





RESEARCH ARTICLE

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

Maria Laura Zoffoli¹ , Pierre Gernez² , Simon Oiry² , Laurent Godet³, Sébastien Dalloyau⁴, Bede Ffinian Rowe Davies²  & Laurent Barillé²

¹Consiglio Nazionale delle Ricerche, Istituto di Scienze Marine (CNR-ISMAR), 00133, Rome, Italy

²Nantes Université, Institut des Substances et Organismes de la Mer, ISOMer, UR 2160, F-44000, Nantes, France

³CNRS, Nantes Université, UMR LETG, B.P. 81223, 44312, Nantes, France

⁴LPO France, Fonderies Royales, 8 rue du Dr Pujos, 17305, Rochefort, France

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Correspondence

Maria Laura Zoffoli, Consiglio Nazionale delle Ricerche, Istituto di Scienze Marine (CNR-ISMAR), 00133 Rome, Italy.

Tel: +39 06 45488213;

Fax: +39 06 45488291;

E-mail: laura.zoffoli@artov.ismar.cnr.it

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Introduction

Seagrasses are key components of the coastal ocean. As ecosystem engineers (*sensu* Jones et al., 1994), seagrasses have a structuring role in sedimentation (Bos et al., 2007), tend to stabilize benthic communities and food webs (Jankowska et al., 2019), and are attractive feeding grounds for fishes (Spalding et al., 2003), birds (Balsby et al., 2017; Robin

Abstract

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

et al., 2015) as well as marine mammals (de Iongh et al., 1995; Sheppard et al., 2007) and sea turtles (Taquet et al., 2006). Seagrass beds provide important ecosystem services to humankind including carbon sequestration, oxygen production, and coastal protection (Nordlund et al., 2016).

The ecological relevance and threats to which seagrass meadows are subjected to boosted ecosystem conservation managers to include seagrass in priority lists for preservation

and observation programmes. Many studies have proposed maps of coverage and spatial dynamics of seagrass beds (e.g. Agostini et al., 2003; Duarte & Sand-jensen, 1990; Godet et al., 2008; Robbins, 1997). In particular, seagrass cover and composition are essential oceanic variables (EOVs) for the monitoring of habitat extent and ecosystem health (Miloslavich et al., 2018), and seagrass taxonomic diversity, species distribution, population abundance, and phenology have been recognized as essential biodiversity variables (EBVs, Pereira et al., 2013). A better understanding of seagrass ecosystem functioning including environmental drivers and trophic interactions is, therefore, required to mitigate anthropic impacts and implement biodiversity conservation (Valentine & Duffy, 2006).

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

Seagrass–herbivores interactions can be investigated at several scales to provide different types of ecological information (Jacobs et al., 1981). One type of information relates to the direct effect of grazing on the individual plant, *i.e.* the immediate reduction of vegetal biomass by herbivore consumption (Ganter, 2000; Sato et al., 2020). Another type of information concerns the seagrass–herbivores relationship at habitat/population level over larger time scales. This interaction is much more complex to investigate because it depends on grazing magnitude and frequency, on seagrass physiological responses with long-term effects (e.g. compensatory growth mechanisms, investment in sexual reproduction), and indirect mechanisms associated with herbivory (e.g. soil fertilization with faeces, seed propagation, relief of competition by other vegetal species) (Shaughnessy et al., 2021; Valentine & Duffy, 2006).

Interestingly, most herbivorous birds feeding on seagrass are migratory birds. Herbivory by migratory animals is a particular case of plant–herbivore interaction. On the one hand, consumers exert pressure on the food resource only during a certain period of time (e.g., a few months).

On the other hand, the population of migratory herbivores is affected by factors related to a large geographical range that includes wintering, stop-over, and breeding sites (Newton, 2007). Thus, both the timing of seasonal cycles of grazers' population and food resources, as well as regional components that drive herbivore population are fundamental factors to understand their complex relationship in a specific site.

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

Several works already documented the crucial role of megaherbivores (waterfowls, turtles, and dugongs) on seagrass ecosystem structure, biomass, and primary production (Scott et al., 2018). Also, there are numerous examples of the potential of Earth Observation (EO) to study seagrass EBVs worldwide (Barillé et al., 2010; Calleja et al., 2017; El-Hacen et al., 2020; Zoffoli et al., 2020). However, to our knowledge, combined analyses of long-term dynamics in herbivorous population and remotely-sensed seagrass distribution have never been attempted. This study focused on Bourgneuf Bay (France, Fig. 1C), an important Brent goose wintering site (Valéry & Schricke, 2013) where satellite observations revealed an increasing trend in both seagrass density and areal extent since the 1980s (Zoffoli et al., 2021). Our objective was to investigate, for the first time, the relationship between remotely-sensed decadal changes in seagrass habitat and bird population. More generally, our work seeks at demonstrating the potential of high-resolution satellite remote sensing for the conservation and ecology of two intertwined and protected species.

Materials and Methods

Remote sensing of seagrass essential biodiversity variables

Along the French Atlantic coast, Bourgneuf Bay is a macrotidal bay hosting a large intertidal seagrass meadow

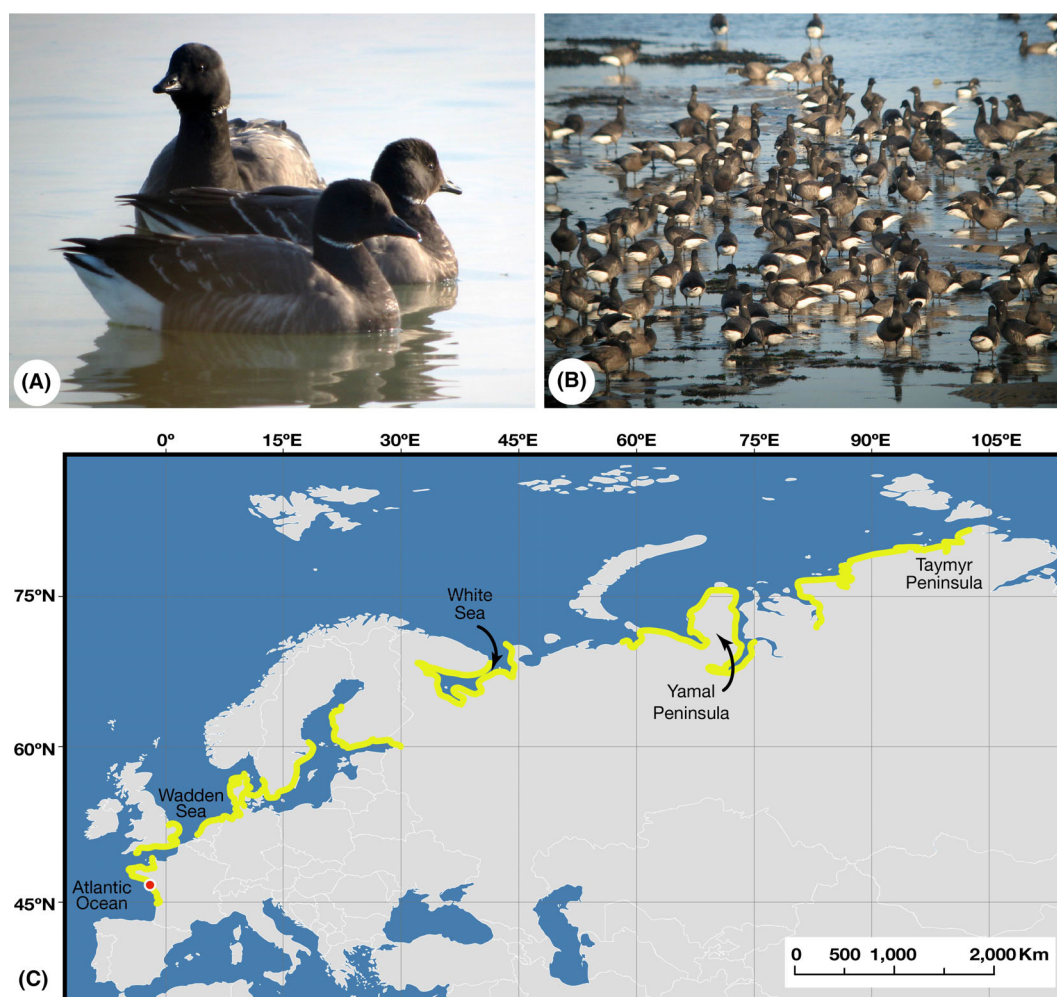


Figure 1. *Branta b. bernicla* individuals (A–B) and its migration flyway (C). The main breeding, stopover and wintering sites are highlighted in yellow (adapted from (Ebbinge et al., 2013)). The red dot shows the location of Bourgneuf Bay (France), a wintering site where seagrass spatial distribution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

dominated by *Zostera noltei*, which is part of a Natura 2000 protected area. At this latitude ($\sim 47^{\circ}\text{N}$), seagrass displays a seasonal cycle with a late summer peak (Zoffoli et al., 2020). In previous work, several seagrass EBVs were computed from long-term high-resolution remote sensing over this site (Zoffoli et al., 2021). Briefly, a multi-mission satellite time series was compiled from Landsat, SPOT, and Sentinel-2 acquisitions. Images were selected for every summer from 1985 to 2020. Maps of seagrass per cent cover (Fig. 2) were computed from the normalised difference vegetation index (NDVI) with an uncertainty of about 14% (Zoffoli et al., 2020), thus making it possible to measure several seagrass indicators at the ecosystem scale. Because seagrass data were missing during 7 years in the initial dataset of Zoffoli et al. (2021), we completed the time series using additional Landsat and SPOT images in 1989, 1992, 1994,

1999, 2000, 2007 and 2014 in order to get a continuous time-series. The new images were slightly suboptimal in terms of acquisition time (*i.e.* they were marginally out-of-time compared to the date of the seagrass summer peak) or cloud cover (and in that case seagrass quantification has been made by a combination of two images acquired during the same summer). Though these data might be subjected to higher uncertainties, they still remained amongst the range of variability observed during the 29 other years and can be consistently used for time-series analysis.

In the present study, we used the following seagrass data: the meadow-averaged seagrass density as an indicator of seagrass above-ground biomass, and two proxies of habitat extent (A20 and A50) corresponding to the surface of the whole and dense seagrass meadow, defined as the area where % cover is higher than 20% or 50%,

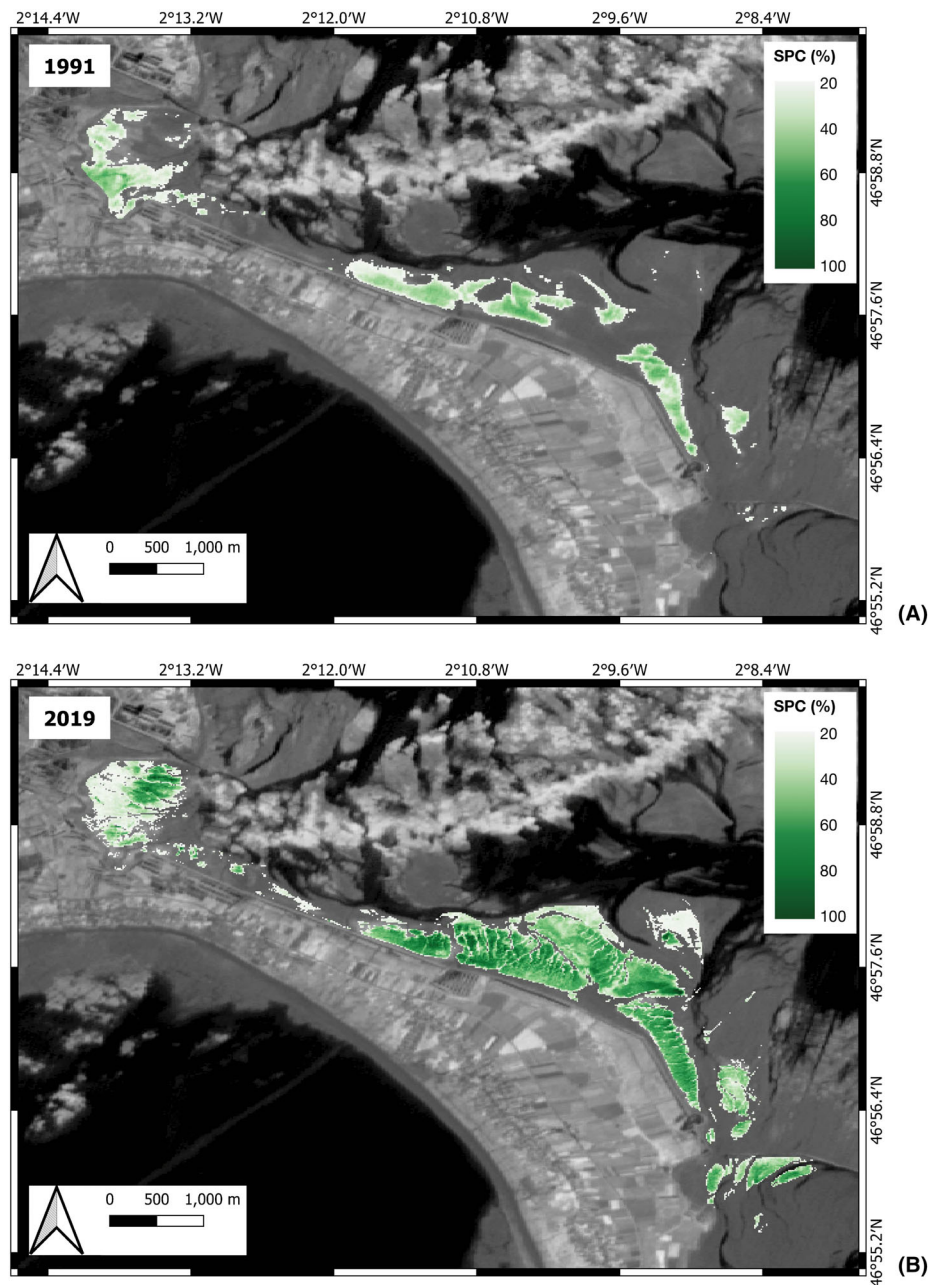


Figure 2. Examples of satellite-derived seagrass map in Bourgneuf Bay, showing seagrass % cover (SPC) at high-resolution over the whole meadow: (A) SPOT-2 image on 28 August 1991; (B) Sentinel-2 image on 16 September 2019. The complete series of SPC maps from 1985 to 2020 is shown in Zoffoli et al. (2021).

respectively. Seagrass density was computed as the mean % cover over the whole meadow. A 20% threshold in seagrass cover was applied to reduce mapping uncertainties (Dolch et al., 2017; Zoffoli et al., 2021). Interestingly, this value is also biologically meaningful for Brent goose as it is close to the per cent cover of 15% indicated as a ‘giving-up’ density below which seagrass leaf cover is not profitable for feeding (Jacobs et al., 1981; Percival & Evans, 1997).

The Landsat time series was also used to detect a possible long-term shift in seagrass phenology over Bourgneuf Bay. A total number of 238 cloud-free images acquired during low tide were selected from 1984 to 2020. Temporal changes in NDVI were used to characterize the seagrass seasonal cycle, as in Zoffoli et al. (2020). Due to limitations in temporal resolution, it was not possible to measure seagrass seasonal variability every year.

Monthly-averaged composite annual cycles were then reconstructed over a 10-year period, and compared between the start (1984–1993) and end (2011–2020) of the Landsat time series.

Brent goose data

In this work, we used two Brent goose datasets in France: one for the goose-size population at Bourgneuf Bay and the other one at the national level. For Bourgneuf Bay, we used monthly records of the Brent goose size population from September to April (period later referred as ‘goose season’), from 1976 to 2021. Bird counts were performed during high tide in 6 different sighting sites within Bourgneuf Bay from the Noirmoutier Island to the Port du Collet. For each goose season, a log-normal model was fitted to the monthly bird numbers ($\log(\text{monthly bird counts}) = f(\text{time})$), with P -value < 0.05 for all years). The date of the maximal goose number was then computed from the fitted curve. The date of arrival and departure was defined as the days when the goose number corresponded to 50% of the seasonal maximum (Valéry & Schricke, 2013).

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

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

Environmental datasets

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

Statistical analyses

Two methods were used to identify the most important factors (environmental and goose abundance) influencing seagrass variables (Density, A20 and A50): the BIOENV

method (Clarke & Ainsworth, 1993) and the Conditional Interference Tree (CIT; Hothorn et al., 2006). The BIOENV method identifies the best subset of environmental variables with the Euclidian distance of scaled environmental variables having the maximum Pearson correlation with the similarity matrix calculated from seagrass parameters. The CIT is a random forest approach used to assess the relative importance of multiple explanatory variables with respect to a single response variable. With the BIOENV method, explanatory variables that are correlated must be removed whilst the CIT is not affected by multicollinearity. The CIT also allows for non-linear relationships unlike BIOENV, which only performs linear relations. BIOENV was run on PRIMER 7 (Clarke & Gorley, 2006) and the CIT analysis with R (Party Kit, Hothorn & Zeileis, 2015). The winter, spring and summer averages of all abiotic parameters were tested using both methods. The tested goose data corresponded to the maximum number recorded during the goose season preceding the seagrass peak (*i.e.* September–April).

The association between Brent goose monthly counts and seagrass density was assessed using Generalized Linear Mixed Effect Models (GLMM). Brent goose counts were modelled as a function of month (October to March), normalized seagrass density (N_i , Eq. 1), year as a random factor, and using a temporal autocorrelation structure based on year. Modelling was performed using the “glmmTMB” package in the R programming language (Brooks et al., 2022; Chadsuthi et al., 2022; R Core Team, 2022) assuming that Brent goose counts followed a Poisson distribution.

$$N_i = \frac{S_i - \mu_S}{\sigma_S} \quad (1)$$

where S_i corresponds to seagrass density in each individual year, μ_S to the mean, and σ_S to its standard deviation. Sample *vs.* fitted residuals, quartile-quartile and autocorrelation of temporally sequential samples were visually assessed to evaluate model assumptions. Seagrass A20 and A50 were likewise modelled.

Results

Explanatory variables for seagrass variability

The BIOENV analysis indicated that the Pearson correlation between seagrass EBVs and the similarity matrices of the investigated factors was maximized at $r = 0.33$ (P -value < 0.05) for maximum goose abundance, suggesting that amongst all the seagrass drivers tested, it was the main factor contributing to seagrass variability. This was confirmed by the result of the CIT model, which showed

that seagrass variability was significantly associated in a first order with maximum goose abundance (P -value <0.01), and in a second order, to average Wave Height in spring (P -value <0.01), suggesting that a higher number of wintering geese promoted a larger and denser seagrass at the end of the following summer.

Mutual interactions between seagrass and Brent geese

Seagrass and Brent goose counts presented increasing trajectories from 1985 to 2020 (Fig. 3). Monthly goose counts were significantly related to all seagrass parameters (GLMM, P -value <0.001). Interestingly, the relationship between monthly goose counts and seagrass density was positive from October to January with the strongest relationships in October and November as evidenced by the steepest slopes in the modelling response (Fig. 4): higher seagrass biomass in summer attracted a higher number of birds during the subsequent goose wintering season. On the contrary, the relationship was negative in March when most of the geese already started their way back towards the Northern breeding sites. GLMM results for seagrass density were similar to the ones obtained for the other seagrass parameters analysed such as A20 and A50 (figures not shown).

Seasonal variability in seagrass and Brent geese

The seagrass phenology did not change over the past 40 years. The averaged seasonal NDVI cycle was the same during the first (1984–1993) and last decade (2011–2020) of the studied time series (Fig. 5). At this latitude, seagrass biomass increases during spring, peaks at the end of

summer (late August/early September), and decreases during autumn and winter. Whilst there was no change in the timing of the seagrass seasonal cycle, there was a difference in its amplitude. NDVI reached a higher peak during the 2011–2020 decade compared to the 1984–1993 decade, consistently with the afore-mentioned long-term increase in seagrass density and extent. Interestingly, a phenological shift in the Brent goose season occurred from 1984 to 2020. Whereas most of the wintering population generally used to arrive in October and depart before the end of March, during the last decade an increasing number of geese have been spotted as early as September and as late as April (Fig. 5). On average, the date of the maximum goose counts shifted from January to November between the first and last considered decades.

The analysis of the whole Brent goose time series from 1976 to 2020 further confirmed the phenological shift of the goose wintering season. According to the log-normal model, the date of maximum goose counts moved about 19 days earlier, from 12 January 1976 to 24 December 2020 (Fig. 6). This trend was accompanied by an extension of the whole wintering season of at least 2 months, with an advance of about 56 days in the date of arrival (from 12 November to 17 September), and a delay of about 17 days in the date of departure (from 16 March to 2 April).

Long-term variability in Brent goose regional, national and global population

The global Brent goose population showed an increasing trend since 1976, peaking at approximately 329,000 individuals in 1992, followed by a reduction and stabilization of around 220,000 individuals since the 2000 s (Fig. 7; Ebbsing et al., 2013). The number of Brent geese wintering in France

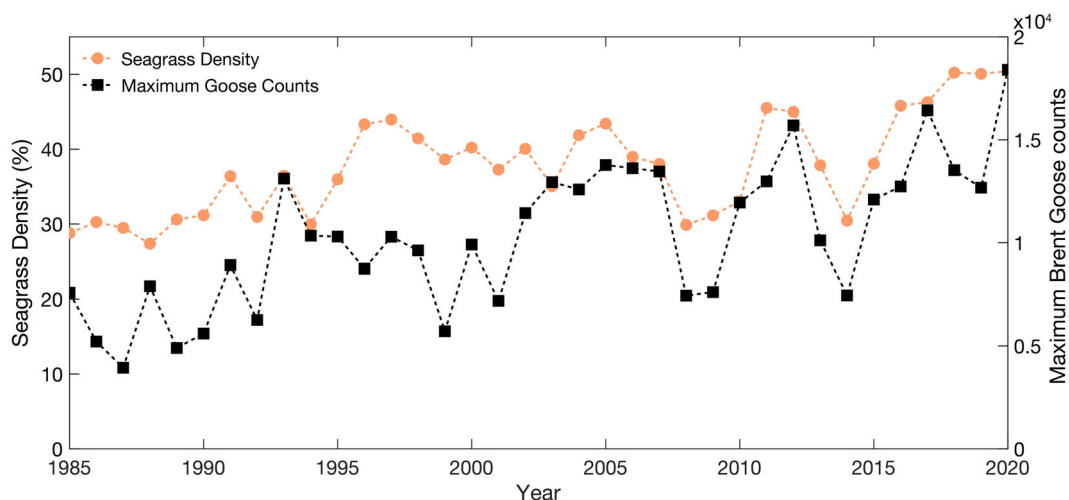


Figure 3. Time-series of variables from 1985 to 2020: meadow-averaged seagrass density (in %) (orange dots) represented in the left y-axis, and maximum Brent goose counts (black squares) in the right y axis.

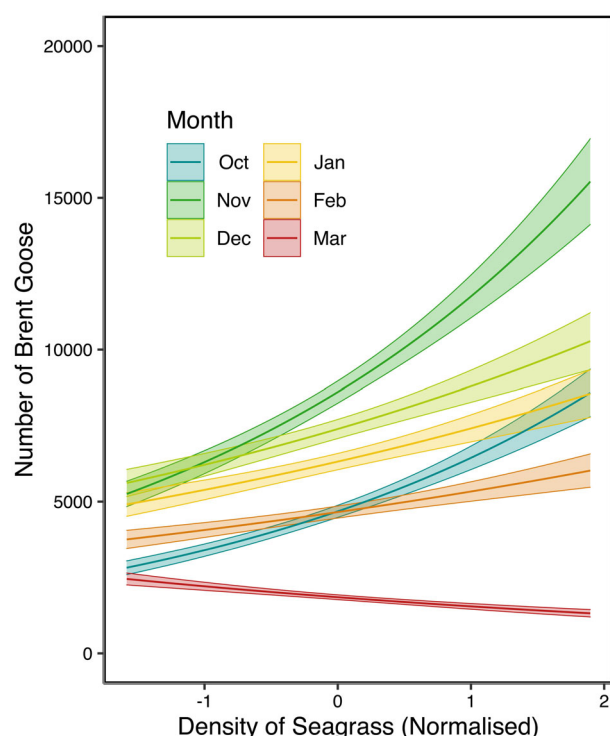


Figure 4. Modelled change in Brent goose counts with normalized seagrass density across months. Lines and shaded areas show GLMM model estimates and standard errors.

and Bourgneuf Bay also increased up to the 1990s, but contrary to the world population, continued to increase afterwards. The French population thus regularly increased up to the early 2010s, stabilizing at around 142,000 individuals over the past decade. The French population thus now represents about 60% of the global goose population. The population in Bourgneuf Bay also displayed an overall increasing trend, reaching a total number of geese fluctuating around 11,500 individuals over the last years. Compared to the French national population, the population in Bourgneuf Bay displayed a high degree of interannual variability, with drastic decreases in 1999, 2001, 2008, 2009 and 2014. Interestingly, the years of strong declines in Brent goose abundance coincided with significant reductions in seagrass surface area and meadow-averaged density, suggesting that a reduction of food supply prompted the migratory birds to overwinter in other sites in France (Fig. 7).

Discussion

Data requirements and challenges to interpret seagrass trajectory

Whilst catastrophic seagrass loss has been globally documented (Green et al., 2021; Waycott et al., 2009) a recent

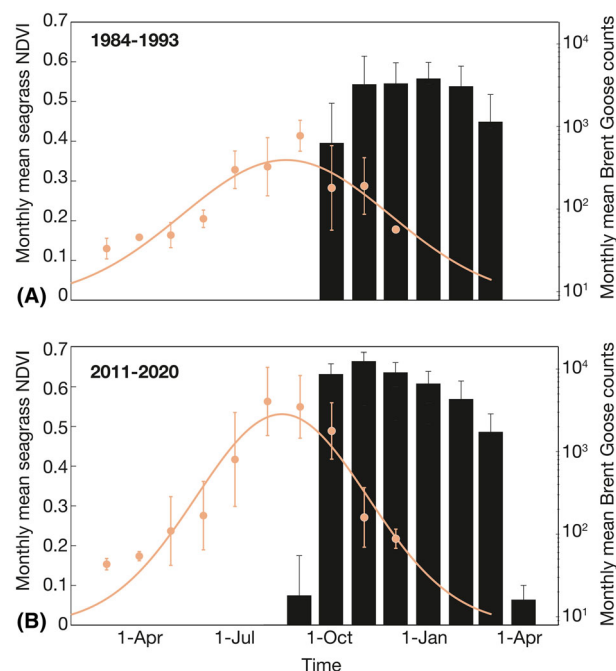


Figure 5. Monthly mean NDVI representing seagrass seasonal cycle (orange circles, left axis), and monthly mean Brent goose counts (black bars, right axis in log-scale). Data correspond to a 10-year average during two time periods: (A) 1984–1993, and (B) 2011–2020. Error bars correspond to standard deviation.

increase in the status of intertidal meadows dominated by *Z. noltei* was reported in several European sites (de los Santos et al., 2019) including Bourgneuf Bay (Zoffoli et al., 2021). The knowledge of seagrass status and its ecological drivers is required to develop predictive models and optimize conservation strategies of these protected habitats, but the determination of such drivers is extremely challenging due to the lack of both seagrass and environmental measurements (Unsworth et al., 2019). The status of the seagrass meadow at the time of its annual maximum corresponds to an ecological response to environmental drivers that acted over the previous months. Thus, the effect of environmental factors should be analysed taking into account the conditions experienced by seagrass during the whole growing season. For that purpose, environmental observations have to be performed at high temporal resolution. Here, the investigated environmental datasets were either acquired using EO, autonomous systems such as meteorological stations and tide gauges or resulting from modelling. This highlights the importance of maintaining coordinated continuous monitoring programs (e.g. satellite missions, *in situ* monitoring networks, autonomous platforms; Papathanasopoulou et al., 2019) collecting data on both EBV and abiotic factors at large spatial and temporal scales to develop an improved understanding of biodiversity and

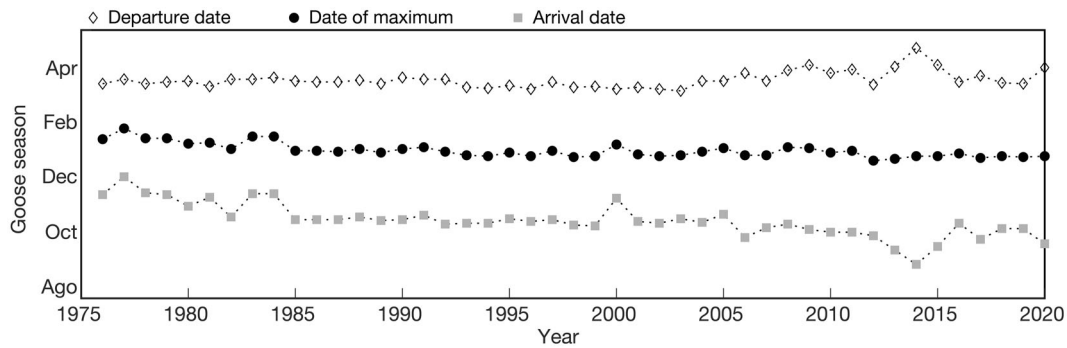


Figure 6. Timing of modelled goose season in Bourgneuf Bay from 1976 to 2020, showing the dates of departure (white diamonds), maximum (black circles) and arrival (grey squares).

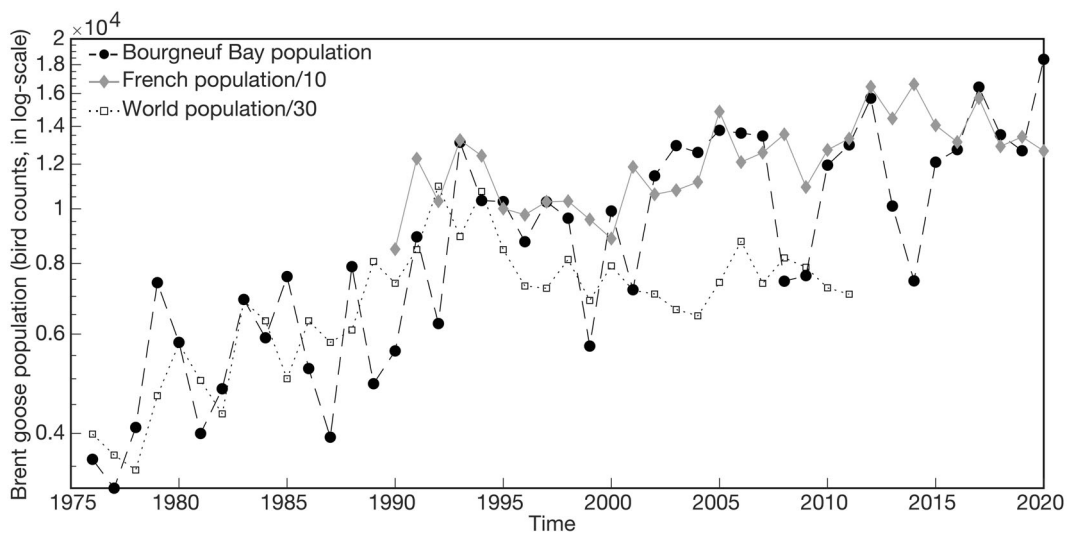


Figure 7. Brent goose population in Bourgneuf Bay from 1976 to 2020 (black circles), in France from 1990 to 2020 (grey diamonds), and in the world from 1976 to 2011 (white squares). For comparative purposes, the French population was divided by 10, and the world population was divided by 30. The vertical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

ecosystem functioning (Navarro et al., 2017; Paganini et al., 2016). Here, monthly data of solar irradiance, air temperature and SST, rainfalls, river flow, wave height and sea level were available. These parameters, however, were not the main explanatory variables for the seagrass dynamics observed in Bourgneuf Bay from 1985 to 2020. Similarly, Lebrasse et al. (2022) did not find any significant relationship between seagrass long-term trends and climatic factors in a subtidal meadow in Florida. Other environmental factors such as sedimentation rate, nutrient concentration, and sediment composition have been pointed out as important seagrass drivers (Guerrero-Meseguer et al., 2021; Qin et al., 2021; Soissons et al., 2018); they were not considered here because of the absence of available long datasets at the required temporal resolution.

Whilst the investigated abiotic factors were not explanatory of seagrass variability in Bourgneuf Bay along the whole time series, some punctual synchronous events are noteworthy. This is the case of a drastic seagrass decline in 2003, which coincided with an intense summer heatwave in Europe (Garcia-Herrera et al., 2010). The low seagrass status observed in 2010 occurred several months after the so-called Xynthia storm, which resulted in dramatic coastal erosion and flooding in Bourgneuf Bay and nearby towns (Chadenas et al., 2014). The limited seagrass extent during the 1980 s and early 1990 s also coincided with a higher occurrence of frost days during the preceding winter whose influence on intertidal seagrass has been previously documented in northern Brittany (Fournier et al., 2006). Due to the absence of correlation between abiotic factors and seagrass trajectory, examples of the synchronous decline in

seagrass and environmental parameters are however to be interpreted with caution, all the more as it is generally easier to highlight coincident abrupt losses rather than to identify other types of changes. Nevertheless, the projected frequency increase of extreme climatic events such as heat-waves, cold waves and droughts in the forthcoming decades (IPCC, 2021) calls for continuous monitoring of EBVs and environmental drivers. Unlike the investigated abiotic data, Brent goose abundance was significantly related to seagrass EBVs. Long-term datasets of waterbirds represent valuable indicators of the conservation status of coastal habitats (Brandis et al., 2018; Ogden et al., 2014). In previous studies, the lack of seagrass time series was highlighted as a limitation to interpret the long-term dynamics in the Brent goose population (Valéry & Schricke, 2013), as well as to document plant–herbivore relationships over large temporal scales (Balsby et al., 2017). In this regard, our work demonstrates that EO makes it possible to further investigate reciprocal interactions between *Z. noltei* and *B. b. bernicla* at the scale of a whole seagrass meadow over several decades.

Ecological interactions between Brent goose and seagrass

One of the most striking results of the present study was that long-term changes in the size of the Brent goose population were related to seagrass EBVs. On the one hand, the positive association between both the seagrass meadow extent and density and goose counts during the subsequent wintering season has a straightforward bottom-up interpretation: a higher seagrass biomass (*i.e.* higher food supply) attracts a higher number of consumers (Ganter, 2000). Furthermore, the results from the GLMM demonstrated that the relationship between the goose population and seagrass was the strongest shortly after the time of the seagrass maximum, also corresponding to the month of the maximal goose counts (October and/or November). On the other hand, grazing pressure could be expected to negatively impact the seagrass population (Sato et al., 2020). As a matter of fact, the influence of grazing by birds on seagrass can be divided into short- and long-term effects (Jacobs et al., 1981). In Bourgneuf Bay, as well as in other temperate wintering sites, the absence of a long-lasting grazing impact could be related to differences in timing between seagrass growth and consumption by migratory birds. Brent geese arrive at the end of the seagrass growing season, and depart before the start of the seagrass reproduction, thus causing little impact on seagrass development (Ganter, 2000). Indeed, Brent geese consume *Zostera* during the seagrass senescent phase, and at a time of the year with a higher frequency of storms. It means that seagrass biomass, if not consumed by geese, would be eventually reduced by

the decomposition of tissues by microorganisms as well as by hydrodynamical processes (Jacobs et al., 1981).

Our results of BIOENV and CIT evidenced a positive, long-lasting effect of Brent geese on seagrass ecology, suggesting that the two species extend beyond a simple plant–herbivore consumptive effect (Heck & Valentine, 2006; Kollars et al., 2017; Valentine & Heck, 1999). Shaughnessy et al. (2021) experimentally demonstrated that Brent goose grazing can stimulate seagrass flowering and compensatory growth mechanisms *via* leaf clipping and fertilization by faecal pellets addition. Previous field experiments in the Wadden Sea showed that Brent geese could promote *Z. noltei* growth by seed propagation and sediment reworking, thus avoiding plant burial by sedimentation (Nacken & Reise, 2000). However, this observational evidence remains to be experimentally evaluated to address the question of whether or not seagrass indicators would continue to show increasing trends in the absence of Brent geese.

Interestingly, the increase in Brent goose population over the 36 years studied was also associated with an extension of their wintering season by about 2 months since the 1980s. Whilst the reasons behind a longer wintering season in Bourgneuf Bay remain unknown, the increase in food supply likely played a role. The analysis of decadal-averaged seagrass cycles using the Landsat archive did not reveal long-term changes in seagrass phenology (comparing the 1984–1993 vs. 2011–2020 cycles), but Landsat limited temporal resolution, as well as the 10-year compositing process, might have masked variations shorter than 1 month. The higher temporal resolution of the S2 time series is expected to improve further analyses of seagrass dynamics, thus bringing new insights on Brent goose ecology to assess whether their later departure (in case it continues to happen) impacts seagrass distribution in Bourgneuf Bay. At larger spatial scales, a cross-analysis of seagrass dynamics and Brent goose migration patterns could also be performed over several stop-over sites all along the north-western European coastline to get a broader picture of the Brent goose migration flyway. Whilst the ‘green wave hypothesis’ (*i.e.* the spring migration towards breeding sites is triggered by plant growth) has been recently investigated for *Branta leucopsis* using MODIS time-series of terrestrial vegetation dynamics at continental scale (Shariatnajaabadi et al., 2014), to our knowledge it remains an open question in the case of Brent goose *B. b. bernicla*.

Conservation and management perspectives

Beyond its regional implications in ecology and biodiversity, the present study aims at demonstrating the benefits of a synergetic use of two atypical datasets: time series of satellite-derived seagrass EBVs and bird census data. By

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

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

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

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

Conclusions

Using a 36-year time-series of seagrass EBVs (namely seagrass extent and meadow-averaged density) derived from high-resolution satellite remote sensing, we analysed the

drivers of biodiversity changes in an intertidal Natura 2000 and RAMSAR protected area along the French Atlantic coast. Whilst none of the investigated abiotic factors (solar irradiance, air temperature and SST, rainfall, river flow, wave height and sea level) was explanatory of the seagrass dynamics, we evidenced a relationship between *Zostera noltei* and *B. b. bernicla*, a migratory herbivorous bird. Our results suggest that a complex and mutualistic plant–herbivore interaction, extending beyond consumption grazing, is key in the increasing trend observed in both species over the last decades. In complement to the increase in bird abundance observed since the 1980s, we observed a phenological change in the goose wintering season. Investigating the reasons for such phenological change would require to perform a global analysis of Brent goose ecology along its entire flyway, from the Taymyr Peninsula to Arcachon Bay.

As a proof-of-concept, our work demonstrates that the original combination of EO with bird census data is of interest to develop an improved understanding of seagrass ecology and biodiversity, as well as to assess the efficiency of any protective measures. As migratory species use resources overpassing administrative and political boundaries, it is noteworthy to remind here that EO makes it possible to provide seamless measures of seagrass status worldwide.

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Author contributions

MLZ, PG, LG and LB conceived the ideas and designed methodology; MLZ, PG, SO, SD and LB collected the data; MLZ, PG, SO, BFRD and LB analysed the data;

MLZ and PG led the writing of the manuscript; LG, SO, SD, BFRD and LB made edits to the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References

- Agostini, S., Capiomont, A., Marchand, B. & Pergent, G. (2003) Distribution and estimation of basal area coverage of subtidal seagrass meadows in a Mediterranean coastal lagoon. *Estuarine, Coastal and Shelf Science*, **56**, 1021–1028. [https://doi.org/10.1016/S0272-7714\(02\)00327-X](https://doi.org/10.1016/S0272-7714(02)00327-X)
- Balsby, T.J.S., Clausen, P., Krause-Jensen, D., Carstensen, J. & Madsen, J. (2017) Long-term patterns of eelgrass (*Zostera marina*) occurrence and associated herbivorous waterbirds in a danish coastal inlet. *Frontiers in Marine Science*, **3**, 285. <https://doi.org/10.3389/FMARS.2016.00285>
- Barillé, L., Robin, M., Harin, N., Bargain, A. & Launeau, P. (2010) Increase in seagrass distribution at Bourgneuf Bay (France) detected by spatial remote sensing. *Aquatic Botany*, **92**, 185–194. <https://doi.org/10.1016/j.aquabot.2009.11.006>
- Bos, A.R., Bouma, T.J., de Kort, G.L.J. & van Katwijk, M.M. (2007) Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. *Estuarine, Coastal and Shelf Science*, **74**, 344–348. <https://doi.org/10.1016/j.ecss.2007.04.006>
- Brandis, K.J., Bino, G., Spencer, J.A., Ramp, D. & Kingsford, R.T. (2018) Decline in colonial waterbird breeding highlights loss of Ramsar wetland function. *Biological Conservation*, **225**, 22–30. <https://doi.org/10.1016/j.biocon.2018.06.022>
- Brooks, M., Bolker, B., Kristensen, K., Maechler, M., Magnusson, A., Skaug, H. et al. 2022. glmmTMB: generalized linear mixed models using template model builder. <https://github.com/glmmTMB/glmmTMB>
- Burgess, M.D., Smith, K.W., Evans, K.L., Leech, D., Pearce-Higgins, J.W., Branston, C.J. et al. (2018) Tritrophic phenological change-mismatch in space and time. *Nature Ecology and Evolution*, **2**, 970–975. <https://doi.org/10.1038/s41559-018-0543-1>
- Calleja, F., Galván, C., Silió-Calzada, A., Juanes, J.A. & Ondiviela, B. (2017) Long-term analysis of *Zostera noltei*: a retrospective approach for understanding seagrasses' dynamics. *Marine Environmental Research*, **130**, 93–105. <https://doi.org/10.1016/j.marenvres.2017.07.017>
- Chadenas, C., Creach, A. & Mercier, D. (2014) The impact of storm Xynthia in 2010 on coastal flood prevention policy in France. *Journal of Coastal Conservation*, **18**, 529–538. <https://doi.org/10.1007/s11852-013-0299-3>
- Chadsuthi, S., Chalvet-Monfray, K., Geawduanglek, S., Wongnak, P. & Cappelle, J. (2022) Spatial-temporal patterns and risk factors for human leptospirosis in Thailand, 2012–2018. *Scientific Reports*, **12**, 1–11. <https://doi.org/10.1038/s41598-022-09079-y>
- Clarke, K.R. & Ainsworth, M. (1993) A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, **92**, 205–219. <https://doi.org/10.3354/meps092205>
- Clarke, K.R. and Gorley, R.N. (2006). PRIMER v6: User Manual/Tutorial (Plymouth Routines in Multivariate Ecological Research). PRIMER-E, Plymouth.
- Dalloyau, S. & Robin, M. (2013) *Distribution des Bernaches cravants à ventre sombre (Branta bernicla bernicla) et disponibilité alimentaire des herbiers à Zostère naine (Zostera noltei): vers une caractérisation de la qualité des habitats intertidaux des Pertuis Charentais*. Rochefort: LPO, p. 77.
- de Iongh, H.H., Wenno, B.J. & Meelis, E. (1995) Seagrass distribution and seasonal biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. *Aquatic Botany*, **50**, 1–19. [https://doi.org/10.1016/0304-3770\(94\)00438-R](https://doi.org/10.1016/0304-3770(94)00438-R)
- de Los Santos, C.B., Krause-Jensen, D., Alcoverro, T., Marbà, N., Duarte, C.M., van Katwijk, M.M. et al. (2019) Recent trend reversal for declining European seagrass meadows. *Nature Communications*, **10**, 1–8. <https://doi.org/10.1038/s41467-019-11340-4>
- Den Hartog, C. (1987) 'Wasting disease' and other dynamic phenomena in *Zostera* beds. *Aquatic Botany*, **27**(1), 3–14. [https://doi.org/10.1016/0304-3770\(87\)90082-9](https://doi.org/10.1016/0304-3770(87)90082-9)
- Desmots, D., Fritz, H., Cornulier, T. & Maheo, R. (2009) Rise in human activities on the mudflats and Brent geese (*Branta bernicla*) wintering distribution in relation to *Zostera* spp. beds: a 30-year study. *Journal of Ornithology*, **150**, 733–742. <https://doi.org/10.1007/s10336-009-0391-5>
- Dolch, T., Folmer, E.O., Frederiksen, M.S., Herlyn, M., van Katwijk, M.M., Kolbe, K. et al. (2017) *Wadden Sea Quality Status Report*. Wilhelmshaven: Common Wadden Sea Secretariat.
- Duarte, C.M. & Sand-jensen, K. (1990) Seagrass colonization: patch formation and patch growth in *Cymodocea nodosa*. *Marine Ecology Progress Series*, **65**, 193–200.
- Dunic, J.C., Brown, C.J., Connolly, R.M., Turschwell, M.P. & Côté, I.M. (2021) Long-term declines and recovery of meadow area across the world's seagrass bioregions. *Global Change Biology*, **27**, 4096–4109. <https://doi.org/10.1111/gcb.15684>
- Ebbinge, B.S., Heesterbeek, J.A., Ens, B.J. & Goedhart, P.W. (2002) Density dependent population limitation in dark-bellied Brent geese *Branta b. bernicla*. *Avian Science*, **2**, 63–75.
- Ebbinge, B.S., Blew, J., Clausen, P., Günther, K., Hall, C., Holt, C. et al. (2013) Population development and breeding success of dark-bellied Brent geese *Branta b. bernicla* from 1991–2011. *Wildf*, **3**, 74–89.
- El-Hacen, E.H.M., Sidi Cheikh, M.A., Bouma, T.J., Olff, H. & Piersma, T. (2020) Long-term changes in seagrass and benthos at banc d'Arguin, Mauritania, the premier intertidal system along the East Atlantic flyway. *Global Ecology and Conservation*, **24**, e01364. <https://doi.org/10.1016/j.gecco.2020.e01364>

- Fournier, J., Dubreuil, V., Olivier, F. & Dekindt, K. (2006) Impact de la variabilité climatique sur l'évolution spatio-temporelle des biocénoses benthiques: le cas des herbiers méditerranéens de phanérogames marines. In: *Annales de l'Association Internationale de Climatologie*. France: Epernay, pp. 255–260.
- Ganter, B. (2000) Seagrass (*Zostera* spp.) as food for Brent geese (*Branta bernicla*): an overview. *Helgoland Marine Research*, **54**, 63–70. <https://doi.org/10.1007/s101520050003>
- García-Herrera, R., Díaz, J., Trigo, R.M., Luterbacher, J. & Fischer, E.M. (2010) A review of the European summer heat wave of 2003. *Critical Reviews in Environmental Science and Technology*, **40**, 267–306. <https://doi.org/10.1080/10643380802238137>
- Godet, L., Fournier, J., van Katwijk, M., Olivier, F., le Mao, P. & Retière, C. (2008) Before and after wasting disease in common eelgrass *Zostera marina* along the French Atlantic coasts: a general overview and first accurate mapping. *Diseases of Aquatic Organisms*, **79**, 249–255. <https://doi.org/10.3354/dao01897>
- Green, A.E., Unsworth, R.K.F., Chadwick, M.A. & Jones, P.J.S. (2021) Historical analysis exposes catastrophic seagrass loss for the United Kingdom. *Frontiers in Plant Science*, **12**, 629962. <https://doi.org/10.3389/fpls.2021.629962>
- Guerrero-Meseguer, L., Veiga, P., Sampaio, L. & Rubal, M. (2021) Sediment characteristics determine the flowering effort of *Zostera noltei* meadows inhabiting a human-dominated lagoon. *Plants*, **10**, 1–13. <https://doi.org/10.3390/plants10071387>
- Heck, K.L. & Valentine, J.F. (2006) Plant-herbivore interactions in seagrass meadows. *Journal of Experimental Marine Biology and Ecology*, **330**, 420–436. <https://doi.org/10.1016/j.jembe.2005.12.044>
- Horn, S., Schwemmer, P., Mercker, M., Enners, L., Asmus, R., Garthe, S. et al. (2020) Species composition of foraging birds in association with benthic fauna in four intertidal habitats of the Wadden Sea. *Estuarine, Coastal and Shelf Science*, **233**, 106537. <https://doi.org/10.1016/j.ecss.2019.106537>
- Hothorn, T., Hornik, K. & Zeileis, A. (2006) Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics*, **15**, 651–674. <https://doi.org/10.1198/106186006X133933>
- Hothorn, T. & Zeileis, A. (2015) Partykit: a modular toolkit for recursive partytioning in R. *Journal of Machine Learning Research*, **16**, 3905–3909. Available at: <https://cran.r-project.org/web/packages/partykit/index.html> [Accessed April 7, 2022].
- Inger, R., Ruxton, G.D., Newton, J., Colhoun, K., Mackie, K., Robinson, J.A. et al. (2006) Using daily ration models and stable isotope analysis to predict biomass depletion by herbivores. *Journal of Applied Ecology*, **43**, 1022–1030. <https://doi.org/10.1111/j.1365-2664.2006.01207.x>
- IPCC. (2021) Summary for policymakers. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S. et al. (Eds.) *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge: Cambridge University Press. In Press.
- Jacobs, R.P.W.M., den Hartog, C., Braster, B.F. & Carriere, F.C. (1981) Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). *Aquatic Botany*, **10**, 241–259.
- Jankowska, E., Michel, L.N., Lepoint, G. & Włodarska-Kowalczyk, M. (2019) Stabilizing effects of seagrass meadows on coastal water benthic food webs. *Journal of Experimental Marine Biology and Ecology*, **510**, 54–63. <https://doi.org/10.1016/j.jembe.2018.10.004>
- Jones, B.L., Cullen-Unsworth, L.C. & Unsworth, R.K.F. (2018) Tracking nitrogen source using $\delta^{15}\text{N}$ reveals human and agricultural drivers of seagrass degradation across the British Isles. *Frontiers in Plant Science*, **9**, 1–10. <https://doi.org/10.3389/fpls.2018.00133>
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**(3), 373–386.
- Kollars, N.M., Henry, A.K., Whalen, M.A., Boyer, K.E., Cusson, M., Eklöf, J.S. et al. (2017) Meta-analysis of reciprocal linkages between temperate seagrasses and waterfowl with implications for conservation. *Frontiers in Plant Science*, **8**, 1–14. <https://doi.org/10.3389/fpls.2017.02119>
- Lebrasse, M.C., Schaeffer, B.A., Coffey, M.M., Whitman, P.J., Zimmerman, R.C., Hill, V.J. et al. (2022) Temporal stability of seagrass extent, leaf area, and carbon storage in St. Joseph Bay, Florida: a semi-automated remote sensing analysis. *Estuaries and Coasts*, **45**, 2082–2101. <https://doi.org/10.1007/s12237-022-01050-4>
- Martínez-Abrán, A. & Jiménez, J. (2016) Anthropogenic areas as incidental substitutes for original habitat. *Conservation Biology*, **30**, 593–598. <https://doi.org/10.1111/cobi.12644>
- Mathers, R.G. & Montgomery, W.I. (1997) Quality of food consumed by overwintering pale-bellied Brent geese *Branta bernicla hrota* and wigeon *Anas penelope*. *Biology and Environment*, **97**, 81–89.
- Miloslavich, P., Bax, N.J., Simmons, S.E., Klein, E., Appeltans, W., Aburto-Oropeza, O. et al. (2018) Essential Ocean variables for global sustained observations of biodiversity and ecosystem changes. *Global Change Biology*, **24**, 2416–2433. <https://doi.org/10.1111/gcb.14108>
- Nacken, M. & Reise, K. (2000) Effects of herbivorous birds on intertidal seagrass beds in the northern Wadden Sea. *Helgoland Marine Research*, **54**, 87–94. <https://doi.org/10.1007/s101520050006>
- Navarro, L.M., Fernández, N., Guerra, C., Guralnick, R., Kissling, W.D., Londoño, M.C. et al. (2017) Monitoring biodiversity change through effective global coordination.

- Current Opinion in Environmental Sustainability*, **29**, 158–169. <https://doi.org/10.1016/j.cosust.2018.02.005>
- Newton, I. (2007) *The migration ecology of birds*. Waltham, Massachusetts: Academic Press, p. 947. <https://doi.org/10.1016/B978-0-12-517367-4.X5000-1>
- Nordlund, L.M., Koch, E.W., Barbier, E.B. & Creed, J.C. (2016) Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS One*, **11**, e0163091. <https://doi.org/10.1371/journal.pone.0163091>
- Ogden, J.C., Baldwin, J.D., Bass, O.L., Browder, J.A., Cook, M.I., Frederick, P.C. et al. (2014) Waterbirds as indicators of ecosystem health in the coastal marine habitats of southern Florida: 2. Conceptual ecological models. *Ecological Indicators*, **44**, 128–147. <https://doi.org/10.1016/j.ecolind.2014.03.008>
- Paganini, M., Leidner, A.K., Geller, G., Turner, W. & Wegmann, M. (2016) The role of space agencies in remotely sensed essential biodiversity variables. *Remote Sensing in Ecology and Conservation*, **2**, 132–140. <https://doi.org/10.1002/rse2.29>
- Papathanasopoulou, E., Simis, S., Alikas, K., Ansper, A., Anttila, S., Attila, J. et al. (2019) Satellite-assisted monitoring of water quality to support the implementation of the Water Framework Directive. *EOMORES White Paper*, p. 28. <https://doi.org/10.5281/zenodo.3463051>
- Percival, S.M. & Evans, P.R. (1997) Brent geese *Branta bernicla* and *Zostera*; factors affecting the exploitation of a seasonally declining food resource. *Ibis*, **139**, 121–128. <https://doi.org/10.1111/j.1474-919x.1997.tb04511.x>
- Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J. et al. (2013) Essential biodiversity variables. *Science*, **339**, 277–278. <https://doi.org/10.1126/science.1229931>
- Qin, L.Z., Suonan, Z., Kim, S.H. & Lee, K.S. (2021) Growth and reproductive responses of the seagrass *Zostera marina* to sediment nutrient enrichment. *ICES Journal of Marine Science*, **78**, 1160–1173. <https://doi.org/10.1093/icesjms/fsab031>
- R Core Team. (2022) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rasmussen, E. (1977) The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In: McRoy, C.P. & Hellferish, C. (Eds.) *Seagrass ecosystems, a scientific perspective*. New York: Marcel Dekker, pp. 1–51.
- Robbins, B.D. (1997) Quantifying temporal change in seagrass areal coverage: the use of GIS and low resolution aerial photography. *Aquatic Botany*, **58**, 259–267. [https://doi.org/10.1016/S0304-3770\(97\)00039-9](https://doi.org/10.1016/S0304-3770(97)00039-9)
- Robin, F., Meunier, F., Corre, F., Joyeux, E., Cayatte, M.-L., Delaporte, P. et al. (2015) Site and prey selection by wintering Black-tailed godwit *Limosa limosa islandica* feeding on seagrass beds and bare mudflats on the central Atlantic coast of France. *Revue d'Ecologie (Terre et Vie)*, **70**, 134–147.
- Sato, F., Tanaka, S., Kirihaara, S. & Tanaka, Y. (2020) The influence of migratory birds on the distribution of the seagrass *Zostera japonica*. *Botanica Marina*, **63**, 521–525. <https://doi.org/10.1515/bot-2020-0045>
- Scott, A.L., York, P.H., Duncan, C., Macreadie, P.I., Connolly, R.M., Ellis, M.T. et al. (2018) The role of herbivory in structuring tropical seagrass ecosystem service delivery. *Frontiers in Plant Science*, **9**, 1–10. <https://doi.org/10.3389/fpls.2018.00127>
- Shariatinaajafabadi, M., Wang, T., Skidmore, A.K., Toxopeus, A.G., Kölzsch, A., Nolet, B.A. et al. (2014) Migratory herbivorous waterfowl track satellite-derived green wave index. *PLoS One*, **9**, 1–11. <https://doi.org/10.1371/journal.pone.0108331>
- Shaughnessy, F.J., Ferson, S.L., Frimodig, A.J., Barton, D.C., Hurst, M. & Black, J.M. (2021) Growth and flowering responses of eelgrass to simulated grazing and fecal addition by Brent geese. *Ecosphere*, **12**, e03690. <https://doi.org/10.1002/ecs2.3690>
- Sheppard, J.K., Lawler, I.R. & Marsh, H. (2007) Seagrass as pasture for seacows: landscape-level dugong habitat evaluation. *Estuarine, Coastal and Shelf Science*, **71**, 117–132. <https://doi.org/10.1016/j.ecss.2006.07.006>
- Soissons, L.M., Haanstra, E.P., van Katwijk, M., Asmus, R., Auby, I., Barillé, L. et al. (2018) Latitudinal patterns in European seagrass carbon reserves: influence of seasonal fluctuations versus short-term stress and disturbance events. *Frontiers in Plant Science*, **9**, 1–12. <https://doi.org/10.3389/fpls.2018.00088>
- Spalding, M.D., Taylor, M.L., Ravilious, C., Short, F.T. & Green, E.P. (2003) The distribution and status of seagrasses. In: Green, E.P. & Short, F.T. (Eds.) *World atlas of seagrasses*. Prepared by the UNEP World Conservation Monitoring Centre. Berkeley, CA: University of California Press, pp. 5–26.
- Stillman, R.A., Wood, K.A., Gilkerson, W., Elkinton, E., Black, J.M., Ward, D.H. et al. (2015) Predicting effects of environmental change on a migratory herbivore. *Ecosphere*, **6**, art114. <https://doi.org/10.1890/es14-00455.1>
- Taquet, C., Taquet, M., Dempster, T., Soria, M., Ciccione, S., Roos, D. et al. (2006) Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Marine Ecology Progress Series*, **306**, 295–302. <https://doi.org/10.3354/meps306295>
- Tinkler, E., Montgomery, W.I. & Elwood, R.W. (2009) Foraging ecology, fluctuating food availability and energetics of wintering Brent geese. *Journal of Zoology*, **278**, 313–323. <https://doi.org/10.1111/j.1469-7998.2009.00578.x>
- Turschwell, M.P., Connolly, R.M., Dunic, J.C., Sievers, M., Buelow, C.A., Pearson, R.M. et al. (2021) Anthropogenic pressures and life history predict trajectories of seagrass meadow extent at a global scale. *Proceedings of the National Academy of Sciences of the United States of America*, **118**, e2110802118. <https://doi.org/10.1073/pnas.2110802118>

- Unsworth, R.K.F. & Butterworth, E.G. (2021) Seagrass meadows provide a significant resource in support of avifauna. *Diversity*, **13**, 1–10. <https://doi.org/10.3390/d13080363>
- Unsworth, R.K.F., McKenzie, L.J., Collier, C.J., Cullen-Unsworth, L.C., Duarte, C.M., Eklöf, J.S. et al. (2019) Global challenges for seagrass conservation. *Ambio*, **48**, 801–815. <https://doi.org/10.1007/s13280-018-1115-y>
- Unsworth, R.K.F., Rasheed, M.A., Chartrand, K.M. & Roelofs, A.J. (2012) Solar radiation and tidal exposure as environmental drivers of *Enhalus acoroides* dominated seagrass meadows. *PLoS One*, **7**, e34133. <https://doi.org/10.1371/journal.pone.0034133>
- Valentine, J.F. & Duffy, J.E. (2006) The central role of grazing in seagrass ecology. In: Larkum, A.W.D., Orth, R.J. & Duarte, C.M. (Eds.) *Seagrasses: biology, ecology and conservation*. Dordrecht: Springer, pp. 463–501. https://doi.org/10.1007/978-1-4020-2983-7_20
- Valentine, J.F. & Heck, K.L. (1999) Seagrass herbivory: evidence for the continued grazing of marine grasses. *Marine Ecology Progress Series*, **176**, 291–302. <https://doi.org/10.3354/meps176291>
- Valéry, L. & Schricke, V. (2013) Trends in abundance and wintering phenology of the dark-bellied Brent goose *Branta b. bernicla* in France between 1982 and 2012. *Wild*, **63**, 57–73.
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S. et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 12377–12381. <https://doi.org/10.1073/pnas.0905620106>
- Zoffoli, M.L., Gernez, P., Godet, L., Peters, S., Oiry, S. & Barillé, L. (2021) Decadal increase in the ecological status of a North-Atlantic intertidal seagrass meadow observed with multi-mission satellite time-series. *Ecological Indicators*, **130**, 108033. <https://doi.org/10.1016/j.ecolind.2021.108033>
- Zoffoli, M.L., Gernez, P., Rosa, P., le Bris, A., Brando, V.E., Barillé, A.L. et al. (2020) Sentinel-2 remote sensing of *Zostera noltei*-dominated intertidal seagrass meadows. *Remote Sensing of Environment*, **251**, 112020. <https://doi.org/10.1016/j.rse.2020.112020>

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Environmental datasets.