11 HERE; SINGLE-COLUMN; COLOUR ONLINE ONLY]

686 3.4. *Modelling applications of optical partitioning*

687 Assessment of the global carbon cycle and sequestration of anthropogenic
688 CO₂ emissions underpins the Paris Agreement (UN, 2015). The oceanic bio-
689 geochemical models used for global carbon cycle assessment remain fairly
690 simplistic and uncertainties are high (Lim & Kug, 2017; Le Quéré et al., 2013,
691 2018; Gruber et al., 2019); increasing the complexity of ecosystem dynamics
692 in models without rendering them unstable is challenging (Anderson, 2005)
693 and different approaches are still being developed (e.g. Hense et al., 2017;
694 Wanninkhof et al., 2013). Optical classes offer an empirical constraint on
695 ecosystem models and provide a dynamic framework for aggregating model
696 outputs and assessing model skill, for example in the prediction of CO₂ up-
697 take or sequestration rates. The preliminary comparison of pCO₂ between
698 optical classes supports both of these applications (Figure 12). Between-
699 class differences in surface partial pressure of CO₂ were significant ($p < 0.01$,
700 $N > 13,000$) for all N5 classes. pCO₂ distributions were mostly bi-modal,
701 reflecting a background latitudinal gradient in class (increasing class num-
702 ber, reflecting increasing chl, to the north) with patches of higher classes to

703 the south. The average pCO₂ value decreased slightly with increasing class
704 number (416±49, 418±48, 404±44, 406±48, 398±48 ppm), in contrast with
705 Nagelkerken et al. (2015) who reported no simple relationship between pri-
706 mary production and CO₂ uptake in this area. Between-class differences in
707 this study were within the version 8 OCO-2 model error for X_{CO₂}, but uncer-
708 tainties in the profile retrieval are not specified (O’Dell et al., 2018). Because
709 of these uncertainties, the scope of this comparison and because too few data
710 were available to test between-area differences, a more complete comparison
711 is reserved for a future study.

712 [FIGURE 12 HERE; TWO-COLUMN; COLOUR ONLINE ONLY]

713 In a fully-realised fuzzy optical classification, multiple colour class mem-
714 berships enable mixed phytoplankton communities (or mixed water types)
715 to be represented and this has been shown to be useful in enhancing the in-
716 terpretation of ocean colour data as well as constraining chl algorithm errors
717 (e.g. Moore et al., 2001, 2009). Better remote sensing information about the
718 ocean surface microbial community feeds into the Conservation on Biodi-
719 versity as well as monitoring and understanding the ecosystem services they
720 provide (CBD, 2010; Tweddle et al., 2018; Roberts et al., 2017). In this study,
721 the Rrs class residuals did not show promise for identifying details of phyto-
722 plankton community composition, but ensemble class biophysical agreement
723 suggests that ecosystem function may be constrained by optical class.

724 3.5. *Management and conservation applications of optical partitioning*

725 Information is lost when Rrs spectra are partitioned into discrete classes,
726 rather than applying an algorithm to produce a continuous biological variable
727 such as chl, but a distinct advantage of this is the possibility of using habitat

728 fragmentation metrics on the class maps. Fragmentation metrics applied to
729 the N5 class maps are shown in Figure 13 for the MPA and the Wiggert-
730 N and -S domains. The lower-chl classes 1 and 2 behaved differently in
731 the three domains: Class 1 patches were of order 5000 km² and generally
732 largest to the south, where they were separated by ca. 200 km. In the
733 MPA, between-patch distances were shorter and stable through time, whereas
734 they fluctuated between 20 and 100 km to the south. The 2011 La Nina
735 period coincided with particularly high separation distances in Wiggert-N
736 (separation ca. 500 km) and with high patch sizes in Wiggert-S (areas up to
737 ca. 15 000 km²; Figure 13). In contrast, class 2 patches were larger overall
738 (O20 000 km²) with higher values to the north, and a maximum coinciding
739 with the 2015 El Nino (mean patch size ca. 50 000 km²). Class 2 patch
740 separation distances fluctuated in Wiggert-N as for class 1 but with a lower
741 range (20 to 70 km). The 2015 El Nino coincided with the highest class 2
742 patch sizes in Wiggert-N (up to ca. 50 000 km²). Classes 1 and 2 represent
743 clear, warm water, which is a foraging habitat used by seabirds preying on
744 flying fish and squid, often in association with subsurface predators (e.g.
745 Weimerskirch et al., 2005; Catry et al., 2009b; Le Corre et al., 2012). The
746 absence of seasonal cycles in the fragmentation metrics for these classes is
747 marked: Prey occurrence, driven by cetaceans and tuna, is stochastic, but
748 patches of similar foraging conditions are predictable at the monthly scales
749 used here, with patch separations that are within the known range of some
750 seabirds (Weimerskirch et al., 2007; Nel et al., 2001; Pinaud & Weimerskirch,
751 2007).

752 [FIGURE 13 HERE: SIGNLE-COLUMN; BLACK AND WHITE]

753 Patch sizes were smaller in the higher-chl classes 3 and 4 (mostly within
754 5000 km²), with separation distances between 20 and 200 km and marked
755 seasonality. For classes 1 to 4 the MPA clearly straddles the Wiggert-N
756 and Wiggert-S conditions, potentially providing stability of resource within
757 foraging range in the event of extreme (Nino/Nina/IOD) conditions. The
758 highest-chl class 5 was not always present (Figure 13e, j, o) and represents the
759 smallest but most intense resource patches (10 to 300 km² in size), separated
760 by 20 to 100 km in the MPA, 40 to 300 km in Wiggert-S and 20 to 1000
761 km in Wiggert-N. Scott et al. (2010) and Trevail et al. (2019) highlight the
762 importance of fine spatial and temporal scales in prey resource; Level 2 (ca.
763 daily, 1 km) or higher spatial resolution data are therefore also of interest.

764 Class 5 patches were largest within the MPA domain up to 2014, after
765 which increasingly large class 5 patches appear in Wiggert-N (Figure 13j).
766 However, the time-series is too short to confirm whether this is a robust
767 trend. Significant temporal trends in fragmentation metrics were only found
768 for fragmentation distance in the MPA, where the average distance between
769 class 2 patches increased over the study period, whilst the distance between
770 class 3 patches decreased ($p < 0.05$, $N = 204$). There is evidence of a shift in
771 the spatial distribution of resources over the study period, but without loss
772 of any of the colour classes, suggesting that the range of niches that seabirds
773 exploit has been maintained across the Wiggert-N and -S domains (Waugh &
774 Weimerskirch, 2003; Catry et al., 2009a; Le Corre et al., 2012). In this study,
775 water depths shallower than 200 m were excluded to avoid land adjacency
776 and bottom reflectance effects, so the MPA domain metrics do not include
777 the near-shore and lagoon waters which may augment class 5.

778 Although mesopelagic biomes have been shown to reflect the spatial dis-
779 tribution of primary production (Proud et al., 2017), the only direct link
780 between optical classes and large, commercially-fished species that could be
781 expected is through water clarity for foraging. To test whether optical classes
782 could provide useful fisheries management information, class maps were com-
783 pared against fisheries records. The Chagos MPA has been a no-take zone
784 since it was established in 2010, and IOTC fishing records amalgamated over
785 the study period (2002 to 2018) are correspondingly lower in waters imme-
786 diately adjacent to the MPA and increase further away (Table 6). However,
787 284 surface fishery records and 43 longline records were reported after 2010
788 in the IOTC gridcells that contain the MPA (-2.3 to -10.8°S, 67.9 to 79.4°E).
789 Figure 14 shows the distribution of average effort, catch and CPUE at in-
790 creasing distances from the MPA for the surface and longline fisheries. In
791 the wider domain (z1000), surface fishery catch and CPUE mostly increased
792 with increasing N5 class, as expected (e.g. Solanki et al., 2015, 2017; Mo-
793 hamed et al., 2018), with significant between-class differences between low-
794 and high-chl waters (Kruskal-Wallis, $p < 0.01$), and effort focussed in class 5
795 waters. Longline fishery effort and catch were highest in class 3, and although
796 a trend for increasing CPUE with increasing class was apparent, it was not
797 statistically significant. Few significant between-class differences were found
798 in the MPA, but CPUE was highest in class 4, whereas effort was decreased
799 from class 2 to 4 (Figure 14d, f). These patterns reflect reported catches, but
800 may be used to infer behaviours of illegal fisheries and so target monitoring
801 resources. This management application of the optical classification is easy
802 to apply using L2 data, but is limited by cloud cover and ca. 1 day data

Table 6: Number of fishing records submitted to the IOTC within the 1° and 5° IOTC gridcells that contain the MPA, then incrementally as boxes of 3 x 3 and 5 x 5 of the 5° IOTC gridcells are added around the MPA area, and finally for entire z1000 domain. LL=long-line fisheries; Surf=surface fisheries; + denotes an increment from the MPA number and Total is the number of records reported within the full z1000 domain.

N5 class	MPA		3x3 x5°		5x5 x5°		z1000		Total	
	LL	Surf	LL	Surf	LL	Surf	LL	Surf	LL	Surf
1	0	73	+15	+131	+84	+254	+792	+948	891	1406
2	14	588	+527	+1375	+650	+2821	+1691	+12078	3152	16862
3	23	668	+648	+1381	+1681	+4674	+3264	+20870	5616	27593
4	6	82	+63	+178	+701	+1665	+2614	+20746	3384	22671
5	0	0	0	0	+25	+100	+1266	+11457	1291	11557

803 latency.

804 [TABLE 6 ROUGHLY HERE]

805 Knowledge of fishing behaviours is also relevant to MPA design and, po-
806 tentially, to the use of dynamic MPA designations. Dynamic protection
807 boundaries serve as a compromise between static MPA boundaries, which
808 protect relatively small areas of rare or valuable habitat (e.g. Opper et al.,
809 2018; Heerah et al., 2019; Handley et al., 2020; Williamson et al., 2019), and
810 the very large foraging domains that are intractable to static protection but
811 where seabirds, cetaceans and large predatory fishes such as tuna are known
812 to collocate in the tropical Indian Ocean (Anderson, 2014; Letessier et al.,
813 2017, 2019; Pinheiro et al., 2019; Hobday et al., 2010).

814 [FIGURE 14 ROUGHLY HERE: 1-COLUMN or 1.5-COLUMN; COLOUR
815 ONLINE ONLY]

816 *3.6. Are there class-specific temporal trends in biological/physical variables?*

817 All conservation and management efforts must consider temporal variabil-
818 ity and the possible impacts of climate change (IPCC, 2013). The 17-year

819 study period used here is sufficient to characterise temporal variability but
820 not to detect long-term change in this region (Henson et al., 2016). However,
821 where biophysical conditions are coupled to large-scale climate indices for
822 which robust, long-term time-series are available, the patterns observed can
823 be extrapolated backwards and, with modelling, forward in time.

824 Time-series of selected variables are shown in Figure 15 for the MPA and
825 Figure S4 for the Wiggert-S domain. A weak tendency for increased chl
826 values in the austral winter was observed, but with no clear seasonal cycle
827 either for the MPA as a whole or within a given class. This is consistent with
828 removal of seasonality by class-switching (c.f. Figure 6). The class 4 and
829 5 chl values overlapped (Figure 15a), with class 4 representing an elevated
830 background level of chl compared with classes 1 to 3, superimposed with
831 stochastic, higher chl events in class 5, which often coincided with increases
832 in nFLH. The strongest chl peak, in 2011, coincided with higher ∇ SSH and a
833 protracted period of positive SOI index (Nina conditions). Higher nFLH:Chl
834 ratios and SSH values were evident for class 1 in both the MPA and Wiggert-S
835 domains, as were lower SST values for class 5. Class 5 chl peaks in the MPA
836 were not synchronised (or time-lagged, judging by visual inspection) with
837 those in the Wiggert-S domain, suggesting small-scale, rather than basin-
838 wide processes are being captured, despite the use of composited Level 3
839 data. Significant trends are not shown on Figures 15 and S4, for clarity, but
840 are summarised in Figure 16a. Chl, nFLH and nFLH:Chl decreased over the
841 study period in most classes and most sub-domains (when appraised using
842 both absolute values and with anomaly time-series). For chl, the rate of
843 change was between -7.5×10^{-6} and $-1.2 \times 10^{-4} \text{ mgm}^{-3}\text{a}^{-1}$ (up to $0.025\% \text{a}^{-1}$

844 in the MPA and $0.055\%a^{-1}$ in z1000, compared with decreases of $0.7\%a^{-1}$
845 reported by Gregg et al., 2017, for the Indian Ocean).

846 Of the abiotic variables, significant trends in all five N5 classes were only
847 found for the MPA, z1000 and Wiggert-N domains, with weaker positive
848 trends in some areas (domain-integrated) and classes for SST, ∇ SSH, u and
849 v, and a positive trend in $\nabla \times \tau$ in Wiggert-S only. Full temporal trend
850 results, including 95% confidence intervals on the rates of change, are given
851 in Table S1, sheet ‘Trends Correlations’.

852 [FIGURE 15 ROUGHLY HERE: SINGLE-COLUMN; PLEASE QUOTE
853 FOR COLOUR PRINTING]

854 [FIGURE 16 ROUGHLY HERE: 1.5 OR SINGLE-COLUMN; PLEASE
855 QUOTE FOR COLOUR PRINTING]

856 No significant correlations were found between the MJO and remotely
857 sensed variables, consistent with the brief residence of MJO events over the
858 TIO as well as the short time-scales of response of chl to MJO events which
859 precludes detection of MJO effects in this Level 3 data analysis (order of
860 days to weeks; Vialard et al., 2009; Jin et al., 2012; Wheeler & Hendon,
861 2004). Surface cooling and enhanced surface primary production have been
862 documented in response to the MJO (Vialard et al., 2009; Resplandy et al.,
863 2009, Supplementary material Figure S5), making the use of higher temporal
864 resolution data desirable where coverage allows. The monthly-averaged MJO
865 index was not correlated with the IOD or SOI indices over the study period.
866 However, a weak, negative correlation was found between the IOD and SOI
867 ($SOI = -0.39 IOD + 0.27$; $n=202$, $p = 0.084$), in contrast to the decoupling of
868 these cycles found using EOF analysis by Saji et al. (1999). Fragmentation

869 metrics for N5 class 3 were related to the SOI (negative relationship for patch
870 density; positive relationship for patch area) and IOD (positive relationship
871 for patch density only). No relationships between fragmentation metrics
872 and any climate index were found for the Wiggert-S domain, whereas for
873 Wiggert-N, patch density increased with increasing IOD for classes 1 and
874 3, and decreased with increasing IOD for classes 4 and 5. Similarly, patch
875 area increased with increasing IOD for classes 1 and 2 and decreased for
876 classes 3 and 4. Fewer significant relationships were found with the SOI, but
877 they mirrored the IOD relationships, consistent with a negative relationship
878 between the two climate indices. These results suggest that within the MPA,
879 if the frequency of Nino events increases as predicted, incurring more negative
880 SOI conditions, the higher chl N5 classes 3 and 4 will yield to larger and more
881 closely spaced patches of lower N5 class 1. If positive IOD events increase
882 in frequency, fewer, smaller N5 class 4 and 5 patches separated by greater
883 distances are predicted. The observed North-South diversity in epipelagic
884 conditions and temporal trends may contribute to resilience of reefs and
885 mobile species in the MPA. However, only surface effects are characterised
886 and, in this study, processes lasting days to weeks, such as MJO events and
887 cyclones that have an impact on vertical mixing (Jin et al., 2012; Webster et
888 al., 2005), may be averaged out.

889 Positive IOD events are associated with elevated SST in the western TIO
890 as the easterly wind driving the SEC converges further west (Saji et al.,
891 1999). Domain-specific correlations between IOD and SST (Table 16) were
892 in agreement, with positive correlations in all but the SCTR-C (eastern-most)
893 domain. Positive relationships were also found for SSH, τ_N and nFLH:chl,

894 whilst negative relationships were found with Chl, FLH, R555:488, EKE and
895 τ_E . Mostly positive, class-specific relationships only were found for ∇ SST,
896 suggesting stronger gradients at the sub-domain spatial scale which can not
897 be explained by the regressions undertaken here as the spatially coarse altime-
898 try products used to calculate ∇ SSH and EKE, which might indicate small-
899 scale processes, tended to decrease with increasing IOD. The SST product (4
900 x 4 km resolution) is more sensitive to mesoscale and perhaps submesoscale
901 processes.

902 Negative impacts of Nino and (positive) IOD conditions on biotic re-
903 motely sensed variables is consistent with surface warming and deepening of
904 the mixed layer in the western TIO, corresponding to down-mixing of phyto-
905 plankton within a strong, westward SEC current extending several hundreds
906 of metres below the surface (Vialard et al., 2009). The response of elevated
907 nFLH:chl ratios (Figure 15) under such a deeply-mixed layer could indicate
908 nutrient stress (e.g. Fe, NO₃) or possibly a thin, surface freshening related to
909 precipitation that is isolating a surface, light-stressed population (Behrenfeld
910 et al., 2009; Chinni et al., 2019; George et al., 2013). The satellite data used
911 for this study can not distinguish between these possibilities and are further
912 limited by their short time-span (Dilmahamod et al., 2016; Landschützer
913 et al., 2019), coarse spatial and temporal resolution (Hosegood et al., 2019;
914 Vialard et al., 2009) and lack of information about depth variability. *In situ*
915 data are needed to interpret many of the possible biophysical interactions in
916 the MPA domain in terms of management application. For example, deep-
917 ening of the mixed layer in the SCTR has been found to be associated with
918 deepening of the DCM with an increase in chl owing to nutrient entrainment

919 (George et al., 2013); or with no net impact on water-column productivity
920 owing to redistribution of light (Resplandy et al., 2009) or with a decrease in
921 chl owing to reduced nutrient entrainment (Ma et al., 2014). Mesopelagic bio-
922 geographies suggest a strong positive relationship between satellite-derived
923 primary production and zooplankton scattering layers (Proud et al., 2017),
924 which is consistent with two of those scenarios. Depending on the response
925 of grazers, a deepened DCM may have a protective effect on pelagic fish
926 that are forced to forage further from the surface (Vialard et al., 2009) but
927 a negative effect for surface-foraging seabirds, so that any future increase in
928 the frequency of these events may have unexpected ramifications at higher
929 trophic levels and for the Chagos MPA reefs (Graham et al., 2018; Fox et al.,
930 2019).

931 **4. Conclusions**

932 Pure, optical classifications of unnormalised satellite remotely sensed re-
933 flectance data have been shown here to constrain physical variables that
934 shape the epipelagic growth environment, making them a potentially useful
935 source of management-relevant information at low- to medium latency. Con-
936 straint of most remotely sensed variables was best when used within spatial
937 sub-domains such as the MPA area, suggesting their use within a seascape
938 heirarchy. Potential applications discussed here include monitoring ecosys-
939 tem services, including CO₂ uptake, and resource distribution, but in all cases
940 *in situ* validation data are needed to elucidate optical biome composition and
941 function.

942 Optical classification provides a snapshot at monthly (or better) time-

943 scales of spatial variability of epipelagic resources that are amenable to habi-
944 tat fragmentation analysis, which suggested a change in the spacing and size
945 of richer surface food resources in response to Nino and IOD events in this
946 study. However, ecological interpretation of the trends and interactions be-
947 tween remotely sensed variables requires knowledge of higher trophic level
948 responses. Inclusion of fragmentation metrics in species distribution models
949 might help to address this, where target species observations are sparse. Al-
950 though ocean colour remote sensing is among the most finely resolved satellite
951 products in space and time, it is limited by cloud cover and does not capture
952 the full range of dynamical interactions that are relevant to habitat structure
953 and use. Increased spatiotemporal coverage is needed and may be provided
954 by combining information from all available sensors (though this is prob-
955 lematic) and by increased *in situ* monitoring using moorings and perhaps
956 unmanned devices. The improved spectral resolution of NASAs forthcoming
957 PACES mission may provide better discrimination of microbial community
958 composition.

959 The suggested applications of optical classifications are globally applica-
960 ble, but the need for more *in situ* data is not restricted to the tropical Indian
961 Ocean. Data requirements include repeat vertical profiles (reflectance, tem-
962 perature, salinity, vertical mixing, nutrient concentrations and carbon cycle
963 parameters) and spatial fields of surface bio-optical and oceanographic condi-
964 tions that resolve sub-pixel variability, so that appropriate spatial scales can
965 be identified for a given question. This scope of fieldwork has been attempted
966 in a few international, inter-disciplinary projects and it is to be hoped that
967 more will take shape under the biogeosciences programme (?).

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1632 **5. Figure captions**

1633 Figure 1: Schematic representation of key biophysical linkages (not ex-
1634 haustive). The flow of information begins with sunlight to the left. Physical
1635 variables that can be detected using remote sensing, followed by the oceano-
1636 graphic variables derived from them, are shown between the sun and the
1637 ocean surface processes. Oceanographic variables of interest that can be de-
1638 rived from remote sensing data are outlined in blue and abbreviations are
1639 explained in Table 1. The other variables shown are of interest to conser-
1640 vation, management or climate change applications but are not amenable to
1641 remote sensing.

1642 Figure 2: Location of the study domain, adapted from Talley et al. (2011);
1643 Aguiar-Gonzalez et al. (2016). SCTR = Seychelles Chagos Thermocline
1644 Ridge; MPA = Chagos Marine Protected Area; SECC = South Equatorial
1645 Countercurrent

1646 Figure 3: Bathymetry of the study domain. Shaded regions denote the
1647 sub-areas related to other published studies. Black line: coast; grey line:
1648 200 m contour; black dashed line: 1000 m contour; thick black line: MPA
1649 boundary.

1650 Figure 4: Central spectra for the 10-band classifications from Level 2
1651 (upper) and Level 3 (lower) datasets with two to nine classes, compared with
1652 the 6-band JSM classification (shaded).

1653 Figure 5: Mapping of the N5, N8 and JSM classes onto published PFT al-
1654 gorithms. SLC=Synechococcus-like cyanobacteria; xDiat was assigned where

1655 the residual PHYSAT-like spectrum resembled the diatom criteria in Al-
1656 vain et al. (2008) but with higher values; SynPro=spectrum matches SLC or
1657 Prochlorococcus except for one waveband, which fell in the other small-cell
1658 category. Algorithm acronyms are explained in section 3.1.

1659 Figure 6: Comparison of class maps produced with the Level 2 and Level
1660 3 Rrs data, classifications N5, N8 and JSM, in 2003. The Chagos MPA
1661 outline, 0 m and 1000 m isobaths are shown in black and the 2000 m isobath
1662 in grey.

1663 Figure 7: Number of classes held at each pixel over the 17 year study
1664 period, by month, for Level 3 data, N=5. The Chagos MPA outline is shown
1665 in black.

1666 Figure 8: Monthly 17-year climatologies of key remote sensing variables.
1667 The Chagos MPA outline and 0 m contour are shown in black, and the 3000
1668 m isobath in grey.

1669 Figure 9: Variability of remotely sensed parameters in the MPA and z1000
1670 domains: Top row = N5; Middle row = N8; Lower row = JSM; black=MPA;
1671 cyan=whole domain with depth > 1000 m (z1000).

1672 Figure 10: Variability of remotely sensed parameters for each sub-domain
1673 using the N5 classification.

1674 Figure 11: Averaged Mann-Kendall-Sen correlation coefficients between
1675 variables within each class for each domain: a) MPA, b) SCTR-W, c) SCTR-

1676 C, d) Wiggert-N, e) Wiggert-S, f) z1000. Only results with a p-value < 0.01 ,
1677 confirmed using bootstrapping to remove autocorrelation and subsampling
1678 effects, are shown.

1679 Figure 12: OCO-2 lowest altitude $p\text{CO}_2$ distributions within the z1000
1680 domain for the N5 classes applied to MODIS Level 2 data, January 2015.

1681 Figure 13: a) to e) Density of patches of each N5 class (a=class 1, e=class
1682 5); f) to j) Average patch area (f=class 1, j=class 5); k) to o) Average
1683 distance between patches (k=class 1, o=class 5) for the MPA, Wiggert-N
1684 and Wiggert-S domains. Note different y-axis limits are used to show detail.
1685

1686 Figure 14: IOTC fishing catch and catch per unit effort for the Indian
1687 Ocean surface (top row; a, b,c) and longline (lower row; d, e, f) fisheries.

1688 Figure 15: Time-series for each N5 class within the MPA for a) Chl, b)
1689 FLH, c) FLH:Chl, d) SST, e) SSH and f) ∇SSH .

1690 Figure 16: a) Summary of the temporal trends found within each do-
1691 main ($p < 0.05$), including ranges of the Sen regression coefficient and rates
1692 of change. Trends for specific classes are denoted by class number; trends
1693 for the entire domain are indicated by block colour (red=positive trend;
1694 blue=negative trend). b) Summary of significant ($p < 0.05$) correlations be-
1695 tween remotely sensed variables and the Indian Dipole Mode Index, including
1696 ranges of the Sen regression coefficient. Correlations for specific classes are
1697 denoted by class number; correlations for the entire domain are indicated

1698 by block colour (red=positive trend; blue=negative trend). Full correlation
1699 results, including 95% confidence intervals on the regression slopes, are given
1700 in Table S1.

1701 **Appendix A. Appendix 1**

Table A.7: Characterisation of variables within each class for the N5, N8 and JSM classification schemes in the whole study site where depth >200 m (total no. pixels 177,145,574)

Variable	Mean $\pm 1\sigma$												
	N5					N8							
	1	2	3	4	5	1	2	3	4	5	6	7	8
Class	13	25	30	22	10	10	15	21	21	17	11	5	<1
N (%)	0.053	0.086	0.122	0.181	0.456	0.049	0.074	0.097	0.126	0.166	0.242	0.612	1.914
chl	± 0.11	± 0.13	± 0.22	± 0.65	± 0.94	± 0.09	± 0.10	± 0.12	± 0.21	± 0.44	± 0.127	± 1.336	± 1.508
flh	0.040	0.045	0.050	0.064	0.107	0.040	0.044	0.046	0.051	0.061	0.076	0.128	0.248
	± 0.21	± 0.22	± 0.27	± 0.40	± 0.77	± 0.21	± 0.21	± 0.22	± 0.28	± 0.37	± 0.050	± 0.087	± 0.163
flh/chl	0.528	0.528	0.409	0.346	0.277	0.822	0.595	0.473	0.399	0.360	0.306	0.264	0.142
	± 0.433	± 0.258	± 0.208	± 0.197	± 0.142	± 0.457	± 0.294	± 0.228	± 0.205	± 0.203	± 0.170	± 0.127	± 0.094
SST	27.62	28.58	28.65	28.02	27.30	27.55	28.22	28.77	28.61	28.10	27.76	27.01	28.67
	± 1.67	± 1.99	± 1.73	± 1.56	± 1.3	± 1.57	± 2.03	± 1.88	± 1.71	± 1.62	± 1.35	± 1.36	± 1.43
SLA	0.083	0.060	0.048	0.038	0.026	0.087	0.067	0.055	0.047	0.039	0.035	0.023	0.074
	± 0.80	± 0.76	± 0.72	± 0.75	± 0.90	± 0.78	± 0.80	± 0.73	± 0.73	± 0.74	± 0.79	± 0.94	± 0.85
VSSH	-23.1	-5.8	-0.3	-1.7	-1.3	-23.8	-13.3	-1.0	-0.4	-3.1	2.8	-1.3	-22.4
	± 62.0	± 52.9	± 49.1	± 55.7	± 72.5	± 62.9	± 56.5	± 49.9	± 49.0	± 54.8	± 59.2	± 80.7	± 67.5
u	-0.059	0.002	0.018	-0.010	0.020	-0.058	-0.031	0.023	0.016	-0.012	0.003	0.029	-0.000
	± 1.46	± 1.88	± 1.96	± 2.11	± 2.44	± 1.41	± 1.77	± 1.93	± 1.96	± 2.07	± 2.23	± 2.57	± 1.71
v	0.012	-0.006	-0.003	0.012	0.021	0.013	-0.000	-0.008	-0.002	0.010	0.016	0.027	-0.028
	± 0.89	± 1.11	± 1.20	± 1.47	± 2.22	± 0.87	± 1.04	± 1.15	± 1.21	± 1.38	± 1.78	± 2.45	± 2.01
EKE	0.017	0.024	0.027	0.034	0.056	0.016	0.022	0.026	0.027	0.032	0.042	0.066	0.037
	± 0.24	± 0.36	± 0.41	± 0.57	± 1.07	± 0.22	± 0.32	± 0.38	± 0.41	± 0.52	± 0.75	± 1.24	± 0.59
τ_E	-0.064	-0.033	-0.023	-0.021	-0.004	-0.066	-0.044	-0.026	-0.023	-0.024	-0.013	0.002	-0.012
	± 0.44	± 0.57	± 0.57	± 0.55	± 0.54	± 0.41	± 0.55	± 0.56	± 0.57	± 0.57	± 0.48	± 0.58	± 0.53
τ_N	0.031	0.024	0.023	0.022	0.008	0.031	0.028	0.023	0.024	0.025	0.011	0.013	0.003
	± 0.27	± 0.34	± 0.38	± 0.48	± 0.64	± 0.25	± 0.33	± 0.35	± 0.39	± 0.46	± 0.54	± 0.69	± 0.46
$\nabla \times \tau$	-1.43	-3.66	-3.80	-2.20	-2.14	-0.86	-3.38	-3.86	-3.76	-2.57	-1.77	-2.12	-0.76
	± 31.8	± 23.2	± 20.8	± 22.9	± 27.0	± 32.9	± 25.7	± 21.7	± 20.7	± 22.8	± 21.8	± 31.7	± 43.4
Depth	4350	4275	3988	3599	3309	4320	4365	4184	3953	3666	3453	3192	677
	± 1005	± 980	± 1047	± 1222	± 1347	± 1002	± 992	± 978	± 1057	± 1197	± 1276	± 1378	± 674
R555:443	0.006	0.022	0.101	-0.90	0.070	0.136	0.156	0.179	0.207	0.272	0.350	0.485	-0.893
	± 8.05	± 9.75	± 23.38	± 32.55	± 30.69	± 0.28	± 0.58	± 0.82	± 0.93	± 1.03	± 1.26	± 1.52	± 31.044
R555:488	-0.352	0.356	0.437	0.262	2.896	0.201	0.218	0.236	0.258	0.309	0.367	0.451	-0.003
	± 88.63	± 15.80	± 50.55	± 22.06	± 482.27	± 0.95	± 0.54	± 0.77	± 0.89	± 0.98	± 1.15	± 1.27	± 16.181
hline													

Table A.8: Characterisation of variables within each class for the N5, N8 and JSM classification schemes within the MPA
(total no. pixels 5,343,309).

Variable	Mean $\pm 1\sigma$														
	N5					N8									
Class	1	2	3	4	5	1	2	3	4	5	4	5	6	7	8
N (%)	8	37	39	16	1	4	20	32	26	15	26	15	3	11	11
chl	0.063 ± 0.008	0.088 ± 0.012	0.123 ± 0.021	0.180 ± 0.046	0.253 ± 0.087	0.058 ± 0.007	0.077 ± 0.009	0.099 ± 0.012	0.128 ± 0.019	0.171 ± 0.036	0.227 ± 0.073	0.244 ± 0.099	0.404 ± 0.108		
flh	0.049 ± 0.022	0.049 ± 0.021	0.060 ± 0.027	0.094 ± 0.037	0.117 ± 0.053	0.050 ± 0.024	0.048 ± 0.020	0.050 ± 0.021	0.062 ± 0.028	0.089 ± 0.035	0.114 ± 0.044	0.081 ± 0.049	0.092 ± 0.002		
flh/chl	0.791 ± 0.376	0.560 ± 0.240	0.482 ± 0.197	0.521 ± 0.190	0.460 ± 0.198	0.868 ± 0.427	0.632 ± 0.269	0.510 ± 0.214	0.479 ± 0.195	0.521 ± 0.191	0.503 ± 0.187	0.357 ± 0.205	0.209 ± 0.070		
SST	29.59 ± 0.77	29.41 ± 0.89	28.71 ± 0.99	27.62 ± 1.06	27.43 ± 1.04	29.55 ± 0.72	29.56 ± 0.87	29.22 ± 0.89	28.60 ± 0.99	27.70 ± 1.08	27.35 ± 0.94	28.05 ± 1.20	28.41 ± 0.41		
SLA	0.147 ± 0.084	0.072 ± 0.074	0.027 ± 0.066	0.008 ± 0.063	0.015 ± 0.042	0.163 ± 0.084	0.100 ± 0.078	0.051 ± 0.070	0.023 ± 0.065	0.009 ± 0.063	0.008 ± 0.057	0.025 ± 0.039	0.110 ± 0.049		
VSSH	24.3 ± 39.4	0.83 ± 34.3	8.52 ± 33.1	2.66 ± 34.6	8.35 ± 32.6	-29.4 ± 38.7	-8.19 ± 37.1	6.74 ± 32.2	8.55 ± 33.5	2.55 ± 34.9	5.38 ± 33.2	14.04 ± 29.3	9.05 ± 15.5		
u	-0.118 ± 0.162	0.018 ± 0.190	0.071 ± 0.193	0.040 ± 0.175	0.048 ± 0.175	-0.138 ± 0.150	-0.038 ± 0.184	0.058 ± 0.192	0.071 ± 0.192	0.041 ± 0.177	0.046 ± 0.169	0.048 ± 0.178	0.110 ± 0.160		
v	0.002 ± 0.089	-0.014 ± 0.090	-0.020 ± 0.088	-0.010 ± 0.093	-0.038 ± 0.111	0.003 ± 0.086	-0.007 ± 0.090	-0.019 ± 0.090	-0.020 ± 0.088	-0.009 ± 0.092	-0.019 ± 0.102	-0.074 ± 0.110	0.038 ± 0.051		
EKE	0.024 ± 0.026	0.023 ± 0.026	0.026 ± 0.033	0.021 ± 0.029	0.024 ± 0.029	0.025 ± 0.026	0.022 ± 0.026	0.025 ± 0.031	0.025 ± 0.033	0.021 ± 0.030	0.021 ± 0.030	0.026 ± 0.027	0.020 ± 0.036		
τ_E	0.003 ± 0.034	-0.007 ± 0.040	-0.027 ± 0.047	-0.056 ± 0.050	-0.047 ± 0.059	0.002 ± 0.034	-0.001 ± 0.037	-0.014 ± 0.042	-0.030 ± 0.048	-0.055 ± 0.049	-0.057 ± 0.051	-0.016 ± 0.068	-0.069 ± 0.0008		
τ_N	0.000 ± 0.017	0.011 ± 0.025	0.027 ± 0.032	0.047 ± 0.034	0.040 ± 0.039	-0.001 ± 0.017	0.005 ± 0.022	0.016 ± 0.027	0.029 ± 0.032	0.046 ± 0.034	0.047 ± 0.034	0.020 ± 0.046	0.057 ± 0.003		
$\nabla \times \tau$	-7.48 ± 17.7	-7.04 ± 16.4	-7.92 ± 16.5	-7.85 ± 17.3	-7.16 ± 26.6	-7.86 ± 18.5	-6.70 ± 16.5	-7.52 ± 16.4	-7.99 ± 16.4	-7.77 ± 16.6	-8.12 ± 22.0	-3.01 ± 25.4	0.00 ± 8.2		
Depth	3891 ± 1143	3730 ± 1083	3598 ± 1173	3396 ± 1368	3011 ± 1433	3938 ± 1149	3785 ± 1102	3688 ± 1087	3574 ± 1193	3441 ± 1343	3129 ± 1446	3113 ± 1471	368 ± 140		
R555:443	-0.113 ± 8.70	0.048 ± 9.88	0.216 ± 21.98	0.250 ± 28.20	0.139 ± 22.04	0.117 ± 0.28	0.147 ± 0.48	0.173 ± 0.80	0.203 ± 0.99	0.260 ± 1.10	0.300 ± 0.84	0.620 ± 1.23	6.934 ± 17.700		
R555:488	-5.161 ± 136.2	0.477 ± 16.07	0.825 ± 51.55	0.179 ± 21.12	15.117 ± 617.4	0.179 ± 5.38	0.207 ± 0.46	0.229 ± 0.76	0.252 ± 0.94	0.295 ± 1.05	0.325 ± 0.75	0.559 ± 0.84	-12.526 ± 40.68		

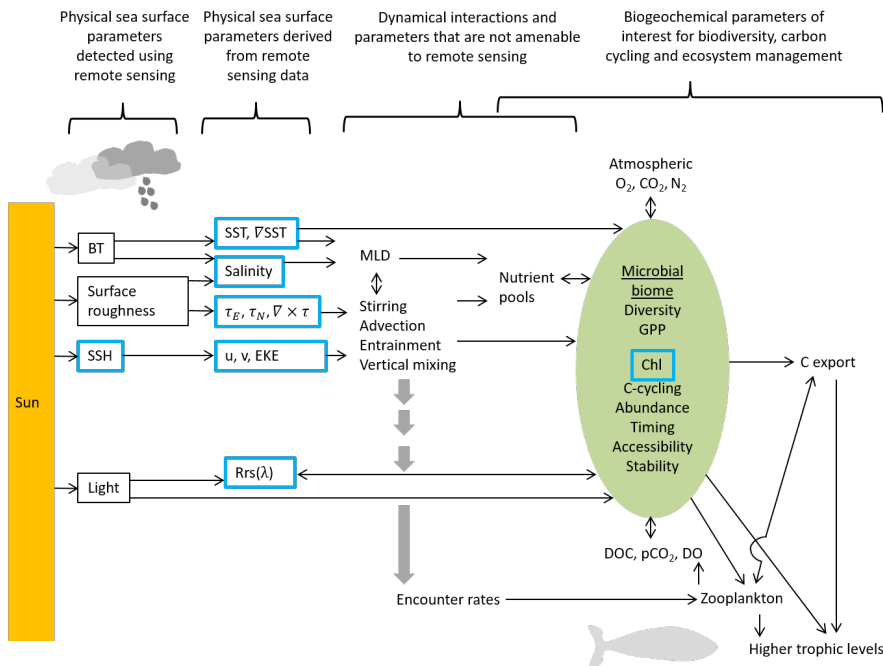


Figure 1: Schematic representation of key biophysical linkages (not exhaustive). The flow of information begins with sunlight to the left. Physical variables that can be detected using remote sensing, followed by the oceanographic variables derived from them, are shown between the sun and the ocean surface processes. Oceanographic variables of interest that can be derived from remote sensing data are outlined in blue and abbreviations are explained in Table 1. The other variables shown are of interest to conservation, management or climate change applications but are not amenable to remote sensing.

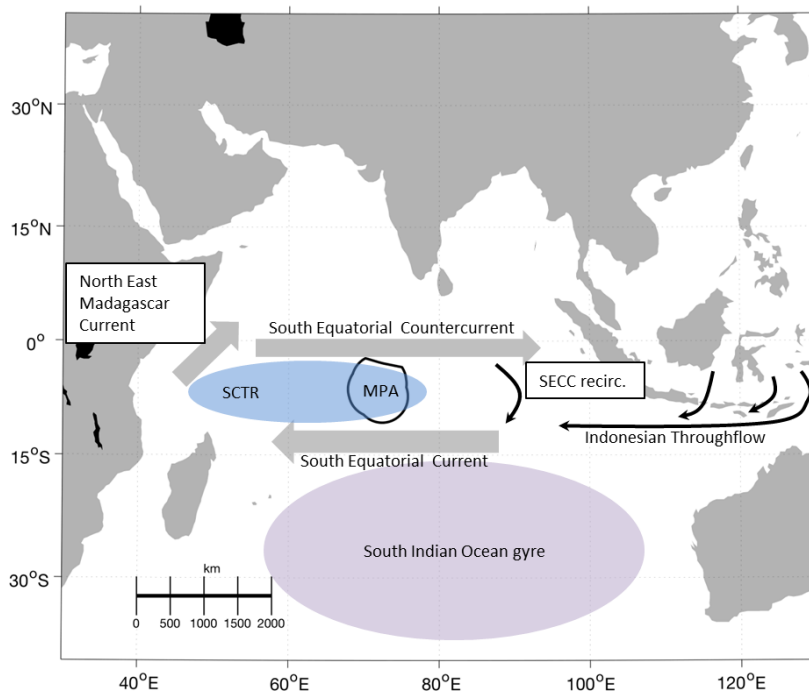


Figure 2: Location of the study domain, adapted from Talley et al. (2011); Aguiar-Gonzalez et al. (2016). SCTR = Seychelles Chagos Thermocline Ridge; MPA = Chagos Marine Protected Area; SECC = South Equatorial Countercurrent

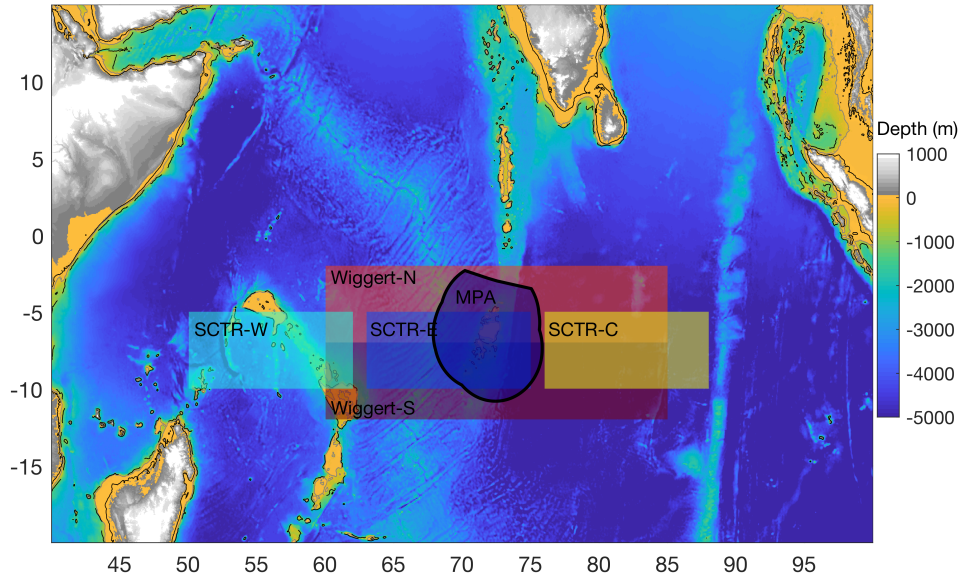


Figure 3: Bathymetry of the study domain. Shaded regions denote the sub-areas related to other published studies. Black line: coast; grey line: 200 m contour; black dashed line: 1000 m contour; thick black line: MPA boundary.

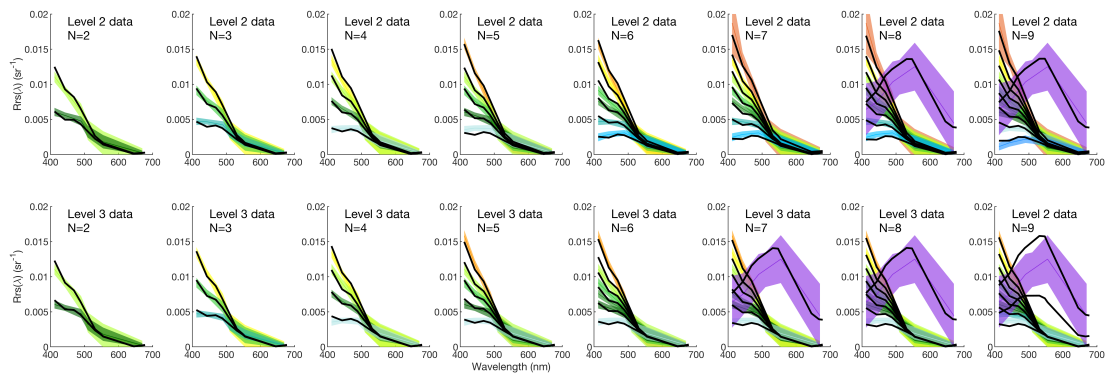


Figure 4: Central spectra for the 10-band classifications from Level 2 (upper) and Level 3 (lower) datasets with two to nine classes, compared with the 6-band JSM classification (shaded).



Figure 5: Mapping of the N5, N8 and JSM classes onto published PFT algorithms. SLC=Synechococcus-like cyanobacteria; xDiat was assigned where the residual PHYSAT-like spectrum resembled the diatom criteria in Alvain et al. (2008) but with higher values; SynPro=spectrum matches SLC or Prochlorococcus except for one waveband, which fell in the other small-cell category. Algorithm acronyms are explained in section 3.1.

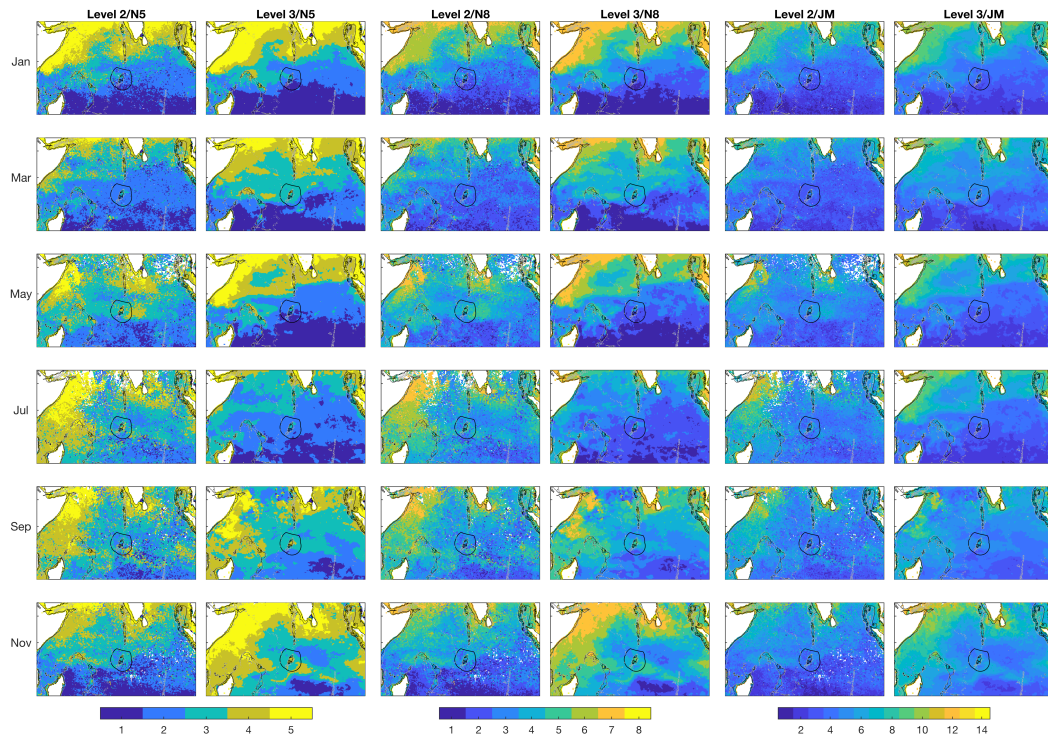


Figure 6: Comparison of class maps produced with the Level 2 and Level 3 Rrs data, classifications N5, N8 and JSM, in 2003. The Chagos MPA outline, 0 m and 1000 m isobaths are shown in black and the 2000 m isobath in grey.

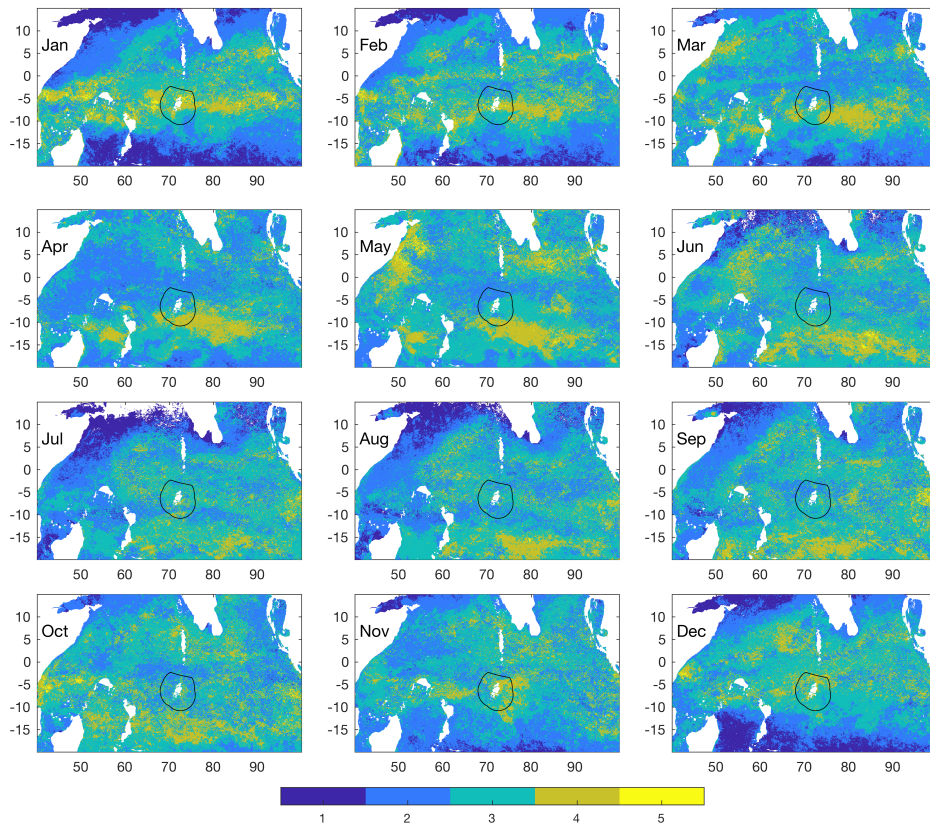


Figure 7: Number of classes held at each pixel over the 17 year study period, by month, for Level 3 data, $N=5$. The Chagos MPA outline is shown in black.

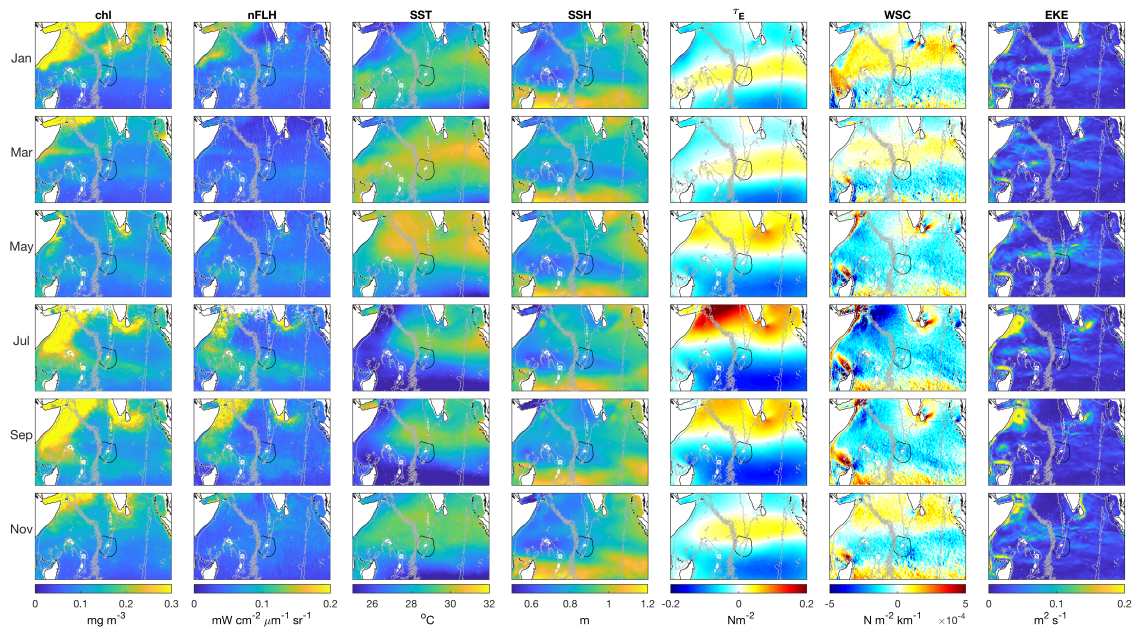


Figure 8: Monthly 17-year climatologies of key remote sensing variables. The Chagos MPA outline and 0 m contour are shown in black, and the 3000 m isobath in grey.

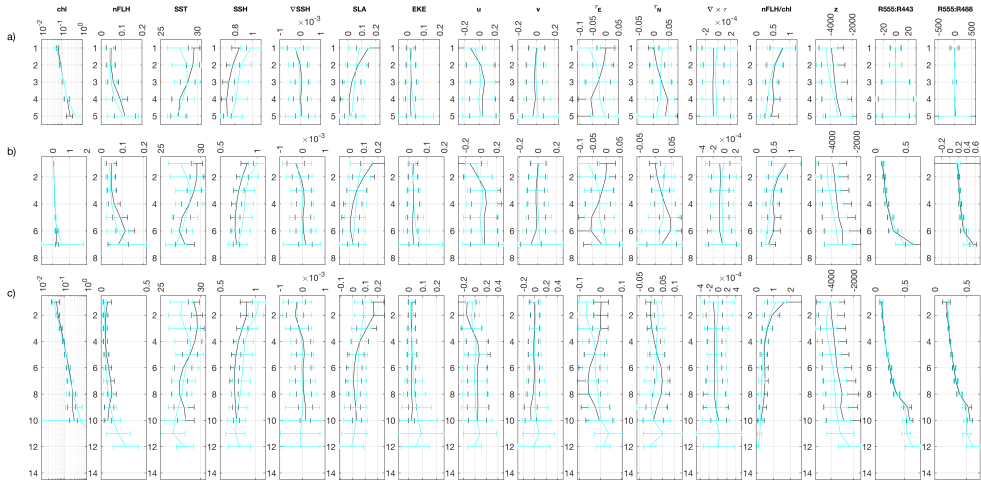


Figure 9: Variability of remotely sensed parameters in the MPA and z1000 domains: Top row = N5; Middle row = N8; Lower row = JSM; black=MPA; cyan=whole domain with depth > 1000 m (z1000).

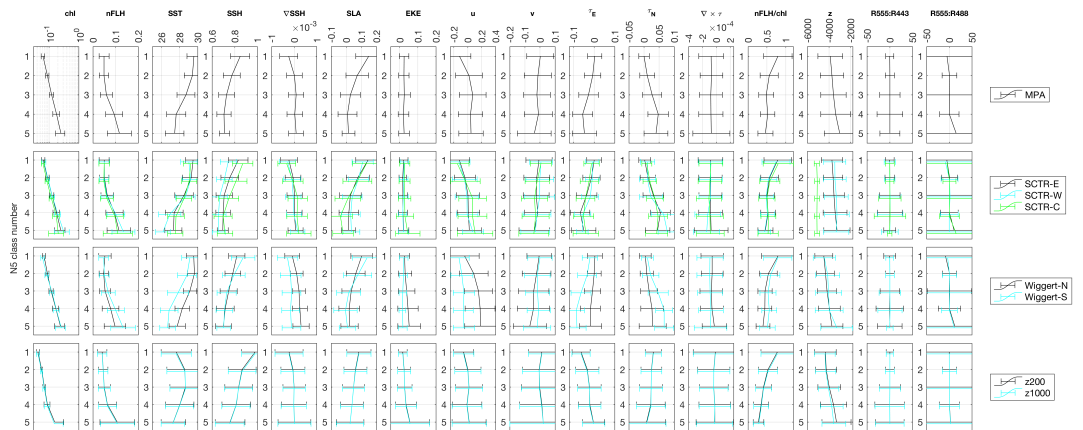


Figure 10: Variability of remotely sensed parameters for each sub-domain using the N5 classification.

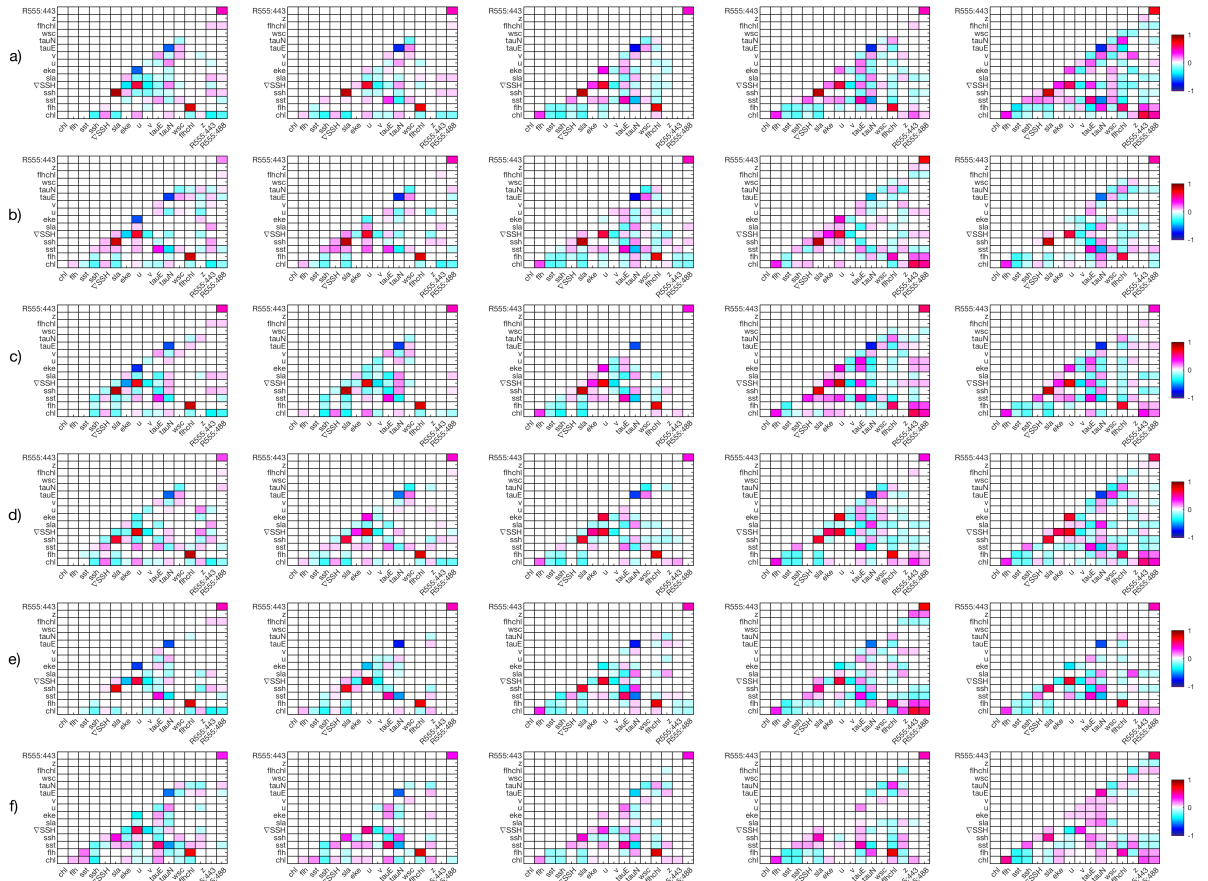


Figure 11: Averaged Mann-Kendall-Sen correlation coefficients between variables within each class for each domain: a) MPA, b) SCTR-W, c) SCTR-C, d) Wiggert-N, e) Wiggert-S, f) z1000. Only results with a p-value < 0.01, confirmed using bootstrapping to remove autocorrelation and subsampling effects, are shown.

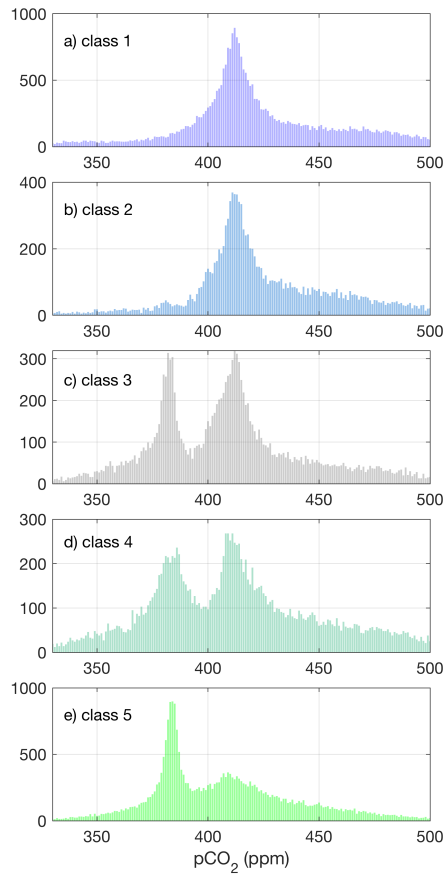


Figure 12: OCO-2 lowest altitude pCO₂ distributions within the z1000 domain for the N5 classes applied to MODIS Level 2 data, January 2015.

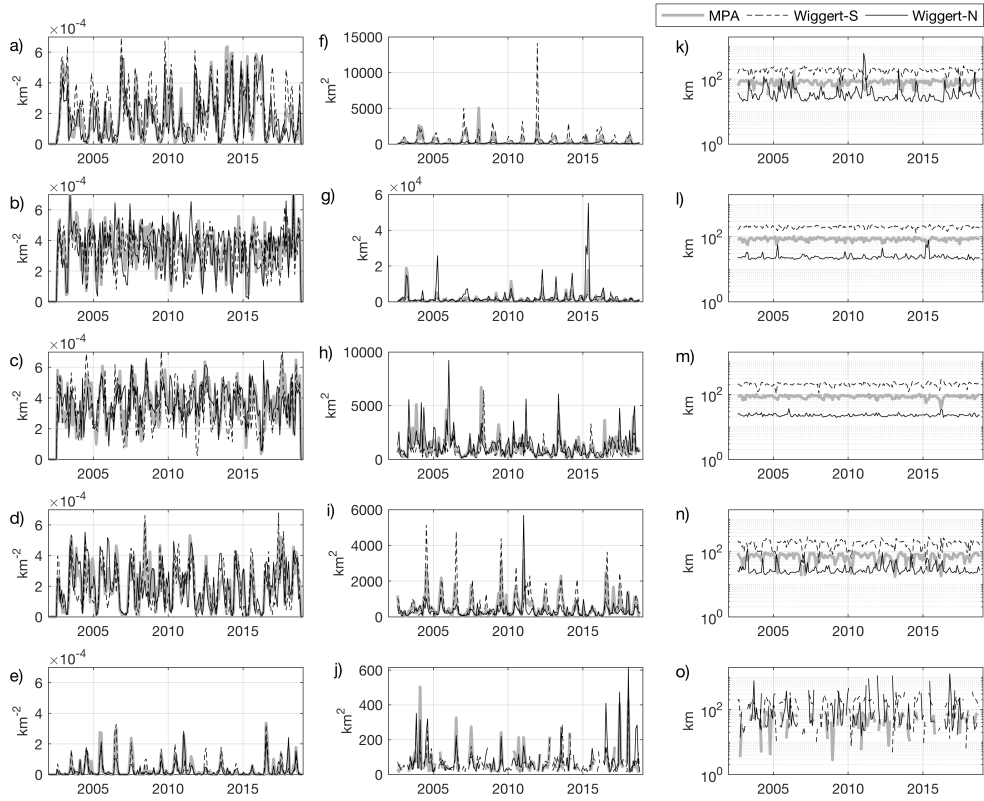


Figure 13: a) to e) Density of patches of each N5 class (a=class 1, e=class 5); f) to j) Average patch area (f=class 1, j=class 5); k) to o) Average distance between patches (k=class 1, o=class 5) for the MPA, Wiggert-N and Wiggert-S domains. Note different y-axis limits are used to show detail.

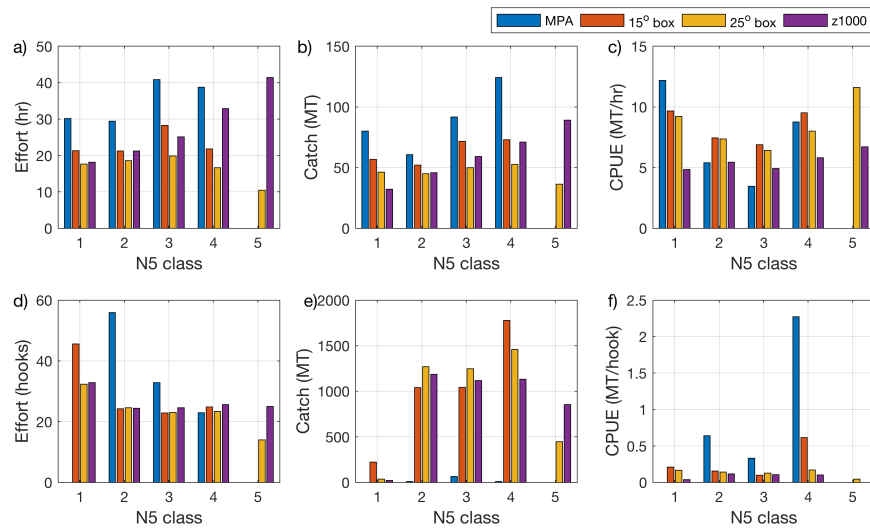


Figure 14: IOTC fishing catch and catch per unit effort for the Indian Ocean surface (top row; a, b,c) and longline (lower row; d, e, f) fisheries.

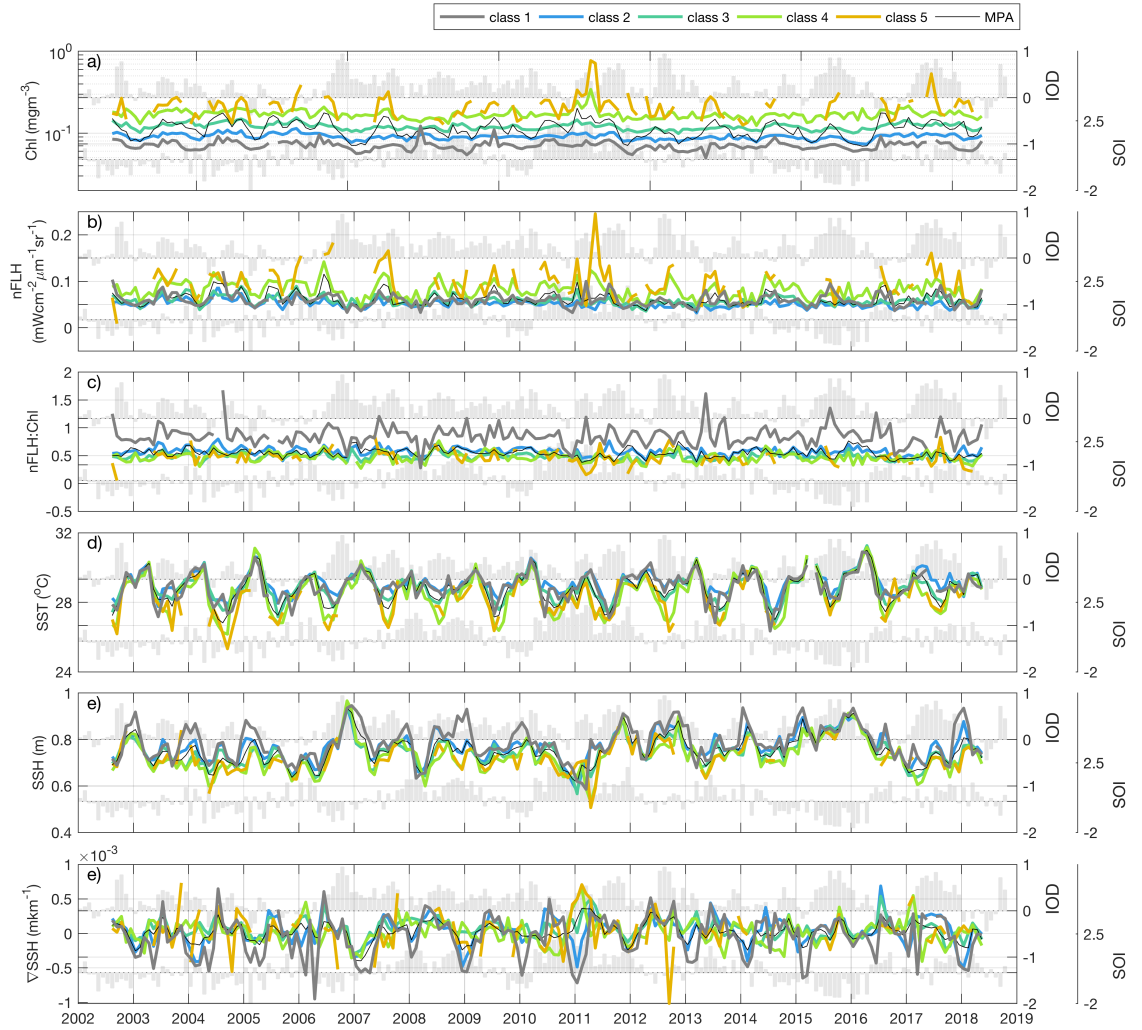


Figure 15: Time-series for each N5 class within the MPA for a) Chl, b) FLH, c) FLH:Chl, d) SST, e) SSH and f) ∇ SSH.

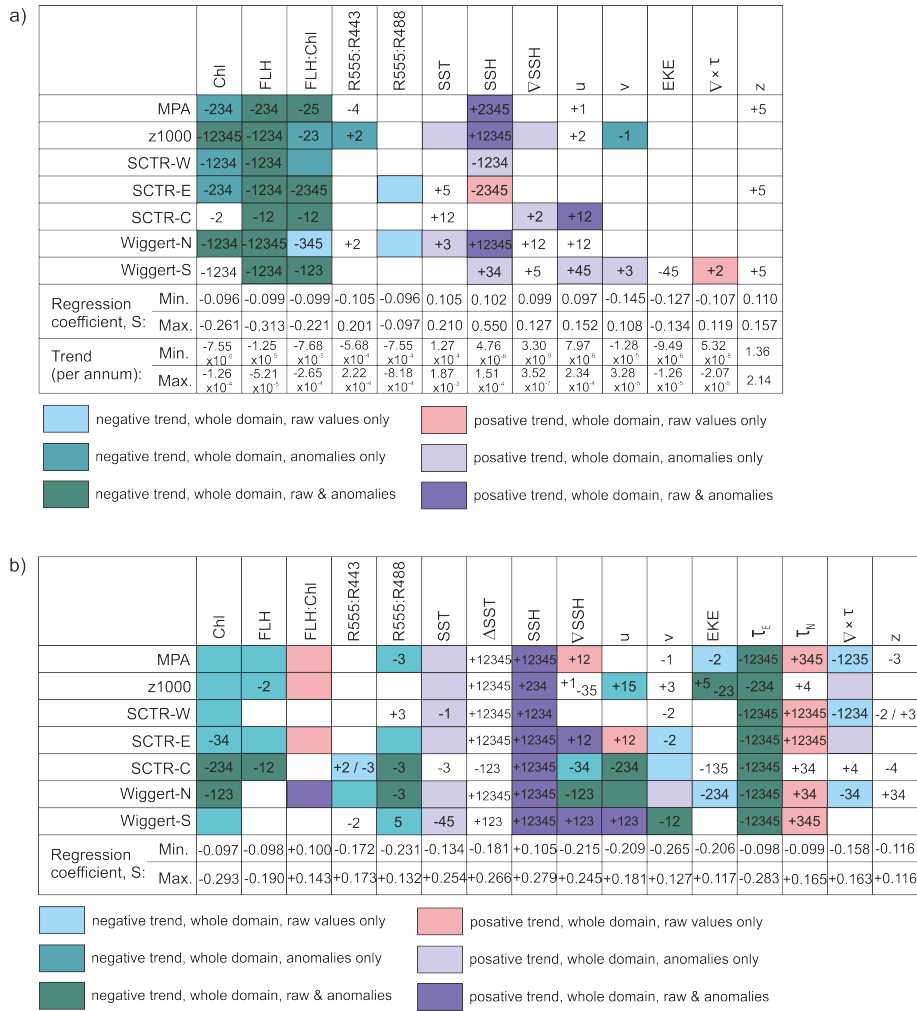


Figure 16: a) Summary of the temporal trends found within each domain ($p < 0.05$), including ranges of the Sen regression coefficient and rates of change. Trends for specific classes are denoted by class number; trends for the entire domain are indicated by block colour (red=positive trend; blue=negative trend). b) Summary of significant ($p < 0.05$) correlations between remotely sensed variables and the Indian Dipole Mode Index, including ranges of the Sen regression coefficient. Correlations for specific classes are denoted by class number; correlations for the entire domain are indicated by block colour (red=positive trend; blue=negative trend). Full correlation results, including 95% confidence intervals on the regression slopes, are given in Table S1.