

1 **Differences in regional oceanography and prey biomass influence the**
2 **presence of foraging odontocetes at two Atlantic seamounts**

3 **Miriam Romagosa^{1,*}, Carlos Lucas², Sergi Pérez-Jorge¹, Marta Tobeña¹, Patrick**
4 **Lehodey³, Jesus Reis², Irma Cascão ¹, Marc O. Lammers^{4,5}, Rui M. A. Caldeira²,**
5 **Mónica A. Silva^{1,6}**

6 1- Okeanos R & D Centre and Institute of Marine Research (IMAR), University of the
7 Azores, and Marine and Environmental Sciences Centre (MARE), Horta, Portugal

8 2- Oceanic Observatory of Madeira, Agência Regional para o Desenvolvimento da
9 Investigação Tecnologia e Inovação, Funchal, Madeira, Portugal

10 3 - MEMMS (Marine Ecosystems Modeling and Monitoring by Satellites), CLS, Space
11 Oceanography Division, Ramonville, France

12 4 -NOAA's Hawaiian Island Humpback Whale National Marine Sanctuary, Kihei, HI, USA

13 5-Oceanwide Science Institute, Honolulu, HI, USA

14 6 - Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts,
15 USA

16 *** Correspondence**

17 MARE - Marine and Environmental Sciences Centre

18 IMAR - Institute of Marine Research

19 DOP - Department of Oceanography and Fisheries

20 University of the Azores

21 Rua Professor Dr. Frederico Machado 4

22 9901-862 Horta

23 Portugal

24 Email: m.romagosa4@gmail.com

25 **Abstract**

26 The importance of seamounts as foraging hotspots for cetaceans depend on interactions
27 between ocean flow and topographical features that concentrate prey. However, the
28 oceanographic processes driving these aggregations are still unclear. Here, we analyzed
29 two months of passive acoustic recordings from two remote seamounts in the Northeast
30 Atlantic, Atlantis and Irving, in relation to regional oceanography and estimates of prey
31 biomass. Delphinids and sperm whales were detected in both seamounts with higher
32 foraging activity at night, indicating feeding on diel migrating prey. There were more
33 detections of delphinids and sperm whales at Atlantis than at Irving. These two
34 seamounts lie in different oceanographic settings created by the Azores Current that
35 separates colder and less saline water masses in the north (Atlantis seamount) from
36 warmer and more saline waters in the south (Irving seamount). Irving seamount is only
37 affected by transient features like eddies that enhance productivity for short time
38 periods. These conditions translate into more productive waters at Atlantis seamount
39 than at Irving, as shown by predicted prey biomasses that ultimately attract top
40 predators. Comparative studies such as this one can help to explain the main drivers of
41 presence of top predators at seamounts.

42

43 **KEYWORDS:**

44 Azores Current, delphinids, foraging ecology, oceanography, odontocetes, passive
45 acoustics, prey, seamount, sperm whale

46

47

48 **1. INTRODUCTION**

49 Cetaceans actively seek and associate with areas of high biological productivity
50 (Barlow, Kahru & Mitchell, 2008; Mannocci et al., 2014). In the open-ocean, where
51 biophysical processes driving biological productivity are highly dynamic, seamounts
52 may provide spatially and temporally persistent prey aggregations and create predictable
53 foraging opportunities for cetaceans (Baumann-Pickering, Trickey, Wiggins and
54 Oleson, 2016; Morato et al., 2008,). Seamount density was found to be a predictor of
55 habitat suitability of short-beaked common (*Delphinus delphis*) and spotted (*Stenella*
56 *frontalis*) dolphins in the Azores, but not of bottlenose (*Tursiops truncatus*) and striped
57 (*S. coeruleoalba*) dolphins (Tobeña, Prieto, Machete & Silva, 2016). Several studies
58 reported significant associations of sperm whales (*Physeter macrocephalus*) to
59 seamounts (Hann, Smith & Torres, 2016; Skov et al., 2008; Tobeña et al., 2016;
60 Waring, Hamazaki, Sheehan, Wood & Baker, 2001; Wong & Whitehead, 2014) while
61 others have not found any significant relationship (Morato et al., 2008; Torres, Smith,
62 Sutton, MacDiarmid & Bannister, 2011). Hann et al. (2016) attributes this discrepancy
63 to differences in the size of the study area, scale, sample size, seamount classification,
64 and data resolution.

65 The importance of seamounts for cetaceans likely depends on local and regional
66 biophysical coupling. The interaction of the abrupt topography with the background
67 ocean circulation may generate a range of physical forcing mechanisms (*e.g.*, currents,
68 internal waves, eddies and fronts) that enhance the horizontal flux and aggregation of
69 food particles and plankton over seamounts (Clark et al., 2010; Genin & Dower, 2007).
70 Oceanographic processes, such as the formation of eddies, vortices, and Taylor caps
71 around seamounts, may also advect and entrain allochthonous plankton and
72 micronekton feeding in surface waters at night. These organisms may become trapped

73 over shallow seamount summits when trying to descend the next dawn ('topographic
74 blockage') (Genin & Dower, 2007; Pusch, Beckmann, Porteiro & Westernhagen, 2004).
75 In addition, seamounts may also provide habitat and refuge for benthic and micronekton
76 fish (Genin, 2004). How local and regional oceanographic conditions influence the
77 seamount effect at aggregating prey and attracting predators, including cetaceans, is
78 unclear (McFarland & Levin, 2002; Morato, Hoyle, Allain, & Nicol, 2010). Studies on
79 predator distribution and behavior at seamounts subject to different oceanographic
80 conditions are needed to understand the drivers promoting and sustaining predator
81 aggregations (Kvile, Taranto, Pitcher & Morato, 2014). The main reason behind the
82 lack of these studies is that seamounts are often in remote locations, which limit the
83 duration of cetacean and oceanographic surveys. One way of overcoming the lack of
84 pelagic cetacean surveys is the use of passive acoustic techniques, which allow the long-
85 term monitoring of vocalizing animals, independently of weather conditions or
86 remoteness (Baumann-Pickering et al., 2016; Giorli et al., 2015; Hastie, Swift, Slesser,
87 Thompson & Turrell, 2005; Soldevilla, Wiggins, Hildebrand, Oleson, & Ferguson,
88 2011, Wong & Whitehead, 2014).

89 Another important limitation is that data on prey distribution are usually not available at
90 desired spatiotemporal scales. Regular transects with active acoustic sounders can offer
91 a series of abundance indices of prey organisms, especially on the vertical migration of
92 the deep scattering layer. However, there is still key issues in the interpretation of such
93 data. Without sampling of organisms inhabiting the water column, the result may be
94 misleading due to differences in target strength of organisms. For instance, gas-bearing
95 siphonophores can produce huge acoustic backscatter that is not representative of the
96 true prey biomass (*e.g.*, Davison, Koslow & Kloser, 2015; Proud, Handegard, Kloser,
97 Cox & Brierley, 2018).

98 A potential useful alternative is emerging with the rapid progress achieved in
99 operational oceanography, combining satellite observations and hundreds of thousands
100 *in situ* data assimilated in numerical models to produce ocean reanalyses (Le Traon et
101 al., 2015). Thanks to data assimilation, predicted temperature and currents are now
102 sufficiently accurate to analyze fine scale movements of remote tracked animals (*e.g.*,
103 Abecassis et al., 2013; Gaspar et al., 2006). Relying on these realistic ocean reanalyses
104 and satellite ocean color data for primary production, the Lower and Mid Trophic Level
105 (LMTL) component of the model SEAPODYM (Spatial Ecosystem and Population
106 Dynamics Model) offers potential additional explanatory variables (micronekton) to
107 study large ocean predator ecology. SEAPODYM-LMTL simulates the biomass of six
108 different functional groups of micronekton in the epipelagic and mesopelagic layers
109 (Lehodey, Murtugudde & Senina, 2010; Lehodey et al., 2015). It has been successfully
110 used to predict turtle habitat and movements (Abecassis et al., 2013), population
111 dynamics of different tuna species (Dragon, Senina, Hintzen & Lehodey, 2017;
112 Lehodey, Senina & Murtugudde, 2008, Senina, Sibert & Lehodey, 2008; Sibert, Senina,
113 Lehodey, & Hampton, 2012) and cetacean habitats (Lambert, Mannocci, Lehodey, &
114 Ridoux, 2014; Roberts et al., 2016) at large regional and basin scales.

115 In this study, we use passive acoustic records collected at two seamounts in the North
116 Atlantic to investigate how local and regional oceanography influence the distribution
117 and the usage of these seamounts by dolphins and sperm whales. In addition to physical
118 oceanographic variables, we use a high-resolution simulation at 0.08° produced with
119 SEAPODYM-LMTL to explore possible explanations of the variability observed based
120 on foraging behavior.

121 **2. METHODS**

122 *2.1 Study area*

123 The Meteor seamount complex is located in the Northeast Atlantic Ocean, ~600 km
124 south of the Azores archipelago and 1,500 km off Northwest Africa. It is a group of
125 seven large banks and a few seamounts extending 550 km from the northernmost to the
126 southernmost seamount. The complex lies between two surface currents: the southern
127 branch of the Azores Current that flows southeastwards and the cold Canary Current
128 flowing offshore from the African coast. Exact directions and intensities of these
129 currents vary seasonally (Johnson & Stevens, 2000; Klein & Siedler, 1989; Kraus,
130 Kaese, & Hinrichsen, 1990). The Azores Current Front System also has deep-sea
131 currents moving opposite to the surface currents with a complex and dynamic
132 mesoscale circulation *i.e.*, meddies (Alves & de Verdière, 1999; Richardson, 1996). In
133 addition, the Meteor complex is also affected by westward propagating surface
134 intensified eddies (Barbosa-Aguiar, Peliz, Cordeiro Pires, & Le Cann, 2011).

135 In this study, two seamounts from the Meteor complex were investigated: Atlantis,
136 which is the northernmost seamount, and Irving located 316 km southeast of Atlantis
137 (Fig. 1). The Atlantis seamount is approximately 410 km², with summit depths ranging
138 from 250 to 400 m (Bednarz, 1991). Its topography is complex with numerous
139 underwater plateaus and pinnacles (Pusch et al., 2004). Irving seamount rises from a
140 broad plateau and has a flat summit of ~8 km radius at 270-290 m depth (Smith &
141 Sandwell, 1997).

142 2.2 Acoustic recordings and analysis

143 Two broad-band static hydrophones, specifically Ecological Acoustic Recorders (EAR)
144 (Lammers, Brainard, Au, Mooney & Wong, 2008), were moored at the Atlantis and
145 Irving seamounts for approximately 2 mo between July and September 2015 at 294 m
146 and 264 m depth, respectively (Table 1). The EARs consist of a sensor Technology

147 SQ26-01 hydrophone with a response sensitivity of -194.17 dB re 1V/ μ Pa for Atlantis
148 and -193.14 dB re 1V/ μ Pa for Irving and a flat frequency response (± 1.5 dB) from 18
149 Hz to 28 kHz. A Burr-Brown ADS8344 A/D converter was used with a zero-to-peak
150 voltage of 1.25 V. EARs were set up at a sampling rate of 50 kHz in order to reach the
151 maximum frequency band capacity of the system (1-25 kHz) and a duty cycle of 20% (3
152 min on, 15 min off) so batteries could last for the whole deployment period (Table 1).

153 Files generated by the EARs were analyzed by manually scanning spectrograms using
154 Adobe Audition 3.0 (Adobe Systems Incorporated, CA, USA). For every 3 min file,
155 detections were entered in a database by logging the start and end time of each one and
156 the type of sound. Although beaked whales were sighted over these seamounts during a
157 visual survey in September of 2015 and have been detected in other seamounts further
158 north (Giorli et al., 2015), the sample rate used in this study (50 kHz) with maximum
159 frequencies of 25 kHz, did not allow us to detect either Cuvier's beaked whales (*Ziphius*
160 *cavirostris*), with clicks centred at 42 kHz (Zimmer, Johnson, Madsen, & Tyack,
161 2005), or Blainville's beaked whales (*Mesoplodon densirostris*), with clicks ranging
162 from 26 to 51 kHz (Johnson, Madsen, Zimmer, Soto, & Tyack, 2006). Sperm whale
163 clicks and delphinid sounds could be successfully detected, and were classified based on
164 descriptions from the literature. Sperm whales produce regularly spaced echolocation
165 clicks below 20 kHz with an interclick interval varying from 0.5 to 1 s, as well as creaks
166 and codas (Goold & Jones, 1995). With the exception of the very distinctive
167 vocalizations produced by Globicephala spp., *Orcinus orca* or *Pseudorca crassidens*,
168 that were not found in our recordings, sounds produced by most delphinids overlap in
169 frequency characteristics, remaining challenging to identify to the level of species.
170 Thus, delphinid vocalizations were classified at family level (excluding the former three
171 genera). Only those delphinid vocalizations attributed to foraging activities, such as

172 echolocation clicks, burst-pulses, buzzes and bray calls (*e.g.*, Au, 1993; Herzing, 2000;
173 Janik, 2000; Santos, Ferreira, & Harzen, 1995), were included in the analysis to
174 investigate usage of these seamounts by foraging dolphins. These foraging vocalizations
175 represented 87.2% of total vocalizations in Atlantis and 91.2% in Irving.

176 The expected detection range of the EARs of delphinid foraging sounds is <4 km (Marc
177 O. Lammers, personal communication¹). Detection range of sperm whale echolocation
178 clicks range from 10 km (Watkins, 1980) up to 16 km (Madsen, Wahlberg & Møhl,
179 2002). Given that the radius of Atlantis and of Irving plateaus is >8 km, we assume that
180 delphinid detections were from animals present over plateau areas, while sperm whale
181 detections could be from whales present above plateaus, slopes of seamounts, or open
182 water.

183 From the database of logged sounds, the following parameters were calculated for each
184 seamount: the percentage of days with detections, the number of consecutive hours with
185 detections, and percentage of time with detections per hour and day.

186 2.3 Oceanographic analysis

187 2.3.1 Regional data

188 The climatological World Ocean Atlas 2013 (WOA13,
189 <https://www.nodc.noaa.gov/OC5/WOD13/>) (Locarnini et al., 2013, Zweng et al., 2013)
190 was used to investigate if differences in oceanographic settings between Atlantis and
191 Irving were representative of long-term patterns. WOA13 is a compound of historical *in*
192 *situ* measures, which are interpolated to produce a high-resolution regional climatology.
193 It consists of a long-term set of climatologies (at annual, seasonal, and monthly periods)

¹ Marc O. Lammers, NOAA's Hawaiian Island Humpback Whale National Marine Sanctuary, Kihei, HI, USA and Oceanwide Science Institute, Honolulu, HI, USA.

194 for temperature, salinity, oxygen, phosphate, silicate, and nitrate. In this study, we used
195 climatologies built using 102 levels from the surface to 5,500 m depth on a 0.25°
196 latitude/longitude grid (27.7 km x 21.3 km). We only used measurements from August
197 and September, corresponding to the study period, from 1955-2012.

198 Based on the WOA13 climatological data, we calculated the geostrophic currents using
199 profiles of density, which is a function of temperature and salinity. The geostrophic
200 current is an oceanic flow in which the pressure gradient force is balanced by the
201 Coriolis effect. The direction of geostrophic flow is parallel to the isobars, with the high
202 pressure to the right of the flow in the Northern Hemisphere. The geostrophic equations
203 are a simplified form of the Navier–Stokes equations in a rotating reference frame. It is
204 assumed that there is no acceleration (steady-state) or viscosity, and that the pressure is
205 hydrostatic.

206 To investigate if climatological data compared well with data from the study period
207 (August and September 2015), regional maps were produced using Absolute Dynamic
208 Topography (ADT) and speed and flow vectors from the MERCATOR-OCEAN
209 operational ocean circulation model PSY2V4R4 ([http://marine.copernicus.eu/services-
210 portfolio/access-to-products/](http://marine.copernicus.eu/services-portfolio/access-to-products/)). This physical configuration is based on the tripolar
211 ORCA grid type (Madec & Imbard, 1996) with a horizontal resolution of 9 km at the
212 equator. The 50-level vertical discretization retained for the system had 1 m resolution
213 at the surface decreasing to 450 m at the bottom, with 22 levels within the upper 100 m.
214 The atmospheric fields forcing NEMO were taken from the ECMWF (European Centre
215 for Medium-Range Weather Forecasts) Integrated Forecast System. A 3 h sampling was
216 used to reproduce the diurnal cycle, in order to force the upper layers of the ocean
217 model, with a thickness of 1 m for the uppermost level. MERCATOR forecasting
218 system did not include tides (see Caldeira et al., 2016 for model details and validation).

219 2.3.2 Local data

220 Daily numerical data of Sea Surface Temperature (SST), salinity, current speed and
221 Mixed Layer Depth (MLD) used for the statistical analysis and boxplots were extracted
222 from MERCATOR – Ocean GLORYS-12v1 (Global Ocean Reanalysis and
223 Simulations product) model, centred at the position of the EARs with a grid size of
224 0.08° latitude/longitude grid (8.8 km x 6.8 km). MERCATOR – Ocean GLORYS-12v1
225 model is a reanalysis, thus it assimilates most of the oceanographic data available for
226 each day. Observations are assimilated by means of a reduced-order Kalman filter,
227 which estimates a joint probability distribution over the variables for each timeframe
228 resulting in a more accurate algorithm than those based on single measurements alone
229 (Kalman, 1960). Track altimeter data (Sea Level Anomaly), satellite SST and Sea Ice
230 Concentration are jointly assimilated with *in situ* temperature and salinity vertical
231 profiles. Moreover, a three-dimensional variational (3D-VAR) assimilation scheme
232 provides a correction for the slowly-evolving large-scale biases in temperature and
233 salinity. This model captures climate signals and trends well and describes mesoscale
234 variability in a realistic manner. A more recent data-model comparison, using a similar
235 approach was partially validated by Drévillon et al. (2008) and evaluated by Caldeira et
236 al. (2016) in the Northeast Atlantic. Weekly potential temperature data were also
237 extracted in order to compare seamounts environment. Potential temperature is the
238 temperature a parcel of water would have if it were moved adiabatically (*i.e.*, without
239 loss of heat) to a reference pressure which allows for comparison between waters of
240 different depths.

241 Chlorophyll-A (CHLA) data were extracted from an agglomeration of optical images
242 collected by different satellites (MODIS and VIIRS). CHLA data were preprocessed by
243 the Plymouth Marine Laboratory Remote Sensing Group and has a horizontal resolution

244 of 1 km. Although there is a daily product, the delayed time data used in this study
245 offers better quality because it uses hindcast data for processing. The algorithms used
246 are presented in McClain et al. (1995) and Smyth, Moore, Hirata & Aiken (2006).

247 The Eddy Kinetic Energy (EKE) was derived using the velocity components of the
248 surface currents obtained by satellite altimetry and calculated as follows:

$$249 \quad \text{EKE} = \frac{(u^2 + v^2)}{2}$$

250 These products were processed by SSALTO/DUACS and distributed by AVISO+
251 (<https://www.aviso.altimetry.fr>) with support from CNES (Centre National d'Études
252 Spatiales) with a 0.25° spatial resolution and a daily periodicity.

253 *2.4 Prey data*

254 Prey data were obtained from the SEAPODYM-LMTL model. This model represents
255 six functional groups of migrant and nonmigrant micronekton in three vertical layers -
256 epipelagic, upper mesopelagic and lower mesopelagic - defined in relation to the
257 euphotic depth (Lehodey et al., 2010, 2015). The boundary between epipelagic and
258 upper mesopelagic layers is defined as 1.5 euphotic depths, while the limit between
259 upper mesopelagic and lower mesopelagic layers is 4.5 euphotic depths, with estimates
260 to a maximum depth of 1,000 m. The model simulates spatial and temporal biomass
261 dynamics of micronekton functional groups based on their diel vertical migration
262 patterns: epipelagic, upper mesopelagic, migrant upper mesopelagic, lower
263 mesopelagic, migrant lower mesopelagic and highly migrant lower mesopelagic. Day
264 and night biomass for each layer were calculated by adding the different micronekton
265 functional groups accordingly (Table 2).

266 Micronekton is comprised of myriads of cephalopods, crustaceans, fishes and jellyfish
267 species with body sizes ranging from 1 to 20 cm in length (Brodeur, Seki, Pakhomov &
268 Suntsov, 2005). Each functional group is modelled as a single multi-species population,
269 with continuous mortality and recruitment controlled by an allometric relationship to
270 water temperature. Organisms are transported by currents according to the time spent in
271 each layer. The model simulation uses 3D temperature and currents provided by the
272 physical operational Mercator model PSY4 (interpolated on a regular grid of 0.08° as
273 for the GLORYS12v1 reanalysis). The primary production and euphotic depth
274 computed from ocean color satellite data was processed in CLS (Collecte Localisation
275 Satellites) using the Vertically Generalised Production Model (VGPM) (Behrenfeld &
276 Falkowski, 1997). The micronekton model outputs have the same horizontal grid and
277 resolution as the physical model ($0.08^\circ \times \text{day}$). The predicted total abundance is linked
278 to the energy transfer efficiency coefficient from primary production to the functional
279 groups. While there is a considerable uncertainty on this coefficient and thus the
280 biomass of mesopelagic micronekton (*e.g.*, Proud et al., 2018), the approach used in this
281 study considers only the relative spatial and temporal variability of these biomass
282 distributions.

283 Prey abundances were extracted from the model grid cells surrounding the hydrophone
284 position according to the presumed detection range of each cetacean group: 4 km for
285 delphinids and 10 km for sperm whales.

286 Small oceanic dolphins feed primarily in the first 200 m of the water column with
287 occasional dives to 400 – 500 m (Klatsky, Randall, & Sweeney, 2007). Thus, we only
288 considered the first two vertical layers with three associated functional groups
289 (epipelagic, upper mesopelagic and migrant upper mesopelagic) for delphinids. Sperm
290 whales are known to forage mostly on cephalopods found in water depths ranging from

291 400 to 1,200 m (Watwood, Miller, Johnson, Madsen & Tyack, 2006). Above
292 seamounts, where depths are below 400 m, only upper mesopelagic groups could be
293 included. Grids surrounding the hydrophone within the detection range of sperm whales
294 were included for the lower mesopelagic micronekton group.

295 *2.5 Statistical analysis*

296 We used Kruskal–Wallis ANOVA to: 1) compare the consecutive number of hours
297 delphinids and sperm whales were detected at each seamount, 2) test for differences in
298 salinity, SST, current speed, MLD, EKE and CHLA between the two seamounts and 3)
299 test for diel differences in micronekton biomass between the two seamounts.

300 A Generalized Additive Mixed Model (GAMM) with a binomial distribution and a logit
301 link function was used to investigate diel variations in delphinid and sperm whale
302 detections. As the diel pattern was similar between seamounts, data from the two
303 seamounts were pooled into a single model. Hour of the day was the predictor variable
304 while presence of detections per hour was the response variable. A temporal
305 autocorrelation structure corAR(1) from package “nmlr” was also included in the
306 model.

307 To investigate which oceanographic and prey variables influenced the presence of
308 foraging delphinids and sperm whales, minutes with detections of each cetacean group
309 were related with biomass of micronekton functional groups and local oceanographic
310 data. Daily biomass of micronekton functional groups as well as delphinid and sperm
311 whale minutes with detections were calculated for day and night periods (based on
312 sunrise and sunset times extracted from the U.S. Naval Observatory Astronomical
313 Applications Department database) to explore how variations of the daily pattern in prey
314 affect predators presence. In the models, period (day and night) was added as an

315 interaction term to allow dissimilar relationships in the two periods (Zuur, 2012). Local
316 oceanographic variables were included in the models at a daily scale, the only available
317 resolution. Prior to running the models, we investigated the collinearity between pairs of
318 covariates using multi-panel scatterplots (Zuur, 2012) (Supl. Material: Fig. 1, 2, and 3)
319 and selected those with a Pearson's correlation coefficient < 0.7 (Dormann et al., 2013;
320 Sutton, Jenner, & Jenner, 2018; Zuur, 2012). As a first step, a Generalized Additive
321 Model (GAM) was built to investigate if explanatory variables had similar effects on the
322 detections at the two seamounts. Results showed considerable differences in several
323 variables so separate models were developed for each seamount. Then a model was run
324 using one predictor at a time to check which of the correlated variables explained best
325 the observed response variable by selecting the one with lowest Akaike Information
326 Criteria (AIC) value. In addition, we checked that the covariates resulting from this best
327 model had low levels of concurvity, which represent nonlinear dependencies among
328 predictor variables, and could lead towards unstable or imprecise estimates of the
329 covariates' functional effects. We also checked if temporal autocorrelation still existed
330 after running the models by looking at the autocorrelation function of residuals and
331 choosing the best model accordingly. Inspection of the data indicated a possible lag
332 between Eddy Kinetic Energy (EKE) and presence of delphinids and sperm whales in
333 Atlantis. To select which temporal lag to use in the final model, we ran models using
334 one lag at a time (0, 7, 14, 21, 28, and 35 d) and selected the one with the lowest AIC
335 (Burnham & Anderson, 2002).

336 GAMs were fit with a Gaussian distribution and an identity link function using
337 restricted maximum likelihood (REML) (Wood, 2011). Predictors with P -values >0.05
338 and estimated degrees of freedom <0.85 were removed (Roberts et al., 2016). Models
339 were checked by looking at Q-Q plots of deviance residuals, histogram of residuals,

340 response vs. fitted values and plots of random quantile residuals versus linear predictor.
341 Sperm whale detections in Irving were not included in the statistical analyses because of
342 small sample size (detections in only 3.8% of days) and the high number of zeros in the
343 response resulted in models with poor fit to the data. All statistical analysis were
344 performed using R software (Rstudio team, 2016. Version 1.0.153).

345 **3. RESULTS**

346 *3.1 Acoustic detections*

347 A total of 277.5 h were recorded in Atlantis seamount and 274.3 h in Irving seamount
348 during 58 and 59 d, respectively. Only days with simultaneous recordings in both
349 seamounts were used (244.8 h recorded during 51 d). Two types of natural sounds were
350 identified; dolphin vocalizations (Fam. Delphinidae) that included high, mid-, and low
351 frequency clicks, click trains, buzzes, bray calls (Fig. 2A), and whistles (Fig. 2B) and
352 sperm whale clicks and creaks (Fig. 2C).

353 Delphinids were detected every day in 14% of the total recording time in Atlantis, and
354 in 73% of days and 6.2% of the recording time in Irving (Fig. 3). Sperm whale clicks
355 were present in 42.3% of the recording days (6% of the total recording time) in Atlantis
356 and in 3.8% of days (0.3% of the total recording time) in Irving (Fig. 4).

357 Delphinids and sperm whales spent more consecutive hours in Atlantis than in Irving
358 (delphinids: KW: 8.715, $P=0.003$; sperm whales: KW: 11.72, $P<0.001$) with a mean of
359 7.4 h for delphinids and 5.2 h for sperm whales in Atlantis and 4.3 h for delphinids and
360 3.5 h for sperm whales in Irving.

361 Hour of the day had a significant effect on delphinid foraging vocalizations (GAMM
362 smoother for hour: edf=2.88, $F=25.11$, $P<0.001$) and sperm whale clicks (GAMM
363 smoother for hour: edf=2.24, $F=3.88$, $P<0.05$) with more detections at night (~2000h –

364 0800h) than during the day (~0800h – 2000h) (Figs. 3 and 4; Supl. Material: Fig. 4A
365 and B).

366 3.2 Regional and local oceanography

367 Data from the WOA13 showed that Atlantis and Irving seamounts were under different
368 oceanographic regimes at a depth of 1,500 m, with Atlantis located in colder and less
369 saline waters relative to Irving (Fig. 5A and B). The frontal system formed between the
370 two seamounts reached 1°C of temperature and 0.15 PSU of salinity. Geostrophic
371 velocities computed along a line separating the two seamounts highlighted these north-
372 south differences. The Azores current (AzC) affected Atlantis from the surface down to
373 1,000 m (Fig. 5C), while Irving was not affected at all by the core of the AzC (Fig. 5D).
374 In fact, at the surface, the geostrophic current affecting Irving flowed in opposite
375 direction relative to the AzC. Also, geostrophic currents that affected Atlantis were
376 stronger (15 cm/s) than those reaching Irving (5 cm/s).

377 Ocean circulation forecasts for August 2015 showed similar results as the climatological
378 scenarios from the WOA13. The Azores Frontal system separating Atlantis from Irving
379 was evident in the ADT plot (Fig. 5E) and speed and flow vectors (Fig. 5F). Atlantis
380 was strongly affected by the Azores surface current, whereas Irving was affected by a
381 cyclonic eddy travelling westwards.

382 At the local scale, differences between the two seamounts were also obvious. During the
383 study period (July-September 2015), Atlantis showed lower salinity (KW: 215.25,
384 $P<0.001$), lower potential temperature (KW: 49.28, $P<0.001$), higher EKE (KW: 99.27,
385 $P<0.001$), and higher CHLA concentration (KW: 22.07, $P<0.001$) than Irving (Fig. 6).

386 3.3 Micronekton model distributions

387 During the study period, Atlantis had higher biomass of epipelagic (KW: 38.46,
388 $P < 0.001$), upper mesopelagic (KW: 42.13, $P < 0.001$), and lower mesopelagic biomass
389 (KW: 42.18, $P < 0.001$) than Irving seamount (Fig. 7). The micronekton biomass in the
390 epipelagic layer was higher at night than during the day (Atlantis: KW: 84.75, $P < 0.001$;
391 Irving: KW: 83.25, $P < 0.001$), with the opposite pattern in the upper and lower
392 mesopelagic layers. At a larger scale, higher biomass of all micronekton functional
393 groups, except the lower mesopelagic, were found in the northern area that includes
394 Atlantis seamount. Further south, where Irving is located, there were scattered patches
395 of high biomass (Fig. 8). Higher biomasses of lower mesopelagic, migrant lower
396 mesopelagic and highly migrant lower mesopelagic micronekton were found in the
397 northwest side of Irving seamount (Fig. 8).

398 *3.4 Delphinid acoustic detections in relation to local oceanography and* 399 *micronekton prey*

400 The best GAM model explaining the presence of foraging delphinids in Atlantis
401 included night epipelagic biomass, MLD and EKE with a 28 d lag (46% of deviance
402 explained) (Supl. Material: Table 1). Minutes with delphinid detections increased with
403 increased night epipelagic biomass and 28-day lag EKE and decreased with deeper
404 MLD (Fig. 9A, B and C; Supl. Material: Table 1). In Irving, the best model included
405 night epipelagic biomass and EKE (31% of deviance explained). Delphinid detections
406 increased with increasing night epipelagic biomass and EKE. (Fig. 9D and E) (Supl.
407 Material: Table 1). For sperm whale detections in Atlantis, none of the predictors used
408 in the model were significant.

409 **4. DISCUSSION**

410 Most delphinid vocalizations found in the recordings (64.2% of recordings in Atlantis
411 and 79.2% in Irving) contained low frequency pulses, named bray calls, described by
412 Santos et al. (1995). This type of vocalization was found in other areas and attributed to
413 bottlenose dolphins engaged in foraging activity (*e.g.*, Hastie, Wilson & Thompson,
414 2006; Janik 2000; King & Janik, 2015). In addition, bottlenose dolphins were the most
415 frequently sighted cetacean during a two-week visual survey at both seamounts in
416 September (Supl. Material: Table 2). Although sightings were made outside of the
417 EARS detection range, night-time recordings of bray calls occurred on the same day that
418 bottlenose dolphins were observed in the area. Therefore, we hypothesize that most of
419 delphinid vocalizations were produced by bottlenose dolphins.

420 Delphinid acoustic activity was higher at night than during the day in both seamounts,
421 consistent with vocal patterns of dolphins in coastal habitats, island slopes and other
422 seamounts (*e.g.*, Au et al., 2013; Giorli & Au, 2017; Hodge, Bell, Kumar & Read,
423 2013). Increased acoustic activity of dolphins at night is believed to be related to higher
424 foraging activity on vertically migrating prey (Hastie et al., 2006; Janik, 2000; King &
425 Janik, 2015; Simonis et al., 2017). Results from our models support this hypothesis and
426 explain the acoustic behavior of delphinids foraging at these seamounts. The biomass of
427 micronekton in epipelagic layers at night was the most important predictor of the
428 presence of foraging delphinids in Atlantis and Irving seamounts. Estimates of the
429 night-time biomass in the epipelagic layers in Atlantis and Irving were 2 times higher
430 than those predicted during the day. Dolphins foraging at night likely benefit from
431 increased prey biomasses that result from the upward migration of mesopelagic
432 organisms from deeper layers. Our study does not account for differences in prey
433 preferences between different species of delphinids. However, only bottlenose dolphins
434 and rough-toothed dolphins (*Steno bredanensis*) were seen over these seamounts during

435 a visual survey in the area (Supl. Material: Table 2). Little is known about the rough-
436 toothed dolphins feeding habits. The few existing reports suggest they feed on a variety
437 of fish and cephalopod species. As a deep-water species frequently associated with
438 other species such as bottlenose dolphins, may suggest they share similar prey
439 preferences and may also take advantage of the night availability of micronekton on the
440 surface (Baird et al., 2008; Miyzaki & Perrin, 1994). Atlantic spotted dolphins (*Stenella*
441 *frontalis*) were also encountered while in transit between seamounts. However, in
442 September this species is known to migrate south to spend winter months off Madeira
443 or the Canary Islands (Silva et al., 2014) and residence time over the seamounts may be
444 short.

445 Sperm whales were also detected more often at night in Atlantis and Irving. Au et al.
446 (2013) found the same diel pattern using EARs deployed off two Hawaiian Islands but
447 another study that used animal-borne tags did not report significant differences in
448 acoustic activity between day or night (Klinck et al., 2012). These differences could be
449 due to the different methodologies used in these studies. While tags record animal
450 acoustic activity independently of their movements, static hydrophones can only detect
451 animals when they are within the instrument detection range. In our study, more sperm
452 whale detections during the night may mean that animals are closer to seamounts during
453 that time. Seamount slopes are potential foraging sites for sperm whales (Clarke, 2007).
454 Cephalopods swim or drift to seamounts for spawning and feeding and may be easier to
455 catch if concentrated against steep topographies (Clarke, 2007; Kaschner, 2007).
456 Oceanic squid species also follow a diel migration feeding at shallow waters on
457 micronekton fish such as Myctophids (Clarke, 2007). Sperm whales may find it easier to
458 catch squid on shallower waters during the night and concentrated against seamount
459 slopes.

460 Delphinids and sperm whales were more frequently detected in Atlantis and spent more
461 time foraging at this seamount than at Irving. Differences in usage between these
462 seamounts can be at least partly explained by their different oceanographic regimes and
463 mesoscale features which ultimately drive productivity and prey distribution. However,
464 simulated prey biomass was not the only variable explaining foraging activity of
465 delphinids at each seamount, and in the case of sperm whales detected in Atlantis, the
466 models did not show a significant relationship with any of the micronekton variables.
467 Furthermore, delphinid foraging activity was associated with different oceanographic
468 variables in each seamount. Together, these results suggest that factors influencing the
469 aggregation of prey and not only prey biomass may influence selection of foraging
470 habitats in these taxa and that oceanographic processes creating favorable foraging
471 conditions differs between the two seamounts.

472 The regional and local oceanographic conditions found during the study period were
473 consistent with the long-term climatologies and should represent well the main
474 oceanographic features at that time of the year. Our results clearly show that Atlantis
475 and Irving seamounts are located in areas with distinct water mass properties, mesoscale
476 variability, and primary productivity. Situated to the north but very close to the mean
477 axis of the AzC ($\sim 34^{\circ}\text{N}$), Atlantis has persistently colder and less saline waters, higher
478 eddy activity, more variable current speeds and higher concentrations of CHLA than
479 Irving, located south of the AzC. These results are supported by previous studies
480 reporting sharp thermal and density gradients across this frontal system, and increased
481 primary productivity inside the frontal zone region, probably associated with upwelling
482 processes. In addition, the high instability of the AzC and the interaction with the
483 shallow bottom topography also result in more intensive meandering and eddy activity
484 in the Atlantis region (Barbosa-Aguiar et al., 2011), in agreement with the higher EKE

485 we observed at this seamount. Moreover, cyclonic and anticyclonic eddies dominating
486 the Atlantis region (Barbosa-Aguiar et al., 2011), can enhance productivity through
487 upwelling of nutrients from ocean depths and concentration and retention of plankton
488 and nekton (Condie & Condie 2016; McGillicuddy et al., 1998). On the other hand,
489 Irving is less affected by the AzC but is occasionally exposed to cyclonic eddies that
490 generate from the outflow of Mediterranean water (*i.e.*, meddies) and propagate
491 westwards across the Northeastern Atlantic (Bashmachnikov, Neves, Calheiros, &
492 Carton, 2015). These transient features could be responsible for temporary enrichments
493 at Irving, by bringing nutrients into the euphotic zone through increased vertical mixing,
494 or by aggregating plankton at the surface through horizontal convergence (Condie &
495 Condie, 2016). Cetaceans appear to concentrate at productive fronts and eddies (Davis
496 et al., 2002), which could make Atlantis seamount a more suitable foraging area than
497 Irving.

498 Results from GAM models reflect these different processes affecting the two
499 seamounts. In addition to prey biomass, EKE was an important predictor of the presence
500 of foraging dolphins with higher number of detections associated with more intense
501 eddy flows at both seamounts. However, in Atlantis, EKE was a significant predictor
502 when lagged 28 d, while in Irving EKE was significant without a lag. The lagged EKE
503 in Atlantis suggests a role of upwelling processes associated with the existence of the
504 AzC front which may be sustained by the numerous passing eddies. Eddies can
505 concentrate and retain phytoplankton that increase productivity with a lagged response
506 in predator's presence (Condie & Condie, 2016). In Irving, where no major upwelling
507 processes exist, temporary increases in EKE may be associated with the passage of
508 cyclonic eddies which retain and aggregate prey explaining the absence of lagged
509 relationship with dolphin detections. The vertical distribution and structure of prey

510 patches also seems to influence the foraging behaviour of dolphins through their effect
511 on accessibility. In Atlantis, the GAM model also selected the MLD with a slightly
512 positive effect of shallower MLD on the number of delphinid detections. Another
513 positive effect of shallower MLD would be through the retention and concentration of
514 small particles like phytoplankton (Gardner, Chung, Richardson & Walsh, 1995; Wolf
515 & Woods, 1988) and the zooplankton feeding on them. Besides, it has been observed
516 that mesozooplankton density declines with increasing mixing depth (Kunz, 2005).
517 Thus, a thin MLD would have a higher concentration of phytoplankton, which in turn
518 would aggregate zooplankton and secondary predators like myctophids. Delphinids may
519 use this MLD-induced prey aggregation to feed more efficiently. At Irving seamount,
520 however, MLD was not a significant predictor of delphinid foraging. It could be due to
521 smaller MLD ranges above this seamount caused by the absence of strong currents
522 and/or different aggregating processes (currents *vs.* temporary eddies) affecting this
523 seamount. Nevertheless, these results should be considered with some caution, as the
524 range of MLD was very limited, and the relevance of such variability to foraging
525 dolphins is questionable. Sperm whale detections in Atlantis were not associated with
526 any predictor used in the model. The small temporal scale of this study, together with
527 the few sperm whale detections, may have an influence on our model results.

528 Consistent with the expectations from the physical dynamics of the region,
529 comparatively higher biomass of epi, upper meso-, migrant upper meso-, migrant lower
530 meso-, and highly migrant lower mesopelagic micronekton were predicted north of the
531 AzC, where Atlantis is located. The SEAPODYM-MTL also predicted increased
532 biomass of micronekton at Irving, coincidental with the passage of a meddie during the
533 study period (August 2015). This feature was observed to pass near Irving seamount
534 with predicted micronekton aggregation on its edge and trapped by the seamount slope

535 in the lower mesopelagic layer, *i.e.*, below 400 m depth. However, the GAM model for
536 sperm whales at Atlantis did not select the micronekton variable. There may be multiple
537 reasons such as the small temporal scale, few sperm whale detections or large spatial
538 scale and resolution of the prey model. Another plausible explanation may be the
539 mismatch between the target prey of sperm whales and those simulated with the
540 micronekton functional groups. The diet of sperm whales caught in commercial whaling
541 in the Azores was mainly composed of squids of the families Histioteuthidae,
542 Octopoteuthidae and Architeuthidae, namely *Histiotheuthis bonnellii*, *Taningia danae*
543 and *Architeuthis dux* (Clarke, 2007). Thus, prey items of sperm whales may exceed the
544 size range of micronekton organisms in the SEAPODYM-MTL (<20 cm) and occupy
545 water depths beyond the 1,000 m considered in the model.

546 At a smaller scale, the interaction of mesoscale and submesoscale features with
547 seamount topography can generate internal waves, permanent or semi-permanent eddies
548 and local upwelling that enrich the productivity of the pelagic water column (Clark et
549 al., 2010; Genin & Dower, 2007). Barbosa-Aguiar et al. (2011) found that bottom
550 topographic features from this area induced variability in eddies and meander activity of
551 the AzC. Therefore, the AzC affecting Atlantis seamount even at depths of 1,000 m
552 could potentially cause nutrient-enriched waters through processes of upwelling and/or
553 enhanced horizontal flux. Since the micronekton model relies on satellite ocean colour
554 data for the primary production, local enrichments are integrated to the dynamics of
555 micronekton functional groups. However, the spatial resolution of the ocean circulation
556 model ($0.08^\circ \sim 9$ km) is likely not enough to properly simulate local effects of the
557 seamount on micronekton biomass. Finally, the micronekton model does not include a
558 representation of the benthos and demersal component on the summit and slopes of the

559 seamount that eventually may be an additional attractive feature for large pelagic
560 predators.

561 In summary, increased productivity and micronekton biomass in Atlantis relative to
562 Irving probably explains why delphinids and sperm whales preferred to forage in
563 Atlantis. Nevertheless, dolphins and sperm whales occasionally foraged in Irving
564 possibly because of the temporarily enriched waters by cyclonic eddies that act as little
565 oasis of productivity in oligotrophic environments (Godø et al., 2012). SEAPODYM-
566 MTL may not represent the fine-scale dolphin prey distribution and accessibility well,
567 which may demonstrate why oceanographic variables (EKE and MLD), proxies of
568 vertical distribution and aggregation, are important predictors in the models.

569 This study provides novel information on cetacean presence in the remote area of the
570 Great Meteor seamount complex and adds to the few studies investigating the influence
571 of regional oceanography on predator distribution. Longer-term studies with more
572 sampling locations including abyssal areas are necessary to describe in more detail the
573 mechanisms influencing the abundance and distribution of marine top predators and
574 their prey.

575

576

577

578

579

580

581 **5. ACKNOWLEDGEMENTS**

582 We are grateful to Rui Prieto, Sergio Ricardo Gómez, Alexandra Rosa, Sérgio Ricardo
583 Gomes and the skippers and crew members of Gago Coutinho and Arquipélago research
584 vessels that helped with the deployment and retrieval of EARs. We are also grateful to
585 Tiago Marques for his statistical feedback during the revision of this manuscript.
586 Comments made by three anonymous reviewers significantly improved the present
587 paper. This work was supported by an EEA grant under project BIOMETORE
588 (PT02_Aviso2_0001), and by Fundação para a Ciência e Tecnologia (FCT) through
589 research project FCT-Exploratory project (IF/00943/2013/CP1199/CT0001) co-funded
590 by FEDER, COMPETE, QREN, POPH, FSE, and the Portuguese Ministry for Science
591 and Education. MR is supported by a DRCT doctoral grant (M3.1.a/F/028/2015 QREN
592 European Social Fund and the Portuguese Ministry for Science and Education). MAS is
593 supported by POPH, QREN, ESF and the Portuguese Ministry for Science and
594 Education through an FCT-Investigator contract (IF/00943/2013). Fieldwork was
595 approved and conducted under scientific permits from the Regional Directorate for the
596 Environment, Regional Government of the Azores (Nº30/2015/DRA). Authors have no
597 conflict of interest to declare.

598

599

600

601

602

603

604

605

606 **6. REFERENCES**

- 607 Alves, M.L.G.R., & Verdière, A. C. (1999). Instability dynamics of a subtropical jet and
608 applications to the Azores Front Current System: eddy-driven mean flow. *Journal of*
609 *Physical Oceanography*, 29, 837-864.
- 610 Abecassis, M., Senina, I., Lehodey, P., Gaspar, P., Parker, D., Balazs, J., & Polovina, J.
611 (2013). A model of loggerhead sea turtle (*Caretta caretta*) habitat and movement in the
612 oceanic North Pacific. *PLoS ONE* 8: e73274.
- 613 Au, W.W. L. (1993). *The sonar of dolphins*. New York, NY: Springer.
- 614 Au, W.W.L., Giorli, G., Chen, J., Copeland, A., Lammers, M., Richlen, M., ...Klinck,
615 H. (2013). Nighttime foraging by deep diving echolocating odontocetes off the
616 Hawaiian islands of Kauai and Ni'ihau as determined by passive acoustic monitors.
617 *Journal of the Acoustical Society of America*, 133, 3119-27.
- 618 Baird, R. W., Webster, L., D., Mahaffy, S. D., McSweeney, D. J., Schorr, G. S., &
619 Ligon, A. D. (2008). Site fidelity and association patterns in a deep-water dolphin:
620 Rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. *Marine*
621 *Mammal Science*, 24, 535-553.
- 622 Barbosa-Aguiar, A. C., Peliz, A. J., Cordeiro Pires, A., & Le Cann, B. (2011). Zonal
623 structure of the mean flow and eddies in the Azores Current system. *Journal of*
624 *Geophysical Research*, 116, C02012.
- 625 Barlow, J., Kahru, M., & Mitchell, B. G. (2008). Cetacean biomass, prey consumption,
626 and primary production requirements in the California Current ecosystem. *Marine*
627 *Ecology Progress Series*, 371, 285-295.

628 Bashmachnikov, I., Neves, F., Calheiros, T., & Carton, X. (2015) Properties and
629 pathways of Mediterranean water eddies in the Atlantic. *Progress in Oceanography*,
630 137A, 149–172.

631 Baumann-Pickering, S., Trickey, J. S., Wiggins, S. M., & Oleson, E. M. (2016).
632 Odontocete occurrence in relation to changes in oceanography at a remote equatorial
633 Pacific seamount. *Marine Mammal Science*, 32, 805-825.

634 Bednarz, U. (1991). Petrologie des Atlantis-Seamount-Komplexes. In Wefer G, Weigel
635 W., & Pfannkuche O. (Eds.). *Eastern Atlantic '90 Expedition, (RV Meteor) Cruise No.*
636 *12, 13th March to 30th June 1990* (pp. 115-123). Meteor-Ber. 91-1. University of
637 Hamburg.

638 Behrenfeld, M.J., & Falkowski. P. G. (1997). Photosynthetic rates derived from
639 satellite- based chlorophyll concentration. *Limnology and Oceanography*, 42, 1-20.

640 Brodeur, R.D., Seki, M.P., Pakhomov, E.A., & Suntsov. A. V. (2005). Micronekton–
641 What are they and why are they important. North Pacific Marine Science Organization.
642 *Pices Press*, 13, 7-11.

643 Burnham, K.P., & Anderson, D. R. (2002). *Model selection and multimodel inference:*
644 *A practical information- theoretic approach*. 2nd ed. NewYork, NY: Springer.

645 Caldeira, R., Couvelard, X., Vieira, R.R., Lucas, C., Sala, I., & Casanova., I. V. (2016).
646 Challenges of building an operational ocean forecasting system for small island regions:
647 Regional to Local. *Journal of Operational Oceanography*, 9, 1-12.

648 Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K. I.,
649 ...Hall-Spencer, J.M. (2010). The ecology of seamounts: structure, function, and human
650 impacts. *Annual Review of Marine Science*, 2, 253-278.

651 Clarke, M. R. (2007). Seamounts and cephalopods. In T. J. Pitcher, T. Morato, P. J. B.
652 Hart, M. R. Clark, N. Haggan & R. S Santos. (Eds). *Seamounts: Ecology, fisheries and*
653 *conservation* (pp. 207-229). Oxford, U.K: Blackwell Publishing.

654 Davis, R. W., Ortega-Ortiz, J. G., Ribic, C. A., Evans, W. E., Biggs, D. C., Ressler, P.
655 H., ...Würsig, B. (2002). Cetacean habitat in the northern oceanic Gulf of Mexico.
656 *Deep-Sea Research Part I*, 49, 121-142.

657 Davison, P. C., Koslow, J. A., & Kloser, R. J. (2015). Acoustic biomass estimation of
658 mesopelagic fish: backscattering from individuals, populations, and communities. *ICES*
659 *Journal of Marine Science*, 7, 1413-1424.

660 Dormann, C. F., Elith, J., Bacher, Buchmann, C., Carl, G., Carré, G., ...Lautenbach, S.
661 (2013). Collinearity : A review of methods to deal with it and a simulation study
662 evaluating their performance. *Ecography*, 36, 027-046.

663 Santos, M.E., Ferreira, A.J. & Harzen, S. (1995). Rhythmic sound sequences emitted by
664 aroused bottlenose dolphins in the Sado Estuary, Portugal. In Kastelein, R.A., Thomas,
665 J.A., & Nachtigall, P.E. (Eds.) *Sensory systems of aquatic mammals* (pp. 325–334).
666 Woerden, NL: De Spil Publishers.

667 Dragon, A.-C, Senina, I., Hintzen, N., & Lehodey, P. (2017). Modelling South Pacific
668 jack mackerel spatial population dynamics and fisheries. *Fisheries Oceanography*, 27,
669 97-113.

670 Drévillon, M., Bourdallé-Badie, R., Derval, C., Lellouche, M., Rémy, E., Tranchant, B.,
671 Benkiran, M., ...Parent, L. (2008). The GODAE/Mercator-Ocean global ocean
672 forecasting system: results, applications and prospects. *Journal of Operational*
673 *Oceanography*, 1, 51-57.

674 Gardner, W.D., Chung, S. P., Richardson, M. J., & Walsh, I. D. (1995). The oceanic
675 mixed-layer pump. *Deep Sea Research Part II: Tropical Studies in Oceanography*, 42,
676 757-775.

677 Gaspar P., Georges J.-Y., Fossette S., Lenoble A., Ferraroli S., & Le Maho Y. (2006).
678 Marine animal behaviour: neglecting ocean currents can lead us up the wrong track.
679 *Proceeding of the Royal Society B: Biological Sciences*, 273, 2697-2702.

680 Genin, A. (2004). Bio-physical coupling in the formation of zooplankton and fish
681 aggregations over abrupt topographies. *Journal of Marine Systems*, 50, 3-20.

682 Genin, A., & Dower, J.F. (2007). Seamount plankton dynamics. In Pitcher, T.J.,
683 Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., & Santos, R.S. (Eds.) *Seamounts:*
684 *Ecology, Fisheries and Conservation* (pp. 85-100). Oxford, UK: Blackwell.

685 Giorli G., Au W.W.L., Ou H., Jarvis S., Morrissey R., & Moretti D. (2015). Acoustic
686 detection of biosonar activity of deep diving Odontocetes at Josephine Seamount High
687 Seas Marine Protected Area. *Journal of the Acoustical Society of America*, 137, 2495-
688 501.

689 Giorli, G., & Au, W.W.L. (2017). Spatio-temporal variation and seasonality of
690 Odontocetes' foraging activity in the leeward side of the island of Hawaii. *Deep Sea*
691 *Research Part I: Oceanography Research Papers*, 121, 202-209.

692 Godø, O.R., Samuelsen, A., Macaulay, G.J., Patel R., Hjøllø, S.S., Horne, J.,
693 ...Johannessen, J.A. (2012). Mesoscale Eddies Are Oases for Higher Trophic Marine
694 Life. *PLoS ONE*, 7, e30161.

695 Goold, J. C., & Jones, S. E. (1995). Time and frequency domain characteristics of
696 sperm whale clicks. *Journal of the Acoustical Society of America*, 98, 1279-1291.

697 Hann, C. H., Smith, T. D., & Torres, L. G. (2016). A sperm whale's perspective: The
698 importance of seasonality and seamount depth. *Marine Mammal Science*, 32, 1470-
699 1481.

700 Hastie, G.D. Swift, R. J., Slessor, G., Thompson, P. M., & Turrell, W. R. (2005).
701 Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic.
702 *ICES Journal of Marine Science*, 62, 760-770.

703 Hastie, G. D., Wilson, B., & Thompson, P. M. (2006). Diving deep in a foraging
704 hotspot: Acoustic insights into bottlenose dolphin dive depths and feeding behaviour.
705 *Marine Biology*, 148, 1181-1188.

706 Herzing, D.L. (2000). Acoustics and social behavior of wild dolphins: implications for a
707 sound society. In Au, W. W. L., & Fay, R. R. (Eds.) *Hearing in whales and dolphins*
708 (pp. 225-272). New York: NY: Springer.

709 Hodge, L. E. W., Bell, J. T., Kumar, A., & Read, A. J. (2013). The influence of habitat
710 and time of day on the occurrence of odontocete vocalizations in Onslow Bay, North
711 Carolina. *Marine Mammal Science*, 29, 411-427.

712 Janik, V.M. (2000). Food-related bray calls in wild bottlenose dolphins (*Tursiops*
713 *truncatus*). *Proceedings of the Royal Society: Biological Sciences*, 267, 923-927.

714 Johnson, J., & Stevens, I. (2000). A fine resolution model of the eastern North Atlantic
715 between the Azores, the Canary Islands and the Gibraltar Strait. *Deep-Sea Research*, 47,
716 875-899.

717 Johnson, M., Madsen, P. T., Zimmer, W. M. X., Soto, N. A. De., & Tyack, P. L. (2006).
718 Foraging Blainville 's beaked whales (*Mesoplodon densirostris*) produce distinct click

719 types matched to different phases of echolocation. *The Journal of Experimental*
720 *Biology*, 209, 5038–5050.

721 Kalman, R.E. (1960). A new approach to linear filtering and prediction problems.
722 *Transactions of the American Society of Mechanical Engineers, Series D, Journal of*
723 *Basic Engineering*, 82, 35-45.

724 Kaschner, K. (2007). Air-breathing visitors to seamounts: marine mammals. In Pitcher,
725 T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., & Santos, R.S. (Eds.)
726 *Seamounts: Ecology, Conservation and Management* (pp. 230-238). Oxford, UK:
727 Blackwell.

728 King, S. L., & Janik, V. M. (2015). Come dine with me: food-associated social
729 signaling in wild bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition*, 18, 969-
730 974.

731 Klatsky, L. J., Randall, S. W., & Sweeney, J.C. (2007). Offshore bottlenose dolphins
732 (*Tursiops truncatus*): Movement and dive behaviour near the Bermuda pedestal.
733 *Journal of Mammalogy*, 88, 59-66.

734 Klein, B., & Siedler, G. (1989). On the origin of the Azores Current. *Journal of*
735 *Geophysical Research*, 94, 6159-6168.

736 Klinck, H., Mellinger, D. K., Klinck, K., Bogue, N. M., Luby, J. C., Jump, W. A., ...
737 Baird, R. W. (2012). Near-real-time acoustic monitoring of beaked whales and other
738 cetaceans using a Seaglider™. *PloS One*, 7, 1–8.

739 Kraus, W., Kaese, R.H., & Hinrichsen, H. H. (1990). The branching of the Gulf Stream
740 southeast of the Grand Banks. *Journal of Geophysical Research*, 95, 13089-13103.

741 Kunz, T.J. (2005). Effects of mixing depth, turbulent diffusion and nutrient enrichment
742 on enclosed marine plankton communities. Dissertation, LMU München: Faculty of
743 Biology.

744 Kvile, K. Ø., Taranto, G. H., Pitcher, T. J., & Morato, T. (2014). A global assessment of
745 seamount ecosystems knowledge using an ecosystem evaluation framework. *Biology*
746 *Conservation*, 173, 108-120.

747 Lambert, C., Mannocci, L., Lehodey, P., & Ridoux, V. (2014). Predicting cetacean
748 habitats from their energetic needs and the distribution of their prey in two contrasted
749 tropical regions. *PLoS ONE*, 9, e105958.

750 Lammers, M.O., Brainard, R.E., Au, W.W.L., Mooney, T.A., & Wong, K.B. (2008).
751 An Ecological Acoustic Recorder (EAR) for long-term monitoring of biological and
752 anthropogenic sounds on coral reefs and other marine habitats. *The Journal of the*
753 *Acoustical Society of America*, 123, 1720-1728.

754 Lehodey, P., Senina, I., & Murtugudde, R. (2008). A spatial ecosystem and populations
755 dynamics model (SEAPODYM) – Modeling of tuna and tuna-like populations.
756 *Progress in Oceanography*, 78, 304-318.

757 Lehodey, P., Murtugudde R., & Senina, I. (2010). Bridging the gap from ocean models
758 to population dynamics of large marine predators: A model of mid-trophic functional
759 groups. *Progress in Oceanography*, 84, 69-84.

760 Lehodey, P., Conchon, A., Senina, I., Domokos, R., Calmettes, B. Jouanno, J., ...
761 Kloser, R. (2015). Optimization of a micronekton model with acoustic data. *ICES*
762 *Journal of Marine Science*, 72, 1399-1412.

763 Le Traon P.-Y., Antoine D., Bentamy A., Bonekamp, H., Breivik, L.A., Chapron, B.,
764 ...Wilkin, J. (2015) Use of satellite observations for operational oceanography: recent
765 achievements and future prospects. *Journal of Operational Oceanography*, 8, 12-27.

766 Locarnini, R. A., Mishonov, A. V., Antonov, J. I., Boyer, T. P., Garcia, H. E.,
767 Baranova, O. K., ...Seidov, D. (2013). World Ocean Atlas 2013, Volume 1:
768 Temperature. In Levitus, S., & Mishonov, A. (Eds.) *Technical Ed.;NOAA Atlas*
769 *NESDIS*. (pp. 40).

770 Madec, G., & Imbard. M. (1996). A global ocean mesh to overcome the north pole
771 singularity. *Climate Dynamics*, 12, 381-388.

772 Madsen, P. T., Wahlberg, M. & Møhl, B. (2002). Male sperm whale (*Physeter*
773 *macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and
774 communication. *Behavioral Ecology and Sociobiology*, 53, 31-41.

775 Mannocci, L., Catalogna, M., Dorémus, G., Laran, S., Lehodey, P., Massart, W., &
776 Ridoux, V. (2014). Predicting cetacean and seabird habitats across a productivity
777 gradient in the South Pacific gyre. *Progress in Oceanography*, 120, 383-398.

778 McClain, C. R., Arrigo, K. R., Esaias, W., Darzi, M., Patt, F. S., Evans, R. H.,
779 ...Kumar, L. (1995). SeaWiFS Algorithms, Part 1. NASA Tech. Memo. 104566, Vol.
780 28 Greenbelt, Maryland: NASA Goddard Space Flight Center.

781 McFarland, W., & Levin, S.A. (2002). Modelling the effects of current on prey
782 acquisition in planktivorous fishes. *Marine and Freshwater Behaviour and Physiology*,
783 35, 69-85.

784 McGillicuddy, D.J. Jr., Robinson, A.R., Jannasch, H.W., Johnsonk, R., Michaels,
785 T.A.F., & Knapk, A. H. (1998). Influence of mesoscale eddies on new production in the
786 Sargasso Sea. *Nature*, 394, 263-266.

787 Morato, T., Hoyle, S.D., Allain, V., & Nicol, S. J. (2010). Seamounts are hotspots of
788 pelagic biodiversity in the open ocean. *Proceedings of the National Academy of*
789 *Sciences of the United States of America*, 107, 9707-9711.

790 Morato, T., Varkey, D. A., Damaso, C., Machete, M., Santos, M. Prieto, R., ...Pitcher,
791 J. (2008). Evidence of a seamount effect on aggregating visitors. *Marine Ecology*
792 *Progress Series*, 357, 23-32.

793 Miyzaki, N., & Perrin, W. F. (1994). Rough-toothed dolphin (Lesson, 1828). In
794 Ridgway, S. H., & Harrison, R. (Eds.) *Handbook of marine mammals*. Volume 5. (pp.
795 1–21). London, U.K: Academic Press.

796 Proud R., Handegard N. O., Kloser R. J., Cox M. J., & Brierley A. S. (2018). From
797 siphonophores to deep scattering layers: uncertainty ranges for the estimation of global
798 mesopelagic fish biomass. *ICES Journal of Marine Science*, fsy037.

799 Pusch, C., Beckmann, A., Porteiro, F. M. & Westernhagen, H. V. (2004). The influence
800 of seamounts on mesopelagic fish communities. *Archive of Fishery and Marine*
801 *Research*, 51, 165-186.

802 Richardson, P. R. (1996). Tracking ocean eddies. In Pirie, R.G. (Eds.) *Oceanography*
803 (pp. 88-104). Third edition. Oxford, UK: Oxford University Press.

804 RStudio Team. 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston.
805 MA. <http://www.rstudio.com/>.

806 Roberts, J. J., Best, B. D., Mannocci, Fujioka, E., Halpin, P. N., Palka, D. L., ...
807 Lockhart, G. G. (2016). Habitat-based cetacean density models for the U.S. Atlantic and
808 Gulf of Mexico. *Nature Scientific Reports*, 6, 22615.

809 Senina, I., Sibert, J., & Lehodey, P. (2008). Parameter estimation for basin-scale
810 ecosystem-linked population models of large pelagic predators: Application to skipjack
811 tuna. *Progress in Oceanography*, 78, 319-335.

812 Sibert, J., Senina, I., Lehodey, P., & Hampton, J. (2012). Shifting from marine reserves
813 to maritime zoning for conservation of Pacific bigeye tuna (*Thunnus obesus*).
814 *Proceedings of the National Academy of Sciences of the United States of America*, 109,
815 18221-18225.

816 Silva, M. a., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Baumgartner, M. F., &
817 Santos, R. S. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic
818 waters around the Azores. *Marine Biology Research*, 10, 123–137.

819 Simonis, A. E., Roch, M. A., Bailey, B. Barlow, J., Clemesha1, R. E. S., Iacobellis, S.,
820 ... Baumann-Pickering, S. (2017). Lunar cycles affect common dolphin (*Delphinus*
821 *delphis*) foraging in the Southern California Bight. *Marine Ecology Progress Series*,
822 577, 221-235.

823 Skov, H., T. Gunnlaugsson, W. P. Budgell, Horne, J. K., Nøttestad, L., Olsen, E.,
824 ...Waring, G. (2008). Small-scale spatial variability of sperm and sei whales in relation
825 to oceanographic and topographic features along the Mid-Atlantic Ridge. *Deep-Sea*
826 *Research Part II: Topical Studies in Oceanography*, 55, 254-268.

827 Smith, W. H. F., & Sandwell, D. T. (1997). Global sea floor topography from satellite
828 altimetry and ship depth soundings. *Science*, 277, 1956-1962.

829 Smyth, T.J., Moore, G.F., Hirata, T., & Aiken, J. (2006). PML Inherent Optical
830 Property model. Semianalytical model for the derivation of ocean color inherent optical
831 properties: description, implementation, and performance assessment. *Applied Optics*,
832 45, 8116-8131.

833 Soldevilla, M.S., Wiggins, S.M., Hildebrand, J.A., Oleson, E.M., & Ferguson, M.C.
834 (2011). Risso's and Pacific white-sided dolphin habitat modeling from passive acoustic
835 monitoring. *Marine Ecology Progress Series*, 423, 247–267.

836 Sutton, A. L., Jenner, K. C. S., & Jenner, M. M. (2018). Habitat associations of
837 cetaceans and seabirds in the tropical eastern Indian Ocean. *Deep Sea Research Part II:
838 Topical Studies in Oceanography*. In press.

839 Tobeña, M., Prieto, R., Machete, M., & Silva, M. A. (2016). Modeling the Potential
840 Distribution and Richness of Cetaceans in the Azores from Fisheries Observer Program
841 Data. *Frontiers in Marine Science*, 3, 202.

842 Torres, L. G., Smith, T. D., Sutton, P., MacDiarmid, A., & Bannister, J. (2011). *Habitat
843 use and distribution patterns of southern right whales and sperm whales discerned from
844 spatial analyses of 19th century whaling records*. National Institute of Water and
845 Atmospheric Research, Ltd. (NIWA) client report WLG2011-52. 135 pp.

846 Waring, G. T., Hamazaki, T., Sheehan, D., Wood, G., & Baker, S. (2001).
847 Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter
848 macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast U.S.
849 *Marine Mammal Science*, 17, 703-717.

850 Watkins, W. A. (1980). Acoustics and the behavior of sperm whales. In Busnel, R.-G.
851 & Fish, J.F. (Eds.) *Animal sonar systems* (pp. 283 – 289). New York, NY: Plenum
852 Press.

853 Watwood, S. L., Miller, P. J. O., Johnson, M., Madsen, P. T., & Tyack, P. L. (2006).
854 Deep-diving foraging behavior of sperm whales (*Physeter macrocephalus*). *Journal of*
855 *Animal Ecology*, 75, 814-825.

856 Wolf, K. U., & Woods, J. D. (1988). Lagrangian simulation of primary production in
857 the physical environment- the deep chlorophyll maximum and nutricline. In Rothschild,
858 B. J. (Eds.) *Toward a theory of biological-physical interactions in the world ocean*.
859 Dordrecht, NL: Kluwer Academic Publishers.

860 Wong, S.N.P., & Whitehead, H. (2014). Seasonal occurrence of sperm whales (*Physeter*
861 *macrocephalus*) around Kelvin Seamount in the Sargasso Sea in relation to
862 oceanographic processes. *Deep-Sea Research Part I: Oceanographic Research Papers*,
863 91, 10-16.

864 Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood
865 estimation of semiparametric generalized linear models. *Journal of the Royal Statistical*
866 *Society: Series B (Statistical Methodology)*, 73, 3-36.

867 Zimmer, W. M. X., Johnson, M. P., Madsen, P. T., & Tyack, P. L. 2005. Echolocation
868 clicks of free-ranging Cuvier's beaked whales (*Ziphius cavirostris*). *Journal of the*
869 *Acoustical Society of America*, 117, 3919-3927.

870 Zuur, A. F. (2012). *A Beginner's Guide to Generalized Additive Models with R*.
871 Newburgh, UK: Highland Statistics Ltd.

872 Zweng, M.M, Reagan, J.R., Antonov, J.I., Locarnini, R.A., Mishonov, A.V., Boyer,
873 T.P., ...Biddle, M. M. (2013). World Ocean Atlas 2013, Volume 2: Salinity. In Levitus,
874 S. & Mishonov, A. (Eds). NOAA Atlas NESDIS 74 (pp. 39). Silver Spring, MD.

875

876

877

878

879

880

881

882

883

884

885

886

887

888

889

890

891 **Tables**

892 Table 1. Summary of acoustic data used in this work including dates, sampling rate,
 893 duty cycle, sensitivity, depth, and position of EARs.

Location	Sample period	Sample rate (kHz)	Duty cycle (%)	Sensitivity (dB re 1V/ μ Pa)	Depth (m)	Position	
						Latitude	Longitude
Atlantis	25 July –	50	20	-194.17	294	34° 8' 37.3"N	-30° 15' 24.1"W
	21 September						
Irving	30 July –	50	20	-193.14	264	32° 2' 47.8"N	-27° 58' 8.04"W
	25 September						

894

895 Table 2. Distribution of micronekton functional group biomass by day and night for
 896 each layer.

Layer	Day	Night
Epipelagic	Epipelagic	Epipelagic + upper migrant mesopelagic + highly migrant upper mesopelagic
Upper mesopelagic	Upper mesopelagic + migrant upper mesopelagic	Upper mesopelagic + migrant lower mesopelagic
Lower mesopelagic	Lower mesopelagic + migrant lower mesopelagic + highly migrant lower mesopelagic	Lower mesopelagic

897

898 **Figures**

899 Figure 1. Map showing the location of Atlantis and Irving seamounts in relation to the
900 Azores archipelago.

901 Figure 2. Long-Term Spectral Average (LTSA) plots (above) and spectrograms (below)
902 of (A) delphinid clicks, whistles and bray calls, (B) delphinid whistles and (C) sperm
903 whale clicks.

904 Figure 3. Heatmaps showing delphinid detections (in minutes) in Atlantis (A) and Irving
905 (B) seamounts for each hour and for each deployment day. Vertical lines indicate time
906 limits between sunset and sunrise (U.S. Naval Observatory Astronomical Applications
907 Department database). On the right: the bar-charts show the number of minutes per day
908 with delphinid detections.

909 Figure 4. Heatmaps showing sperm whale detections (in minutes) in Atlantis (A) and
910 Irving (B) seamounts for each hour and for each deployment day. Vertical lines indicate
911 time limits between sunset and sunrise (U.S. Naval Observatory Astronomical
912 Applications Department database). On the right: the bar-chart showing the number of
913 minutes per day with sperm whale detections.

914 Figure 5. Maps of temperature (A) and salinity (B) at 1,500 m depth and geostrophic
915 velocities (cm/s) at the surface (C) and at 1,000 m depth (D) for Atlantis and Irving
916 corresponding to August and September climatology from WOA13 data set. Maps of
917 forecasted ADT (E), and speed and flow vectors (F) for mid-August of 2015 in the
918 Great Meteor area. Lines represent the bathymetry around these seamounts.

919

920 Figure 6. Boxplots of Salinity (A), Potential temperature (B), Speed current (C), Mixed
921 layer depth (D), Eddy kinetic energy (E), and Chlorophyll A (F) data from July through
922 September of 2015.

923 Figure 7. Boxplots of day and night epipelagic (A), upper mesopelagic (B) and lower
924 mesopelagic biomass (C) at Atlantis and Irving seamounts for the deployment period
925 (July-September 2015).

926 Figure 8. SEAPODYM modelled biomass of epipelagic (A), upper mesopelagic (B),
927 migrant upper mesopelagic (C), migrant lower mesopelagic (D), highly migrant lower
928 mesopelagic (E), and lower mesopelagic micronekton (F) averaged across the
929 deployment period (27th of July to 22nd of September 2015) at a grid resolution of 0.25°
930 latitude/longitude.

931 Figure 9. Results from the best GAM with detections of delphinids in Atlantis relative
932 to epipelagic micronekton biomass at night (A) EKE lagged 28 d (B) and MLD (C) and
933 in Irving relative to epipelagic micronekton biomass at night (D) and EKE (E). Solid red
934 line represents the fitted function with 95% confidence bands denoted by blue dashed
935 lines. Grey dots indicate observations.