Description and assessment of neuston communities present in the South Indian Ocean

By

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Abstract

Animal communities living at the sea-surface are relatively poorly known, despite the fact that this biotope is globally distributed, it acts as an important nursery area for many commercially important taxa and supports significant amounts of anthropogenic waste. This lack of knowledge applies particularly to the Indian Ocean. Here, I describe the structure of non-copepod neuston assemblages across the Southern Indian Ocean Gyre using samples collected between 26 June – 16 July 2015 from 35 stations along a transect line at 20° S. Neuston was sampled using triplicated manta trawls at each station, while environmental parameters were assessed using a CDT. All non-copepod neuston were identified to morphospecies, with the exception of siphonophores, which were identified to species.

At the time of the study, two anticyclonic eddies were present between 75 – 85° E and these were characterised by warmer surface waters, deeper fluorescence maxima and elevated total fluorescence, by comparison with surrounding areas. Salinity was lowest to the east. Assemblages were dominated by Ostracods, though mysids, juvenile chaetognaths, siphonophores and amphipods were also common: the majority of specimens collected were facultative neuston. The greatest number of morphospecies were observed in Amphipoda and Siphonophora. While facultative neuston were more common at night than by day, euneuston showed little diel variation in abundance. Meroplanktonic neuston were more abundant at longitudinal extremes and were uncommon in the centre of the area.

There was a significant spatial pattern to the structure of assemblages, with those in the centre of the transect (between 75 - 85° E) being distinct from those to either the east or west. Samples collected in the far east of the region were different from the balance of samples, which tended to show some rotational symmetry around assemblages at the core. The key environmental factors that were linked to assemblage structure were associated with longitude – salinity, fluorescence and temperature at 200 m, emphasising the interaction between Indonesian Throughflow Water, eddy-related process and settlement of

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49 meroplankton. The study highlights the value of using morphospecies in studies of plankton

50 assemblages.

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53 **Keywords:** Air-sea interphase, biogeography, biological communities, Indian Ocean,

54 neuston, plankton, Subtropical Gyre

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Declaration

I, Yasmeen Parker declare that:

"Description and assessment of neuston communities present in the South Indian Ocean", is my own work, and that:

1. It has not been submitted for any degree or examination at any other university;
2. When data (neuston samples) were not collected by me, the sources were acknowledged;
3. All the literature sources that I have used and quoted have been acknowledged in my reference list.

Full name: Yasmeen Parker

Signature:

Date: 30 November 2021

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5

113   To my near and dear friends, Aarifah Jakoet, Aseeqah Davids and Lyle Wilson, your

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115   amazing. Just sitting and chatting with you, sharing knowledge and life experiences have

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117   wellbeing that comes with having the strong backbone of a friendship that the three of you

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122   and have been inspired and motivated to do the same. Thank you for helping me where you

123   could make things easy since we are expecting our first child and my health was up and down

124   for a while. Last but certainly not least, thank you to my family for their unwavering support

125   and love, this includes my niece and nephews who provide those small bursts of

126   entertainment that gave me the energy to keep pushing on.

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Introduction

The Indian Ocean is the world's third- largest ocean, covering an area of over 68.5 million km^2, and is bounded by land masses on three sides. The Indian Ocean stretches 9 600 km from the Bay of Bengal in the North to Antarctica in the South, and 7 600 km from Africa to Australia (Demopoulos et al. 2003) encompassing seven geographical limits (Figure 1, A-G). The Indian Subtropical Gyre Province (ISSG) extends from the hydrochemical front to the Subtropical Convergence (10-15˚S to approximately 30˚S) (Longhurst 1998).
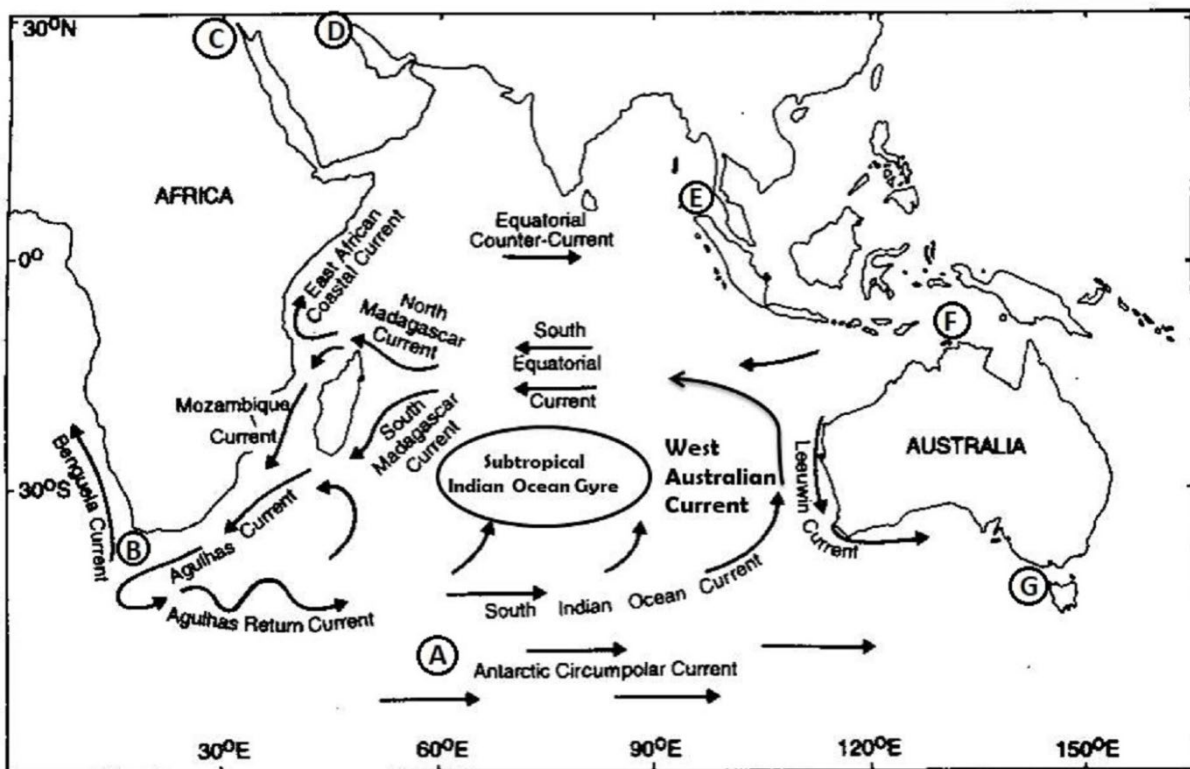
Figure 1: Map of the Subtropical Indian Ocean Gyre showing the currents and the geographical limits of the Indian Ocean. **A**, The northernmost limit of the Southern Ocean at a latitude of 60˚ South ,**B**, the southernmost point of the African continent at Cape Agulhas, **C**, the Suez Canal, **D**, the northernmost regions of the Persian Gulf, **E**, the Strait of Malacca, **F**, from the Singapore Strait to the eastern boundary of the Timor Sea (this includes the Java, Flores and Banda Seas within the archipelagic waters of Indonesia) and, **G**, the west coast of Tasmania (not including the waters of Bass Strait)(Pearce 1993, Allan et al. 1995, O'Loughlin and Luke 2010)

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174 The Indian Ocean region encompasses 36 key nations and supports more than 25%

175 (O'Loughlin and Luke 2010) of the world's ever-increasing population (Hood et al. 2016),

176 while it's nine marine ecosystems house over 35 000 marine species (Colgan 2017). A

177 number of sub regions within the Indian Ocean have previously been recognised as having

178 very high levels of biodiversity (Colgan 2017). This biodiversity is threatened by a number of

179 factors including global warming and ocean acidification (Hood et al. 2016), as well as more

180 immediate pressures associated with the increasing human populations in the bordering states

181 (Hood et al. 2016). It is due to these stressors that understanding and predicting the changes

182 in the Indian Ocean have become imperative within recent years (Hood et al. 2016).

183 The Indian Ocean was identified as one of the least studied ocean basins by the Scientific

184 Committee on Ocean Research (SCOR) and the Intergovernmental Oceanographic

185 Commission (IOC) in the middle part of the twentieth century (Hood et al. 2016). As a

186 consequence, these bodies motivated for the International Indian Ocean Expedition (IIOE),

187 which ran from 1960 until 1965 (Hood et al. 2016). It was argued that human societies in this

188 region would benefit from studies aimed at understanding the annual monsoon cycle and its

189 wider effects on the Indian Ocean fisheries and weather (Hood et al. 2016).

190 The outputs from the IIOE included advancements on understanding monsoon variability and

191 dynamics, the emergence of the first description of complex surface ocean circulation in

192 response to monsoon forcing and a more detailed understanding of the complex topography

193 of the Indian Ocean Basin. Other outputs include a comprehensive hydrographic atlas of the

194 Indian Ocean basin (Wyrtki 1971, Schott and McCreary 2001) and the first survey of

195 monsoon circulation in the Somali Current (Swallow and Bruce 1996, Schott and McCreary

196 2001). A number of studies have been conducted on the Somali, Agulhas and Leeuwin

197 Currents (Stramma and Lutjeharms 1997), and these have served to improve our

198 understanding of the oceanography in the boundary regions of the Southern Indian Ocean.

199 However, our understanding of the dynamic processes such as the wind-driven, anticyclonic

200 circulation of the Southern Indian Ocean, which is significantly different to that of the South

201 Atlantic Ocean, remains weak (Peterson and Stramma 1991, Stramma and Lutjeharms 1997).

202 Since their first expedition to Somalia in 1975, the Norwegian research vessel *Dr Fridtjof*

203 *Nansen* has undertaken 40 surveys in the Western Indian Ocean, with the history of the

204 surveys being reviewed by Groeneveld and Koranteng (2017). The Western Indian Ocean is

205 dominated by two western boundary currents, the Agulhas to the south and the Somali to the

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206 north (Groeneveld and Koranteng 2017). The Western Indian Ocean consists of dynamic

207 ocean currents and upwelling cells that regulate the climate and influence the weather

208 patterns, sea temperature, water chemistry, productivity, biodiversity and fisheries

209 (Groeneveld and Koranteng 2017). Mesoscale eddies also influence biological production by

210 interacting with the continental slope on the western side of the Mozambique Channel which

211 causes the upwelling of cooler, nutrient-rich, waters. (Ternon et al. 2014; Lamont et al. 2014;

212 Hugget and Kyewalyanga 2017).

213 Global winds driven by latitudinal pressure gradients, transfer energy to surface waters to

214 create shallow currents which, under the influence of the Coriolis force and through

215 interactions with continental land masses, form gyres in the central ocean basins north and

216 south of the equator (Mann and Lazier 2006). Those of the subtropics circulate in an

217 anticyclonic motion, while those in boreal subpolar regions rotate in a cyclonic motion: there

218 are no clear subpolar gyres in the Southern Hemisphere.

219 Subtropical gyres transport large quantities of heat away from the equator in western

220 boundary currents. These currents meander and cut off large gyrating bodies of water forming

221 cold and warm-core rings. Since the oceanic waters of anticyclonic gyres are permanently

222 stratified, the surface waters tend to have low average levels of nutrients (Mann and Lazier

223 2006). It was previously assumed that the subtropical gyres were areas of low productivity

224 but the currents along with the rings have unique properties which are used by different

225 organisms for breeding and migration to higher productivity sites in the temperate latitudes

226 (Mann and Lazier 2006). The productivity of subtropical gyres is greatly increased by the

227 presence of eddies and Ekman transport from peripheral gyres (Mann and Lazier 2006). Due

228 to the seasonal influence of monsoon winds over the Indian Ocean the circulation of the

229 Southern Indian Gyre is more variable than the Pacific and Atlantic subtropical Gyres

230 (Longhurst 1998).

231 Surface water circulation in the southern Indian Ocean is dominated by the Subtropical

232 Anticyclonic Gyre (Demopolous et al. 2003, Sultan et al. 2007). The gyre is largely located

233 on the western half of the Indian Ocean (Demopolous et al. 2003, Sultan et al. 2007), with the

234 eastern part being blocked by the South East Indian Ocean Ridge (Rogers et al. 2009). The

235 western boundary of the gyre is associated with a strong southward transport of water

236 associated with the Agulhas Current (Rogers et al. 2009). There is no gyre in the northern

237 Indian Ocean owing the position of the Asian continental landmass, but winds there blow

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238 from the northeast from November to February (winter monsoon) and from the southeast

239 from May to September (summer monsoon) (Shankar et al. 2002). A transition period with

240 weak winds occurs between March to April and October (Shankar et al. 2002). A seasonally

241 reversing circulation in the upper north Indian Ocean is caused by the strong winds

242 experienced during the summer monsoon (Shankar et al. 2002).

243 In response to the lack of knowledge about the Southern Indian Ocean Gyre, a series of

244 surveys were undertaken from 2015 through to 2020 across the southern part of the Indian

245 Ocean in support of the IIOE-2. The first survey began in 2015 on-board the *Dr Fridtjof*

246 *Nansen*. The survey, in preparation for the 2nd International Indian Ocean Expedition (IIOE-

247 2), hosted scientists and technicians from six Western Indian Ocean countries. The first leg of

248 the survey, which collected data on the Southern Indian Ocean Gyre, began in Jakarta,

249 Indonesia, and ended in Port Louis, Mauritius (Groeneveld and Koranteng 2017). Preliminary

250 results from the survey regarding the anticyclonic circulation of the southern Indian Ocean

251 (Subtropical Indian Ocean Gyre) indicated that the gyre consisted of a number of smaller

252 eddies which impacted the flow regime and productivity within the gyre (Toresen et al.

253 2015). The preliminary results suggest that there was an increase in surface chlorophyll

254 within these eddies but the processes driving this are unknown (Toresen et al. 2015). The

255 anticyclonic circulation yielded low biological production within the gyre, but relatively

256 higher biological production away from the centre and towards the edges of the gyre

257 (Groeneveld and Koranteng 2017). Dufois et al. (2017) later hypothesized several processes

258 responsible for enhancing surface chlorophyll in the eddies in the South Indian Ocean.

259 The majority of the previous studies done on zooplankton communities across oceans have

260 been of a latitudinal rather than a longitudinal nature (e.g. McGowan and Walker 1979, 1985,

261 de Puelles et al. 2019) and have tended to focus on the change in community structure with

262 depth rather than with longitude. de Puelles et al. (2019) showed that the abundance of

263 zooplankton decreased with depth in the subtropical and tropical latitudes across the Atlantic,

264 Pacific and Indian Oceans. This decrease in abundance was noted in all oceans where the

265 influence of the surface layer is known to extend over 400 m with high zooplankton

266 abundance values found close to upwelling areas. de Puelles et al. (2019) concluded that

267 depth rather than oceans or biogeographical provinces was the primary factor structuring the

268 habitat and communities of zooplankton. McGowan and Walker (1979), in their study of the

269 structure of the copepod community of the North Pacific Central Gyre, showed that the only

270 group of species with a clear, general, seasonality of abundance was the most shallow-living

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271 group and that members of this group live in a zone of strong temperature seasonality but
272 with no apparent seasonal change in primary production.

273 Previous studies done on the abundance and diversity of zooplankton in the Central South
274 Pacific Gyre (González et al. 2019) and the South Atlantic Gyre (Piontkovski et al. 2003)
275 have shown that the zooplankton biomass decreased towards the centre of both (Piontkovski
276 et al. 2003, González et al. 2019). The results from González et al. (2019) showed that there
277 was a significant segregation of the zooplankton communities divided into four zones
278 (eutrophic, mesotrophic, oligotrophic and the ultra-oligotrophic) with the gyre being the
279 ultra-oligotrophic zone.

280 Within the Southern Indian Ocean Gyre, mesopelagic fish densities were low but tended to
281 follow biological production. The highest density of plastics or micro-plastics was collected
282 along the gyre's edges and the majority of plastics were derived from the eastern edge.
283 Plastics were present in the majority of the water samples (Groeneveld and Koranteng 2017).
284 The presence of plastics within the Indian Ocean, in particular the ocean surface, sea-air
285 interface, threatens the existence of many marine organisms, in particular neustonic
286 zooplankton (zooneuston) living at/on the surface of the ocean.

287 Zooplankton are animals that "float" in the water column. They are the primary consumers of
288 the oceans and comprise many different animal groups such as crustaceans, molluscs,
289 cnidarians, and even fish in larval form. Zooplankton occur in a variety of sizes, from tiny,
290 microscopic ciliates to enormous jellyfish (Naumann 1917, Collard et al. 2015).
291 Holoplankton are zooplankton which remain on the surface of the ocean throughout their
292 lifecycle and comprise mostly of floating and rafting animals (e.g. Hydrozoa, Siphonophorae,
293 Gastropoda, Copepoda, Ostracoda, Euphausiacea, Chaetognatha) whereas meroplankton are
294 the zooplankton which comprise of individuals which have life stages at both the surface and
295 benthos of the ocean (e.g. Stomatopoda, Decapoda, fish larvae and fish eggs) (Santos et al.
296 2019). Zooneuston, hereafter simply referred to as neuston, are those animals that inhabit the
297 sea-air interface whereas zooplankton inhabit the subsurface layer (Naumann 1971, Collard et
298 al. 2015). The surface layer is a very important niche area for feeding and breeding of fish; in
299 particular commercially valuable fish species (Cardinale et al. 2003, Pusineri et al. 2005,
300 Collard et al. 2015).

301 As already noted, neuston comprises a variety of animals such as crustaceans (copepods,
302 mysids, euphausids, amphipods, isopods, Ostracods and Decapod larvae), fish larvae,

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303 polychaetes and their larvae, a wide variety of molluscs and their larvae, cnidarians

304 (hydromedusae, siphonophores and scyphozoans), insects (water striders), protostomes

305 (chaetognaths) and tunicates (salps, doliolids and appendicularians) (Marshall and Burchardt

306 2005). Due to their position at the sea-air interface, neuston are exposed to many

307 environmental and oceanographic stressors including high light intensity, wind stress,

308 turbulence and high (and low) temperatures, as well as high levels of predation from above

309 and below (Collard et al. 2015, Olivar et al. 2015). Most neustonic species have evolved

310 morphological and/or ecophysiological adaptations to this environment, which makes them

311 different from more typical zooplankton (Collard et al. 2015). Hydrozoans such as *Velella*

312 *velella* and *Physalia physalis* have a large part of their bodies occurring above the sea

313 surface, and they have adapted to their neustonic lifestyle by being able to withstand

314 prolonged desiccation and exposure to direct solar radiation (Liss and Duce 2005). Smaller

315 neustonic organisms are less susceptible to sinking and are able to float on the surface of

316 water due to the cohesive forces between water molecules which provide surface tension,

317 allowing them to float (Marshall and Burchardt 2005).

318 The stresses of life at the sea surface mean that comparatively few species occupy the

319 neuston permanently and choose rather to inhabit this ecotone temporarily (Olivar et al.

320 2015). Neuston can be categorised into three major ecological groups; euneuston (consisting

321 of epineuston and pleuston), facultative neuston and pseudoneuston (Hempel and Weikert

322 1972). The euneuston are adult organisms permanently inhabiting the neustonic realm, day

323 and night, and are most abundant in the direct vicinity of the ocean surface (Holdway and

324 Maddock 1983). Examples of euneuston are species of *Halobates* (water striders) and

325 floating and rafting animals (or pleuston), which have submerged bodies and aerial flotation

326 devices (e.g. *Velella velella*, *Porpita porpita* and *Physalia physalis*). Facultative neuston

327 inhabit the surface of the ocean temporarily, during part of their diel vertical migration

328 (Hempel and Weikert 1972, Holdway and Maddock 1983). Examples of facultative neuston

329 are neustonic larvae and juvenile stages of planktonic, nektonic or benthic species (Holdway

330 and Maddock 1983).

331 During diel vertical migration, zooplankton and fish move up and down the water column in

332 generally synchronised movement. Generally, plankton migrate towards the surface waters at

333 dusk and descend back to depth at dawn, with reverse patterns occurring as well (Brierley

334 2014). Neuston use diel vertical migration to escape predators that feed using sight and

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possibly to avoid ultraviolet radiation due to its damaging effects. Metabolic clocks might maintain diel vertical movement in the absence of light for example in the deep sea, cloud cover, eclipse etc. (Brierley 2014).

Pseudoneuston occupy a depth range that extends to deeper layers: they are not confined to the near-surface environment. Rather, the surface represents the uppermost extent of their distribution (Holdway and Maddock 1983). The occurrence of neuston is dependent on the time of day since a large number of animals enter the surface waters only during the night (Hempel and Weikert 1972). Further classification of neuston can be made separating them into epineuston and hyponeuston. Epineuston are those individuals living on the upper side of the surface film of water or subaerially and are solely represented by the genus *Halobates* (Cheng 1973, Holdway and Maddock 1983). Hyponeuston are those individuals living on the lower side of the surface film of water extending to a depth of 5 cm (Marshall and Burchardt 2005, Gladyshev and Malyshevskiy 1982).

Euneuston and pleuston occurring in subtropical and tropical surface waters are well adapted due to the unfavourable environmental conditions of irradiance, but environmental conditions are uniform year-round with reduced wave action compared to the Boreal areas (Hempel and Weikert 1972). In Boreal areas irradiance is lower and mixing by wave action in more intensive, this results in the differences between the biotypes of neuston and plankton being much reduced. The pseudoneuston (and very few euneuston e.g., the copepod *Anomalocera patersoni*) only avoid the uppermost layer of the sea at noon when light-intensities are extremely high (Hempel and Weikert 1972).

The sea surface is unfortunately home for more than just animals, and a large amount of anthropogenic debris is known to occur and accumulate here (Thiel and Gutow 2004). Moore et al. (2001) reported that in the North Pacific, the highest abundances of plastic microlitter were recorded from the North Pacific Central Gyre having over 330 000 items of microlitter per km^{-2} (Thiel and Gutow 2004). These plastics are frequently ingested by seabirds, pelagic filter feeders and, when they settle on the seabed, by many benthic deposit feeders (Vlietstra and Parga 2002, Thiel and Gutow 2004, Duis and Coors 2016). A tremendous amount of anthropogenic debris enters the ocean regularly, approximately between 5 to 13 million tonnes each year (Geyer et al. 2017). Microplastics are synthetic organic polymers smaller than 5 mm in diameter, which have been recognised since the 1970s (Duis and Coors 2016). There is an abundance of microplastics in the upper 20 cm of the sea surface in the gyres of

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367 the North and South Atlantic, the North and South Pacific and the Indian Ocean (Duis and

368 Coors 2016). The circulation caused by gyral currents serves as a retention mechanism,

369 preventing plastics from escaping and moving to mainland coasts (Moore et al. 2001). A

370 surface current modelling study showed that many particles can be retained in a gyre for at

371 least 12 years (Inngraham and Ebbesmeyer 2000, Moore et al. 2001). The accumulation of

372 microplastics in the ocean, over time, ranges from low background levels to localized

373 "hotspots", with gyres being particular hotspots for microplastics (Goldstein et al. 2012,

374 Wright et al. 2013).With an increase in the human population and consequently increasing

375 pollution and fishing activity, the assemblages of neuston could undergo drastic changes

376 (Collard et al. 2015). These changes could have a negative effect on the underlying

377 ecosystem. Therefore, an understanding of neustonic ecology is very important (Collard et al.

378 2015).

379

380 The aim of this study is two-fold. Firstly, it is to describe non-copepod neuston assemblages

381 across the Southern Indian Ocean Gyre and secondly it is to examine changes in assemblage

382 structure across the region, and to link such changes (where possible) to variations in the

383 oceanographic environment. It is hypothesised, following González et al. (2019) that

384 abundances will be lower in the centre of the gyre and that assemblages at the edge of the

385 gyre will be distinct from others. Following Hoeksema (2007) it is also anticipated that

386 assemblages closer to landmasses will comprise greater numbers of meroplanktonic taxa and

387 that there would be a higher abundance of neuston during the night than during the day

388 (Holdway and Maddock 1983).

389

15

Materials and methods

Field sampling

A total of 35 stations were sampled at regular intervals (100 nm, 150 nm) along a transect line extending from Jakarta, Indonesia to Port Louis, Mauritius, between 26 June - 16 July 2015 (Figure 2) (Toresen et al. 2015). At each station, information on vertical changes in temperature, salinity, oxygen and fluorescence were collected using a Seabird 911+ CTD fitted with a Turner Design fluorometer.
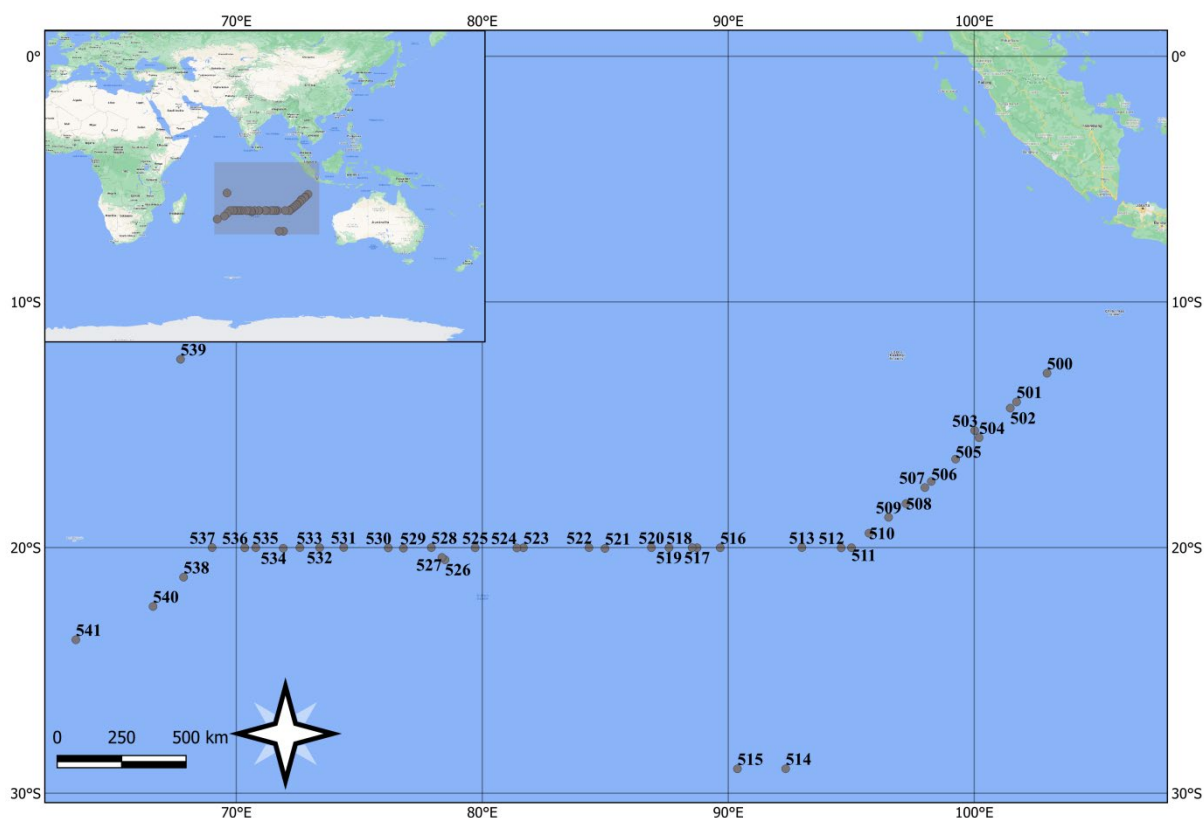
Figure 2: Neuston stations sampled during the IOS leg 1 survey of the southern Indian Ocean (QGIS version 3.16.3).

At each station, three neuston samples were collected using a rectangular manta trawl, with a mouth frame measuring 19 cm high and 61 cm wide balanced by two wings and fitted with a net having a 335 μm mesh and a 100 ml bottle fitted at the cod end (Figure 3). A mechanical flow meter was fitted to the mouth of the net in order to determine the volume of water

16

406 filtered by the net. The manta net was only deployed in relatively calm weather and was
407 towed for a period of 15 minutes at a speed of 2-3 knots, horizontally at the ocean surface
408 (Toresen et al. 2015).

409 On retrieval, samples were immediately examined under a stereo microscope at various
410 magnifications, and all micro-plastics were removed. Thereafter the neuston was fixed and
411 preserved in either 96% ethanol or 4% buffered seawater formalin for later processing in the
412 laboratory (Toresen et al. 2015).

413

414
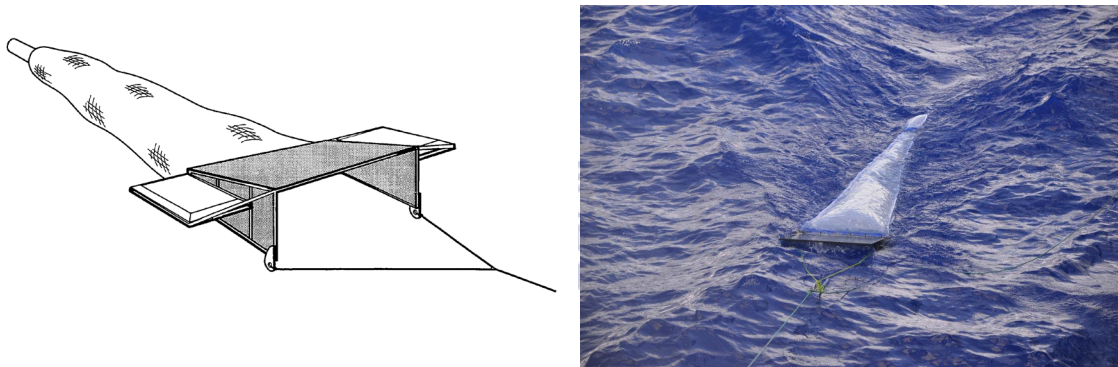
417 **Figure 3:** Diagram of a manta trawl, with a photograph showing how the manta trawl is used
418 to sample the sea-surface environment (Sandknop et al. 2002, Toresen et al. 2015).

419

Laboratory methods

421 Prior to microscopic examination, those samples in formalin were drained through a 180 μm
422 sieve and material was suspended in freshwater: samples in ethanol were examined without
423 rinsing. All samples were examined (and counted) without sub-sampling and specimens were
424 identified to morphospecies (Appendix A), except siphonophores, which were identified to
425 species level.

426 It is customary in ecological studies to identify sampled specimens to the lowest taxonomic
427 level using morphological characters. Ideally, this is to the level of species, as defined by the
428 Darwinian concept of a species (Darwin 1859, Mallet 2008, Pos et al. 2014). In practise,
429 however, this becomes difficult when samples are diverse and contain a large number of very

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430 different taxonomic groups, because the expertise needed to identify all sample members to
431 species level is not available. In such circumstances, there is a tendency to focus on a
432 taxonomically distinctive and well-known taxon – a taxocene (Morin 2011). It is then
433 generally assumed that observations from the well-known can be extrapolated to the
434 unknown (Morin 2011). Although this assumption can sometimes be supported (e.g. Kuyper
435 et al., 2020), depending on the question being asked, there are instances when it cannot
436 (Morin 2011).

437 When attempts are made to identify everything to the lowest taxonomic level, individuals that
438 cannot be distinguished are often recorded as "indets", and the number of indets will increase
439 as the dataset increases (Pos et al. 2014). Deciding whether to incorporate or ignore these
440 individuals in subsequence analyses can become tricky as they are associated with their own
441 errors. Consequently, there is little agreement among ecologists on how indets should be
442 treated and to what degree they may compromise the results (Pos et al. 2014).

443 An attempt is made here to be as inclusive as possible, and to use all the material in the
444 samples. However, given our lack of taxonomic expertise, it has been decided to use
445 morphospecies. As samples were processed, specimens with a readily identifiable
446 morphology were photographed, removed as vouchers and provided with unique labels, so
447 that it was possible to validate and cross-reference subsequent identifications. Indets are
448 consequently accorded taxon-level recognition because, with the exception of siphonophores,
449 all specimens are indets. It is acknowledged that in some cases, one morphospecies may
450 comprise more than one real species and it is understood that in other cases more than one
451 morphospecies could be assigned to a single species – especially in the case of larval
452 Decapods where different developmental stages may look quite different from one another.
453 However, the error is assumed to be consistent as only one person was involved in
454 morphospecies designation and sample analysis.

455

456 Data analyses

457 Temperature, salinity and chlorophyll/fluorescence were recorded in order to see if there
458 were any cohesive changes in the environment across the transect. Vertical profiles of the
459 temperature, salinity and chlorophyll/fluorescence were constructed using the computer
460 package Ocean Data View version 5.2.0. Even though neuston occur within the upper 20 cm
461 of the water column (Naumann 1971), the vertical profiles were constructed to a depth of 200

18

462 m in order to describe and assess the environment of migratory species. It should be

463 remembered that most of the samples were collected in an equatorial region, where

464 productivity is typically low at the surface and biomass generally peaks at some depth

465 (Stramma and Lutjeharms 1997).

466

467 In order to examine multivariate patterns in the assemblages sampled across the Southern

468 Indian Ocean Gyre, data were analysed using various software at the level of morphospecies,

469 (Appendix A). Patterns in community structure were assessed, *a priori*, by binning samples

470 into a) 5° longitudinal classes and b) Time of Day (day, dusk, night). The rationale behind

471 this was twofold. Firstly, our aim was primarily to determine if there were east-west changes

472 in the structure of neuston assemblages across the subtropical gyre. Owing to the patchy

473 nature of samples, it was necessary to bin them into 5-degree bins. And secondly, it is

474 understood that the composition and structure of neuston assemblages varies with time of day

475 (Hays 2003). Time of day was assessed from the sample log with reference to The NOAA

476 Solar Calculator (https://www.esrl.noaa.gov/gmd/grad/solcalc/) remembering that the ships

477 log was set as UTC (GMT): dawn and dusk were designated as the times of sunrise and

478 sunset, plus/minus 1 hr, respectively.

479 The biological data were first root-root transformed and a Bray-Curtis similarity matrix was

480 computed between samples. In order to determine if there was an effect of both longitude and

481 time of day on overall assemblage structure, data were analysed using a PERMANOVA

482 (permutational MANOVA), with the factors Longitude and Time of Day set as fixed and

483 random, respectively. Otherwise default settings were used: Type III sum of squares,

484 permutation of residuals under a reduced model and fixed effects sum to zero for mixed terms

485 (Anderson et al. 2008). These analyses were performed using PRIMER v7 + PERMANOVA

486 software (Clarke and Gorley 2015).

487 Given the significant effect of Time of Day on assemblage structure (see Results, below),

488 data were analysed separately for Day and Night samples; there being too few Dusk and

489 Dawn samples for analyses. Separate similarity matrices were constructed for Day and Night

490 samples, and the significance of a spatial pattern was tested using a one-way ANOSIM. A

491 matrix of pairwise R values between longitudinal bins was computed, which was visualised

492 using cluster analysis with group-average sorting. These analyses were conducted using

493 PRIMER v7 software (Clarke and Gorley 2015).

19

494   To test for differences in the average abundance of neuston across samples by Time of Day

495   (Day vs Night) and longitude, a two-way full factorial ANOVA was performed. Similar tests

496   were computed for the other univariate measures that summarise assemblages, namely

497   species richness and diversity (H'). Species diversity per sample was computed using the

498   Shannon Index (H'), following Krebs (2002). While sample averages were used to test for

499   changes in diversity across the transect as just outlined, all samples per longitudinal bin were

500   pooled to determine overall bin diversity, and error values around these were computed using

501   jack-knife methods (Magurran 2003).

502   The morphospecies responsible for 70% of the similarity (identity) of samples by Time of

503   Day and longitudinal bin were determined using a Similarity Percentage analysis (SIMPER).

504   Data were pooled by longitudinal bin and Time of Day, respectively, in these analyses owing

505   to the fact that there were too few data to generate robust patterns if they had been

506   partitioned. These analyses were conducted using PRIMER v7 software (Clarke and Gorley

507   2015).

508   A Distance Based Linear Model (DistLM) was computed to determine the environmental

509   variables driving community structure across longitudinal bins, by Day and Night separately.

510   The predictors used included seas surface temperature and salinity, the temperature and

511   salinity at 200 m, the depth of the upper mixed layer and of the fluorescence maximum as

512   well as integrated fluorescence and, the fluorescence value at the fluorescence maximum.

513   Marginal and sequential tests were performed by stepwise selection and the significance of

514   model outputs was assessed using adjusted R^2. Owing to some fairly large gaps in the

515   environmental data (especially for fluorescence), analyses were confined **only** to those

516   samples with matching environmental data. The outputs of all DistLMs were visualised using

517   distance-based redundancy analysis (dbRDA) (Clarker and Gorley 2015).

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Results

Hydrography

The vertical temperature profiles indicates that surface waters were generally warmer than 24°C across the transect, being warmest off Christmas Island to the east (Figure 4). Warmer than surrounding waters were centred on the two anticyclonic gyres reported in the region at ~ 76° E and ~88° E (Dufois et al. 2017). While the ocean temperature remained above 23°C down to 100 m, an upward doming of cooler isotherms is noted east of ~90° E, reflecting the cyclonic gyre noted in that region (Dufois et al. 2017). The lowest temperature at 200 m (17°C) was recorded off Christmas Island.

Salinity was lower at the surface than it was at depth across the width of the transect, being lowest at the surface in the easternmost stations (Figure 4). Interestingly, the distribution of surface salinities mirrored the distribution of temperatures, being slightly higher in cooler than warmer waters. Indeed, there was a significant negative relationship between the two variables (Pearson's R=-0.94, p<0.05). An apparent upward doming of high salinity water (> 35.5 psu) was evident to 100 m, west of ~100° E.

There was a relatively deep fluorescence maximum across the transect, centred at ~ 120 m, except in the extreme west where it occurred at ~45 m (Figure 4). Dufois et al. (2017) noted that the vertical position of the chlorophyll maximum closely tracked the mixed-layer depth, hence it approximates the distribution of deeper isotherms and isohalines.

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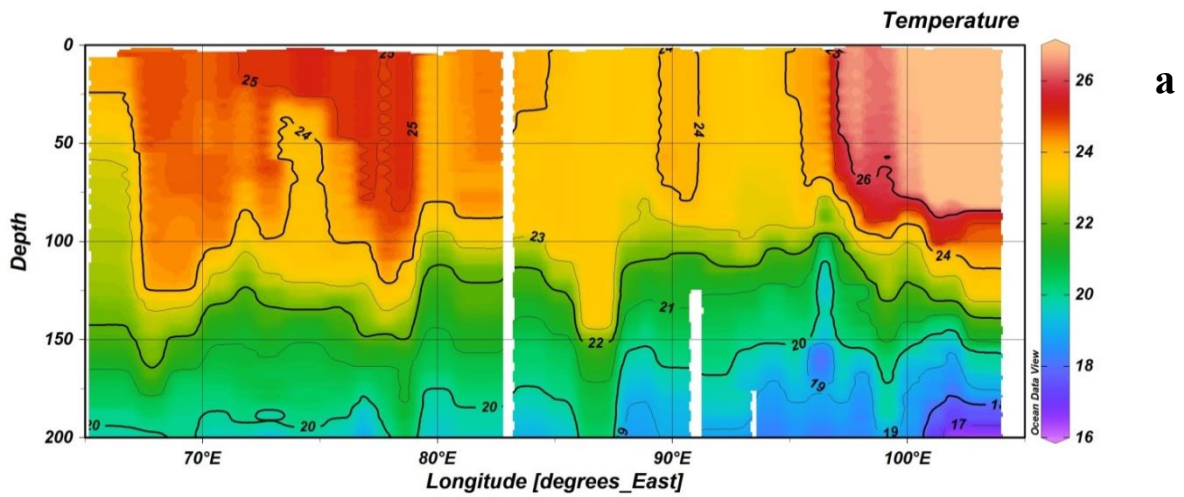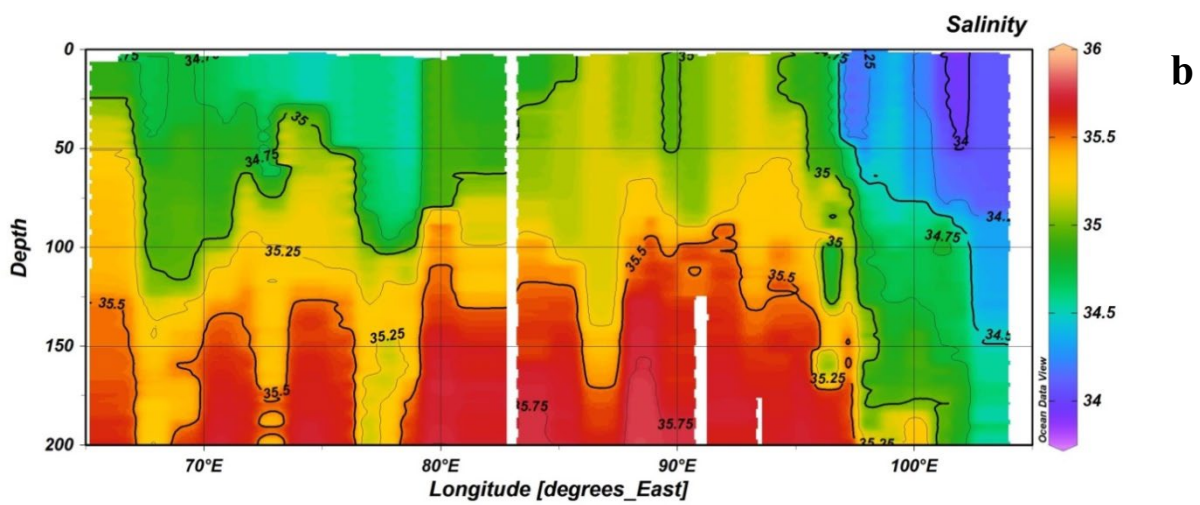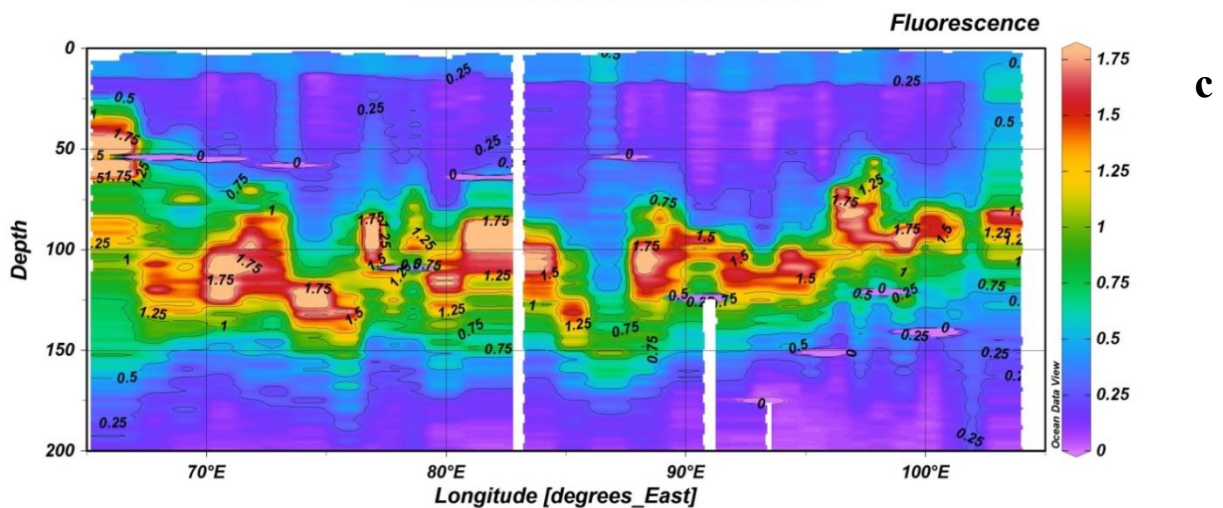
Figure 4: Vertical profiles in temperature (a), salinity (b) and fluorescence (c) during the IOS
leg 1 survey of the southern Indian Ocean (using Ocean Data View version 5.2.0(ODV)).

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Neuston

Assemblage composition

Overall, the non-copepod neuston was dominated by Ostracods though mysids, juvenile chaetognaths, siphonophores and amphipods were also common (Table 1). The greatest number of morphospecies was observed amongst Amphipoda (19 Hyperiida, six Gammarida) and Siphonophora (21 Calycophorae, three Physonectae, one Cystonectae). Gastropods were represented by 20 morphospecies (17Pteropoda, one Littorinimorpha, one Nudibranchia, one Caenogastropoda); there were ten Thaliacea (eight Salpida, two Pyrosomatida, one Doliolida) and seven each of Stomatopoda, fish larvae and Decapoda. The taxon that was most frequently recorded across all samples was Siphonophora, which occurred in 83 of the 87 samples, followed by Gastropoda (72 samples), non-siphonophoran Hydrozoa (71) and Ostracoda (70) (Table 1). Of the siphonophores, *Abylopsis eschscholtzii* was most abundant followed by *Chelophyes contorta* and *Bassia bassensis.*

The majority of the specimens collected (88%), and the greatest variety of morphospecies, were facultative neuston (Appendix A). Of the balance, ~10% comprised euneuston (pleuston) *Porpita* and *Velella* (Hydrozoa), *Physalia* (Siphonophora) and epineuston, Water Strider, *Halobates* (Insecta) and ~2% were hyponeuston [morphospecies of *Spirula* (Cephalopoda), *Janthina* and *Glaucus* (Gastropoda)]. Although the relative proportions of the different types of neuston varied little across the transect, facultative neuston were slightly more common by night (~90%) than day (86%).

Holoplanktonic morphospecies dominated neuston by day (~84.5%) and night (85.5%). The contribution by meroplanktonic morphospecies was greater at the longitudinal extremes of the transect than it was at the centre of transect (Figure 5), especially by night.

23

571   **Table 1:** The average abundance, diversity (number of morphospecies) and frequency of

572   occurrence of the major taxa recovered in neuston samples across the Southern Indian Ocean

573   Gyre of the Indian Ocean during 2015. Their relative rankings also shown.

Taxon	Average abundance	Rank	no morphospecies	Rank	no samples	Rank
Amphipod	27,28	5	25	1	70	5
Barnacle	0,06	22	3	14	4	22
Cephalopod	0,07	20	4	11	6	19
Chaetognath	50,15	3	1	18	65	7
Decapod	18,63	6	7	5	66	6
Doliolid	0,84	15	1	18	26	14
Euphausiid	1,78	13	2	16	5	20
fish eggs	1,00	14	1	18	28	13
Fish Juvenile	0,11	19	5	8	7	18
Fish larvae	1,84	12	7	5	50	10
Gastropod	10,47	7	20	3	72	2
Hydrozoa	9,70	8	4	11	71	3
Isopod	0,30	17	4	11	11	16
Mysid	59,11	2	1	18	57	9
Ostracod	80,03	1	5	8	71	3
Polychaete	0,33	16	5	8	11	16
Salp	2,40	10	10	4	60	8
Scyphozoa	0,07	20	2	16	5	20
Siphonophore	31,45	4	25	1	83	1
Sipunculid	0,01	23	1	18	1	23
Stomatopod	2,24	11	7	5	34	12
Water strider	4,46	9	3	14	47	11
Zooanthidae	0,28	18	1	18	19	15

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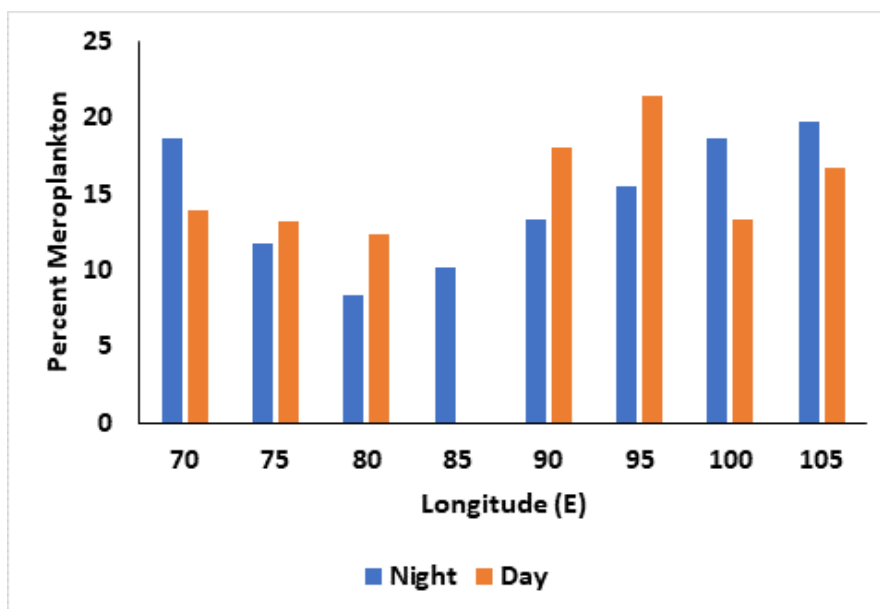
Figure 5: Changes in the relative contribution by meroplanktonic morphospecies to neuston
abundance across the Southern Indian Ocean Gyre in the Indian Ocean during 2015 with
longitude and time of day.

Effects of longitude and time of day

The results from the PERMANOVA routine indicated that both *a priori* factors influenced
the structure of neuston assemblages across the transect, individually and interactively,
despite the high residual sums of squares (Table 2). As a consequence, data have been treated
separately by Time of Day in all subsequent analyses.

Table 2: PERMANOVA results to examine the effects of Time of Day and Longitude on the
structure of neuston assemblages across the IOS Leg 1 survey in the southern Indian Ocean.

Source	DF	SS	MS	Pseudo-F	P(perm)	No Unique Permutations	P(MC)	Estimate of components of variation
Longitude	7	30626	4375,1	1,495	0,042	998	0,029	157,67
Time of Day	3	17953	5984,4	4,653	0,001	998	0,001	316,89
Longitude x Time of Day	9	26668	2963,1	2,304	0,001	997	0,001	408,92
Residual	64	82308	1286,1					1286,1

25

The results of the two-way, full factorial ANOVA indicate that the total abundance of the neuston in the samples was significantly impacted by Time of Day ($F_{1,52}$=34.49, $p<0.0001$), Longitude ($F_{6,52}$=4.38, $p<0.005$) and the interaction between both factors ($F_{6,52}$=3.01, $p<0.05$). Abundance was higher during the night than the day, and tended to be higher at the extremes of the transect and lowest around 80° E. (Figure 6a)
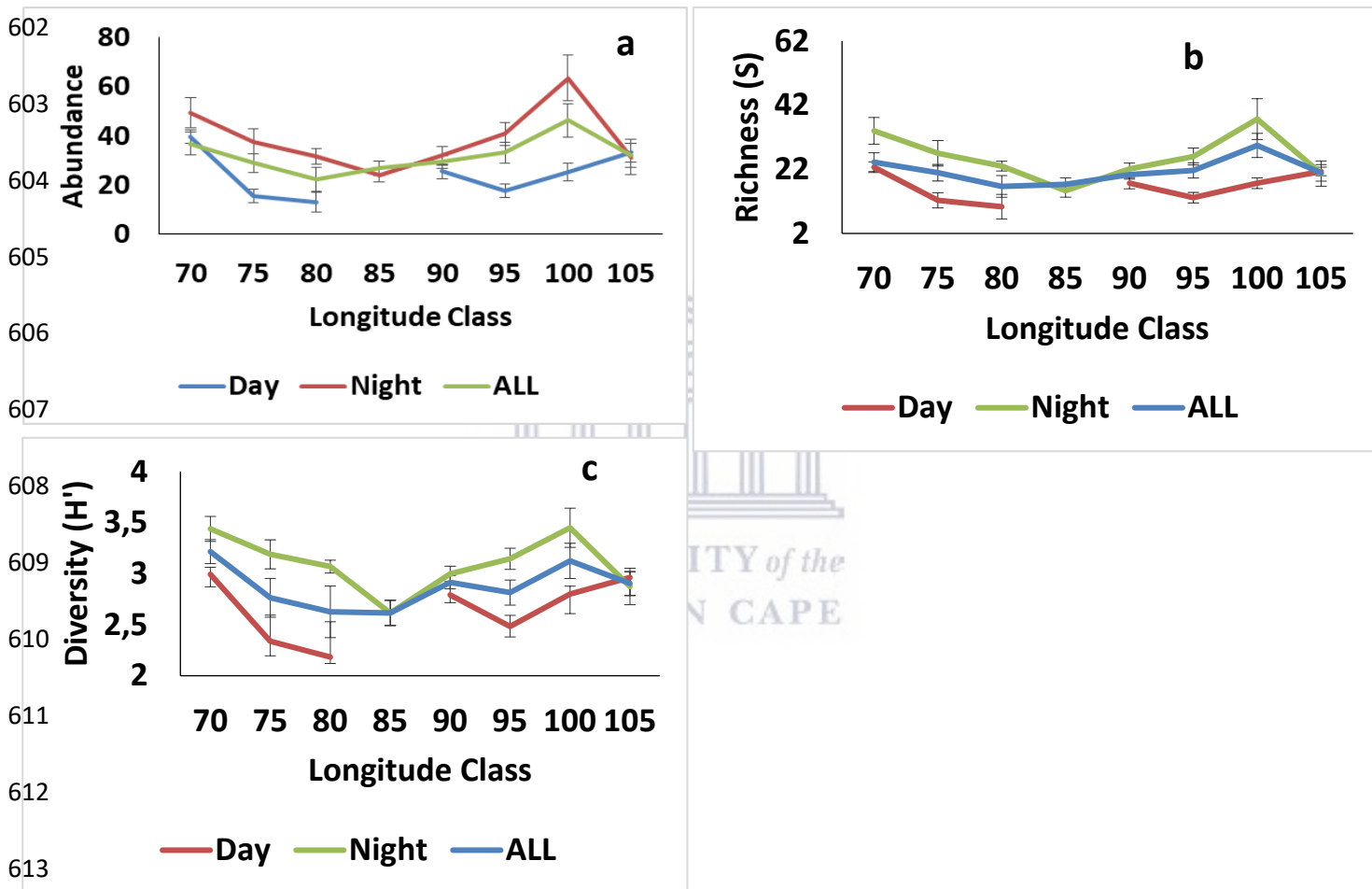
Figure 6: Diel variability in the mean abundance (a), richness (morphospecies, b) and diversity (H', c) of the non-copepod neuston collected across the Southern Indian Ocean Gyre in 2015. Error bars are standard error.

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619 Effectively similar temporal and spatial results were observed in terms of sample diversity,

620 either measured as richness or diversity (H': Table 3, Figure 6b, c). Diversity was higher in

621 samples collected at night than during the day, and was greater at the extremes of the transect

622 than around 80° E.

623

624 **Table 3:** Effect of Longitude, Time of Day and Longitude and Time of Day on sample

625 diversity and species richness.

Measure	Abundance		Species Richness		*H'*	
Statistic/Significance	*F*	*p*	*F*	*P*	*F*	*P*
Intersect	531,52	<0.0001	632,56	<0.0001	4132,74	<0.0001
Longitude	4,38	<0,005	2,97	<0,05	2,37	<0,05
Time of Day	34,49	<0,0001	38,38	<0,0001	32,52	<0,0001
Longitude and Time of Day	3,01	<0,05	2,30	<0,05	2,46	<0,05

626

627 Composition

628 The average abundance (± se) of those morphospecies that were responsible for 70% of the

629 dissimilarity (SIMPER analysis) between Day and Night samples (across all longitudinal bins

630 are shown in Figure 7: those responsible for differences between longitudinal bins (across

631 Time of Day) are shown in Figure 8.

632 As noted previously, the majority of taxa increased in abundance at night. With the exception

633 of water striders, the other members of the euneuston (*Janthina, Velella*) did not differ much

634 in abundance with Time of Day: only *Enneagonum hyalinum*, *Lucifer* and Ostracod 4 were

635 more common during the day than at night.

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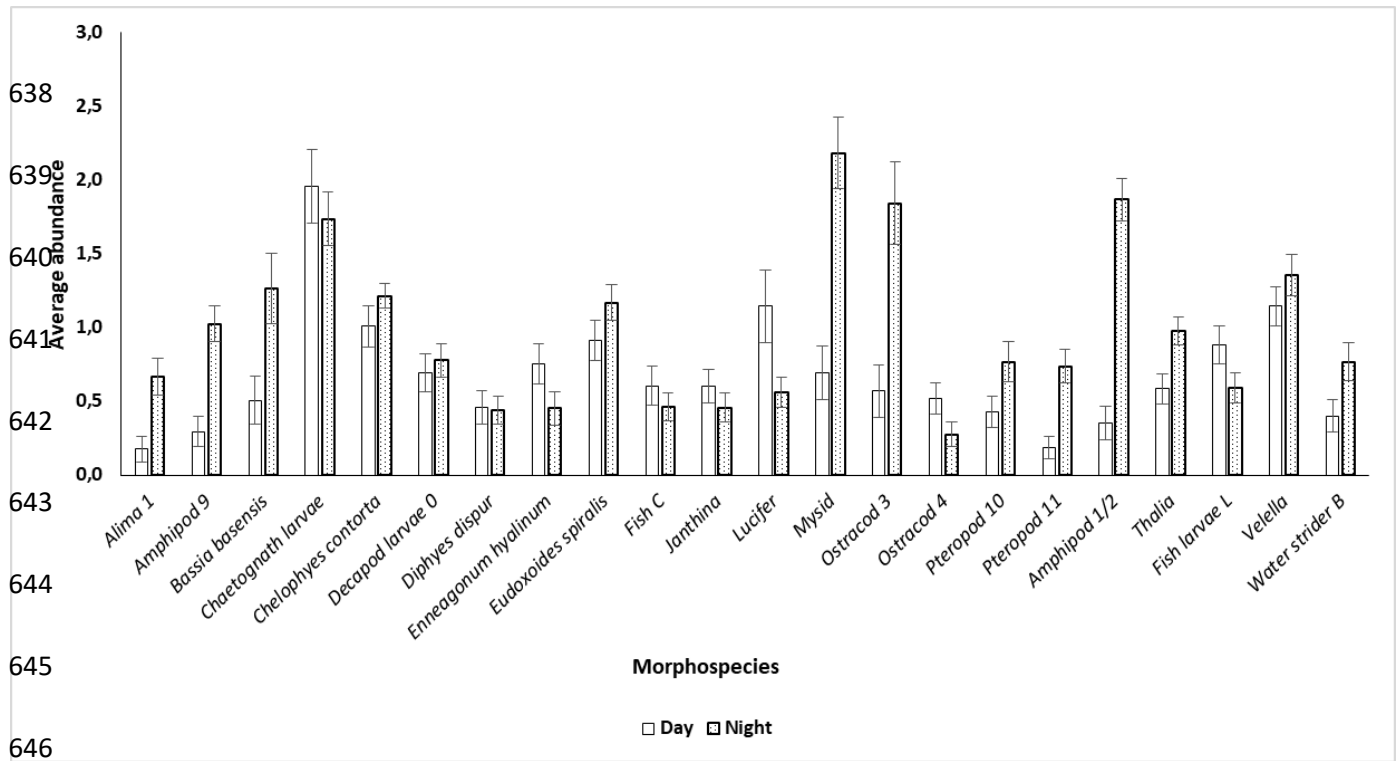
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Figure 7: The average abundance of the morphospecies responsible for 70% dissimilarity between day and night samples collected in the IOS Leg 1 survey of the southern Indian Ocean. Data pooled by longitudinal bin. Error bars are standard error.

The data shown in Figure 8 indicate that all the taxa that were responsible for the identity of each longitudinal bin were found across the transect, though some did display a pattern of spatial distribution. For example, the siphonophores *Abylopsis eschscholtzii* and *Enneagonum hyalinum* were more common in the west (grids 70, 75, 80), whilst *Alima* 1, chaetognath larvae, mysids and Ostracod 3 were more abundant in the east (grids 95, 100, 105). Few taxa were most abundant in the central part of the transect (grids 80, 85, 90, 95), though water striders were notably uncommon there, by comparison with the extremes of the transect.

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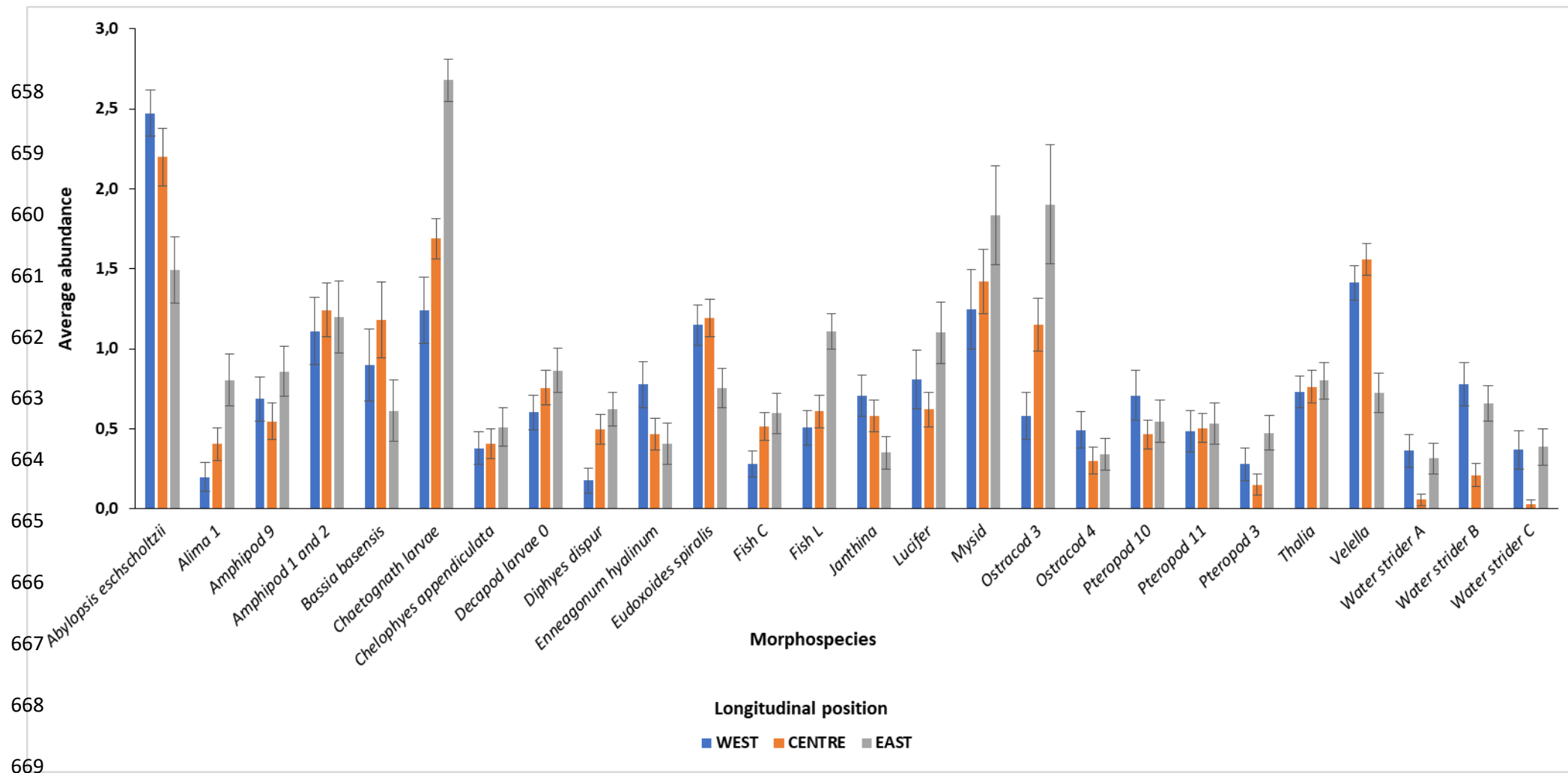
Figure 8: The average abundance of the morphospecies responsible for 70% dissimilarity between neuston samples collected in the centre (75 - 85° E), East (95 - 105° E) and balance of the IOS Leg 1 survey in the southern Indian Ocean. Data pooled by time of day bin. Error bars are standard error. .

29

Assemblage structure

The results of the ANOSIM indicate that there was a significant difference in the structure of assemblages across the transect, by Day (global $R=0.381$, $p<0.005$), Night (global $R=0.413$, $p<0.005$) and overall (global $R=0.229$, $p<0.005$). The cluster analyses generated from the matrices of pairwise R values are shown in Figure 9 and reveal some interesting patterns. The night-time samples indicate that assemblages between 80 - 85° E are very distinct from the balance, and that those at the extremes of the transect (between 65 - 75° E; 95 - 105° E) are more similar to each other than to those immediately surrounding 85° E (Figure 9a). In the case of the samples collected during the day, those between 75 - 80° E were very different from the balance: no samples were collected during the between 80 - 85° E. The rest of the samples fall into two groups that span 75 - 80° E, with those collected between 100 - 105° E being dissimilar (Figure 9b). Examination of the cluster analysis for all data indicate that samples from between 75 - 85° E were more similar to each other than to the rest of the samples, which otherwise clustered out into groups that were approximate longitudinal opposites of each other (Figure 9c).

The results of the cluster analyses shown in Figure 9 are graphically re-interpreted in Figure 10. Although there are some differences in the way that the different longitudinal bins relate to each other by Time of Day, in general it would appear that there is a symmetry to the pattern either side of a "core" between 75 - 85° E.

The results of a SIMPER analysis exploring the taxa that are responsible for similarities within, and differences between the three clusters identified in Figure 9c are graphically illustrated in (Table 6). From this it can be seen that assemblages between 75 - 85° E are characterised by siphonophores and few mesozooplankton. Amphipods, chaetognaths, mysids, water-striders and *Lucifer* were more common at the other stations, with those to the east (95-105° E) supporting greatest numbers of meroplanktonic crustaceans.

Owing to their high richness and widespread distribution across the region, the siphonophores, amphipod and gastropod data can be analysed separately. In the case of the former, there was no overall diel (ANOSIM $R=0.07$, $p>0.05$) or longitudinal (ANOSIM $R=-0.09$, $p>0.05$) change in assemblage structure. Although there was also no distinct longitudinal pattern in amphipod assemblage structure across the transect (ANOSIM $R=0.09$, $p>0.05$), assemblages were different, by day and night (ANOSIM $R=0.29$, $p<0.005$), being

705 both more abundant (13 vs 4 per haul, respectively) and diverse (20 vs 12 morphospecies) at

706 night. Although there was no apparent longitudinal pattern to the distribution of assemblages

707 of neustonic gastropods (ANOSIM R=0.11, p>0.05), there were significant diel differences in

708 assemblage structure (ANOSIM R=0.34, p<0.005). Overall, day time samples were less

709 species rich than night-time samples (12 vs 18 morphospecies, respectively), and contained

710 fewer individuals (4.6 vs 33.4, respectively). Both morphospecies of *Creseis* were more

711 common by day than night, whilst heteropods (*Atlanta* and Pterotracheidae) were more

712 common at night.

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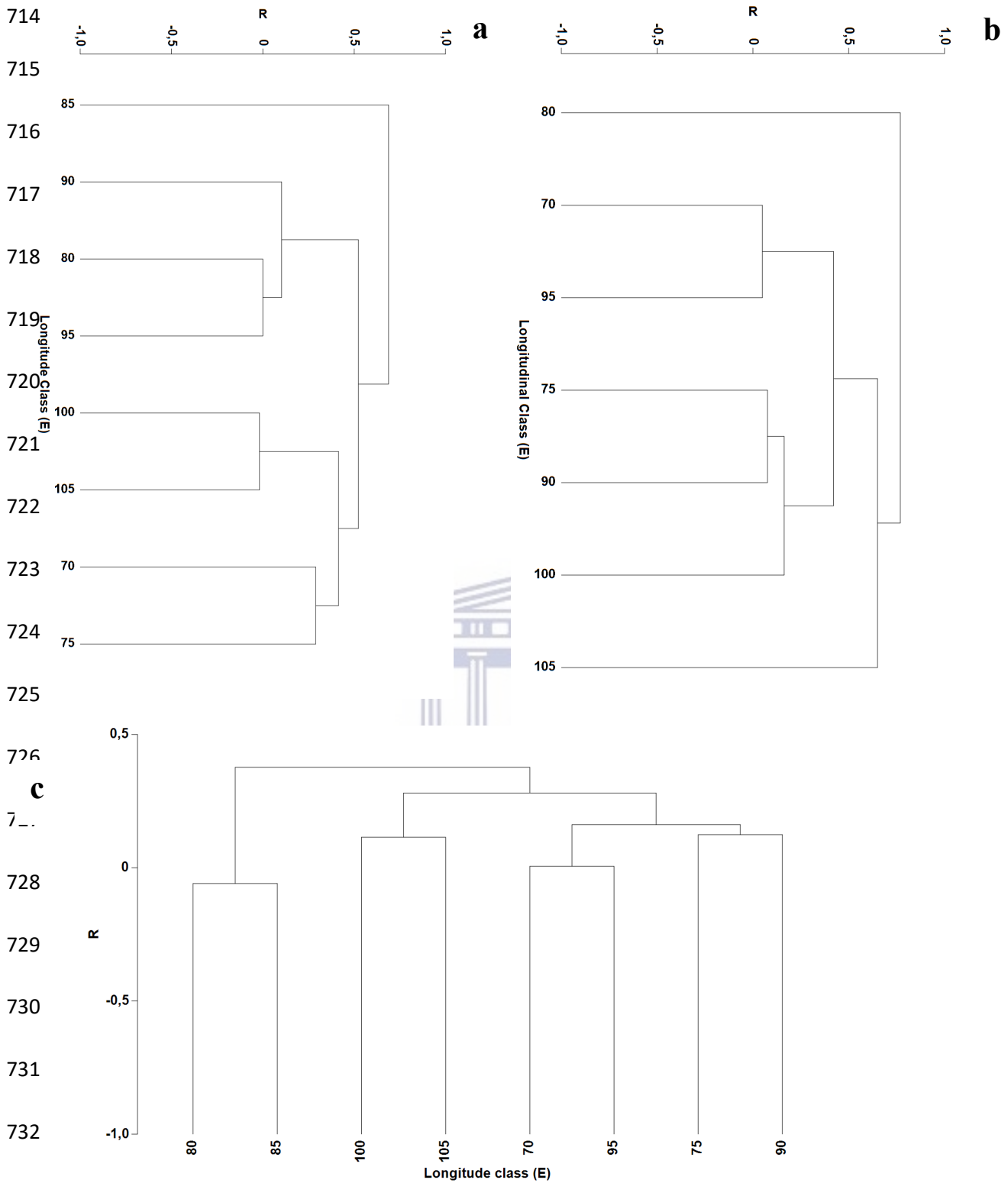
Figure 9: Cluster analyses showing the significant difference in the structure of assemblages across the transect during the night-time (a), day-time (b)and all data (c).

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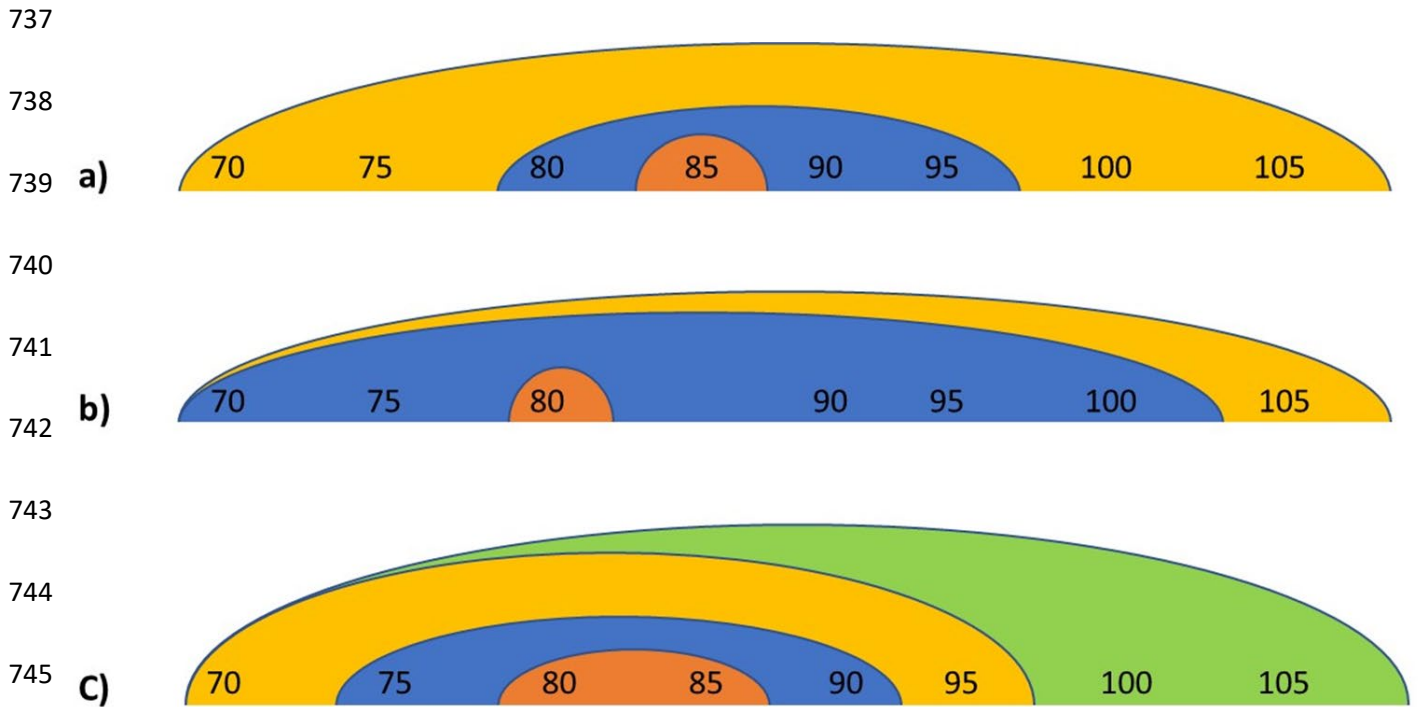
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749 **Figure 10:** Graphical re-interpretation of cluster analyses shown in Figure 9 for night-time
750 (a), day-time (b) and all samples collected during IOS Leg 1 survey of the southern Indian
751 Ocean.

752

753 The results of the DistLM are shown in Tables 4 and 5, for Day and Night samples,

754 respectively. The results of the marginal tests indicate that none of the predictors associated

755 with fluorescence were significantly related to the longitudinal structure of the day-time

756 assemblages (Table 4a). That said, three (depth of the fluorescence maximum, sea surface

757 fluorescence and integrated fluorescence) were included in the final model (R^2=0.49, adjusted

758 R^2=0.33; Table 4b). The dbRDA plot for the day-time samples is shown in Figure 11, the first

759 two axes of which explain 56% of fitted and 27% of total variation.

760

Table 4a: Marginal test results of the DistLM exploring the effect of different environmental variables on the structure of day-time neuston assemblages observed across the IOS Leg 1 survey in the southern Indian Ocean.

Variable	SS(trace)	Pseudo-*F*	*P*	Prop.
Latitude	4001,5	2,180	0,006	0,072
Longitude	4075,8	2,223	0,01	0,074
Sounding	1157,3	0,597	0,876	0,021
SST (sea surface temperature)	3551,3	1,918	0,033	0,064
Temperature at 200 m	4952,4	2,748	0,001	0,089
SSS (sea surface salinity)	3490,7	1,883	0,029	0,063
S (salinity) at 200 m	4242,1	2,321	0,007	0,077
SSFl (Sea surface fluorescence)	3189,9	1,710	0,055	0,058
D Fl max (deep fluorescence maximum)	2247	1,184	0,259	0,041
Fl at Chl max (fluorescence at chlorophyll maximum)	3126,5	1,674	0,068	0,056
Integr Fl (Integrated fluorescence)	3244,1	1,741	0,061	0,059

Table 4b: Sequential test results of the DistLM exploring the effect of different environmental variables on the structure of day-time neuston assemblages observed across the IOS Leg 1 survey in the southern Indian Ocean. See Table 4a for full labels to variables.

Variable	Adj R^2	SS(trace)	Pseudo-*F*	*P*	Prop.	Cumul.	res.df
+Temp at 200 m	0,057	4952,4	2,7483	0,002	0,089	0,089	28
+S at 200 m	0,111	4607,5	2,7133	0,002	0,083	0,173	27
+D Fl max	0,155	3882,3	2,4053	0,005	0,070	0,243	26
+SSS	0,206	4019,3	2,648	0,003	0,073	0,315	25
+Integr Fl	0,237	2946,9	2,0207	0,023	0,053	0,368	24
+SSFl	0,266	2739,1	1,9528	0,033	0,049	0,418	23
+SST	0,324	3837,9	2,9706	0,002	0,069	0,487	22

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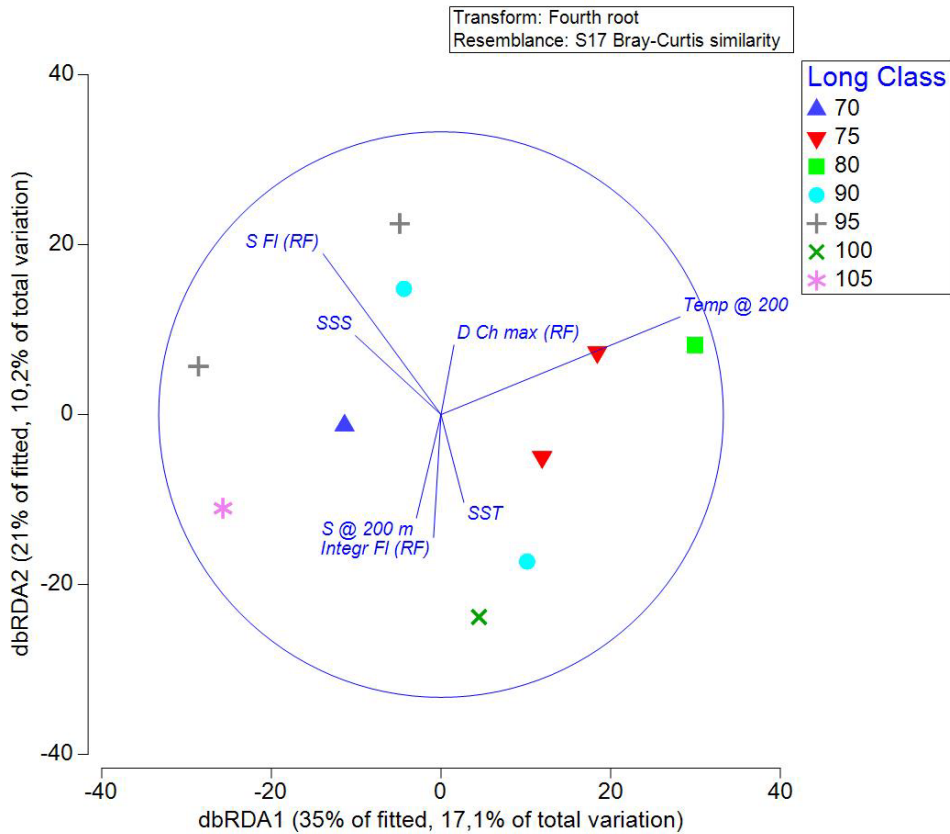
Figure 11: dbRDA plot illustrating the relationship between environmental predictors and the structure of day-time neuston assemblages observed across the IOS Leg 1 survey in the southern Indian Ocean.

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Interestingly, and perhaps tellingly, in the case of the night- time samples, only the depth of the fluorescence maximum was not significantly related to the structure of assemblages along the transect; both measures of chlorophyll biomass were significant (Table 5a). That said, only the depth of the fluorescence maximum was included in the full, sequential model (R^2=0.62, adjusted R^2=0.45; Table 5b). The first two axes of the dbRDA plot (Figure 12) explain 61% of fitted and 38% of total variation. Note the lesser number of stations included in the night- time than day time model owing to gaps in the environmental data (Fig 11 vs Figure 12).

784

785 **Table 5a:** Marginal test results of the DistLM exploring the effect of different environmental
786 variables on the structure of night-time neuston assemblages observed across the IOS Leg 1
787 survey in the southern Indian Ocean. See Table 4a for full labels to variables.

788

Variable	SS(trace)	Pseudo-*F*	*P*	Prop.
Latitude	3586,5	2,233	0,009	0,092
Longitude	6640,5	4,525	0,001	0,171
Sounding	4785	3,083	0,001	0,123
SST	6258,7	4,215	0,001	0,161
Temp at 200 m	3986	2,510	0,006	0,102
SSS	5779,5	3,836	0,001	0,148
S at 200 m	5483,9	3,607	0,001	0,141
SSFl	3472,5	2,155	0,016	0,089
D Fl max	1995,3	1,189	0,254	0,051
Fl at Chl max	5188,9	3,383	0,001	0,133
Integr Fl	4315,3	2,743	0,002	0,111

789

790 **Table 5b:** Sequential test results of the DistLM exploring the effect of different
791 environmental variables on the structure of night-time neuston assemblages observed across
792 the IOS Leg 1 survey in the southern Indian Ocean. See Table 4a for full labels to variables.

793

Variable	Adj R^2	SS(trace)	Pseudo-*F*	*P*	Prop.	Cumul.	res.df
+Longitude	0,133	6640,5	4,525	0,001	0,171	0,171	22
+SSS	0,205	4023,3	2,990	0,002	0,103	0,274	21
+ D Fl max	0,248	2798,5	2,198	0,008	0,072	0,346	20
+SSFl	0,321	3628,3	3,157	0,001	0,093	0,439	19
+Latitude	0,382	3020,3	2,889	0,001	0,078	0,517	18
+Sounding	0,424	2230,3	2,286	0,014	0,058	0,574	17
+Temp at 200 m	0,452	1757,6	1,896	0,04	0,045	0,619	16

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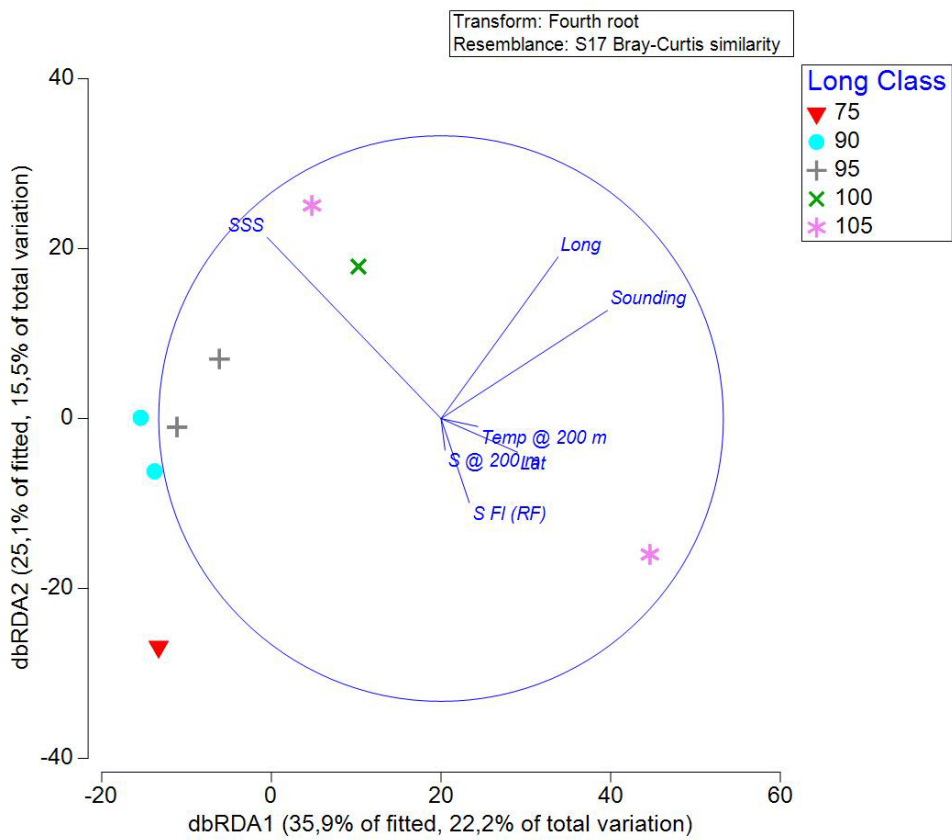
Figure 12: dbRDA plot illustrating the relationship between environmental predictors and
the structure of night-time neuston assemblages observed across the IOS Leg 1 survey in the
southern Indian Ocean.

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Discussion

Vertical profile for environmental data

During the austral winter, the Subtropical Gyre in the southern Indian Ocean is generally characterised by anticyclonic eddies and elevated surface chlorophyll concentrations (references in Dufois et al. 2017). In their study, which was conducted on the same cruise as the present data were collected, Dufois et al. (2017) used Bio-Argo floats and *in situ* sampling to understand the mechanisms responsible for this chlorophyll enrichment. They noted the presence of three eddies: one cyclonic eddy near 89º E and two anticyclonic eddies at approximately 78.5° E and 87º E (Dufois et al. 2017). The cyclonic eddy was the smallest of the three and had a lifespan of 70 days, while the anticyclonic eddies had a lifespan between 117 - 132 days (Dufois et al. 2017).

Dufois et al. (2017) concluded that the anticyclonic eddies "can trap productive waters through horizontal advection and/or locally modify the chlorophyll distribution through enhanced convective mixing" (p 3262). They noted that the warm waters in the west, associated with the largest of the eddies, were drawing in waters from the north, which themselves originated in part from the Indonesian Throughflow and had been propagated westward – hence the lower salinity. Usually, higher sea surface temperatures are associated with high levels of evaporation and salinity but south of the equator, Indonesian Throughflow Water transports freshwater from Indonesian seas to the south eastern tropical Indian Ocean, which maintains a low Sea Surface Salinity (SSS) (Du and Zhang 2015). The anticyclonic movement of the Indian Ocean Gyre recirculates the low salinity water and maintains a negative SSS south of the equator (Du and Zhang 2015).

Neuston

On balance, the neuston communities examined here are broadly similar to those of previous studies, as recently reviewed by Helm (2021). That said, most of the work that has been conducted on neuston has tended to focus on specific taxonomic groups, often with a focus on fish larvae (e.g. Davenport and Rees 1993), and comprehensive research on regional communities as a whole are scant. Zaitsev (1970) reviewed the work that he and colleagues had led in the Black Sea and other areas; Hempel and Weikert (1972) studied neuston in the North Atlantic Ocean, whilst Holdway and Maddock (1983) reported on the neuston collected along a transect extending from Indonesia, across the Indian Ocean and into the

Mediterranean Sea. Brodeur et al. (1987) briefly examined the neritic neuston of the NE

Pacific, with reference to the salmon resources there, while Echelman and Fishelson (1990)

and Mantha et al. (2019) have documented communities in the Red Sea. Otherwise

comprehensive studies that can be used for comparative purposes have been hard to find. For

example, a recent study of 54 neuston samples collected in the NE Pacific, taken to

contextualise the fauna of the Great Pacific Garbage Patch, failed to report the presence of

many key neuston groups (Egger et al. 2021) and cannot be used here.

Common taxa.

The eueneuston collected here is broadly similar to that noted by others and comprises

floating and rafting animals that permanently inhabit the surface film of the ocean (Weikert

1970, Grave 1971, Zaitsev 1971, Hempel and Weikert 1972). These animals do not display

diel vertical migration and are constantly on the ocean surface regardless of time of day

(Weikert 1970, Grave 1971, Zaitsev 1971, Hempel and Weikert 1972). That said,

morphospecies of *Halobates* were more common by night than by day. The two species of

Halobates that inhabit the Indian Ocean are *Halobates micans* and *Halobates germanus* both

of which occur in water with a temperature greater than 25 ̊C (Harada 2005). *Halobates*

micans is the only species that can be found in all three ocean basins, while *H. germanus* is

widely regarded as occurring mostly in coastal waters (Cheng 1985; Harada et al. 2013). It is

suggested here that the lower abundance of *Halobates* in day-time trawls reflects net

avoidance and night blindness, as these animals detect food by sight or via the sensory

detection of water ripples created by struggling prey at the ocean surface (Sagaydachnyy

1975; Cheng 1985), suggesting a sensory disadvantage during the night.

As noted earlier, the other species/morphospecies that were slightly more common by day

than night were *Enneagonum hylinum*, *Lucifer* and Ostracod 4. Of the seven recognised

species of *Lucifer/Belzebub* (Vereshchaka et al. 2016), all have been identified in the Indo-

Pacific (Antony 2005; Naomi et al. 2006). Although most species seem to reach greatest

abundances in coastal and neritic waters rather than in the open ocean (Antony 2005), they

may nevertheless dominate zooplankton biomass at mesopelagic depths in oligotrophic

waters (Steinberg et al. 2008). That said, although Holdway and Maddock (1983) noted the

presence of *Lucifer* in neuston samples collected across the Indian Ocean, it was not abundant

– an observation in agreement here. There is limited information on the DVM of *Lucifer* in

867 oceanic waters, though it does display strong DVM in coastal waters (Woodmansee 1966;

868 Moreira et al. 2007). In the oligotrophic waters off Hawaii, Steinberg et al. (2008) noted that

869 *Lucifer* did not show pronounced DVM. In other crustacean species, the powers of DVM may

870 develop ontogenetically, with adults displaying stronger DVM than juveniles (e.g. Ringelberg

871 2009). Mature females tend to carry eggs in a loose sac for at least a short time following

872 fertilisation, and none of the specimens collected here supported any egg sacs. While it could

873 be argued that these "small" specimens were all juvenile, and so therefore perhaps less likely

874 to display pronounced DVM, it should be remembered that all species of *Lucifer/Belzebub*

875 are small in size and that the eggs sacs can be readily dislodged on capture (Naomi et al. 2006

876 and references therein).

877 Ostracods are frequently the second most abundant taxon in the plankton after copepods

878 (Angel 1999), and more than 200 species are known from different depths in the world ocean.

879 Purushothaman (2015) documents 26 species from 17 stations in the Arabian Sea, while

880 Drapun and Smith (2012) note over 40 species from more extensive sampling in the same

881 area: Graves and Angel (2017) record 41 species from a single station in the Gulf of Ohman.

882 The majority of species are found at depths greater than 200 m, but some species can be

883 collected in abundance in near surface waters (Angel 1999; Morales-Ramírez and Jakob

884 2008). Information on the DVM of planktonic Ostracods is scant, and this behaviour remains

885 undocumented for the majority of species (Angel 1999). Some species do show very

886 pronounced DVM, whilst others do not, and this behaviour does not appear to be linked to

887 occupational depth (Angel 1999). In some species, the early juvenile stages may occupy

888 shallower depths than the adults and if the species undertakes a seasonal or any other form of

889 migration, it might reflect an absence in the sampling if the full range is not covered (Angel

890 1999). Most carnivorous zooplankton will feed on Ostracods, as too will many mesopelagic

891 fishes (Uchikawa et al. 2001; Bernal et al. 2015) and the siphonophores *Hippopodius*

892 *hippopus*, *Diphyes dispur* and *Chelophyes appendiculata* appear to favour Ostracods as food

893 (Angel 1999). The higher night than day abundance of Ostracod 3 is not therefore

894 unexpected, especially as some species appear able to detect the net and to display net

895 avoidance (Angel et al. 2007), but quite why the abundance of Ostracod 4 was higher by day

896 than night is unknown. Ostracods were reported commonly in the nocturnal samples of

897 neuston collected by Holdway and Maddock (1983), especially from the central Indian Ocean

898 (their Area 4). Ostracod sp 3 was more abundant in neuston samples in the east of the transect

899 sampled here (Figure 8), which agrees too with the observations of Holdway and Maddock

900 (1983), who noted greatest contributions by Ostracods to the neuston in (their) Areas 2 and 3,
901 which correspond to the Banda, and Banda and Java Seas, respectively.

902 Although Rezai et al. (2019) recorded few siphonophores in the neuston of the NE Persian
903 Gulf, Holdway and Maddock (1983) found them to be common across all the transects they
904 investigated, as too they were here. Of the 23 species noted, eight were recorded in all
905 longitudinal bins (Table 6) and, as noted previously, *Abylopsis eschscholtzii* was most
906 abundant followed by *Chelophyes contorta* and *Bassia bassensis* (Table 6). Although similar
907 species (and numbers of species) were recovered amongst assemblages of very-near surface
908 siphonophores in the Colombian Pacific, Uribe-Palomino et al. (2019) noted that *Diphyes*
909 *dispar, Eudoxoides mitra, C. contorta* and *Muggiaea atlantica* were the most common
910 species, respectively. The fact that the latter of these was not recovered here reflects its
911 coastal distribution (e.g. Thibault-Botha et al. 2004), and is no surprise. Interestingly, Uribe-
912 Palomino et al. (2019) recorded few specimens of *B. bassensis*, which together with *A.*
913 *eschscholtzii* here dominated assemblages around 85° E. This species can be very abundant in
914 subtropical waters (e.g. Pagès et al. 2001) but tends to be uncommon closer to the shelf (e.g.
915 Pagès and Gill 1992). *Abylopsis eschscholtzii* dominated siphonophore assemblages in the
916 tropical Sargasso Sea (Lüskow et al. 2019), where it failed to display DVM. Neither did this
917 latter species appear to display DVM in the Celebes or Sulu Seas (Grossmann et al. 2015),
918 though these authors did note that it was one of the most shallow-living of the 90-odd species
919 recovered.

920 In their study of neuston in the North Atlantic, Hempel and Wikert (1972) observed that
921 chaetognaths made a generally small contribution to the neuston, an observation in agreement
922 with that of Brodeur et al. (1987) in the NE Pacific. Grant (1991) recorded 17 species of
923 chaetognaths in the hyponeuston of the Mid-Atlantic Bight, noting that they were generally
924 less common there than in sub-surface waters. That said, Grant (1991) did comment upon the
925 fact that species with warm-water and subtropical affinities were more regularly encountered
926 in the hyponeuston than at greater depths. By contrast, Nair et al. (1989) noted that
927 chaetognaths were common in the central Arabian Sea, Rezai et al. (2019) noted that they
928 were not uncommon in the NE Persian Gulf, and they were the second most abundant taxon
929 recorded by Holdway and Maddock (1983), especially in the coastal waters off Somalia.
930 They were the sixth most abundant taxon recovered in this study, though notably absent from
931 longitudinal bin 85, and all specimens were juveniles. This is in contrast to the results of
932 previous studies (e.g. Grant 1991), where it is assumed all collected material was adult since

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933   no reference to the presence of juveniles is made. Kehayias et al. (1994) have observed that

934   juveniles of mesopelagic species of chaetognaths in the Eastern Mediterranean may occur at

935   shallower depths than adults, as too did Besiktepe and Unsal (2000) in the SW Black Sea.

936   The latter authors observed that while adult chaetognaths displayed DVM, individuals less

937   than 5 mm in length (juveniles) did not.

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943 **Table 6:** Taxa responsible for similarities within, and differences between the three clusters

944 identified in Figure 10c.

Longitudinal Bin	95-105 (42.6%	Others (41,75%)	75-85 (37,98%)	(95-105) vs Others (61,74%)		(95-105) VS (75-85) (69,38%)		(75-85) vs Others (62,91%)	
				95-105	Others	95-105	75-85	Others	75-85
Morphospecies									
Abylopsis eschscholtzi	0,82	1,14	1,25	0,82	1,14	0,82	1,25	0	0
Alima 1	0,54	0	0	0,54	0,38	0,54	0,09	0,38	0,09
Amphipod 1=2	0,00	0	0	0	0	0	0	0	0
Amphipod 11	0	0	0	0	0	0	0	0,17	0,17
Amphipod 12	0	0	0	0,49	0,15	0,49	0,18	0	0
Amphipod 13	0	0	0	0	0	0	0	0,13	0,2
Amphipod 16	0	0	0	0,43	0,04	0,43	0,09	0	0
Amphipod 21	0	0	0	0	0	0	0	0,23	0,08
Amphipod 9	0,68	0	0	0,68	0,56	0,68	0,19	0,56	0,19
Bassia basensis	0	0	0,7	0,29	0,5	0,29	0,7	0,5	0,7
Chaetognath larvae	1,27	0	0	1,27	0,97	1,27	0,38	0,97	0,38
Chelophyes appendiculata	0	0	0	0	0	0	0	0	0
Chelophyes contorta	1,05	0,91	0,91	1,05	0,78	0	0	0,78	0,91
Decapod larvae 0	0	0	0	0,48	0,69	0,48	0,18	0,69	0,18
Decapod larvae 2 (crab larvae)	0	0	0	0,55	0,19	0,55	0,08	0	0
Diphyes bojani	0	0	0	0,34	0,28	0,34	0,25	0,28	0,25
Diphyes dispur	0	0	0	0,47	0,36	0,47	0,17	0,36	0,17
Doliolid sp.	0,58	0	0	0,58	0,25	0,58	0,25	0,25	0,25
Enneagonum hyalinum	0	0	0	0,36	0,47	0,36	0,27	0,47	0,27
Eudoxoides mitra	0	0	0	0,35	0,23	0,35	0,17	0,23	0,17
Eudoxoides spiralis	0	0,8	0,8	0,4	0,89	0,4	0,8	0,89	0,8
Euphausiid	0	0	0	0,11	0,34	0,11	0,5	0,34	0,5
Euphausiid larvae	0	0	0	0,31	0,22	0,31	0,26	0,22	0,26
Fish B	0	0	0	0	0	0,17	0,43	0,13	0,43
Fish C	0,54	0	0	0,54	0,44	0,54	0,18	0,44	0,18
Janthina	0	0	0,62	0,28	0,59	0,28	0,62	0,59	0,62
Lensia hotspur	0	0	0	0	0	0	0	0,18	0,34
Lensia subtilis	0	0	0	0	0	0	0	0,19	0,17
Lucifer	0,75	0,75	0	0,75	0,55	0,75	0,17	0,55	0,17
Mysid	1,00	1	0	1	0,81	1	0,61	0,81	0,61
Ostracod 1	0	0	0	0	0	0,12	0,33	0,28	0,33
Ostracod 3	0,98	0,98	0,62	0,98	0,53	0,98	0,62	0,53	0,62
Ostracod 4	0	0	0	0,35	0,42	0,35	0,35	0,42	0,35
Physalia	0	0	0	0,45	0,09	0,45	0	0	0
Porpita	0	0	0	0,17	0,24	0	0	0,24	0,08
Pteropod 1	0	0	0	0	0	0	0	0	0
Pteropod 10 (Shell A)	0	0,5	0	0,5	0,59	0,5	0,18	0,59	0,18
Pteropod 11	0	0	0	0,51	0,43	0,51	0,63	0,43	0,63
Pteropod 3	0	0	0	0	0	0	0	0	0
Pteropod 8 (Atlanta sp)	0	0	0	0,35	0,27	0	0	0,27	0,17
Sulculiolaria biloba	0	0	0	0,29	0,17	0,29	0,25	0,17	0,25
Thalia	0,70	0	0	0,7	0,75	0,7	0,46	0,75	0,46
unidentified fish larvae	0,86	0,86	0	0,86	0,62	0,86	0,17	0,62	0,17
Vellela	0	0	1,12	0,42	1,03	0,42	1,12	0	0
Water strider A	0,53	0,53	0	0,53	0,19	0,53	0,08	0	0
Water strider B	0,88	0	0	0,88	0,39	0,88	0,17	0,39	0,17
Water strider C	0,56	0	0	0,56	0,14	0,56	0,17	0	0
Zooanthidae larvae	0	0	0	0,33	0,23	0,33	0,08	0,23	0,08

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Meroplankton was represented by a wide variety of taxa but was dominated, for the most part, by larvae of Decapods, Stomatopods and fish. Larvae of brachiopods, polychaetes, bryozoans, gastropods, bivalves and echinoderms were rare, though they were conspicuous in the study of Holdway and Maddock (1983) from across this same area. Indeed, the latter authors noted that meroplankton represented about 33% of the non-copepod neuston, whereas here they constituted between 9% and 21%, being more abundant at the longitudinal extremes of the transect than at the centre. If we accept that waters along the transect have their origin, in part, from the east and from the Indonesian throughflow jet (Dufois et al. 2017 and references therein), then perhaps the high numbers of meroplankton found in samples collected close to Jakarta and Christmas Island can be explained by their proximity to the coral or East Indies triangle (Hoeksema 2007; Veron et al. 2009). Coral reefs support very rich associated communities, especially of Decapods (Klompmaker et al. 2013 and references therein) and Stomatopods (Barber et al. 2002), many of which have planktonic larval development. As this advected water moves westward from the coast and into open ocean water, it is likely that the meroplanktonic species drop out of assemblages, as has been noted by Ayata et al. (2011) for polychaetes in the Bay of Biscay and Meerhof et al. (2018) for Decapod larvae around Easter Island. It is then perhaps no surprise that the number of such benthic meroplankton are low between 75-85° E. Moving further westward still, the numbers of zoanthid and Decapod larvae and Stomatopod alima once again begin to increase, which could reflect the southward advection of waters from the Mascarene Plateau, because the diversity of both taxa is known to be relatively high off the east coast of Africa (Reaka et al. 2008; Head et al. 2018).

Mysids were found across the sampling area, being slightly more common in the east than the west, which is subtly at odds with the observations of Holdway and Maddock (1983). The latter authors noted that these crustaceans were more abundant in the Indian Ocean than elsewhere, but that they were slightly more common close to the African coastline than they were in the Banda and Java Seas. Mysids were significantly more common in samples collected at night than they were during the day, which agrees with previous observations (e.g. Hempel and Wieckert 1972; Holdway and Maddock 1983). While mesopelagic species of mysid may not display pronounced DVM (Andersen and Sardou 1992; Hopkins et al. 1994), this behaviour is frequently noted by shallow water (e.g. Kouassi et al. 2006) and lotic species (Beeton and Bowers 1982). Epipelagic species of mysid are generally uncommon in the open ocean and are characterised by *Siriella thompsoni* and *Anchialina typica* (Murano

979 and Mauchline1999), which tend to be associated with warm water. Hempel and Wieckert
980 (1972) noted that both species descended to about 200 m during the day before reappearing in
981 surface waters at night.

982 Whilst doliolids were scarce, salps, including morphospecies of *Thalia* (as well as
983 *Traustedtia* and *Salpa*) were relatively common across the sampling area, and were slightly
984 more numerous in night-time than day-time tows. Holdway and Maddock (1983) also noted
985 the presence of both taxa in their Indian Ocean samples, at frequencies that what would
986 appear to be similar to those noted here. That said, few other students of neuston have
987 remarked on the presence of thaliaceans in their collections, despite the fact that these
988 organisms are known to graze microplastics very effectively (Brandon et al. 2020). Although
989 some species of salp are known to display pronounced DVM for reproductive purposes
990 (Madin et al. 1996), it is clear that others do not (Gibbons 1997) and attempts to interpret the
991 data recovered here would be speculative in this regard. More work on this group remains to
992 be done, because they are not generally regarded as members of the neuston (but see also
993 Mantha et al. 2019).

994 Tropical and warm water assemblages of pelagic amphiods are typically more diverse than
995 those in cooler waters (Vinogradov 1999), and after Copepoda, Amphipoda is probably the
996 most diverse group of holopelagic crustaceans. Given this, their richness in neustonic samples
997 is perhaps no surprise. The absence of any distinct latitudinal pattern in amphipod assemblage
998 structure across the transect agrees with the observations of Vinogradov (1999). The latter
999 author noted that "… species compositions are relatively homogeneous within the vast
1000 tropical anticyclonic gyres, and dominant species are also more or less similar in the
1001 various collections…". The distinct diel difference in assemblages undoubtedly reflects
1002 DVM (Vinogradov 1999; Holdway and Maddock 1983) and the movement into the surface
1003 waters of species that typically reside at greater depths during the day.

1004 The sea-surface represents an important nursery area for many epi- and mesopelagic fish
1005 species, and a wide variety of forms can be found there, usually as eggs and larvae (e.g.
1006 Doyle 1992), where they may represent important diet items for marine birds, mammals and
1007 larger fishes (Olivar et al. 2015). Although there are relatively few studies of the neustonic
1008 ichthyofauna in the open Indian Ocean, Olivar et al. (2015) recorded 14 larval taxa in their
1009 transect from west to east at ~25°S, and assemblages were dominated by Myctophidae and
1010 Exocoetidae. Here, only eleven morphospecies were recovered (no eggs), in very low

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numbers, and although most failed to display clear day-night differences in abundance (as Holdway and Maddock 1983, but unlike Olivar et al. 2015), Morphospecies C was more common by day than night. In the absence of any identification, however, it is not possible to explain this behaviour. Neustonic fish larvae are notoriously patchy in their distribution (Olivar et al. 2015), and this could explain the absence of any spatial pattern to the distribution of assemblages here. That said, diversity and abundance were greater at the eastern part of the transect than in the centre or to the west, probably as a result of contributions from the Indonesian Throughflow jet (see above).

Hempel and Weikert (1972) also observed species of *Creseis* to be more common by day than night, while Holdway and Maddock (1983) noted heteropods to be more more common at night than day. Diel vertical migration by Pteropods was noted by van der Spoel and Dadon (1999), while Richter and Seapy (1999) refer to the occasional abundance of heteropods in neuston samples, which is thought to be for reproductive purposes. Interestingly, the latter authors report that *Halobates* may use floating heteropod egg masses for oviposition. Sea-swallows (*Glaucus* sp.) were rare, and while *Janthina* were recorded across the region they were slightly more common to the west. Both these latter species are predators of the neustonic hydrozoans *Porpita, Velella* and *Physalia* (Lepoint et al. 2016; Pinotti et al. 2019), but there was no correlation (Pearson's *R*) between the abundance of the two groups ($p > 0.05$).

Less common taxa

Isopods are known to occur in neuston samples, though not frequently and not in large numbers (Holdway and Maddock 1983; Brodeur et al. 1987). As here, where a total of 11 individuals from four morphospecies were observed (Table 1; Figure 13). Isopods of the genus *Idotea* and *Eurydice* are typically more common in neuston samples from near-coastal waters (Holdway and Maddock 983; Brodeur et al. 1987; Echelman and Fishelson 1990), where they can also be associated with rafting algae and other flotsom (Thiel and Gutow 2004 and references therein). The absence of *Sargassum* or other floating debris may account for the general scarcity of isopods in our samples.

Euphausiids were relatively uncommon across the transect (Table 1) and only two morphospecies were identified, putatively *Euphausia brevis* and *Stylocheiron* sp. While

neither morphospecies was caught regularly in the centre of the transect, the former was more common in the west and the latter in the east. Both species were slightly more abundant by night than day, an observation in agreement with previous studies (Holdway and Maddock 1983; Brodeur et al. 1987; Echelman and Fishelson 1990). As in previous studies, larvae (some calyptopes but mostly furcilia) were always more abundant than adults, but like adults they too were more common at night than by day (as Holdway and Maddock, 1983). Euphausiids are often regarded as micronekton and are known to perform pronounced DVM (e.g. Pillar et al. 1992).

Although polychaetes occurred at low average abundances, five morphospecies were observed. These included one *Tomopteris*, three Alciopidae and miscellaneous larvae (considered here as one morphospecies) (Table 1: Figure 13). With the exception of the larvae, about which little can be said, the other taxa are regarded as holoplanktonic (Fernández-Alamo and Thuesen 1999). The absence of (e.g.) nereids suggests floating substrata were absent from neuston samples (as noted too above with regard to isopods), as these benthic taxa may commonly occur amongst *Sargassum* and other flotsom (Baker et al. 2018). The taxa recorded here were noted too by Brodeur et al. (1987). Polychaetes were more common towards the east (Holdway and Maddock 1983) and were found exclusively at night (Table 7). Information regarding the DVM of pelagic polychaetes is thin: deeper-living species of *Tomopteris* in cooler water do not appear to display any change in vertical distribution (Guglielmo et al. 2014), though tomopterids and alciopids in the Sargasso Sea have been shown to be very strong migrators (Eden et al. 2009).

Gastropod larvae (of unknown origin) were uncommon (Figure 13), as observed too by Holdway and Maddock (1983) in the Indian Ocean, which is perhaps no surprise if they are the product of benthic forms. In neuston samples collected in coastal waters of the northern Red Sea and Gulf of Aqaba, however, Gastropoda (identity not stated) were almost as abundant as copepods, and were more abundant at night than by day (Mantha et al. 2019). Given that bivalve larvae were also very numerous in the latter study, as too were a number of other meroplanktonic forms, it is likely that the Gastropoda recovered by Mantha et al. (2019) were larvae. Liparoto et al. (2017) found in the Western Mediterranean and Southern Adriatic Sea that apart from the eueneuston, gastropod veligers were the most widely distributed taxa and were found at all the stations sampled. Which again is no surprise given the neritic nature of the environment sampled.
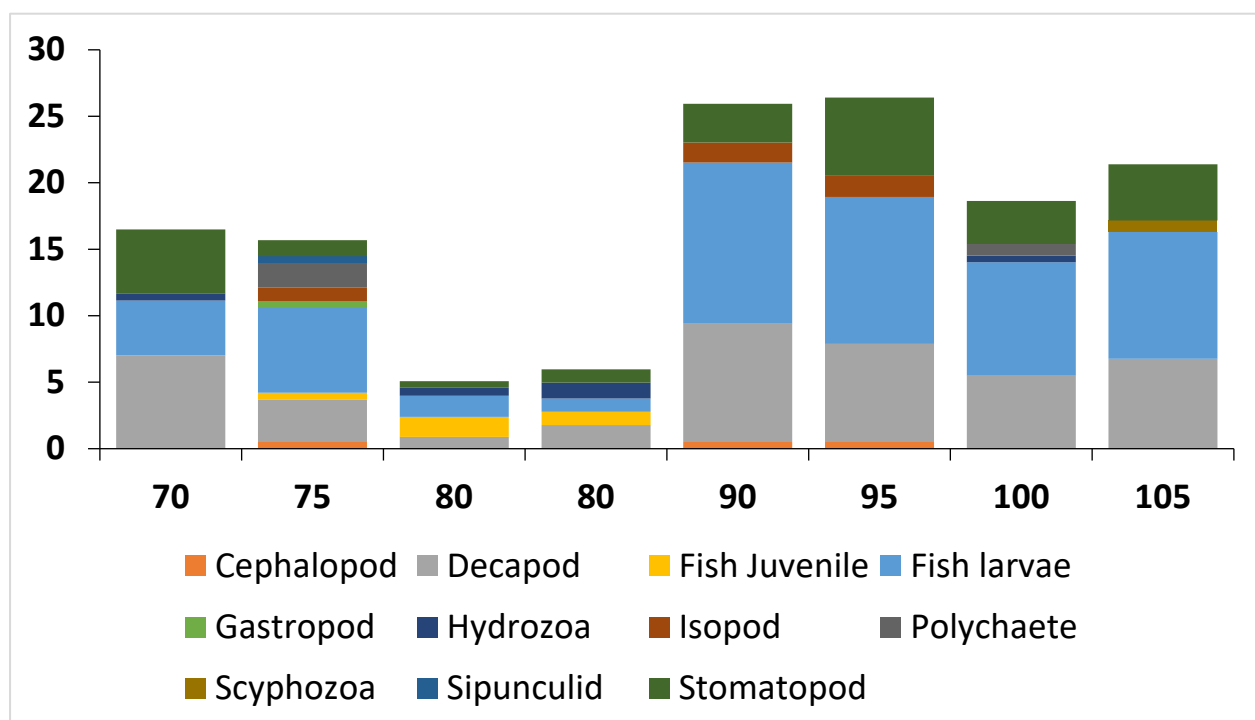
Figure 13: Average abundance of non-major taxa across all longitudinal classes.

Diel vertical migration

The diversity and abundance of the neuston was higher at night than during the day, as euneuston was supplemented with facultative neuston following DVM (Figures 6a, c). As noted above in reference to the individual taxa, many facultative members of the neuston move into the surface waters at night in order to feed and escape predators (Williamson et al. 1996). The significant role that the time of day plays in shaping the structure of neuston assemblages has long been recognised (Hempel and Weikert 1972), but it means that unless there is an equal balance of samples across day and night time-series, it is very difficult to rigorously investigate the role played by any other factors simultaneously. Hence, as here, further analyses were partitioned by time of day.

The marginal tests of the DistLM indicate aspects of the chlorophyll environment (sea surface fluorescence, integrated fluorescence, depth of the fluorescence maximum and value of fluorescence at the fluorescence maximum) were all correlated with assemblage structure at night. But not during the day. The euneuston is dominated by carnivores: *Physalia* (Bieri 1970; Holdway and Maddock 1983), *Velella* (Purcell et al. 2015; Betti et al. 2019), *Porpita* (Sahu et al. 2020), *Janthina* (Churchill et al. 2011), *Glaucus* (Thompson and Bennett 1970; Sahu et al. 2020), *Halobates* (Cheng 1985), as are chaetognaths (Stuart and Verheye 1991; Albuquerque et al. 2021), siphonophores (Mackie et al. 1988) and most hyperiid amphipods

1102   (Shulenberger 1977). The link between these species and the fluorescent environment is

1103   therefore indirect. By contrast, herbivorous/detritivorous taxa (including Pteropods, salps,

1104   mysids, euphausiids and Ostracods), which tended to be at least twice as common in neuston

1105   samples at night than by day (Table 7), are likely to be directly influenced by fluorescence. It

1106   is perhaps not surprising then that overall assemblage structure was more influenced by

1107   fluorescence at night than during the day. That said, in the full DistLMs generated for night

1108   and day assemblages, aspects of the fluorescence environment were incorporated into both

1109   (with similar overall weightings, Tables 4b and 5b), implying perhaps that its impact is "felt"

1110   both directly and indirectly.

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1113 **Table 7:** Diel changes in the abundance of major taxa, averaged across samples per station;

1114 data as root-root numbers per trawl.

Taxon	Day	Night
Amphipod	1,232	4,201
Barnacle	0	0
Cephalopod	0	0,077
Chaetognath	0,983	0,955
Decapod	1,368	1,668
Doliolid	0,271	0,349
Euphausiid	0,296	0,787
Fish Juvenile	0,067	0,051
Fish larvae	1,479	1,328
Gastropod	1,871	3,025
Heteropod	0,033	0
Hydrozoa	0,980	1,141
Isopod	0,067	0,155
Mysid	0,478	1,026
Ostracod	0,929	1,713
Polychaete	0,000	0,316
Salp	0,582	1,191
Scyphozoa	0	0,107
Siphonophore	5,509	6,796
Sipunculid	0	0,026
Stomatopod	0,209	0,813
Water strider	0,590	1,162
Zooanthidae	0,170	0,205

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Longitudinal patterns displayed by neuston

The use of morphospecies complicates clear interpretation of the longitudinal patterns because, as noted earlier, a single morphospecies may comprise more than one sibling species, whilst different developmental stages of the same species, may be regarded here as representing separate morphospecies. The latter is especially likely to occur in the case of larval Decapods, polychaetes and even fish larvae, whose anatomy and outward appearance may change quite markedly during development (Williamson 2013). The other taxon that is particularly problematic in this regard isPteropoda, species of which can usually be identified by the nature of their calcareous shell (e.g. Boltovskoy et al. 1996 cited in Boltovskoy 1999). Unfortunately, following prolonged exposure to formalin, the shells of Pteropods had all but dissolved, and animals were separated on the basis of the shape of the remaining body mass and wing-like feet; when the latter had not been retracted. Regardless, every effort was made to be consistent in specimen categorisation to morphospecies and so it is hoped that errors were consistent across the samples.

If we accept the above, and are conservative in our interpretation of the results, then the results suggest the following. Firstly, that assemblages between 75 - 85° E (corresponding to Grids 80 and 85) are distinct (Figures 9 and 10). Secondly, that the easternmost assemblages of the balance (corresponding to Grids 100 and 105) are distinct (Figure 9c), and thirdly that there is an approximate symmetry of the remaining samples around 75 - 85° E (Figure 9c).

During the 12 months prior to the survey, the "centre" of the Southern Indian Ocean Gyre lay approximately along latitude 20°S, and extended from ~95° E westwards to the coastline of Madagascar at ~50° E. At the time of the cruise, its mean position was strongly disrupted by a series of mesoscale eddies (both cyclonic and anticyclonic) ranging in size from 50 - 150 km diameter (Toresen et al. 2015). Two distinct, anticyclonic, warm core eddies, with elevated sea surface heights were detected between 75 - 85° E (Dufois et al. 2017). Conditions in these eddies were distinct from those at the edge, with elevated concentrations of chlorophyll being attributed to deeper convective mixing (Dufois et al. 2017). Assemblages of plankton in the centre of eddies are often distinct from those outside (Dufois et al. 2017; Bernal et al. 2020) due to the horizontal advection of productive waters and deeper vertical mixing in the anticyclonic eddies causing an increase in surface chlorophyll in the anticyclonic eddies in winter in the Southern Indian Ocean Gyre (Dufois et al. 2017). And it is likely that the neuston were behaving similarly here. Interestingly, however, assemblages in this region were generally less abundant, species-rich and diverse than those to either the

1151   east or the west, and were characterised by relatively high numbers of siphonophores and

1152   some holozooplankton (Ostracod 1, Pteropod 11) but low levels of all meroplankton except

1153   fish larva 4. The near absence of meroplankton is perhaps no surprise, given that the majority

1154   of taxa would likely be of benthic forms (Schnack-Schiel and Isla 2005) and the great

1155   distance of this region from the coast; as has been argued above.

1156

1157   The high diversity and distinct nature of assemblages between 95 - 105° E no doubt reflects

1158   the impact of water emerging from the Java and Banda Seas in the Indonesian throughflow.

1159   As noted previously, the East Indies Triangle is a global biodiversity hotspot (e.g. Roberts et

1160   al. 2002) for many benthic or reef associated taxa and is likely to have levels of plankton

1161   diversity too (e.g. Yasuhara et al. 2012). This area was characterised by relatively high

1162   temperatures and low salinities at the surface and neuston assemblages delimited by water-

1163   striders, doliolids and high numbers of chaetognath larvae, *Lucifer* and mysids: zoanthid

1164   larvae were also common. Morphospecies of *Thalia* were also common, but like Pteropod 10,

1165   they were also common in the longitudinal bins around the core at 75 - 85° E.

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Conclusions

Overall, the results of the study were in accordance with much of the previous literature in terms of the general taxa present, though they differed in some respects. The preponderance of Ostracods and juvenile chaetognaths in samples was unusual, while the lack of flotsam meant that many of those organisms that inhabit such structures were missing. The fact that assemblages were generally more diverse towards the margins of the transect is no surprise, given that holoplankton was being supplemented with meroplankton – especially in the east with water from the Indonesian Throughflow: this is as originally hypothesised. Communities were strongly influenced by the time of day, reflecting the diel vertical migration of facultative members, whose abundances and diversity were all greater at night: which again comes as no surprise.

There was a strong agreement between the structure of assemblages and the structure of the physical environment, and it is clear that assemblages in the core of the anticyclonic eddies were distinctly different from those outside, as initially hypothesised. In part this may reflect the drop-out of meroplanktonic forms, but there is a suggestion in the data that the chlorophyll environment may have some role to play in this. More work that couples the physical environment with the neuston is clearly needed, though this study emphasises the value of simultaneously collected data sets in this regard.

This study used morphospecies as identification units, rather that recognised species (with the exception of siphonophores), and I believe this approach holds much promise for future work. It does have its drawbacks as articulated previously, but it does allow, by comparison with (e.g.) ZooScan, a greater resolution in taxonomic identification (Gorsky et al. 2010), without the need for full-blown training in the taxonomy of individual taxa. It is unlikely to be as thorough in its resolution of species units as e-DNA (Garcia-Vasquez et al. 2021) or molecular approaches to identification (Bucklin et al. 2021), but in an African context where the cost of such technologies is so high (let alone the specialist laboratories needed to undertake the work), it does have its advantages (see also Machida et al. 2021).

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1587 **Appendices**

1588

Appendix A

List of morphospecies recovered from neuston samples collected during the IOS Leg 1 survey of the southern Indian Ocean, June-July 2015. Also shown are higher levels of taxonomic classification, the number of CTD tations from which each was recovered and their allocated numbers (see Appendix B).

Number	Morphospecies	Taxon 1	Holo/Mero	Epi/Hypo/Fac	No stations
1	Amphipod 10	Amphipod	Holoplankton	facultative	8
2	Amphipod 11	Amphipod	Holoplankton	facultative	12
3	Amphipod 12	Amphipod	Holoplankton	facultative	11
4	Amphipod 13	Amphipod	Holoplankton	facultative	11
5	Amphipod 15	Amphipod	Holoplankton	facultative	2
6	Amphipod 16	Amphipod	Holoplankton	facultative	6
7	Amphipod 17	Amphipod	Holoplankton	facultative	5
8	Amphipod 18	Amphipod	Holoplankton	facultative	9
9	Amphipod 19	Amphipod	Holoplankton	facultative	3
10	Amphipod 20	Amphipod	Holoplankton	facultative	6
11	Amphipod 21	Amphipod	Holoplankton	facultative	14
12	Amphipod 22	Amphipod	Holoplankton	facultative	1
13	Amphipod 23	Amphipod	Holoplankton	facultative	2
14	Amphipod 24	Amphipod	Holoplankton	facultative	2
15	Amphipod 25	Amphipod	Holoplankton	facultative	1
16	Amphipod 26	Amphipod	Holoplankton	facultative	2
17	Amphipod 27	Amphipod	Holoplankton	facultative	1
18	Amphipod 6	Amphipod	Holoplankton	facultative	10
19	Amphipod 7	Amphipod	Holoplankton	facultative	3
20	Amphipod 8	Amphipod	Holoplankton	facultative	4
21	Amphipod 9	Amphipod	Holoplankton	facultative	20
22	*Phronima* Amphipod 5	Amphipod	Holoplankton	facultative	4
23	*Synopia* Amphipod 1=2	Amphipod	Holoplankton	facultative	21
24	*Vibilia* Amphipod 4	Amphipod	Holoplankton	facultative	6
25	Barnacle larvae - cypris	Barnacle	Meroplankton	facultative	1
26	Cephalopod larvae 1	Cephalopod	Meroplankton	facultative	2
27	Cephalopod larvae 2	Cephalopod	Meroplankton	facultative	2
28	*Spirula*	Cephalopod	Holoplankton	Hypo	1
29	Chaetognath larvae	Chaetognath	Holoplankton	facultative	26
30	Sergestidae	Decapod	Holoplankton	facultative	4
31	Decapod larvae 0	Decapod	Meroplankton	facultative	23
32	Decapod larvae 10	Decapod	Meroplankton	facultative	1
33	Decapod larvae 12	Decapod	Meroplankton	facultative	1
34	Decapod larvae 2	Decapod	Meroplankton	facultative	11
35	Decapod larvae 5=6	Decapod	Meroplankton	facultative	4
36	*Lucifer*	Decapod	Holoplankton	facultative	20
37	Doliolid sp.	Doliolid	Holoplankton	facultative	17
38	*Euphausia brevis*	Euphausiid	Holoplankton	facultative	1
39	Euphausiid	Euphausiid	Holoplankton	facultative	14

40	Euphausiid larvae	Euphausiid	Holoplankton	facultative	15
41	*Stylocheiron* (furcilia)	Euphausiid	Holoplankton	facultative	3
42	Fish A	Fish Juvenile	Meroplankton	facultative	1
43	Fish I	Fish juvenile	Meroplankton	facultative	2
44	Fish J	Fish juvenile	Meroplankton	facultative	1
45	Fish K	Fish juvenile	Meroplankton	facultative	1
46	Fish B	Fish larvae	Meroplankton	facultative	8
47	Fish C	Fish larvae	Meroplankton	facultative	19
48	Fish D	Fish larvae	Meroplankton	facultative	3
49	Fish E	Fish larvae	Meroplankton	facultative	2
50	Fish F	Fish larvae	Meroplankton	facultative	1
51	Fish G	Fish larvae	Meroplankton	facultative	6
52	Fish H	Fish larvae	Meroplankton	facultative	4
53	Fish I	Fish larvae	Meroplankton	facultative	22
54	*Creseis* sp (1)	Gastropod	Holoplankton	facultative	9
55	*Creseis* sp (2)	Gastropod	Holoplankton	facultative	2
56	*Creseis* sp (3)	Gastropod	Holoplankton	facultative	13
57	Gastropod larvae	Gastropod	Meroplankton	facultative	1
58	*Glaucus* sp.	Gastropod	Holoplankton	Hypo	1
59	*Janthina*	Gastropod	Holoplankton	Hypo	20
60	LargePteropod 15	Gastropod	Holoplankton	facultative	1
61	Pteropod 1	Gastropod	Holoplankton	facultative	7
62	Pteropod 10 (Shell A)	Gastropod	Holoplankton	facultative	19
63	Pteropod 11 (Shell B)	Gastropod	Holoplankton	facultative	19
64	Pteropod 12	Gastropod	Holoplankton	facultative	2
65	Pteropod 13	Gastropod	Holoplankton	facultative	1
66	Pteropod 14	Gastropod	Holoplankton	facultative	1
67	Pteropod 2	Gastropod	Holoplankton	facultative	4
68	Pteropod 4	Gastropod	Holoplankton	facultative	3
69	Pteropod 5	Gastropod	Holoplankton	facultative	2
70	Pteropod 6	Gastropod	Holoplankton	facultative	3
71	Pteropod 7	Gastropod	Holoplankton	facultative	1
72	Pteropod 8 (*Atlanta* sp)	Gastropod	Holoplankton	facultative	15
73	Pteropod 9	Gastropod	Holoplankton	facultative	8
74	Heteropod larvae (pterotrachidae)	Heteropod	Holoplankton	facultative	1
75	*Bougainvillia* sp	Hydrozoa	Meroplankton	facultative	4
76	*Porpita*	Hydrozoa	Holoplankton	epi	11
77	Rhopalonematidae	Hydrozoa	Holoplankton	facultative	1
78	*Vellela*	Hydrozoa	Holoplankton	epi	25
79	Isopod	Isopod	Meroplankton	facultative	8
80	Mysid	Mysid	Holoplankton	facultative	24
81	Ostracod 1	Ostracod	Holoplankton	facultative	9
82	Ostracod 3	Ostracod	Holoplankton	facultative	19
83	Ostracod 4	Ostracod	Holoplankton	facultative	18
84	Ostracod 5	Ostracod	Holoplankton	facultative	5
85	Ostracod 7	Ostracod	Holoplankton	facultative	2
86	*Vanadis* sp2)	Polychaete	Holoplankton	facultative	3
87	Polychaete 2	Polychaete	Holoplankton	facultative	2
88	Polychaete 3 (larvae)	Polychaete	Meroplankton	facultative	2

89	*Vanadis* sp1	Polychaete	Holoplankton	facultative	2
90	*Tomopteris* sp	Polychaete	Holoplankton	facultative	1
91	*Iasis zonaria*	Salp	Holoplankton	facultative	5
92	*Pegea*	Salp	Holoplankton	facultative	2
93	*Salpa*	Salp	Holoplankton	facultative	7
94	*Thalia*	Salp	Holoplankton	facultative	27
95	*Trastedia multitentaculata*	Salp	Holoplankton	facultative	2
96	*Pyrosoma*	Salp	Holoplankton	facultative	2
97	Ephyrae	Scyphozoa	Meroplankton	facultative	1
98	*Nausithoe* sp	Scyphozoa	Holoplankton	facultative	1
99	*Pelagia* sp.	Scyphozoa	Holoplankton	facultative	3
100	Scyphozoan 1	Scyphozoa	Holoplankton	facultative	1
101	Scyphozoan 2	Scyphozoa	Holoplankton	facultative	1
102	*Abyla trigona*	Siphonophore	Holoplankton	facultative	6
103	*Abylopsis eschscholtzi*	Siphonophore	Holoplankton	facultative	27
104	*Abylopsis tetragona*	Siphonophore	Holoplankton	facultative	9
105	*Agalma elegans*	Siphonophore	Holoplankton	facultative	1
106	*Agalma okeni*	Siphonophore	Holoplankton	facultative	1
107	*Bassia basensis*	Siphonophore	Holoplankton	facultative	18
108	*Chelophyes appendiculata*	Siphonophore	Holoplankton	facultative	17
109	*Chelophyes contorta*	Siphonophore	Holoplankton	facultative	27
110	*Diphyes bojani*	Siphonophore	Holoplankton	facultative	17
111	*Diphyes dispur*	Siphonophore	Holoplankton	facultative	18
112	*Enneagonum hyalinum*	Siphonophore	Holoplankton	facultative	22
113	*Erenna* sp.	Siphonophore	Holoplankton	facultative	1
114	*Eudoxoides mitra*	Siphonophore	Holoplankton	facultative	11
115	*Eudoxoides spiralis*	Siphonophore	Holoplankton	facultative	26
116	*Hippopodius hippopus*	Siphonophore	Holoplankton	facultative	6
117	*Lensia campanella*	Siphonophore	Holoplankton	facultative	2
118	*Lensia hotspur*	Siphonophore	Holoplankton	facultative	7
119	*Lensia subtilis*	Siphonophore	Holoplankton	facultative	6
120	*Physalia*	Siphonophore	Holoplankton	epi	9
121	*Sulculiolaria biloba*	Siphonophore	Holoplankton	facultative	12
122	*Sulculiolaria chuni*	Siphonophore	Holoplankton	facultative	8
123	*Vogtia glabra*	Siphonophore	Holoplankton	facultative	4
124	Sipunculid larvae	Sipunculid	Meroplankton	facultative	1
125	Alima 1	Stomatopod	Meroplankton	facultative	17
126	Alima 2	Stomatopod	Meroplankton	facultative	1
127	Alima 3	Stomatopod	Meroplankton	facultative	3
128	Stomatopod 1	Stomatopod	Meroplankton	facultative	2
129	Stomatopod 2	Stomatopod	Meroplankton	facultative	2
130	Stomatopod 3	Stomatopod	Meroplankton	facultative	1
131	Stomatopod 4	Stomatopod	Meroplankton	facultative	3
132	Water strider A	Water strider	Holoplankton	epi	12
133	Water strider B	Water strider	Holoplankton	epi	20
134	Water strider C	Water strider	Holoplankton	epi	12
135	Zooanthidae larvae	Zooanthidae	Meroplankton	facultative	14

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1596

1597   Appendix B.

1598   Average abundance (root-root numbers) of neuston morphospecies (see Appendix A for

1599   details) recovered from samples collected during the IOS Leg 1 survey of the southern Indian

1600   Ocean, June-July 2015. Also shown are details regarding the time of day (day, D; Night, N:

1601   Dusk, Dk; Dawn, Dn) of sample capture and gridded longitudinal bin (e.g. 65 - 70° E = 70).

1602

Longitude Bin	105	105	105	100	100	100	95	95	95	95	95	90	90	90	90	90	85	85	80	80	75	75	75	75	75	70	70
Time of Day	D	N	N	N	D	Dk	D	Dk	N	D	N	N	D	D	N	N	Dk	N	N	D	D	N	D	Dk	N	Dn	N
Number	500	503	504	506	508	509	511	512	513	514	515	516	517	518	519	520	523	524	527	529	531	532	534	535	536	537	539
1	0,439	0	0	0	0	0,498	0	0	0,396	0	0	0	0	0	1,016	0	0	0,333	0	0	0	1,917	0	0,978	0	0	0
2	0	0	0,333	0,835	0	0	0	0,333	0,333	0	0,396	0,333	0,439	0	0,333	0	0,333	0	0,333	0	0	0,333	0	0	0	0	1,029
3	0	1,217	0,333	1,593	0,333	0,498	0	2,349	0	0	0	0	0	0	0	0	0,396	0	0,522	0	0,333	0	0	0	0,333	0	0,895
4	0	0,73	0	0,439	0	0,835	0	0	0	0	0,333	0	0,396	0	0	0,333	1,351	0	0	0	0	0	0	0,333	0,333	0	0,439
5	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0
6	0	1,84	0	0,855	0	0,73	0	0	0	0	0,333	0	0	0	0	0	0,439	0	0	0	0	0	0	0	0,333	0	0
7	0	0,439	0	0,396	0	1,083	0	0,911	0	0	0	0	0	0	0	0	1,503	0	0	0	0	0	0	0	0	0	0
8	0	0,498	0	0,333	0	0,333	0	1,107	0	0	0,439	0	0	0,667	0	0	0,333	0	0	0	0	0	0	0	0,593	0	0,439
9	0	0	0	0	0	0	0	0,333	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0
10	0,333	0	0	0,333	0	0,835	0	0,894	0	0	0	0	0	0,333	0	0	0,561	0	0	0	0	0	0	0	0	0	0
11	0,838	0,333	0	0,333	0	0	0,471	0,333	0,396	0	0,667	0,333	0	0	0,333	0	0,333	0	0	0	0	0,333	0	0	0	0,333	0,471
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0
13	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0
14	0	0	0	0	0	0,561	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0,705	0	0	0	0	0	0	0,607	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333
18	0	0,498	0	0,396	0	0	0	1,12	0	0	0,498	0	0	0	0	0	0	0	0,333	0	0	0,396	0	0	0,939	0,439	0,793
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,396	0	0	0,396	0	0	0,333	0	0	0	0	0	0
20	0,333	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0,396	0	0	0	0	0	0,333	0	0	0	0	0	0
21	1,357	1,679	0,333	1,417	0	0,805	0	0,471	1,833	0,333	0,772	0,835	0	0	1,534	0,667	0,471	0	0,561	0	0,333	1,165	0	1,307	1,334	0	1,184
22	0	0	0	0	0	0,73	0	0	0	0	0	0	0,333	0	0	0	0	0	0,333	0	0	0	0	0,333	0	0	0
23	0	2	0	3,083	0,835	2,905	0	0,333	2,615	0	2,251	1,29	1,636	0,396	2,309	1,876	1,249	0,667	1,863	0	0	1,742	0,333	1,59	2,09	0	2,516
24	0	0	0	0,667	0	0	0	0	0,333	0	0	0	0	0	0,396	0	0	0,396	0	0	0	0,333	0	0	0	0	0,396
25	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0
28	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	3,193	2,987	1,738	3,411	2,648	1,959	2,991	4,226	3,317	1,594	2,228	1,61	1,333	2,258	2,047	0,868	0,333	0	2,014	0	0,439	0,396	0,793	0,753	0,396	1,251	1,564
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0,333	0	0	0,993	0	0	0	0	0,396
31	0,793	1,839	0	0,73	0,396	0	0,73	1,475	1,719	0,73	0,832	1,291	0,73	1,059	0,73	0,333	0	0,333	0,593	0	0,333	0	0,333	0,772	0,667	0,333	1,063
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,396	0	0	0	0	0	0	0	0	0	0	0
34	0,333	1,546	0	1,988	0	0,772	0	0	0,333	0	0	0	0,333	0	0	0,73	0,333	0	0	0	0	0	0	0	0,805	0,333	1,461
35	0	0	0	0,542	0	0	0	1,66	0	0,577	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0
36	3,035	0,333	0,832	1,452	0	1,231	1,89	2,072	0,957	1	0,396	0,667	0	1,052	0,333	0,333	0	0	0,805	0	0,868	0	0	0	0,333	0,333	0,835
37	0,793	1,455	0	0,772	0,333	0,73	0,667	1,2	0,396	0	0	0	0,396	0	0,333	0	0,333	0,396	0,333	0	0,333	0	0	0	0,333	0	1,274
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,498	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0,73	0	0,333	0,333	0,333	0,333	0	1,487	0	0,542	0,667	1,736	0,396	1,485	0	0	0	0	1,082	1,219	0	1,825
40	1,038	0,333	0	0,822	0	0,439	0,333	0,471	0,667	0	0,333	0,439	0	0	0,471	0	0,439	0	0,73	0	0	0	0	0,805	0,439	0	1,386
41	1,157	0	0	0	0	0	0	0	0,772	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0
43	0	0	0	0	0	0,333	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,667	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0
46	0	0	0	0	0	1,063	0	0	0	0	0	0,667	0,333	0	1,063	0	1,201	0,333	0	0,333	0	0,333	0	0,333	0	0	0
47	0	0,333	0,895	0,396	2,004	0,73	0	0,333	0,333	0,667	0,73	0	1,211	0,772	0,73	0,868	0	0,868	0	0	1,063	0	0,333	0,333	0,835	0,333	0

Longitude Bin	105	105	105	100	100	100	95	95	95	95	95	90	90	90	90	90	85	85	80	80	75	75	75	75	75	70	70
Time of Day	D	N	N	N	D	Dk	D	Dk	N	D	N	N	D	D	N	N	Dk	N	N	D	D	N	D	Dk	N	Dn	N
Number	500	503	504	506	508	509	511	512	513	514	515	516	517	518	519	520	523	524	527	529	531	532	534	535	536	537	539
48	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0,396	0	0,396	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	0,805	0	0,333	0,667	0	0,333	0	0	0	0	0,396	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0
52	0	0	0,333	0,793	0	1	0	0	0	0	0,396	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	1,294	1,294	1,063	1,168	0,667	0,333	0,73	2,459	0,868	1,524	1,39	0	0,73	1,376	0	0,333	0,333	0	0,333	0	1,264	0	0,439	0,439	0	1,201	1,231
54	0,471	1,35	0	0,333	0	0,577	0	0,911	0	0	0	0,667	0,333	0,522	0	0	0	0	0	0	0	0,471	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0,439	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	1,543	1,29	0	0,772	0	0	0,333	0,793	0	0	0,333	0	0,333	0,471	0	0	0	0	0	0,333	0,333	0,333	0	0	0,333	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,439	0	0
59	0,333	0	0	0,73	0	0,73	0,333	1,375	0	1,211	0,542	0,876	0	1,126	0	1,168	1,347	0	0,333	1,377	1,126	0,667	0	0,439	0,918	1,542	0,73
60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,396
61	0,396	0,396	0	0,73	0	0,333	0	0,333	0	0	0,439	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0
62	0	1,201	0	1,824	0	1,214	0,333	0,832	0	0,667	0,894	0,805	1,379	0,396	0	1,105	0,91	0	0	0	0,333	1,612	0,333	0	1,59	1,377	0,97
63	0	0,73	0	1,905	0	2,042	0	0,73	0,667	0,805	0,667	0,667	0	0,333	0,396	0,667	1,383	0,73	1,105	0	0,333	0,799	0,396	1,299	1,251	0	0
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,396	0	0,498	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0
67	0	0	0	0	0	0,396	0	0	0	0	0	0	0,333	0,333	0	0	0	0	0	0	0	0,396	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0,333	0	0	0	0,333	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0,667	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0,396	0	0	0	0,333	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0
72	0,333	0,73	0	0,73	0	0,577	0	0	0	0	1	0,396	0,333	0	0,439	0,333	0	0,333	0,333	0	0	0,333	0	0,439	0,835	0	1,126
73	0,396	0	0	0,333	0	0,835	0	0,333	0	0	0,333	0	0	0	0	0,396	0	0	0	0	0	0	0	0,333	0	0	0,667
74	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0,396	0	0	0	0	0	0,333	0	0	0,333
76	0	0	0	0,333	0,73	0	0	0,835	0,333	0	0	0	0,333	0	0	0	0	0	0,333	0	0,439	0	0	0,333	0,835	2,031	0,396
77	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0,333	0	0	1,168	1,835	0,333	1,438	1,639	0,96	2,062	1,479	2,025	1,674	1,393	2,384	1,676	2,33	1,063	1,353	0,894	1,436	1,455	1,53	1,472	1,927	2,035
79	0	0	0	0	0	0	0	1,063	0,73	0,333	0	0,333	0	0,333	0,333	0	0	0	0	0	0	0,333	0	0	0,333	0	0
80	1,642	3,701	0	4,44	0,73	3,655	0,333	1,517	2,917	0	2,731	2,477	2,38	0,333	2,166	1,168	2,173	0,333	2,215	0	0,439	1,245	0	2,336	0,73	0,396	4,28
81	0	0	0	0	0,805	0	0	0	1,166	0	0	0,333	0	0	1,685	0	0	0,333	1	0	0	1,168	0	0,832	1,231	0	0
82	2,624	3,925	0	6,203	0,333	2,957	0,333	0	2,412	0	1,3	2,196	1,946	0	1,88	1,439	0,793	0,439	1,396	0,471	0	0	0	1,217	1,059	0	1,71
83	0,333	0	0	1,479	0,333	0,333	0	1,704	0	0,561	0,333	0	0,772	0,333	0	0	0	0	0,73	0	0,868	0,667	0,667	0,73	0,667	1,105	0,396
84	0	0,656	0	0	0	0	0	0	0	0	0	0,333	0	0	0,333	0	0	0	0	0	0	0	0	0,333	0	0	0
85	0	0	0	0	0	0	0	0,667	0	0	0,73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0,396	0	0,333
87	0	0,333	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0,577	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,244	0
89	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333
90	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0,522	0,471	0	0,522	0	0,396	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333
92	0	0	0	0	0	0,333	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0,333	0	0,835	0	0	0	0	1,258	0	0,333	0	0	0	0,667	0	0,396	0	0	0	0	0	0	0	0	0	0,396
94	0,498	0,772	1,063	1,314	0,396	0,868	0,667	0,333	1,347	0,333	0,805	0,73	1,168	0,333	1,333	0,73	0,868	1,238	0,471	0	1,063	0,793	0,333	0,868	0,835	1	1,274

Longitude Bin	105	105	105	100	100	100	95	95	95	95	95	90	90	90	90	90	85	85	80	80	75	75	75	75	75	70	70
Time of Day	D	N	N	N	D	Dk	D	Dk	N	D	N	N	D	D	N	N	Dk	N	N	D	D	N	D	Dk	N	Dn	N
Number	500	503	504	506	508	509	511	512	513	514	515	516	517	518	519	520	523	524	527	529	531	532	534	535	536	537	539
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0,396	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0,667	0
97	0	0,577	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0,73	0	0,333	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0,333	0,333	0	0,333	0	0	0,333	0	0	0	0	0,333	0,333	0	0	0	0	0	0	0
103	1,138	0	0,835	1,534	2,516	1,856	1	3,065	1,82	2,472	2,114	1,73	2,087	2,013	3,857	1,805	2,646	3,286	2,445	1,77	2,132	2,843	2,256	2,915	2,72	2,031	2,015
104	0,333	0	0,498	0	0	0	0	0	1,103	0,396	0	0	0	0,396	0,62	0	0	0	0,333	0	0	0	0	0	0	0	0,667
105	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0
107	0	0,577	0	0,333	1,228	0	0	0	3,033	0,333	0	0,396	0,396	0	4,261	0,805	0,333	2,937	2,02	0	0,471	1,334	0	2,909	0,73	0,439	0
108	0,73	0	0	0,96	0,439	0,333	1,063	1,032	0,876	0	0,522	0,73	0	0	0,868	0	0,439	0	0,793	0	0	0,333	0	0,667	0,396	0	0,667
109	1,614	1,634	1,126	1,933	1,8	0,73	0,396	1,166	1,294	0,333	0,805	1,165	1,818	0	0,835	0,667	1,031	1,512	0,772	1,437	1,366	1,515	0,333	1,924	1,42	0,73	1,126
110	0,333	0,333	0	0,73	0,396	0,333	0,333	0,333	0,333	0	0	0,333	0	0	0,333	0,333	0	0,73	0,333	0	0	0,333	0	1,063	0,73	0	0
111	0,868	0	0	0,895	1,211	0,333	0,396	0,396	0,667	0,333	1,211	0	0,793	0,607	1,165	0	0	0,772	0	0	0,396	0,333	0	0,396	0,333	0	0,333
112	0,73	0	0,471	0,396	0,832	0,333	0	0,333	0,333	0,877	0	0,333	1,272	0,333	0,667	0,396	0	0,577	0	0,805	1,287	0,561	0,957	0,522	1,833	0	0,333
113	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0,333	0	0	1,357	0,333	0,439	0	0	1,138	0	0	0,667	0	0	0,396	0,793	0	0	0,772	0	0	0	0	0,73	0,667	0	0
115	0	0,772	0,333	0,333	0,835	0,396	0,667	1,51	1,748	1,078	1,02	0,333	1,412	1,253	2,33	1,27	0,805	1,745	0,667	0,772	1,201	1,703	0	1,498	1,696	0,772	1,231
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0,333	0	0,333	0	0,667	0,333	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0,333	0	0	0
118	0	0	0	0	0	0	0	0	1,168	0,396	0	0	0	0	1,671	0	0	0,396	1	0	0	0	0	0,333	0	0	0
119	0	0	0	0	0,396	0	0	0	1,347	0	0	0	0	0	0,926	0	0	0	0,73	0	0,333	0	0	0	0	0	0
120	0	0,333	0,667	0,805	0,667	0,333	0	0	0,333	0	0	0	0	0,333	0	0	0	0	0	0	0	0,333	0	0	0	0,667	0
121	0,471	0,73	0	0	0	0,667	0	0	0,911	0	0	0	0	0	0	0,333	0	0,396	0	0,333	0,333	0	0	0	0,73	0,805	0,471
122	0	0,439	0	0	0,396	0	0	0	0,73	0	0	0	0	0	0,667	0	0	0,333	0	0,396	0	0,333	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0,396	0	0	1,103	0	0	0	0,667	0	0	0	0	0	0	0,577	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0
125	0	1,825	0,667	1,491	0	0,333	0,396	1,849	0,542	0,957	1,36	0,877	0	0,396	0,333	0	0,396	0	0	0	0	0	0	0,333	0,805	0,439	0,772
126	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0,333	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,73
128	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,063
129	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,333
131	0	0	0	0	0	0,396	0	0	0	0	0	0	0	0	0	0,333	0	0	0	0	0	0	0	0	0	0	0,333
132	0	0	1,063	1,091	0,333	1,382	0	0	0,333	0	0	0	0	0	0	0	0	0	0,333	0	0	0,333	0,333	0,333	0,73	0,333	1,168
133	0,396	0,943	1,705	1,829	0,73	2,25	0,333	0	0	0	0	0	0,333	0	0,333	0,793	0	0,396	0,333	0	1,481	0,97	0,333	0,667	1,21	0,333	1,487
134	0	0,868	1,127	0,498	0,989	1,254	0	0	0	0	0	0	0	0	0	0	0,333	0	0	0,333	0,333	0	0,439	0,396	0,805	0	1,031
135	0,333	0,333	0,333	0,333	0,333	0,333	0	0	0	0	0	0	0	0,333	0,667	0	0	0	0,333	0	0	0,333	0	0,667	0,333	1,105	0