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Largest baleen whale mass mortality during strong El Niño event is likely related to harmful toxic algal bloom

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29 **ABSTRACT**

30 While large mass mortality events (MMEs) are well known for toothed whales, they have

31 been rare in baleen whales due to their less gregarious behaviour. Although in most cases the

32 cause of mortality has not been conclusively identified, some baleen whale mortality events

33 have been linked to bio-oceanographic conditions, such as harmful algal blooms (HABs). In

34 southern Chile, HABs can be triggered by the ocean-atmosphere phenomenon El Niño. The

35 frequency of the strongest El Niño events is increasing due to climate change. In March 2015,

36 by far the largest reported mass mortality of baleen whales took place in a gulf in southern

37 Chile. Here we show that the synchronous death of at least 343, primarily sei, whales can be

38 attributed to HABs during a building El Niño. Although considered an oceanic species, the sei

39 whales died while feeding near to shore in previously unknown large aggregations. This

40 provides evidence of new feeding grounds for the species. The combination of older and newer

41 remains of whales in the same area indicate that MMEs have occurred more than once in recent

42 years. Large HABs and reports of marine mammal MMEs along the north-east Pacific coast

43 may indicate similar processes in both hemispheres. Increasing MMEs through HABs may

44 become a serious concern in the conservation of endangered whale species.

6

7

INTRODUCTION

Although most populations of whales have been fully protected from industrial hunting for half a

century, some were reduced to such low levels that recovery is still very slow (Baker &

Clapham, 2004). Today, whales face additional threats, such as ship strikes, entanglement and

by-catch, underwater noise, pollution and habitat loss (Clapham et al., 1999). Moreover, since

ocean conditions directly influence quality and availability of the prey species of baleen whales,

the effects of climate change will become a concern (Simmonds & Isaac, 2007).

8

9

53   Mass mortality events (MME) of marine mammals generally involve social species such

54   as dolphins or sea lions, but are rare in baleen whales due to their less gregarious behaviour

55   (Perrin et al., 2009a). When MMEs have occurred in baleen whales they have often extended

56   over several months and large areas, involving mostly coastal whales (Table 1). In the Northeast

57   Pacific, seven to eight times more gray whales (*Eschrichtius robustus*) washed ashore during the

58   years 1999 and 2000 than is usual in such a time span. Of these, 106 died within a three-month

59   period in Mexico (Gulland et al., 2005). In the course of 2012, 116 southern right whales

60   (*Eubalaena australis*), mostly calves, washed ashore at their breeding ground in Valdés

61   Peninsula, Argentina (Anonymous, 2015). During 2009, 46 humpback whales (*Megaptera*

62   *novaeangliae*) stranded in Australia (Coughran et al., 2013) and 96 in Brazil during 2010, most

63   of them calves and juveniles (Rowntree et al., 2013). Less frequent and much smaller in

64   magnitude are sudden and locally restricted baleen whale mortalities. The largest of those

65   involved 14 humpback whales which died around Cape Cod during five weeks in November

66   1987 (Geraci et al., 1989) (Table 1). The causes of most MMEs have not been conclusively

67   identified (e.g. Anonymous, 2015; Coughran et al., 2013; Gulland et al., 2005); however,

68   paralytic shellfish poisoning during harmful algal blooms (HABs) has been argued as one of the

69   main likely causes (and this is also the case for other marine vertebrate mass mortalities; Geraci

70   et al., 1989; Durbin et al., 2002; Doucette et al., 2006; Rowntree et al., 2013; Cook et al., 2015;

71   D'Agostino et al., 2015; Wilson et al., 2015; Lefebre et al., 2016).

10

72   Harmful algal blooms have an extended record in southern Chile (particularly the genus

73 *Alexandrium* with production of Paralytic Shellfish Toxins (PST). HABs have been of concern

74 to fishermen and Patagonian communities since at least 1972, when the first mass intoxication

75 was recorded (Suárez and Guzmán, 2005). Since then, the geographic region in which blooms

76 have been detected has increased to over 1000 km north-south extent (Molinet et al. 2003).

77 HABs have also become more frequent, becoming annual events with blooms normally

78 occurring in large areas during the summer and fall (Guzmán et al., 2002). Due to the danger

79 posed by these toxins, the Chilean government funds a monitoring program with over 200

80 sampling stations throughout the southern part of Chile, where phytoplankton and shellfish

81 samples are obtained and later analysed for the presence of microalgae and their toxins

82 (paralytic shellfish toxin PST, amnesic shellfish toxin AST, diarrheic shellfish toxin DST)

83 (Suárez and Guzmán, 2005). Unfortunately, mainly due to the difficulty accessing many sites,

84 these biotoxin data are only available for a limited coastal area of southern Chile.

12

85   Chilean Patagonia is a complex environment that hosts one of the largest and most

86 extensive fjord regions, with a north-south extent of approximately 1,500 km (42ºS to 55ºS),

87 covering an area of over 240,000 km² and with a coastline of more than 80,000 km, made up of

88 numerous fjords, channels and islands. At the same time this is one of the least scientifically

89 understood marine regions of the world (Försterra, 2009; Försterra et al., in press). Precipitation

90 can locally exceed 6,000 mm per year and the tidal range can exceed 7 m. The prevailing strong

91 westerly winds make its exposed shores amongst the most wave-impacted in the world

92 (Försterra, 2009). These factors are responsible for the inaccessibility of a large part of this

93 region. Chilean Patagonia is subdivided into the North, Central and South Patagonian Zone (for

94 a summary of biogeography of the region see Häussermann and Försterra, 2005 and Försterra et

95 al., in press). The remote area around Golfo de Penas and Taitao Peninsula (Fig. 1) is situated in

96 the Central Patagonian Zone between 47 ºS and 48ºS. Except for two Chilean Navy lighthouses

97 at Cabo Raper and San Pedro, the closest human settlements are more than 200 km away (Tortel,

98 Puerto Aysén and Puerto Edén).

14

99   In general, Chilean Patagonia is influenced by the West Wind Drift, a largescale eastward

100   (onshore) flow which diverges at the coast to form the northward Humboldt Current and the

101   southward Cape Horn Current (Thiel et al., 2007). The fjordic nature of the coastline produces

102   significant local complexity, with many inlets and dispersed freshwater sources. High productiv-

103   ity in these coastal waters (Fig. 2) is driven by the availability of both terrestrial nutrients, car-

104   ried by large rivers originating at the Northern and Southern Patagonian Icefields, and marine

105   nutrients (González et al., 2010; Torres et al., 2014). While this region experiences coastal winds

106   that favor net coastal downwelling, intermittent and/or localized upwelling, in particular in sum-

107   mer and north of Taitao Peninsula (47°S), is expected to enhance the supply of marine nutrients

108   to coastal waters, and the relative balance between upwelling and downwelling varies from year

109   to year.

110   During a vessel-based scuba diving expedition, "Huinay Fiordos 24" (HF24), focused on

111   benthic fauna between Golfo Tres Montes (northern Golfo de Penas, 46°30'W) and Puerto Eden

112   (49°S), dead baleen whales and skeletal remains were discovered south of Golfo de Penas and at

113   Golfo Tres Montes. Here we describe by far the largest ever recorded MME of baleen whales at

114   one time and place. Our analyses focus on the location and cause of the mortality.

115

116   **MATERIALS AND METHODS**

117   **Field surveys**

118   The vessel-based HF24 scuba diving expedition, from April 15 to May 8, 2015, aimed to

119   inventory the benthic fauna of the area between Golfo Tres Montes (northern Golfo de Penas,

120   46°30'W) and Puerto Edén (49°S). By chance, VH and her team discovered recently dead baleen

121   whales and skeletal remains in and close to the entrance of the 14 km long Estero Slight and in

122   the Canal Castillo situated 235 km to the south (Figs. 1, 3, Table 2). Georeferences and

123   photographs of different views were taken, whales measured, and species and sex identified

124   whenever possible. Between May 25 and 31, the Chilean Fisheries Service (SERNAPESCA),

125   with the support of the Chilean Navy (Armada) and the Criminal Investigation Department of

126   the Civil Police (PDI), organized a vessel-based trip to the location of the dead whales in Estero

127   Slight to investigate possible anthropogenic reasons behind the mortality. During this trip,

128   genetic samples for species identification were taken, one ear bone was extracted and stomach

129   and intestine contents of two whales were tested for presence of PST and AST (Fiscalía de

130   Aysén, 2015). During a subsequent aerial survey on-board a high wing airplane Cessna 206,

131   between June 23 and 27, 2015, CSG, VH and FH surveyed the coasts along the shores of Golfo

132   de Penas. This aerial survey covered the coastal area between the Jungfrauen Islands (48°S) and

133   Seno Newman (46°39'S) from altitudes between 100m and 850m and at speeds between

134   100km/h and 200km/h (Figs. 1, 4, Table 2). Due to limited flying time (unstable weather

135   conditions and the inability to refuel in the area) data collection was focused on counting whale

136   carcasses, recording GPS positions and taking photographs. A GoPro camera filmed

137   continuously until reaching Seno Newman. The researchers on the flight counted carcasses and

138   marked their coordinates while an audio recorder captured the carcass number, position,

139   orientation, photo number, photographer and geomorphology of the beach. Whale counts were

140   repeated in all areas except Seno Newman due to adverse weather conditions. Since there are no

18

141   landing opportunities in this remote and unpopulated area it was not possible to take samples or

142   close-up photos, or to search for additional whale bones.

143   In addition to the whale carcasses and skeletons from the two surveys, some whale

144   carcasses and skulls were reported between February and June 2015 by boat crews navigating

145   the west coast of Taitao Peninsula and the coast between 49°15' and 51°S (Table 2). Between

146   January 23 and March 1, 2016 (Expedition Huinay Fiordos 27) and between April 27 and May

147   30, 2016 (Expedition Huinay Fiordos 29), two additional vessel-based expeditions were carried

148   out, each to Seno Escondido, Seno Newman and Estero Slight, with the aim of searching for

149   new carcasses, taking samples for genetic and red tide analyses, and performing oceanographic

150   transects. Data from those surveys are included here, but most of the analyses of the samples

151   will be published in a separate paper.

152   Samples of marine invertebrates were collected under permit of Subsecretaria de Pesca y

153   Acuicultura (R.EX. 1295 del 27.04.2016). Samples of cetacean carcasses were authorized by

154   SERNAPESCA, Region de Aysen (Acta Numbers 2016-11-10 and 12).

155

156   **Satellite image**

157   A high resolution satellite image was taken of Seno Newman on August 13, 2015 using

158   the Pleiades-1 Satellite. The 16-Bit ortho-rectified GeoTIFF Multispectral (R-G-B-NIR) and

159   Panchromatic files have been analyzed to count whale carcasses and determine their geographic

160   positions (Fig. 5). The whales identified in the satellite image were compared to the photos and

161   GPS locations obtained during the overflight, and cross matched with reference to nearby

162   geomorphological features.

163

164   **Taxonomic analysis**

165   Whales were identified in situ during the vessel-based expedition based on morphological

166   characteristics. The species identification of the specimens from which tissue was sampled

167   during the SERNAPESCA expedition to Estero Slight was confirmed genetically by MJP

168   (Fiscalía de Aysen, 2015). A 675 bp fragment of mitochondrial DNA control region was

169   amplified using the primers using the primers M13 Dlp1.5 5'-

170   TGTAAAACGACAGCCAGTTCACCCAAAGCTGRARTTCTA-3' and 8G 5

171   ´GGAGTACTATGTCCTGTAACCA (Dalebout et al. 2005) and sequenced in both directions.

172   Amplification reactions were performed in a total volume of 25 µl with 5 µl PCR buffer 10X, 2

173   µl MgCl2 50 mM, 1 µl of each primer, 2 µl dNTP 200 mM and 0.3 µl Taq DNA polymerase

174   (Invitrogen Life Technologies) and 50 ng DNA. The PCR temperature profile was as follows: a

175   preliminary denaturing period of 2 min at 94 ºC followed by 30 cycles of denaturation for 30 s at

176   94 ºC, primer annealing for 40 s at 56 ºC and polymerase extension for 40 s at 72 ºC. A final

177   extension period for 10 min at 72 ºC was included.

178   **Taphonomy**

22

179   Analysis was carried out, following biostratinomic criteria, on different subsets of the

180   whale remains recorded during the overflight and the vessel-based surveys. Characterization of

181   the depositional state of the carcasses was based on a *post hoc* analysis of the assemblage,

182   exclusively through photographs, classifying the carcasses into three taphonomic classes

183   according to previous studies of biostratinomic processes in marine mammals (Pyenson et al.,

184   2014, Liebig et al., 2003, 2007, Schäfer, 1972). The aspects considered were: anatomic position

185   of the carcasses (ventral, dorsal or lateral side up; n=201), deposition site (rocky or sandy,

186   n=295), and the disarticulation and degree of decay of the carcasses. These final two aspects

187   were sorted into classes to estimate the sequence of disarticulation/decay addressing two

188   aspects: time since death (n=245) and drift time/distance of the carcass (as a proxy to estimate

189   the relative location of death, n=151).

190   To assess the time since death, three categories were defined, reflecting a straightforward

191   order from the least decomposed to the most disarticulated carcass/skeleton. "Class 1" refers to

192   carcasses in the lowest to relatively medium state of decomposition for these assemblages.

193   Included in this category are complete carcasses with skin, complete carcasses without skin, and

194   complete carcasses with partially exposed bones (see Fig. 6A). "Class 2" includes carcasses in a

195   relatively greater state of decomposition but still maintaining their longitudinal axis, although

196   some bones may be scattered (see Fig. 6B). Finally, "Class 3" refers to isolated skeletal remains

197   with no soft tissue, such as skulls, dentaries or postcranial remains (see Fig. 6C). Thus, the

198   sequence of "time since death" should reflect ranges from less than 3 months (Class 1), several

199   months, but probably less than 6 months (Class 2), to a year or more (Class 3).

24

200   The analysis of the location of death, namely whether the carcasses are para-

201 autochthonous or allochthonous, was addressed by evaluation of the time that the carcasses had

202 remained floating in the water column and at the surface (see Schäfer, 1972). For this, we

203 defined two classes, depending of the presence or absence of the skull, as a proxy for the time

204 floating and the potential distance between the site of mortality and the observed site of

205 deposition (Fig. 7) (Toots, 1965; Voorhies, 1969; Behrensmeyer 1973; Holz and Simoes, 2002;

206 Liebig, 2003). Thus, "Class A" includes carcasses that preserve the skull and "Class B" includes

207 those without a skull. For this analysis we excluded skeletons which were considered older than

208 a year (minimum age, based on field observations of AVT from 2016 expedition to the site of the

209 mortality).

210   A geomorphological analysis was made using photographs and Google Earth

211 (Terrametrics, 2015). We classified the type of depositional locality (i.e. sand/pebble dominated

212 beach or rocky outcrop) (Table 2) in order to assess the relationship between these aspects and

213 the taphonomic categories mentioned above; for instance, whether carcasses that had been

214 transported further and disarticulated (allochthonous) were more prevalent at high energy sites

215 (i.e. rocky outcrops) and articulated (para-autochthonous) carcasses more prevalent in low

216 energy environments (i.e. sandy beaches).

26

217   To compare the density of the death assemblages at Golfo de Penas with known extinct

218   and extant death assemblages recorded in the literature, we measured linear dimensions of the

219   geomorphological units (i.e. length and width of the beach), through the measure tool in Google

220   Earth, using the highest resolution satellite images available, at sites where assemblages were

221   found. In this manner, the geographic areas corresponding to the death assemblages were

222   calculated and the density determined by dividing the number of specimens in each assemblage

223   by its area.

224

225   **Analysis of the petrotympanic complex (ear bone)**

226   CSG studied the bones of the middle and inner ear of one whale, collected during the

227   SERNAPESCA expedition. A volumetric computed tomography in the Morita tomograph (box

228   of 60 mm, 500 cuts) was carried out. The images were visualized with Osirix Dicom viewer v

229   5.6 32-bit in search for fractures or micro-fractures, which would appear as black gaps in the

230   bony tissue.

231

232   **Analysis for toxins (PST/AST)**

28

233   Bivalve tissue was sampled in Estero Slight on April 22 and on May 25, 2015 (2 samples in

234   total), and in Estero Slight, Seno Newman and Seno Escondido between January 23 and March

235   1, and April 27 and May 30, 2016 (22 samples in total). The stomach content and intestine

236   content of two whales from Estero Slight were sampled on May 25, 2015. On February, 2016,

237   one sample of duodenum content was obtained from a freshly dead whale observed in Estero

238   Slight. At the same period, one sample of surface-swimming *Munida* spp. was collected at 46º

239   29.730'S, 74°55.722'W. All samples were analyzed *in situ* for presence of PST using the protocol

240   already described for the shellfish tissue and stomach content samples. Samples from 2015 were

241   analyzed by DC, while the samples from 2016 were analysed by KMC. The tissue was

242   homogenized using a blender and mixed in a 1:1 ratio with a field extraction fluid composed of

243   2.5 parts of rubbing alcohol (70%) to one part white vinegar. The mixture was then

244   homogenized manually and filtered through a paper filter (paper filter #4). The extract obtained

245   after filtration was then used to detect the presence of toxins through rapid field test kits from

246   Scotia Rapid Testing for PST and AST. For this, 100 μl of the extract was placed in a test tube

247   containing running buffer, mixed and then 100 μl of this mixture was placed in a lateral flow

248   ELISA (enzyme-linked immunosorbent assay) test strip with antibodies specific for PST

249   (saxitoxin and its derivative toxins) and AST (domoic acid). These tests were left to develop for

250   1 hour before the results were read.

30

251   Twenty-two phytoplankton samples were collected in Estero Slight, Seno Newman and

252   Seno Escondido between January 23 and March 1, and April 27 and May 30, 2016, using a 20

253   μm mesh size plankton net in a vertical tow from 15 m depth. The phytoplankton present in

254   these samples was concentrated using the net, and a 100 μl subsample was placed in a tube with

255   0.1 M acetic acid and mixed. 100 μl of this mixture were then added to a test tube containing

256   running buffer and an aliquot of this mixture of the same volume was placed in a ELISA test

257   strip for PST and left to develop for one hour before results were read.

258   These qualitative PST test strips are extremely sensitive due to the local toxin profile,

259   which is high in GTX2/3, resulting in detection limits below 32 μg STX Eq/100 g of tissue. The

260   detection limit for the AST tests was reduced to 2 ppm of domoic acid by modifying the

261   standard sample preparation protocol by eliminating the dilution of the sample before mixing it

262   with the buffer.

263   A graphical analysis of the geographic and temporal distribution of PSP events, presence

264   of harmful microalgae and environmental variables in the affected region (43°S-51°S) from

265   2007 to July 2015 and from March 2016 was performed with the data obtained from the red tide

266   monitoring program conducted by the SERNAPESCA (RS Galdames RS, personal

267   communication, 2015), in which mytilid samples are analyzed at several stations throughout

268   Chilean Patagonia approximately once a month by the "Laboratorios SEREMI Salud", from

269   Aysén and Magallanes regions at southern Chile.

270

271   **Drift model**

32

272 Floating objects are directly affected by surface currents, wind and waves. Wind both drives the

273 Ekman drift of surface water (Ardhuin et al., 2009) and exerts a direct drag on the emerged

274 surface of an object (Breivik et al., 2012). Stokes drift, the net forward transport due to non-

275 closed particle trajectories resulting from passing waves, also contributes to the transport of

276 floating objects. The drift of whale carcasses was simulated by parametrising the contribution of

277 these components, based on objects of a similar size from search and rescue models (Breivik et

278 al., 2012; Peltier et al., 2012). Due to the large uncertainty in carcass drift characteristics,

279 parameters were varied stochastically within a wide range of possible values.

280   Use was made of existing current and wave products, the HYCOM daily 1/12 simulation

281 (Wallcraft et al., 2009), and waves from ECMWF ERA-Interim reanalysis (Dee et al., 2011).

282 Winds were taken from a custom downscaling of NCEP NFL boundary conditions using the

283 WRF model (Skamarock et al., 2008) to a sub-4 km grid size. Drift scenarios were run by

284 stepping forward in time from hypothetical sites and times of mortality. All of these sites were in

285 shallow water, since carcasses resulting from mortality in deep water have a tendency to sink

286 and not resurface (Smith et al., 2015). A horizontal diffusion coefficient of 10 m^2s^{-1} was included

287 in drift tracks to represent unresolved physical processes. While the resolution of the current and

288 wave datasets is inadequate to represent detailed coastline or seabed geometry, or the interior of

289 the fjords, the drift model does clarify the expected distribution and spread of carcasses from

290 localized sources.

291

292 **Large scale wind stress**

293   The large-scale tendency toward upwelling or downwelling provides a key driver of

294   coastal ecosystems. This was assessed using ECMWF ERA-Interim reanalysis data (Dee et al.,

295   2011). It is the alongshore component of wind stress that drives Ekman transport normal to the

296   coast and consequent upwelling or downwelling. Since upwelling and downwelling are

297   cumulative processes, a time-integrated wind stress was calculated (e.g. Pierce et al., 2006) from

298   a base time of the vernal equinox (September 21). Stress was estimated from reanalysis winds at

299   10 m elevation according to Large and Pond (1981). The large scale change in coastal

300   orientation was taken into account in extracting the alongshore wind component, although

301   localized inlets, bays (including the Golfo de Penas) and islands were not considered.

302

303   **RESULTS**

304   **Field surveys and toxicity tests**

305   Of the total of dead whales observed in all expeditions and reports in 2015 (367), 35

306 recently dead whales and 12 skeletal remains were discovered during the HF24 expedition: 31

307 carcasses and 12 skeletal remains were found in and close to the entrance of the 14 km long

308 Estero Slight and four carcasses in Canal Castillo, situated 235 km to the south, as well as many

309 whale bones on different beaches (Fig. 3, Table 2). Three-hundred and five carcasses were

310 mapped during the overflight between the Jungfrauen Islands (~48ºS) and Seno Newman

311 (46º39'S). In addition to this total of 284 whale carcasses and 21 skeletons from the two surveys,

312 51 whale carcasses and 11 whale skulls were reported between February and June 2015 by boat

313 crews navigating the west coast of Taitao Peninsula and the coast between 49°15' and 51°S

314 (Table 2, Fig. 4).

36

315   On some photos what could have been carcasses of smaller animals (possibly dolphins

316   and/or sea lions) were seen, but due the flying altitude, speed and weather conditions, the photo

317   quality and resolution did not allow their conclusive identification as actual carcasses. In Estero

318   Slight, one dead pinniped was found on the shore from the vessel. During the SERNAPESCA

319   expedition one Otariidae skull was found and photographed in the same channel but the

320   correspondence of the carcass and the skull could not be established.

321   The 28 whale carcasses that could be identified unambiguously to species level were all

322   sei whales (*Balaenoptera borealis*); 15 of these identifications were confirmed genetically.

323   Seven specimens could be identified as males and ten as females. One hundred and twenty-nine

324   carcasses were identified as baleen whales of the Balaenopteridae family or rorquals. The 30

325   whales examined in detail in Estero Slight during the vessel-based expedition were between 6 m

326   and 15 m long, hence included both juvenile and fully grown specimens.

327   None of the examined whales showed any evidence of disease or traumatic damage. The

328   anatomic structures of the ear bone were in good condition showing no damage; the stapes were

329   articulated in place, and the bony tissue showed no fractures (Fig. 8). The analysis of locally

330   collected mytilids in April and May 2015 and of the stomach and intestine content of two whales

331   in May 2015 showed presence of PST and AST.

38

332   In 2016, 16 fresh carcasses were observed during the HF27 and HF29 vessel-based

333 expeditions to Golfo Tres Montes; five further were reported by boat crews navigating the

334 southern part of Chilean Patagonia. None of the examined whales showed any evidence of

335 disease or traumatic damage. Thirty-six rapid tests on PST were run using mussels (12 tests),

336 *Munida* (2 tests), and phytoplankton (22 tests) in Seno Escondido, Seno Newman and Estero

337 Slight. Most of the samples collected during the 2016 expeditions proved to be negative for the

338 presence of PST, nevertheless, both expeditions detected the presence of PSP in the

339 phytoplankton collected at the entrance of Seno Newman. A sample collected at the head of

340 Seno Newman was negative for PST, indicating that the toxic phytoplankton was preferentially

341 located at the mouth of this inlet and nearby areas of the Canal Chaicayán.

342

343 **Biostratinomic analysis**

344   Of the 367 dead whales observed in 2015, 305 carcasses were mapped between Seno

345 Newman (46º39'S) and Jungfrauen Islands (~48ºS). Those carcasses could be grouped into five

346 assemblages (Figs. 1, 9, Table 2), defined as a group of carcasses in close proximity. The

347 assemblages were called Golfo de Penas, Jungfrauen Islands, Seno Escondido, Seno Newman

348 and Estero Slight.

349   Some carcasses were floating (11), but most (284) were deposited ashore (Figs. 3 to 5). In

350 general, they were tide-oriented (parallel to the coast line) and all of the classified carcasses

351 from the overflight were lying on their back or side (ventral up, 44.3%; lateral up, 55.7%) (Table

352 3, Fig. 11C), while only one specimen (from HF24) was found in a dorsal up position (data not

353 included in analysis due to different time of observation).

41

354   With respect to the classification of "time since death", 68.8% of the carcasses were

355   classified in class 1 (less than 3 months), 24.9% in class 2 (less than 6 months) and 6.3% in class

356   3 (more than a year) (Fig. 11A-B, Table 4). With respect to "time at sea", 147 (87%) of the

357   carcasses were classified in class A (short time/distance of drift), while only four (13%) were

358   identified as class B (long time/distance of drift) (Fig. 11 C, Table 4). There was no pattern

359   relating the geomorphological unit (sandy: 34%, pebble: 27%, rocky beach: 34%) to the

360   taphonomic classes.

361   The carcasses found in April in Estero Slight were classified in stage 2 of Geraci and

362   Lounsbury (2005) indicating a few days to weeks since death; this would be classified as class 1

363   in the taphonomic classes of the present study.

364   The density of whale carcasses was in average 1050/km², considering all assemblages

365   recognized (Table 5).

366

367   **Carcass drift and potential source locations**

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368   The distribution of beached carcasses was simulated from four illustrative source

369   locations (Fig. 12A-D). In each case, calculations tracked 13000 hypothetical carcasses,

370   reflecting source times spanning a 2-month period from mid-February to mid-April 2015 and a

371   range of drift model parameters. The spread of stranding locations therefore represents

372   variability of the current, wind and wave environment during this period as well as the

373   uncertainty in model parameters and a diffusive component to the drift tracks. While each of the

374   illustrated source locations leads to strandings distributed over several hundred kilometres of

375   coastline, there are important differences in these distributions. A simulated source in Golfo Tres

376   Montes (northern Golfo de Penas) leads to strandings throughout the Golfo de Penas (Fig. 12A),

377   including in the Golfo Tres Montes itself. No other source location (Fig. 12B-D) leads to

378   strandings in Golfo Tres Montes due to the direction of prevailing currents and the sheltering

379   effect of Peninsula Taitao. Similarly, only a source to the north of Peninsula Taitao leads to

380   strandings in that region (Fig. 12B). Carcasses originating in the Golfo de Penas have a tendency

381   to be transported to the south by prevailing currents (Fig. 12A, C, D).

382

383   **Inter-annual variation in upwelling or downwelling**

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384   Comparison between the cumulative alongshore wind stress for the year in question and

385   the previous 20 years (Fig. 13) reveals that the months immediately prior to the mortality event

386   were anomalous. North of the study area, at 45°S, there was an anomalously strong tendency

387   toward upwelling (an upward trend in Fig. 13), making this one of the most upwelled years of

388   the period. At the latitude of Golfo de Penas and further south there was a net tendency to

389   downwelling (a downward trend in Fig. 13), but punctuated by upwelling events, making this

390   one of the least downwelled years of the period.

391

392   **DISCUSSION**

393   Possible causes of death (Table 6) need to be analysed for a mechanism that is capable of

394   synchronous killing of hundreds of whales, apparently all or most of the same species (with few

395   exceptions, i.e. one confirmed pinniped). Baleen whales, in contrast to odontocetes, are less

396   social and do not use echolocation to navigate (Perrin et al., 2009b). The latter characteristics are

397   key aspects used to explain mass mortalities in odontocetes.

398   Possible causes for the death of hundreds of baleen whales include a lethal and highly

399   contagious unknown virus or infection, noise-related mechanisms at sea, and intoxication by

400   biotoxins (domic acid, saxitocin, etc; Geraci et al., 1989; Fire et al., 2010; Lefebvre et al., 2016;

401   Pyenson et al. 2014, Table 6). In this assemblage the individuals could not be tested for viruses

402   or bacteria, due to their advanced state of decomposition. There was no evidence of pathological

403   modifications that could be attributed to such a cause, however, it is not possible to completely

404   discard this hypothesis.

46

405   The only potentially lethal noise-related mechanism for a baleen whale are very intense

406   noises associated with blasting in close proximity (Ketten 1992). This could injure the animal

407   and cause haemorrhage or provoke panic, disorientation and favour entrapment (not yet

408   described for baleen whales, Goldbogen et al. 2013). Although there was no evidence of bony

409   damage or micro-fracture of the one examined periotic, this cannot be excluded for the other

410   individuals. Any other noise-related damage could neither be ruled out due to the decomposition

411   of the soft tissue structures, nevertheless there is no evidence that for baleen sonar and ground

412   noise could trigger more than non-lethal behavioural and temporary effects (Goldbogen et al.

413   2013). The strongest argument against this hypothesis is that whales died synchronously along

414   hundreds of kilometres of shore line and at least five different sources of carcasses were

415   identified (see discussion on drift models), which could only be explained by a large number of

416   blastings along the coast during a very restricted time period. The study carried out by

417   SERNAPESCA (Fiscalía de Aysén, 2015; Ulloa et al., 2016, available upon request from

418   SERNAPESCA authorities) based on partial necropsies of two whales in late May 2015, found

419   no evidence of any trauma or human interaction. The whales were already in decomposition

420   stage 3 to 4 and class 1 of taphonomic classes used here.

421

49

422   Paralytic shellfish toxin (PST) is known to accumulate in the pelagic stage of the squat

423   lobster *Munida gregaria* (MacKenzie & Harwood, 2014), an important prey of sei whales

424   (Matthews, 1932). Older reports (Tabeta & Kanamura, 1970) and recent observations by boat

425   crews (pers. comm. Keri-Lee Pashuk, 2015) indicate that squat lobster abundance fluctuates

426   strongly and can reach extremely high concentrations, especially in Golfo Tres Montes (Tabeta

427   & Kanamura, 1970). The presence of PST in mytilids from the area and in the whale carcasses

428   and the absence of evidence for other causes of death leaves paralytic shellfish poisoning (PSP)

429   as the most probable cause of death (Table 6). Although AST was also detected in one of the

430   stomach content samples, it is not believed to be the cause of the MME as it was not detected by

431   the toxin monitoring stations. A mixed assemblage of 40 skeletons from the Miocene in the

432   north of Chile, dominated by rorqual whales and attributed to four recurrent HAB events, shows

433   many similarities to the assemblages described here (Pyenson et al., 2014). The characteristics of

434   the MME and the repetition in the same locality are common features for HAB-mediated

435   mortalities (Brongersma-Sanders, 1957) (see Table 6, 7). MMEs through PSP in rorquals are

436   thus not a recent phenomenon in the South East Pacific. Nevertheless, whale bone

437   accumulations and reports of mortalities in Chilean Patagonia of up to 15 rorquals going back to

438   at least 1977 suggest an increase in the frequency of mortalities (Table 8). Since the early 1990s

439   HABs have been recorded every year in spring and autumn along the entire Patagonian coast but

440   patterns are patchy and generally restricted to bays and fjords. The same is true the coast of the

441   Northeast Pacific where HAB events have been increasing in strength and extension (Cook et

442   al., 2015). This MME coincided with increased mortality of baleen whales along the west coast

443   of North America in 2015 (NOAA, 2015b), and with the most extended and longest lasting HAB

444   event registered there (NOAA, 2015c). A positive correlation between the occurrence of PST

50

51

445   blooms and the ENSO indices in northern and central Patagonia has been shown (Cassis et al.,

446   2002; Guzmán & Pizarro, 2014). A similar correlation between the abundance of toxic harmful

447   algae and surface temperatures, which in turn are affected by ENSO, was observed in Aysén by

448   Cassis et al., (2002). El Niño events have increased in frequency and strength due to global

449   warming (Cai et al., 2014). A strong El Niño event began to build in September 2014, which

450   became the strongest El Niño of all time (NOAA, 2015a). The calculated cumulative windstress

451   (Fig. 13) suggests that during this period there was an anomalous tendency towards coastal

452   upwelling and associated nutrient delivery. Exceptionally high levels of PST, ten times higher

453   than usual peaks, were reported in March 2015 from the closest monitoring site 120km north of

454   the mortality area (Isla Canquenes, Fig. 14).

455   The presence of PST during February 2016 was accompanied by deep red/brown surface

456   water discoloration due to the high abundance of *Alexandrium catenella*. This harmful algal

457   bloom was coincidental with an unusually large bloom of the same toxic species in the waters

458   around Chiloé island (42°S) (Hernández et al, 2016). The May 2016 expedition did not observe

459   water discolouration at this location, nevertheless the phytoplankton samples obtained at the

460   mouth of Seno Newman were also positive for PST, indicating that this toxic species can be

461   present in the area for long periods of time during the summer. The PST levels at Isla Canquenes

462   were not elevated in 2016; however, at two sites in the Messier Channel levels four and seven

463   times higher than usual peaks, were measured (Fig. 15)

52

464   Rorqual whales sink shortly after death (Smith et al., 2015). Once carcasses have sunk

465   below a depth of 50 m to 100 m, they tend not to re-float since hydrostatic pressure compresses

466   decomposition gases (Smith et al., 2015). The bathymetry in the Golfo de Penas area and off the

467   steeply sloping Taitao Peninsula (Fig. 12) requires that the whales that washed ashore all died

468   near the shore. Thus, we conclude that despite common belief (Perrin et al., 2009a) sei whales

469   opportunistically feed close to shore and may even follow their prey into narrow and shallow

470   inlets and channels. This hypothesis is supported by the fact that live Sei whales were observed

471   nearshore in Golfo de Penas and Estero Slight on several occasions (Table 8).

54

472 The drift model suggests that the observed carcasses originated from multiple sites. The

473 carcasses found in the two fjordic inlets of Seno Newman and Estero Slight (62% of the total)

474 probably died not far from where they stranded, either in the Golfo Tres Montes or within the

475 inlets themselves (Figs. 1, 9), since source locations elsewhere in Golfo de Penas or north of

476 Taitao Peninsula do not lead to carcasses in this region (Fig. 12B-D). Although the inlets

477 themselves are not resolved in the drift model, the net seaward surface outflow of a fjord would

478 only allow carcasses to collect toward its head (as observed) if wind and waves in that direction

479 dominated their drift, or if they died close to the site where they were found. Modeled winds

480 were occasionally toward the head of Seno Newman, on March 20 and during April 14 -18, but

481 almost never in the case of Estero Slight (Fig. 16), so it is highly likely that the carcasses found

482 within these inlets were the result of mortality within the inlets themselves. Carcasses from

483 within these inlets could, however, be exported to nearby coastal waters and then distributed

484 around Golfo de Penas as seen in the drift simulations for a source in Golfo Tres Montes (Fig.

485 12A), so mortality within the inlets of Seno Newman and Estero Slight could have been the

486 source for carcasses found elsewhere in Golfo Tres Montes or Golfo de Penas.

487 The accumulation of carcasses in the convoluted and extremely shallow Estero Escondido

488 is similarly unresolvable by the drift model, but it also appears highly likely that these carcasses

489 resulted from mortality within the inlet itself. It is however unclear why dozens of large whales

490 would swim into a narrow inlet which in most parts is only between 2 and 7 m deep (maximum

491 depth 15 m just inside extremely shallow entrance) (Fig. 17).

492   Drift predictions from sources within Golfo de Penas, or to the south (Fig. 12A, C-D),

493   never led to carcasses on or to the north of Taitao Peninsula, therefore the observed carcasses on

494   the exposed shoreline in that region (Estero Cono) likely originated close to shore, either locally

495   or to the north. The carcasses found between the southern end of Golfo de Penas and 49°S

496   either died very close to where they washed ashore or were transported from the large

497   concentrations in Golfo de Penas by clockwise flow within the gulf. The five whales between

498   49°S and 51°S probably died locally.

499   Surveys in the Golfo de Penas area have sighted sei whales in all seasons, with up to 600

500   individuals, some even near to the shore of Golfo de Penas and Estero Slight (Table 8).

501   Therefore, the number of whales that have been exposed to toxins could be considerable. It has

502   been calculated that less than 10% of the gray whales that are estimated to die each year in the

503   eastern North Pacific are washed ashore, while most sink and do not resurface (Rugh et al.,

504   1999). Assuming a similar ratio, our observations may greatly underestimate the actual

505   magnitude of this mortality event. Many whales may have sunk and never re-surfaced, and a

506   significant number of carcasses may have been washed ashore on the many remote beaches that

507   could not be surveyed due to adverse weather conditions. Others may have been destroyed by

508   wave action from winter storms on the high-energy rocky shores that dominate the area.

509   In other reported MMEs, the period of the time of a massive mortality was determined by

510   considering the number of carcasses, and their temporal and spatial extent. This ranged from two

511   years (gray whales; Gulland et al., 2005) to a few weeks (Humpback whales of cape Code;

512   Geraci, 1989). To determine the time span of this MME, the classification of carcasses was

513   carried out following the disarticulation sequence proposed by Schäfer (1972).

514   Time since death and time of transportation at sea of the carcass are slightly different in

515   terms of articulation and state of decomposition. Following Schäfer (1972), the first breakage of

516   the outer tissue of a carcass at sea should occur within a week to a month, although in Chilean

517   Patagonia the time span could be a little greater due to the low temperature. In addition, some

518   carcasses could have drifted for some weeks, arrived intact on shore, and then decayed more

519   rapidly exposing the bones, while other carcasses could have floated longer until skull, tail and

520   limbs were disarticulated, but decayed more slowly due to the colder water temperatures. This

521   was in agreement with the comparisons of the disarticulation of carcasses in the field assessed

522   through the photographs of the different expeditions to the same area (Estero Slight, in April and

523   May 2015). Nevertheless, at the present assemblage, the time until the bones were exposed was

524   extended from 1 to around 3 months (class 1) and time of disarticulation was shifted from 3 to 6

525   months (class 2), due to the low average temperature in the study area.

526   Considering available information on MMEs time scales, it is reasonable to suppose this

527   event occurred over a time span of approximately three to maximum six months (November

528   2014 to April 2015). Nevertheless, the record of other crews (Table 2) and modeled

529   oceanographic conditions (see "Carcass drift and potential source locations", above) point to the

530   beginning of the die off around February at Golfo de Penas. Thus the class 2 carcasses would

531   indicate another pulse of corpses arriving at the same area in a different taphonomic condition,

532   which could suggest: a) longer drift time/distance transport; b) equal arrival but different time of

533   death; or c) higher energy environment. The classification of "time at sea" analysis suggested

534   that drift time was in its majority the same with a similar proportion of class a (short drift

535   time/distance). The analysis of the anatomic positions suggests the allochthonous nature of the

536   deposits in all assemblages (see Pyenson et al., 2014). Only two carcasses were found in a dorsal

537   up position which suggests live stranding.

538   The average density of Golfo Tres Montes assemblages is equivalent to one third of the

539   density calculated for Cerro Ballena, a Late Miocene (~9 m.y.a.) fossil red tide linked

540   assemblage of northern Chile (3000/km^2, Pyenson et al., 2014) (Table 5). However, this

541   difference is likely to have a sampling bias since in Golfo Tres Montes and Golfo de Penas we

542   could only could the carcasses along the coastline, but not on the seafloor.

543

544   **CONCLUSIONS**

545

546   1. The whales died at sea, close to where they beached. About 90% of the whales died during

547   one MME (94.7% for time since death and 87% for time at sea analysis), most probably

548   between February and April 2015. No major mortality has occurred in the same area in 2016,

549   but mortalities in other areas cannot be excluded (see Fig. 15 for 2016 toxin levels).

550   2. Since it is likely that all or most of the affected whales were sei whales, the documented

551   mortality may represent a significant increase over the usual death rate of Southern

552   Hemisphere sei whales (Reilly et al., 2008). If the frequency and magnitude of MMEs

553   increase due to climate change this would have a significant impact on the local population

554   and threaten the recovery of this endangered species, which in the Southern Hemisphere was

555   reduced by whaling from about 100,000 to 24,000 individuals by 1980 (Perrin et al., 2009a).

556   3. This MME and historical data suggest that, at least during years with abundant squat

557   lobsters, the Golfo de Penas is one of the most important feeding grounds for sei whales,

558   hosting the largest and densest known sei whale aggregations outside the polar regions.

559   1. The MME reported herein and its probable connection to El Nino-caused red tide events

560   throughout the eastern Pacific could indicate that marine mammals are among the first

561   oceanic megafauna victims of global warming.

562   4. Discoveries of dead whales in this remote area are chance finds. To clarify the extent,

563   frequency and magnitude of MMEs, an assessment and systematic monitoring of whale

564   populations in Central Chilean Patagonia is necessary. We suggest to do this through regular

565   satellite images.

566

567

568 **Acknowledgements**

We particularly thank the organizers and participants of the expedition organized by the Chilean

Fisheries Service (SERNAPESCA), especially B. Caceres, G. Garrido, M. Ulloa, F. Viddi, J.

Acevedo, T. García, C. Calderón and L. Bedriñana. Thanks also to R. Brownell, N. Pyenson, L.

Pastene, E. Poulin, F. Beaujot, U. Pörschmann, P. Pascoe, S. Kraft, K.-L. Pashuk and V. Beasley.

Thanks to Bidema PDI, Fiscalía de Aysén and Armada de Chile for field support. We are

thankful to many more people for assisting with field-work, technical support and logistics, for

sharing or facilitating data and information, and for discussions. This is publication number 134

of Huinay Scientific Field Station.

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823 **Figure and table captions**

824 **Fig. 1:** Location of dead whales and skulls found in Chilean Patagonian. Boat track: green (HF24), flight track: blue

825 (HF25) A) Golfo de Penas, B) Golfo Tres Montes, C) Seno Escondido.

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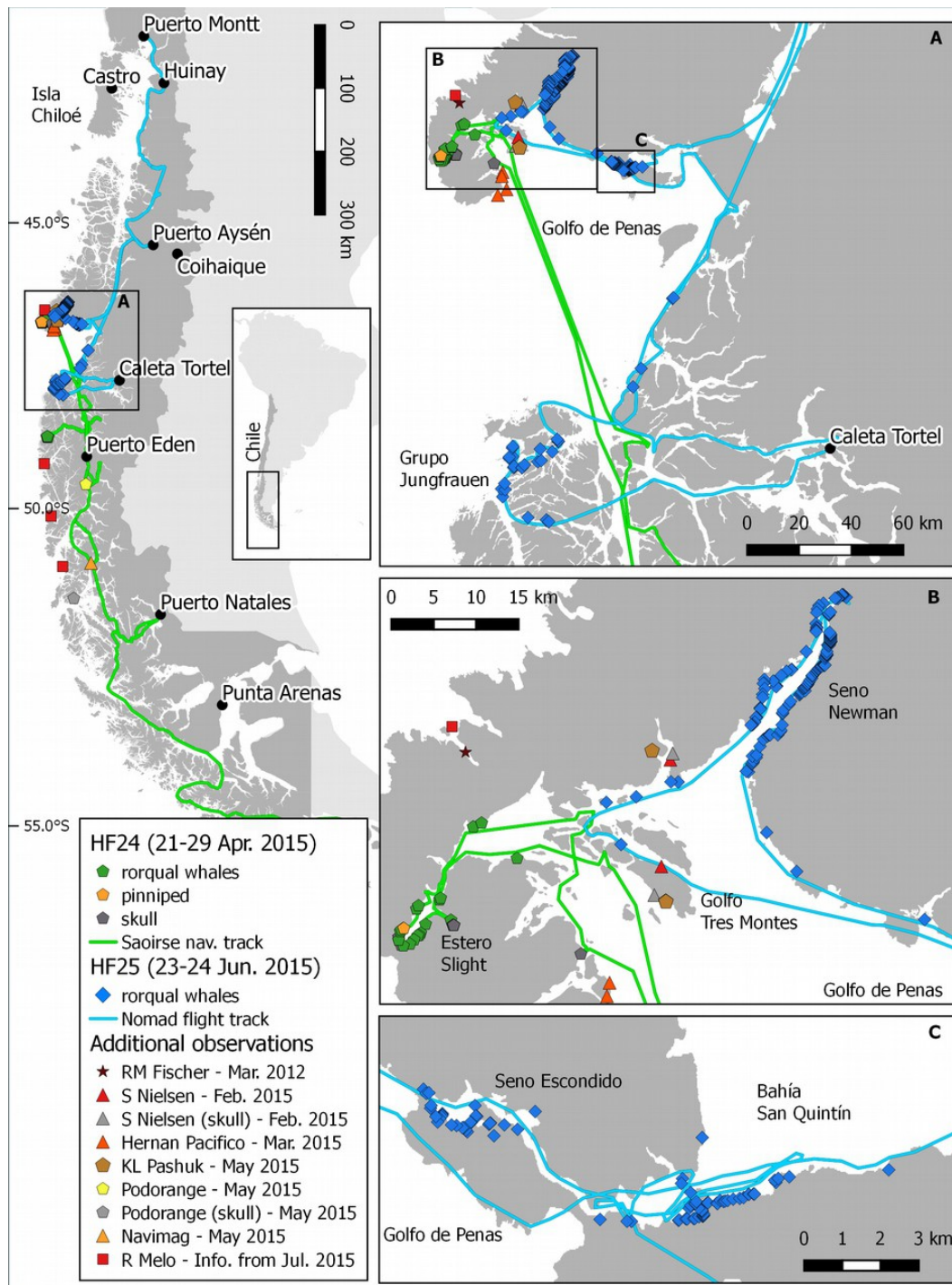
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842 **Fig. 2:** Satellite image (MODIS Aqua) showing the concentration of chlorophyll a on March 23rd, 2015. Areas

843 where most whales were found are circled.
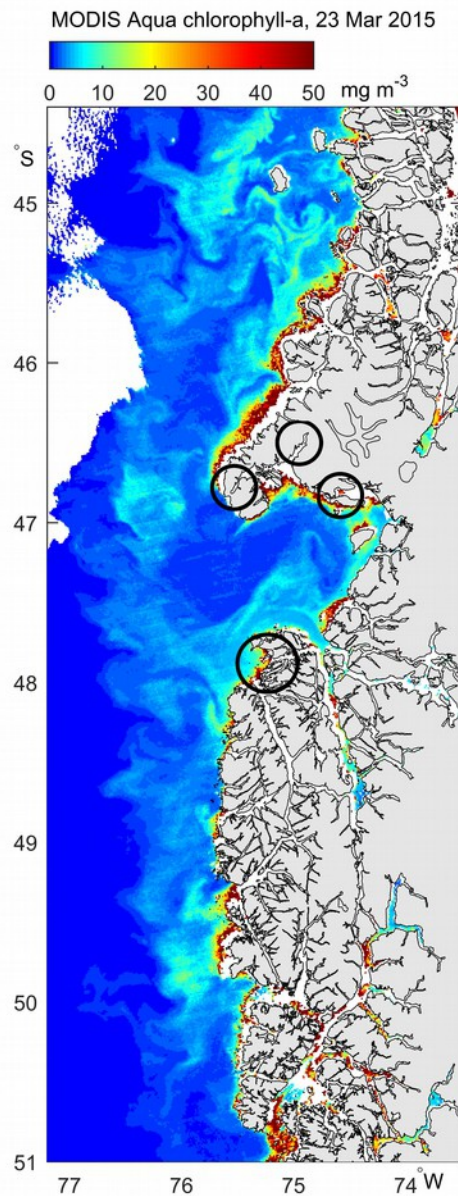
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845   **Fig. 3:** Documented whale carcasses and skeletal remains during a vessel survey in April 21st 2015 in Caleta Buena,

846   Estero Slight. A) and B) skeletal remains C) Recently dead sei whale. Photos: Keri-Lee Pashuk, all rights reserved.

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849   **Fig. 4:** Documented whale carcasses and skeletal remains during an overflight on June 25st 2015, Seno Escondido.

850   The numbers correspond to the whale identification numbers in Table 1. Photos: Vreni Häussermann, all rights

851   reserved.
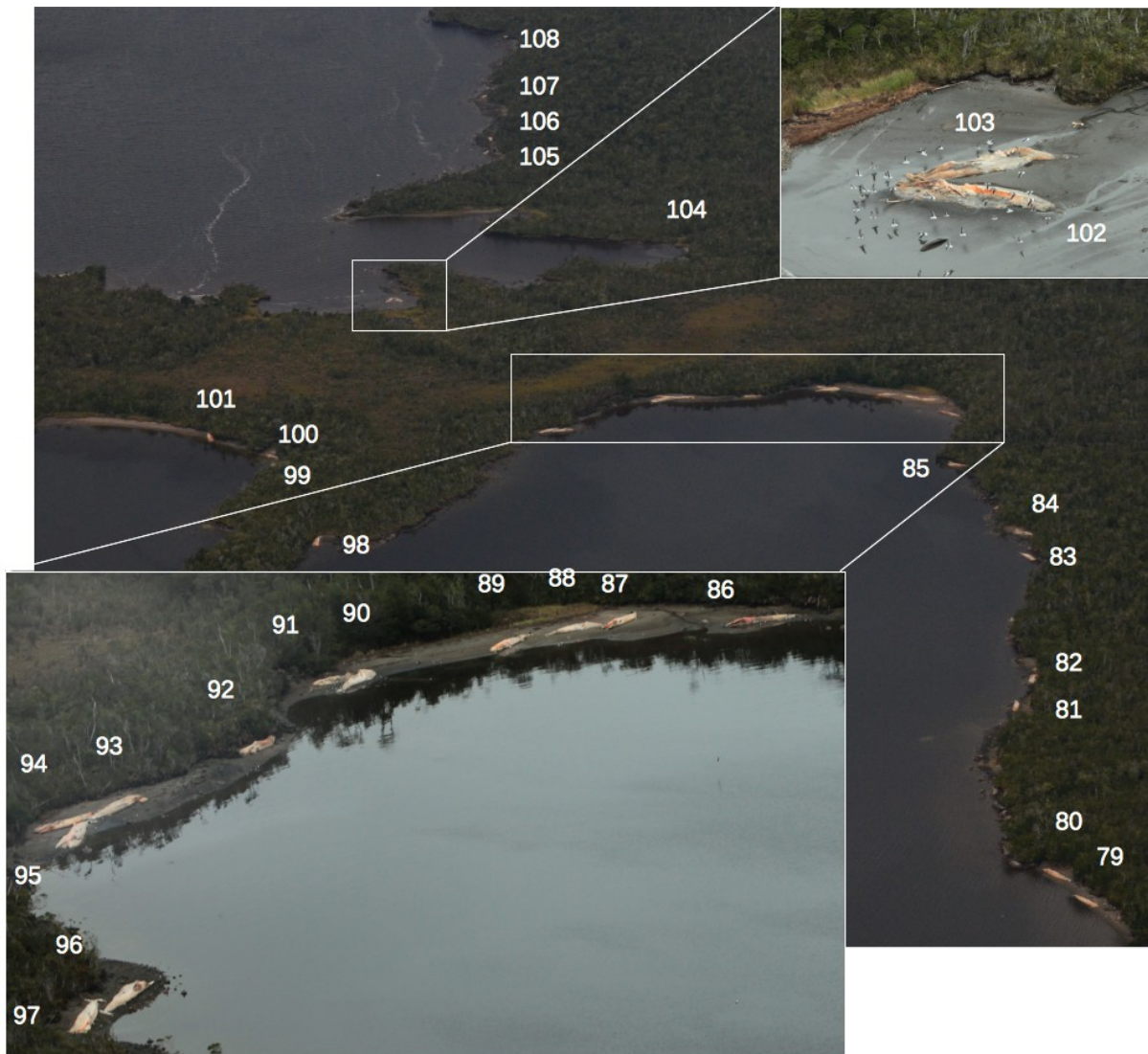
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855 **Fig. 5:** A. A. Satellite image on August 13th 2015, used to count the carcasses along Seno

856 Newman. B-C-D. Detail of the carcasses highlighted in A.
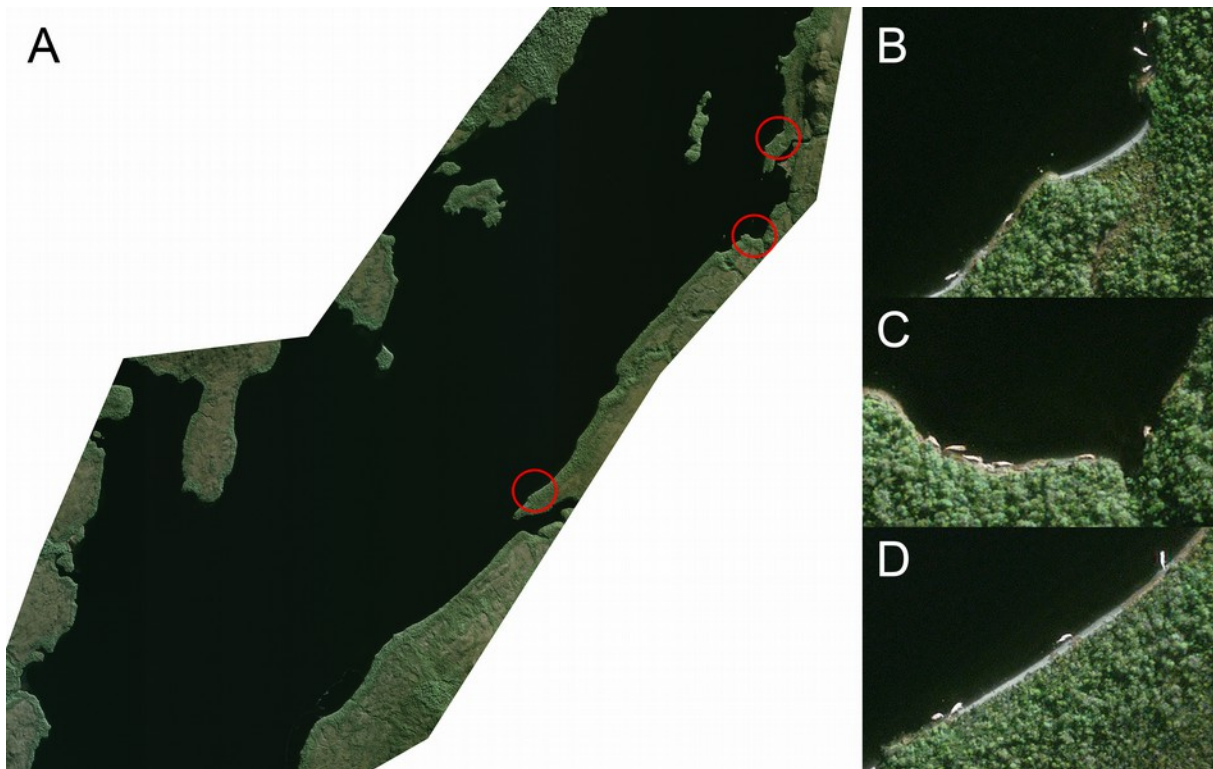
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864 **Fig. 6**: Biostratinomic classification addressing the decomposition/desarticulation of carcasses/skeletal remains

865 assessing to the time since death. A-B) Class 1, carcasses in the lowest to relatively medium state of decomposition,

866 C-D) Class 2, carcasses in a relatively greater state of decomposition, but still maintaining their longitudinal axis,

867 although some bones may be scattered, E-F) Class 3, isolated skeletal remains with no soft tissue.
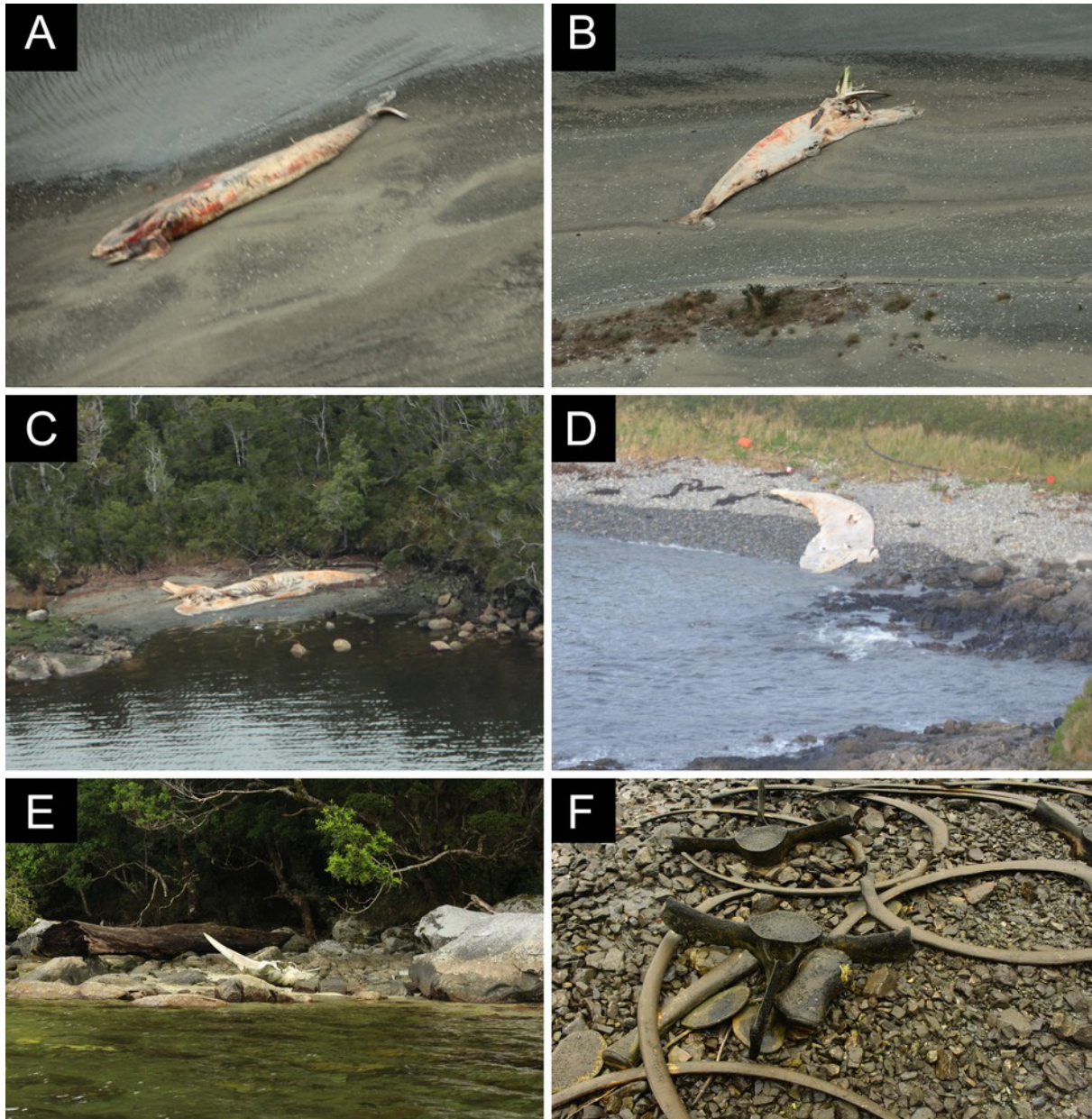
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870　**Fig 7:** Biostratonomic classification of the location of death of carcasses/skeletal remains A)

871　Carcasses preserving the skull, B) Carcasses lacking the skull.
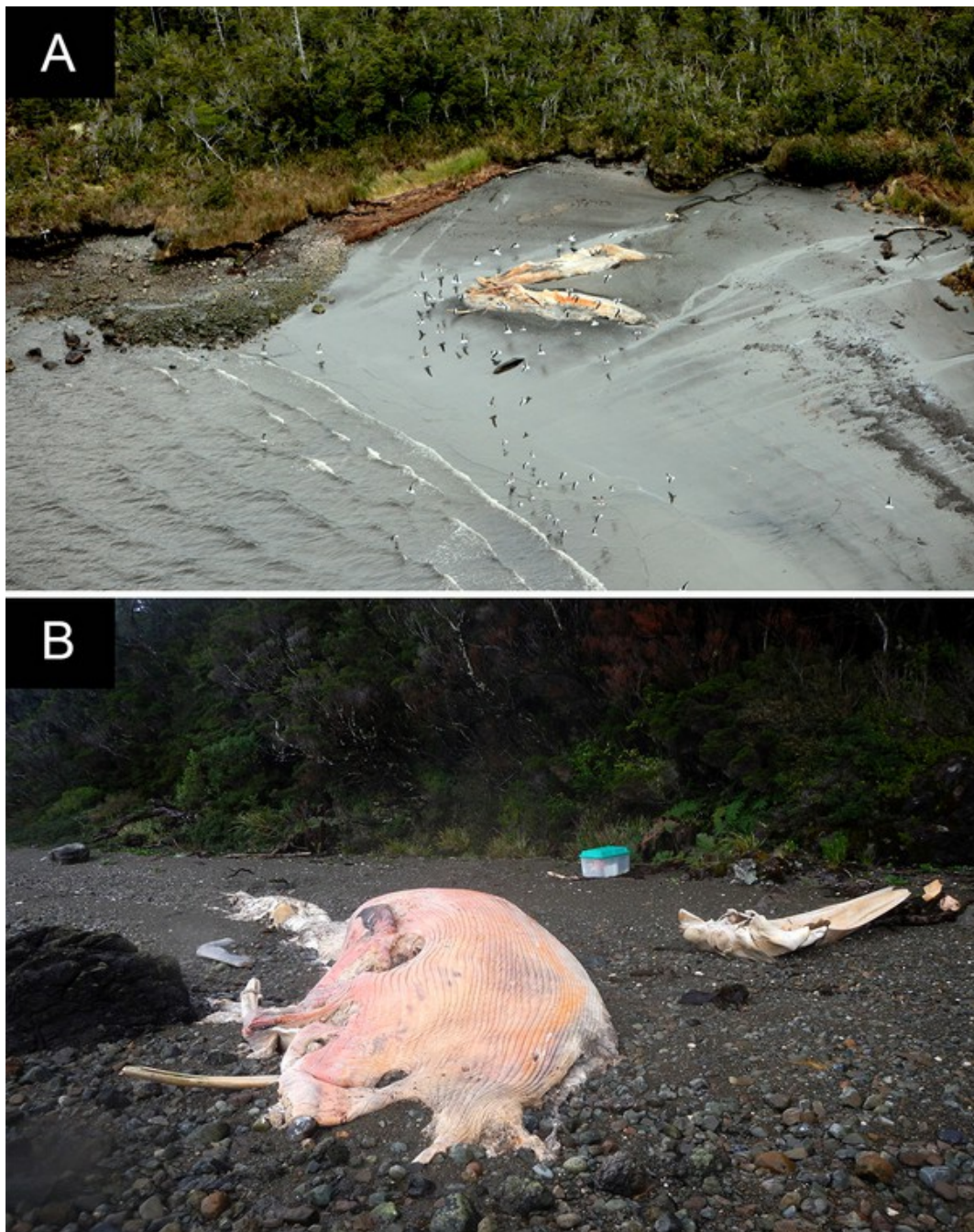
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874 **Fig. 8:** Digital images obtained through computed volumetric tomography (CVT) scanned at Morita Tomography

875 (box of 60 mm, 500 slices). All acoustic anatomical structures of the middle ear (ossicles: stapes), internal ear

876 (cochlea: spiral lamina) and the semicircular canals are seen in perfect condition.

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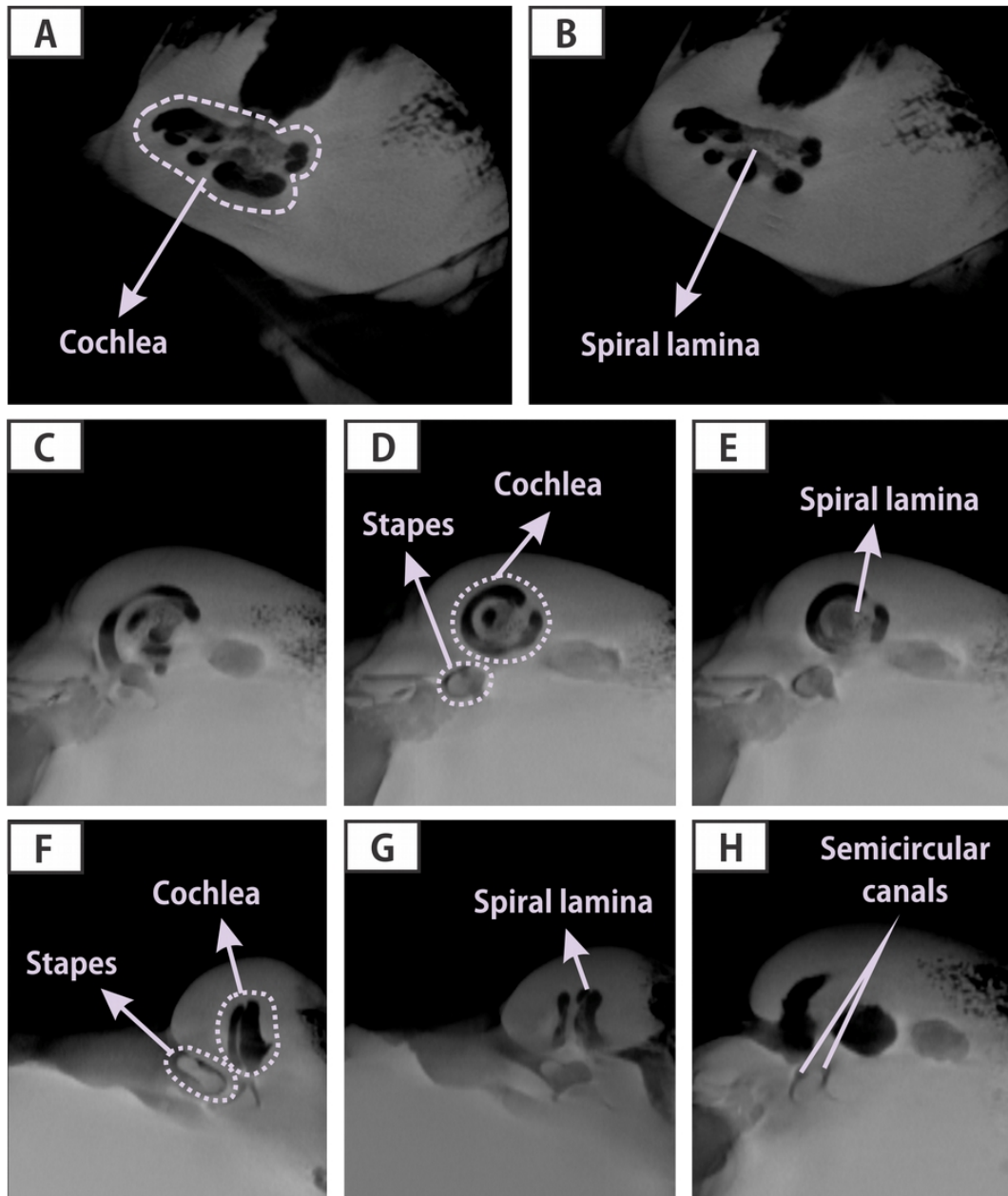
Fig. 9: Maps showing the five assemblages of whale carcasses. (A) Golfo de Penas, (B) Seno

Escondido, (C) Seno Newman, (D) Estero Slight, (E) Jungfrauen Islands. State of decomposition

color-coded: Yellow (state 1; least decomposed, all articulated), orange (state 2, intermediate

decomposed), red (state 3; isolated remains).
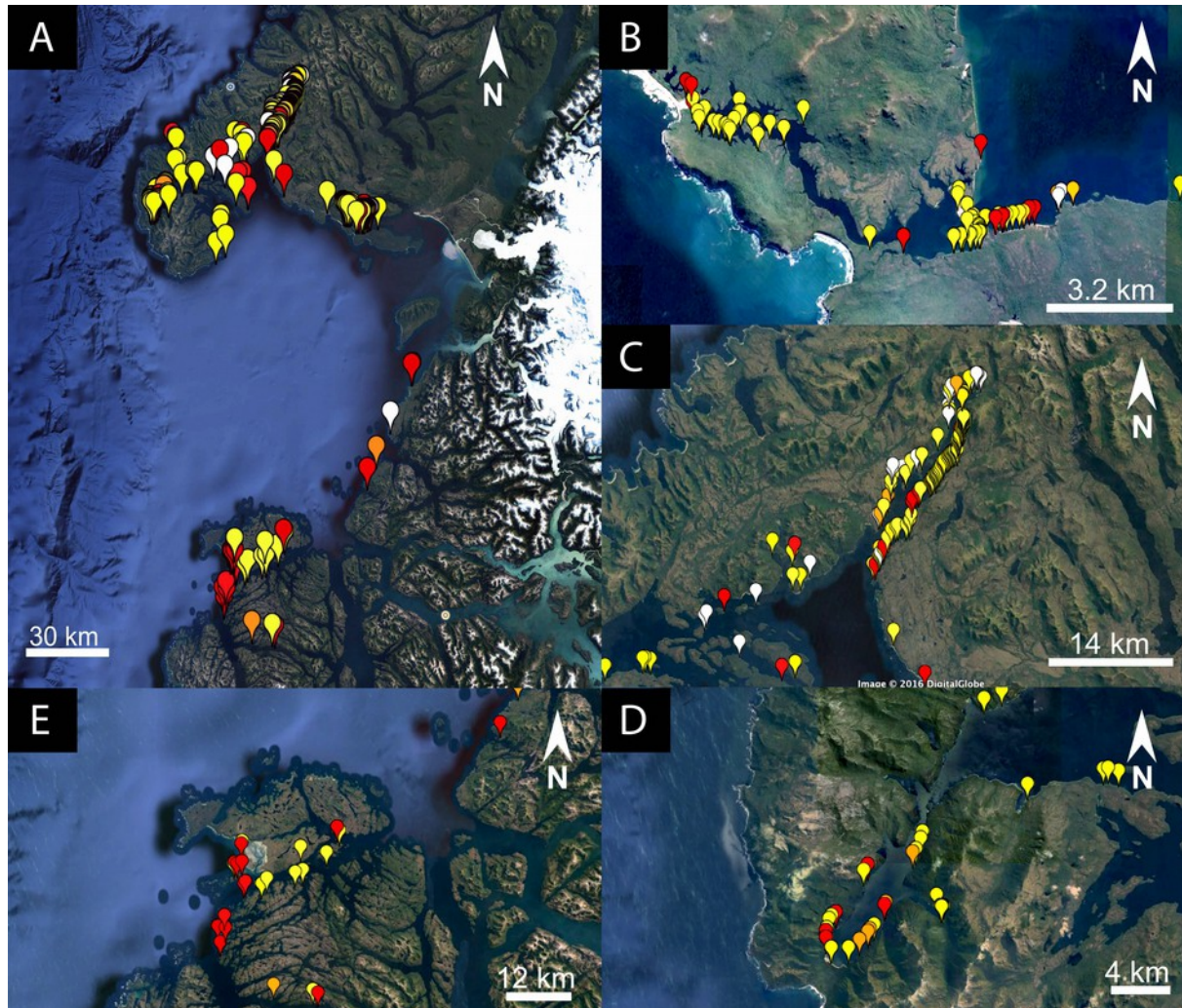
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887 **Fig. 10**: Inflation of the tongue and its implication for whale carcass deposition. The greater

888 proportion of carcasses deposited in a lateral position and to a lesser extent in the ventral-up

889 position reflects the hydrodynamics of the body in the sea as determined by the inflation of the

890 abdominal region (*9*) and mainly of their tongues. A) inflated tongue in a very recently dead sei

891 whale (weeks) indicated by the arrow head. B) Close-up of the mouth with dislocate mandibles

892 due to the previous inflation of the tongue (arrow head), which is decayed and removed by

893 scavengers. C) Whale carcass seen from the overflight deposited in lateral position and its

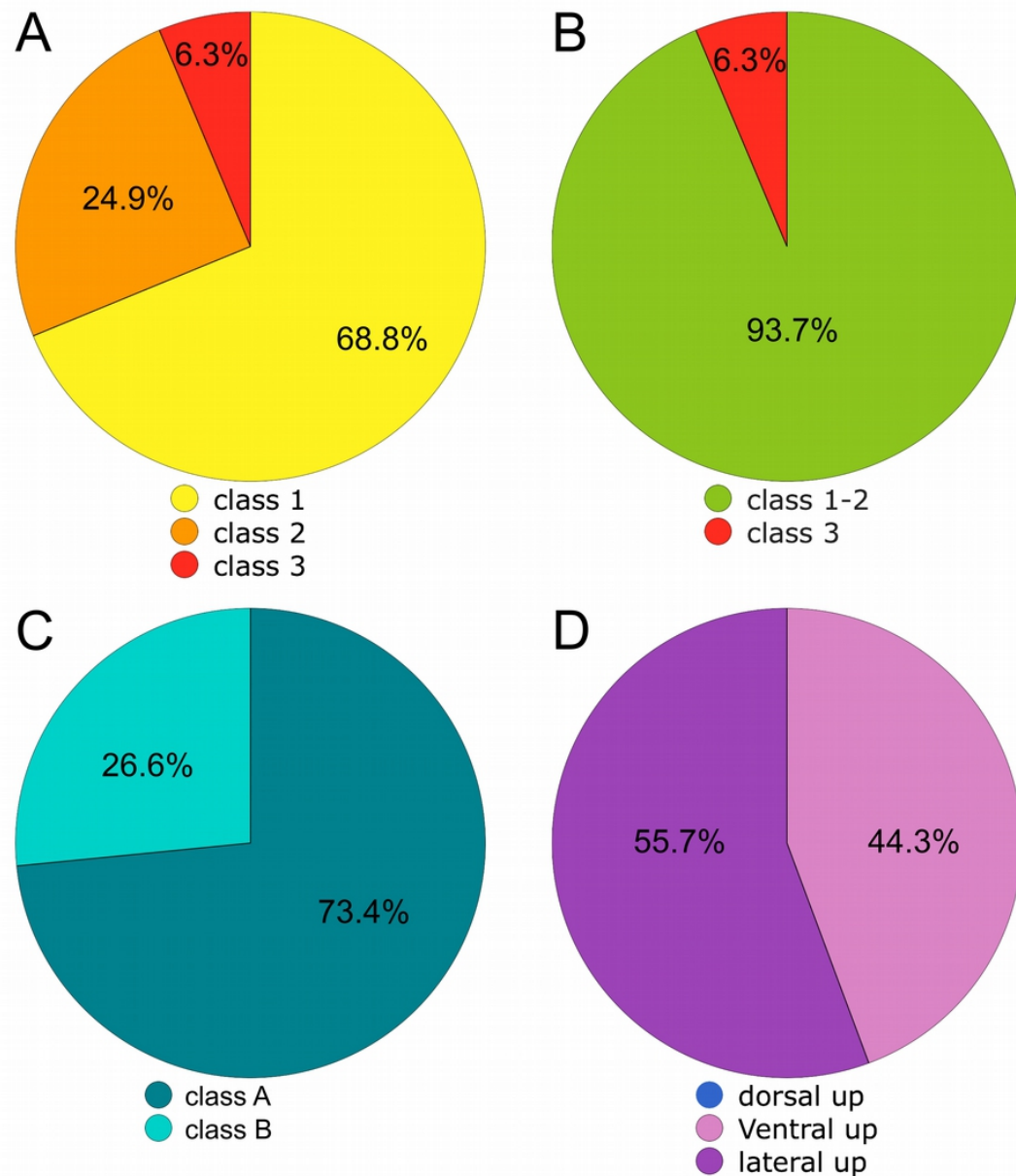894 protuberant inflated tongue (arrow head).


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900 **Fig. 11**: Graphs showing the proportion of the total classified carcasses in the biostratonomic

901 analysis. A) Time since death, B) Time since death, combining Class 1 and 2, C) location of

902 death, D) Anatomical positions of carcasses (lateral, ventral and dorsal-up).

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905 **Fig. 12:** Location of beached carcasses (blue) predicted by the drift model from four possible

906 mortality locations (red stars). Mortalities during a 2-month period are simulated, from mid

907 February to mid April 2015, with multiple carcasses (n=200) of varying drift properties released

908 each day to predict the range of resulting carcass locations. Green vectors show time-averaged

909 surface currents for this period (HYCOM model). Depth contours at 50 m and 100 m are

910 indicated (GEBCO), although nearshore waters and inlets are not resolved.
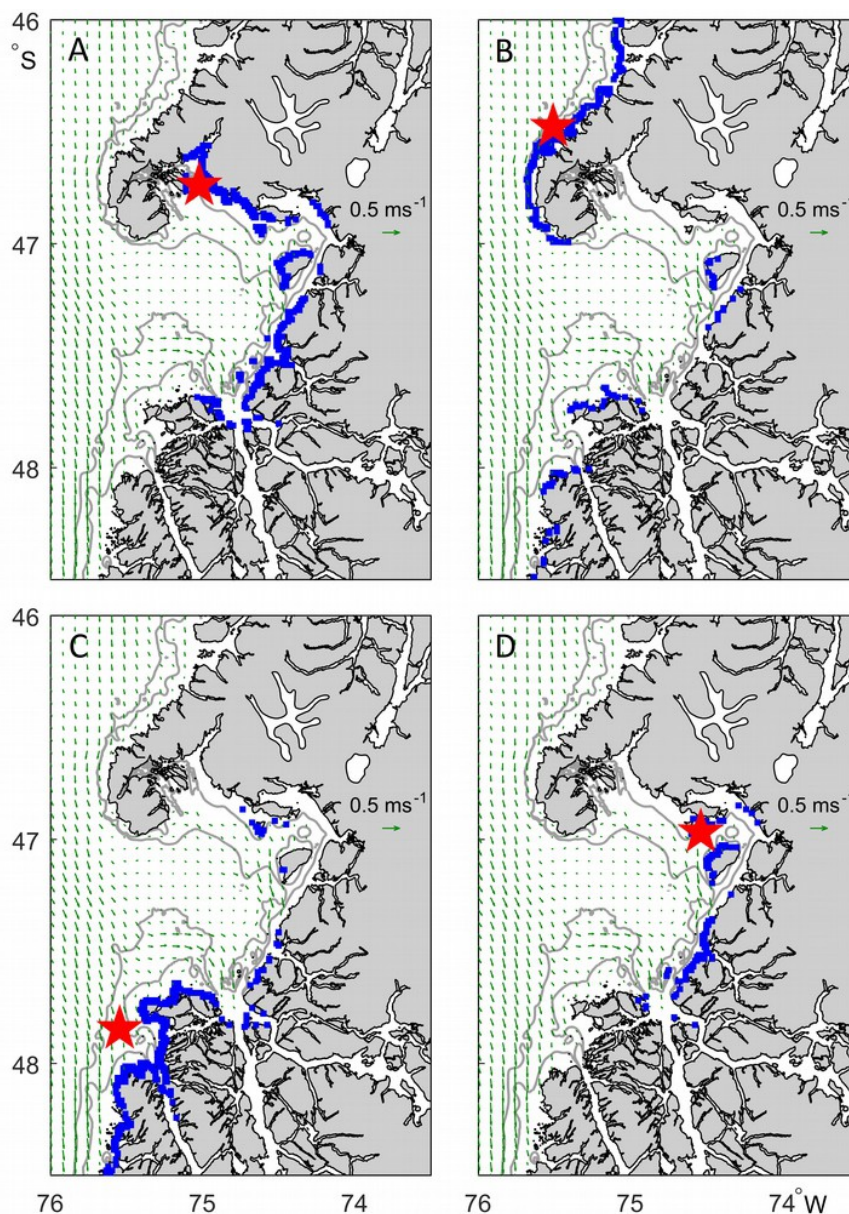
911 **Fig. 13:** Cumulative alongshore component of near-shore wind stress (red) from ECMWF ERA-

912 Interim reanalysis winds at three latitudes, with an origin time of the vernal equinox, September

913 21, 2014. Gray shading shows the envelope of variability experienced during 1995−2014, with

914 darker shading indicating one standard deviation from the mean for this period. Vertical lines

915 show the timing of vessel (green) and aerial (blue) observations of whale carcasses.

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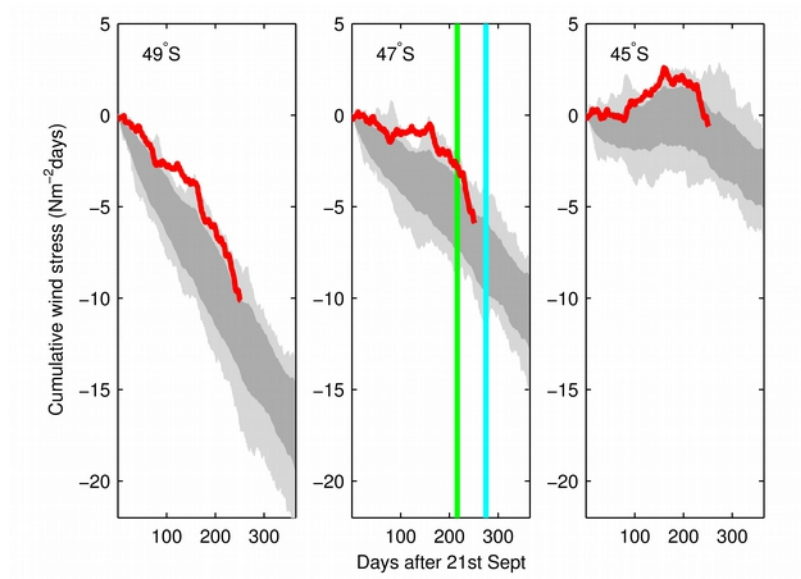
919 **Fig. 14:** Spatial distribution of PST (STX. Eq./100g tissue) as measured in mytilids and the

920 relative abundance of *Alexandrium catenella* between 43°S and 51°S in March 2015. Insert

921 shows the toxin level at the closest site to the Golfo de Penas, Isla Canquenes (45°43´31"S;

922 74°06´51"W) measured between March 2010 and March 2015. Shellfish consumption is unsafe

923 for humans if values rise above 80μg STX. Eq./100g tissue.

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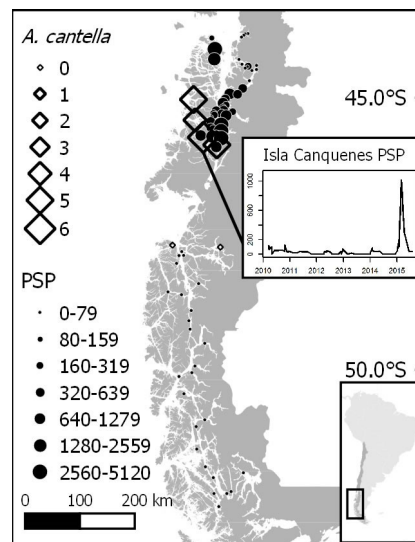
926 **Fig. 15:** Spatial distribution of PST (STX. Eq./100g tissue) as measured in mytilids between

927 43°S and 51°S in March 2016. In 2016, the PST levels in the Golfo Tres Montes region were not

928 elevated. However, values four to seven times higher than usual peaks were measured in the

929 channels of Central Patagonia. Shellfish consumption is unsafe for humans if values rise above

930 80μg STX. Eq./100g tissue.

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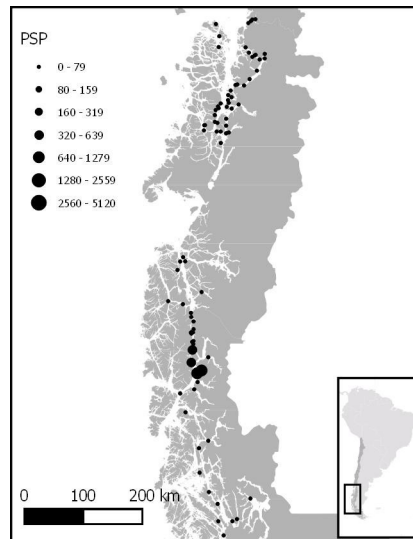
934 **Fig. 16:** Wind roses at the entrance to two inlets, Seno Newman (A) and Estero Slight (B),

935 derived from a local high-resolution implementation of the WRF model. Spoke lengths indicate

936 the frequency of occurrence of winds from each direction. Colors represent speed. Seno Newman

937 has a significant up-inlet component (winds from SSW) but Estero Slight does not (winds from

938 NNE).

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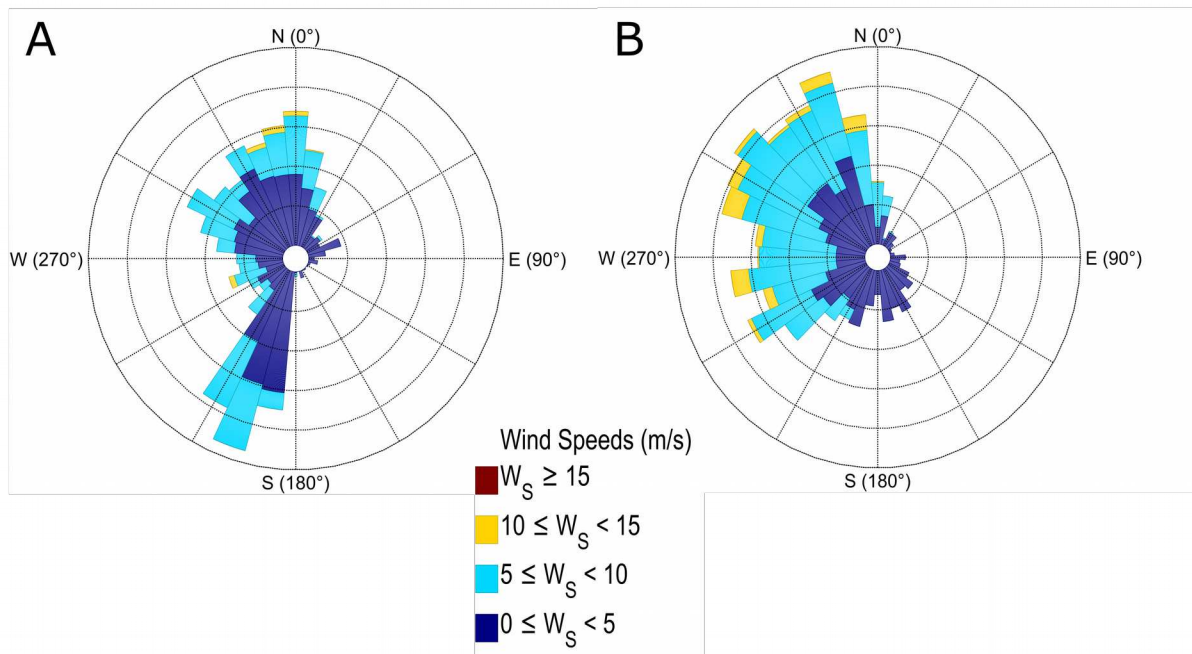
942 **Fig. 17:** Nautical maps of Escondido and Slight Inlet. A) Section of the Bahia San Quintin

943 showing Escondido Inlet (maximum depth 15m). B) Section of Hoppner Bay showing Estero

944 Slight (maximum depth 152m). Sources: Map nr 8820 and 8810 from armada de Chile. Newman

945 Inlet is poorly charted with only five depths indicated along the inlet, the largest being 82m.

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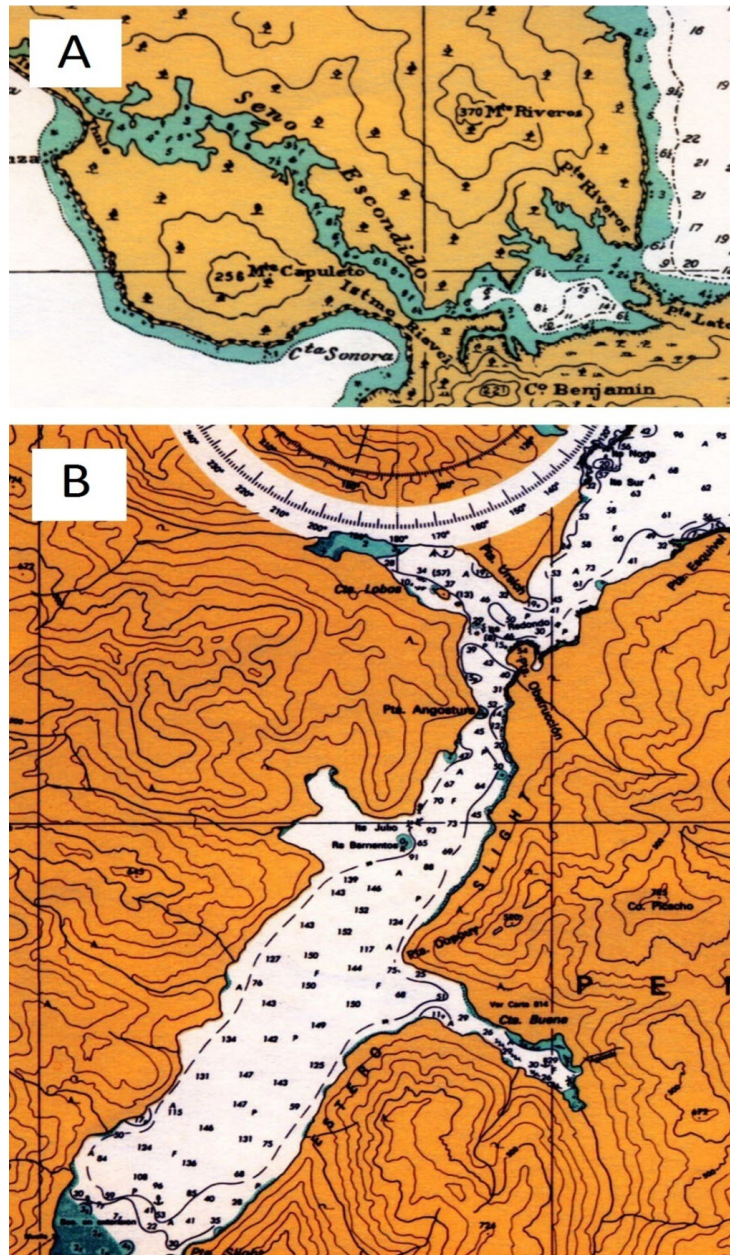
947 **Table 1:** Recorded mass mortality events of baleen whales (updated from Table 1 in Rowntree et
948 al. (2013))

Region/site	Time span	Species	Number	Age classes	Cause of death	Source
Caleta Buena/Slight Inlet, Southern Chile	November/December 1977	rorqual	4 fresh, numerous skeletons		unknown	Pers. Comm. Salas M, 2015
Cape Cod (USA)	5 weeks (11/1987)	humpback	14		HAB (saxitoxin)	Geraci et al., 1989
Upper Gulf of California (Mexico)	? (1995)	fin, minke and bryde[1]	8		unknown	Vidal & Gallo-Reynoso, 1996
Eastern North East Pacific	throughout 1999	gray	283[2]	mostly adults	malnutrition?	Gulland et al., 2005
Eastern North East Pacific	throughout 2000	gray	368	mostly adults	malnutrition?	Gulland et al., 2005
Upper Gulf of California (Mexico)	? (2009)	unknown	10		unknown	Rowntree et al., 2013
Australia	throughout 2009	humpback	46	mostly calves and juv.	unknown	Coughran et al., 2013
Brazil	throughout 2010	humpback	96	mostly calves and juv.	unknown	Rowntree et al., 2013
Peninsula Valdés (Argentina)	2005-2011[3]	southern right	420	mostly calves	unknown (HAB-related?, starvation?, kelp gull harassment?)	D'Agostino et al., 2015; Wilson, 2015
Puerto Edén area (Chile)	March 2011	sei and/or minke	3		unknown	this paper
Estero Cono (Chile)	March 2012	sei and/or minke	15		unknown	Pers. comm. Fischer RM, 2015
Puerto Edén area (Chile)	January 2014	sei and/or minke	5		unknown	Pers. comm. Cristie C, 2015
Between 46° and 51°S, mainly Golfo de Penas (Chile)	February to early April 2015[4]	probably all sei	305	all	HAB	this paper
Alaska/British Columbia (USA/Canada)	Mai/June 2015	fin, humpback, grey	38		unknown (HAB?)	NOAA, 2015b

949 [1] In total, 400 cetaceans died, including 8 baleen whales
950 [2] 106 in Mexico during 3 months
951 [3] 116 died during 2012
952 [4] 271 died within one month

953   **Table 2 (separate file)**

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960   **Table 3 –** Proportion of carcasses in each anatomical position as recorded from the overflight

961   survey and posterior photographic analysis.

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Anatomical position of Carcass	Unkown	Dorsal Up	Ventral Up	Lateral Up	Total
Count	187	0	43	54	**97**
Proportion (%)	65.84%	0	15.14%	19.01%	**100**
Proportion (%) based on classified individuals only	-	0	44%	56%	**100**

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966 **Table 4** – Minimal number of individuals (MNI) and proportion of carcasses in each of the
967 classes of decomposition / disarticulation stages recorded at Golfo de Penas.
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	Class	MNI	Proportion (%)
Classes of decomposition			
Time since death	1	141	68.78
	2	51	24.88
	3	13	6.34
	Total	**205**	**100**
Time at sea	A	147	97.35
	B	4	2.64
	Total	**151**	**100**

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971
972 **Table 5**. Density of specimens in assemblages (specimens/km²).
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	Area (km²)	No. of specimens	Density (specimens/km²)
Assemblage 1 - Jungfrauen Group	0.19	30	156
Assemblage 2 - Escondido Inlet	0.02	47	1906
Assemblage 3 - Escondido Inlet	0.01	32	1987
Assemblage 4 - Newman Inlet	0.60	149	248
Assemblage 5 - Slight Inlet	0.04	40	952
Total area of assemblages/specimens	0.87	298	341
Average	0.17	59	1050

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976 **Table 6:** Comparison of the usual causes of death with the evidence encountered at Golfo the Penas (GP).

Cause of death for marine mammals	Main feature	Type of evidence (confirm-discard)	Observation at Golfo de Penas	Expected in rorqual event	Oceanographic conditions near time of death	Rorqual Species recorded	References	Oceanographic Conditions Observed at GP
Starvation by abundance surpassing carrying capacity	Thin blubber layer, or empty stomach, or numbers around 5% of population	Measurements, necropsy and population numbers nearby carrying capacity	Not likely, Sei whales are still recovering from whaling, last species to be hunted	Reported in one species	Low productivity event	Unknown. Reported in gray whales (*Eschrichthius robustus*).	Gulland et al. 2005	High productivity event
Epidemic Disease	Morbillivirus: Contagious-epidemic, emaciated, external and internal parasites, lesions and inflammatory reactions	Histology, parasitology-virology test	No signs of external or internal lesions in the whales of Estero Slight. Stomach content present. No test available.	Low numbers, young individuals.	Shift in temperature, anthropogenic contamination, mutation of virus.	Juveniles and calves fin whales, *Balaenoptera physalus*	Brongersma-Sanders 1957, Jauniaux et al. 2000, Shimizu et al 2013, Van Bressem et al. 2014, Mazzariol et al. 2016	Unknown
Military exercise with Sonar	Only confirmed in dolphins	ear damage and – or haemorrhage nearby the ears	Unknown	Unknown	No military exercises public programed, chilean law for the protection of whales	Unknown	Goldbogen et al. 2013, Nowacek et al. 2007, Southall et al. 2007	Not reported
Poisoning by toxins of Harmful Algal Bloom	Massive, multispecific, recurrent in time	HAB reported, shift in oceanographic conditions, El Niño event	Yes	Yes	High productivity event, El Niño influence	*Balaenoptera physalus, Megaptera novaeangliae, Balaenoptera acutorostrata*	Geraci et al. 1989, Fire et al. 2010, Pyenson et al. 2014, Brongersma-Sanders 1957. (Present work)	Yes, at the closest station of red tide monitoring.
Trauma: Ship collision/ entanglement	Evidence of trauma, small number (i.e. 8 deaths in 19 years in U.S.A.)	Lesions, hematoma,	No sign of internal or external lesion.	Yes (small number of individuals at a time)	Not related.	*Eubalaena glacialis*	Kraus, 1990; Moore et al. 2004, Vanderlann y Taggart, 2007.	Not related.

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980 **Table 7** – Main biostratinomic pathways and their significance in understanding the thanatocenosis.

Time since death	Condition of the carcasses	Age proportions	Sex proportions	Geographic position	Observed
Catastrophic – single event	Highly homogenous. Majority within one to a few classes (*42*)	Same as population rate	Same as population rate	Homogenous	Homogenous; see Tab. S2
Time averaged	Highly heterogeneous. Several classes present.	Same as proportion of annual mortality of the population.	No pattern, different from ratio of population.	Heterogeneous	Homogenous; see Tab. S2

Location of death	Condition of the carcasses	Anatomic position expected	Anatomic position expected	Orientation	Anatomic position observed
Authoctonous	Very well preserved, low disarticulation	Position of life: dorsal up (*5*).	Dorsal up	No trend	Dorsal up: 1.00%
Allocthonous	Disarticulation and scattering present, depending on time and distance to final deposit	Heterogeneous depending on time since death or time of drift. Majority ventral to lateral up (*5*, see Fig. S5).	Ventral up – lateral up	One main direction (current-wind) and/or two main directions (tide)	Ventral up: 20.40% Lateral Up: 78.61%

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