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1       **Remote sensing in seagrass ecology: coupled dynamics between migratory herbivorous**  
2                   **birds and intertidal meadows observed by satellite during four decades**

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25 **Abstract**

26 Taking into account trophic relationships in seagrass meadows is crucial to explain and predict  
27 seagrass temporal trajectories, as well for implementing and evaluating seagrass conservation  
28 policies. However, this type of interaction has been rarely investigated over the long-term and at  
29 the scale of a whole seagrass habitat. In this work, reciprocal links between an intertidal seagrass  
30 species, *Zostera noltei*, and an herbivorous bird feeding on this seagrass species, the migratory  
31 goose *Branta bernicla bernicla*, were investigated using an original combination of long-term  
32 Earth Observation (EO) and bird census data. Seagrass Essential Biodiversity Variables (EBVs)  
33 such as seagrass abundance and phenology were measured from 1985 – 2020 using high-  
34 resolution satellite remote sensing over Bourgneuf Bay (France), and cross-analysed with *in situ*  
35 measurements of bird population size during the goose wintering season. Our results showed a  
36 mutual relationship between seagrass and Brent geese over the four last decades, suggesting that  
37 the relationship between the two species extends beyond a simple grass – herbivore consumptive  
38 effect. We provided evidence of two types of interactions: (i) a bottom-up control where the late-  
39 summer seagrass abundance drives the wintering population of herbivorous geese, and (ii) an  
40 indirect top-down effect of Brent goose on seagrass habitat, where seagrass development is  
41 positively influenced by the bird population during the previous wintering season. Such  
42 mutualistic relationship has strong implications for biodiversity conservation because protecting  
43 one species is beneficial to the other one, as demonstrated here by the positive trajectories  
44 observed from 1985 – 2020 in both seagrass and bird populations. Importantly, we also  
45 demonstrated here that exploring the synergy between EO and *in situ* bird data can benefit  
46 seagrass ecology and ecosystem management.

47 Key words: Time-series; Earth Observation; Essential Biodiversity Variables; *Zostera noltei*;  
48 *Branta bernicla bernicla*, trophic relationships

49

## 50 **Résumé**

51 Les interactions trophiques sont rarement considérées dans les études à long-terme et macro-  
52 échelle des habitats formés par les angiospermes marines. Pourtant, leur prise en compte  
53 permettrait de mieux comprendre les trajectoires temporelles des herbiers marins, d'anticiper leur  
54 évolution future, et d'améliorer les mesures de gestion et de protection des écosystèmes côtiers.  
55 Dans cette étude, nous avons analysé, en combinant de manière originale des séries temporelles à  
56 long-terme issues de la télédétection spatiale et du suivi de terrain de l'avifaune marine, les  
57 relations mutuelles entre un herbier intertidal de zostère, *Zostera noltei*, et la bernache cravant,  
58 *Branta bernicla bernicla*, une oie migratrice herbivore. Les variables essentielles de biodiversité  
59 telles que l'abondance et la phénologie des zostères ont été mesurées par des satellites  
60 d'observation de la Terre à haute résolution spatiale de 1985 à 2020. Ces observations ont été  
61 analysées conjointement avec les comptages pluriannuels de la population de bernaches  
62 hivernant en Baie de Bourgneuf (France). Nous avons mis en évidence une relation entre les  
63 zostères et les bernaches lors des quatre dernières décennies, suggérant que les interactions entre  
64 les deux espèces ne sont pas limitées à une simple relation d'herbivorie. Notre interprétation met  
65 en lumière deux types d'interactions : (i) une relation de type "bottom-up" par laquelle la  
66 population hivernante de bernaches est régulée par l'abondance estivale de zostère, et (ii) une  
67 relation indirecte de type "top-down" par laquelle le développement annuel de l'herbier est  
68 influencé par la population de bernaches séjournant dans l'herbier lors de l'hiver précédent. Dans  
69 un contexte général de conservation de la biodiversité, une telle relation mutualiste est

70 particulièrement importante car la protection d'une des deux espèces est bénéfique à l'autre,  
71 comme le démontre l'augmentation à long-terme observée de 1985 à 2020 de manière parallèle  
72 de l'abondance de zostères et de bernaches. En outre, notre étude met en lumière l'intérêt  
73 d'analyser en synergie les suivis d'avifaune et les observations issues de la télédétection spatiale  
74 pour l'étude et la gestion des écosystèmes côtiers.

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## 79 **1. Introduction**

80 Seagrasses are key components of the coastal ocean. As ecosystem engineers (*sensu* Jones *et al.*,  
81 1994), seagrasses have a structuring role in sedimentation (Bos *et al.*, 2007), tend to stabilize  
82 benthic communities and food webs (Jankowska *et al.*, 2019), and are attractive feeding grounds  
83 for fishes (Spalding *et al.*, 2003), birds (Robin *et al.*, 2015; Balsby *et al.*, 2017) as well as marine  
84 mammals (de Iongh *et al.*, 1995; Sheppard, Lawler and Marsh, 2007) and sea turtles (Taquet *et*  
85 *al.*, 2006). Seagrass beds provide important ecosystem services to humankind including carbon  
86 sequestration, oxygen production, and coastal protection (Nordlund *et al.*, 2016).

87 The ecological relevance and threats to which seagrass meadows are subjected to boosted  
88 ecosystem conservation managers to include seagrass into priority lists for preservation and  
89 observing programs. Many studies have proposed maps of coverage and spatial dynamics of  
90 seagrass beds (e.g., Agostini *et al.*, 2003; Duarte and Sand-Jensen, 1990; Godet *et al.*, 2008;  
91 Robbins, 1997). In particular, seagrass cover and composition are essential oceanic variables  
92 (EOVs) for the monitoring of habitat extent and ecosystem health (Miloslavich *et al.*, 2018), and

93 seagrass taxonomic diversity, species distribution, population abundance and phenology have  
94 been recognized as essential biodiversity variables (EBVs, Pereira *et al.*, 2013). A better  
95 understanding of seagrass ecosystem functioning including environmental drivers and trophic  
96 interactions is therefore required to mitigate anthropic impacts and implement biodiversity  
97 conservation (Valentine and Duffy, 2006).

98 Previous works have identified several drivers of seagrass trajectories, such as solar radiation and  
99 tidal exposure (Unsworth *et al.*, 2012), diseases (Rasmussen, 1977; Den Hartog, 1987), as well  
100 as anthropic pressures related to eutrophication (Jones *et al.*, 2018), coastal development (Dunic  
101 *et al.*, 2021), a variety of human activities (Desmonts *et al.*, 2009), water quality (Dunic *et al.*,  
102 2021, Turschwell *et al.*, 2021), and fisheries (Turschwell *et al.*, 2021). While many  
103 environmental drivers have been documented in the literature, less attention has been paid to  
104 investigate the influence of trophic interactions on seagrass dynamics (e.g., Balsby *et al.*, 2017;  
105 Horn *et al.*, 2020; Kollars *et al.*, 2017). Herbivory is a crucial interaction to consider because  
106 grazing influence seagrass biomass via top-down control and, in turn, changes in seagrass  
107 abundance affect herbivore population size via bottom-up control (Unsworth and Butterworth,  
108 2021; Valentine and Duffy, 2006).

109 Seagrass – herbivores interactions can be investigated at several scales to provide different types  
110 of ecological information (Jacobs *et al.*, 1981). One type of information relates to the direct  
111 effect of grazing on the individual plant, i.e., the immediate reduction of vegetal biomass by  
112 herbivore consumption (Ganter, 2000; Sato *et al.*, 2020). Another type of information concerns  
113 the seagrass – herbivores relationship at habitat/population level over larger time scales. This  
114 interaction is much more complex to investigate because it depends on grazing magnitude and  
115 frequency, on seagrass physiological responses with long-term effects (e.g., compensatory

116 growth mechanisms, investment in sexual reproduction), and on indirect mechanisms associated  
117 to herbivory (e.g., soil fertilization with faeces, seed propagation, relief of competition by other  
118 vegetal species) (Shaughnessy *et al.*, 2021; Valentine and Duffy, 2006).

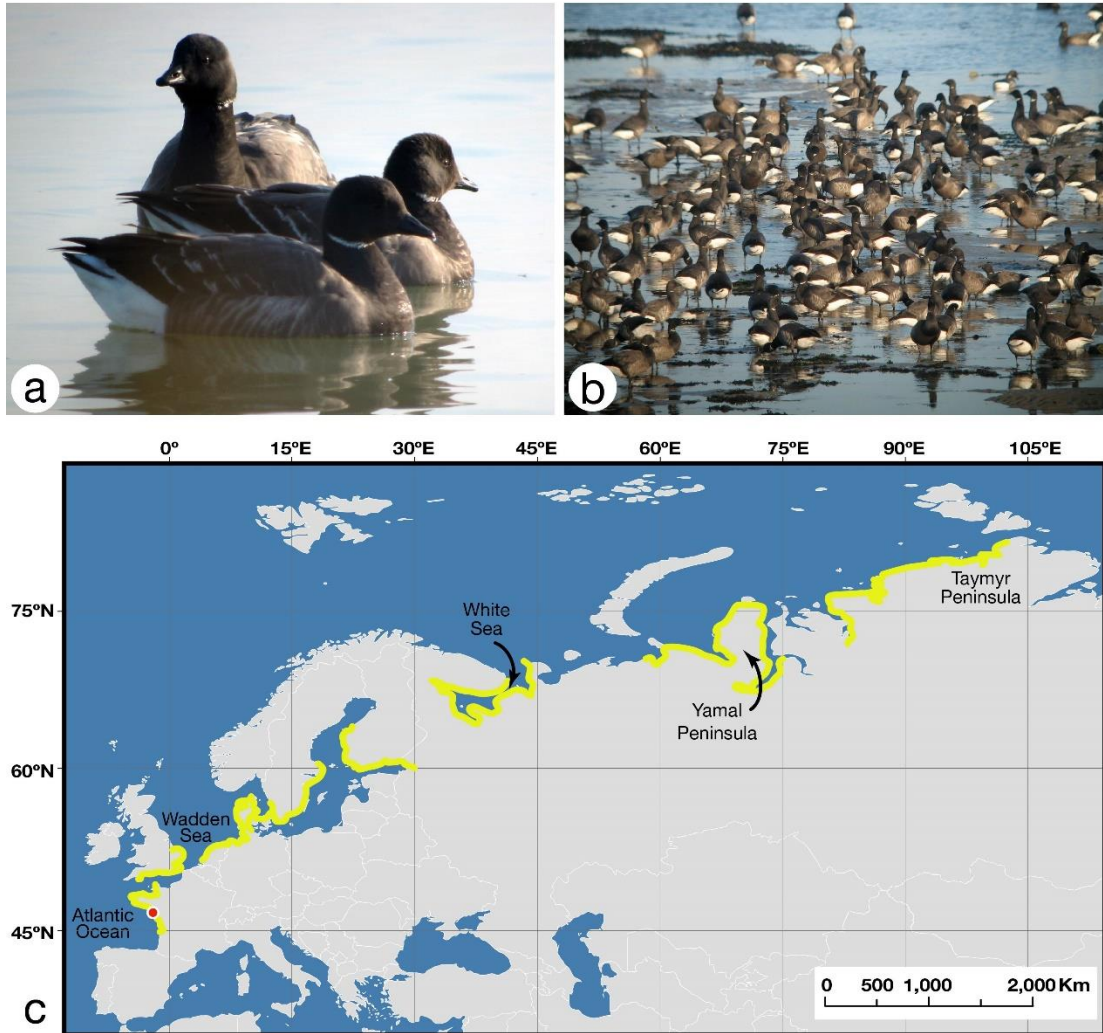
119 Interestingly, most herbivorous birds feeding on seagrass are migratory birds. Herbivory by  
120 migratory animals is a particular case of plant – herbivore interaction. On the one hand,  
121 consumers exert pressures over the food resource only during a certain period of time (e.g., a few  
122 months). On the other hand, the population of migratory herbivores is affected by factors related  
123 to a large geographical range that includes wintering, stop-over, and breeding sites (Newton,  
124 2007). Thus, both the timing of seasonal cycles of grazers' population and food resource, as well  
125 as regional components that drive herbivore population are fundamental factors to understand  
126 their complex relationship in a specific site.

127 The dark-bellied Brent goose (*Branta bernicla bernicla*, Fig. 1a, b) is an herbivore waterfowl  
128 that migrates from arctic Russia to the French Atlantic coast (Fig. 1c). It breeds during summer  
129 in the Taymyr Peninsula (~76.3° N) and migrates south- and westward in order to spend the  
130 autumn and winter in Western Europe. Sixty percent of the global Brent goose population winter  
131 in France across 18 sites, down to Arcachon Bay (~ 44.6° N) in the Atlantic Coast (Dalloyau and  
132 Robin, 2013). Brent goose has several stop-overs in the White, Baltic, and Wadden Seas. Its  
133 main food resource is constituted by seagrass of the *Zostera* genus (either *Z. marina* or *Z. noltei*).  
134 When seagrass is not available, Brent goose can switch diet to feed on green macroalgae (*Ulva*  
135 spp.), saltmarsh vegetation (*Puccinellia maritima*), or agricultural crops (Inger *et al.*, 2006;  
136 Mathers and Montgomery, 1997; Tinkler *et al.*, 2009).

137 Several works already documented the crucial role of megaherbivores (waterfowls, turtles, and  
138 dugongs) on seagrass ecosystem structure, biomass, and primary production (Scott *et al.*, 2018).

139 Also, there are numerous examples of the potential of Earth Observation (EO) to study seagrass  
140 EBVs worldwide (Barillé *et al.*, 2010; Calleja *et al.*, 2017; El-Hacen *et al.*, 2020; Zoffoli *et al.*,  
141 2020). However, to our knowledge, combined analyses of long-term dynamics in herbivorous  
142 population and remotely-sensed seagrass distribution have never been attempted. This study  
143 focused on Bourgneuf Bay (France, Fig. 1c), an important Brent goose wintering site (Valéry  
144 and Schricke, 2013) where satellite observations revealed an increasing trend in both seagrass  
145 density and areal extent since the 1980s (Zoffoli *et al.*, 2021). Our objective was to investigate,  
146 for the first time, the relationship between remotely-sensed decadal changes in seagrass habitat  
147 and bird population. More generally, our work seeks at demonstrating the potential of high-  
148 resolution satellite remote sensing for the conservation and ecology of two intertwined and  
149 protected species.





150 **Figure 1.** *Branta b. bernicla* individuals (a – b) and its migration flyway (c). The main breeding,  
 151 stopover, and wintering sites are highlighted in yellow (adapted from (Ebbinge *et al.*, 2013)). The  
 152 red dot shows the location of Bourgneuf Bay (France), a wintering site where seagrass spatial  
 153 distribution has been documented using satellite remote sensing since 1985.  
 154  
 155

156 **2. Material and methods**

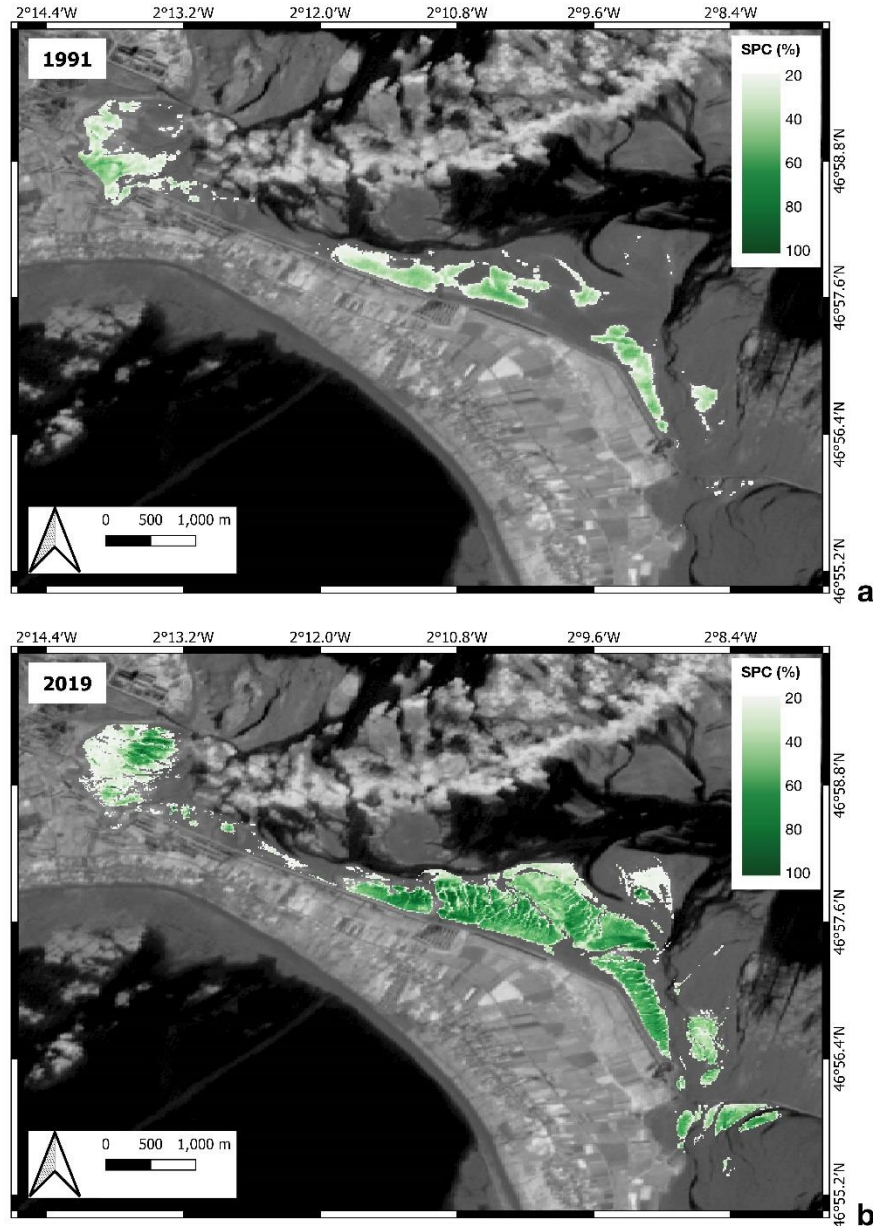
157 **2.1 Remote sensing of seagrass essential biodiversity variables**

158 Along the French Atlantic coast, Bourgneuf Bay is a macrotidal bay hosting a large intertidal  
 159 seagrass meadow dominated by *Zostera noltei*, which is part of a Natura 2000 protected area. At  
 160 this latitude (~47° N), seagrass displays a seasonal cycle with a late summer peak (Zoffoli *et al.*,  
 161 2020). In a previous work, several seagrass EBVs were computed from long-term high-

162 resolution remote sensing over this site (Zoffoli *et al.*, 2021). Briefly, a multi-mission satellite  
163 time-series was compiled from Landsat, SPOT, and Sentinel-2 acquisitions. Images were  
164 selected for every summer from 1985 – 2020. Maps of seagrass percent cover (Fig. 2) were  
165 computed from the normalized difference vegetation index (NDVI) with an uncertainty of about  
166 14% (Zoffoli *et al.*, 2020), thus making it possible to measure several seagrass indicators at  
167 ecosystem scale. Because seagrass data was missing during 7 years in the initial dataset of  
168 Zoffoli *et al.* (2021), we completed the time-series using additional Landsat and SPOT images in  
169 1989, 1992, 1994, 1999, 2000, 2007, and 2014 in order to get a continuous time-series. The new  
170 images were slightly suboptimal in terms of acquisition time (i.e., they were marginally out-of-  
171 time compared to the date of seagrass summer peak) or cloud cover (and in that case seagrass  
172 quantification has been made by a combination of two images acquired during the same  
173 summer). Through these data might be subjected to higher uncertainties, they still remained  
174 among the range of variability observed during the 29 other years, and can be consistently used  
175 for time-series analysis.

176 In the present study, we used the following seagrass data: the meadow-averaged seagrass density  
177 as an indicator of seagrass above-ground biomass, and two proxies of habitat extent (A20 and  
178 A50) corresponding to the surface of the whole and dense seagrass meadow, defined as the area  
179 where % cover is higher than 20% or 50% respectively. Seagrass density was computed as the  
180 mean % cover over the whole meadow. A 20% threshold in seagrass cover was applied to reduce  
181 mapping uncertainties (Dolch *et al.*, 2017; Zoffoli *et al.*, 2021). Interestingly, this value is also  
182 biologically meaningful for Brent goose as it is close to the percent cover of 15% indicated as a  
183 “giving-up” density below which seagrass leaf cover is not profitable for feeding (Jacobs *et al.*,  
184 1981; Percival and Evans, 1997).

185 The Landsat time-series was also used to detect possible long-term shift in seagrass phenology  
186 over Bourgneuf Bay. A total number of 238 cloud-free images acquired during low tide was  
187 selected from 1984 – 2020. Temporal changes in NDVI were used to characterize seagrass  
188 seasonal cycle, as in Zoffoli *et al.* (2020). Due to limitations in temporal resolution, it was not  
189 possible to measure seagrass seasonal variability every year. Monthly-averaged composite  
190 annual cycles were then reconstructed over a 10-year period, and compared between the start  
191 (1984 – 1993) and end (2011 – 2020) of the Landsat time-series.



192  
 193 **Figure 2.** Examples of satellite-derived seagrass map in Bourgneuf Bay, showing seagrass %  
 194 cover (SPC) at high-resolution over the whole meadow: a) SPOT-2 image on 28 August 1991; b)  
 195 Sentinel-2 image on 16 September 2019. The complete series of SPC maps from 1985 – 2020 is  
 196 shown in Zoffoli *et al.* (2021).  
 197

## 198 2.2 Brent goose data

199 In this work we used two Brent goose datasets in France: one for the goose size population at  
 200 Bourgneuf Bay, and the other one at national level. For Bourgneuf Bay, we used monthly records  
 201 of Brent goose size population from September to April (period later referred as “goose season”),

202 from 1976 – 2021. Bird counts were performed during high tide in 6 different sighting sites  
203 within Bourgneuf Bay from the Noirmoutier Island to the Port du Collet. For each goose season,  
204 a log-normal model was fitted to the monthly bird numbers ( $p$ -value < 0.05 for all years). The  
205 date of maximal goose number was then computed from the fitted curve. The date of arrival and  
206 departure was defined as the days when the goose number corresponded to 50% of the seasonal  
207 maximum (Valéry and Schricke, 2013).

208 The national Brent goose wintering population data was available for the period 1990 – 2020, as  
209 part of the French Brent network (Goose Specialist Group / Wetlands International) framework.  
210 Monthly counts were based on the Wetlands protocol and were carried out at mid-month from  
211 September to April. The data retained correspond to the sum of each site performed in all French  
212 wintering sites at the time of the national abundance peak, which may occur mainly in  
213 November, less frequently in December.

214 The world population of Brent goose from 1976 – 2011 was compiled from previously published  
215 results. It corresponded to the sum of all mid-January counts performed in France, United  
216 Kingdom, The Netherlands, Germany and Denmark (Ebbinge *et al.*, 2002, 2013).

217

### 218 **2.3. Environmental datasets**

219 The potential influence of environmental parameters on seagrass extent and density was  
220 investigated from 1984 – 2020 using monthly time-series of abiotic factors such as air  
221 temperature, sea surface temperature, cumulative rainfall, flow of the nearby Loire River, surface  
222 solar radiation, wave height, and sea level. The details regarding the environmental data are  
223 provided in Supplementary Information.

224

## 225 2.4. Statistical analyses

226 Two methods were used to identify the most important factors (environmental and goose  
227 abundance) influencing seagrass variables (Density, A20 and A50): the BIOENV method  
228 (Clarke and Ainsworth, 1993) and the Conditional Interference Tree (CIT; Hothorn *et al.*, 2006).  
229 The BIOENV method identifies the best subset of environmental variables with the Euclidian  
230 distance of scaled environmental variables having the maximum Pearson correlation with the  
231 similarity matrix calculated from seagrass parameters. The CIT is a random forest approach used  
232 to assess the relative importance of multiple explanatory variables with respect to a single  
233 response variable. With the BIOENV method, explanatory variables that are correlated must be  
234 removed while the CIT is not affected by multicollinearity. The CIT also allows for non-linear  
235 relationships unlike BIOENV which only performs linear relations. BIOENV was run on  
236 PRIMER 7 (Clarke and Gorley, 2006) and the CIT analysis with R (Party Kit, Hothorn and  
237 Zeileis, 2015). The winter-, spring- and summer-averages of all abiotic parameters were tested  
238 using both methods. The tested goose data corresponded to the maximum number recorded  
239 during the goose season preceding the seagrass peak (i.e., September – April).  
240 The association between Brent Goose monthly counts and Seagrass Density was assessed using  
241 Generalized Linear Mixed Effect Models (GLMM). Brent Goose counts were modelled as a  
242 function of Month (October to March), normalised Seagrass Density ( $N_i$ , Eq. 1), Year as a  
243 random factor, and using a temporal autocorrelation structure based on Year. Modelling was  
244 performed using the “glmmTMB” package in the R programming language (R Core Team, 2022;  
245 Brooks *et al.*, 2022; Chadsuthi *et al.*, 2022) assuming that Brent Goose counts followed a Poisson  
246 distribution.

$$247 \quad N_i = \frac{S_i - \mu_S}{\sigma_S} \quad (\text{Eq. 1})$$

248 where  $S_i$  corresponds to seagrass Density in each individual year,  $\mu_S$  to the mean, and  $\sigma_S$  to its  
249 standard deviation. Sample vs. fitted residuals, quartile-quartile, and autocorrelation of  
250 temporally sequential samples were visually assessed to evaluate model assumptions. Seagrass  
251 A20 and A50 were likewise modelled.

252

### 253 **3. Results**

#### 254 **3.1. Explanatory variables for seagrass variability**

255 The BIOENV analysis indicated that the Pearson correlation between seagrass EBVs and the  
256 similarity matrices of the investigated factors was maximized at  $\rho = 0.33$  ( $p$ -value  $< 0.05$ ) for  
257 Maximum Goose Abundance, suggesting that among all the seagrass drivers tested, it was the  
258 main factor contributing to seagrass variability. This was confirmed by the result of the CIT  
259 model, which showed that seagrass variability was significantly associated in a first order to  
260 Maximum Goose Abundance ( $p$ -value  $< 0.01$ ), and in a second order, to average Wave Height in  
261 spring ( $p$ -value  $< 0.01$ ), suggesting that a higher number of wintering geese promoted a larger  
262 and denser seagrass at the end of the following summer.

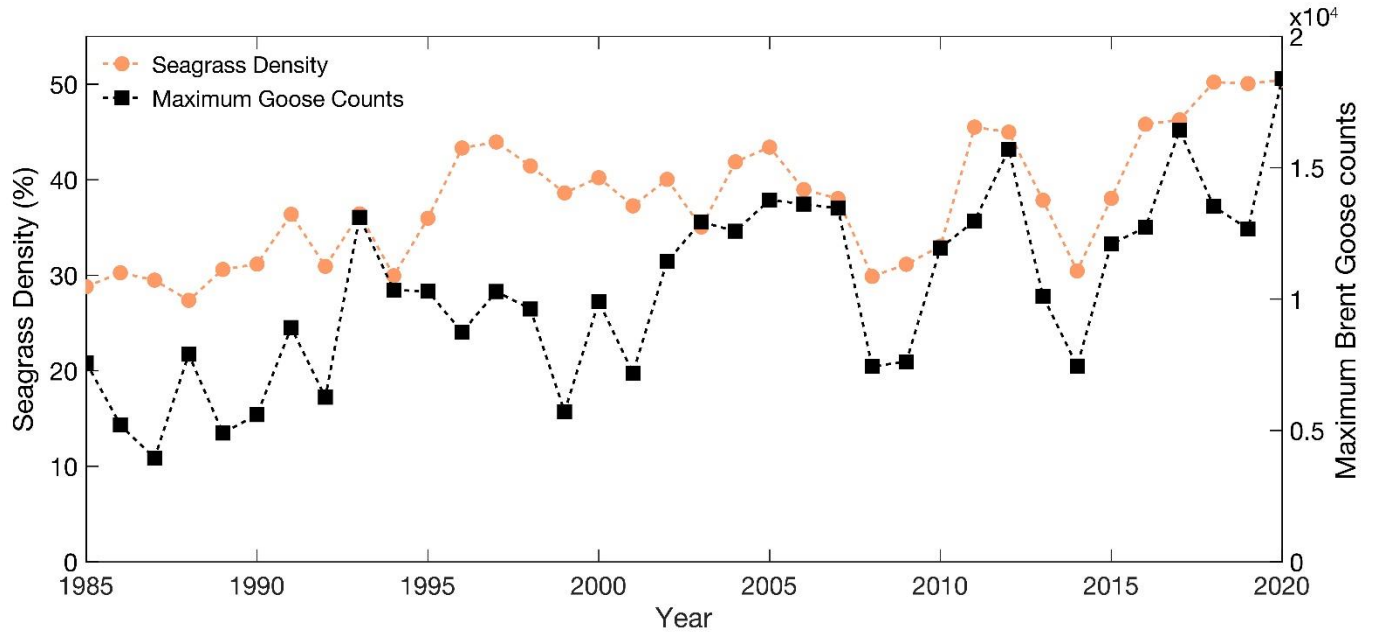
263

#### 264 **3.2. Mutual interactions between seagrass and Brent geese**

265 Seagrass and Brent goose counts presented increasing trajectories from 1985 – 2020 (Fig. 3).  
266 Monthly goose counts were significantly related to all seagrass parameters (GLMM,  $p$ -value  $<$   
267 0.001). Interestingly, the relationship between Monthly Goose Counts and seagrass Density was  
268 positive from October to January with the strongest relationships in October and November as  
269 evidenced by the steepest slopes in the modelling response (Fig. 4): higher seagrass biomass in  
270 summer attracted a higher number of birds during the subsequent goose wintering season. On the

271 contrary, the relationship was negative in March when most of the geese already started their  
272 way back towards the Northern breeding sites. GLMM results for seagrass Density were similar  
273 to the ones obtained for the other seagrass parameters analysed such as A20 and A50 (figures not  
274 shown).

275

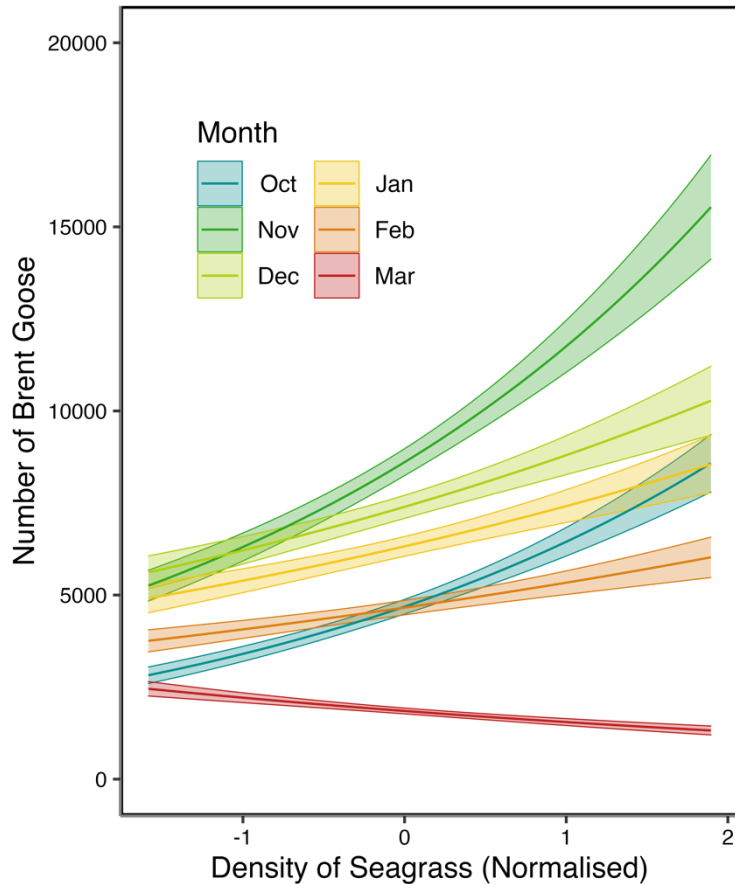


276

277 **Figure 3.** Time-series of variables from 1985 – 2020: meadow-averaged Seagrass Density (in %)   
278 (orange dots) represented in the left y-axis, and maximum Brent Goose counts (black squares) in   
279 the right y-axis.

280



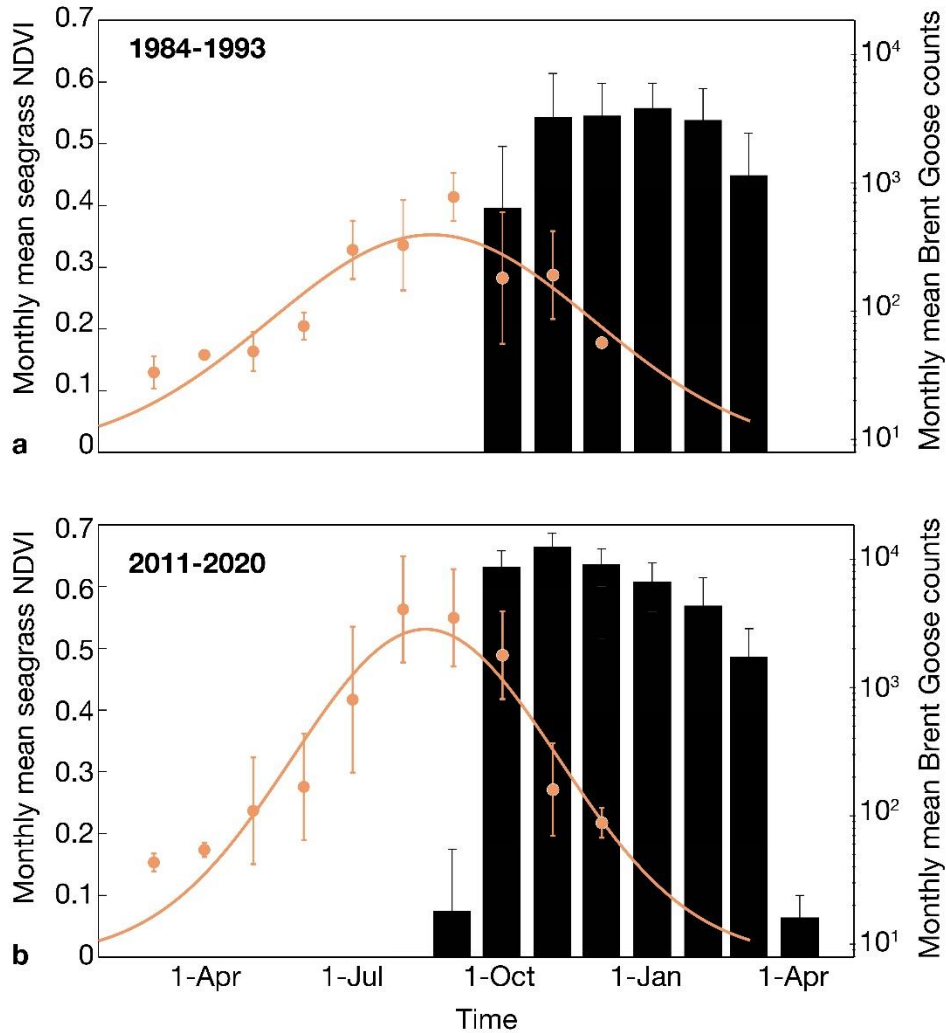


281 **Figure 4.** Modelled change in Brent Goose counts with Normalised Seagrass Density across  
 282 Months. Lines and shaded areas show GLMM model estimates and standard errors.  
 283  
 284

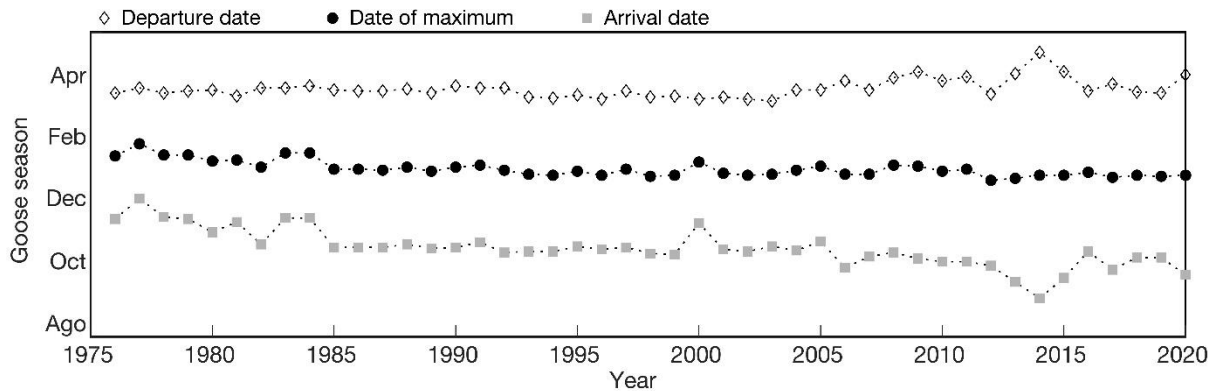
### 285 3.3. Seasonal variability in seagrass and Brent geese

286 The seagrass phenology did not change over the past 40 years. The averaged seasonal NDVI  
 287 cycle was the same during the first (1984 – 1993) and last decade (2011 – 2020) of the studied  
 288 time-series (Fig. 4). At this latitude, seagrass biomass increases during spring, peaks at the end of  
 289 summer (late August / early September), and decreases during autumn and winter. While there  
 290 was no change in the timing of the seagrass seasonal cycle, there was a difference in its  
 291 amplitude. NDVI reached a higher peak during the 2011 – 2020 decade compared to the 1984 –  
 292 1993 decade, consistently with the afore-mentioned long-term increase in seagrass density and  
 293 extent. Interestingly, a phenological shift in the Brent goose season occurred from 1984 – 2020.

294 Whereas most of the wintering population generally used to arrive in October and depart before  
295 the end of March, during the last decade an increasing number of geese have been spotted as  
296 early as September and as late as April (Fig. 4). In average, the date of the maximum goose  
297 counts shifted from January to November between the first and last considered decades.  
298 The analysis of the whole Brent goose time-series from 1976 – 2020 further confirmed the  
299 phenological shift of the goose wintering season. According to the log-normal model, the date of  
300 maximum goose counts moved about 19 days earlier, from 12 January in 1976 to 24 December  
301 in 2020 (Fig. 5). This trend was accompanied by an extension of the whole wintering season of  
302 at least 2 months, with an advance of about 56 days in the date of arrival (from 12 November to  
303 17 September), and a delay of about 17 days in the date of departure (from 16 March to 2 April).  
304



305  
 306 **Figure 5.** Monthly mean NDVI representing seagrass seasonal cycle (orange circles, left axis),  
 307 and monthly mean Brent goose counts (black bars, right axis in log-scale). Data corresponds to  
 308 10-year average during two time periods: (a) 1984 – 1993, and (b) 2011 – 2020. Error bars  
 309 correspond to standard deviation.  
 310



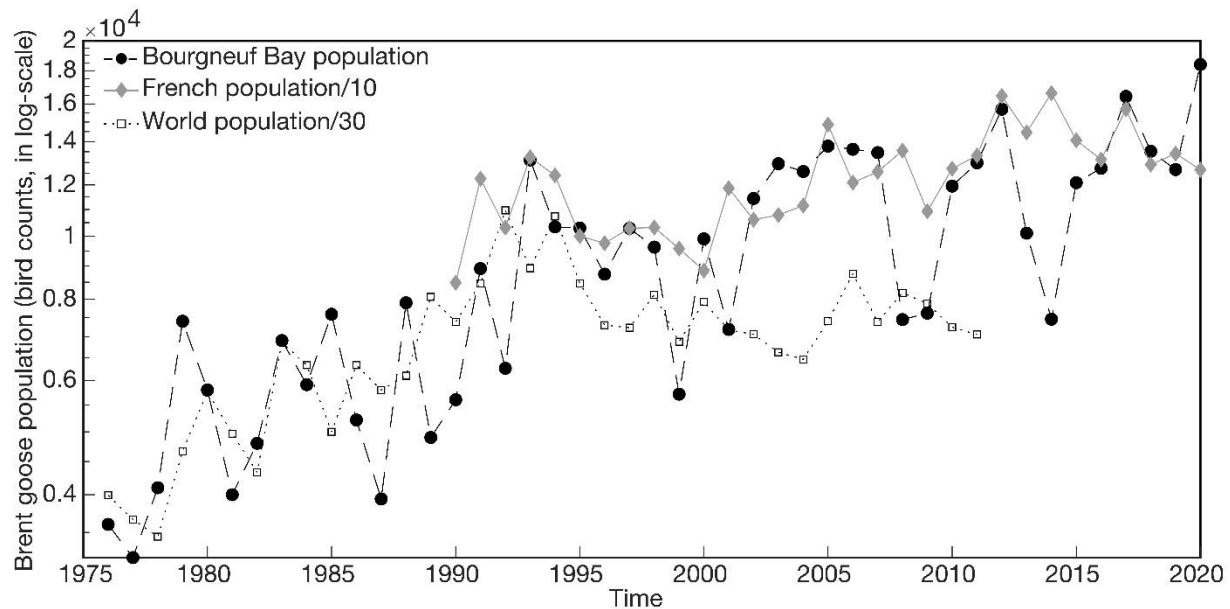
311  
 312 **Figure 6.** Timing of modelled goose season in Bourgneuf Bay from 1976 – 2020, showing the  
 313 dates of departure (white diamonds), maximum (black circles) and arrival (grey squares).

314 **3.4. Long-term variability in Brent goose regional, national and global population**

315 The global Brent goose population showed an increasing trend since 1976, peaking to  
316 approximately 329,000 individuals in 1992, followed by a reduction and stabilization around  
317 220,000 individuals since the 2000s (Fig. 6; Ebbinge *et al.*, 2013). The number of Brent geese  
318 wintering in France and in Bourgneuf Bay also increased up to the 1990s, but contrary to the  
319 world population, continued to increase afterwards. The French population thus regularly  
320 increased up to the early 2010s, stabilizing around 142,000 individuals over the past decade. The  
321 French population thus now represents about 60% of the global goose population. The  
322 population in Bourgneuf Bay also displayed an overall increasing trend, reaching a total number  
323 of geese fluctuating around 11,500 individuals over the last years. Compared to the national  
324 population, the population in Bourgneuf Bay displayed a high degree of interannual variability,  
325 with drastic decreases in 1999, 2001, 2008, 2009 and 2014. Interestingly, the years of strong  
326 declines in Brent goose abundance coincided with significant reductions in seagrass surface area  
327 and meadow-averaged density, suggesting that a reduction of food supply prompted the  
328 migratory birds to overwinter in other sites in France.

329

330



331 **Figure 7.** Brent goose population in Bourgneuf Bay from 1976 – 2020 (black circles), in France  
 332 from 1990 – 2020 (grey diamonds), and in the world from 1976 – 2011 (white squares). For  
 333 comparative purpose, the French population was divided by 10, and the world population was  
 334 divided by 30. The vertical axis is graduated in log-scale.  
 335

336  
 337  
 338 **4. Discussion**

339 **4.1. Data requirements and challenges to interpret seagrass trajectory**

340 While catastrophic seagrass loss has been globally documented (Waycott *et al.*, 2009; Green *et*  
 341 *al.*, 2021) a recent increase in the status of intertidal meadows dominated by *Z. noltei* was  
 342 reported in several European sites (de los Santos *et al.*, 2019) including Bourgneuf Bay (Zoffoli  
 343 *et al.*, 2021). The knowledge of seagrass status and its ecological drivers is required to develop  
 344 predictive models and optimize conservation strategies of these protected habitats, but the  
 345 determination of such drivers is extremely challenging due to the lack of both seagrass and  
 346 environmental measurements (Unsworth *et al.*, 2019). In the present study, a long-term seagrass  
 347 time-series has been analysed using satellite observations acquired during its annual maximum to  
 348 avoid biases caused by seasonal variations. The status of the seagrass meadow at this time  
 349 corresponds to an ecological response to environmental drivers that acted over the previous

350 months. Thus, the effect of environmental factors should be analysed taking into account the  
351 conditions experienced by seagrass during the whole growing season. For that purpose,  
352 environmental observations have to be performed at high temporal resolution. Here, the  
353 investigated environmental datasets were either acquired using EO, autonomous systems such as  
354 meteorological stations and tide gauges, or resulting from modelling. This highlights the  
355 importance of maintaining coordinated continuous monitoring programs (e.g., satellite missions,  
356 *in situ* monitoring networks, autonomous platforms; Papathanasopoulou et al., 2019) collecting  
357 data on both EBV and abiotic factors at large spatial and temporal scales to develop an improved  
358 understanding of biodiversity and ecosystem functioning (Navarro et al., 2017; Paganini *et al.*,  
359 2016). Here, monthly data of solar irradiance, air temperature and SST, rainfalls, river flow,  
360 wave height and sea level were available. These parameters, however, were not the main  
361 explanatory variables for the seagrass dynamics observed in Bourgneuf Bay from 1985 – 2020.  
362 Similarly, Lebrasse *et al.* (2022) did not find any significant relationship between seagrass long-  
363 term trends and climatic factors in a subtidal meadow in Florida. Other environmental factors  
364 such as sedimentation rate, nutrient concentration, and sediment composition have been pointed  
365 out as important seagrass drivers (Guerrero-Meseguer *et al.*, 2021; Qin *et al.*, 2021; Soissons *et*  
366 *al.*, 2018); they were not considered here because of the absence of available long datasets at the  
367 required temporal resolution.

368 While the investigated abiotic factors were not correlated with seagrass variability in Bourgneuf  
369 Bay, some synchronous events are noteworthy. This is the case of a drastic seagrass decline in  
370 2003, which coincided with an intense summer heatwave in Europe (Garcia-Herrera *et al.*,  
371 2010). The low seagrass status observed in 2010 occurred several months after the so-called  
372 Xynthia storm, which resulted in dramatic coastal erosion and flooding in Bourgneuf Bay and

373 nearby towns (Chadenas *et al.*, 2014). The limited seagrass extent during the 1980s and early  
374 1990s also coincided with a higher occurrence of frost days during the preceding winter whose  
375 influence on intertidal seagrass has been previously documented in northern Brittany (Fournier *et*  
376 *al.*, 2006). Due to the absence of correlation between abiotic factors and seagrass trajectory,  
377 examples of synchronous decline in seagrass and environmental parameters are however to be  
378 interpreted with caution, all the more as it is generally easier to highlight coincident abrupt losses  
379 rather than to identify other types of changes. Nevertheless, the projected frequency increase of  
380 extreme climatic events such as heatwaves, cold waves and droughts in the forthcoming decades  
381 (IPCC, 2021) calls for a continuous monitoring of EBVs and environmental drivers. Unlike the  
382 investigated abiotic data, Brent goose abundance was significantly related to seagrass EBVs.  
383 Long-term datasets of waterbirds represent valuable indicators of conservation status of coastal  
384 habitats (Ogden *et al.*, 2014; Brandis *et al.*, 2018). In previous studies, the lack of seagrass time-  
385 series was highlighted as a limitation to interpret the long-term dynamics in Brent goose  
386 population (Valéry and Schricke, 2013), as well as to document plant – herbivore relationships  
387 over large temporal scales (Balsby *et al.*, 2017). In this regard, our work demonstrates that EO  
388 makes it possible to further investigate reciprocal interactions between *Z. noltei* and *B. b.*  
389 *bernicla* at the scale of a whole seagrass meadow over several decades.

390

#### 391 **4.2. Ecological interactions between Brent goose and seagrass**

392 One of the most striking results of the present study was that long-term changes in the size of the  
393 Brent goose population was related with seagrass EBVs. On the first hand, the positive  
394 association between both the seagrass meadow extent and density and goose counts during the  
395 subsequent wintering season has a straightforward bottom-up interpretation: a higher seagrass

396 biomass (i.e., higher food supply) attracts a higher number of consumers (Ganter, 2000).  
397 Furthermore, the results from the GLMM demonstrated that the relationship between goose  
398 population and seagrass was the strongest shortly after the time of the seagrass maximum, also  
399 corresponding to the month of maximal goose counts (October and/or November). On the other  
400 hand, grazing pressure could be expected to negatively impact seagrass population (Sato *et al.*,  
401 2020). As a matter of fact, the influence of grazing by birds on seagrass can be divided into  
402 short- and long-term effects (Jacobs *et al.*, 1981). In Bourgneuf Bay, as well as in other  
403 temperate wintering sites, the absence of a long-lasting grazing impact could be related to  
404 differences in timing between seagrass growth and consumption by migratory birds. Brent geese  
405 arrive at the end of the seagrass growing season, and depart before the start of the seagrass  
406 reproduction, thus causing little impact on seagrass development (Ganter, 2000). Indeed, Brent  
407 geese consume *Zostera* during seagrass senescent phase, and at a time of the year with a higher  
408 frequency of storms. It means that seagrass biomass, if not consumed by geese, would be  
409 eventually reduced by the decomposition of tissues by microorganisms as well as by  
410 hydrodynamical processes (Jacobs *et al.*, 1981).

411 Our results of BIOENV and CIT evidenced a positive, long-lasting effect of Brent geese on  
412 seagrass ecology, suggesting that the two species extends beyond a simple plant – herbivore  
413 consumptive effect (Heck and Valentine, 2006; Kollars *et al.*, 2017; Valentine and Heck, 1999).  
414 Shaughnessy *et al.* (2021) experimentally demonstrated that Brent goose grazing can stimulate  
415 seagrass flowering and compensatory growth mechanisms via leaf clipping and fertilization by  
416 faecal pellets addition. Previous field experiments in the Wadden Sea showed that Brent geese  
417 could promote *Z. noltei* growth by seed propagation and sediment reworking, thus avoiding plant  
418 burial by sedimentation (Nacken and Reise, 2000). However, this observational evidence



419 remains to be experimentally evaluated to address the question of whether or not seagrass  
420 indicators would continue to show increasing trends in the absence of Brent geese.  
421 Interestingly, the increase in Brent goose population along the 36-years studied was also  
422 associated with an extension of their wintering season by about 2 months since the 1980s. While  
423 the reasons behind a longer wintering season in Bourgneuf Bay remain unknown, the increase in  
424 food supply likely played a role. The analysis of decadal-averaged seagrass cycles using the  
425 Landsat archive did not reveal long-term changes in seagrass phenology (comparing the 1984 –  
426 1993 vs. 2011 – 2020 cycles), but Landsat limited temporal resolution as well as the 10-year  
427 compositing process might have masked variations shorter than one month. The higher temporal  
428 resolution of the S2 time-series is expected to improve further analyses of seagrass dynamics,  
429 thus bringing new insights on Brent goose ecology to assess whether their later departure (in case  
430 it continues to happen) impacts seagrass distribution in Bourgneuf Bay. At larger spatial scales, a  
431 cross-analysis of seagrass dynamics and Brent goose migration patterns could also be performed  
432 over several stopover sites all along the north-western European coastline to get a broader picture  
433 of the Brent goose migration flyway. While the “green wave hypothesis” (i.e., the spring  
434 migration towards breeding sites is triggered by plant growth) has been recently investigated for  
435 *Branta leucopsis* using MODIS time-series of terrestrial vegetation dynamics at continental scale  
436 (Shariatnajafabadi *et al.*, 2014), to our knowledge it remains an open question in the case of  
437 Brent goose *B. b. bernicla*.

438

### 439 **4.3. Conservation and management perspectives**

440 Beyond its regional implications in ecology and biodiversity, the present study aims at  
441 demonstrating the benefits of a synergetic use of two atypical datasets: time-series of satellite

442 derived seagrass EBVs and bird census data. By providing continuous, long-term, and spatially  
443 resolved measurements of seagrass dynamics (Paganini *et al.*, 2016), EO made it possible to get  
444 a consistent picture of biodiversity changes in the (seasonal) habitat of a migratory waterfowl  
445 over four decades. As both *B. b. bernicla* and *Zostera noltei* are protected species, such a  
446 mutualistic plant – herbivore relation has implications for conservation because protection of the  
447 seagrass habitat is beneficial to Brent goose. Then, documenting the ecological status of an  
448 ecosystem/meadow that can guide conservation actions expected to protect seagrass meadows,  
449 herbivorous waterfowl, as well as a variety of marine avifauna (Stillman *et al.*, 2015; Unsworth  
450 and Butterworth, 2021). On the other hand, knowledge about the effect of the seagrass food webs  
451 is fundamental for an efficient management of these habitats (Valentine and Duffy, 2006).

452 As migratory bird, Brent geese are subjected to different biological controls along the whole  
453 flyway, thus interconnecting very distant coastal ecosystems (Newton, 2007). Habitat  
454 degradation or destruction in any point of the flyway can have far reaching consequences in the  
455 Brent goose global population (Newton, 2007). As those long routes usually overpass national  
456 frontiers, the protection of biodiversity calls for coordinated conservation partnerships at  
457 continental and global scales (Navarro *et al.*, 2017).

458 As mentioned earlier, the mutually positive effect of the relationship between seagrass beds and  
459 geese is probably due to the fact that geese start their wintering during the senescence of the  
460 seagrass bed. However, since the wintering period of the geese is getting longer, we can assume  
461 a future potential phenological mismatch of this mutually positive effect. Such a temporal  
462 mismatch between a predator and its trophic resource, often attributed to climate change, has  
463 already been documented in different bird species, such as blue tits, great tits and pied  
464 flycatchers (Burgess *et al.*, 2018).

465 Finally, the conservation of this “seagrass-geese tandem” seems necessary in terms of  
466 conservation management in the coastal area. Like other herbivorous birds, geese can indeed  
467 move to other habitats when their trophic resource becomes scarce. Leaving their original  
468 habitats (*sensu* Martínez-Abraín and Jiménez, 2016), the substitute habitats (*sensu* Martínez-  
469 Abraín and Jiménez, 2016) will be probably the peripheral agricultural fields, which may lead to  
470 conflicts with farmers. The conservation of seagrass beds is therefore necessary so that geese are  
471 not considered in the future as simple pest species creating agricultural damages.

472

## 473 **5. Conclusions**

474 Using a 36-year time-series of seagrass EBVs (namely seagrass extent and meadow-averaged  
475 density) derived from high-resolution satellite remote sensing, we analysed the drivers of  
476 biodiversity changes in an intertidal Natura 2000 and RAMSAR protected area along the French  
477 Atlantic coast. While none of the investigated abiotic factors (solar irradiance, air temperature  
478 and SST, rainfall, river flow, wave height, and sea level) was explanatory of the seagrass  
479 dynamics, we evidenced a relationship between *Zostera noltei* and *B. b. bernicla*, a migratory  
480 herbivorous bird. Our results suggest that a complex and mutualistic plant-herbivore interaction,  
481 extending beyond consumption grazing, is key in the increasing trend observed in both species  
482 over the last decades. In complement to the increase in bird abundance observed since the 1980s,  
483 we observed a phenological change in the goose wintering season. Investigating the reasons of  
484 such phenological change would require to perform a global analysis of Brent goose ecology  
485 along its entire flyway, from the Taymyr Peninsula to Arcachon Bay.

486 As a proof-of-concept, our work demonstrates that the original combination of EO with bird  
487 census data is of interest to develop an improved understanding of seagrass ecology and

488 biodiversity, as well as to assess the efficiency of any protective measures. As migratory species  
489 use resources overpassing administrative and political boundaries, it is noteworthy to remind  
490 here that EO makes it possible to provide seamless measures of seagrass status worldwide.

491

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505

## 506 **Author contribution**

507 *MLZ, PG, LG* and *LB* conceived the ideas and designed methodology; *MLZ, PG, SO, SD* and *LB*  
508 collected the data; *MLZ, PG, SO, BFRD* and *LB* analysed the data; *MLZ* and *PG* led the writing  
509 of the manuscript; *LG, SO, SD, BFRD* and *LB* made edits to the manuscript. All authors  
510 contributed critically to the drafts and gave final approval for publication.

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718 **Supplementary material**

719 **Environmental datasets**

720 **Monthly average of air temperature (AT, in °C) and Cumulative precipitations (PP, in mm)**

721 corresponded to *in situ* measurements acquired at the meteorological station in Saint Sauveur, Ile  
722 d'Yeu (France) (46.69°N – 2.33°W). They corresponded to monthly measurements spanning the  
723 period 1/Jan/1984 – 31/Mar/2021. Meteorological data were downloaded from  
724 [www.infoclimat.fr](http://www.infoclimat.fr).

725 **Sea Surface Temperature (SST, in °C):** The “European North West Shelf/Iberia Biscay Irish  
726 Seas” product produced by the Copernicus Marine Service (CMEMS,  
727 <https://marine.copernicus.eu/>) was used. The product is based on satellite data from infrared and  
728 microwave radiometers. Its spatial resolution was 0.05° for 1/Jan/1984 – 31/Dec/2019 and 0.02°  
729 for 1/Jan/2020 – 31/Mars/2021. The acquired SST product consisted on daily values and was  
730 aggregated as a monthly average for the area comprising the coordinates: 46.8 °N – 47.1°N and  
731 2°W – 2.5°W.

732 **Loire river flow (in m<sup>3</sup> sec<sup>-1</sup>):** It corresponded to the daily average of flux of the Loire River  
733 measured *in situ* at the station located in Monjean-sur-Loire (France) (47.39°N – 0.86°W). This  
734 station is located at approximately 120 km from the Loire River mouth and is the latest fluvial  
735 station, i.e., it is not affected by tides and, then, it provides information about freshwater inputs  
736 to the bay. Data were downloaded from the *Institut Français de Recherche pour l'Exploitation de*  
737 *la Mer* (FREMER) portal ([http://www.ifremer.fr/co-](http://www.ifremer.fr/co-en/eulerianNetwork?contextId=386&lang=en)  
738 [en/eulerianNetwork?contextId=386&lang=en](http://www.ifremer.fr/co-en/eulerianNetwork?contextId=386&lang=en)) from January/1984 – March/2021. From daily  
739 river flow measurements, monthly averages were computed.

740 **Surface solar radiation downwards (SSRD, in  $\text{J m}^{-2}$ ) and Significant height of combined**  
741 **wind waves and swell (Height waves, in m):** They were produced as a part of the reanalysis  
742 dataset of the fifth generation of the European Centre for Medium-Range Weather Forecasts  
743 (ERA5), provided by the Copernicus Climate Change Service within the Climate Data Store  
744 (CDS) (<https://cds.climate.copernicus.eu/cdsapp#!/search?type=dataset>). SSRD corresponds to  
745 the amount of total solar radiation (including direct and diffuse components) that reaches the  
746 horizontal Earth surface. Height waves represented the surface ocean and sea waves produced by  
747 wind and swell. Hourly data from Jan/1984 – Mar/2021 were downloaded in a spatial resolution  
748 of  $0.25^\circ \times 0.25^\circ$  for SSRD and  $0.5^\circ \times 0.5^\circ$  for height waves, and aggregated as the monthly  
749 average of the area comprising the coordinates:  $46.5^\circ\text{N} - 47.5^\circ\text{N}$  and  $2^\circ\text{W} - 3^\circ\text{W}$ .

750 **Sea level (in m):** Hourly data were acquired from the *Service hydrographique et*  
751 *océanographique de la Marine* (SHOM). They corresponded to measurements at the *in situ*  
752 station closest to the seagrass meadow “L’Herbaudière” ( $47.025^\circ\text{N} - 2.299^\circ\text{W}$ ). Missed data  
753 were filled out either with measurements at the station “Pointe Saint Gildas” ( $47.140^\circ\text{N} -$   
754  $2.246^\circ\text{W}$ ) or modelled data. Hourly sea level data were monthly averaged.