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1 **The MADRidge Project: Bio-Physical coupling around three shallow seamounts in the**
2 **South West Indian Ocean**

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19 **ABSTRACT**

20 Compared with other ocean basins, little is known scientifically about the seamounts in the
21 Indian Ocean. Nonetheless, fishers have plundered these fragile ecosystems for decades, and
22 now mining is becoming a reality. We introduce a multidisciplinary project referred to as
23 MADRidge that recently focused on three shallow seamounts in the South West Indian
24 Ocean between 19°S and 34°S. The larger Walters Shoal (summit at 18 m) discovered in
25 1963 occupies the southern part of the Madagascar Ridge and has long received attention
26 from the fishing industry, and only recently by scientists. In contrast, nothing is known of the
27 northern region of the ridge, which is characterised by a prominent, steep-sided seamount that
28 has a flat circular summit at 240 m and width of ~20 km. This seamount is some 200 km
29 south of Madagascar and unnamed; it is referred to here as the MAD-Ridge seamount.
30 MAD-Ridge is the shallowest of a constellation of five deeper (>1200 m) seamounts on that
31 part of the ridge, all within the EEZ of Madagascar. It lies in a highly dynamic region at the
32 end of the East Madagascar Current, where mesoscale eddies are produced continuously,

33 typically as dipoles. The Madagascar Ridge appears to be an area of great productivity, as
34 suggested by the foraging behaviour of some tropical seabirds during chick-rearing and a
35 longline fishery that operates there. The third seamount, La Pérouse, is located between
36 Réunion Island and Madagascar. With a summit 60 m below the sea surface, La Pérouse is
37 distinct from MAD-Ridge and Walters Shoal; it is a solitary pinnacle surrounded by deep
38 abyssal plains and positioned in an oligotrophic region with low mesoscale activities. The
39 overall aim of the MADRidge project was to examine the flow structures induced by the
40 abrupt topographies, and to evaluate whether biological responses could be detected that
41 better explain the observed increased in fish and top predator biomasses. The MADRidge
42 project comprised a multidisciplinary team of senior and early career scientists, along with
43 postgraduate students from France, South Africa, Mauritius and Madagascar. The
44 investigation was based around three cruises using the French vessels RV *Antea* (35 m) and
45 RV *Marion Dufresne* (120 m) in September 2016 (La Pérouse), November/December 2016
46 (MAD-Ridge) and May 2017 (Walters Shoal). This manuscript presents the rationale for the
47 MADRidge project, the background, a description of the research approach including the
48 cruises, and a synopsis of the results gathered in the papers published in this Special Issue.

49

50

51

52 *Keywords:* Madagascar Ridge, Walters Shoal, La Pérouse, seamounts, current-topography
53 interaction, biological productivity, foodweb, fisheries and governance

54

55

56 1. Seamounts and their importance

57

58 Distinctive and often spectacular, seamounts are typically extinct volcanoes that rise abruptly
59 above the surrounding deep-ocean floor but do not reach the sea surface; they are often
60 referred to as undersea mountains (Wessel, 2007). Most are deep, but some come to within
61 100 m of the sea surface. They also commonly exist along ocean ridges. An example is the
62 South West Indian Ridge that stretches 7700 km from Bouvet Island in the South Atlantic
63 Ocean (54°25'S, 3°22'E) to the Rodriguez triple junction at 70°E in the Indian Ocean
64 (Munsch and Schlich, 1989; Sauter and Cannat, 2010; Figure 1a). Other examples are
65 found in the northern Pacific, the volcanic 5800-km-long Hawaii-Emperor chain having >80
66 seamounts, and in the southern Pacific, the 4300-km-long Louisville Seamount Trail
67 (Koppers et al., 2011). Seamounts arise from tectonic plate dynamics and mantle-melting
68 anomalies (i.e. deep-mantle plumes known as hotspots).

69

70 Ship acoustic soundings are understandably limiting in terms of spatial coverage, but
71 nowadays satellite altimetry can confidently detect seamounts taller than ~1.5 km, and studies
72 have produced seamount catalogues holding some 14 000 seamounts (Kitchingman et al.,
73 2007) as shown in Figure 1a. Of these, 62% are in the Pacific, 20% in the Atlantic, 12% in
74 the Indian, and 6% in the Southern oceans. Based on the size-frequency relationship for
75 larger seamounts, Kitchingman et al. (2007) predicted more than 100 000 seamounts >1 km
76 in height that remain uncharted. Globally, 50% are within Exclusive Economic Zones (EEZ),
77 but the proportion drops to 32% in the West Indian Ocean (FAO area 51). Harris et al.
78 (2014), using a new digital global seafloor geomorphic features map (GSFM) recognised a
79 total of 9951 seamounts and 283 guyots (seamounts with flat summits attributable to wave
80 erosion), covering a total area of 8 796 150 km² — approximately 30% of the global shelf
81 region. As a consequence of more-restrictive criteria on (conical) seamount shape excluding
82 reef-shaped features, Harris et al. (2014) counted less seamounts than in previous studies
83 (Kitchingman et al., 2007; Yesson et al., 2011).

84

85 Seamounts represent a very special kind of biological hotspot in the deep ocean, often
86 maintained by peculiar physics and resultant but fragile ecosystems. They often interact with
87 ocean currents, creating high levels of variability in the mesoscale domain. Nearfield effects
88 of seamounts have been predicted theoretically for several decades, but only recently has

89 theory been confirmed by observation. Apart from altering flow patterns, the flow-
90 topography interaction can cause Taylor columns and quasi-stationary eddies over and near
91 seamounts, impacting both the benthic and pelagic communities overlying seamounts (White
92 et al., 2007). Such interactions also cause downstream effects such as eddy fields (Huppert
93 and Bryan, 1976; Herbette et al., 2003). These physical processes induce vertical water
94 movement, resulting in nutrients moving into the photic layer of the ocean. Consequently, it
95 is often hypothesised that seamounts carry above-average-size plankton populations that
96 subsequently attract fish aggregations, which in turn fall prey to further predation, making
97 seamounts important biological hotspots (Pitcher and Bulman, 2007). Suspension-feeding
98 animals tend to dominate the summit and flanks of seamounts, creating dense benthic
99 communities of cold-water stony corals, sea fans, black corals and sponges that in turn create
100 habitat for numerous animals including dense aggregations of fish (Buhl-Mortensen et al.,
101 2010). Rowden et al. (2010) found that seamounts support higher epibenthic megafaunal
102 biomass than adjacent continental slopes. This increased productivity and aggregational
103 effect is also an enticement for foraging seabirds that at times travel hundreds of kilometres
104 to these feeding grounds. Haney et al. (1995) demonstrated that, relative to adjacent waters in
105 the Central North Pacific, seabird density and biomass within the vicinity of seamount
106 summits were 2.4 and 8 times higher, respectively, and highlighted that some seabird taxa
107 can even be up to 40× more abundant around the studied seamount than in the wider Central
108 North Pacific.

109

110 However, seamounts are also not all the same. They differ in form, size, depth and location,
111 which combined with the ambient oceanography, creates unique local environmental and
112 biogeographical conditions that impact faunal composition (Samadi et al., 2007). Along with
113 geographic isolation, seamounts have been likened to oceanic islands, where endemism and
114 species richness can be great (Barton, 1998). Certainly Taylor columns promote larval
115 retention and aggregation (Boehlert and Mundy, 1993; Rogers, 1994; Mullineaux and Mills,
116 1997). Mullineaux and Mills (1997) and Richer de Forges et al. (2000) suggested that
117 geographic isolation and retentive mechanisms could lead to a reduction in gene flow.
118 Although the issue of the “island effect” and consequently unique seamount ecosystems is
119 still unresolved, a review by Clark et al. (2010) concluded that seamounts do host diverse and
120 abundant benthic communities, but often the composition is broadly similar to that of
121 adjacent continental slopes. The same authors further indicate that whereas high levels of

122 endemism on seamounts is found, the concept of “islands in the sea” is not well supported.
123 This is because connectivity levels between seamounts varies considerably, with some taxa
124 having limited dispersal capabilities and hence localized distributions, and others with
125 dispersal ranges of hundreds to thousands of kilometres.

126

127 The aggregation effect of seamounts is well-known by the commercial fishing industry, with
128 many seamounts supporting (or formerly supporting) extensive fisheries, both pelagic
129 (Fonteneau, 1991; Marsac et al., 2014) and benthic (Clark et al., 2007; Pitcher et al., 2010). In
130 the 1960s, deep-sea trawlers in search of new fish stocks began to trawl seamounts and
131 discovered large aggregations of commercially important fish species, targeting orange
132 roughy (*Hoplostethus atlanticus*), oreos (*Neocyttus rhomboidalis*, *Pseudocyttus maculatus*),
133 alfonsinos (*Beryx splendens*), grenadiers (*Coryphaenoides rupestris*) and toothfish
134 (*Dissostichus* spp.) (Clark et al., 2007). Heavily built bottom trawls are towed from the
135 summit down the flanks of seamounts to capture these fish. Many of the species are slow-
136 growing, long-lived and mature at a late age, so have low reproductive potential (Morato and
137 Clark, 2007). Consequently, seamount fisheries typically collapse within a few years of
138 initiation, with trawlers then moving on to other unexploited seamounts to maintain the
139 fishery (Roberts, 2002; Norse et al., 2011). These long-lived seamount-associated fish species
140 take a long time to recover, impeding seamount ecosystems restoring to their pristine
141 conditions (Clark et al., 2019).

142

143 The heavy depletion of some fish stocks is not the only concern associated with seamount
144 fishing. Trawling of seamounts can cause extensive damage to fragile coral communities,
145 bringing up not only fish, but large numbers of corals, sponges and other benthic animals
146 associated with the corals (FAO, 2006). Comparisons with unfished seamounts have shown
147 the extent of habitat damage and loss of species diversity brought about by trawling, with the
148 dense coral habitats reduced to rubble and devastating the ecosystem (Clark et al., 2019).
149 Bottom fishing has not been limited to bottom trawls (70% of the vessels), but also includes
150 demersal longlines, demersal gillnets and traps (Bensch et al., 2009). Unsurprisingly,
151 seamount fisheries have become controversial. Several regional fisheries management
152 organisations have recognised vulnerable marine ecosystems (VMEs) and some have
153 established fishing closures for trawling on seamounts (e.g. the Northwest Atlantic Fisheries
154 Organization, NAFO, in 2006, Southern Indian Ocean Fisheries Agreement, SIOFA, in

155 2018), along with compulsory bottom fishing impact assessment measures. However, as
156 already noted, some 50% of seamounts exist in areas beyond national jurisdiction (ABNJ) in
157 the global ocean, which brings additional difficulty in controlling and regulating fishing
158 activities on them. Fishing represents one threat, but deep-sea mining and drilling activities
159 would add another threat to benthic ecosystems of seamounts with mineral resources
160 (Wessel, 2007). So far, only exploration contracts have been granted by the International
161 Seabed Authority, ISA (Figure 1b), but through the Mining Code, protection measures have
162 to be implemented by the contractors, including environmental management plans (ISA,
163 2019). Note here that the South West Indian Ridge is receiving particular attention.

164

165 Despite the large number of seamounts in the global ocean and the negative anthropogenic
166 attention they have attracted, it appears that the future of such ecosystems lies in a delicate
167 balance between protection and exploitation.

168

169 **2. Indian Ocean has fewest and least known seamounts**

170

171 As mentioned by Demopoulos et al. (2003), the seamounts of the Indian Ocean are among the
172 least explored. As seen in Figure 1a, the majority of seamounts are located in the western
173 part of the basin with the South West Indian Ridge (SWIR) being particularly conspicuous.
174 Throughout the South West Indian Ocean (SWIO), the Soviet fleet targeted red mullet, also
175 sometimes known as redbait (*Emmelichthys nitidus*) and rubyfish (*Plagiogeneion*
176 *rubiginosus*), with catches peaking around 1980 and then decreasing in the mid-1980s (Clark
177 et al., 2007; Rogers et al., 2017). Fishing switched to alfonsino in the 1990s as new
178 seamounts were exploited. Some exploratory trawling was carried out on the Madagascar
179 Ridge and SWIR by French vessels in the 1970s and 1980s, particularly targeting the Walters
180 Shoal and Sapmer Bank (Collette and Parin, 1991). In the 1990s and early 2000s new
181 fisheries developed in both regions. Along the SWIR, a major fishery developed on the high
182 seas targeting orange roughy, black cardinal fish (*Epigonus telescopus*), pelagic armourhead
183 (*Pseudopentaceros wheeleri*), oreos (Oreosomatidae) and alfonsino (Clark et al., 2007). In
184 both cases, fisheries were characterised by a very rapid expansion of effort followed by a
185 collapse in catches (Boyer et al., 2001; Branch, 2001; Clark et al., 2007). Thereafter, fishing
186 shifted to the Madagascar Ridge, Mozambique Ridge and Mid-Indian Ocean Ridge, where
187 they again targeted alfonsino and rubyfish (Clark et al., 2007). Much of this fishing is

188 undertaken using bottom trawls with a high likelihood of significant adverse impacts on the
189 vulnerable marine ecosystems such as the cold-water coral habitat, predicted or known on the
190 seamounts in the region (Tittensor et al., 2009).

191

192 Two Soviet/Ukrainian research institutes (YugNIRO and Yugrybpoisk) undertook a huge
193 research and exploratory fishing effort (mostly bottom and midwater trawls) on the SWIR
194 (Romanov, 2003; FAO, 2017); more than 80 expeditions were conducted over three decades
195 (1972-2000). The objective was to assess the fishing potential of this largely unknown area,
196 with a focus on seamounts (Figure 2). Oceanographic and environmental observations were
197 made during the expeditions. However, despite these and a series of intensive efforts during
198 the unprecedented International Indian Ocean Expedition (IIOE) between 1959 and 1965
199 (Zeitzschel, 1973), the basin-scale ecology and the fauna inhabiting seamounts of the Indian
200 Ocean, including the SWIR, are poorly known. This in part is due to the ocean's remoteness
201 from nations with large-scale oceanographic research programmes. In an attempt to redress
202 this knowledge deficit, the International Union for the Conservation of Nature (IUCN) in
203 partnership with the United Nations Development Programme (UNDP) and the Global
204 Environment Facility (GEF), supported a ship-based study between 2009 and 2013 to focus
205 on the oceanography and pelagic ecology associated with six seamounts on the SWIR —
206 Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Bank and Atlantis
207 Seamount — and one unnamed seamount on the Madagascar Ridge near Walters Shoal
208 (Figure 3). Summit depths ranged from 90 to 1000 m. The brief was to understand how
209 pelagic ecosystems are influenced by the presence of seamounts, and of course the converse,
210 how pelagic ecosystems interact with seamounts. The first expedition in 2009 used the RV
211 *Dr Fridtjof Nansen* in affiliation with the Agulhas and Somali Current Large Marine
212 Ecosystem (ASCLME) project, and focused on pelagic fauna. The second, in 2011, was
213 devoted to the benthic realm using the RRS *James Cook* (Rogers et al., 2017).

214

215 The findings of the IUCN project represented a step change in the understanding of pelagic
216 ecosystems and processes associated with seamounts in the SWIO. Results showed water
217 mass to have a major effect on community structure across this complex and dynamic region,
218 including the bacterioplankton, phytoplankton, pelagic invertebrates, other micronekton (fish)
219 and even predators such as seabirds (Rogers et al., 2017). Processes likely to influence the
220 distribution of both benthic and pelagic communities of megafauna, including species of

221 fisheries interest, included internal tides and biological phenomena such as provision of
222 additional habitat for prey species including micronektonic crustaceans and cephalopods
223 (Rogers et al, 2017). The study emphasised that even limited sampling effort can significantly
224 improve knowledge of the biodiversity and ecology of that remote part of the Indian Ocean,
225 and moreover, contribute to understanding of seamount ecology in general.

226

227 **3. Seamounts in the vicinity of the Madagascar Ridge — regions of high productivity?**

228

229 *3.1 Prominent seamounts*

230 The Madagascar Ridge is an area extending south of the Madagascar landmass with
231 dimensions of some 400 km in width and 1300 km in length (Figure 3). Water depths over
232 most of the plateau are between 2000 and 3000 m. The southern half of the ridge rises to the
233 prominent Walters Shoal seamount, which comes within 18 m of the surface. South of
234 Walters Shoal, the water depth increases rapidly to more than 3000 m. Beyond this, the 4000
235 m isobath joins the SWIR. The ‘top’ of the seamount has collapsed, and has an average depth
236 around 50 m, with a broken and jagged relief at the edge (more detailed maps are presented
237 later, in Figure 7). The summit is rather bare and covered with massive blocks of calcareous
238 coralline algae (P. Bouchet, pers. comm.). The northern part of the ridge also has several
239 seamounts (>750 m), and one, referred to in our study as the MAD-Ridge seamount, rises to a
240 depth of 240 m below the sea surface (27°29’S, 46°16’E). The western side of the ridge is a
241 steep scarp that runs down into the 5000 m deep Mozambique Basin. The slope of the eastern
242 flank is gentler, leading into the 5000-6000 m deep Madagascar Basin.

243

244 The La Pérouse seamount is located farther north (19°43’S, 54°10’E) than the two other
245 seamounts, 160 km northwest of Réunion Island. It is an extinct volcano reaching 60 m
246 below the sea surface and is surrounded by an abyssal plain at 5000 m — making it a very
247 isolated pinnacle. Owing to the collapse of one side of the seamount, La Pérouse as we know
248 it today has a crescent-shaped summit instead of the more common conical shape of MAD-
249 Ridge and Walters Shoal.

250

251 *3.2 Seabirds and marine mammals*

252 Unlike the eastern Indian Ocean, the western portion is interspersed with islands, which
253 provide a sanctuary for seabirds, a breeding habitat for an estimated 7.4 million pairs totalling

254 31 species (Le Corre et al., 2012). Telemetry tracking data collected between 2003 and 2011
255 by Le Corre et al. (2012) revealed oceanic areas with particularly high seabird density in
256 relation to breeding and foraging (Figure 4a). Seychelles and the Madagascar Ridge (south to
257 the Walters Shoal) are the most populated areas, with a few dense spots also found in the
258 Mozambique Channel and in the Mascarene Basin.

259

260 The Madagascar Ridge area is a major foraging ground of two seabird species — the red-
261 tailed tropicbird (*Phaethon rubricauda*) and Barau's petrel (*Pterodroma barau*) (Le Corre et
262 al., 2012). The red-tailed tropicbird has nine breeding sites in the western Indian Ocean, with
263 the islands of Europa and Nosy Vé in the southern Mozambique Channel hosting almost half
264 the entire population (Le Corre and Jouventin, 1997; Le Corre and Bemanaja, 2009). Barau's
265 petrel, an endemic and endangered species from Réunion Island, also uses the Madagascar
266 Ridge as foraging ground (Pinet et al., 2012; Le Corre et al., 2012; Figure 4b). They alternate
267 between long and short foraging trips during the chick-rearing period (January-April),
268 foraging over the Walters Shoal to replenish the adult reserves (Pinet et al., 2012). Isotope
269 ratios measured on feathers indicate that the Black Bourbon's petrel (*Pseudobulweria*
270 *aterrima*), another endemic and endangered species from Réunion Island, also feeds near Fort
271 Dauphin on the southern Madagascar shelf, where upwelling is regular (Ramanantsoa et al.,
272 2018) and farther south on the Madagascar Ridge (S. Jaquemet, unpublished data). In the
273 Mascarene Basin, the only notable seabird hotspot is Tromelin Island (15°53'S, 54°31'E),
274 characterised by two species of booby (*Sula dactylatra* and *S. sula*), and do not move far
275 offshore (Le Corre et al., 2012). Interestingly, seabird tracking shows no activity in the
276 vicinity of La Pérouse.

277

278 Feeding habitat chosen by seabirds is usually a good indicator of high ocean productivity.
279 The majority of tropical seabirds feed upon small epipelagic prey (Le Corre and Jaquemet,
280 2005) that are distributed within the upper 50 m of the water column. Many seabirds, not
281 being able to dive deeper than a few metres, often rely on surface-dwelling predators such as
282 tuna and dolphins, while hunting, to force fleeing prey up towards the surface making them
283 accessible to seabirds (Harrison, 1990, Jaquemet et al., 2004, 2005, Potier et al., 2007, Hebshi
284 et al., 2008). It is also well-known that tuna are attracted to seamounts (Dubroca et al., 2013,
285 Marsac et al., 2014) making these ecosystems of paramount importance for higher trophic
286 levels.

287

288 It is furthermore noteworthy that the Madagascar Ridge is located on the migration route of
289 several whale species from the SubAntarctic, especially the blue whale *Balaenoptera*
290 *musculus* (Best et al., 2003) and the humpback whale *Megaptera novaeangliae* (Best et al.,
291 1998). The Walters Shoal has been recognised as a possible ‘staging post’ in December for
292 whales migrating south to the Antarctic. Humpback whales are also seen in abundance along
293 the east and southwest coast of Madagascar in austral winter, along with the less numerous
294 southern right whales *Eubalaena australis* (Rosenbaum et al., 2001). At La Pérouse, as
295 revealed by satellite tagging, humpback whales gather and breed in the surrounding areas of
296 the seamount during austral summer (Dulau et al, 2017).

297

298 3.3 Fishing

299 Apart from deep-sea trawling, the region around the Madagascar Ridge is also subject to
300 pelagic longlining by Asian fleets (since the 1960s) and by Spanish, Portuguese and Réunion
301 Island-based French longliners, since the 1990s (IOTC database, [www.iotc.org/data-and-](http://www.iotc.org/data-and-statistics)
302 [statistics](http://www.iotc.org/data-and-statistics)). As shown in Figure 5, there are regional differences in the SWIO among the
303 dominant species caught. Unlike the Mozambique Channel, where yellowfin tuna (*Thunnus*
304 *albacares*) makes up the bulk of the longline catch, the situation is more diversified around
305 the Madagascar Ridge, with swordfish (*Xiphias gladius*) the dominant species in the catch,
306 supplemented by yellowfin and bigeye (*T. obesus*) tuna and albacore (*T. alalunga*). The
307 Madagascar Ridge is in the middle of a west–east decreasing gradient in catches, with an
308 average of 1000-1500 tonnes per 5° square over the period 1995-2017 (IOTC database,
309 www.iotc.org/data-and-statistics). In the vicinity of La Pérouse, tuna and billfish are only
310 exploited by Réunion-based French longliners, which mostly fish the region between
311 Réunion Island and Madagascar (Evano and Bourjea, 2012). Albacore and swordfish are the
312 two species primarily targeted and caught around La Pérouse and other topographic rises
313 west of Réunion Island (www.iotc.org/data-and-statistics).

314

315 The SWIO region, particularly south of Madagascar, is also subject to illegal, unreported and
316 unregulated fishing (IUU), as elsewhere in the high seas (MRAG, 2005). At-sea-trans-
317 shipment is one possible way for illegal catches to be merged with catches from legal fleets,
318 and for that reason, trans-shipment activities must comply with strict rules established by the
319 Indian Ocean Tuna Commission (IOTC) to combat IUU fishing. Boerder et al. (2018) used

320 Automatic Identification System (AIS) vessel-tracking data to locate a IUU trans-shipment
321 hotspot in the vicinity of the Madagascar Ridge.

322

323 **4. Oceanography in the vicinity of the three prominent seamounts**

324

325 Most of what we know about the oceanography near the Madagascar Ridge has been gleaned
326 from satellite observations and ocean models. Few oceanographic expeditions have been
327 there, including during the era of the IIOE (1959-1965). Basic oceanographic data were
328 collected by the Soviet and Ukraine fisheries expeditions in the 1970s and 1980s, but these
329 are scant and not digitised (Romanov, 2003). In more recent years, the most notable scientific
330 surveys have been in the northern region and include the Agulhas Current Sources
331 Experiment in 2001 (ASCEX; Lutjeharms et al., 2000; de Ruijter et al., 2005), the
332 Madagascar Experiment in 2005 (MadEx; Quartly, 2006), and the Agulhas Somalia Current
333 Large Marine Ecosystem (ASCLME) Madagascar cruise in 2008 (Vousden et al., 2008). In
334 2013, a multidisciplinary cruise was undertaken to the Walters Shoal as part of the African
335 Coelacanth Ecosystem Programme (ACEP); however, those data have not been published.

336

337 The longitudinal orientation and length of the Madagascar Ridge is such that it spans
338 contrasting oceanographic conditions. The northern region is subject to high (total) kinetic
339 energy (TKE) because of the termination of the southern branch of the East Madagascar
340 Current (S-EMC) (Figure 6a). The S-EMC is a strong western boundary current that flows
341 along the linear east Madagascar coast with speeds of 1.5 m s^{-1} (Voldsund et al., 2017). On
342 reaching the southern end of the shelf, the flow is understood to undergo several
343 configurations (branches), each of which may only exist intermittently: (1) turns west
344 towards the Agulhas Current (e.g. Gründlingh, 1993); (2) or northwards into the Mozambique
345 Channel (i.e. along the west coast of Madagascar (Srokosz et al., 2004), (3) retroflexion
346 eastwards (similar to the Agulhas Current) to join the shallow South Indian Ocean Counter
347 Current (Palastanga et al., 2007; Siedler et al. 2009; Halo et al., 2014; Menezes et al., 2014),
348 and (4) generation of eddies. At a mesoscale, the high kinetic energy observed in Figure 6b
349 is mostly caused by cyclonic and anticyclonic eddies that spin up adjacent to the shelf, which
350 then propagate west towards the African continent, at times as dipoles (de Ruijter et al., 2004;
351 Ridderinkhof et al., 2013). Eddies are generated monthly with waves/trains of dipoles evident
352 on time-scales of 3–4 months (Siedler et al, 2009). Models suggest that some 50% of the total

353 S-EMC transport heads toward the Agulhas Current and that about 40% flows back into the
354 central Indian Ocean, some via the South Indian Ocean Counter Current. Owing to the
355 southward flow of the warm S-EMC, sea surface temperatures over the northern ridge are
356 high, ranging seasonally between 23 and 26°C (climatological values; [Vianello et al, 2020a](#)).

357

358 Seasonal upwelling also develops on the continental shelf south of Madagascar ([Lutjeharms
359 and Machu, 2000; Machu et al., 2002; Ramanantsoa et al., 2018](#)), which, apart from local
360 ecological benefits, may also provide biological production (plankton) towards the northern
361 part of the Madagascar Ridge, as seen in satellite observations depicting lengthy chlorophyll
362 filaments extending off the shelf (e.g. [de Ruijter et al., 2004](#); their Figure 1). This coastal
363 upwelling appears to be driven by the easterly trade wind and at times the S-EMC
364 ([Ramanantsoa et al., 2018](#)). The MAD-Ridge seamount at 27°29'S (200 km offshore), which
365 rises to 240 m below the sea surface, is located in this very dynamic environment of eddies
366 and retroflection of the S-EMC, and may also benefit from the biological production of the
367 upwelling cell south of Madagascar.

368

369 The shallower Walters Shoal on the southern part of the Ridge at 33°S lies within a
370 completely different dynamic environment — namely at the southern boundary of the South
371 Indian Subtropical Gyre. As seen in [Figure 6b](#), this seamount is located in a region of low
372 kinetic energy (TKE), indicative of less mesoscale eddy activity. High TKE values are found
373 south of the Walters Shoal, caused by eddy shearing of the Agulhas Return Current and
374 Subtropical Front ([Pollard and Read, 2015](#)). With Walters Shoal being in the Gyre, surface
375 currents tend to be weaker. Sea surface temperature climatologies indicate a seasonal range
376 between 23 and 18°C ([Vianello et al., 2020a](#)).

377

378 The Madagascar Ridge is also located in a region of high internal tide energy ([Zhao et al.,
379 2016](#)). Indeed, the entire Mascarene Sill–Madagascar Ridge–Mozambique Channel
380 topographic complex is the epicentre of high internal tide generation in the Indian Ocean.
381 Internal tides are generated by barotropic tidal currents flowing over steep bottom topography
382 in the stratified oceans ([Baines, 1982](#)). Intense internal tidal energy is known to produce
383 vertical mixing and diapycnal upliftment, which can stimulate local biological productivity
384 ([da Silva et al., 2002](#)). Only two studies of internal tides have been undertaken in the SWIO
385 to date. [da Silva et al. \(2009\)](#) found an internal tide generation hotspot at 20-21°S on the

386 Sofala shelf in the Mozambique Channel, with a ray path towards the northern Madagascar
387 Ridge. [da Silva et al. \(2011\)](#), also observed internal waves at the Mascarene Plateau. Satellite
388 images (synthetic-aperture radar) reveal powerful internal waves radiating both to the west
389 and east from a central sill near 13°S, 60°54'E, between the Saya de Malha and Nazareth
390 Banks. Nothing is known of internal waves south of Madagascar.

391

392 The La Pérouse seamount is also located in the South Indian Subtropical Gyre Province
393 ([Longhurst, 2007](#)), as Walters Shoal is, but at a much lower latitude of 19°43'S. Hence La
394 Pérouse experiences warmer temperatures all year round ([Noyon et al., 2020](#)). La Pérouse is
395 similarly subject to low TKE ([Figure 6b](#)), but is situated in the path of the west-flowing
396 South Equatorial Current. Of all three seamounts, La Pérouse is situated in the most
397 oligotrophic environment, highlighted by satellite observations of extremely low surface
398 chlorophyll-*a* concentrations with low variability, all year round ([Jena et al., 2013](#); [Noyon et](#)
399 [al., 2020](#)).

400

401 **5. The MADRidge Project (2016-2017)**

402

403 *5.1 Aims and Objectives*

404 As stated above, seamounts are often used as habitat and feeding grounds for fish and top
405 predators. Certainly, fish catches and seabird observations show the Madagascar Ridge
406 region with its varying shallow and deep seamounts to be an attractant. However, nothing is
407 known of the underlying physical and biological mechanisms that promote the aggregations,
408 or so-called hotspots of biodiversity. The overall aim of the MADRidge project was therefore
409 to investigate this 'observed' heightened productivity, including the responsible physical
410 processes, and to see whether seamounts are the underlying trigger. More precisely, the
411 project aimed to obtain a first description of the pelagic ecosystems in the vicinity of the three
412 regionally prominent shallow seamounts — MAD-Ridge (240 m), La Pérouse (60 m) and the
413 Walters Shoal (18 m). From the large body of published knowledge, we hypothesised that
414 interactions between currents and the seamount topographies were important contributors to
415 enhanced productivity. We hoped to find evidence of enrichment through the vertical
416 movement of deeper nutrient-rich water, and retention by Taylor columns. The spread of
417 these seamounts also made a good case study for testing the influence of latitudinal effects
418 (20-33°S) and ambient contrasting hydrodynamic environments — with all three seamounts

419 showing the presence of marine top predators (pelagic fish, marine mammals or seabirds) at
420 least part of the year. Although benthos sampling was not possible in the MADRidge project,
421 the spread, isolation and geographic location of the seamounts relative to the surrounding
422 landmass also provided an opportunity to investigate connectivity in the region.

423

424 More specific scientific quests in the MADRidge project are given below. These provided
425 guidance for the subcomponent studies published in this special issue.

- 426 a) What physical mechanisms are at play around seamounts and which are important for
427 moving nutrients into the photic zone, in other words, the existence and role of
428 mesoscale eddies, Taylor columns, slope upwelling, hydraulic jumps and vertical
429 diapycnal mixing mechanisms such as internal tides, lee waves, and bores? All of
430 these processes operate on temporal and spatial scales ranging from milliseconds to
431 weeks, and from millimetres to hundreds of kilometres.
- 432 b) Do these physical processes linked to seamounts have a significant effect on the local
433 ecosystem, i.e. is there upwelling and does production reside on the seamounts long
434 enough for trophic transfer towards the upper levels of the foodweb?
- 435 c) In the case of MAD-Ridge, which is in an eddy-rich region, do seamount effects add
436 extra productivity that makes the region special, i.e. is phytoplankton biomass
437 increased at the top and on the slopes of the seamount? If so, do the assemblages
438 differ from the open ocean? Is there a response in the zooplankton component, i.e.
439 influencing biomass and taxa composition of the zooplankton communities on the
440 slopes and around the seamount?
- 441 d) Is micronekton enhanced around the seamounts, i.e. do species composition and
442 biomass of micronekton communities on the slopes and around the seamount differ?
443 Also, does the presence of the seamount have any influence on the vertical day-night
444 migration of micronekton?
- 445 e) Does the taxonomic composition of zooplankton and micronekton differ with latitude
446 within the WIO?
- 447 f) Are seamounts conducive for spawning? If so, which species, and are larvae
448 maintained near the seamount, and what are their connectivity with surroundings
449 areas, i.e. which regions would benefit?

450

451 Overarching these scientific issues, the MADRidge project aimed to provide scientific
452 knowledge for a better understanding of seamount ecosystem functioning, which ultimately
453 might be used to promote and design new management and conservation protocols for the
454 seamounts of the SWIO (FFEM, 2019; Marsac et al, 2020b).

455

456 *5.2. A team of French-South Africa-Madagascar collaboration*

457 A multidisciplinary team of scientists, engineers and students was assembled representing the
458 Institut de Recherche pour le Développement (France), Université de Bretagne Occidentale
459 (France), Ifremer (France), Nelson Mandela University (South Africa), Branch Oceans and
460 Coasts (DEA, South Africa), Université de la Réunion (ECOMAR), University of Cape
461 Town (South Africa), Bayworld Centre for Research and Education (South Africa) and the
462 Institut d’Halieutique et des Sciences Marines (IHSM), (Tuléar) Madagascar. Vessel time
463 was provided by France, with some financial assistance from the Nelson Mandela University
464 for the mooring recovery cruise out of Mauritius. Workshops were held in both South Africa
465 and France to work the data into papers.

466

467 The MADRidge project was also supported by the FFEM-SWIO programme on the
468 “Conservation and sustainable exploitation of deep-sea ecosystems of the South-West Indian
469 Ocean away from national EEZ”, funded by the Fonds Français pour l’Environnement
470 Mondial (FFEM) and conducted by IUCN (FFEM, 2019)

471

472 *5.3 Ships, dates, surveys*

473 The MADRidge project was based mainly on observations around the summits of the three
474 prominent seamounts (Figure 7) — MAD-Ridge (240 m), Walters Shoal (18 m) and La
475 Pérouse (60 m). Two cruises were undertaken using the French vessels RV *Antea* (35 m) and
476 one cruise with RV *Marion Dufresne* (120 m). The RV *Antea* has a scientific complement of
477 10 people. The RV *Marion Dufresne*, being larger, has an increased scientific complement,
478 with part of her time dedicated to the logistics in the French TAAF (Terres Australes et
479 Antarctiques Françaises). In all, 25 scientists were on board that vessel for the Walters Shoal
480 cruise, 8 of which were from the MADRidge team. La Pérouse was surveyed between 15 and
481 30 September 2016 (RV *Antea*, doi: 10.17600/16004500), the MAD-Ridge seamount
482 between 8 and 25 November 2016 for the first leg (RV *Antea*, doi: 10.17600/16004800) and
483 26 November to 13 December 2016 for the second leg (RV *Antea*, doi: 10.17600/16004900)

484 and the Walters Shoal between 22 April and 18 May 2017 (RV *Marion Dufresne*, doi:
485 10.17600/ 17002700). Cruise data can be accessed by contacting the cruise chief scientists
486 with reference to the doi ID of the cruises.

487

488 All three seamounts were sampled in similar ways, using a traditional suite of oceanographic
489 instruments. Temperature, salinity, dissolved oxygen, fluorescence and light profiles through
490 the water column were measured at all stations using a CTD-O₂. A ship-mounted (75 kHz)
491 and Lowered (300 kHz) ADCP were used for along-track (0-600m depth range) and station
492 current profiling, respectively. Seawater was sampled at different depths to measure nutrients
493 (NO₂, NO₃, PO₄, Si(OH)₄) in the upper 1000 m as well as phytoplankton pigments (within the
494 euphotic layer), and to analyse the stable isotope signature of particulate organic matter
495 (POM) and the picoplankton community (only MAD-Ridge Leg 1). Mesozooplankton and
496 ichthyoplankton were collected using obliquely towed Bongo nets (200 and 500 µm) or a
497 multinet (200 µm). Micronekton distribution and biomass were studied using a hydro-
498 acoustic approach (Simrad EK 60 using 38, 70, 120 and 200 kHz) as well as midwater trawls
499 (YGPT mesopelagic trawl with 10 mm mesh at La Pérouse and MAD-Ridge and an Isaacs-
500 Kidd Midwater Trawl with 5 mm mesh at Walters Shoal). Temperature and salinity in the
501 surface waters were also measured continuously using a thermosalinograph (TSG), which
502 contributed to identifying mesoscale features during the cruises.

503

504 At La Pérouse, 11 hydrographic stations (CTD and plankton nets) were sampled, with 4
505 stations far from the seamount for comparison controls (**Figure 7b**). Ten trawls were
506 deployed. The first leg of the MAD-Ridge cruise focused on the hydrography and circulation
507 around the seamount, using a south-north and east-west sampling transect intersecting over
508 the seamount summit (**Figure 7c-d**). In all, 31 stations were sampled over 17 days using a 12-
509 h operational schedule. Leg 2 consisted of a continuous survey made up of several triangles
510 surrounding the seamount (not shown) and focused on the micronekton (hydro-acoustics and
511 mesopelagic trawl). The Walters Shoal cruise, with its wider scope and being shared with the
512 IUCN biodiversity project, consisted of a survey of two weeks of work onsite, with just 12 h
513 per day dedicated to the pelagic component. The second half of each day was dedicated to the
514 benthic component, which is not reported in this Special Issue. Owing to the shallow depth
515 (18-50 m) and the size of the vessel, the centre of the seamount was not sampled. Stations (24

516 in total) were selected around the summit and ranged in depth between 50 m and 1000 m,
517 with CTDs and plankton nets being deployed at each station ([Figure 7e-f](#)).

518

519 Two ADCP (75 kHz) moorings with 400 m temperature and salinity (*Seacat*) arrays were
520 deployed either side of the summit at the MAD-Ridge seamount in a depth of 600 m. These
521 were left for 2 years and only recovered in October 2018, using a chartered private vessel
522 *MV La Curieuse* from Mauritius. These data were too late for inclusion in this issue.

523

524 **6. MADRidge project output synopsis**

525

526 From all the data collected, 13 papers (including this one) have been compiled, and are
527 presented in this volume as a sequence covering ocean physics, ocean colour, plankton,
528 ichthyoplankton, micronekton, connectivity, and seamount governance issues. As indicated
529 above, the overall aim is to provide new knowledge to build an understanding of pelagic
530 ecosystem functioning around seamounts in the SWIO.

531

532 The oceanography papers start by providing broad perspectives centred around the
533 Madagascar Ridge of ocean circulation, eddy kinetic energy (EKE), and meridional gradients
534 of sea surface temperature (SST), mixed layer depth (MLD), Total Heat Flux and chlorophyll
535 (*chl-a*), all based on 20-year climatologies of satellite remote sensing data ([Vianello et al.,
536 2020a](#)). For the ocean circulation in this seldom visited region, a novel approach is used.
537 ‘Virtual moorings’ are created using a time-series of geostrophic currents derived from
538 satellite altimetry. Together, the data highlight the contrasting environments experienced by
539 the three prominent seamounts, and emphasise the overall longitudinal effect on the SWIO. A
540 new technique based on generating a *chl-a* enrichment index (EI) for the entire SWIO, is also
541 developed, then used to demonstrate enhanced productivity at some of the seamounts as well
542 as other features such as the continental shelves ([Demarcq et al., 2020](#)). The two studies
543 mentioned in this paragraph serve as a backdrop to the other, more specialised papers.

544

545 The circulation and hydrography in the immediate vicinity of MAD-Ridge and La Pérouse
546 are then investigated by [Vianello et al., \(2020b\)](#) and [Marsac et al., \(2020a\)](#), respectively.
547 MAD-Ridge being in a very energetic environment, it was expected that the mesoscale
548 dynamics there in the form of strong eddies and dipoles would be found to be the overriding

549 driver of the physical processes, strongly influencing water masses, nutrient and chl-*a*
550 distributions (Vianello et al., 2020b), and moreover in our ‘snapshot’ cruise survey,
551 somewhat obscuring any *in situ* observations of current-topography interactions and
552 processes. Nevertheless, currents at MAD-Ridge were strong, and definitely (albeit small)
553 changes in vertical density and temperature structures were observed around the summit and
554 upper 400 m of slope, but any biological repercussions were outweighed by the presence of a
555 powerful eddy dipole at the time of sampling. Analyses based on altimetry data showed the
556 occurrence of eddies over MAD-Ridge to be common.

557

558 The classical seamount quest to observe retention cells, such as a Taylor column, at the three
559 shallow seamounts is addressed in several papers. However, as with many seamount studies
560 the world over, no conclusive *in situ* observational evidence is found. Theoretical
561 considerations (calculations) using seamount shape, hydrological environment and ocean
562 dynamics around the structures were generally not in favour of the development and
563 maintenance of a Taylor column at certainly MAD-Ridge and La Pérouse (Annasawmy et al.,
564 2020a), but was potentially possible around Walters Shoal (Demarcq et al., 2020).

565

566 The La Pérouse seamount received less attention in the physical oceanography, a
567 consequence of a shorter field campaign (2 weeks), which had to collect many types of
568 measurements — CTD stations, zooplankton tows, midwater trawls and attempts to sample
569 demersal fish at the summit (Marsac et al., 2020a). Close examination of vertical current
570 profiles, as well as nutrients and chl-*a*, showed strong, submesoscale flow instabilities
571 adjacent (0-3 km) to the seamount, with slightly higher zooplankton biomass on the leeward
572 (west) flank of the seamount relative to the eastern flank. These instabilities were generated
573 by the seamount topography, and suggest an island-wake effect. Nevertheless, no remarkable
574 biological enrichment directly associated with La Pérouse could be detected at the time of the
575 cruise. This is an interesting finding, perhaps supported by the fact that neither seabird
576 observations nor tuna catches are notably high in the vicinity of that seamount (Marsac et al.,
577 2020a).

578

579 The impact of seamounts on the pelagic ecosystem is first tackled by Rocke et al. (2020),
580 who focused on the MAD-Ridge seamount. They provide a description of the pico- and
581 nanoplankton communities using flow cytometry. Both the mesoscale environment (dipole)

582 and topographic effects were reflected in the abundance of picoplankton (higher in the
583 anticyclonic eddy and on the slopes of the seamount) and nanoplankton (dominating in the
584 cyclonic eddy). The differences in abundance found above the slopes of the seamount relative
585 to farther afield are perhaps indicative of small-scale current turbulence caused by the
586 topography and the mesoscale activity. [Noyon et al. \(2020\)](#) compared the mesozooplankton
587 communities on the three seamounts using a size-based approach. They demonstrated no
588 significant effect of the topography on zooplankton communities. Possibly not expected, the
589 Walters Shoal had a lesser abundance and different size spectra than the two northern
590 seamounts (MAD-Ridge and La Pérouse), where communities were typical of oligotrophic
591 pelagic ecosystems dominated by small organisms. Seasonal variability is expected at the
592 more temperate latitude of the Walters Shoal, whereas the influence of dynamic mesoscale
593 structures could have masked seamount effects at the two other seamounts.

594

595 Of interest is the role of seamounts in being biodiversity hotspots and especially places in the
596 deep ocean for larval recruitment. In this regard, the paper by [Harris et al. \(2020\)](#) analysed
597 ichthyoplankton assemblages around all three of the seamounts. As for the mesozooplankton,
598 no clear effect of seamount topography was observed on the fish larvae communities.
599 However, a notable result is that neritic larvae were collected in high concentration on the
600 MAD-Ridge seamount, emphasising the influence of the nearby Madagascar shelf in seeding
601 the adjacent offshore environment ([Crochelet et al., 2020](#); [Noyon et al., 2019](#)). Often in
602 satellite observations, filaments of high chlorophyll are visible sweeping offshore for
603 distances of several hundreds of kilometres, following contours of mesoscale structures such
604 as eddies ([de Ruijter et al., 2004](#)).

605

606 Expanding this theme, [Crochelet et al. \(2020\)](#) used an Individually-Based Model (IBM) to
607 further consider the degree of connectivity across and between these prominent seamounts.
608 Results show a weak connectivity between La Pérouse, MAD-Ridge and the Walters Shoal
609 and nursery grounds, as batches of ‘artificial’ larvae (particles) released at each seamount did
610 not reach other suitable areas in substantial numbers. This suggests a mix of self-recruitment
611 and immigration of larvae from nearby coastal areas must be happening at the seamounts,
612 which is confirmed by [Harris et al. \(2020\)](#). Particle retention around the seamounts was
613 greatest at Walters Shoal (~10%), with decreasing magnitudes at the MAD-Ridge seamount
614 and La Pérouse ([Crochelet et al., 2020](#)).

615

616 Micronekton form a crucial link in pelagic foodwebs connecting lower and upper trophic
617 levels. [Annasawmy et al. \(2020a\)](#), using complex hydro-acoustic techniques, examined the
618 micronekton distribution at the La Pérouse and MAD-Ridge seamounts. The data showed
619 that, at the mesoscale, the micronekton distribution responded mostly to the eddy dynamics,
620 following the diurnal dynamics of lower trophic levels (phyto- and zooplankton), with no
621 strong evidence of any ‘seamount effect’ at both sites. However, at a local scale, the acoustic
622 data clearly showed fish aggregation close to the summits of both seamounts, with trawl
623 catches confirming the presence of seamount-associated species ([Annasawmy et al., 2020a](#)).

624

625 [Cherel et al. \(2020\)](#) extended this work and examined the micronekton taxonomy on the three
626 seamounts. They found three families of mesopelagic fish dominating at all three seamounts
627 (myctophids, gonostomatids and sternoptychids), most of them being high-seas species. Few
628 myctophids were pseudo-oceanic fish, highlighting the association with landmasses. The
629 study by [Annasawmy et al. \(2020b\)](#) followed energy fluxes through the food chain using
630 carbon and nitrogen stable isotope analyses on samples collected at La Pérouse and MAD-
631 Ridge. These ranged from particulate organic matter (POM) to micronekton (including
632 gelatinous). Discrepancies between isotopic signatures for the two sites appeared at the
633 lowest trophic levels, mostly reflecting the differences between the oligotrophic environment
634 at La Pérouse and the more productive northern Madagascar Ridge. Overall, it appears that
635 micronekton organisms occupy similar trophic positions at both seamounts despite varied
636 feeding modes.

637

638 Returning to the MADRidge project aims, we confidently believe that we have provided
639 comprehensive first descriptions of the pelagic ecosystems for the MAD-Ridge, La Pérouse
640 and Walters Shoal seamounts. Our *in situ* data showed no evidence of Taylor columns and
641 conspicuous current-topographic driven upwelling at these seamounts, although satellite data
642 highlighted chlorophyll enrichment, particularly at the Walters Shoal. The lack of retentive
643 mechanisms at the seamounts, combined with the results of the modelled connectivity study
644 suggest that “oceanic island” effects are absent and therefore that high levels of endemism is
645 unlikely. This is important for conservation measures. The WIO-wide climatologies of
646 satellite-derived wind, SST, MLD, Total Heat Flux, EKE, Chl-*a*, show stark longitudinal (20-
647 33°S) change in these parameters, but hydrodynamic processes, especially at MAD-Ridge,

648 conceal this effect on the biota. We also need to point out that important aspects that further
649 complement these findings, such as mixing due to internal tides at MAD-Ridge and the
650 formation of cross-shelf chl-*a* filaments south of Madagascar, will be published later.

651

652 Finally, in keeping with the overarching aim of the MADRidge project, i.e. to provide
653 scientific knowledge for the promotion and design of new management and conservation
654 protocols for seamounts in the SWIO, we conclude this Special Issue with a final paper that
655 raises seamount-related governance issues in the SWIO, with an emphasis on fisheries and
656 conservation. In it, the Walters Shoal seamount, fished more than any other and located
657 within an Area Beyond National Jurisdiction (ABNJ), is taken as a case study to explore a
658 new format for marine protected areas (MPAs) that include seamounts in the high seas
659 (Marsac et al., 2020b).

660

661 7. Science into Governance

662

663 The MADRidge project provides the first in-depth investigation of topographically coupled
664 pelagic systems at three prominent shallow seamounts in the SWIO. The work adds to the
665 regional body of knowledge already collected by the IUCN Seamounts project (Rogers et al.,
666 2017). The IUCN project surveyed six seamounts on the SWIR, and one on the Madagascar
667 Ridge north of the Walters Shoal (Figure 3). The MADRidge project presented here now
668 adds the MAD-Ridge, Walter Shoals and La Pérouse seamounts to this body of knowledge.

669

670 In their review of key scientific areas required for improved management and conservation of
671 seamounts, Clark et al. (2012) listed four important areas of required improvements
672 (objectives): (1) new physical and biological research, (2) a global data repository, (3) new
673 analysis tools, and (4) new impact research. We therefore now attempt to measure the
674 scientific outputs of the IUCN Seamounts and MADRidge projects against the first two of
675 these objectives (3 and 4 require additional resources and stakeholders).

676

677 The physical and biological knowledge acquired here makes good progress in describing
678 many of the processes associated with seamounts, across a large latitudinal gradient (19-
679 41°S) and range of morphologies and depths (18-1000 m). As stated by Clark et al. (2012),
680 we confirm that the diverse geological and oceanographic settings explain heterogeneity

681 between seamounts in terms of flow instabilities along the slopes and biological responses, at
682 least in the pelagic realm. The connectivity patterns, investigated by Lagrangian models at
683 various spatial scales, are now better visualised in the SWIO and can be used in planning
684 conservation measures. This is essential to identify the corridors that can drive gene flows
685 between a series of seamounts. However, our description of the biodiversity at the three
686 seamounts remains incomplete. Despite the pelagic biodiversity (represented by zooplankton,
687 fish larvae, and micronekton, including fish, shrimps and squid, being measured at these
688 seamounts, large knowledge gaps remain for the benthic biodiversity (with the exception of
689 the Walters Shoal, where this was addressed during the cruise in 2017 – P. Bouchet, pers.
690 comm.). Furthermore, for completeness, the structure of these ecosystems needs to be
691 modelled. Only then can we have a complete or at least better understanding of the
692 ecosystems.

693

694 Previously, only two areas have been surveyed scientifically, the seamounts of the
695 Mozambique Ridge (25-30°S along 35°E; [Parin et al., 2008](#)) in the 1970s/1980s, and the
696 Walters Shoal with intermittent expeditions since 1964 ([Clark, 1972](#); [Collette and Parin,](#)
697 [1991](#); [Parin et al., 1993](#)), including the *Marion Dufresne* MD208 (doi: 10.17600/17002700)
698 mounted by the MAD-Ridge project. Yet, corals and sponges represent the most fragile and
699 diversified components of seamount biota, and are the first to be damaged by bottom trawls
700 and mining. Benthic biodiversity surveys are undoubtedly activities that need to be promoted
701 in future seamount expeditions. Such knowledge is essential to evaluate whether a seamount
702 has fragile, rare or endemic species, or whether similarities exist with neighbouring
703 seamounts in order to set up management measures at a larger spatial scale. Both the IUCN
704 Seamounts and the MAD-Ridge projects have also contributed to improvements of seamount
705 bathymetries in the SWIO (using single- and multi-beam sounders). These data too are
706 essential for delimiting conservation areas, and have been provided to relevant data
707 depositories.

708

709 To conclude, the scientific information collected on the SWIO seamounts is indeed
710 incomplete and needs to be supplemented. Nevertheless, what is known today after these
711 expeditions can allow refinement of management strategies and perhaps kick-off a science-
712 policy dialogue with WIO member states and regional management bodies specifically
713 focused on seamounts. The Nairobi Convention (UNEP) is a key organisation competent in

714 dealing with areas under national jurisdiction (EEZs), and possibly in the near future, in the
715 ABNJ via the international legally binding instrument (ILBI) for the conservation and
716 sustainable use of marine biodiversity, currently negotiated under the United Nations
717 Convention for the Law of the Sea (UNCLOS). Indeed, seamounts are becoming a topic of
718 concern at the Nairobi Convention (discussed at its 9th Conference of Parties in 2018), under
719 the scientific guidance of the Western Indian Ocean Marine Science Association (WIOMSA)
720 and the IUCN. The Southern Indian Ocean Fisheries Agreement (SIOFA) is another key
721 stakeholder in this dialogue, because it has already established five provisionally designated
722 benthic protected areas that regulate fishing on seamounts.

723

724 In closing, although the MADRidge project has contributed a new, large body of knowledge
725 on seamount functioning, it is clear that more seamount studies should be pursued in the
726 SWIO to reveal the richness of the biota in this unique and seldom visited region. Only with
727 this knowledge can we develop risk assessments and management strategies that have real
728 impact.

729

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731

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743

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745

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1044 **Figure Legends**

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1046 **Figure 1:** (a) Global distribution of seamounts. Based on GEBCO_2014 bathymetric data
1047 (adapted after Rogers, 2019). The South West Indian Ridge is highlighted, as examples of
1048 well-studied chains. The three seamounts examined by the MAD-Ridge project are depicted.
1049 (b) Global distribution of marine mining and exploration contracts (after Rogers, 2018).

1050

1051 **Figure 2:** Map of seamounts explored by the Russian/Ukrainian fishing fleet in the South-
1052 western Indian Ocean between 1972 and 2000 (after Romanov, 2003).

1053

1054 **Figure 3:** Bathymetry (see depth scale) of the Western Indian Ocean highlighting the
1055 Madagascar Ridge (Plateau), the unnamed MAD-Ridge seamount (240 m) and the Walters
1056 Shoal seamount (18 m) on the northern and southern parts of the ridge respectively, and the
1057 La Pérouse seamount (60 m) northwest of Réunion Island (white text). Grey lines delineate
1058 EEZs. Red dots indicate seamounts sampled during the IUCN Seamounts Project.

1059

1060 **Figure 4:** Seabird hotspots in the western Indian Ocean, based on satellite tracking data. (a)
1061 Number of tracking detections calculated per cell of $1^\circ \times 1^\circ$ (after Le Corre et al., 2012). (b)
1062 Density distributions of Barau's petrels during the breeding season, short trips vs. long trips
1063 of 10 birds (after Pinet et al., 2012).

1064

1065 **Figure 5:** Longline catches (by 5° square) of yellowfin (YFT) and bigeye (BET) tuna,
1066 albacore (ALB) and swordfish (SWO) in tonnes between 1995 and 2017, combining all
1067 longline fleet data operating in the Indian Ocean. The 2000 m isobath is represented by a
1068 black line (data sources: IOTC C/E database, 2018, and ETOPO1 database).

1069

1070 **Figure 6:** (a) Modelled speed and velocity at 100 m, as a 5-day average, around 21 May 1997
1071 highlighting major ocean current features of the SWIO (after Biastoch et al., 2009). (b) TKE
1072 (total kinetic energy, $\text{cm}^2 \text{s}^{-2}$) indicating highly energetic regions (1993-2017 average, from
1073 altimetry).

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1075 **Figure 7:** Sampling patterns used for the various cruises and legs. (a) Overview map; (b) La
1076 Pérouse September 2016; (c) MAD-Ridge Leg 1 November 2016; (d) Zoom-in over the
1077 summit; (e) and (f) Walters Shoal April/May 2017.

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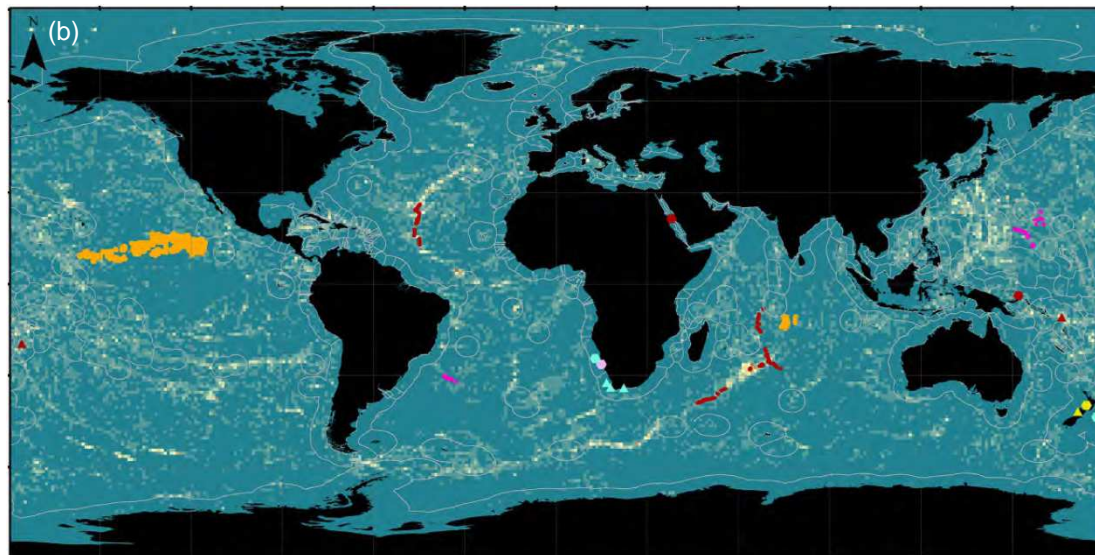
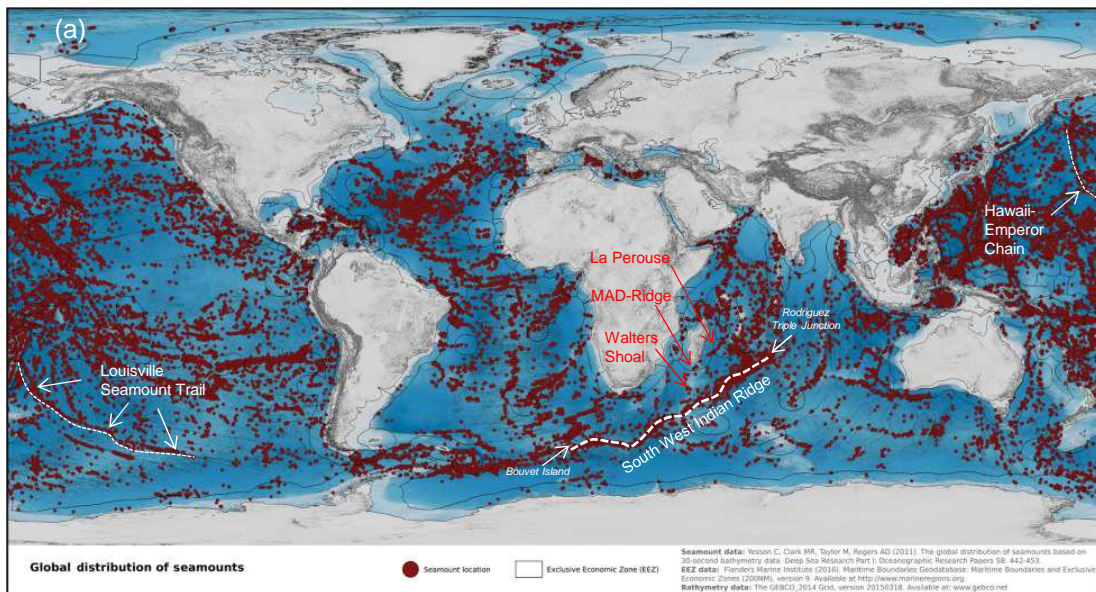


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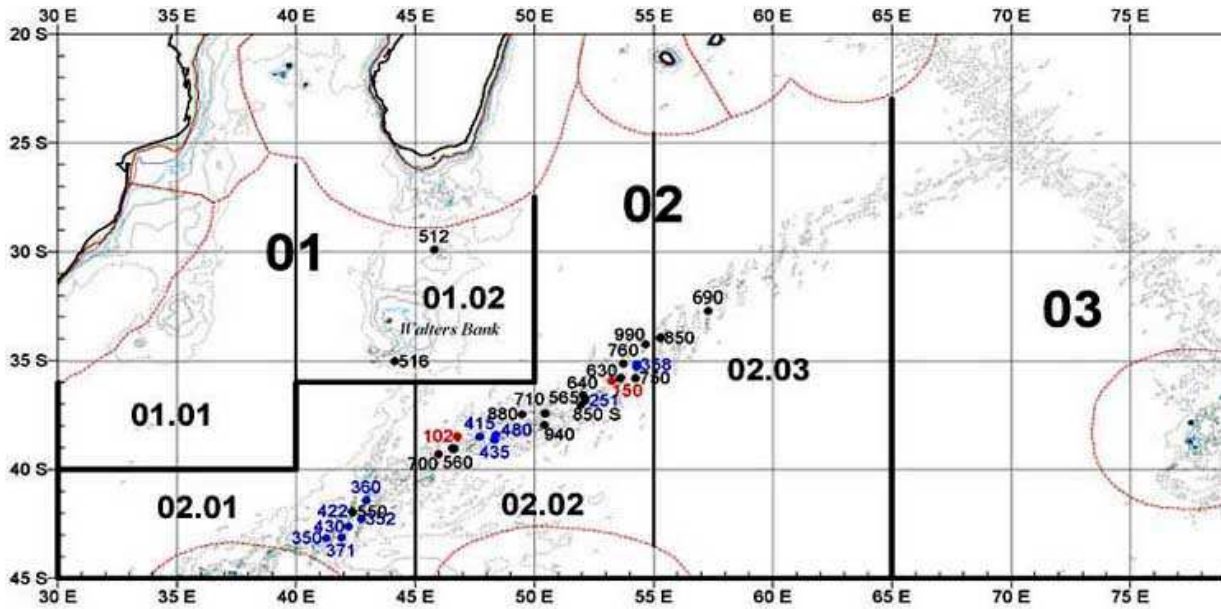


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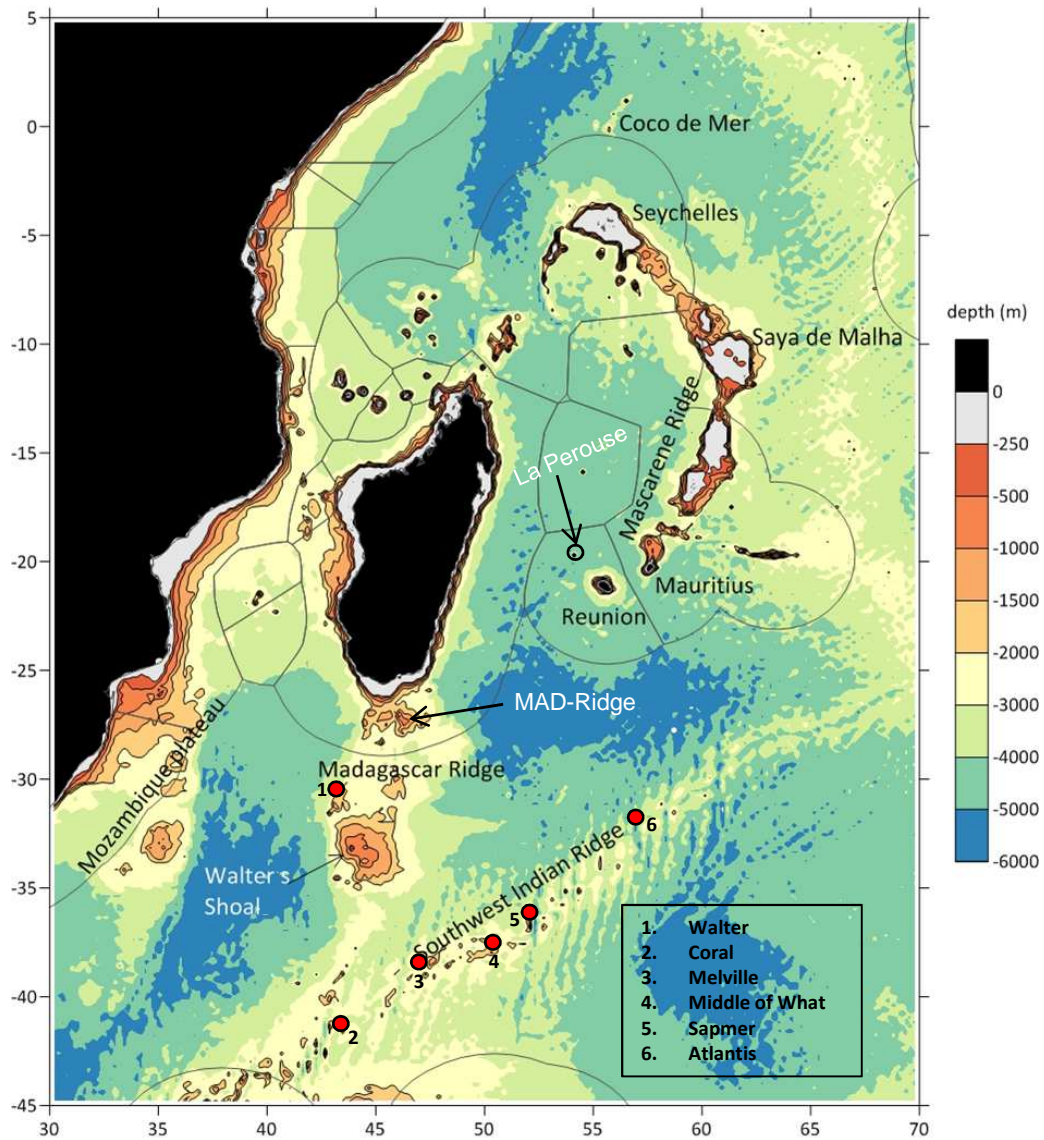


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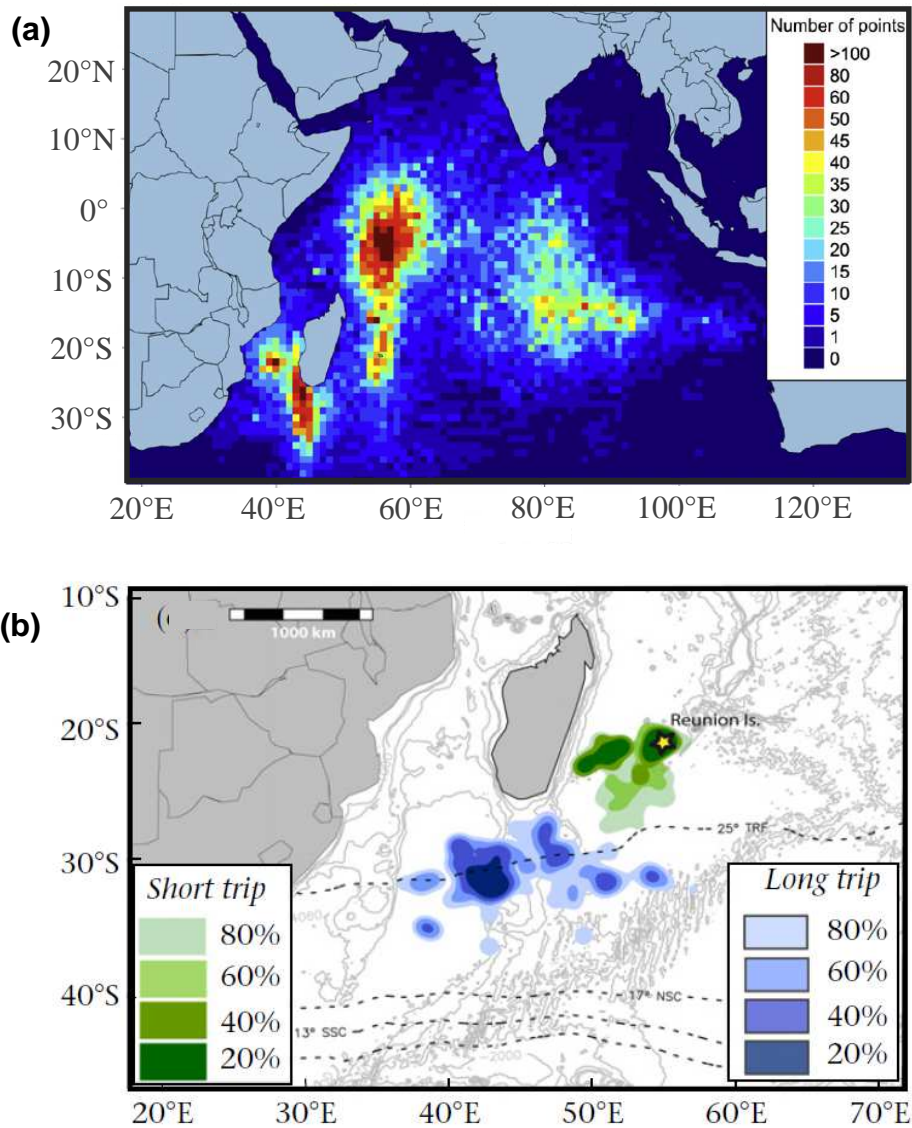


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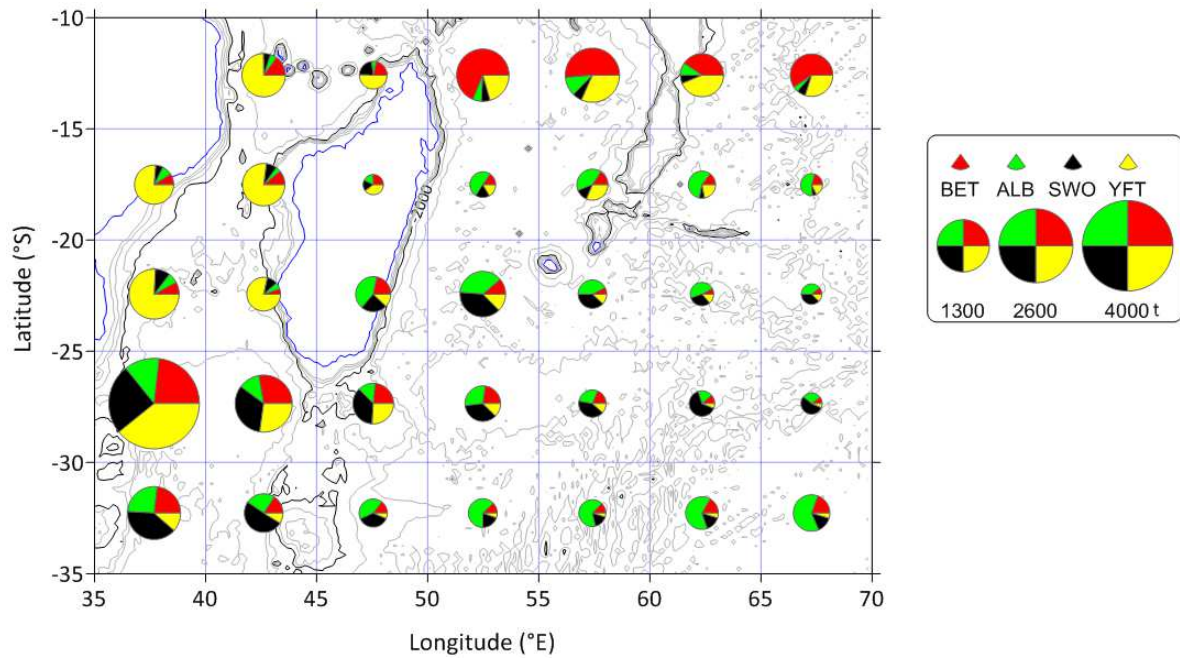


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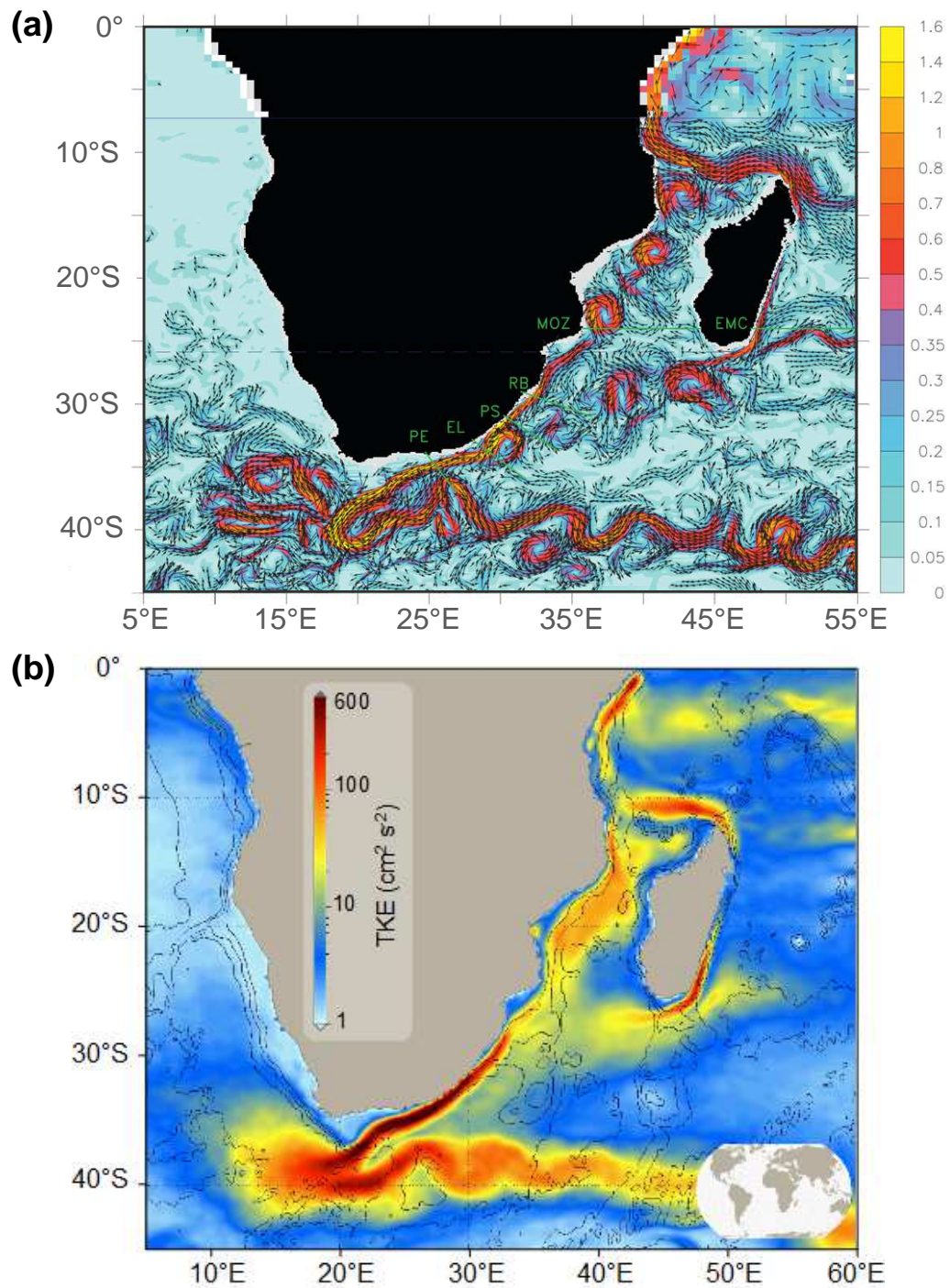


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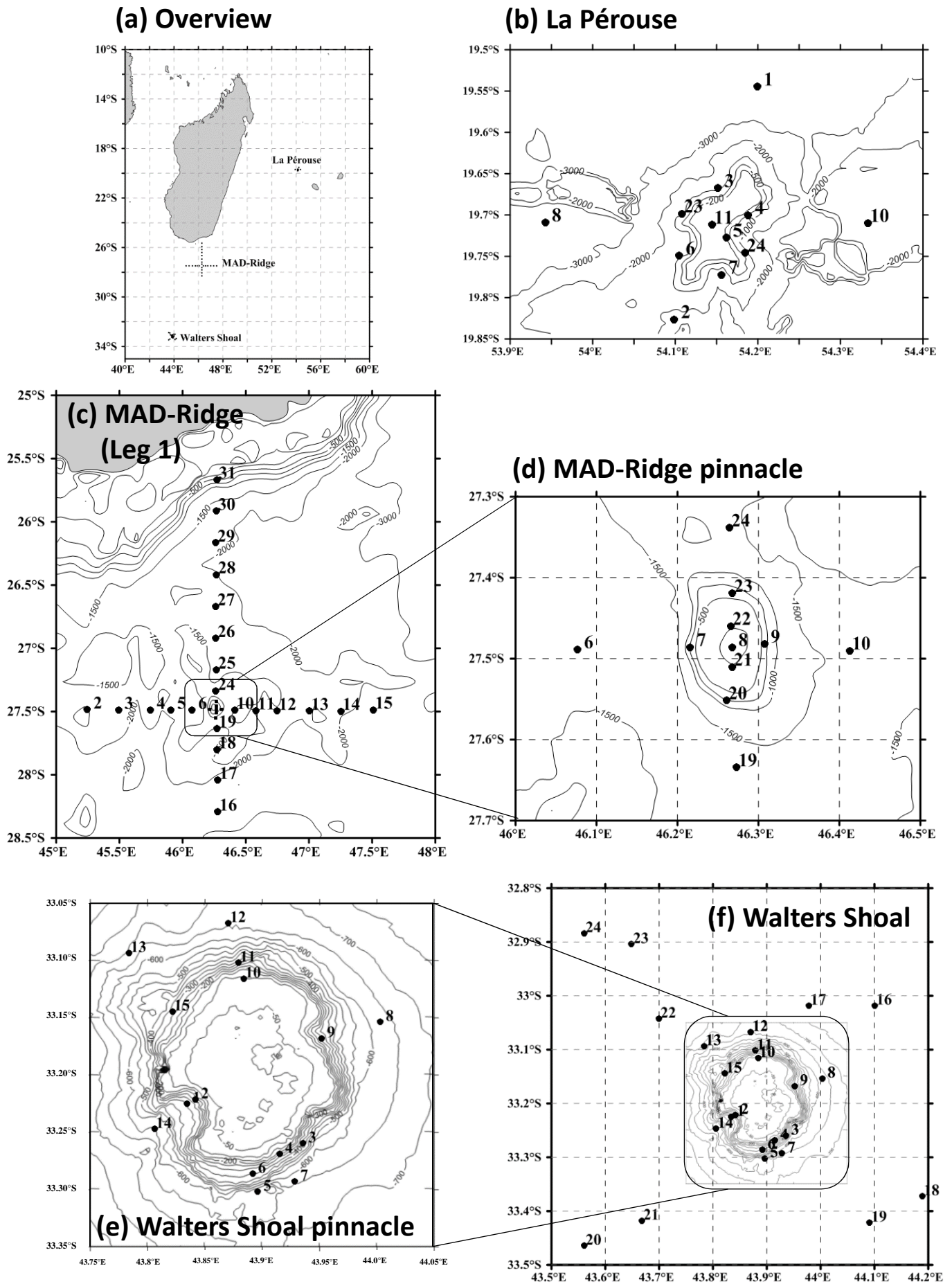


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