1	THE CONTRIBUTION OF STRANDING DATA TO MONITORING AND CONSERVATION STRATEGIES FOR
2	CETACEANS: DEVELOPING SPATIALLY EXPLICIT MORTALITY INDICATORS FOR COMMON
3	DOLPHINS (DELPHINUS DELPHIS) IN THE EASTERN NORTH-ATLANTIC
4	
5	Peltier H. * ^{1,2} , Jepson P. D. ³ , Dabin, W. ² , Deaville, R. ³ , Daniel, P. ⁴ , Van Canneyt, O. ² ,
6	Ridoux, V. ^{1,2}
7	
8	¹ Laboratoire Littoral Environnement et Sociétés, UMR 7266, Université de La Rochelle, 2
9	rue Olympe de Gouges, 17000 La Rochelle, France
10	² Observatoire <i>PELAGIS</i> , UMS 3462- Université de La Rochelle-CNRS, Centre de Recherche
11	sur les Mammifères Marins, Université de La Rochelle, 5 allées de l'océan, 17000 La
12	Rochelle, France
13	³ Cetacean Strandings Investigation Programme, Institute of Zoology, Zoological Society of
14	London, Regent's Park, NW1 4RY London, United-Kingdom
15	⁴ Météo France, Dprevi/MAR, 42 avenue Coriolis, 31057, Toulouse, Cedex, France
16	
17	*Contact author : Helene PELTIER, hpeltier@univ-lr.fr
18	Observatoire PELAGIS, UMS 3462- Université de La Rochelle-CNRS, Centre de Recherche
19	sur les Mammifères Marins, Université de La Rochelle, 5 allées de l'océan, 17000 La
20	Rochelle, France.

21 Phone : +33 5 16 49 67 82/ +33 6 82 74 08 41

22 Abstract

Cetacean strandings are an important source of information on cetacean population status and 23 of biological samples. Nevertheless, collecting stranding data remains opportunistic and their 24 representativity must be improved. The aim of this study was to improve the ecological 25 significance of strandings, through the determination of stranded common dolphin origin 26 found along the coasts of the Channel and the Bay of Biscay, by using the drift prediction 27 model MOTHY. In order to map inferred distribution of dead dolphins, origin of strandings 28 were weighted by the probability that cetaceans dying at sea become stranded. The difference 29 between observed stranding origin and origin of expected strandings under the hypothesis of 30 spatial and temporal uniformity of dead cetaceans, constituted the anomaly in stranding 31 32 origin. Between 1990 and 2009 6,182 common dolphin strandings were reported by the UK and French stranding networks. Distribution inferred from strandings suggested that common 33 dolphins died mostly in the neritic Bay of Biscay. The anomaly in stranding origin was 34 maximal in the southern Bay of Biscay, highlighted as an area of high relative abundance or 35 strong mortality for common dolphin. The monthly decomposition of this anomaly showed 36 that positive anomaly was located in the southern Bay of Biscay in winter and expanded 37 northward over the whole Bay of Biscay and western Channel in spring and summer. These 38 results were consistent with current knowledge on common dolphin distribution and provide 39 new insight on strandings as cetacean population indicators. These parameters are essential 40 components for assessing the conservation status of vulnerable populations. 41

42

Keywords: Indicators, origin of strandings, monitoring, anomaly, common dolphin *Delphinus delphis*, Bay of Biscay, Channel.

45 1- Introduction

Environmental monitoring is "the collection and analysis of repeated observations or 46 measurements to evaluate changes in condition and progress toward meeting a management 47 objective" (Elzinga et al., 2001). Monitoring top predators is a major concern in the context of 48 biological conservation (Asseburg et al., 2006; Boyd et al., 2006; Mace and Baillie, 2007; 49 Sergio et al., 2008, 2006; Len Thomas, 1996; Wanless et al., 2007). An optimum monitoring 50 method would be based on three fundamental principles: its ecological significance, its 51 statistical credibility and its cost-effectiveness (Hinds, 1984). The ecological significance 52 implies that monitoring data must be simple and well-defined measurements, and ensures that 53 measured ecological process responds to changes in the population being considered. 54 However monitoring wild species in their habitat remains very expensive (Elzinga et al., 55 2001) and high cost of monitoring techniques is a hindrance to efficiency (Caughlan and 56 Oakley, 2001). This is particularly true for marine megafauna because of the very high costs 57 of dedicated cruises at sea, if large oceanic areas consistent with the size of conservation units 58 for such mobile animals are to be covered on a regular basis. The use of indicators is therefore 59 needed. Indicators are defined as "measures established from verifiable data that include more 60 information than data themselves do" (Bubb et al., 2005). They are often developed by 61 scientists (Schiller et al., 2001) and constitute communication tools between scientists and 62 policy-makers or stake-holders (Mace and Baillie, 2007; Müller and Lenz, 2006; Turnhout et 63 al., 2007). 64

Many regulatory frameworks (European Union Habitats Directive, Marine Strategy Framework Directive and Common Fisheries Policy; US Endangered Species Act and Marine Mammal Protection Act; ...) require that population status of marine top predators be assessed. The population status is generally defined as the current distribution and abundance relative to reference distribution and abundance at equilibrium in undisturbed ecosystem. The

true reference situation is generally unknown, except in a few specific cases for which long 70 data time series are available and make it possible to model past abundance. Additionally, 71 even the best population estimates are associated to uncertainties that limit our ability to 72 73 detect small changes in abundance. Therefore, assessing the current status of most populations of small cetaceans on the basis of abundance estimates only remains difficult. Consequently 74 other sources of information are necessary to fully depict cetacean population status. Relative 75 76 densities, frequency of occurrence, health and body condition, key demographic parameters, causes of death, and the risk and gravity of interaction with anthropogenic pressures are 77 valuable parameters to be considered jointly in a monitoring strategy. 78

Many of these features can be collected from stranded cetaceans. Their use as a source of 79 ecological indicators is still limited because of the reported lack of sampling strategy (Epperly 80 et al., 1996; Siebert et al., 2006). The ecological relevance of stranding data is poorly 81 understood, mostly because the geographical origin of a sample is unknown, and their 82 83 statistical credibility is disputed, because sampling is mostly opportunistic in nature. Yet, it is admitted that stranded animals represent a minimum measure of at-sea mortality (Epperly et 84 al., 1996). Strandings are underused resources (Pikesley et al., 2011) and the collection of 85 stranding data for decades in Europe constitutes an underexploited monitoring dataset at large 86 spatial and temporal scale. Attempts for using stranding data to elaborate indicators of at-sea 87 mortality were made mostly in seabirds (Bibby and Lloyd, 1977; Hlady and Burger, 1993; 88 Lloyd et al., 1974; Piatt and Ford, 1996; Piatt et al., 1990), sea otters (Degange et al., 1994; 89 Garshelis, 1997), sea turtles (Epperly et al., 1996; Hart et al., 2006; Koch et al., 2013) and 90 91 more recently cetaceans (Maldini et al., 2005; Peltier et al., 2012, 2013; Pyenson, 2011, 2010; Williams et al., 2011). The comparatively low cost of monitoring plans based on strandings is 92 a very important feature and it motivated the development of indicators based on stranding 93 94 data. However, "the art of developing indicators is to simplify without losing scientific 95 credibility" (Bubb et al., 2005). In other words, developing indicator implies understanding 96 the relationship between the indicator and the population being dealt with. Cetacean 97 strandings follow a complex function of a biological component composed of abundance and 98 mortality rate, a physical component which includes all processes that determine carcass drift 99 (tides, wind, currents, and carcass buoyancy) and a societal component which determines 100 reporting conditions.

- 101
- 102

$N_{stranding} \sim N_{individual}$.mortality.buoyancy.drift.reporting

103

104 The development of indicators based on strandings have to take into account all processes that 105 link stranding data with cetacean population at sea, in order to improve the ecological 106 significance of strandings and to allow comparisons with other monitoring techniques.

The present study focuses on common dolphins (Delphinus delphis) in the Bay of Biscay and 107 108 western English Channel. The species is the most frequently encountered small cetacean over the eastern North Atlantic continental shelf (Certain et al., 2008; Kiszka et al., 2007; McLeod 109 et al., 2009) and the commonest species in stranding records recorded from the Bay of Biscay 110 (Castège et al., 2013) and Channel coasts (Leeney et al., 2008). Additionally, in the eastern 111 North Atlantic, common dolphins are frequently impacted by fishery activities, but this threat 112 113 is still insufficiently documented to be properly assessed (Kirkwood et al., 1997; Kuiken et al., 1994; Leeney et al., 2008; Mannocci et al., 2012; Morizur et al., 1999; Murphy et al., 114 2009; Northridge et al., 2007, 2006; Rogan and M. Mackey, 2007). 115

116 The first goal of this study was to analyse common dolphin stranding time series in the 117 eastern North Atlantic. Observed strandings were compared to predictions of strandings under 118 the assumption that stranding frequency was only driven by drift conditions. We set a

hypothetical flat uniform distribution and mortality of common dolphins (named null 119 hypothesis) (Peltier et al., 2013). Secondly, we aimed at inferring distribution of dead 120 common dolphins by back-calculating the drift of observed strandings. Spatial and temporal 121 comparisons between expected and observed strandings would improve the statistical 122 credibility of strandings as they allow the use of a formal statistical analysis of stranding time 123 series (Peltier et al., 2013). Understanding the areas of origin would improve their ecological 124 significance as it would allow interpreting strandings in the light of ecological processes and 125 human activities that take place across their area of likely origin. This brand new approach is 126 aimed at developing indicators based on strandings that would provide relevant information to 127 monitor common dolphin populations (and more widely marine megafauna), identify changes 128 in their condition at sea and therefore set up adapted management strategies. 129

130 2- Materials and methods

131 2.1 Definitions

We defined the prior distribution of dead dolphins, or the null hypothesis, as the reference distribution that allows expected stranding data sets to be calculated by using the drift model MOTHY. This prior distribution constitutes the origin of expected strandings. Here, the prior distribution is set flat (uniform in space and constant in time).

136 Stranding probability ($P_{stranding}$) is the probability that a cetacean dying at sea would reach the 137 coast and get stranded. This probability is calculated for each of the 113 cells constructed in 138 the study area and climatology maps of stranding probability can be averaged over the study 139 period (1990-2009) for various temporal resolution, here monthly.

Expected strandings are strandings predicted under the null hypothesis. They vary with driftconditions only.

Observed strandings are strandings recorded across study area. In the present study observed strandings are the common dolphin stranding data sets provided by the French and UK stranding schemes.

The terms "unusual mortality events" or "multiple strandings" were used to define high numbers of strandings that occurred within a restricted geographical and temporal range with a common cause of death. The threshold was set at 30 stranding events of common dolphins over 10 consecutive days.

149 The origin of observed strandings was determined by back-calculating the drift of observed150 strandings.

151 The inferred distribution is defined as the origin of observed strandings multiplied by 152 $1/P_{stranding}$.

The difference between observed and expected strandings predicted under the null hypothesis was defined as the anomaly of strandings. Positive (*vs* negative) anomalies suggest that more (*vs* less) strandings were observed than expected under the null hypothesis.

The difference between inferred stranding origin and expected stranding origin constitutes the anomaly in stranding origins. When prior distribution is set uniform and constant as in the present work, this anomaly is a function of local dolphin density and mortality rate.

159

160 2.2 General experiment design

The study area encompasses the Channel and the Bay of Biscay and was sub-divided into four
sub-areas: eastern Channel and western Channel (British and French coasts pooled together),
northern Bay of Biscay, (48.5°N to 47°N) and southern Bay of Biscay (47°N to 43.5 °N). The

analysis was based on stranding datasets reported from 1990-2009 by the French and UKstranding schemes (figure 1) and followed two main steps.

Firstly, in order to determine baseline variation in stranding frequency due to drift conditions, 166 strandings expected under a null hypothesis were calculated along the Bay of Biscay and 167 Channel coasts (Peltier et al., 2013). The null hypothesis was constructed from a prior 168 distribution of dead dolphins based on the assumption of spatial and temporal uniformity at 169 sea and by using the drift prediction model MOTHY, developed by Météo-France (Daniel et 170 al., 2002); 30-day long drift simulations were calculated by using wind archives and model 171 outputs of tidal current every 10 days over the period 1990-2009. Predicted strandings 172 constituted the stranding dataset expected under the null hypothesis. Moreover, these drifts 173 allowed the probability to get stranded (or stranding probability) to be mapped across the 174 whole study area, both as annual and monthly climatologies averaged over the study period. 175 Stranding anomaly time series were constructed from along the Bay of Biscay and the 176 Channel coasts from 1990 to 2009. 177

Secondly, the origin of stranded dolphins was identified by back calculating the drift of each 178 individual. Corrected by the stranding probability, this constituted the inferred distribution of 179 mortality. All segments of trajectories were weighted by a drift duration probability function 180 determined from a photograph-based distribution of carcass decomposition conditions 181 converted into post-mortem drift duration from the results of a decomposition experiment 182 (Peltier et al., 2012). Anomalies in dolphin stranding origins were examined for any spatial 183 structure. All maps were constructed with the same spatial coverage and a grid cell size of 184 0.75°. 185

186 2.3 The drift prediction model MOTHY

The drift of cetacean carcasses was modelled with the drift prediction model MOTHY 187 (Modèle Océanique de Transport d'HYdrocarbures), initially developed by Météo-France to 188 predict the drift of oil slicks and adapted later on to solid objects (Pierre Daniel et al., 2002). 189 MOTHY predicts trajectories of floating objects by calculating the vertical profile of currents 190 and the wind effect on the emerged part of the object. MOTHY can be used forward (from 191 drift start to landing point) or backward (from landing location to drift origin) (Daniel et al., 192 2002). Atmospheric data were provided by the European Centre for Medium-Range Weather 193 and tides are modelled using a purely hydrodynamic tidal model. Object characteristics were 194 adapted to small cetaceans (size: 2 m; thickness: 0.32m) and immersion rate was 195 196 experimentally estimated at 90% (Peltier et al., 2012).

197 2.4 Construction of the null hypothesis

The null hypothesis consisted in a hypothesis of spatial and temporal uniformity in dead dolphins at sea and was represented by a grid of equally spaced theoretical cetaceans. Their 30 day drift was predicted every 10 days by the drift prediction model MOTHY from 1990 to 2009, and the proportion of predicted strandings defined stranding probability in each cell of the grid. These probabilities were averaged on either a monthly or a yearly basis.

Stranding predictions were used to build expected stranding time series and maps, under thenull hypothesis.

205 2.5. Common dolphin strandings

The 1990-2009 time series data of common dolphin observed stranded along the Bay of Biscay and the Channel coasts were provided by the British and French stranding schemes. In this study, only dead stranded cetaceans have been considered, since they represent 95.8% of stranding records in the study area over the years 1990-2009 (ULR and CSIP, unpublished reports).

211 2.5.1 UK stranding scheme

The British stranding network is the oldest organisation that collects data on marine mammal stranding events. This network was generalised to the whole United-Kingdom in 1990, through the establishment of the Cetacean Stranding Investigation Program (CSIP) that coordinates and scientifically supervises the stranding scheme. Many volunteers contribute to examining top predator stranding following a standardized protocol.

217 2.5.2 French stranding scheme

The French stranding network is co-ordinated by Observatoire PELAGIS, (formerly the 218 Centre de Recherche sur les Mammifères Marins, CRMM) at the University of La Rochelle, 219 France). It is constituted of about 260 trained volunteers distributed along the whole French 220 coast who collect data according to a standardized observation and dissection protocol 221 (Kuiken and Hartmann, 1993). The network was established in the early 1970's and its 222 223 organisation and procedures are considered unchanged since the mid 1980's. Data are centralized into a single database held by Observatoire PELAGIS at University of La 224 Rochelle. 225

226 2.6 Stranding anomalies

Differences between observed and expected common dolphin strandings were tested by 227 Wilcoxon test for non-parametric paired samples. Ruptures in stranding anomaly time series 228 were detected by using an algorithm for detecting breaks in time series (Zeileis et al., 2003, 229 2002). They were analysed by an autocorrelation function (ACF) analysis, using the software 230 R (Cowpertwait and Metcalfe, 2009; Ihaka and Gentleman, 1996). The ACF analysis showed 231 the degree of autocorrelation in the time series at each lag (from 1 to 24 months), in order to 232 reveal the existence of any seasonal signal or temporal trend in the stranding anomaly data 233 series. 234

235 2.7 Origin of common dolphin strandings

A 30 day long backward drift was calculated for each common dolphin found stranded along the Bay of Biscay and the Channel coasts. Each 10 hour segment of trajectories was weighted according a drift duration function (Peltier et al., 2012). The obtained gridded maps represent the origin of observed strandings.

240 2.8 Inferred distributions of dead dolphins

Origin of observed strandings were weighted by $P_{stranding}$, the probability of dolphins dying in each cell to get stranded, to produce the inferred distribution of dead common dolphins (equation 2).

244 Inferred distribution = Origin of observed strandings \cdot Probability of strandings⁻¹

This calculation deals with floating dolphins only and thus makes the assumption that the proportion of dolphins that float or sink after death is independent of death location.

Inferences were truncated for $P_{stranding} < 0.1$ because the offshore most cells of the map correspond to the greatest uncertainty (few stranding originating from these cells) and would receive the highest multiplication factor (1/ $P_{stranding}$).

250 2.9 Anomaly in stranding origin

251 Finally, anomalies in stranding origin were constructed following equation 3 in each cell:

Anomaly in stranding origin = number of observed stranded dolphins inferred to originate from a given cell – number of dead dolphin expected to get stranded under the null hypothesis.

256 3- Results

257 3.1 Stranding probability

Monthly maps represent the probability that a small cetacean dying in each cell reach the coast and get stranded (figure 2). In the Channel, the probability of stranding remained over 0.3 during the whole year. In the Bay of Biscay, highest stranding probability areas expand over the slope from November to February and shrinks to coastal areas in the summer. The Bay of Biscay represents From April to September; cetaceans dying in offshore cells of central Bay of Biscay would never reach the coast.

264 3.2 Common dolphin stranding data

A total of 6,182 common dolphin strandings was collected by the UK and French stranding networks along the Bay of Biscay and Channel coasts. Very few of them were reported from the eastern Channel (0.5%) mainly in winter and, therefore, this sub-region was not considered any further in the present study.

Annual stranding numbers were very variable between 1990 and 2009 (figure 3). From 1990
to 1996, around 100-200 strandings of common dolphins per year were recorded. From 1997
onwards, yearly totals of stranded common dolphins were most often >400 individuals.

An extreme seasonal pattern was found, characterized by highest values in winter (figure 4). As much as 73% of all common dolphin strandings in a year were recorded from January to March. Very low numbers were observed in the other months. The main 3 sub-regions: western Channel, northern Bay of Biscay and southern Bay of Biscay showed quite similar seasonal patterns, with the highest stranding numbers observed during winter months (65% of total strandings in the western Channel, 61% in the northern Bay of Biscay and 81% in the

southern Bay of Biscay. Because of the high similarity of seasonal patterns in the differentsub-regions, all subsequent analyses are carried out across the whole study area.

280 3.3 Stranding anomalies: time series analysis

281 Long term time series of stranding anomaly, established at a monthly resolution, significantly differed from 0 (figure 5) (P=0.023). Stranding anomaly was generally negative, except 282 during acute stranding events that lasted for about 1 month at a time. This suggests that 283 abundance and/or mortality of common dolphins were lower than predicted under the 284 hypothesis of uniformity during the whole year, except during these events. In these episodes, 285 observed strandings were much higher than expected strandings. No breakpoint was detected 286 in this difference, mostly because high stranding numbers appeared as short-duration events 287 and baseline levels between these events remain fairly stable. 288

The ACF analysis confirmed the lack of long term trend in stranding anomaly and its strong seasonal pattern (figure 6). Positive autocorrelations at lags 11-13 suggested a positive linear relationship between variables separated by a 12 month period. In contrast, a negative linear relationship was detected between records separated by 6 month period, which is in line with the time series being mostly dominated by the seasonal pattern.

Strandings expected under the null hypothesis showed a slight seasonality, with maxima predicted from October to March. Minima observed in the summer represented 61% of maxima (figure 7). Observed and expected strandings were statistically different (P=0.002). Stranding anomaly monthly decomposition showed that stranding anomaly was strongly positive between January and March and negative the rest of the year.

299 3.4 Origin of observed strandings

Backward drifts of 6,182 stranded common dolphins were weighted by the drift duration 300 probability for stranded common dolphins. Their origins showed that carcasses found along 301 the Bay of Biscay and the Channel coasts came mostly from the continental shelf (figure 8). 302 Highest densities were observed very close to the coast, particularly in the southern Bay of 303 Biscay and south of Cornwall. As much as 58% of stranded dolphins were estimated to 304 originate from within the 500m-isobath in the Bay of Biscay. The western Channel was the 305 origin of around 27% of stranded dolphins. The rest originated from the oceanic part of the 306 Bay of Biscay and from the eastern Channel. 307

During unusual mortality events, 76% of stranded common dolphins came from within the 500m-isobath of the Bay of Biscay and only 14% from the western Channel (figure 9A). Very few stranded animals were estimated to originate from areas off the continental slope. Out of these unusual mortality events, origin of stranded animals was more widely distributed as 49% of stranded common dolphins originated from the continental shelf of the Bay of Biscay and as much as 40% from the western Channel (figure 9B). As much as 8% of stranded animals were estimated to originate from the oceanic part of the Bay of Biscay.

Average origins of stranded dolphins were analysed with a monthly resolution (figure 10). 315 From January to March, between 58% and 76% of stranded dolphins originated from the shelf 316 of the Bay of Biscay, 14% to 37% died in the the western Channel and less than 10% 317 originated within the 500m-isobath of the Bay of Biscay. From May to September, almost all 318 stranded common dolphins were estimated to originate from waters within the 500 m isobaths 319 320 over the whole study area. Highest densities were observed in very coastal waters, along the Bay of Biscay and the Cornish coasts. In October and November, as much as 40% of stranded 321 322 dolphins originated from the western Channel.

323 3.5 Inferred distribution

Origins of observed strandings were divided by stranding probability in order to map common dolphin mortality irrespective of distance to coast. Inferred distribution between 1990 and 2009 showed that high densities of dead common dolphins were observed in the whole Bay of Biscay and western Channel, but mostly on the continental shelf (figure 11). About 82% of common dolphins died within the 500 m isobaths (Bay of Biscay and western Channel), whereas this area represents 49% of cells where $P_{stranding} > 0.1$. Only 18% of dolphins died in the deeper waters of the Bay of Biscay (21% of considered cells).

During unusual mortality events, common dolphin death locations was concentrated over the continental slope of the Bay of Biscay (70%) (figure 12A) and 11% died in the western Channel. Out of these events, dead dolphins were quite uniformly distributed in the study area even if higher densities were observed in the western Channel (36% of dead dolphins) only 44% of common dolphins were estimated to die within the 500 m isobaths of the Bay of Biscay and 20% out of the continental slope (figure 12B).

From January to March, dolphin mortality was inferred to occur over the whole study area, mostly in the southern Bay of Biscay over the continental slope and in Cornwall (figure 13). During the rest of the year, dead dolphins at sea were more randomly distributed. In April and December, lower densities of dead dolphins were found even if a hotspot remained visible south of Cornwall. From May to October, common dolphins were mostly found in coastal waters and over the western Channel and very few dolphins were inferred to be dying over deep waters of the Bay of Biscay.

344 3.7 Anomalies in stranding origin

From 1990 to 2009, anomalies were statistically different from 0 (P=0.023). In the southern coastal Bay of Biscay and in southern Cornwall, numbers of dead dolphins were much higher than expected under the null hypothesis, whereas anomalies were only slightly positive in the

rest of the Bay of Biscay (figure 14A). In the eastern Channel and southern Irish Sea, numbersof dead dolphins were lower than expected.

During unusual mortality events highest positive anomalies were observed in the southern 350 Bay of Biscav over the continental shelf (figure 14B); whereas in the oceanic part of the Bay 351 of Biscay and in the Channel, observed dead dolphin densities were lower than expected, 352 except along the southern Cornish coasts. Out of these acute stranding episodes, anomalies 353 were less spatially contrasted, with anomalies in the Bay of Biscay being only slightly 354 positive (figure 14C). Along southern Cornwall, anomalies remained strongly positive, 355 whereas the rest of the Channel, eastward to Dover Strait, showed strongly negative 356 anomalies. 357

Monthly variation in stranding origin anomalies were statistically significant from 0 for the 358 whole year (P < 0.001), except in July (P = 0.225). In January, positive anomalies were found in 359 the southern Bay of Biscay, from the coast to over the slope, and off southern Cornwall 360 (figure 15). Differences were negative in the rest of the calculation areas. In February, 361 positive anomalies were found in the south-eastern Bay of Biscay and expanded northward 362 covering the whole Bay of Biscay in March. Positive anomalies decreased in March and 363 April, and shrank to coastal waters of the Bay of Biscay and the western Channel. From May 364 to November, spatial patterns in anomalies of stranded dolphin death locations become poorly 365 defined throughout study area, and regions of slightly positive anomalies expand to the whole 366 continental shelf, from southern Ireland to northern Bay of Biscay. From December onwards, 367 areas of positive anomaly concentrate again in the southern Bay of Biscay and western 368 Channel. 369

370 Negative differences observed along the Spanish coast are an artefact due to Spanish371 stranding data not being incorporated in the analysis.

372 4- Discussion

373 4.1 General

The aim of is study was to improve the ecological significance of stranding data as well as 374 375 their statistical credibility through the case study of common dolphins in the Bay of Biscay and English Channel, in the perspective of developing new population indicators. Ecological 376 significance was improved by calculating of the origin of common dolphins found stranded 377 along the coasts. To do this, their backward trajectories were calculated by using the drift 378 prediction model MOTHY. These trajectories were weighted by a drift duration probability 379 function fitted to experimental data (Peltier et al., 2012). Origin of observed strandings was 380 estimated to be mainly in neritic waters of the southern Bay of Biscay and off Cornwall 381 southern coasts. During acute mortality events, around 80% of stranded animals were 382 383 estimated to originate from the continental shelf of the Bay of Biscay. Over the study period, dead dolphins were estimated to be distributed across the whole area, but during acute 384 stranding episodes, dolphins were estimated to die mostly over the slope and shelf of the 385 southern Bay of Biscay. 386

The strong seasonality of stranding anomalies suggested that the huge stranding numbers 387 observed in winter could not be explained by drift conditions only; indeed drift conditions 388 alone would predict a ratio of approximately 1 to 2 between lower (summer) and higher 389 (winter) stranding numbers, whereas observed values vary from 1 to 20; additionally the 390 phenology of expected stranding (maxima from October to February) did not match the 391 392 phenology of common dolphin observed stranding (maxima from January to March). Anomalies in stranding origin could be mapped across the whole computation area and 393 showed that dead dolphin numbers were higher than expected under the null hypothesis in 394 neritic waters of the southern Bay of Biscay and south of Cornwall. More dead dolphins were 395

observed in winter (from December to March) in the southern shelf and slope of the Bay of
Biscay and in western Channel. Spatial patterns of anomalies in stranding origin were less
defined during the rest of the year and they moved geographically to south of Ireland and to
the northern Bay of Biscay.

There is a large potential for this new approach in interpreting stranding data both temporally and spatially. It can be applied to all small cetacean species and can cover large spatial and temporal ranges. For the first time, stranding data allowed mortality to be mapped.

It has been shown that between 12.9% and 18.4% of cetacean carcasses could float and therefore drift (Peltier et al., 2012), whereas carcasses with a negative buoyancy would sink and be rapidly consumed by bottom dwelling carrion eaters (Baco and Smith, 2003; Jones et al., 1998; Smith and Baco, 2003). Cetacean inferred distribution could therefore be corrected by the proportion of floating dead animals in order to estimate number of dead cetaceans at sea, corrected for drift conditions and floating probability.

Drift duration probability used to weight backward trajectories of stranded common dolphins was calculated from experimental data collected in winter (Peltier et al., 2012). This function was appropriate for drift back-calculations in winter in the Bay of Biscay. The assumption was made that a temperature difference of 3°C between sea surface temperatures in the Bay of Biscay and in the English Channel during winter (http://envlit.ifremer.fr) might not significantly change the decomposition kinetic or buoyancy of common dolphins.

Another mechanism likely generated some blurring of death location maps at all seasons along the prevailing wind direction (which is on average from a westerly direction). The drift duration probability function, which was used in weighting the trajectories back-calculated over 30 days, implies that locations calculated for increasing drift durations have decreasing but non null probability to occur, until the very end of the trajectories. Using the actual drift duration for each carcass (would it be measurable for all individuals) would reduce
uncertainty along the drift track, since we would replace the weighted trajectory by a single
position with a value of 1 individual.

Anomalies in stranding origins can be explained by the inter- and intra-annual variations in the distribution of common dolphins or of their mortality, either natural or man-induced. Combined with other spatial dataset such as the distribution of fishery activities or other human pressures and the distribution of common dolphins obtained from visual surveys, inferred distributions and stranding origin anomalies derived from stranding data could be interpreted in the aim of disentangling variations in abundance and mortality.

429 4.2 The potential of stranding data as indicators of common dolphin populations

Maps of inferred distribution represented changes in relative abundance or mortality of 430 common dolphins. Summer anomalies were only slightly positive in the Bay of Biscay and 431 432 the Celtic shelf and slightly negative elsewhere. This would suggest that common dolphin abundance or mortality would show only weak geographic patterns at this time of the year and 433 within the computation area. This is consistent with sighting surveys from platforms of 434 opportunity, which showed that common dolphins were mostly observed in shelf and slope 435 waters of the northern half of the Bay of Biscay between April and September (Certain et al., 436 2008; Kiszka et al., 2007; McLeod et al., 2009). The Channel east of 4°W is clearly an area of 437 negative common dolphin origin anomaly, quite in agreement with available data on the 438 species distribution (J. B. Reid et al., 2003). 439

From October to March, the occurrence of common dolphins is reported to increase in the western Channel (McLeod et al., 2009), which is consistent with positive anomaly of stranding origin estimated between October and December. High positive anomalies were observed on the shelf of the southern Bay of Biscay and southern Cornwall. These anomalies 444 were recorded during acute mortality events too, which occurred mostly from January to 445 March. It is unclear to which extent high positive anomaly observed between January and 446 March was mostly due to a local increase of common dolphin mortality or to the contraction 447 of the common dolphin range in two hotspots, the western Channel and the southern Bay of 448 Biscay.

The comparison between these indicators and other datasets highlighted and validated the context of interpretation of strandings. It suggested that strandings can provide relevant lowcost cetacean population indicators, being applicable worldwide for many marine predators (cetaceans, sea-turtles, seabirds...).

453 4.3 Strandings as a monitoring tool

Bycatch is by far the most frequent cause of death reported for stranded common dolphins (on 454 average 75% of necropsied carcasses), mostly during multiple stranding events (Kirkwood et 455 456 al., 1997; Kuiken et al., 1994; Leeney et al., 2008). Common dolphins are mostly reported bycaught in the seabass (Dicentrarchus labrax) and albacore (Thunnus alalunga) pelagic 457 trawlers (Morizur et al., 1999; Northridge et al., 2006; Rogan and M. Mackey, 2007). In 2005, 458 459 common dolphin mortality in the albacore and sea bass fisheries (ICES areas VII and VIII) was estimated at 1,567 common dolphins (CV=2.07) and 586 for the French sea bass (575 in 460 ICES area VIII and 11 in ICES area VII) (Northridge et al., 2006). In areas VI, VII and VIII, 461 240 and 300 common dolphins were estimated to be bycaught in French sea bass pair trawlers 462 respectively in 2007 and 2008 [56,57]. Hence, data collected during fishery monitoring 463 programs are collected by implementing a rigorous protocol designed a priori 464 (notwithstanding difficulties in their implementation); yet they produce information that is 465 466 clearly negatively biased, because important segments of the relevant fisheries are not monitored. Therefore, because bycatch data are sparse and hard to collect (Lewison et al., 467

2004) the joint use of stranding origin anomalies and fishery monitoring data would highlyimprove scientific knowledge of interactions between small cetaceans and fisheries.

470 Causes of death and mortality remain hard to determine for top predators. Nevertheless, these 471 parameters are crucial in management strategies. For marine top predators, strandings 472 constitute the main source of information for providing a minimal estimation of mortality and 473 provide an inventory of death causes. The improvement of stranding data analyses to provide 474 population indicators will ensure relevant perspectives for cetacean monitoring and 475 management strategies.

476

477 5-CONCLUSION

This study consisted in the development of new indicators based on stranding data. These 478 indicators were the distribution inferred from strandings and the anomaly in stranding origins. 479 They provide important information on natural or man-induced mortality of small cetaceans 480 481 and changes in distribution of dead dolphins. Moreover, the cost-effectiveness of a monitoring strategy based on stranding is an additional asset (Caughlan and Oakley, 2001). This approach 482 consisted in developing indicators, exploring their significance and comparing them with 483 other studies. The validation of indicators with other datasets was an essential step in their 484 development (Dale and Beyeler, 2001; Heink and Kowarik, 2010). The development of 485 indicators was possible through the improvement of their statistical credibility by using 486 prediction of stranding under the null hypothesis and their ecological significance by back-487 calculating the origin of stranded dolphins and further mapping inferred distribution. Map-488 489 based indicators were therefore provided, which are most attractive for decision-makers and stake-holders (Bubb et al., 2005). Detecting changes in populations by using map-based 490 indicators is fairly uncommon, especially since map-based datasets rarely deal with time 491 492 series (Bubb et al., 2005).

494 Acknowledgments:

495	We warmly thank all members of the French and UK stranding networks for their continuous
496	effort in collecting stranding data.

497 CRMM is funded by the ministry in charge of the environment, and by Communauté
498 d'Agglomération de la Ville de La Rochelle, with support of Région Poitou-Charentes and the
499 European Union. The PhD thesis of H. Peltier was supported by the Centre National de la
500 Recherche Scientifique and by Région Poitou-Charentes.

- 501 The UK Cetacean Strandings Investigation Programme is funded by Defra in England and the
- 502 Devolved Administrations in Scotland and Wales.

503

505 Bibliography

- Asseburg, C., Harwood, J., Matthiopoulos, J., Smout, S., 2006. The functional response of generalist predators and its implications for the monitoring of marine ecosystems., in: Top Predators in Marine Ecosystems, Conservation Biology. Boyd, I., Wanless, S., Camphuysen, C.J., New-York, pp. 262–274.
- Baco, A.R., Smith, C.R., 2003. High species richness in deep-sea hemoautotrophic whale
 skeleton communities. Mar. Ecol. Prog. Ser. 260, 109–114.
- Bibby, C., J., Lloyd, C., S., 1977. Experiments to determine the fate of dead birds at sea. Biol.
 Conserv. 12, 295–309.
- Boyd, I.L., Wanless, S., Camphuysen, J., 2006. Introduction, in: Top Predators in Marine
 Ecosystems. Boyd, Wanless and Camphuysen, pp. 1–11.
- 516 Bubb, P., Jenkins, M., Kapos, V., 2005. Biodiversity Indicators for National Use.
- Castège, I., Soulier, L., Hémery, G., Mouchès, C., Lalanne, Y., Dewez, A., Pautrizel, F., d'
 Elbée, J., D'Amico, F., 2013. Exploring cetacean stranding pattern in light of variation
 in at-sea encounter rate and fishing activity: Lessons from time surveys in the south
 Bay of Biscay (East-Atlantic; France). Journal of Marine Systems 109–110,
 Supplement, S284–S292.
- 522 Caughlan, L., Oakley, K.L., 2001. Cost considerations for long-term ecological monitoring.
 523 Ecological Indicators 1, 123–134.
- 524 Certain, G., Ridoux, V., Van Canneyt, O., Bretagnolle, V., 2008. Delphinid spatial
 525 distribution and abundance estimates over the shelf of the Bay of Biscay. ICES
 526 Journal of Marine Science 65, 1–11.
- 527 Cowpertwait, P.S.P., Metcalfe, A.V., 2009. Introductory Time Series with R, Springer. ed,
 528 Use R!
- Dale, V.H., Beyeler, S.C., 2001. Challenges in the development and use of ecological indicators. Ecological Indicators 1, 3–10.
- Daniel, Pierre, Jan, G., Cabioc'h, F., Landau, Y., Loiseau, E., 2002. Drift Modeling of Cargo
 Containers. Spill Science & Technology Bulletin 7, 279–288.
- Degange, A.R., Doroff, A., M., Monson, D., H., 1994. Experimental recovery of sea otter
 carcasses at Kodiak Island, Alaska, following the Exxon Valdez oil spill. Marine
 mammal science 10, 492–496.
- Elzinga, C.L., Salzer, D.W., Willoughby, J.W., Gibbs, J.P., 2001. Monitoring plant and
 animal populations, Blackwell Science. ed.
- Epperly, S.P., Braun, J., Chester, A.J., Cross, F.A., Merriner, J.V., Tester, P., Churchill, J.H.,
 1996. Beach Strandings as an indicator of at-sea mortality of sea turtles. Bulletin of
 Marine Science 59, 289–297.
- Garshelis, D.L., 1997. Sea Otter Mortality Estimated from Carcasses Collected after the
 Exxon Valdez Oil Spill. Conservation Biology 11, 905–916.
- Hart, K.M., Mooreside, P., Crowder, Larry B., 2006. Interpreting the spatio-temporal patterns
 of sea turtle strandings: Going with the flow. Biol. Conserv. 129, 283–290.
- Heink, U., Kowarik, I., 2010. What criteria should be used to select biodiversity indicators?
 Biodivers Conserv in press.
- 547 Hinds, W.T., 1984. Towards monitoring of long-term trends in terrestrial ecosystems.
 548 Environmental Conservation 11, 11–18.
- Hlady, D., A., Burger, A., E., 1993. Drift-Block Experiments to Analyse the Mortality of
 Oiled Seabirds off Vancouver Island, British Columbia. Mar. Pollut. Bull. 26, 495–
 501.
- Ihaka, R., Gentleman, R., 1996. R: a language for data analysis and graphics. J. Comput. Sta.
 Graph. Anal. 5, 299–314.

- Jones, E.G., Collins, M., Bagley, P.M., Addison, S., Priede, I.G., 1998. The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal north-east Atlantic Ocean. Proceedings of the Royal Society B 265, 1119–1127.
- Kirkwood, J.K., Bennet, P.M., Jepson, P.D., Kuiken, T., Simpson, V.R., Baker, J.R., 1997.
 Entanglement in fishing gear and other causes of death in cetaceans stranded on the coasts of England and Wales. Vet. Rec. 141, 94–98.
- Kiszka, J., MacLeod, K., Van Canneyt, O., Walker, D., Ridoux, V., 2007. Distribution,
 encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay
 and adjacent waters from platform-of-opportunity data. ICES Journal of Marine
 Science 64, 1033–1043.
- Koch, V., Peckham, H., Mancini, A., Eguchi, T., 2013. Estimating At-Sea Mortality of
 Marine Turtles from Stranding Frequencies and Drifter Experiments. PLoS ONE 8,
 e56776.
- Kuiken, T., Hartmann, M.G., 1993. Cetacean pathology: dissection techniques and tissue
 sampling., in: Proceedings of the European Cetacean Society Workshop. Presented at
 the European Cetacean Society, Kuiken, T., Hartmann, M.G., Leiden, Netherlands, p.
 39.
- Kuiken, T., Simpson, V.R., Allchin, C.R., Bennet, P.M., Codd, G.A., Harris, E.A., Howes,
 G.J., Kennedy, S., Kirkwood, J.K., Law, R.J., 1994. Mass mortality of common
 dolphins (Delphinus delphis) in south west England due to incidental capture in
 fishing gear. Veterinary Record 134, 81–89.
- Leeney, R.H., Amies, R., Broderick, A.C., Witt, Matthew J., Loveridge, Jan, Doyle, J.,
 Godley, Brendan J., 2008. Spatio-temporal analysis of cetacean strandings and
 bycatch in a UK fisheries hotspot. Biodiversity and Conservation 17, 2323–2338.
- Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of
 fisheries bycatch on marine megafauna. Trends in Ecology and Evolution 19, 598–
 604.
- Lloyd, C., S., Bogan, J.A., Bourne, W.R.P., 1974. Seabird mortality in the North Irish Sea and
 Firth of Clyde early in 1974. Mar. Pollut. Bull. 5, 136–140.
- Mace, G.M., Baillie, J.E.M., 2007. The 2010Biodiversity Indicators: Challenges for Science
 and Policy. Conservation Biology 21, 1406–1413.
- Maldini, D., Mazzuca, L., Atkinson, S., 2005. Odontocete stranding patterns in the main
 Hawaiian Islands (1937-2002): How do they compare with live animal surveys?
 Pacific Science 59, 55–67.
- Mannocci, L., Dabin, W., Augeraud-Véron, E., Dupuy, J.-F., Barbraud, C., Ridoux, V., 2012. 589 590 Assessing the Impact of Bycatch on Dolphin Populations: The Case of the Common Dolphin the Eastern North PlosOne 7, 591 in Atlantic. e32615. doi:10.1371/journal.pone.0032615. 592
- McLeod, K., Brereton, T., Martin, C., 2009. Changes in the occurrence of common dolphins,
 striped dolphins and harbour porpoises in the English Channel and Bay of Biscay.
 Journal of the Marine Biological Association of the United Kingdom 89, 1059–1065.
- Morizur, Y., Berrow, S.D., Tregenza, N.J.C., Couperus, A.S., Pouvreau, S., 1999. Indidental
 catches of marine-mammals in pelagic trawl fisheries of the northeast Atlantic.
 Fisheries Research 41, 297–307.
- Müller, F., Lenz, R., 2006. Ecological indicators: Theoretical fundamentals of consistent applications in environmental management. Ecological Indicators 6, 1–5.
- Murphy, S., Winship, A., Dabin, W., Jepson, P.D., Deaville, R., Reid, R.J., Spurrier, C.,
 Rogan, E., Lopez, A., Gonzalez, A.F., Read, F.L., Addink, M., Silva, M., Ridoux, V.,
 Learmonth, J.A., Pierce, G.J., Northridge, S.P., 2009. Importance of biological

604	parameters in assessing the status of Delphinus delphis. Mar. Ecol. Prog. Ser. 388,
605	273–291.
606	Northridge, S.P., Kingston, A., Thomas, L., Mackey, A., 2007. Second annual report on the
607	UK cetacean bycatch monitoring scheme. (Contract report to DEFRA). Sea Mammal
608	Research Unit.
609	Northridge, S.P., Morizur, Y., Souami, Y., Van Canneyt, O., 2006. PETRACET: Project
610	EC/FISH/2003/09 Final report to the European Commission 1735R07D.
611	Peltier, H., Baagoe, H.J., Camphuysen, K.C.J., Czeck, R., Dabin, W., Daniel, P., Deaville, R.,
612	Haelters, J., Jauniaux, T., Jensen, L.F., Jepson, P.D., Keijl, G.O., Siebert, U., Van
613	Canneyt, O., Ridoux, V., 2013. The stranding anomaly as population indicator: the
614	case of harbour porpoise Phocoena phocoena in north-western Europe. PLoS ONE.
615	Peltier, H., Dabin, W., Daniel, P., Van Canneyt, O., Dorémus, G., Huon, M., Ridoux, V.,
616	2012. The significance of stranding data as indicators of cetacean populations at sea:
617	Modelling the drift of cetacean carcasses. Ecological Indicators 18, 278–290.

- Piatt, J.F., Ford, R.G., 1996. How many seabirds were killed by the Exxon Valdez oil spill?
 American Fisheries Society Symposium 18, 712–719.
- Piatt, J.F., Lensink, C.J., Butler, W., Kendziorek, M., Nysewander, D., 1990. Immediate
 impact of the Exxon Valdez oil spill on marine birds. Auk 107, 387–397.
- Pikesley, S.K., Witt, M. J., Hardy, T., Loveridge, J., Loveridge, J., Williams, R., Godley, B.
 J., 2011. Cetacean sightings and strandings: evidence for spatial and temporal trends?
 Journal of the Marine Biological Association of the United Kingdom Available on
 CJO 2011 doi:10.1017/S0025315411000464.
- Pyenson, N.D., 2010. Carcasses on the coastline: measuring the ecological fidelity of the
 cetacean stranding record in the eastern North Pacific Ocean. Paleobiology 36, 453–
 480.
- Pyenson, N.D., 2011. The high fidelity of the cetacean stranding record: insights into
 measuring diversity by integrating taphonomy and macroecology. Proceedings of the
 Royal Society B.
- Reid, J.B., Evans, P.G.H., Northridge, S.P., 2003. Atlas of Cetacean Distribution in North West European Waters. Joint Nature Conservation Committee.
- Rogan, E., Mackey, M., 2007. Megafauna bycatch in drift nets for albacore tuna (Thunnus alalunga) in the NE Atlantic. Fisheries Research 86, 6–14.
- Schiller, A., Hunsaker, C.T., Kane, M.A., Wolfe, A.K., Dale, V.H., Suter, G.W., Russell,
 C.S., Pion, G., Jensen, M.H., Konar, V.C., 2001. Communicating ecological indicators
 to decision makers and the public. Conservation Ecology 5, 19.
- Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., Hiraldo, F.,
 2008. Top predators as conservation tools: ecological rationale, assumptions, and
 efficacy. Annu. Rev. Ecol. Evol. Syst. 39, 1–19.
- Sergio, F., Newton, I., Marchesi, L., Pedrini, P., 2006. Ecologically justified charisma:
 preservation of top predators delivers biodiversity conservation. Journal of Applied
 Ecology 43, 1049–1055.
- Siebert, U., Gilles, A., Lucke, K., Ludwig, M., Benke, H., Kock, K.-H., Scheidat, M., 2006. A
 decade of harbour porpoise occurence in German waters- Analyses of aerial surveys,
 incidental sightings and strandings. Journal of Sea Research 56, 65–80.
- Smith, C.R., Baco, A.R., 2003. Ecology of whale falls at the deep-sea floor. Oceanography
 and Marine Biology: an Annual Review 41, 311–354.
- Thomas, Len, 1996. Monitoring long-term population change: why are there so many analysis
 methods? Ecology 77, 49–58.
- Turnhout, E., Hisschemöller, M., Eijsackers, H., 2007. Ecological indicators: between the two
 fires of science and policy. Ecological Indicators 7, 215–228.

- Wanless, S., Frederiksen, M., Daunt, F., Scott, B.E., Harris, M.P., 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. Progress in Oceanography 72, 30–38.
- Williams, R., Gero, S., Bejder, L., Calambokidis, J., Kraus, S.D., Lusseau, D., Read, A.J.,
 Robbins, J., 2011. Underestimating the damage: interpreting cetacean carcass
 recoveries in the context of the Deepwater Horizon/BP incident. Conservation Letters
 4, 228–233.
- Zeileis, A., Kleiber, C., Krämer, W., Hornik, K., 2003. Testing and dating of structural
 changes in practice. Computational Statistics & Data Analysis 44, 109–123.
- Zeileis, A., Leisch, F., Hornik, K., Kleiber, C., 2002. strucchange: An R Package for Testing
 for Structural Change in Linear Regression Models. Journal of Statistical Software 7,
 1–38.
- 666

667 Figure captions

Figure 1: Study area and sub-regions. EC: Eastern Channel, WC: Western Channel, BB: Bayof Biscay.

Figure 2: Monthly maps of stranding probability in the study area, from 1990 to 2009. Thedarker the colour, the highest the probability of stranding.

Figure 3: Annual numbers of observed common dolphin strandings (n) from 1990 to 2009.

673 Figure 4: Monthly decomposition of observed common dolphin strandings (n) in western

674 Channel, northern Bay of Biscay and southern Bay of Biscay from 1990 to 2009.

Figure 5: Long term common dolphin stranding anomaly (n) from 1990 to 2009.

676 Figure 6: Correlograms of common dolphin stranding anomaly.

677 Figure 7: Monthly decomposition of common dolphin observed strandings (black bars),

expected strandings (grey bars) and stranding anomaly (white bars) from 1990 to 2009.

Figure 8: Origin of observed stranded common dolphins between 1990 and 2009.

Figure 9: Origin of observed stranded common dolphins between 1990 and 2009, during
multiple stranding events (A) and out of these events (B).

Figure 10: Monthly origin of observed stranded common dolphins between 1990 and 2009.

Figure 11: Distribution inferred from strandings of common dolphins between 1990 and 2009.

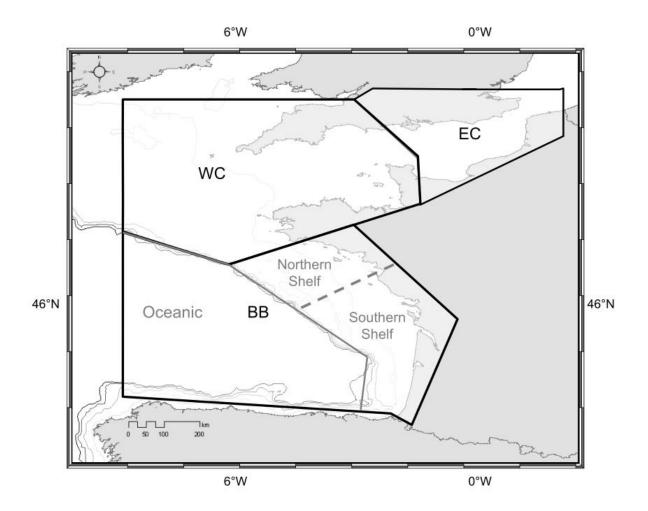
Figure 12: Distribution inferred from strandings of common dolphins between 1990 and 2009

685 during multiple stranding events (A) and out of these events (B).

Figure 13: Monthly distribution inferred from stranded common dolphins between 1990 and2009.

- Figure 14: Anomaly in stranding origin between 1990 and 2009, from 1990 to 2009 (A),
- 689 during multiple stranding events (B) and out of these events (C)
- Figure 15: Monthly anomaly in stranding origin between 1990 and 2009.

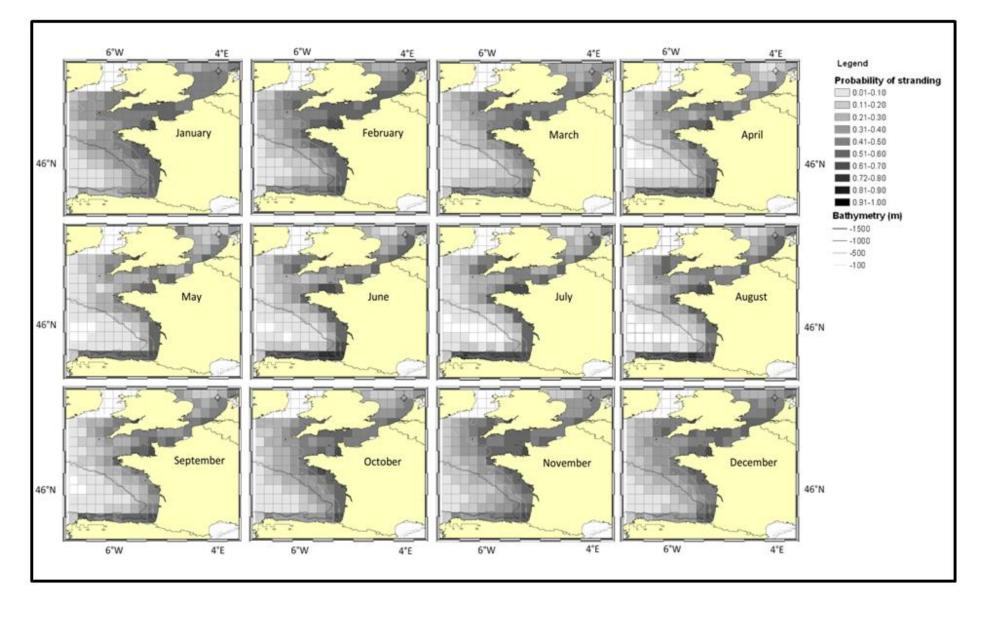
694 Figure 1



695

696





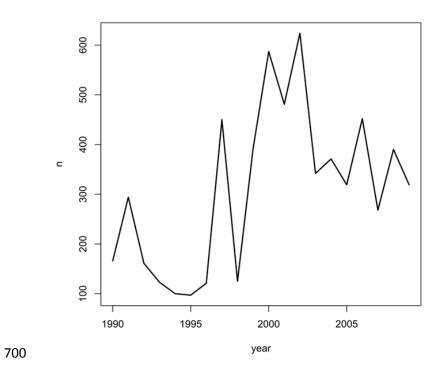
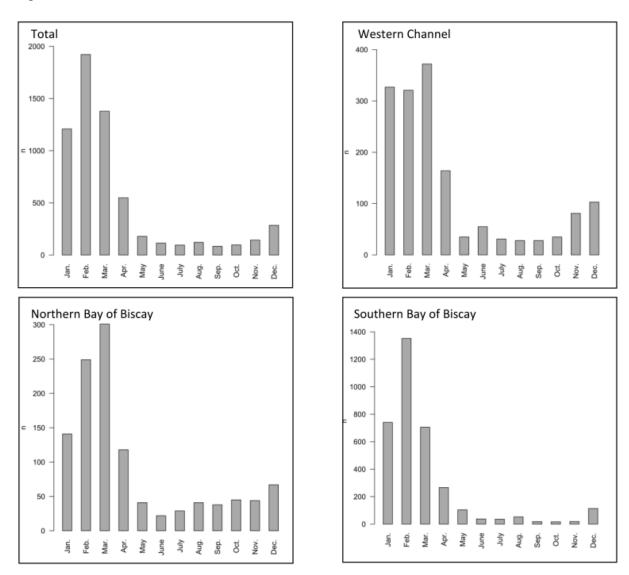
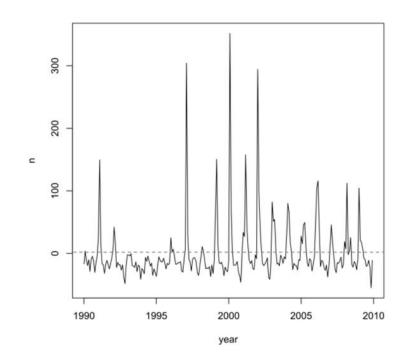


Figure 4

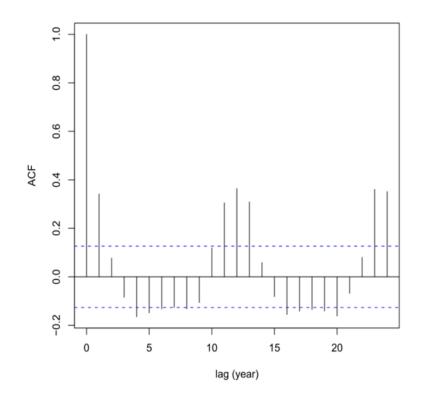


702

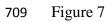


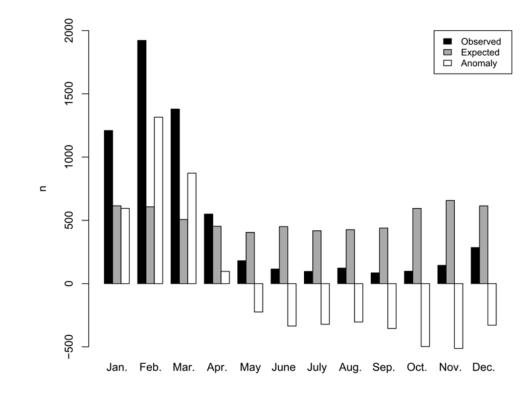


706 Figure 6



708

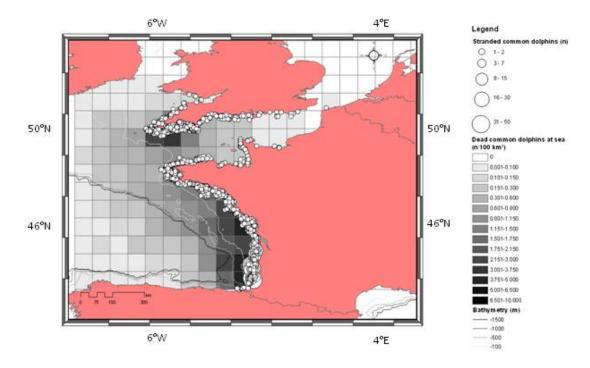


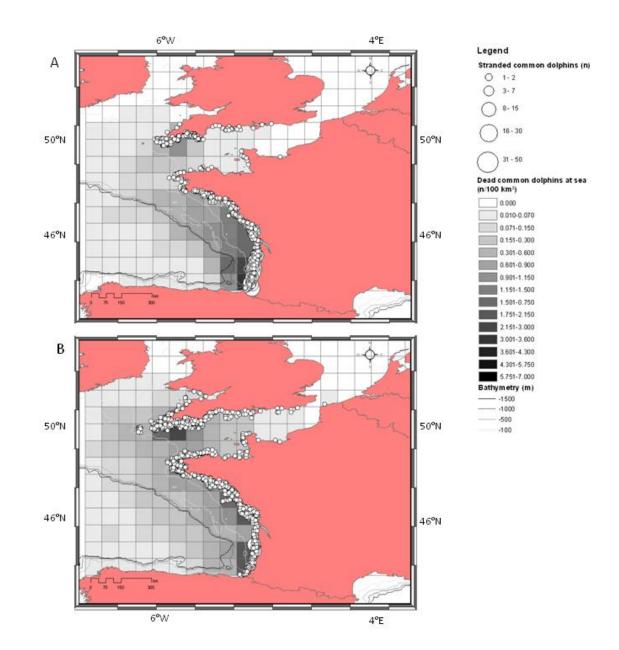


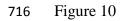


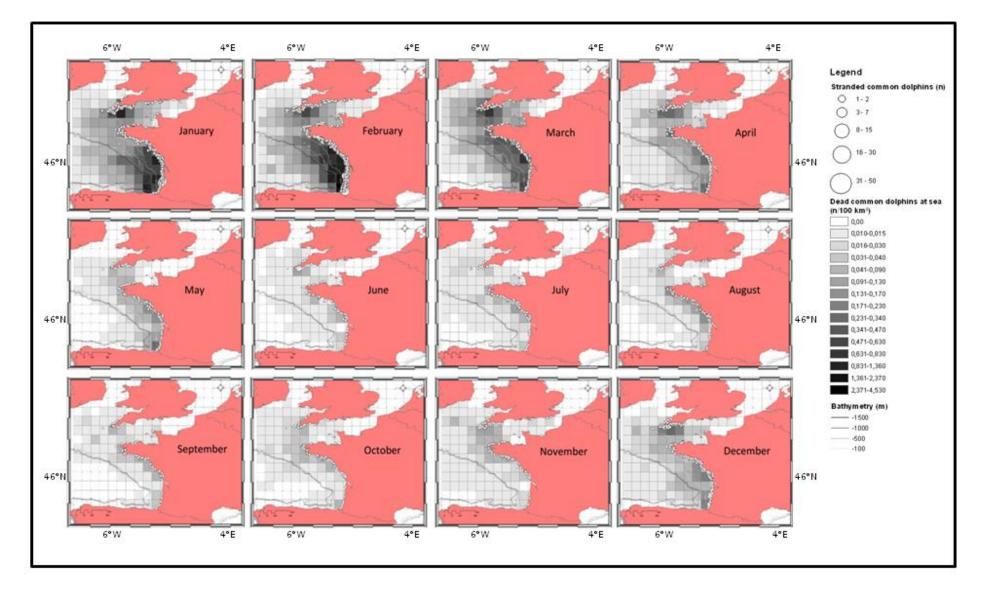


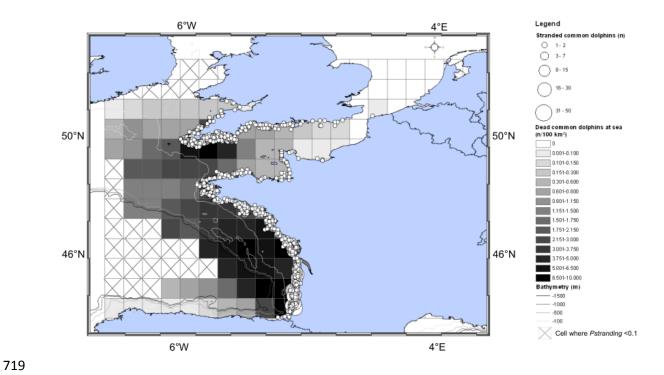
712 Figure 8

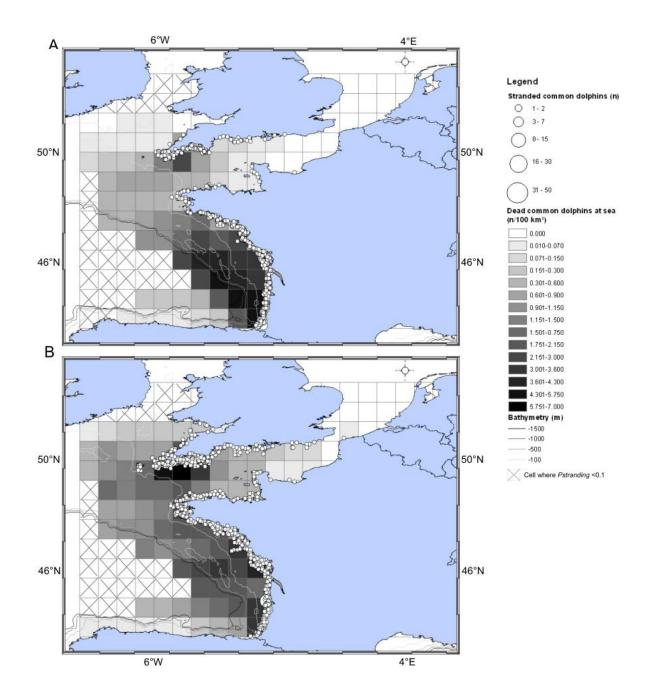












722

