The effect of deep oceanic flushing on water properties and ecosystem functioning within atolls in the British Indian Ocean Territory

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ES, PH, MA & JM conceived this research, ES, JM & DT gathered the data, ES, PH, CG & MW analysed the data. All authors wrote the manuscript.

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Abstract

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Within atolls, deep water channels exert significant control over local hydrodynamic conditions; which are important drivers of planktonic distributions. To examine planktonic responses to oceanography, this study tested the effect of proximity and exposure to deep oceanic flushing through these channels on water properties and planktonic assemblages across four atolls (Diego Garcia, Salomon, Egmont and Peros Banhos) in the British Indian Ocean Territory Marine Reserve. As this is the largest, most isolated and sparsely inhabited atoll complex in the world, it provides the perfect experimental conditions to test the effect of oceanic flushing without confounding factors related to anthropogenic development. Results are discussed in the context of ecosystem functioning. A total of 30 planktonic taxa and 19,539 individuals were identified and counted. Abundance was significantly different between atolls and significantly greater within inner regions in all atolls except southeast Egmont. Planktonic assemblage composition significantly differed between atolls and between inner and outer stations; exhibiting higher similarity between outer stations. Within outer stations of Diego Garcia, Peros Banhos and Egmont, evidence suggesting oceanic flushing of cold, saline and dense water was observed, however a longer time series is required to conclusively demonstrate tidal forcing of this water through deep water channels. Planktonic variability between inner and outer atoll regions demonstrates that broad comparisons between oceanic and lagoon regions fail to capture the complex spatial dynamics and hydrodynamic interactions within atolls. Better comprehension of these distributional patterns is imperative to monitor ecosystem health and functioning, particularly due to increasing global anthropogenic pressures related to climate change. The extensive coral bleaching described in this paper highlights this concern.

Contribution to the field

This manuscript provides the first account of plankton communities and deep oceanic flushing processes, within atolls across the Chagos archipelago. We show how flushing processes are potentially shaping plankton distribution patterns within and between atolls, which could explain the distribution patterns of larger pelagic organisms such as manta ray, turtles and sharks. The diversity of benthic habitats and the extent of pristine coral bleaching are also reported and contextualised in the frame of ecosystem functioning.

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15

16 **Abstract**

17

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19 conditions; which are important drivers of planktonic distributions. To examine planktonic

20 responses to oceanography, this study tested the effect of proximity and exposure to deep

21 oceanic flushing through these channels on water properties and planktonic assemblages across

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Keywords: Plankton, Chagos Archipelago, Indian Ocean, Atoll, Marine Protected Area, ecosystem functioning, exposure, oceanography, coral bleaching.

1. Introduction

Coral atolls are often characterized by a rich biodiversity of fishes, corals and coralline algae, highly mobile consumers such as manta rays (McCauley et al., 2014) and sea turtles

46 (Mendonca, 1982)**,** and apex predators (Sheppard et al., 2012) such as reef sharks (Tickler et

47 al., 2017)**.** The greater productivity within atolls relative to the surrounding oligotrophic

48 tropical waters (Rayner and Drew, 1984;Letessier et al., 2016) likely supports such diverse

49 assemblages**.** As such they have been claimed to be 'oases of life in an oceanic desert' (Odum,

50 1955;Johannes and Gerber, 1974)**.**

51 Such atoll productivity may be maintained by high nutrient recycling, through microbial food

52 webs and coral symbionts (Hatcher and Frith, 1985;Falter et al., 2004), and geomorphology.

53 Geomorphological features such as deep water channels are thought to affect productivity

54 within atolls, by facilitating oceanic exchange between lagoon and oceanic waters; controlled

55 by the tidal forcing (Pugh and Rayner, 1981;Kench, 1998;Chevalier et al., 2017;Green et al.,

56 2018). Without this oceanic exchange, temperature, salinity and oxygen may reach extreme,

57 uninhabitable levels (Pugh and Rayner, 1981). Thus, the nutrient enrichment (Thompson and

58 Golding, 1981;Thomson and Wolanski, 1984;Wolanski et al., 1988) and environmental

59 stability exerted by these deep water channels through water renewal likely plays a key role in

60 ecosystem functioning.

61 Investigating the role of atoll hydrodynamics on natural ecosystem functioning is almost

62 always confounded by anthropogenic influences such as nutrient input through urban run-off,

63 overfishing, sedimentation, coastal development, pollution and tourism (Knowlton and

64 Jackson, 2008;Riegl et al., 2012;Firth et al., 2016)**.** However, atolls within the Chagos

65 Archipelago, Indian Ocean, represent a unique opportunity to investigate these relationships in

66 the absence of direct human pressures. The Chagos Archipelago is a large area of atolls and

67 submerged banks within the British Indian Ocean Territory (BIOT), situated in the southern

68 region of the Lakshadweep-Maldives-Chagos ridge (Sheppard et al., 2012). Established within

69 BIOT is a designated no-take marine reserve of approximately 550,000 km². The marine

70 reserve includes all of the atolls and waters of the BIOT Exclusive Economic Zone (EEZ), with

71   the exception of the atoll of Diego Garcia (Sheppard et al., 2012). There are no human

72   inhabitants within the archipelago, save for those associated with the military base on Diego

73   Garcia. As such, the BIOT marine reserve is the largest, most isolated uninhabited atoll

74   complex in the world**.**

75   Plankton are extremely important to the functioning of atoll lagoon systems. They are key to

76   conserving biodiversity and productivity (Bozec et al., 2004;Alldredge and King, 2009) as they

77   play a vital role in food webs, linking primary producers to multiple trophic levels e.g. reef

78   fishes, manta rays and reef sharks (Niquil, 1998 ;Alldredge and King, 2009;Tickler et al.,

79   2017), participate in biogeochemical cycles (Roman, 1990;Legendre and Le Fèvre, 1991) and

80   their abundance is known to influence pelagic and benthic faunal recruitment (Hughes, 2000

81   ;Grorud-Colvert, 2009). Given their importance to ecosystem functioning (Hébert et al., 2017),

82   investigating the spatial distribution, abundance and diversity of plankton is vital for the

83   monitoring of marine biodiversity and ecosystem health.

84   Within planktonic assemblages, zooplankton comprise taxa which reside in the plankton for

85   early larval stages (meroplankton) and taxa which are planktonic for their entire life cycle

86   (holoplankton) (Kennish, 2001). There are also small, often benthic animals translocated into

87   the water column by hydrographic and behavioural processes (tychoplankton) (Kennish, 2001).

88   Typically the abundance of zooplankton is greater within lagoons, compared to adjacent

89   oceanic areas (Gerber, 1981;Pagano et al., 2012) and is dominated by meroplankton (Gerber,

90   1981;Achuthankutty et al., 1989;Pagano et al., 2017). This pattern highlights the importance

91   of atolls as 'nursery grounds' for the larval planktonic stages of tropical invertebrates and

92   fishes.

93   A number of oceanographic processes are known to influence the distribution and community

94   structure of zooplankton throughout the open ocean such as ocean fronts, mesoscale eddies and

95   upwelling (Kiørboe, 1997;Huggett, 2014;Lamont et al., 2014). Within lagoons, however,

96   hydrodynamic drivers including tidal flushing and wind-driven circulation, and the associated

97   variations in salinity and temperature, are highly influential (Dumas et al., 2012;Dupuy et al.,

98   2016). Additionally, particulate organic matter and chlorophyll (Le Borgne et al.,

99   1989;Carassou et al., 2010), increased terrestrial runoff and nutrient input (Carrillo Baltodano

100   and Morales Ramírez, 2016;Dupuy et al., 2016) and zooplankton swimming behaviour within

101   tidal-currents may also affect the retention/aggregation of zooplankton in lagoons (Genin et al.,

102   2005). Cold oceanic water spilling into atolls from deep channels may underpin zooplankton

103   spatial and temporal distribution within the lagoons.

104

105   This study compared zooplankton metrics (number of taxa, abundance, and assemblage

106   composition) between inner more sheltered regions with outer more exposed regions. To

107   examine the hypothesis that deep oceanic water is flushed into the atoll, differences in water

108   properties were compared between inner and outer regions. Four atolls in the BIOT were

109   surveyed; Salomon, Egmont and Peros Banhos in the marine reserve, and Diego Garcia.

110

2. Materials and methods

111

112

113   To enable comparison of these data between atolls and to other comparable locations, site

114   characterisation was first undertaken. Intertidal and subtidal samples were taken using cores

115   and towed video respectively (Figure 1). Plankton samples and CTD vertical profiles were

116   collected concurrently following a transect, to capture the different regions of exposure in four

117   coral reef atolls in the British Indian Ocean Territory (Diego Garcia, Salomon, Egmont and

118 Peros Banhos), in the central Indian Ocean between 04°54' to 07°39'S and 70°14' to 72°37'E

119 (Tickler et al., 2017) (Figure 1). Each transect started in the most sheltered part of the atoll and

120 ended at the exposed lagoon entrance (weather depending). Sampling took place from a 4 m

121 skiff during daylight hours between 11th- 22nd May 2016. Permission was granted to undertake

122 the work by the United Kingdom Foreign and Commonwealth Office.

123

2.1 Site characterisation

125

126 Within each atoll, 3-5 intertidal sites and 1-5 subtidal sites were haphazardly selected to gain

127 optimal coverage of each atoll, time allowing (Figure 1). To assess the intertidal sediment size,

128 organic content and infauna, 3 replicates were sampled at the waterline of each site. Each

129 replicate gathered a sediment sample using a small plastic corer (50 mm L x 50 mm D) to

130 assess particle size and organic content, and an infauna sample using a bespoke stainless steel

131 corer (250 mm L, 100 mm D) (Supplementary Figure 1) (Sheehan et al., 2015). Sediment

132 processing was conducted using a standard approach as described in (Sheehan et al., 2010).

133 Sediments from the large corer were sieved over a 1 mm mesh sieve. The samples did not

134 contain any living fauna, bar 5 individuals of a featureless species of polychaete, hence no

135 infauna data are presented. To assess habitat type and coral health, 3 x video transects of the

136 subtidal sea bed at each site were recorded. Transects were recorded for 5 minutes and towed

137 at <0.2 knots using a bespoke, non-contact, towed array, fitted with a Go Pro 4 silver and laser

138 scaling (Supplementary Figure 1) for 3 x 5 minute tows at each subtidal site (Figure 1). To

139 analyse sub-tidal video transect recordings, each transect was split into frames at 3 second

140 intervals. Poor quality and overlapping frames were removed, leaving high quality frames for

141 analysis (Sheehan et al., 2013). The dominant habitat type and its bleaching status for each

142 frame was recorded (Corals: Bommies, Rubble, Branching and Massive; Sediment: Sand or

143 Mounds in sand). In addition, any live corals (hard or soft), encrusting coralline algal/hydroid

144 turf that colonises dead coral, or reef fish were noted. Percent occurrence of dominant habitat

145 and percent presence of the other variables were calculated for each replicate tow.

146

147 2.2 Plankton & Water property profiles
148

149 Along each transect, samples were taken at discrete stations separated 1 nautical mile apart for

150 the larger atolls (Diego Garcia and Peros Banhos) and 0.5 nautical miles apart for the smaller

151 atolls (Egmont and Salomon) (Figure 1). The position of each station was logged using a GPS

152 Garmin Etrex 20x. At each station, a seabed-surface vertical sample was obtained by a plankton

153 net (250 mm frame with a 250 µm mesh) and a Maestro CTD (RBR Maestro conductivity-

154 temperature-depth sensor equipped with a Rinko dissolved oxygen sensor and a Seapoint

155 Chlorophyll-α fluorometer, sampling at 12 Hz) (Supplementary Figure 1). Salinity data are

156 henceforth expressed in practical salinity units (PSU). Each transect was completed between

157 30 and 70 minutes, minimising the influence of non-steady dynamics, likely attributable to

158 tides, on the results. From the density values derived from the Maestro CTD, the Brunt-Vaisala

159 frequency, N;

160

$$N = \sqrt{-\frac{g}{\rho_o}\frac{\partial\rho(z)}{\partial z}}$$

161

162

163   where g=9.81 m s^{-2} is the acceleration due to gravity, ρ_o is a reference density and z is the

164   vertical distance, was calculated for 1 metre vertical increments. Data were subsequently bin-

165   averaged at 1 m vertical resolution in post-processing.

166

167   In addition to the vertical profiles, Valeport mini-CTDs were deployed at a depth of 3 m and

168   approximately 2 m above the bed at the entrances to each lagoon, except Salomon in which the

169   CTD malfunctioned (Figure 1). The mini-CTDs sampled at 1 Hz and were deployed at each

170   site for a complete semidiurnal tidal cycle, with the intention of observing temporal changes in

171   the water properties entering and leaving the lagoon. The deployments were coincident with

172   the Maestro CTD vertical profile transects, enabling an assessment to be made of the temporal

173   variability that may influence the interpretation of the spatial variability depicted by the

174   Maestro CTD data. Due to entrapment of particles in the conductivity cell of the mini CTDs,

175   the salinity data were unreliable, therefore only the temperature data from these instruments

176   could be reliably used to indicate the susceptibility of a given site to cold water flushing from

177   the open ocean.

178   Plankton samples were stored in 100% ethanol and later filtered through a 200 µm mesh and

179   identified using light microscopy. Taxon were identified as described by (Conway et al., 2003)

180   to the highest level of taxonomic resolution as was feasible. For copepod abundance

181   specifically, individuals were distinguished first by order and then a size fraction (small = < 2

182   mm, large= >2 mm). Identification was then conducted within these fractions.

183

184   Identifications were made using stereo microscopes: Leica MZ6 (magnification x9.45-x60);

185   Zeiss Discovery. V8 (magnification x6.3-x120) and a bespoke compound microscope

186   (magnification x62.5-x625). For each microscope, size distinctions were made using an

187   eyepiece graticule calibrated to a stage micrometer. Identification and enumeration was

188   completed on 39 samples. Samples were counted in their entirety, excluding a singular occasion

189   in which the abundance of gastropod larvae surpassed 5,500. In this sample (southwest Egmont

190   Station 2, Figure 1), the count for this taxon was based on extrapolation of abundance within

191   half the sample.

192

193

194

195   **2.3 Data analysis**

196

197

198   **2.3.1   Site characterisation**

199

200   Site characterisation data were tabulated but not analysed as there were no a priori hypotheses

201   to test.

202

203   **2.3.2   Plankton & Water property profiles**

204

205   Transects comprised evenly dispersed stations and ran from the most sheltered part of each

206   atoll towards the primary channel where it was most exposed. To statistically compare plankton

207   assemblages between inner sheltered and outer exposed regions, stations in the first half of

208   each transect were considered "inner" and the remaining stations considered "outer" unless

209   water property data provided a more informed division between categories. (Figure 2, Figure

210   3, Supplementary Figure 2-5). It was anticipated that deep oceanic flushing would be

211   characterised by vertical isopycnals indicating lateral gradients in water properties as oceanic

212 water entered the lagoon. Inner unflushed lagoons instead would demonstrate a degree of

213 vertical stratification, as the absence of flushing by oceanic water enables persistent diurnal

214 warming to enhance the near surface thermocline. As these data were limited to single time

215 points, flushing extent could be underestimated. To further extrapolate these data, this study

216 would need to be replicated to account for tidal, daily, seasonal and annual variability.

217

218 Permutational multivariate analysis of variance in Primer 7 (Anderson, 2001;Clarke and

219 Warwick, 2001) was used to test for differences between Atolls (Fixed, 5 levels: Diego Garcia,

220 Salomon, southwest Egmont, southeast Egmont and Peros Banhos) and Exposure (Fixed, 2

221 levels: Inner and Outer) using two univariate metrics (number of taxa and abundance) and one

222 multivariate metric (assemblage composition). All data were fourth root transformed and

223 univariate data were based on Euclidean distance, while multivariate data were based on the

224 Bray–Curtis similarity index (Bray and Curtis, 1957). Non-metric multi-dimensional Scaling

225 (nMDS) was used to visualise differences between factors, while SIMPER routine (Clarke and

226 Warwick, 2001) was used to interpret trends, which drove observed differences in assemblage

227 composition.

228

229 ## 3. Results

230

231 ### 3.1 Atoll habitat

232

233　The intertidal sediments in all four atolls comprised medium to very coarse sand (Folk and

234　Ward, 1957) that had very poor to medium sorting similar levels of low organic content and

235　almost no infauna present (Supplementary Table 1).

236

237　The subtidal habitats were more variable (Supplementary Table 2). The habitat in Diego Garcia

238　was dominated by a matrix of sandy mounds created by benthic organisms, covered in trails

239　made by gastropods and hermit crabs (40 %), areas of bleached Bommies (22.8 %) on sand

240　and coral rubble (26.3 %). There was very little occurrence of live coral (hard= 6.9 %; soft=0.4

241　%). While some corals appeared to be recently bleached, others had been bleached for some

242　time and were covered in red algae, green algae and other encrusting organisms (8.9 %). The

243　breaking down of coral structure was evident throughout, with giant clams falling out of

244　decomposing coral structure. Reef fishes still populated areas of bleached coral and were seen

245　in 13.7 % of the frames.

246

247　Across the four atolls, Salomon was the only place where live coral was recorded as a dominant

248　habitat (43 %). There was still bleached branching corals (9.1 %) and bleached massive corals

249　(13.2 %) between areas of sand (10.5 %) and mounds in sand (22.7 %). Here only 13.5 % of

250　frames contained colonising crust on the bleached coral and 43.2 % of frames were populated

251　with reef fishes.

252

253　Egmont was characterised by mostly bleached massive corals (64 %), bleached branching

254　corals (36 %) and turf algae (32 %). Reef fishes occurred in 68 % of the frames. Although

255　extensively bleached, there were still some live hard (3 %) and soft corals present (4.4 %).

256

257 In Peros Banhos, the south west site had steep slopes of degrading corals down to flatter sandy

258 areas, especially table corals that had broken and were littered upside down across the slopes.

259 The rest of the sites were fairly homogenous flat areas, characterised mostly by bleached

260 massive coral (84.9 %). There were examples of recently bleached branching corals with

261 symbiotic porcelain crabs still present next to those that had bleached some time ago, evidenced

262 by the encrusting pink algae (89.4 %). Live hard (3 %) and soft corals (4.4 %) were observed

263 across the massive dead hard coral reef. Despite the dead coral habitat, 76 % of the frames were

264 populated with reef fishes and sharks were also recorded. Subtidal habitat examples are shown

265 in Figure 4.

266

267 **3.2 Atoll oceanography**
268

269 The CTD time series data (Figure 3) was consistent with the hypothesis that these atolls are

270 subject to intermittent inundations at depth of cold, oceanic water. CTD time series, presented

271 as t, decimal year day for 2016, in particular demonstrated the extent to which the tidal currents

272 may be flushing the lagoons with water of oceanic origin, thereby providing a potential source

273 of nutrients. However, a longer time series is needed to conclusively demonstrate this.

274 CTD data from the time series moorings and the depth profile transects (Figure 2 &

275 Supplementary Figures 2-5) demonstrate that the region is strongly stratified, potentially from

276 nonlinear internal waves of depression that are supported by near-surface stratification and

277 manifest themselves as short period elevations in temperature (Hosegood et al., 2019). These

278 effects may promote shear-induced mixing and the downward diffusion of heat accumulated

279 in the surface layers during daytime.

3.2.1 Diego Garcia

The transect within Diego Garcia (Figure 2) began at the far southern extent of the lagoon in 10.68 m water depth, where the water is sheltered from the effects of the open sea and whose only entrance into the lagoon is approximately 20 km to the north, where the maximum depth recorded was 28.79 m. As such, there is no possibility of water entering the lagoon by any other means, such as over a surrounding reef. Temperature (T) was vertically homogenous throughout the lagoon and implies efficient vertical mixing throughout the water column. A lateral gradient was apparent as temperature decreased from $\sim$31.05 °C in the inner southern extent of the lagoon to <30.4 °C towards the northern entrance. Similarly, salinity (S) was highest in the inner stations and reached 34.1, diminishing in an approximately linear manner horizontally towards outer stations, where S$\sim$33.9. It should be noted that the apparent vertical homogeneity in T and S and simultaneous pronounced stratification in the density field is a relic of the colour scale bar. Density only ranges from 20.83 to 20.99, a difference of 0.16, and a similarly subtle temperate and salinity gradient also exists but is not expressed in Figure 2. Density alternates between regions of stable but weaker stratification, in which $N^2 \sim 10^{-4.5}$ s^{-2}, and regions in which isopycnals exhibited a significant inclination to the vertical, within which $N^2 > 10^{-4}$ s^{-2}. The regions of maximum stratification coincided with parts of the lagoon in which dissolved oxygen (DO) was minimum, specifically the central part of the lagoon in which the channel narrows, and the southern extent of the lagoon where S was lowest. This suggests terrestrial input of freshwater, given the temperatures were highest.

303 Notably, there was evidence of a cold intrusion of deeper water entering the outer stations of

304 the lagoon; the cold, saline, and therefore dense water was accompanied by decreased DO but

305 had a negligible signature in chlorophyll-α (chl-α), which varied only in the horizontal.

306 Distinctly higher concentration of chl-α >1 mg l^{-1}, was observed at the enclosed inner end of

307 the lagoon and dropped to background levels of <0.3 mg l^{-1} towards the extent of the outer

308 stations.

309

310 CTD time series showed evidence of colder water entering the lagoon near the bed (Figure 3).

311 Whilst a semidiurnal variation in temperature was apparent near the surface, where temperature

312 decreased from 30.83 °C at t = 131.7 to 30.55 °C approximately 6.5 hours later, before

313 recovering back to initial values. The temperature at a depth of 19 m decreased more abruptly

314 at t = 131.95 and 132.125, reaching 30.2 °C from an initial temperature of 30.6 °C. The

315 accelerated decrease in temperature at these points suggests pulses of cooler water were

316 advected into the lagoon and is consistent with the near-bed intrusion of cold water observed

317 during the Maestro CTD transect.

318
319 **3.2.2 Salomon**
320

321 Despite the similar water depth range recorded within Salomon (11.62 m – 28.72 m) compared

322 to Diego Garcia (10.68 m – 28.78 m), the vertical structure in Salomon was markedly different

323 (Supplementary Figure 2). Pronounced and persistent stratification was evident across the

324 entire transect. In the inner eastern portion of the transect, temperatures were lowest, T<29.4

325 °C, and increased towards the centre the lagoon where a pronounced maximum of T > 29.8 °C

326 occurred in the surface layer of 5 m depth. The S did not replicate the vertical structure,

327 indicating a lateral gradient that was strongest, O (0.05 km^{-1}), towards the western inner portion

328   of the transect, but decreased such that the S in the central lagoon was approximately

329   homogenous with S~34.3 compared to 34.5 in the west. In the centre of the lagoon, closest to

330   the entrance in the north, there was no evidence of deep, cold water exchange with the open

331   ocean.

332   Similarly to Diego Garcia, DO was minimum where the stratification was strongest. In this

333   case towards the beginning of the transect, where $N^2 > 10^{-3.5}$ s^{-2}, and DO <4.4 mg l^{-1}.

334   Stratification was elevated in a near surface layer, in the outer region, that is consistent with

335   insolation effects, i.e. the generation of a diurnal thermocline, but also near the bed in a layer

336   of 5 m thickness, that deepens from 10 m depth at the outer extent of the transect to 20 m

337   towards the centre of the lagoon. Chlorophyll-α was low, at <0.3 mg l^{-1}, in the inner portion of

338   the lagoon but increased substantially to >1 mg l^{-1} near the bed in the centre of the lagoon. This

339   is directly beneath a localised near surface region of elevated DO, but adjacent to the near bed

340   minimum in DO.

341

342   3.2.3 Egmont

343

344   The CTD transect starting in the southeast of Egmont had a depth range of 4.99 m – 21.57 m

345   (Supplementary Figure 3) and exhibited highest salinity, S~34.26, near to the land (furthest

346   from the entrance). The transect beginning in the southwest (9.15 m – 24.34 m depth range)

347   (Supplementary Figure 4) indicated minimum salinities in the innermost stations, S~34.18,

348   increasing vertically downwards to 34.28 at the bed towards the centre of the lagoon but with

349   little lateral variability. As S increased with depth, so did chl-α to a maximum concentration of

350   0.7 mg l^{-1} at 15 m depth. In comparison, chl-α in the southwest transect reached 1.2 mg l^{-1} in

351   inner stations. S and chl-α appear to therefore be positively correlated, with higher S suggesting

352 higher chl-α concentrations. As T did not necessarily follow S (Figure 3), due to insolation

353 effects that vary on short timescales of hours, the chl-α appears to be related to the incursion

354 of oceanic water from outside the atolls.

355

356 In outer Egmont, temperature exhibits a general increasing trend during deployment, with

357 occasional, abrupt decreases in temperature, demonstrated by the CTD time series, suggest the

358 intrusion of colder water into the outer lagoon as pulses, such as at t = 132.02 (Figure 3).

359

360 3.2.4 Peros Banhos

361

362 The maximum water depth in Peros Banhos was not reached by the plankton net or the maestro

363 CTD as there were concerns that the kit may become entangled and lost. The maximum water

364 depth reached in Peros Banhos was 7.09 m – 37.95 m. The Peros Banhos transect began at the

365 northern edge of the lagoon near to an open channel that was not the primary channel. It was

366 the most sheltered part of this lagoon, howeverpenetration of cold, saline water through this

367 channel into the lagoon was detected (Supplementary Figure 5). Temperature <29.2°C and S

368 >34.5 at depths of >30 m in the inner extent of the transect were markedly different from the

369 overlying water properties. Near surface stratification (N^2 >$10^{-3.5}$ s^{-2}) was consistent with

370 diurnal heating, particularly given the timing of the transect during the afternoon, but the high

371 density of the near-bed intrusion also generated a strong density interface at a depth of 30 m,

372 across which N^2 ~10^{-3} s^{-2}. The water of apparent oceanic origin exhibited high levels of chl-α,

373 >1.5 mg l^{-1}, and low DO ~4.0 mg l^{-1}. The concentrations of chl-α in the near-bed layer were

374 the highest observed within all of the lagoons. The persistent stratification throughout the water

375 column, but especially at the top of the near-bed chlorophyll-rich layer, would have prevented

376 the diffusion of chl-α vertically to the overlying water.

378   CTD time series (Figure 3) demonstrated high frequency fluctuations in temperature

379   throughout the tidal cycle. A pronounced decrease in temperature at t = 137.21, contribute to

380   our hypothesis that the lagoons we studied may be subject to intermittent inundations at depth

381   of cold, oceanic water. There is a lack of clear tidal periodicity associated with these

382   temperature time series, although we note that a weak tidal signal may be obscured by lower

383   frequency variability over a given 12 hour period. Longer time series should be undertaken to

384   evidence tidal influence.

3.3 Number of taxa and abundance

389   The plankton samples contained 30 taxa (holoplankton = 17 & meroplankton =13) and 19,539

390   individuals (Figure 5, Supplementary Table 3). Frequently observed holoplankton included

391   crustaceans such as calanoid copepods >2mm (Figure 5a),chordates such as appendicularians

392   (Figure 5b), radiolarians such as acantharians, chaetognaths (Figure 5c) and calanoid copepods

393   <2mm (Figure 5d). Common meroplankton included crustaceans such as decapod larvae

394   (Figure 5e) and molluscs such as gastropod larvae (Figure 5f). Fairly large fish larvae (~4mm)

395   were also encountered (Fig 5g) and annelids such as polychaete larvae (Fig 5h).

397   The following data are presented as mean ± SE. Number of taxa were not statistically different

398   between atolls or between inner and outer regions (Supplementary Table 4). However, the

399   abundance was significantly different between atolls and inner (In) and outer (Out) regions

400   (Atoll: $P = 0.001$, $Pseudo\text{-}F = 0.87$; Exposure: $P = 0.01$, $Pseudo\text{-}F = 4.36$, Supplementary

401 Table 4). Abundance was consistently higher within inner regions across all atolls, excluding

402 southeast Egmont (Figure 6). The greatest abundance occurred within inner stations in

403 southwest Egmont (In= 2636 ± 1434.08, Out= 185.50 ± 26.80, Supplementary Table 3).

404 Additionally, southwest Egmont had the largest difference between exposure regions (2450.50

405 individuals), driven by an extremely high abundance of gastropod larvae within the inner

406 stations. Diego Garcia possessed the next greatest mean abundance (In=458.57 ± 83.29,

407 Out=322 ± 60.28), followed by southeast Egmont (In =150 ± 20.42, Out= 359.33 ± 194.01),

408 Peros Banhos (In= 242.67 ± 49.65, Out= 87 ± 36.67), and Salomon (In= 141.25 ± 45.94, Out=

409 117 ± 47.62).

410

411 3.4 Zooplankton assemblage structure

412

413 The assemblage composition was significantly different between atolls (*P*= 0.0001, *Pseudo-*

414 *F*= 6.39, Supplementary Table 4) and between inner and outer stations (*P*= 0.005, *Pseudo-F*=

415 2.94). The interaction between atoll and exposure was also significantly different (*P*= 0.0002,

416 *Pseudo-F*= 2.29). The two atolls in the north, Peros Banhos and Saloman were most similar to

417 each other, Diego Garcia is the most isolated atoll of the group and was significantly different

418 to the other three atolls, as was Egmont SW, however Egmont SE was similar to assemblages

419 in Peros Banhos inner and outer regions, but only the outer region for Salomon with a

420 significantly different assemblage to the inner region (Supplementary Table 4). Overall, the

421 assemblage compositions within inner stations were more dispersed than those in outer stations

422 (MVDISP: Inner= 1.06, Outer= 0.92, Figure 7).

423

424   Of the holoplankton, calanoid copepods <2 mm comprised *Acartia spp., Acrocalanus spp.,*

425   *Bestolina spp., Calanidae* (Juvenile)*, Calanopia spp., Calanopia spp.* (Juvenile)*, Calocalanus*

426   *pavo, Candacia catula, Candacia spp., Candacia spp.* (Juvenile)*, Canthocalanus spp.,*

427   *Centropages furcatus, Centropages orsinii, Centropages spp., Clausocalanus spp.,*

428   *Cosmocalanus darwinii, Labidocera laevidentata, Labidocera spp., Paracalanidae* (Juvenile),

429   *Paracalanus spp., Tortanus spp.* Calanoid copepods >2 mm included *Calanopia spp.,*

430   *Labidocera spp., Labidocera stylifera, Labidocera styliferi/koryeri, Nannocalanus spp.,*

431   *Paraeuchaeta spp., Subeucalanus spp., Tortanus spp., Undinula spp.* Poecilostomatoid

432   copepods <2 mm included *Corycaeus spp., Farranula spp., Oncaeidae.* Cyclopoid copepods

433   <2 mm were represented by *Oithona spp.* The singular Monstrilloid copepod <2 mm was

434   *Monstrilla sp.*

435   Calanoid copepods <2 mm were the most dissimilar group between inner and outer regions

436   (3.87 mean dissimilarity ± 1.25). They were most common to inner regions (In=3.57, Out=3.05,

437   Figure 8, Supplementary Table 3). This trend was consistent among all atolls, except southeast

438   Egmont which supported a higher abundance at outer stations. Additionally, within Egmont

439   atoll, a calanoid copepod (<2 mm) from the family Tortanidae was observed and is believed to

440   be a species that is not yet described. Calanoid copepods >2mm were more abundant within

441   outer regions (In=1.09, Out=1.22). This was also true for Salomon, southeast Egmont and Peros

442   Banhos. Within southwest Egmont, they were uniformly abundant, though within Diego Garcia

443   they were present at greater abundance within inner stations. Similarly, chaetognaths relatively

444   dissimilar between regions (3.37 mean dissimilarity ± 1.19) and typically occurred more

445   frequently within outer stations (In= 1.8, Out= 1.85). This was reflected in all atolls except

446   Peros Banhos. Contrary to this, appendicularians were more common at inner regions (In= 1.2,

447   Out= 0.92). This occurrence was mirrored across all atolls barring southwest Egmont and

448   within Peros Banhos where they were only present in the inner region of the atoll.

450 Of the meroplankton, gastropod larvae were the most dissimilar (4.26 mean dissimilarity ±

451 0.91) and dominated inner regions (In= 1.91, Out= 1.17). This pattern was consistent in Diego

452 Garcia and southwest Egmont, and Peros Banhos, where gastropod larvae were only present

453 within inner stations. However, within Salomon and southeast Egmont more individuals were

454 found within outer stations. Decapod larvae were the second most dissimilar meroplankton

455 group (2.23 mean dissimilarity ± 1.01) and were present at greater abundance within inner

456 stations (In= 2.11, Out= 1.7) and this was consistent across atolls, except Diego Garcia.

457 Polychaete larvae, however, were encountered more often within outer regions (In=0.1,

458 Out=0.45). This was detected within Salomon and across southwest Egmont, and Peros Banhos

459 wherein polychaete larvae only occurred within the outer region of the atoll. Polychaete larvae

460 were not observed within Diego Garcia or southeast Egmont. There were no obvious trends in

461 fish larval abundance across BIOT. Fish larvae were observed only within Diego Garcia, the

462 outer region of Southwest Egmont and the inner region of Peros Banhos; abundance was

463 consistently low.

464

4. Discussion

467 Diego Garcia, Salomon, Egmont and Peros Banhos all shared similar intertidal beach habitats

468 characterised by course sands with low organic content. Subtidally, the extent of bleaching was

469 the most consistent and extensive feature. Diego Garcia was dominated by bleached bombies

470 and sandy mounts, Egmont and Peros Banhos were characterized by bleached massive and

471 degrading corals, whereas Salomon still supported live corals as a dominant habitat type.

472 Despite bleaching effects, reef fishes were still observed in all atolls.

473   Zooplankton assemblages comprised different compositions depending on whether they were

474 in the inner or outer atoll regions. Assemblages also varied between the atolls that were located

475 furthest apart (Diego Garcia to all other atolls), and were more similar between atolls that were

476 closer (Peros Banhos and Salomon). Overall, in the outer regions of BIOT atolls, planktonic

477 assemblages were more similar between atolls, than inner station assemblages between atolls;

478 which were more diverse. The water property and the plankton data support the hypothesis that

479 atolls have regional differences which is likely to be the result of increased isolation of inner

480 stations from oceanic exposure relative to outer regions. Shorter water residence time and

481 frequent flushing with increasing proximity to channels within these outer regions, likely

482 selects for community similarities by facilitating planktonic transport both in and out of the

483 atolls. These exchanges are known to not only modify the composition of the planktonic

484 community but also the abundance (Hamner et al., 2007;Pagano et al., 2017). Evidence

485 suggesting the flushing of oceanic water was observed within outer regions of Diego Garcia,

486 Peros Banhos and Egmont; typically demonstrated by cold, saline and dense water. However,

487 a longer time series is required to conclusively demonstrate tidal forcing of this water through

488 deep water channels. Tidal forcing through atoll channels has been documented (Green et al.,

489 2018) and the pumping of cold water from depth demonstrated within canyons (Walter et al.,

490 2012;Walter and Phelan, 2016) and to shallow coral reefs, driven by tidal bores (Leichter et

491 al., 1996;Woodson, 2018). Given the density and low temperatures of these oceanic intrusions,

492 deeper within the water column, it is clear that this flushing could not have originated from

493 surface flow over the shallow reefs that surround some atolls. No evidence of oceanic flushing

494 was found within outer stations in Salomon atoll, which was the only atoll where live coral was

495 observed as a dominant habitat type. This may be a result of the tidal phase at the time of

21

496   sampling, which may have been conducive for the flushing out of oceanic water and/or oceanic

497   exchange may be occurring in a location not represented within the transect. Further detail on

498   water properties within Chagos atolls, specifically temperature, can be found in (Sheppard et

499   al., 2017).

500

501   Abundance of plankton was shown to be consistently lower within outer regions, except

502   southeast Egmont. Transport of plankton through channels adjacent to the coral reef may

503   account for this reduction, as lower abundance of zooplankton following passage over the coral

504   rim of atolls is well documented and has been linked to ingestion by the reef (Fabricius and

505   Metzner, 2004;Wyatt et al., 2010) and planktivorous fish (Achuthankutty et al., 1989;Hamner

506   et al., 2007). Increased surface temperatures and chlorophyll within some of the inner regions

507   may also be driving the distinctions between inner and outer assemblages (Carassou et al.,

508   2010).

509

510   The greater abundance of zooplankton present within outer stations in southeast Egmont is

511   intriguing. Although not formally tested in this study, internal waves could perhaps account for

512   this pattern as they are known to influence planktonic distributions (Shanks, 1983;Lennert-

513   Cody and Franks, 1999) and have been observed in the BIOT (Hosegood et al., 2019).

514   Turbulence associated with internal waves (Moum et al., 1992) may increase predator-prey

515   contact rates and have an overall positive effect on plankton feeding rates (Kiørboe, 1997;Saiz

516   et al., 2003), thus altering the structure of planktonic assemblages. In addition, variability in

517   oceanographic parameters believed important to planktonic distributions, such as temperature,

518   salinity, water velocity and chlorophyll, may be associated with internal bores created by

519   breaking internal waves (Leichter et al., 1996).

520

521 Egmont atoll was also distinctive due to the greatest difference between number of taxa in inner

522 and outer stations, on the south-westerly transect. The remarkable abundance of zooplankton

523 within the inner stations is represented mostly by an extreme abundance of gastropod larvae.

524 Abundance of gastropod larvae has previously been positively related to solar radiation

525 duration (Carassou et al., 2010); given the insolation effects evident within Egmont atoll it is

526 possible that this might be influencing their abundance and distribution. Alternatively, the

527 sampling may have captured a spawning event. This increased occurrence of gastropod larvae

528 in inner regions is replicated across most atolls with other meroplankton, such as decapod

529 larvae, also common to these areas. Increased occurrence of meroplankton within atolls is

530 commonly documented (Gerber, 1981;Achuthankutty et al., 1989;Pagano et al., 2017) and

531 specifically within the Chagos Archipelago, greater availability and longer residence of larvae

532 has been linked to the weaker currents within lagoons (Riegl et al., 2012). Therefore, the co-

533 occurrence of increased zooplanktonic biomass within these areas perhaps suggests the

534 importance of these inner, less exposed areas as nursery grounds for larval species.

535

536 Although oceanographic processes are known drivers of zooplankton distribution and

537 abundance (Kiørboe, 1997;Huggett, 2014;Lamont et al., 2014) and interactions within this

538 study are evident, it is possible that behavioural responses and life history traits may also play

539 a role, particularly for copepods; a major contribution to the zooplanktonic taxa in this study.

540 Copepods have been observed to maintain position by active movements against the flow,

541 migrating down to low current regions and attaching to substrate (Genin et al., 2005;Shang et

542 al., 2008). As such their retention within lagoons has been observed. Of the copepods, calanoids

543 <2 mm were more commonly found within inner regions, and the opposite was true for those

544   greater than 2 mm. Larger and oceanic copepods are likely present in higher densities at outer

545   stations due to the inward flushing of ocean currents. The lower numbers observed within inner

546   stations could also indicate higher predation rates, as it has been suggested that larger-sized

547   individuals are actively-selected by predators (Suchman and Sullivan, 2000;van Deurs et al.,

548   2014). The dominance of smaller copepods in inner regions of atolls, could therefore suggest

549   a size-based predation refuge. Additionally, these regions are likely to experience greater

550   fluctuations in water properties, due to lack of interaction with regulatory, stable water bodies.

551   The dominating presence of calanoids <2 mm, mostly represented by Acartia spp. and

552   Centropages spp., in these areas could be indicative of this. Species of these genera produce

553   resting eggs, which allow the persistence of copepod taxa when environmental conditions

554   become unfavourable for growth and reproduction (Guerrero and Rodriguez, 1998)**.** Greater

555   retention of eggs within areas of reduced flushing could account for the increased abundance

556   observed.

557

558   The variability in zooplankton distribution and assemblage composition within atolls, with

559   respect to oceanic exposure, demonstrates that past studies detailing broad comparisons

560   between oceanic and lagoon areas may underestimate differences, if samples are only taken in

561   the outer regions of atolls. Interactions with the water properties in these systems is clearly

562   complex and requires more extensive studies to identify and determine how deep water flushing

563   influences planktonic communities as they are transported both in and out of atolls. If a

564   predictable planktonic zonation exists within these systems, comprehension of such ecological

565   patterns is imperative for an indication of ecosystem health and functioning, particularly when

566   such patterns are likely to be disrupted in the near future by global anthropogenic pressures

567   such as climate change (Beaugrand, 2003). This is particularly concerning given the

568   importance of zooplankton to ecosystem functioning (Hébert et al., 2017). Given the

569 widespread bleaching evident in this study, both from past and recent bleaching events, such

570 changes are likely already at work. BIOT atolls are clearly not exempt from global issues such

571 as climate change, and the high degree of localised protection does not change that. However,

572 irrespective of such bleaching, the diversity and abundance of holoplankton and reef-associated

573 fauna in the meroplankton in the region demonstrates that these atolls are dynamic and

574 potentially resilient systems (Sheppard et al., 2012), and as such are important to preserve.

575

576 Continued monitoring of relatively pristine sites such as the Chagos archipelago presents an

577 invaluable opportunity to assess near-natural ecosystem functioning within coral atolls, provide

578 ecological baselines and demonstrate best-case scenarios for impacts of climate change to reef

579 systems. However, the lack of ecological and oceanographic data to currently support such

580 investigations is a major hindrance. Further investigation of the spatiotemporal dynamics of

581 these planktonic communities in response to oceanographic processes within BIOT is therefore

582 necessary to continue and sustain management of these habitats, in the midst of such

583 environmental uncertainty world-wide.

584

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585

586

592

Author Contribution Statement

594 ES, PH, MA & JM conceived this research, ES, JM & DT gathered the data, ES, PH, CG &

595 MW analysed the data. All authors wrote the manuscript.

596

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598

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789

790 # Figure legends

791 Figure 1. Map of BIOT with sampled atolls and their primary channels. Transects of plankton

792 and water property profiles are shown, alongside CTD time series, intertidal cores and

793 subtidal video.

794

795 Figure 2. Example CTD transect, of Diego Garcia, indicating changes in temperature (T),

796 salinity (S), density (σ_θ), chlorophyll-α (chl-α), dissolved oxygen saturation (DO), and the

797 Brunt-Vaisala frequency squared (N^2) with depth (m) and horizontal position (km), with

798 depth (m) and horizontal position (km). Black line indicates exposure boundaries, left (inner)

799 & right (outer).

800

801 Figure 3. Temperature time series from Valeport miniCTDs deployed at the entrance to **(A)**

802 Diego Garcia, **(B)** Peros Banhos and **(C)** Egmont lagoons. With the exception of Egmont for

803 which only the deep CTD was recovered, CTDs were located at a depth of approximately 4 m

804 and a height above the bed of 2 m. For each instrument the mean depth throughout the record

805 is indicated.

806 Figure 4. Images of the dominant habitat types **(A)** Bleached coral Bommie on sand in Diego

807 Garcia **(B)** Examples of living coral in Salomon **(C)** Bleached coral encrusted with coralline

808 algae in Peros Banhos **(D)** Broken bleached table coral in Peros Banhos

809

810 Figure 5. Images of zooplankton of interest to this study, holoplankton **(A)** Calanoid Copepod

811 <2mm (Centropages spp. 1.55mm length) **(B)** Appendicularian (2.07mm) **(C)** Chaetognath

812 (6.88 mm) **(D)** Calanoid copepods >2mm (*Labidocera stylifera*, 2.88mm) and meroplankton

813 **(E)** Decapod larvae (~2mm) **(F)** Gastropod larvae (~1mm) **(G)** Fish larvae (~4mm), **(H)**

814 Polychaete larvae (~3.5mm). Images A-G were taken with an Infinity camera mounted to a

815 Zeiss Discovery. V8

816

817 Figure 6. Mean abundance (± SE) at Inner and Outer stations, within each of the four atolls

818

819 Figure 7. Non-metric Multidimensional Scaling Plot of the assemblage composition of

820 zooplankton, between atolls and regions of Inner and Outer stations.

821

822 Figure 8. Mean abundance (± SE) for common taxa and/or taxa of ecological interest, at Inner

823 and Outer stations across all atolls. **(A)** Taxa group 1**, (B)** Taxa group 2, [a] Taxa have been

824 separated into groups for graphical representation,
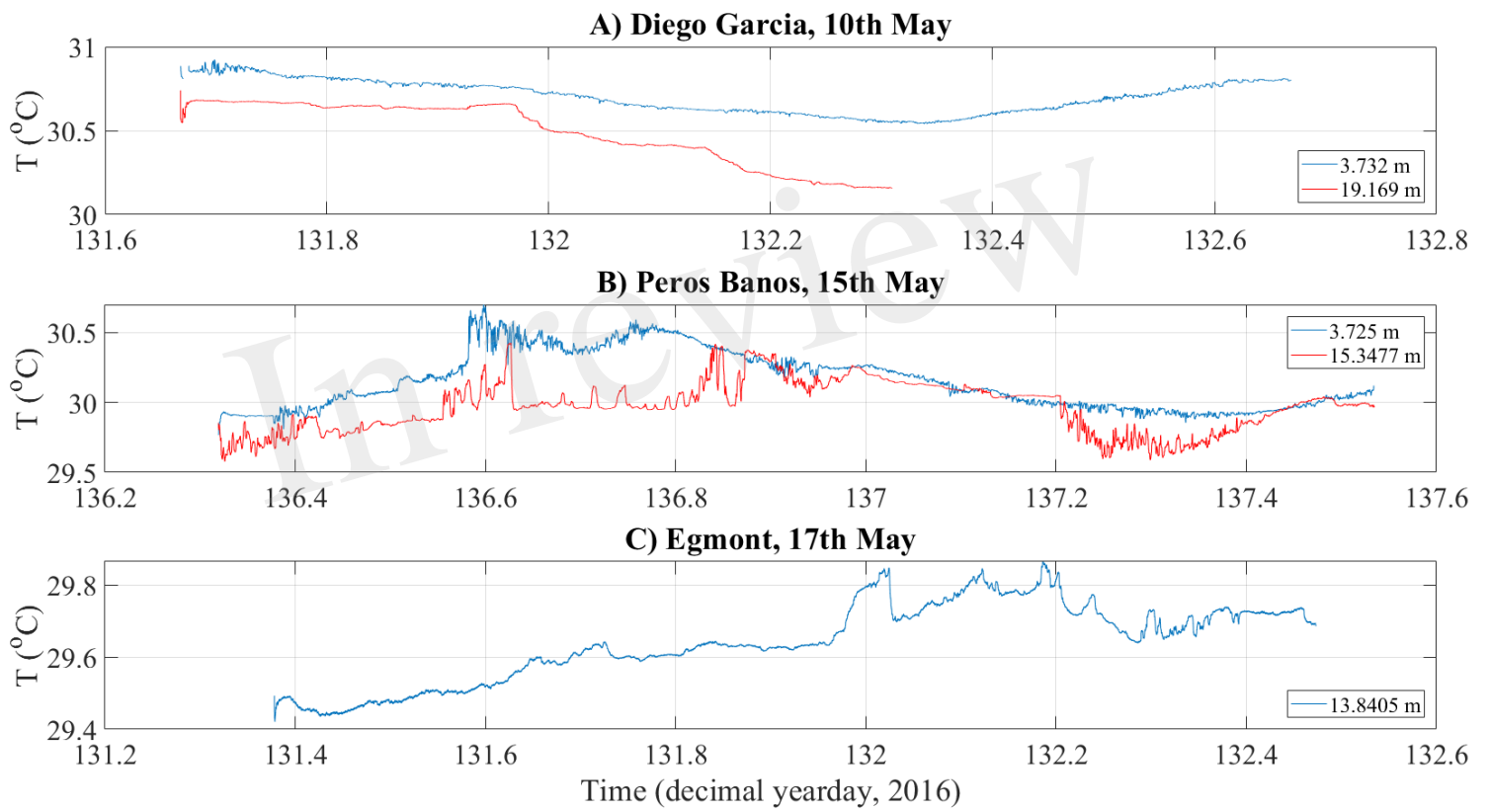
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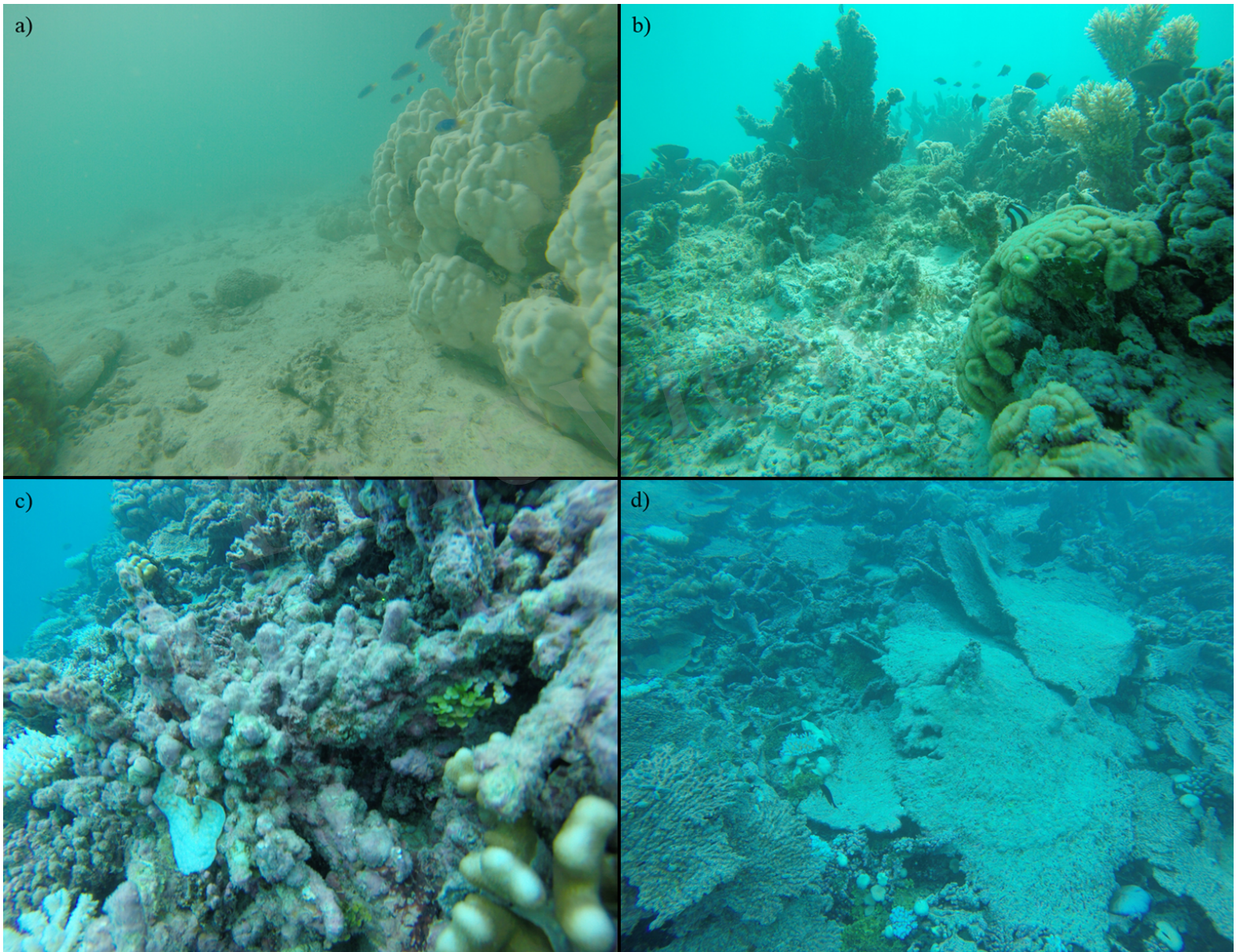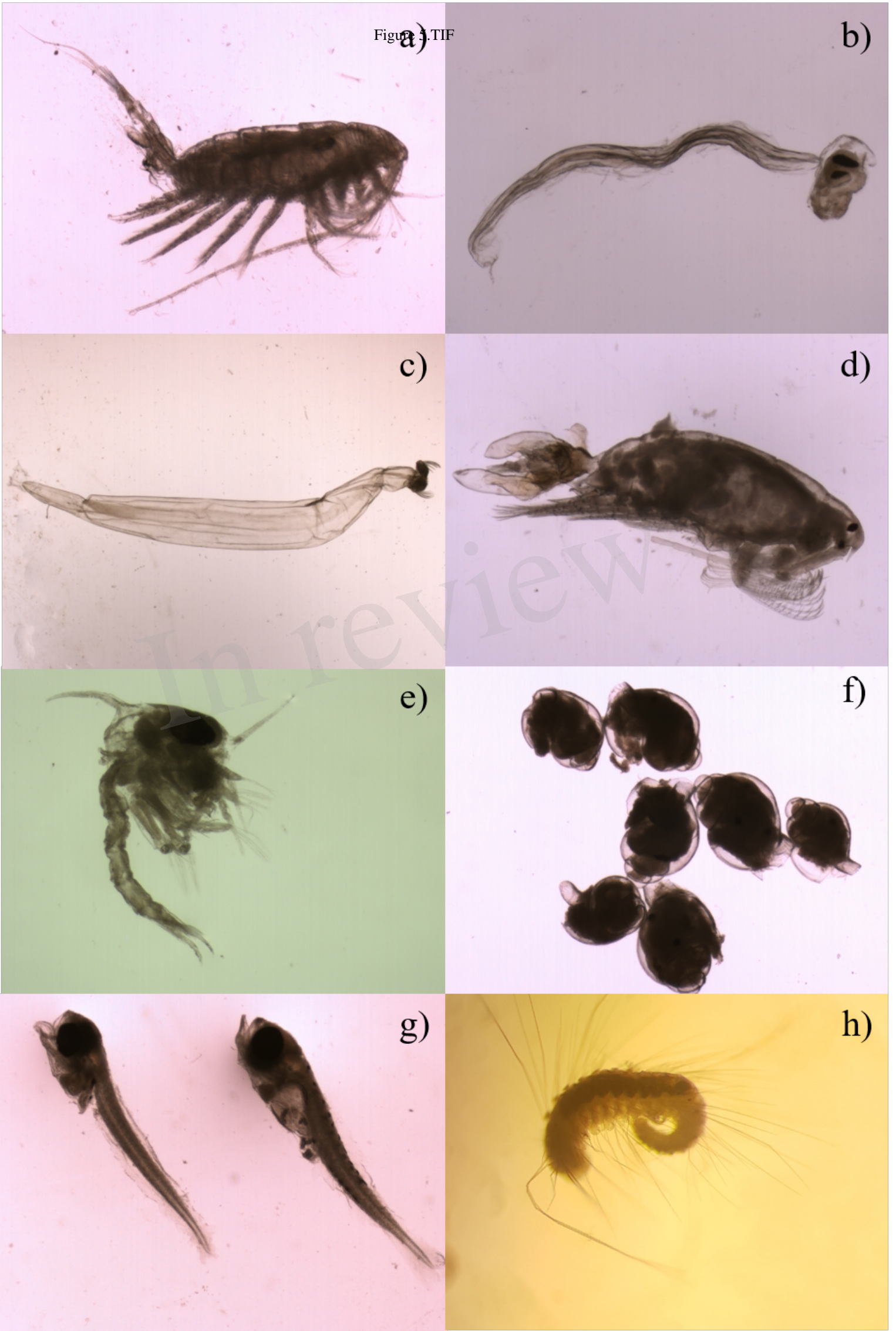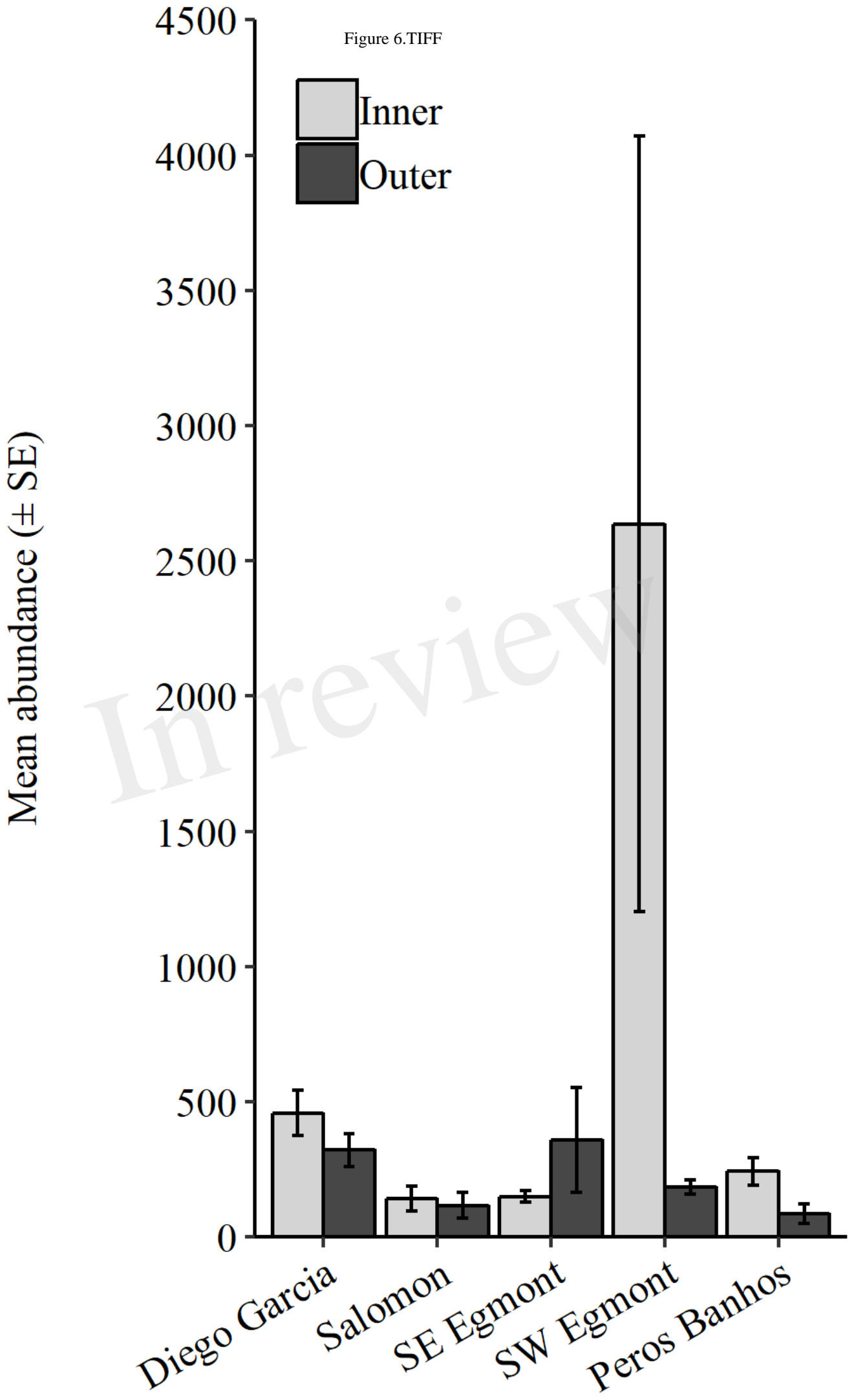826

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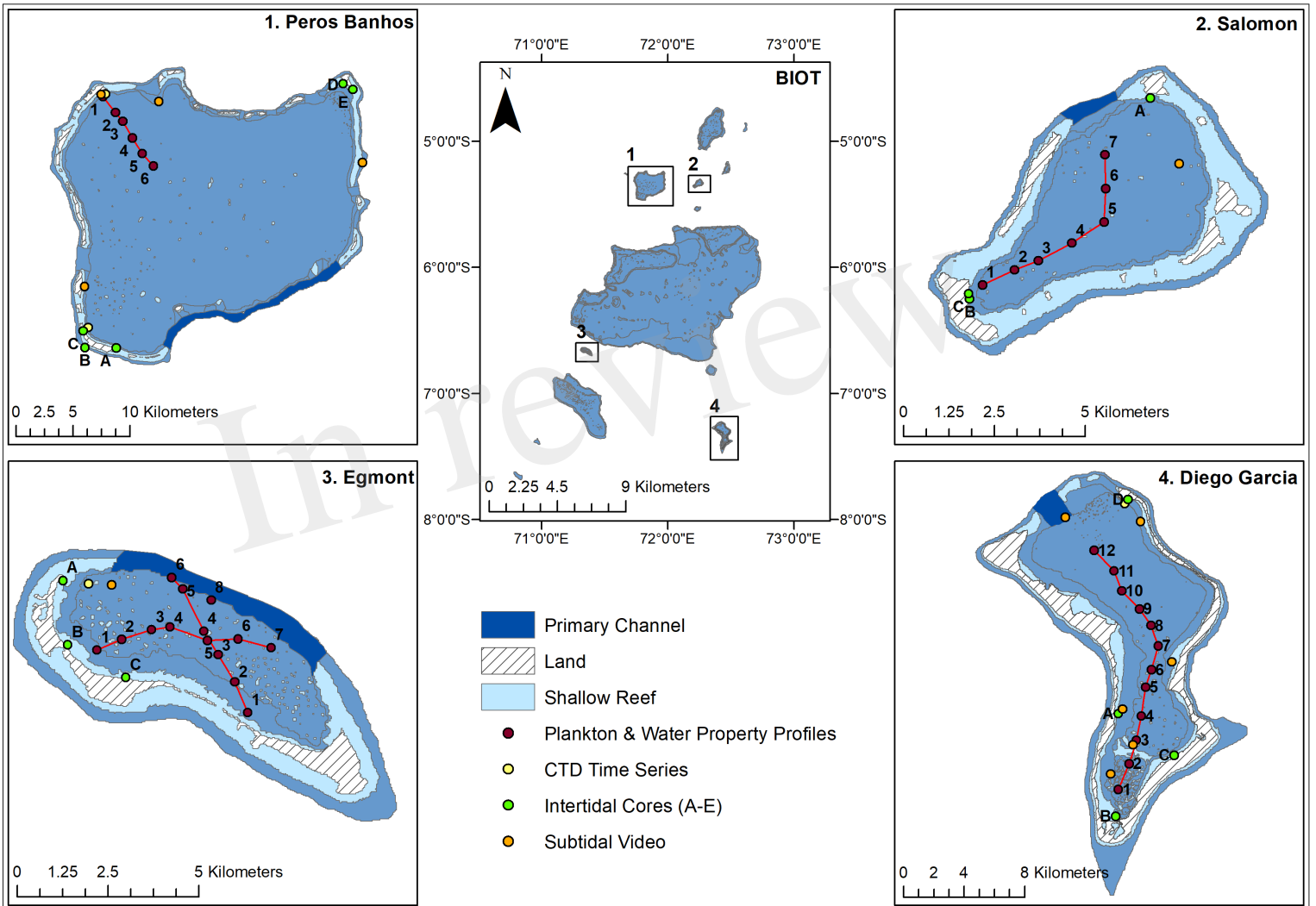
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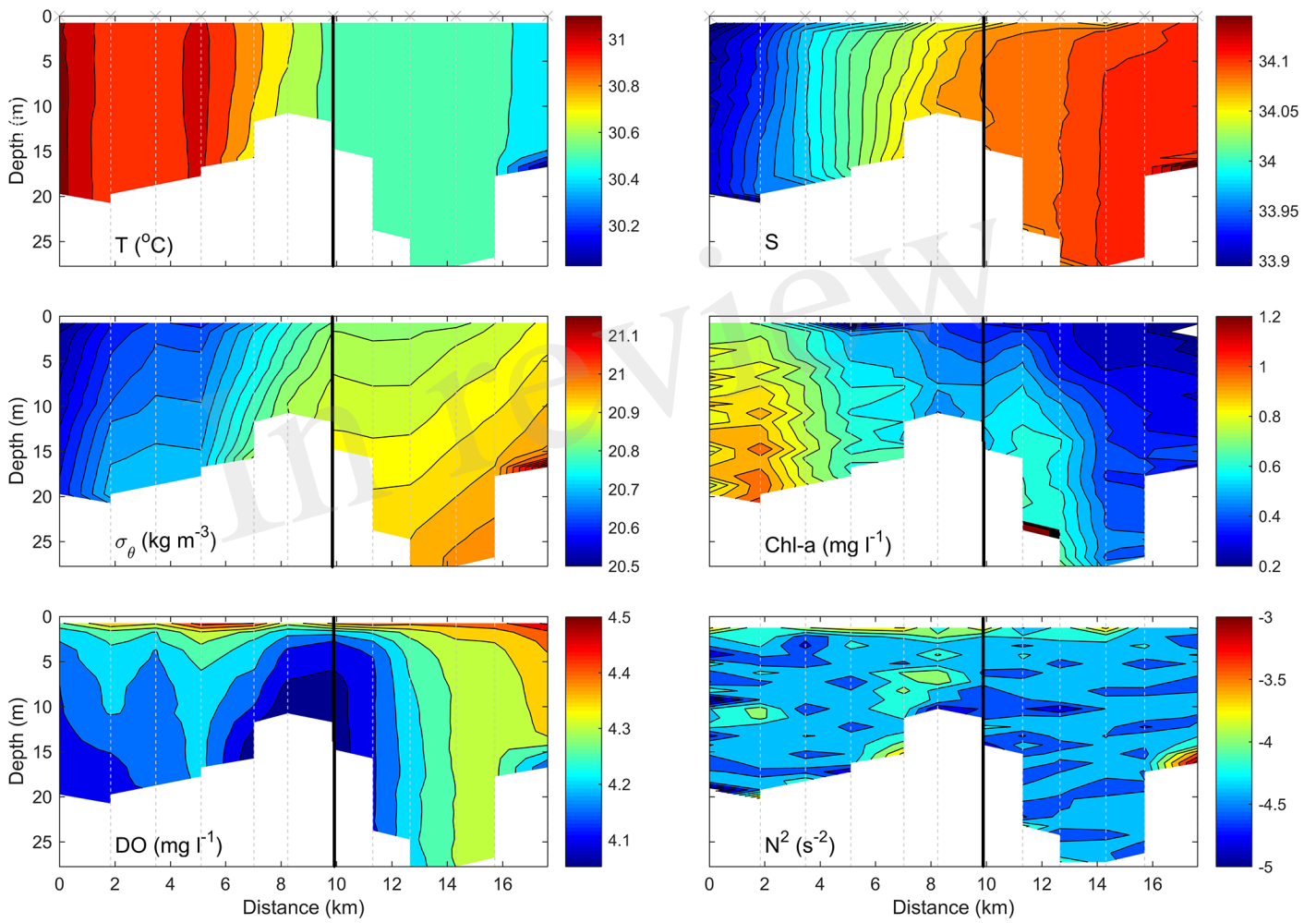
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