One of the least disturbed marine coastal ecosystems on Earth: Spatial and temporal persistence of Darwin’s sub-Antarctic giant kelp forests

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Abstract

Aim: Marine habitats and their dynamics are difficult to systematically monitor, particularly those in remote locations. This is the case with the sub-Antarctic ecosystem of the giant kelp *Macrocystis pyrifera*, which was already noted by Charles Darwin in his accounts on the *Voyage of the Beagle* and recorded on the nautical charts made during the *Beagle* voyage.
1 | INTRODUCTION

There is an increasing awareness of the need to protect the last remaining terrestrial forest ecosystems with limited anthropogenic impact (Watson et al., 2018). Intact forests on continents are periodically monitored by remote sensing systems to better understand changes in the quantity and quality of these ecosystems (Hansen et al., 2013; Potapov et al., 2008, 2017). In contrast, there has been less attention to the status of intact or pristine underwater ecosystems, particularly kelp forests. Kelps are considered ‘foundation’ species, as their presence increases the number and diversity of species by the control of the physical environment in the water column, also known as physical engineering (Lamy et al., 2020; Miller et al., 2018). In many regions of the planet, kelp forests are degrading under multiple stressors such as ocean warming, pollution or over-harvesting (Krumhansl et al., 2016; Wernberg et al., 2019).

A missing area in the recent account of the global trends of kelp forests is the sub-Antarctic region (Krumhansl et al., 2016), which paradoxically was one of the first kelp ecosystems mentioned in natural history studies. In Voyage of the Beagle, Charles Darwin commented on the conspicuous forests of the giant kelp (Macrocystis pyrifera) surrounding Tierra del Fuego, saying ‘I can only compare these great aquatic forests of the southern hemisphere, with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp’ (Darwin, 1845). These tenets forged the pillars of kelp ecology (Miller et al., 2018). Darwin was not the first to record the giant kelp: the first written description of *M. pyrifera* was made by Juan Ladrilleros during his expedition through the Strait of Magellan in 1557–1558, which illustrates how prevalent this alga was in the region (Martinic Beros, 1982).

The combined extent of the giant kelp canopies of *M. pyrifera* on the sea surface (kelp forests hereafter) detected with satellite imagery of the Chilean Fjords, Falkland Islands (Malvinas), and the island of South Georgia is 8067.7 km², which accounts for more than 47% of its known distribution (Mora-Soto et al., 2020). Recent evidence suggests that this ecosystem is adapting to environmental change (Palacios et al., 2021). A previous study reported that the abundances and composition of the
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kelp forests at Isla de los Estados (Argentina, 54°47′S 64°15′W) experienced little changes over the last four decades (Friedlander et al., 2020). Furthermore, kelp forests in a nearby fjord (Yendegaia, Beagle Channel, Chile, 54°52′S 68°44′W) showed physiological tolerance to the indirect effects of glacier melting such as reduced light availability and increased turbidity (Huovinen et al., 2019; Palacios et al., 2021). Contrary to other kelp regions suffering thermal stress, the sub-Antarctic currents at present do not show signs of tropicalisation (Vergés et al., 2014).

The sub-Antarctic kelp forests in this region are found along a high gradient of geographical coastal diversity, from the Fjordlands of Southern Chile, to the extensive coastal shelf of the Falkland Islands and the rugged and heavily glaciated landscapes of South Georgia. These coastlines have been subject to direct and indirect influences of humans for thousands of years. Indigenous peoples in the Chilean Fjordland region have utilised M. pyrifera and other local seaweed species for food and medicine over at least 14,000 years BP (Dillehay et al., 2008). The Falkland Islands and South Georgia, without human occupation before European arrival, have seen successive waves of economic activity since the mid-18th century, such as livestock grazing and seal and whale hunting (Alonso Marchante, 2014; Bridges, 1988; Palomares & Pauly, 2015), but the impact of these activities on kelp forests is unknown. At present, the spread of the salmon farming industry in Chile has had a devastating impact in the northern Patagonia coastal region, and is now threatening the coastal and fjord ecosystems in the southernmost regions of the country (Friedlander et al., 2018; Quiñones et al., 2019). Still, the nature and extent of the impacts of this activity on kelp forests are poorly understood.

In the present study, we aim to characterise key aspects of the biophysical characteristics of sub-Antarctic giant kelp forests, and to observe the long-term patterns in their distribution as inferred from observational records. By addressing these questions, we aim to develop a broad biogeographical conceptual model of the environmental adaptations and long-term trends in these unique ecosystems.

1.1 Characterising the abiotic habitat

Abiotic variables such as depth, complexity of the rocky substrate and wave stress are essential in determining kelp presence and persistence (Young et al., 2016). However, detailed bathymetric data of the sub-Antarctic are sparse, which precludes a comprehensive overview of the ecosystem. For this reason, this paper will analyse the abiotic niche of kelp forests based on the geomorphology of the coastline, exposure to the ocean, and sea surface temperatures.

Geomorphology informs on the general patterns of rocky nearshore ecosystems. In glacial and paraglacial regions with parallel glacial history such as in the Chilean Fjordland and South Georgia (Hodgson et al., 2014), coastal and submarine geofoms like lateral or terminal moraines, erratic rocks and sills, may provide available rocky substrates at the borders of trough valleys or U-shaped fjords. In contrast, the Falkland Islands experienced limited glacial presence (Clapperton, 1990) with a large shelf, which provided an ecological refugium during the Pleistocene for some marine species (González-Wevar et al., 2012; Leese et al., 2008). Following this premise, similar geomorphological processes may be linked to similar coastal configurations and spatial patterns of kelp forests. Consequently, if the geomorphological origin of a rocky substrate has been under a slow geological pace of marine sedimentation, the substratum for kelp forests should remain persistent within modern records, unless direct disturbance led to local extinctions.

Oceanographic variables such as exposure to currents can also support habitat persistence or shifts. Kelp generally grows best under high hydrodynamic regimes due to the increased flow of nutrients and inorganic carbon (Parnell et al., 2010; Wernberg et al., 2019). On exposed coastlines, kelp attains higher biomass and growth rates in open waters with more water movement, as observed by Van Tussenbroek (1989b) in the Falkland Islands and by Dayton (1985b) at Isla de Los Estados and southern Tierra del Fuego. However, we have limited evidence of kelp forest sizes in exposed or sheltered areas in sub-Antarctic kelp ecoregions, or whether strong storms are able to remove kelp forests in the most exposed areas.

In addition, sea surface temperature (SST) records can help to confirm temperature ranges for kelp persistence. At latitude 42°S, north of the Chilean Fjordland, SST >15-17°C was observed to increase the mortality of annual populations of kelp sporophytes (Buschmann et al., 2014). It is not yet clear whether sub-Antarctic SST records for the last decades are fully within the optimal thermal tolerance of kelp.

1.2 Long-term persistence

Estimating long-time resilience of kelp forest ecosystems in these three different ecoregions is challenging, considering the limited temporal range of ecological studies in this region (Barnes et al., 2006; Castilla & Moreno, 1982; Dayton, 1985b; Santelices & Ojeda, 1984; Van Tussenbroek, 1989c). Instead, the concept of persistence (sensu Connell & Sousa, 1983) refers to a population that did not go extinct, or if it did go extinct locally or regionally, it recolonised during a given period of time in a given area.

To gain perspective on the long-term persistence of sub-Antarctic kelp forests, we compared the first detailed cartographical records made during the voyages of the HMS Beagle and Adventure in 1826-1836 (King et al., 1836) and similar early charts from South Georgia made in 1882-1931 with surveys and remote sensing imagery from the second half of the 20th century up to the present.

2 MATERIALS AND METHODS

2.1 Study area

Our area of study encompasses the western side of South America from Peninsula Tres Montes at latitude 47°S to Cape Horn at latitude 56°S; and from longitudes 35°W to 76°W along the Chilean coastline to South Georgia (Figure 1a). This area includes the marine ecoregions of Channels and Fjords of Southern Chile, the Falkland Islands...
and the island of South Georgia (excluding the South Sandwich Islands; Spalding et al., 2007), and is oceanographically connected with the Pacific and the Atlantic oceans by the Cape Horn Current, the Falkland Current and the Circumpolar Antarctic Current around the South Georgia Shelf (Brandon et al., 2000). The Channels and Fjords ecoregion is connected by a network of channels (called Channels hereafter, described in González et al., 2013) and the Strait of Magellan that separates the South American continent from Tierra del Fuego. The Falkland Islands ecoregion is bisected by Falkland Sound, which separates the West and East Falkland Islands. In this study, we consider the Patagonian Shelf ecoregion that includes Puerto Deseado (Argentina) and the Chiloense ecoregion (Chile, latitude 41–46°S) for historical analysis only because the kelp forests in the former occur within a region of large tidal ranges, which may render them invisible to satellite sensors (Mora-Soto et al., 2020), while in the latter kelp forests are less stable, with weaker attachments to the substrate (Darwin, 1845; Dayton, 1985b).

### 2.2 The abiotic niche

#### 2.2.1 Spatial identification of a sample of present kelp forests (2016–2019)

We extracted present giant kelp canopy extents using remote sensing imagery. The extent of each canopy on the sea surface was...
detected with the Kelp Filter (KF) algorithm developed by Mora-Soto et al. (2020) and applied to Sentinel-2 Level-1C (Copernicus Service) satellite imagery from the Austral Spring 2015, starting on 21st September through to Austral Summer 2020, ending on 21st March. KF highlights the presence of kelp canopies through the difference of the red-edge (Band 6, 740 nm) and red reflectance (Band 4, 665 nm) of the Sentinel-2 spectral bands at 20 m resolution. The algorithm further masks values to discard other land or ocean elements, except for Ulvophyceae (a class of green algae) in intertidal areas, due to their similar reflectance. We applied this algorithm in seasonally-averaged images to increase the detection of kelp forests, as they often otherwise remain invisible due to heavy cloud cover, potentially persistent swell, or very small canopies over the study area. Subsequently, all seasons were averaged to calculate a representative extent of kelp canopy for the total range of time.

We aimed to obtain a representative sample of kelp forests per ecoregion. In QGIS (version 3.14.15), a random multipoint layer was created within the limits of each ecoregion. If any of those random points were in a range of 500 m near a kelp forest as identified by the KF algorithm, the forest was selected as a sample, and the process was repeated until the number of samples was close to 100 per ecoregion. The final number of sites were 108, 114 and 87 for Falkland Islands, Channels and South Georgia, respectively. For each of these kelp forests, a polygon was delineated covering the maximum extent of the observed canopy, including an inland range of 500 m if the forest was next to a coastline. Sites were double-checked with visible canopies on very high-resolution Google Earth true colour images to avoid false positives (Mora-Soto et al., 2020). If the Google Earth image had low resolution, or was obstructed by cloud cover, we used KF pixels that showed a permanent overlay of pixels identified as kelp in concentrated areas, avoiding estuarine or beach areas. The polygon drawing scale ranged from 1:5,000 to 1:20,000.

2.2.2 Statistical analyses

Kelp forests were characterised by their coastal geospatial attributes (Table 1). Orientation, level of exposure to the open ocean, and the coastal setting of the surrounding land (geof orm) were manually classified using Sentinel-2 and a topographic layer (Advanced Land Observing Satellite Global Digital Surface Model—ALOS AW3D30; Tadono et al., 2016) for context. For kelp forests next to land, the maximum slope in a range of 500 m was calculated with ALOS and the Zonal Statistics tool in QGIS version 3.14. Kelp forest size was classified according to the median size of the complete number of samples (6.6 ha, rounded to 7 ha), in two classes: ‘small’ (<7 ha) and ‘large’ (>7 ha).

A Kruskal–Wallis (1952) rank sum test was applied to determine whether kelp forest size was significantly different along the categorical variables exposure to the ocean, geof orm, ocean current and aspect per each ecoregion. Significant p-values were adjusted and compared with the Benjamini and Hochberg (1995) method. Additionally, Kaiser–Meyer–Olkin (KMO) and Bartlett’s Tests (R version 4.0.2, package: ‘psych’; Revelle & Revelle, 2015) were used to assess the adequacy of each factor. Spearman’s rank-order correlation (Spearman, 1987) was used to identify whether kelp forest size was correlated with the continuous variables of adjacent land slope, longitude and latitude. Statistically significant categorical variables were included in a conditional inference tree (Hoithorn et al., 2006; R package: ‘partykit’; Hothorn & Zeileis, 2015) to investigate the association between forest size and geospatial variables, using 80% of all forests of the three bioregions combined (N = 254) for calibration and the remaining 20% (N = 55) as an evaluation dataset.

2.2.3 Decadal trends of SST (1981–2020)

We obtained long-term daily SST records surrounding sub-Antarctic kelp forests. SST trends were analysed using the NOAA CDR OISST: Optimum Interpolation Sea Surface Temperature product (Reynolds, Banzon, & NOAA, 2008) employing the Google Earth Engine API. As this imagery dataset has a coarser scale (0.25 arc degrees) than the one used for delimitating kelp forests, we selected two representative points for each ecoregion between the kelp forests and the open ocean (Figure 1a). Daily records from 01 September 1981 to 30 March 2020 were tested for stationarity using the Augmented Dickey–Fuller Test (R package: ‘adf.test’; Fuller, 2009). The selected sites were as follows: (1) Channels and Fjords ecoregion: Punta Carrera, in the Strait of Magellan; Grevy Island in the Cape Horn Archipelago; (2) Falkland Islands ecoregion: Sea Lion Island, at the South of East Falkland; Pebble Islet, at the North of West Falkland; (3) South Georgia ecoregion: Annenkov Island at the western side of the island; Stromness Bay at its eastern side.

2.3 Long-term persistence

2.3.1 Long-term kelp canopy extent monitoring

To examine the variability of kelp forest extent over the longest observational time frame possible, we made use of historical nautical charts, airborne (from aircraft and unmanned aerial vehicles [UAVs]) and satellite imagery, spanning the period 1829–2020.

(a) 1829–2019. Nautical charts and visual assessments of kelp forests

The original HMS ‘Beagle’ Nautical Charts of the Strait of Magellan, Tierra del Fuego and Falkland Islands (1829–1834; King et al., 1836), along with the HMS ‘Sappho’ (1905), HMS ‘Dartmouth’ (1920), RRS ‘Discovery’ (1925–1930) and German International Polar Year Expedition (1882–1914) Nautical Charts of South Georgia were manually scanned at the archives of the United Kingdom Hydrographic Office (UKHO) using a hand-held scanner. The images were georeferenced in QGIS using a first-order polynomial transformation and ground control points using distinctive coastal features.
TABLE 1 Attributes of the giant kelp (*Macrocystis pyrifera*) forests used in this study.

| Name                  | Definition and levels                                                                 | Type of variable and test                      |
|-----------------------|----------------------------------------------------------------------------------------|------------------------------------------------|
| Size<sup>a</sup>      | Total area covered by canopy, in hectares.                                              | Continuous, Spearman rank-order correlation     |
| Slope<sup>b</sup>     | Maximum topographic slope in degrees (source: ALOS AW3D30) of the surrounding land in a range of 500 m. |                                                |
| Latitude, Longitude<sup>b</sup> | Coordinates in decimal degrees (WGS 84).                                               |                                                |
| Size class<sup>a</sup> | Small (<7 ha) or Large (>7 ha).                                                        | Categorical, Kruskal–Wallis rank-sum test (compared with Size in hectares and Size class). |
| Slope class<sup>b</sup> | Classification of topographic slope ranges: <4° = level, 4–15° = sloping, 15–35° = steep, >35° = Very steep. |                                                |
| Exposure<sup>b</sup>  | Exposition to the open sea: wave exposed or sheltered.                                 |                                                |
| Geoform<sup>b</sup>   | Visual assessment of the geomorphological setting of the forest site: concave (bay), convex coastline, straight coastline, small island, intertidal rock (islet). |                                                |
| Orientation<sup>b</sup> | Visual assessment of the orientation or aspect of the kelp forest next to a coastline (flat or circular is omitted): North, North East, East, South East, South, South West, West, North West. |                                                |
| Current<sup>b</sup>   | Oceanic currents: Antarctic Circumpolar, Cape Horn, Falkland Islands. Straits and sounds: Channels (in the Chilean fjordland), Falkland Sound, Strait of Magellan. |                                                |
| Ecoregion<sup>b</sup> | Channels and Fjords of Southern Chile, Falkland Islands, South Georgia.                 |                                                |

<sup>a</sup>Dependent variable.

<sup>b</sup>Independent variable.

Choosing the georeference with the minimum root mean square (RMS) error (Figure 1b–d). With this transformation, we opted to maintain the main coordinates of the historical chart rather than stretching the chart to fit the actual coastline, in consideration of the cartographic technology at the time. The observed kelp forest areas, depicted with symbols of stipes and blades, were delineated as polygon shapefiles along a wide perimeter around the fronds, following the protocol of Costa et al. (2020). The range of the drawing scale was 1:5,000–1:10,000.

2.3.2 | Second half of the 20th century

(b) Airborne imagery

Aerial photographic archives containing kelp forests from Port Stanley and surrounding area (Falkland Islands) were scanned and georeferenced along with the nautical charts. The date of the aerial survey was 14–22 March 1976 (Sortie number: 1186). The flight was conducted at ~1800 m with a camera of focal length of 152:46 mm at a scale of 1:12,000. The boundaries of the kelp canopies were manually drawn in shape polygons following the same protocol as with the aerial photography.

Sketches and observations from geolocated diving surveys and footage records using a Chasing Gladius Mini underwater drone were included in this analysis in addition to the visual assessment of kelp canopies. Surveys were conducted in the Strait of Magellan, Yenegaia Fjord (Beagle Channel), the Magdalena Channel (Aysén Region, Chilean Patagonia) and Tussac Islands (Falkland Islands) from January to July 2019.

(c) Historical kelp surveys (1972–1987)

The first ecological and ecophysiological studies on sub-Antarctic kelp were conducted in the 1970s and 1980s (Dayton, 1985b; Moreno & Jara, 1984; Ojeda & Santelices, 1984; Santelices & Ojeda, 1984; Van Tussenbroek, 1989a, 1989b, 1989c, 1989d, 1993). We located the surveys on the map and verified whether satellite-detected kelp forests exist in the vicinities of the locations indicated in these studies (either in maps or registered coordinates), using the same layered procedure as mentioned above. Finally, we compared the charts with data on human impact using geographical records of historical and current land use from Geographical Information Systems of the local governments and institutions (Chile: Región de Magallanes (GORE-Magallanes, 2020); UK Overseas Territories (BAS, 2020; SAERI, 2020) as main sources.

(d) Multi-decadal assessments of kelp forests with satellite imagery (1984–2019)

Charted kelp forests drawn on the UKHO historical nautical charts were compared with the extent of kelp forests from the satellite imagery provided by Google Earth Engine (Gorelick et al., 2017). The detection algorithms were as following: Normalised Difference Vegetation Index (NDVI; Tucker, 1979) derived from the Landsat 5 TM Tier 1 calibrated top-of-atmosphere (TOA) reflectance of 30 m
resolution (Nijland et al., 2019); and the KF derived from Sentinel-2 (note that KF cannot be computed from Landsat due to lack of adequate reflectance bands). As the available Landsat 5 TM images from 1984 to 2011 were few in comparison to Sentinel-2 images from 2016 to 2019, all images were averaged annually. Only Sentinel-2 images were available for South Georgia.

The following protocol was applied to the annually-averaged Landsat 5 TM: cloud masking with the aid of the Quality Assessment band (USGS, 2021); land masking of elevation values >0 m using the Advanced Land Observing Satellite Global Digital Surface Model (ALOS AW3D30; Tadono et al., 2016); NDVI calculation and filtering of values ≥0.01; selection of annual images with filtered NDVI pixels over the targeted kelp forests. In the case of Sentinel-2, we followed the KF protocol mentioned above.

Kelp canopies can be covered by persistent clouds resulting in underestimation of their total extent, and kelp areas in the historical nautical charts were not outlined precisely and are thus prone to non insignificant margins of error. Therefore, the polygons corresponding to each canopy drawn on the UKHO charts were overlaid with the satellite-detected kelp areas to analyse spatial concordance, and we classified this visual assessment in four categories:

1. The satellite-detected kelp areas covered the charted kelp in similar form and extent.
2. The satellite-detected kelp areas had spare pixels over the target kelp canopy: this may mean that the forest is small or with sparse fronds, largely undetected by the satellite sensor.
3. The satellite-detected kelp areas showed patterns not associated with kelp forests.
4. No satellite-detected kelp pixels over the targeted kelp.

### 3 | RESULTS

#### 3.1 | Characterising the abiotic niche

##### 3.1.1 | The landscape/seascape of present kelp forests

The landscape and seascape characteristics allowed the identification of key characteristics defining the kelp forests in the three studied ecoregions: for example, the mean size of individual kelp forests in the Falkland Islands ecoregion is three times larger than that of the forests in the Channels and Fjords ecoregion, and 20 times larger than the forests in the South Georgia Ecoregion (Table 2). The largest forests are associated with the Falklands Current, Falklands Sound and the Cape Horn Current, whereas smaller forests are found in areas that are influenced by the less powerful currents of the Channels, Strait of Magellan and the Antarctic Circumpolar Current near South Georgia (Figure 2a). Post-hoc pairwise comparison indicates that forest size is not significantly different between Falklands Current and Falklands Sound, and between Strait of Magellan and Cape Horn and Channels. However, forest canopies are larger when their surrounding coastline is oriented towards the dominant oceanic currents. This corresponds with directions from southwest to east in Channels, and from south to northeast at both the Falkland Islands and South Georgia (Figure 1a; Figure S1.1).

Kelp forests differ in size and number according to the slope class of the nearby land, but follow different patterns in each ecoregion (Figure 2b; Table S1.1). The majority and the larger kelp forests are adjacent to steep (15–35°) to very steep (>35°) terrain in the Channels and Fjords; in South Georgia, slightly larger kelp forests are associated with sloping lands (4–15°; Figure 2b). In the Falkland Islands, most of the kelp forests are located around flat to gently sloping gradients. Regarding geoforms, in the Channels and Fjords ecoregion and in South Georgia, larger kelp forests are associated with convex headlands and straight coastlines, and dominate in number in bays and around intertidal rocky islets. In the Falkland Islands ecoregion, larger forests are found around islands or intertidal rocky islets (Figure 2c). Finally, a significant difference is observed among forests in sheltered versus exposed areas facing the main ocean currents in both Channels and Fjords and the Falkland Islands (Figure 2d).

The continuous variables of longitude, latitude and slope display significant correlations with the size of the kelp forests. These are overall weak and tend to confirm the patterns displayed by categorical variables. Kelp forest size is negatively correlated with longitude ($\rho = -0.19; \ p < 0.001$; i.e., in a hump-shaped relationship from the continent to the very large forests of the Falkland Islands and becoming smaller towards South Georgia in the east). Similarly, kelp forest size decreases with increasing latitude ($\rho = 0.26; \ p < 0.001$). Kelp forest size is negatively correlated with land slope, although this relationship is not as strong as with latitude or longitude ($\rho = -0.14; \ p = 0.015$).

The significant variables are used in a conditional inference tree to predict the size of the kelp forests (Figure 3). Small forests are linked to the Antarctic Circumpolar Current on the South Georgia Shelf (94.6%) and the Channels of Southern Chile (76.6%). Larger forests are related to the main oceanic currents (Cape Horn, Table 2

| Ecoregion       | N forests | Mean (ha) | St. Dev | Median (ha) | 1st Qu (ha) | 3rd Qu (ha) | Min (ha) | Max (ha) |
|-----------------|-----------|-----------|---------|-------------|-------------|-------------|----------|----------|
| Falklands       | 108       | 60.72     | 94.6    | 35.73       | 14.70       | 77.79       | 0.28     | 820.53   |
| Channels        | 114       | 19.84     | 34.1    | 6.03        | 2.11        | 21.24       | 0.08     | 220.51   |
| South Georgia   | 87        | 2.38      | 2.9     | 1.54        | 0.49        | 2.97        | 0.07     | 18.69    |

**Abbreviation:** Qu, quartile.
Falkland Current, Falkland Sound and Strait of Magellan, \( p < 0.001 \), but they vary in relation to how exposed they are to the open ocean. In sheltered areas, including the Strait of Magellan and Falkland Sound, small forests make up 40% of the total, whereas larger forests dominate in the open oceanic areas facing the Cape Horn and Falkland currents, accounting for 77% and 100% of the kelp forests, respectively. The prediction level of the conditional inference tree is 81% \( (p = 0.001) \).
3.1.2 Multi-decadal SST trends

The long daily record (1981–2020) of NOAA SST data shows stationary trends for all the representative pixels (Dickey–Fuller test = stationary; \( p = 0.01 \) for all the sites; Figure S1.2). Minimum SST record is \(-1.74^\circ C\) at Stromness, South Georgia, while the maximum recorded temperature is \(12.77^\circ C\) at Pebble Island in the Falkland Islands (Table S1.2). No temperatures above the thermal range of kelp survival are recorded between 1981 and 2020. This record demonstrates that SSTs have been stable during the last three decades in the study area.

3.2 Long-term persistence

The complete coverage of UKHO Nautical Charts and satellite-detected kelp forests can be found in the following online resource: https://biogeoscienceslab.oxfordusers.earthengine.app/view/beagle-ekelp-charts. Multi-annual kelp time series, detected with KF from Sentinel-2 and NDVI derived from Landsat 5 TM, show spatial coincidence with contemporary kelp forests, with differences mostly attributable to cloud cover in the averaged satellite images. A multi-decadal assessment of kelp forest area was not possible due to lack of continuous cloudless data, but the overlay of annual detected kelp forest shows patterns of spatial coincidence, indicating a persistence of kelp forests from 1984 to 2019. All of the surveys made in the 1970s and 1980s are in the vicinity of the recent satellite-detected kelp areas.

Contemporary kelp forests also displayed a general spatial coincidence with kelp canopies drawn on the historical UKHO survey charts (Table 3). The cartographical details of the UKHO charts vary greatly in their accuracy; consequently, some sheltered coastlines have generally more details, suggesting more elaboration time, usually including kelp canopies as a warning for navigation. The best equivalence between past and present inferred kelp forests is in the Falkland Islands charts, with 200 out of 223 kelp forests along the complete coastline, and only four non-detected forests in exposed areas of Choiseul Sound, Eagle Passage, Falkland Sound and Berkeley Sound. South Georgia has 231 out of 304 satellite-detected kelp forests with similar presence and shape of charted kelp forests in the areas of Larsen Harbour, Royal Bay, Cumberland Bay, Stromness Bay, Fortuna Bay, Possession Bay, Bay of Isles, Prince Olaf Harbour, Right Whale Bay, Elsehul, Undine Harbour and Bird Islands, with few confirmed kelp forest removals in the exposed areas of Barff Point, Elsehul, and Prince Olaf Harbour. The Channels and Fjords of the Southern Chile ecoregion has less coincidence of kelp forests (21 out of 38) along the Strait of Magellan, Navarino and Wollaston Island, Hardy Peninsula, and south of Tierra del Fuego, with 11 areas of sparse pixels and six noisy areas in the middle of the first and second narrows of the Strait of Magellan. The Patagonian Shelf ecoregion has four out of eight areas with similar presence and shape near Puerto Deseado, Cape Virgins and southeast coast of Tierra del Fuego, one missing area from Cape Espiritu Santo to Peninsula El Paramo, and two missing kelp forests in the exposed area of Puerto Deseado.

### TABLE 3 Summary of the total of kelp forests drawn on the UKHO nautical charts and satellite-detected kelp

| Marine ecoregion         | Channels and Fjords of Southern Chile | Falkland Islands (Islas Malvinas) | South Georgia | Patagonian Shelf |
|--------------------------|--------------------------------------|----------------------------------|----------------|------------------|
| Historical nautical charts | Number of charts                     | 11                               | 4              | 24               | 4                |
|                          | Year of elaboration                  | 1834                             | 1834–35        | 1882–1931        | 1929–1834        |
|                          | Number of charted kelp forests       | 38                               | 223            | 304              | 8                |
| Kelp forests on nautical charts versus contemporary detections | Similar shape                      | 21                               | 200            | 231              | 4                |
|                          |                                      | 55.3%                            | 89.7%          | 76%              | 50%              |
|                          | Spare pixels                         | 11                               | 19             | 48               | 1                |
|                          |                                      | 29%                              | 8.5%           | 15.8%            | 12.5%            |
|                          | Noise                                | 6                                | 0              | 0                | 0                |
|                          |                                      | 16%                              |                |                  |                  |
|                          | Empty                                | 0                                | 4              | 25               | 3                |
|                          |                                      | 1.8%                             | 8.2%           | 37.5%            |                  |
Relatively small patches of kelp are abundant in bays and rocky islets in South Georgia, in contrast to the large extent of kelp forests in the Falkland Islands. This may reflect paraglacial patterns (Hodgson et al., 2014) of fjords and moraines and restricted glacial history and extensive shallow shelf (Clapperton, 1990), respectively. This pattern is also supported by the surrounding land slope and anecdotal observations in the field. The spatial extent of sub-Antarctic kelp forests along coastlines is broader on flat to inclined slopes and narrower along vertical slopes. Level to sloping lands dominate at the Falkland Islands, steep to vertical lands dominate in South Georgia and Chilean Fjords. Vertical and over-hanging walls are a niche for animal forests like bivalves, polychaetes and soft-corals, which can coexist with macroalgae (Cárdenas & Montiel, 2017). Regarding the external boundary for *M. pyrifera* forests, previous surveys in the Channels and Fjords and Falkland Islands have reported that some forests are bordered by a narrow band of *Lessonia flavicans*, small boulders and sand, although *L. flavicans* can grow intermixed with *M. pyrifera* (Beaton et al., 2020; Dayton, 1985b; Santelices & Ojeda, 1984; Van Tussenbroek, 1989d). We illustrate this general conceptual model of kelp forest habitats in Figure 4. The patchy response of *M. pyrifera* to a variety of abiotic (geomorphology, SST) and biotic (competitive interactions) between species of kelps presents analytical challenges: understanding their differentiation/integration in response to contemporary environmental pressures would benefit modelling and monitoring of kelp forests in all regions.

In the ecoregions of Channels and Fjords and Falkland Islands, the dominant orientation of larger kelp forests towards the oceanic currents corroborates previous findings (Dayton, 1985b; Van Tussenbroek, 1989b, 1993), supporting the concept that water motion and turbulence play a primary role on nutrient assimilation for kelp (Dayton, 1985a). This prevalent quality ends when maximum wave energy limits kelp canopy, resulting in a hump-shaped relationship between kelp forest size and wave energy (Young et al., 2016). On the other hand, in areas of very low energy, that is, the fjords of South Georgia and the internal Channels of Southern Chile, kelp forests are strongly influenced by freshwater coming from glaciers and snow fields and rainfall. Previous work in the Beagle Channel has shown that *M. pyrifera* has adapted their photosynthetic activity to this paraglacial environment, including overshadowing due to high turbidity (Palacios et al., 2021) or adopting a loose-lying form on the bottom and small pneumatocysts, undetectable from the surface (Gerard & Kirkman, 1984; Van Tussenbroek, 1989c). Therefore, kelp forests in fjords can persist despite being considered stressed (Dayton, 1985b; Mora-Soto et al., 2020), even with the increased glacial melting rates of the last three decades (Meier et al., 2018).

In the current global context, kelp forests are severely affected by marine heatwaves, ocean acidification, increased frequency of storms and over-harvesting (Krumhansl et al., 2016; Wernberg et al., 2019). However, kelp persistence seems to follow a neutral relationship with SST at higher latitudes, i.e., bull kelp *Nereocystis luetkeana* in Oregon (Hamilton et al., 2020). Furthermore, our SST analysis confirms that the currents near our study areas show no trends of tropicalisation, a major cause of thermal stress and shifts on kelp distributions in other regions, i.e., Western Australia (Wernberg et al., 2013), or Tasmania, with a sharp decline of kelp canopies since the year 2000 (Butler et al., 2020). The low SST ranges in South Georgia, located south of the Antarctic Polar Front (Moore et al., 1999), could mean that this ecosystem may cope well with polar temperatures, which might be a signal for potential colonisation of the Antarctic, but the small sizes of their canopies might also mean they are close to their lower temperature limit. On the other hand, acidification could have a negative impact on the development of calcareous organisms that feed on kelp, but not the kelp itself (Brown et al., 2014). An increased frequency of subpolar westerly winds and strong storms is affecting the distribution of some species like the bull kelp *Durvillaea antarctica* (Fraser et al., 2018). Although SSTs have remained stable and the present study supports the long-term stability observed in this marine ecosystem (Friedlander et al., 2018, 2020), more local long-term studies on persistence after storms are needed to confirm this region as a climatic refugium for kelp.

Our work compared present time with late-modern records. The large number of kelp forests drawn in the nautical charts is explained by the words of Captain FitzRoy of the HMS Beagle: ‘there is no danger in any of the Falkland harbours that is not distinctly buoyed by kelp’ (FitzRoy, 1839, p. 265). The process of georeferencing the charts with modern techniques confirmed the remarkable accuracy of the coordinates calculated in the Beagle charts, which meant a significant improvement from the previous cartography made in the times of the Spanish Empire (King et al., 1836). South Georgia charts have more errors, but they improved in accuracy in successive editions from 1882 to 1931, refining the outline of the coastlines and charted kelp area. However, the location of very exposed kelp forests may be less accurate than kelp forests close to land. Similar sources of data to estimate kelp persistence were also used with success by Costa et al. (2020) in British Columbia, and Pfister et al. (2018) in the state of Washington. This research confirms their convenience for integrated historical studies.

The results of the temporal comparison showed 0%, 1.8%, 8.2% and 37.5% of empty kelp areas in Channels and Fjords of Southern Chile, Falkland Islands, South Georgia and Patagonian Shelf, respectively. For present-time records, our kelp-detecting method with satellite imagery might have generated false negatives (empty cells) in narrow kelp canopy fringes or in canopies of low density, as the resolution of the satellites (30 m for Landsat TM and 20 m for Sentinel-2) might be too coarse to detect them, and in the eastern side of Tierra del Fuego and the Patagonian Shelf, kelp forests can be hidden under high tides (Mora-Soto et al., 2020). In South Georgia, empty areas could be explained by the marginal distribution of the species, a high dynamism of the coastline due to glacial activity, or direct anthropogenic intervention. Some Landsat-5 TM images can also show some noisy stripes at the border of the original images. In the middle of the Strait of Magellan (Paso Ancho), a higher number of false positives (16%) was detected than elsewhere. A possible cause for this could be due to local areas of higher photosynthetic activity
associated with phytoplankton (Saggiomo et al., 2011) or to floating kelp (Wichmann et al., 2012).

The remote sensing approach used in this study was based on previous studies that used KF (Mora-Soto et al., 2020) and NDVI (Nijland et al., 2019), with high levels of overall accuracy at detecting kelp canopy extent in remote locations. However, this study does not include ground-truthed estimations of kelp canopy biomass, frond density and kelp density linked with satellite imagery. Those variables could help to explain the environmental dynamics of the forests further, but would need a significant long-term sampling effort through SCUBA diving, as done in previous works developed in the Southern California coastline (Bell et al., 2018; Cavanaugh et al., 2011, 2013). The baseline presented in this study could be expanded to a similar kind of environmental research in the future.

4.1 | Anthropogenic changes and kelp persistence

A number of places in our area of study have experienced important landscape changes in the last two centuries caused by direct or indirect human interventions in the environment. Nevertheless, kelp forests have generally persisted in the same areas (Table S1.3). The main landscape alterations are the following:

\[ \text{FIGURE 4} \] A general model of the sub-Antarctic kelp forest in relation to coastal geomorphology. The area of a kelp forest depends on the available substrate originated by geological orogeny followed by glacial, marine, alluvial or organic weathering and/or sedimentation. Topographic slope classes: (a) Level to sloping; (b) steep; (c) vertical and over-hanging walls. Exposure to the ocean has an inverse correlation with the growth rate and positive correlation with the life span of the canopies (Van Tussenbroek, 1989a, 1989c)
a. Glacier retreat: The German International Polar Year Expedition stayed at Royal Bay (South Georgia) between 1882 and 1883, where they mapped the bay including Molkte Harbour and Ross Glacier, a tidewater glacier. Although the map had some errors, the trends of this glacier show a slight advancement until 1965 (Hayward, 1983) followed by a high rate of retreat since the 1990s (Cook et al., 2010) with an area loss of $0.88 \pm 0.04 \text{ km}^2 \text{ year}^{-1}$ between 2003 and 2016 (Farias-Barahona et al., 2020). The kelp forests of Molkte Harbour are still in the same location despite the distance to the ice front (currently $<10$ km; Figure S1.3). Other retreating glaciers with persistent kelp forests are Turnback and Purvis glaciers, among others.

b. Indigenous (Yaghan) people: Yaghan people, local canoe sailors, lived traditionally in the intertidal environment of the Beagle Channel and the Cape Horn Archipelago (south of Tierra del Fuego). Kelp forests were an essential source of food and meant a central part of their worldview (Ojeda et al., 2018). The most detailed charts of these coastlines were made on Goree Roads on the 7th, Packsaddle Bay on the 18th, and Middle Cove (Wollaston Island) on the 19th of February 1833, where Yaghans were in close contact with the HMS Beagle crew (FitzRoy, 1839). The number of Yaghan people declined dramatically after the first contacts with Europeans, Chileans and Argentinians during the 19th and 20th centuries, and Yaghan descendants now live in Ushuaia (Argentina) and Puerto Williams and Puerto Natales (Chile). Although we do not know if the Yaghan had a positive or negative impact on kelp forests, our results indicate that kelp forests have persisted in historical Yaghan areas.

c. Urban development: The Beagle Expedition finished their surveys of South America and the Falkland Islands in 1834. Some years later, in 1843, the city of Port Stanley (Falkland Islands) was founded in Port William (Royle, 1985), and in 1848 the city of Punta Arenas (Chile) was founded in the Strait of Magellan (Martinic Beros, 2002). Both cities have seen population and infrastructure growth since their founding, but kelp forests persist around both settlements, as does the kelp forest near the city of Puerto Deseado (Argentina).

d. Whaling/sealing areas: The Beagle anchored in Thetis Bay, between St. Vincent and St. Diego capes on 21st February 1834 (Keynes, 2001). Between 1940 and 1948, a pinniped slaughterhouse operated in the bay, where 200 people worked; more than 30,000 sea lions were killed until the installation was closed and abandoned (Vázquez & Santiago, 2014). The southern elephant seals (Mirounga leonina) and whales that were processed in South Georgia from the mid-19th to mid-20th centuries (Palomares & Pauly, 2015) in the factories of Leith, Grytviken, Husvik, Prince Olaf and Stromness Harbours, among others, suffered a similar fate, all of which had detailed charts indicating kelp forests that are still present today.

Estimations of past distributions of sub-Antarctic kelp forests remain an open question. Terrestrial references indicate that the maximum extent of the Patagonian Icefields occurred around 14,600 years BP and was followed by a relatively gradual warming (Glasser et al., 2004) that opened coastal spaces for conifers and moorlands (Villagran, 2001), whereas closed-canopy Nothofagus forests in Patagonia have been in place since ~10,000 cal year BP (Moreno et al., 2019). Shell middens along the Beagle Channel indicate human occupation of the coastline during at least the last 6,500 years, with a stable marine biota (Estévez et al., 2001). A 14,000 year multiproxy record of seabird guano and tussock grass (Poa flabellata) in the Falkland Islands showed an abrupt establishment of P. flabellata and seabird colonies ~5000 year BP (Groff et al., 2020), which, in turn, could have meant massive nutrient inputs for kelp growth. In turn, seabirds like the kelp gull Larus dominicanus can forage on bivalves growing on kelp blades like Gaimardia trapesina (Friedlander et al., 2020; Hockey, 1988). Molecular studies have suggested a northern hemisphere origin of giant kelp, with a later dispersal to the southern hemisphere (Astorga et al., 2012; Coyer et al., 2001; Macaya & Zuccarello, 2010). Specifically, Coyer et al. (2001) indicate that multiple inter-hemisphere crossings occurred between 3.1 Mya and as recent 0.01 Mya. More specific research is needed to complement these convergent lines to estimate an age of sub-Antarctic kelp forests.

The observed persistence does not necessarily imply that sub-Antarctic kelp forests are not threatened by local anthropogenic factors. To the north of our study area, kelp forests are harvested with different levels of protection in central and northern Chile. This has a strong overall influence on kelp forest morphology and biomass (Gouraguine et al., 2021; Krumhansl et al., 2016; Vásquez, 2008). The effect of marine traffic on kelp canopies in the region, particularly near the Strait of Magellan and the Cape Horn is a question that requires future research. The major impending threat to the region is probably the rapid expansion of salmon farming; however, overexploitation of fisheries stocks, destructive fishing practices and threats associated with climate change will all require proactive management actions to mitigate potential negative impacts (Friedlander et al., 2021). To sustain this ecosystem in the long term, it is imperative to develop specific plans for conservation, like the creation of marine protected areas (Friedlander et al., 2018, 2020; Rozzi et al., 2007), regulation of kelp harvesting, intensive salmon farming, destructive fishing practices, and pollution (Hinojosa et al., 2011; Iriarte et al., 2010), evaluation of carbon sequestration and ecosystem services (Bayley et al., 2021) as well as encouraging indigenous rights for the protection of the maritorio (seascape) in Patagonia.

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DATA AVAILABILITY STATEMENT
All the historical nautical charts, previous surveys and the current kelp distribution layers were uploaded to an online open visualisation viewer: https://biogeoscienceslab.boxford.users.earthengine.app/view/beaglekelpcharts with the aim of encouraging scientists and the public to explore the layers interactively.

The datasets generated during the current study are available in the Beagle Kelp charts repository: https://doi.org/10.5061/dryad.bcc2fqzck.

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BIOSKETCH
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Author contributions: A.M-S and M.M-F conceived the ideas; A.M-S, M.P., N.G. and T.H. conducted the fieldwork, A.M-S collected and analysed the data, and led the writing; A.C., A.M.F., M.P., P.B., N.G., P.K.D., B.V.T., A.M., W.G., C.V-C., T.H., E.C.M., A.P-M, and M.M-F critically reviewed and edited the manuscript.

SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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