Mapping Long-Term Changes in Eelgrass Meadows Using Aerial Photography

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"*Last but not least…I wanna thank me. I wanna thank me for believing in me. I wanna thank me for doing all this hard work. I wanna thank me for having no days off. I wanna thank me for never quittin'*"

- Snoop Dogg

Pernille Eyde Nerlie

Abstract

Coastal ecosystems are threatened by a changing climate and growing human impacts. Among these are seagrass meadows, which provide numerous valuable ecosystem services. Concerningly, seagrass ecosystems have declined globally at accelerating rates. Mapping efforts have overall increased on a global scale, but remain low in Norway, where the dominant seagrass is eelgrass (*Zostera marina*). Thus, there is a lack of knowledge on the historic and present extent of eelgrass meadows, and the processes that govern these ecosystems in Norway. To protect and manage these ecosystems in a sustainable way, there is a strong need to fill these knowledge gaps. With advancements in remote sensing technology, aerial photography has been increasingly used for mapping seagrass. In Norway there is a large database containing readily available, geo-referenced aerial photographs, which is one of the only sources of historic information on eelgrass extent. However, this has remained an untapped source.

In this study we examined to what extent aerial photography can be used for mapping Norwegian eelgrass meadows, assessed temporal changes in eelgrass meadow extent in southern Norway, and indicated likely causes from available data on pressures. The results showed that aerial photography can be successfully used as a tool for mapping shallow meadow extent. Using this method, we revealed that temporal trends in eelgrass meadow extent have varied greatly between stations, but during the last two decades there seem to be a shift in trajectories, from high variability to predominantly expansion. These results suggest there is an ongoing natural recovery of eelgrass meadows in southern Norway. The variability in trends between stations indicate that temporal change is a result of local changes in water quality, an seems highly dependent on local conditions.

Aerial photography can serve as a useful and cost-effective tool for increasing mapping efforts of eelgrass meadow extent in shallow waters in Norway, and to gain insight into historic extent. Furthermore, it can serve as a baseline for further monitoring, and as a complimentary approach for modelling. The results also reveal that the responses to stressors are highly localised, and that managing these ecosystems entail assessing how different stressors may act on both regional and local scales.

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1. Introduction

In a world where the effects of climate change become more and more pressing (IPCC, 2022), it has never been more important to take care of our ecosystems. Coastal ecosystems are considered one of our most threatened habitats (Waycott et al., 2009), and are under increasing pressure from both land and sea. These key ecosystems make up a small group of marine angiosperms (flowering plants), which can form extensive meadows in shallow soft-sediment coastal habitats (Green & Short, 2003). They are distributed globally, with the exception of the highest polar regions, and their distribution is often classified into six bioregions (seven, when dividing the temperate North Atlantic into East and West) (Dunic et al., 2021; Short et al., 2007). The lowest diversity is found in the North Atlantic bioregion, where eelgrass (*Zostera marina*) is the dominant seagrass species (Short et al., 2007).

Seagrass meadows are recognized as one of our most valuable ecosystems, due to the many ecosystem services they provide (Costanza et al., 1997). These ecosystems are of high ecological and socio-economic importance, supporting societies directly and indirectly through provisioning and regulating services (Cullen-Unsworth et al., 2014; Nordlund et al., 2016). As primary producers they contribute to the oxygenation of the ocean and sediments (Borum et al., 2006), and make up highly productive communities (Duarte & Chiscano, 1999). They are foundation species that promote biodiversity by providing habitat, nursery areas, food and refuge for numerous fish, invertebrates, microbes and birds (Beck et al., 2001; Bertelli & Unsworth, 2014; Duarte, 2002; Green & Short, 2003; Heck et al., 2003; Hughes et al., 2009; Orth et al., 2020; Renkawitz et al., 2011). Several of these seagrass-associated species are also considered either threatened or vulnerable, including seahorses, bivalves, fish and rays, green turtles and sirenians (dugongs and manatees) (Hughes et al., 2009; Preen & Marsh, 1995). Furthermore, many seagrass-associated species support commercially important species of fish, bivalves and crustaceans (Cullen-Unsworth et al., 2014; Lefcheck et al., 2017), emphasizing the role of seagrasses in supporting the world’s fisheries.

Seagrasses also promote ecosystem health and provide coastal protection by modifying their environment. Seagrasses can alter their physical environment by modifying hydrodynamics such as wave energy and current velocities. Through wave attenuation and reduction of current velocity seagrasses reduce sediment resuspension and increase sedimentation (Hansen & Reidenbach, 2012). Sediment can be further stabilized by extensive root and rhizome structures, thus contributing to coastal protection by mitigating the risk of coastal erosion and flooding

(Ondiviela et al., 2014). Furthermore, Seagrasses obtain nutrients from both their surrounding environment and from sediments. Seagrass canopies can work as effective filters, trapping the surrounding particles, which then accumulate in the sediment (Hendriks et al., 2008). Ultimately, these processes improve water quality by reducing turbidity and consequently increasing light availability. Although seagrasses occupy only a small fraction of the world's oceans, it is estimated that they account for more than 10% of the yearly carbon burial in the ocean (C. M. Duarte et al., 2005), with more recent estimates indicating it could be double (Fourqurean et al., 2012). Carbon is stored in both above and below ground seagrass biomass, and a significant amount of carbon is also stored in the sediment (C. M. Duarte et al., 2005; Kennedy et al., 2010). As such, seagrasses can act as important, and possibly long-term, nutrient and carbon sinks (Almroth-Rosell et al., 2016; Saderne et al., 2020), thus contributing to both reducing eutrophication, and to climate mitigation (Duarte et al., 2013).

It is important to note that the ecosystem services provided by seagrasses vary on a spatial-temporal scale, both between and within species (Nordlund et al., 2016; Ondiviela et al., 2014). For instance, the number of ecosystem services provided by seagrasses are positively associated with genus size, however size varies even within species geographically (Nordlund et al., 2016). Nevertheless, the role of seagrasses in promoting ecosystem health, and in climate change mitigation and adaption, highlights the importance of protecting these valuable ecosystems.

Concerningly, seagrass meadows are declining globally, and have done so at an accelerating rate over the last century. Dunic *et al.* (2021) found that seagrass meadow area had a net loss of 19.1% of the total area surveyed between 1880 and 2018, reflecting a net loss of 5602 km^2. They also found that decline was the general trajectory for all seven seagrass bioregions, with the largest declines happening in the Tropical Atlantic, Temperate North Atlantic East, Temperate Southern Oceans and the Tropical Indo-Pacific (2021). The largest declines were found after 1980, with a loss of 35% of seagrass area. Rates of loss for the declining meadows also accelerated from <1% yr^{-1} before 1940, while after 1980 the rate was 5% yr^{-1}. However, there are large variations between bioregions. While regions such as the Tropical Atlantic and Mediterranean stabilized by the 1980s, the Temperate North Atlantic West has declined since the 2000s. In contrast, the Temperate North Atlantic East has slightly increased since the 2000s.

The global decline in seagrass meadows is a result of numerous threats that these ecosystems face. Although the causes of decline are often poorly documented (Dunic et al., 2021; Waycott et al., 2009), several important threats have been identified. These threats include mechanical damage from coastal development, boat propellers, dredging and destructive fishing practises, overfishing, disease, invasive species, pollution, weather extremes, and eutrophication and deteriorate water quality (Duarte, 2002; Dunic et al., 2021; Waycott et al., 2009). The near-shore distribution of seagrass also leaves them vulnerable to disturbances from both land and sea, and coastal ecosystems are considered some of the most threatened habitats on earth (Waycott et al., 2009).

The most well documented disturbances leading to seagrass loss are related to deteriorate water quality (de los Santos et al., 2019; Dunic et al., 2021; Waycott et al., 2009). Seagrasses have high light requirements, which in turn leaves them vulnerable any disturbances that reduce light availability. In fact, seagrasses have some of the highest light requirements compared to other plant groups (Dennison et al., 1993). Minimum light requirements vary greatly within and between seagrass species (Duarte, 1991), but is estimated to range between 2-37% of surface irradiance (SI) (Lee et al., 2007). This is also comparably higher than other marine primary producers such as phytoplankton and macroalgae, which requires of only 1-3% SI (Lee et al., 2007). Disturbances that reduce light availability, either natural or anthropogenic, pose a great threat to seagrass ecosystems.

Anthropogenic disturbances are the most frequently cited threats to seagrass ecosystems. Eutrophication, as a result of nutrient loading from river and sediment run-off, has been identified as a major threat to seagrass meadows, and is largely attributed to anthropogenic input (Artioli et al., 2008; Orth et al., 2006; Short & Wyllie-Echeverria, 1996). It is often related to run-off from agricultural practices and nutrient input from sewage and wastewater, which has increased with the growing human population (Artioli et al., 2008; Greening et al., 2014; Harding Jr & Perry, 1997). Nutrient enrichment of the coastal ocean stimulates algal blooms (Harding Jr & Perry, 1997), including phytoplankton, macroalgae and growth of epiphytic algae on seagrass leaves, which in turn causes both increased shading and increased competition for light (Valiela et al., 1997). Furthermore, eutrophication can increase the risk of oxygen depletion due to the decomposition of organic material, especially in sheltered water where mixing is limited (Valiela et al., 1992). The effects of eutrophication can also be exacerbated by overfishing. Depletion of top predators can cause cascading effect through the food web, by decreasing the amount of mesograzers that would otherwise feed on epiphytic algae growing on seagrass, especially in areas with high nutrient input (Baden et al., 2010; Heck et al., 2000). This highlights the importance of trophic interactions, and the complexity of disturbance pathways.

Deteriorated water quality is also caused by increased turbidity, which is found to be highly associated with rapid declines in seagrass meadows (Turschwell et al., 2021). Anthropogenic disturbances such as coastal development and dredging are major threats to seagrass ecosystems (Waycott et al., 2009), and can cause direct mechanical damage or indirect effects such as increased resuspension of sediment and increased pollution (Bernard et al., 2007; Duarte, 2002; Kendrick et al., 2002). When seagrass meadows decline below a threshold, the loss of seagrass area will diminish the meadow's ability to stabilize sediment, which further promotes resuspension of sediment and increases turbidity in a positive feedback loop (Maxwell et al., 2017; Moksnes et al., 2018). Such processes can also favourise less light-dependent species such as algae, and potentially result in a regime shift (Moksnes et al., 2018).

Although less common (Waycott et al., 2009), natural disturbances can have detrimental effects on seagrass. The so-called wasting disease that occurred in the 1930s caused large-scale losses of eelgrass (*Zostera marina*) meadows. The disease was caused by the slime mould *Labyrinthula sp.*, and the epidemic almost eliminated populations of eelgrass across the North Atlantic, with reported losses estimated to 90% (Tutin, 1942). More recently, seagrass loss has been attributed to disturbances such as storms, heatwaves, floods and other extreme events, and such disturbances can cause mechanical damage, resuspension of sediment and unfavourable conditions resulting in physiological stress (Duarte, 2002; Dunic et al., 2021; Short & Wyllie-Echeverria, 1996). Loss of seagrass meadows due to extreme events is rarely sited, but is known to have had negative impacts, especially marine heatwaves and events that reduce water transparency (Campbell & McKenzie, 2004; Lefcheck et al., 2017; Moore et al., 2014). Concerningly, climate extremes are expected to increase in frequency due to climate change (IPCC, 2022).

With the accelerating loss of seagrass area and the many threats that are facing, managing these ecosystems becomes more important. Although natural disturbances certainly contribute to seagrass decline, anthropogenic disturbances far outweigh the natural (Waycott et al., 2009). Human expansion is considered a driver of current seagrass habitat loss, especially the effects of anthropogenic inputs to the coastal ocean (Short & Wyllie-Echeverria, 1996). This is concerning, as human pressure on the coastal zone is expected to increase (Mcgranahan et al., 2007; Nicholls & Small, 2002). Furthermore, with the expected increase in climate extremes, (IPCC, 2022) the importance of conservation and protection becomes increasingly important.

Although seagrass area has declined globally, meadows in Europe show signs of optimism. Similar to the global trend there was a long period of decline in Europe, with as much as onethird of the European seagrass area lost between 1869-2016 (de los Santos et al., 2019). This was mainly caused by disease, deteriorated water quality, and coastal development (de los Santos et al., 2019). Eelgrass accounted for the largest net loss, with of 57% of the maximum documented area. Losses accelerated over the second half of the 20th century, with loss rates reaching a peak of -33.6% decade^{-1} in the 1970s. However, the loss rates slowed towards the end of the century, and for the first time since the 1950 the net rate of change was reversed form negative to positive. The trend reversal was mostly due to losses slowing down, and a simultaneous increase in recovery of *Zostera noltei* and *Z. marina*, representing 86.2 and 11.1% of the total gains, respectively.

With a growing recognition of the values of seagrass ecosystems, and their global decline, they have gained more attention (Orth et al., 2006). In the Rio declaration (Chap. 18, part D 17.86 d), seagrass meadows are identified as critical ecosystems that should be prioritized for protection, due to their high levels of productivity and biodiversity. Management and protection of seagrass ecosystems are also addressed, implicitly or directly, under several convention and directives (Krause-Jensen et al., 2022). Due to seagrasses' sensitivity to reductions in light availability, seagrass depth limits can serve as useful bioindicators of water quality (Krause-Jensen et al., 2005), and have been implemented as such in the EU Water Framework Directive, which aims at maintaining good ecological status for European waters. As a result, seagrass monitoring efforts have increased in Europe (Marbà et al., 2013).

With the increased attention to seagrass ecosystems and efforts to minimize human disturbances, management action has shown effective in improving seagrass ecosystems. In Europe, the recovery of seagrass meadows has been mostly attributed to management action (de los Santos et al., 2019). Such initiatives have proven successful also outside Europe, with reduction of nutrient loadings and wastewater run-off resulting in recovery of meadows in Tampa Bay and Chesapeake Bay in the US (Greening et al., 2014; Lefcheck et al., 2018). However, management actions that reduce nutrient input and run-off have proven less effective in other places (Bernard et al., 2007; Kendrick et al., 2002; Krause-Jensen et al., 2021; Moksnes et al., 2018). Western Australia, France and Sweden experienced large-scale losses of seagrass area, but the following initiatives to reduce silt and nutrient inputs did not result in recovery of meadow areas. In such cases it has been hypothesized that there is a case of ecological hysteresies (Bernard et al., 2007), in which the re-establishment of the ecosystem requires even better environmental conditions than what could be tolerated for an already established meadow. Feedback mechanisms acting as a hindrance for re-establishment and restoration

(Moksnes et al., 2018) also highlight the importance of protecting and conserving these ecosystems before large losses occur. These example calls for stronger conservation efforts and strategies for managing seagrass meadows, and a deeper understanding of the processes governing seagrass ecosystems.

A key hindrance preventing effective management and understanding of the effects of seagrass disturbances is the lack of knowledge of the areal extent of seagrass meadows. Although monitoring and restoration efforts of seagrass has increased (Orth et al., 2006), there is still an extensive knowledge gap on the extent of seagrass area. Although improved in recent years, there is still a lack of mapping in areas like the east coast of South America and the west coast of Africa. Furthermore, efforts to estimate global seagrass area show vastly different results. The first global seagrass distribution map, generated in 2003, estimate a total seagrass area of 177 000 km^2 (Green & Short, 2003). This has later been revised, with a current estimated area of 321 682 km^2 (UNEP-WCMC & Short, 2021). Another recent study by McKenzie et al. (2020) calculated the global seagrass area based on published literature to be between 160 387 km^2 and 266 562 km^2. With technological advancements, modelling has emerged as a potential method for mapping seagrass, but also this method shows vastly different results. Modelling based on irradiance and seagrass light requirements have estimated potential seagrass area to be 4 320 000 km^2 (Gattuso et al., 2006), whereas modelling that included a wider selection of environmental variables predicted potential seagrass area to be 1 646 788 km^2 (Jayathilake & Costello, 2018). However, when compared to previously mapped areas, the model frequently over-estimates seagrass area, and still, actual mapped area often fell outside of the predicted area. Hence, the potential seagrass area may be far different from actual seagrass area. The accuracy of such models is likely to be improved, but it requires increased knowledge on the processes that determine the seagrass distribution.

In Norway, efforts of mapping seagrass have been low (Boström et al., 2014). Eelgrass *(Zostera marina*), which is the main seagrass in Norway, is known to occur along the whole coast, from Oslofjord and all the way up to Porsangerfjord (Gundersen et al., 2018). Following the wasting disease in the 1930s, occurrence and cover of Norwegian eelgrass has been registered yearly as a part of the Beach Seine Series since 1933 (Johannessen et al., 2012). However, cover data is only on a qualitative scale, and there is no registration of area extent. Moreover, eelgrass is explicitly mentioned in the OSPAR treaty, where it is listed as threatened and in need for further protection and conservation, followed by recommendations of more systematic mapping of the quality and distribution of eelgrass extent (OSPAR 12/22/1, Annex 13). Norway has also implemented the Water Framework Directive (WFD, EU Directive 2000/60/EC) in the Norwegian legislation, resulting in eelgrass depth limit being used as a bioindicator for assessing water quality through the ØKOKYST monitoring program (Fagerli et al., 2018). As a response to the UN Rio convention and the implementation of the WFD, the Norwegian National Program for Mapping and Monitoring Biodiversity was initiated in 2003, which led to the first large-scale mapping of eelgrass area in Norway. The program was carried out in 2007-2011 and included eelgrass meadows at selected stations from Oslo to Troms, which were mapped using field methods (Bekkby et al., 2013). Such mapping is challenging, as it is time consuming and costly, especially in countries like Norway with a wide eelgrass distribution and a long and convoluted coastline. The current registered eelgrass area is 62 km^2, but it is assumed that the total area is approximately 93 km^2. Since then, only one larger-scale mapping and historical comparison of eelgrass area has occurred (Jørgensen & Bekkby, 2013), which showed declines in eelgrass area in northern Norway (Troms county). Thus, due to large knowledge gaps of the historic extent of Norwegian eelgrass meadows, as well as large uncertainties in the estimates of the current extent, it is difficult to assess the ecological status of eelgrass meadows, which calls for a strong need for comprehensive mapping and monitoring. Such knowledge is necessary to understand the threats and processes that affect Norwegian eelgrass meadows, and to inform policy makers on how to manage these ecosystems effectively and sustainably.

One possibility for improving knowledge on the current and historic extent of Norwegian eelgrass meadows is through the use of aerial photography. With technological advancements, the use of remote sensing (RS) methods such as aerial photography, satellite imagery and acoustics for mapping seagrass has become more common (Hossain et al., 2014). Aerial photography has been used in a wide range of seagrass mapping initiatives for years, mostly in areas with large shallow bays or tidal flats, which are very different from the bathymetry of the convoluted Norwegian coast. In Norway there is a large database containing readily available, geo-referenced aerial photographs, but despite our lack of knowledge on eelgrass extent it has remained an untapped source for mapping eelgrass.

The objectives of this thesis are to

1. examine the extent to which aerial photography can be used for mapping eelgrass meadow extent along the Norwegian Skagerrak coast,
2. assess temporal changes in eelgrass meadow extent in Southern Norway, and
3. indicate likely causes from available data on pressures.

I hypothesize that temporal changes in eelgrass meadow extent in southern Norway will reflect the global trend of decreasing meadow area. Some meadows in the North Atlantic bioregion are increasing as a result of management actions. However, despite reductions in nutrient loading, eelgrass meadows along the Swedish Skagerrak coast have declined since the 1980s, and show little evidence of any natural recovery (Baden et al., 2003; Moksnes et al., 2018). It is therefore likely that the circumstances are similar for meadows along the Norwegian Skagerrak coast.

2. Materials and Methods

2.1 Study Area and Site Selection

The study was performed in Agder county in the southern part of Norway, along the western part of the Skagerrak Sea (Fig. 1). The area is characterized by a convoluted coastline, including multiple rivers, several smaller fjords, archipelagos and islands, and a narrow continental shelf that gradually slopes down to the 500-650 m deep Norwegian Trench. The near-shore sea is shallow (0-50 m), with sea surface temperatures dropping to below 0°C during winter and exceeding 20 °C during summer. Southern Norway is also an area that is being increasingly affected by marine heatwaves (MHW) (Filbee-Dexter et al., 2020). Agder has a growing population, with coastal cities ranging in size from around 6000 to 115 000 people (https://www.ssb.no/). There are many agricultural areas, and it is also a popular area for visitors during summer, and the number of second homes has been steadily increasing. Hence eelgrass meadows in Agder are under increasing pressure from both land and sea.

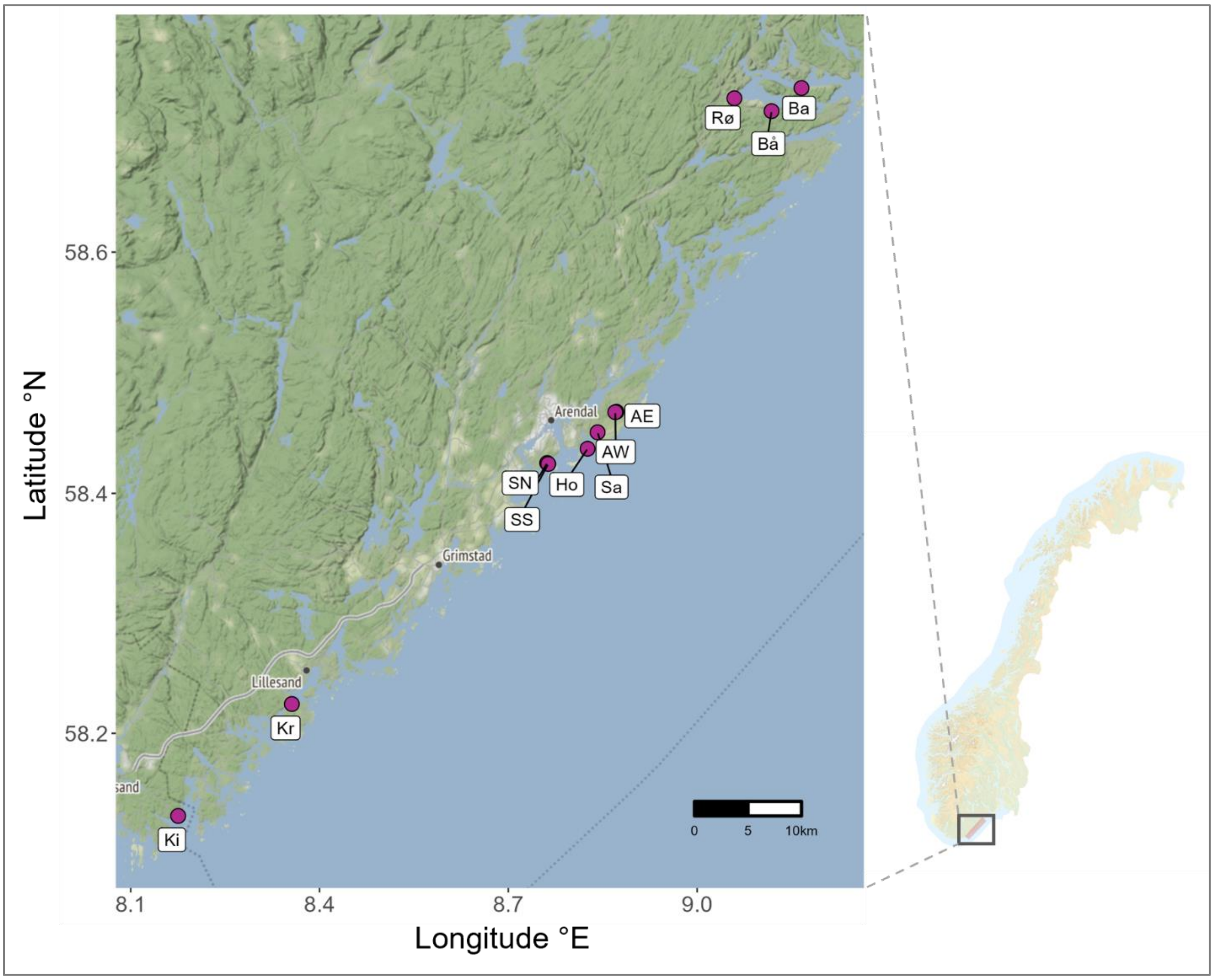

Figure 1: Map of the study area showing the location of the 11 stations (purple points) and their station ID.

A list of 55 potential stations was generated based on previous observations of eelgrass meadows at those stations, either from the Beach Seine Survey (Johannessen et al., 2012), previous marine habitat mapping, by researchers that are familiar with the area, or observations made by the public. These stations were then ranked based on their relative accessibility by car or by boat from Flødevigen Research Station, and the availability of aerial photography of the area. We wanted each station to have at least five aerial photos, with at least one photo taken before 1980. This resulted in a selection of 11 stations (see Appendix A for photos of each station) that were mapped in the field (Table 1). Most of the stations were located in inner fjord areas and are moderately to highly sheltered, except the two Stølsvigen stations, which are quite exposed. The stations Barmen, Båssvika, Kilen, Røedsfjorden, Sandumkilen and Stølsvigen are located close to river outlets, and all stations are close to at least one pier or marina. The stations were assigned to three geographic areas: Arendal, Risør, and Lillesand/Kristiansand (Table 1).

Table 1: The geographic area, station name, station ID, and the latitude (°N) and longitude (°E) in decimal degrees for the 11 stations.

Area	**Station**	**Station ID**	**Latitude (°N)**	**Longitude (°E)**
Arendal	Alvekilen East	AE	58.467774	8.871718
Arendal	Alvekilen West	AW	58.467425	8.869910
Risør	Barmen	Ba	58.735352	9.165746
Risør	Båssvika	Bå	58.716349	9.118184
Arendal	Hovekilen	Ho	58.437078	8.825912
Lillesand/ Kristiansand	Kilen	Ki	58.130856	8.175458
Lillesand/ Kristiansand	Krossvigsundet	Kr	58.224470	8.356065
Risør	Røedsfjorden	Rø	58.726953	9.059106
Arendal	Sandumkilen	Sa	58.450761	8.841772
Arendal	Stølsvigen North	SN	58.425242	8.761707
Arendal	Stølsvigen South	SS	58.424455	8.763360

2.2 Field Sampling

The data sampling was conducted during September 2022. Eelgrass meadows at the 11 stations were mapped in the field by snorkelling. First, a stand-up paddleboard (SUP) was used to paddle around the seagrass meadow to get an overview of the margin of the beds, and to plan an approximate snorkelling track. After planning the track, the eelgrass beds were mapped by snorkelling, using a Garmin 76CX GPS to track my position. I swam along the landward edge of the eelgrass meadows along the shore and stopped the track when it got too deep (about 3-4 m) to see the eelgrass.

2.3 Aerial Photography

To gather information on the historic extent of eelgrass, aerial photographs of the mapped stations were downloaded from the online data source *Norge i bilder* (https://www.norgeibilder.no/). This website contains more than 1.3 million georeferenced aerial photographs, covering all of Norway, from 1935 until present. This includes color, infrared (IR), color-infrared (CIR) and panchromatic (black and white) photos. These can be downloaded, and can serve as a potential valuable source of historical information about eelgrass. In the case of using aerial photos for eelgrass mapping, there are some limitations. Reflection from the sea, as well as strong wind and large waves, can highly limit the possibility to see underwater vegetation. A low solar angle casting shadows and lower resolution for some photos can also make it difficult to distinguish structures in the photo. Another important limitation is that at a certain depth, it is impossible to distinguish whether there is eelgrass or whether it is simply too dark to see it. This makes aerial photography suitable for mapping eelgrass only in relatively shallow areas.

Photos of the selected stations were downloaded as tagged image file formats (TIFFs). Only photos taken within the eelgrass growth season, June throughout September, were selected, and photos with too low resolution, high reflection or too much shadow were removed. This resulted in six to eight photos for each station (See Appendix B for reference list), with a resolution ranging from 0.1 to 0.25 m, depending on what was available. The earliest photos were from 1946 and the most recent photos from 2021, covering a year span of 56-76 years depending on the station. The selection includes colour, panchromatic (black and white), IR and CIR photos (See Appendix C for details).

2.4 Data Processing

Eelgrass meadow extent today was assessed from field data and compared with historic extents analysed from aerial photo using QGIS version 3. 26.3. First, I defined the mapped area, using the GPS tracks from the field sampling. GPS tracks were imported into the Garmin MapSource program and saved as an Excel file. The Excel file was then cleaned, removing everything but the waypoint number, latitude, and longitude, and saved as a text file. Aerial photos from each station were then imported into QGIS, and the coordinate reference system (CRS) ESPG:25832 ETRS89 / UTM zone 32N was used to get the right projection. The GPS track text files were then imported into QGIS and added as a vector layer onto the aerial photo from the respective station, as point coordinates. GPS tracks were then cleaned so that only the point coordinates where I swam around the meadow margins were left.

After defining the mapped area, I drew polygons of the non-eelgrass area in QGIS, for each photo at each station. To ensure that potential changes in the non-eelgrass area could be attributed only to the changes in seagrass extent, I drew a shoreline polygon for each station, using the GPS point coordinates to define the mapped area. These shoreline polygons were then used as a base for drawing polygons of the non-eelgrass area for all aerial photos within the same station (Fig. 2A). For each photo, the shoreline polygon of the respective station was added as a vector layer, and the QGIS vertex tool was used to fit the polygon to the seagrass meadow edge (Fig. 2B). All aerial photographs were interpreted at a resolution of 1:1000. The shoreline polygons were also used to draw the 2022 polygon, but instead of fitting it to a seagrass meadow edge it was fitted to the GPS point coordinates (Fig. 2D).

The Røedsfjorden station had two separate eelgrass meadows, one on each side of the bay, and the station was therefore divided into two separate polygons (North and South). On the 1999 photo from Krossvigsundet, there were some disturbances in parts of the photo, which would make the photo inadequate for area analysis for the eastern part of the station. To avoid losing data from 1999, the station was divided into two polygons, Krossvigsundet East and Krossvigsundet West.

It was not always entirely obvious on the photos where the meadow edge was, and I therefore drew two polygons for each photo – one conservative drawing (Fig. 2B) and one liberal drawing (Fig. 2C). The conservative polygon was drawn where I could say with high certainty that the eelgrass meadow edge stretched at least so far, while the liberal polygon reflected best judgement of the meadow edge.

For some stations I made a few minor modifications during the polygon drawing. At the Barmen station the eelgrass meadow edge was located on, or around, a slope. This made it hard to follow the edge for parts of the meadow, as it was sometimes too deep to see the eelgrass. During the field mapping I therefore divided the meadow into two parts, and swam once along each part. When drawing the 2022 polygon I used 5 vertices from the 2021 liberal polygon to connect the two parts, as it made more sense to map the meadow as one continuous meadow.

In two instances, (Båssvika and Røedsfjorden in 2011), the photos were edited in QGIS as they were quite dark. For these two photos gamma was set to 2, and the saturation and contrast were set to 20. In the 2021 and 2021 CIR photos for Alvekilen West, shadow on a small part of the meadow made it hard to see the meadow edge. I therefore used 3 and 6 vertices from the 2022 GPS points to draw the 2021 conservative and 2021 liberal polygon, respectively, and 8 vertices for both 2021 CIR polygons.

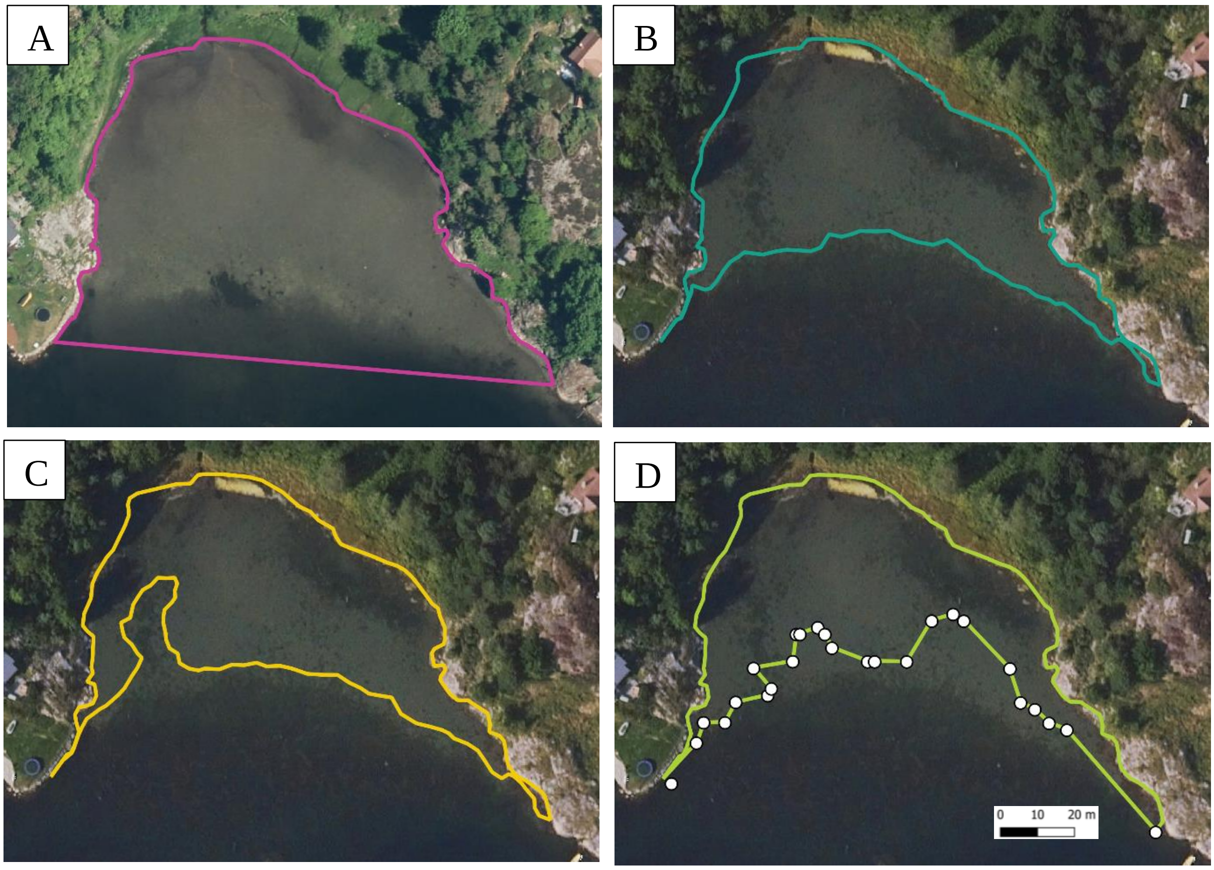

Figure 2: The methodical approach for mapping the non-eelgrass area in QGIS is exemplified by using aerial photos of Alvekilen East. Figure 2A shows the shoreline polygon drawn using the 2012 aerial photo. 2B shows the shoreline polygon conservatively fitted to the shallow edge of the eelgrass meadow on the 2021 photo. 2C showing the shoreline polygon liberally fitted to the shallow edge of 2021 polygon. 2D showing the shoreline polygon fit to GPS coordinates (white points) from the field mapping.

2.5 Data Analysis

2.5.1 Area and Overlap

To examine to what extent aerial photography could be used for mapping temporal changes in eelgrass meadows, I compared eelgrass meadow extent from field data with eelgrass meadow extent analysed from aerial photography. To avoid differences in eelgrass meadow extent caused by year-to-year variation, the ideal would be to compare field data with eelgrass meadow extent analysed from aerial photography from 2022. However, there were no available aerial photos from 2022 that fit the selection criteria. Therefore, the field data was compared to seagrass meadow extent analysed from two aerial photos from 2021 – one colour photo and one CIR photo.

How well the polygons drawn from aerial photo analyses fit with the polygon made from the GPS track was assessed by finding the area, overlap and differences between polygons in QGIS

(Fig. 3). The 2022 polygon was compared to the 2021, 2021 liberal, 2021 CIR and the 2021 CIR liberal polygons. First, I had to find the area of the polygons, using the $area function in the QGIS field calculator. The overlap between polygons was found using the Vector Geoprocessing Tool called Intersection, using the 2022 polygon as input layer and the 2021 polygon as overlay layer. The non-overlapping polygon areas were found using the Vector Geoprocessing Tool Difference. Using the 2022 polygon as input layer and the 2021 polygon as overlay layer gave the overestimated area (seagrass area larger than what was mapped in the field), while using the 2021 polygon as input layer and the 2022 polygon as overlay layer gave the underestimated area (seagrass area smaller than what was mapped in the field). This was done for all stations, and for all four 2021 polygons. The area of the overlap, over-estimation and under-estimation were then calculated relative to the 2022 polygon area of the respective station.

How well the 2021 polygons fit with the 2022 polygon form the field mapping was quantified by estimating the percentage overlap, over-estimation, and underestimation relative to the 2022 polygon. All calculation were made in RStudio (version 4.2.2) using the *tidyverse* package (Wickham *et al.*, 2019).

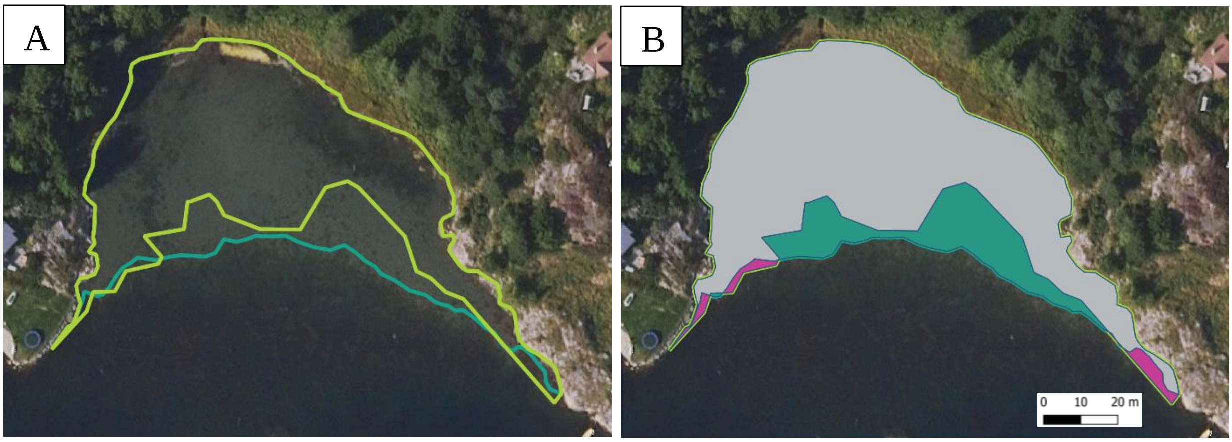

Figure 3: The methodical approach for estimating the overlap of the non-eelgrass area, and the over- and under-estimation of seagrass area in QGIS is exemplified in Figure 3 by using the 2021 aerial photo of the Alvekilen East. Figure 3A show the 2022 polygon (light green) and the 2021 polygon (dark green). Figure 3B shows the overlapping area between polygons (grey), the over-estimated seagrass area (pink) and the under-estimated seagrass area (dark green).

2.5.2 Temporal Change in Eelgrass Meadows

Temporal changes in eelgrass extent were assessed by calculating the area of the polygons for each year at each station, relative to the first mapped year. As we could not see the deeper (seaward) edge of the meadows neither on aerial photos nor during field mapping, it was not possible to map the total area of the eelgrass meadows. Rather, we assessed how the shallow (landward) edge of the eelgrass meadow has changed over time by calculating the change in non-eelgrass area over time and determining whether the meadows have retracted or expanded towards land.

Before estimating the change, some modifications were made. Stations located right next to each other, or stations divided into two sub-stations during the polygon drawing, were combined into single stations. This applied to the Alvekilen East and West, Krossvigsundet East and West, Stølsvigen North and South, and Røedsfjorden North and South. For these stations, the change was calculated based on the combined station area (1).

$$Combined\ station\ area = \frac{(Area\ station_{x1} + Area\ station_{x2})}{(Area\ station_{x1} + Area\ station_{x2})} \qquad (1)$$

After finding the area of all polygons, using the field calculator as described above, I found the temporal change by calculating the inverse proportion of non-eelgrass area as compared to the first mapped year (2). This was done for each year at each station, and resulted in positive values for smaller non-eelgrass area (more eelgrass) and negative values for larger non-eelgrass area (less eelgrass).

$$Change = \frac{Area\ year_0 - Area\ year_n}{Area\ year_0} \qquad (2)$$

For Alvekilen 1975 and Krossvigsundet 1999, the non-eelgrass area could only be analysed for one of the sub-stations. Change in the non-eelgrass area for these two years was therefore calculated based on the sub-station area. For the Kilen station we were able to map the total area of the eelgrass meadow, but for better comparison between stations, estimations of change in eelgrass area, and the overlap, over-estimation, and underestimation are done as described above. Total eelgrass meadow area for Kilen can be found in Appendix D.

All calculations and illustrations were made in RStudio (version 4.2.2) using the package *tidyverse* (Wickham *et al.*, 2019). For years where there were two photos (i.e. two polygons representing one year) the mean area of the two polygons were used when calculating the inverse proportion of the non-eelgrass area.

2.6 Anthropogenic Impact

2.6.1 Coastal Development

Anthropogenic pressure, and especially coastal development, is known to be a threat to seagrass ecosystems (Dunic et al., 2021; Waycott et al., 2009). To assess if there was any connection between the changes in eelgrass extent and coastal development, I looked at potential disturbances near the eelgrass meadows. These disturbances included piers (floating or stationary), construction (roads, buildings, land-claim development, and other construction), beach creation and dredging. I used aerial photos from *Norge i bilder* to find development that have occurred in the vicinity of the eelgrass meadows. The number of years between aerial photos varied, and therefore the exact time of the disturbance is not known. Timing of the disturbances was set to the mean year between the year when the disturbance occurred in a photo and the year of the nearest previous photo. The accuracy of the time in which the disturbance occurred varies from <1 year to +/- 16 years.

2.6.2 Human Population

Population data was collected as a proxy for diffuse human impact (human pressure) which we could not account for otherwise. The data includes population within the catchment area of Agder, which includes Agder and the former county of Telemark, and was retrieved from Statistics Norway (https://www.ssb.no/). Between 1933 and 1986 the population was registered every 10 years, and population in between those years were interpolated. Since 1986, the population has been registered every year.

2.7 Environmental Variables

To assess possible causes for observed trends in eelgrass extent, available data for environmental variables known to affect seagrass meadows was collected.

2.7.1 Salinity and Wave Exposure

To be able to look for impacts due to wave exposure on the mapped eelgrass meadows, we used data from a simple wave exposure model, using information of fetch and wind, developed at IMR (Halvorsen *et al.*, 2020) to generate statistical measurements of long-term average wave height at each station. The model operates on high resolution bathymetric data (50 x 50 m), which were collected from the online data source *Geonorge* (https://data.geonorge.no/sosi/dybdedata), hosted by the Norwegian Mapping Authority. Additional data applied with this model is a decadal long time series of wind from a nearby Meteorological station and offshore swell statistics from a operational wave model, both operated and hosted by the Norwegian Meteorological Institute (https://seklima.no and https://thredds.met.no, respectively). For the Kilen station, the wave exposure was estimated to be erroneously high (0.46 m) compared with how sheltered this station is. The reason is that the Kvåsefjorden bathymetry (i.e. the coastline) was too coarse in this area, resulting in 2-3 geographical sectors becoming directly exposed to offshore swells, hence the total wave height was estimated too high. A value of 0.05 m was then chosen for Kilen, based on the quantified wave heights for other similar stations (Jon Albretsen, pers. comm., 16 May, 2023).

Salinity data was extracted from IMR's hydrodynamic model system NorFjords-160, which is a high-resolution version of the open-source Regional Ocean Modelling System (ROMS) for the Norwegian fjords. The model provides realistic salinity estimates with high accuracy along with surface salinity variability which corresponds well with observations. For further details on the model system and validation results from a similar model simulation of the Hardangerfjord at the west coast of Norway, see Dalsøren, Albretsen and Asplin (2020). The wave exposure and salinity variation at each station was then assigned to either low, moderate or high level, based on comparisons between station (Table 2).

Table 2: Wave height (m) and the assigned wave exposure level, median salinity, salinity variation (+/- SD), and the assigned salinity variation level of the mapped stations.

Station	Wave height (m)	level	Salinity	Salinity variation	Level
Alvekilen East	0.06	Low	29.96	2.23	Low
Alvekilen West	0.05	Low	29.96	2.23	Low
Barmen*	0.07	Low	26.06	3.98	High
Båssvika*	0.06	Low	26.71	3.22	Moderate
Hovekilen	0.09	Moderate	28.56	2.25	Low
Kilen*	0.05	Low	30.83	1.89	Low
Krossvigsundet	0.06	Low	30.33	1.94	Low
Rødsfjorden*	0.07	Low	25.84	4.44	High

Sandumkilen**	0.07	Low	28.84	2.35	Low
Stølsvigen North*	0.16	High	28.30	4.45	High
Stølsvigen South*	0.13	High	28.09	4.37	High

** Station near river outlet.*
*** Station near river outlet, but freshwater discharge considered negligible (Jon Albretsen, pers. comm., 16 May, 2023)*

2.7.2 Temperature

Temperature data are from measurements at Flødevigen research station (58.426106 °N, 8.754805 °E). Until December 2008, the water temperature was measured manually by a thermometer at 1 m depth around 8:00 UTC every day. Since January 2009 the 8:00 UTC-values have been extracted from continuous measurements by a digital sensor. We used these daily temperatures from 1st May-30th September to calculate annual mean and maximum sea surface summer temperatures (Fig. 7). All calculations were done in RStudio (version 4.2.2) using the *tidyverse* package (Wickham *et al.*, 2019). Graphs were made using *ggplot2* (Wickham, 2016) and *patchwork* (Pedersen, 2022).

2.7.3 Nutrients

Nutrient data (total nitrogen and total phosphorus) in the inner Oslofjord was extracted from NIVA (Staalstrøm, 2020) which compiled data covering 1920 to 2013. Data from 1920-1980 is collected from Bergstøl, Feldborg and Olsen (1981), and data from 1985 and 1990-2013 is collected from Berge et al. (2015). This data was then used for modelling the nutrient levels for the 2015, using NIVA Fjord Model (NFM), a multidisciplinary model describing the physical, chemical, and biological conditions in the inner fjord basin.

3. Results

3.1 Use of Aerial Photos for Mapping Eelgrass Meadows

To what extent aerial photos could be used for mapping was examined by calculating how well the polygon from the analysed aerial photos fit with the area mapped in the field, in terms of overlap, over-estimation and under-estimation (Fig. 4). The boxplot in Figure 4 shows the comparison between all four types of 2021 polygons, relative to the 2022 polygon.

Overall, the non-eelgrass area analysed from aerial photos from 2021 largely overlaps with the non-eelgrass area mapped in the field in 2022. All 2021 polygons had a median overlap of >90% with the 2022 polygon. However, the liberal polygons overlap slightly less than the conservative, with a median overlap of 90.7% and 94.5% for 2021 lib and the 2021 CIR lib, respectively. The liberal polygons also show a wider range in the minimum and maximum values compared to the conservative, and the CIR liberal polygon has three clear outliers.

The over-estimation of seagrass area ranges from 3.1-9.3%, with the liberal polygons showing the largest median over-estimation of 5.5% for CIR and 9.3% for the colour photo. The over-estimated values have a larger spread for the liberal polygons, with the 2021 lib polygon having the largest range, and the 2021 CIR polygons has three clear outliers.

The under-estimation of seagrass area ranges from 4.3-12.0%, with the 2021 conservative and liberal polygons having the larges spread in values. The conservative polygons have the largest median under-estimation, with 12.0% the 2021 polygon, and 10.0% for the 2021 CIR polygon.

Overall, the polygon that fit best with the 2022 polygon from the field mapping was the 2021 CIR liberal polygon. When taking into account both over and-estimation (% over-estimation + % under-estimation), the 2021 CIR liberal polygon had a total difference of 11.2%, followed by the 2021 conservative polygon with 13.8%.

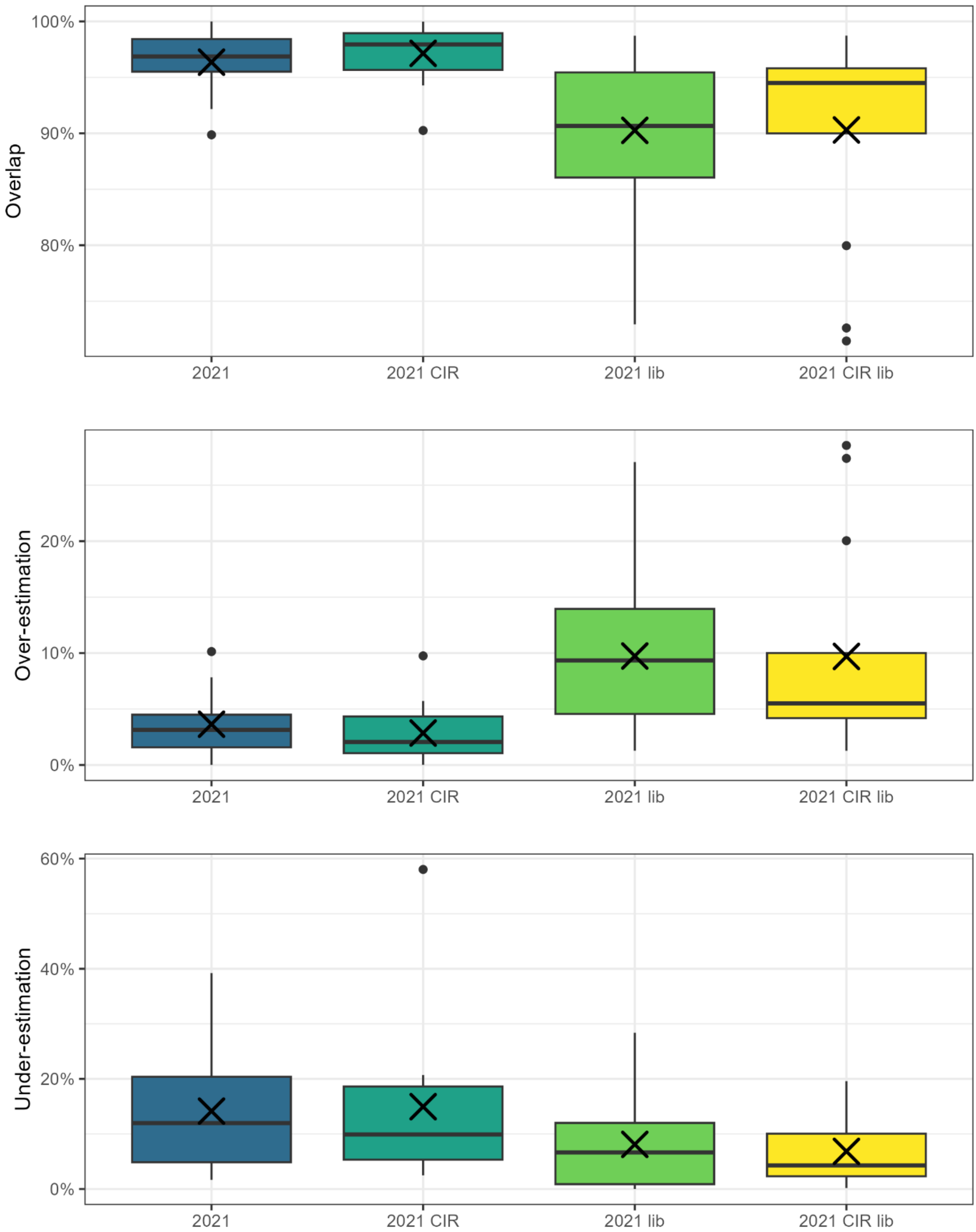

Figure 4: Boxplot showing the percentage overlap of the mapped non-eelgrass area (upper panel), over-estimation of seagrass area (middle panel), and under-estimation of the seagrass area (lower panel) of the four different 2021 polygons analysed from aerial photos (x-axis), compared to the 2022 polygon from the field mapping. The boxes show the interquartile range, with a black line and black cross inside the box representing the median and mean, respectively. Whiskers represent the smallest and largest value within 1.5x the interquartile range, and black points are outliers (>1.5 and <3 times the interquartile range).

3.2 Temporal Changes in Eelgrass Meadow Extent

3.2.1 Coastal Development

Temporal trends in eelgrass extent were assessed by calculating the inverse proportion of the non-eelgrass areas relative to the first mapped year and is shown in Figure 5. Temporal trends were variable between stations and did not show any consistent trend within a geographical area. Overall, the temporal trends are more varied before the early 2000s, while within the last decade or two, meadows extent seem to stabilize or expand. Alvekilen, Sandumkilen, Båssvika and Krossvigsundet all had a noticeable retraction toward the early 2000s, but the most profound changes are seen in Sandumkilen and Alvekilen. In Sandumkilen, eelgrass extent has a large expansion towards land until the end of the 1970, followed by a large retraction to about -70% in the early 2000s. In Alvekilen, the eelgrass extent steadily retracted until it, similar to Sandumkilen, reaches its lowest recorded extent of almost -70% in the early 2000s. A similar trend, although not as extreme, is seen for Båssvika, which has a ~20% retraction toward the early 2000s. For all three stations, the eelgrass meadows expand towards land again after the early 2000s. The Krossvigsundet meadow is stable until an abrupt retraction of -25% over an approximate 10-year period from 1999-2010, followed by an increase towards present.

The Hovekilen, Stølsvigen, Barmen and Røedsfjorden meadows were relatively stable. The Stølsvigen meadows showed a small expansion of ~15% towards the 1970s, and have since then been stable with an approximate +/-10% change over the last two decades. Both the Barmen and Røedsfjorden meadows had a small expansion over the study period. Most stable of all were the Hovekilen meadow, with less than +/-10% change throughout the whole study period. Kilen was the only station where there was no eelgrass meadow at the beginning of the mapping period. Here, no meadow appeared until after 2010, but over the last decade a meadow covering ~30% of the mapped area has emerged.

To assess potential effects of anthropogenic disturbances on eelgrass meadow extent, coastal development near the eelgrass meadows and the time of the occurrence were registered. A total of 62 anthropogenic disturbances (coastal development) were registered during the study period, and the number of disturbances at each station ranged from 0 (Barmen) to 13 (Stølsvigen and Krossvigsundet) between stations (Fig. 5). The most common disturbance was piers (38) and construction (22), with beach creation and dredging only accounting for 1 each. The number of disturbances was spread out over the study period, with an overweight of disturbances occurring after 1970. No consistent pattern was observed between temporal changes in eelgrass extent and the number of disturbances.

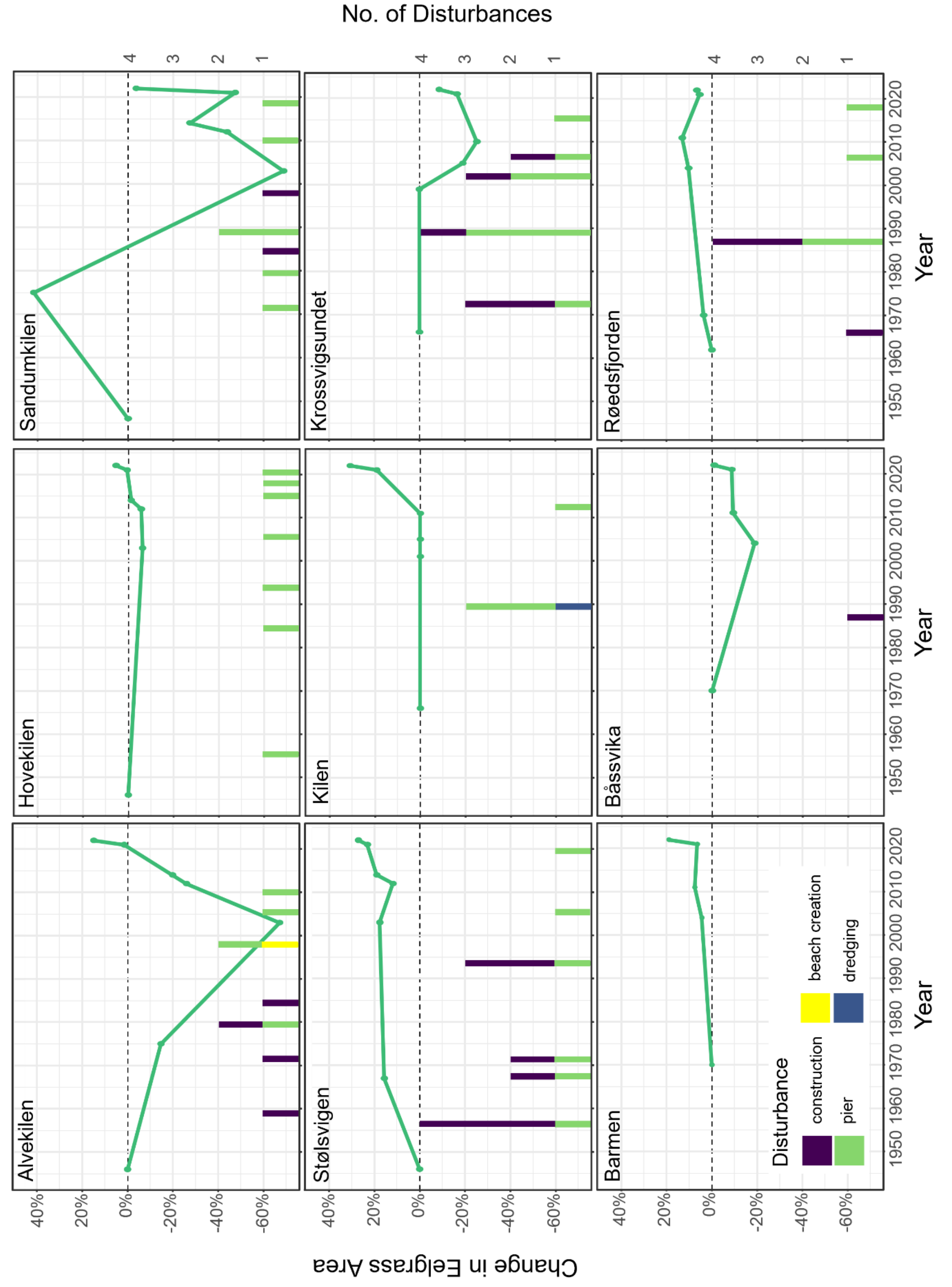

Figure 5: Change in eelgrass extent in percentage relative to the first mapped year (dotted line) is shown on the left-hand y-axis, with the solid green line showing the temporal trend. Number of anthropogenic disturbances (n) per year are represented by bars and are shown on the right-hand y-axis. Disturbances are divided into 4 types of coastal development: construction (purple), pier (green), beach creation (yellow), and dredging (blue).

3.2.2 Salinity Variation and Wave Exposure

To assess the how salinity variation and wave exposure may effect changes in eelgrass extent, the level of exposure was compared with temporal trends in the three geographical areas (Fig. 6). Salinity variation differed between stations (Fig. 6, column), with low salinity variation being most common. Low salinity variation was found for three of the Arendal stations, and both stations in Lillesand/Kristiansand. Only one station, Båssvika, has moderate salinity variation. High salinity was registered for Stølsvigen in Arendal, and Røedsfjorden and Barmen in Risør. Temporal trends in eelgrass extent were more stable at stations with high salinity variation, while for stations with a low salinity variation the trajectories were more variable. Low wave exposure was estimated for all stations, except for Hovekilen and Stølsvigen (Fig. 6, column). Hovekilen and Stølsvigen, which are the two least sheltered stations, are exposed to moderate and high wave height, respectively. Temporal trends in eelgrass extent were highly variable among stations with low level of wave exposure, while both stations with moderate and high wave exposure were relatively stable.

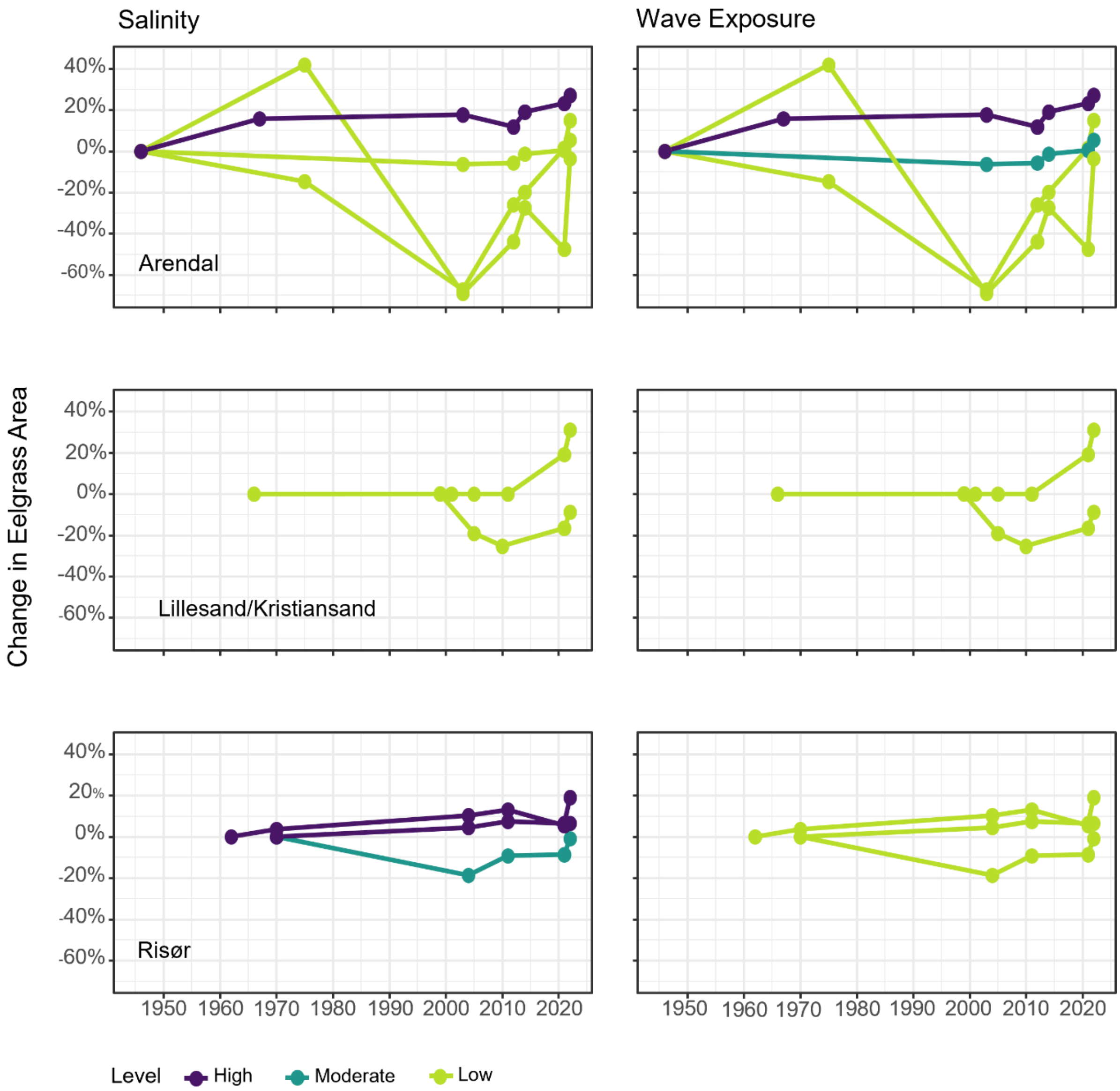

Figure 6: Temporal trend of eelgrass extent at stations in three geographical areas (Arendal, Lillesand/Kristiansand, and Risør). The colour of each line represents the level of salinity variation (left column) and wave exposure (right column), assigned to either high (purple), moderate (blue) or low (green) exposure level.

3.2.3 Human Population, Temperature and Nutrient Input

Effects of diffuse human impact was assessed by using human population as a proxy. Population within the catchment area of Agder has increased steadily since the 1930s and has accelerated slightly since 2010 (Fig. 7). Since 1970, there has been a decoupling of population growth and nutrient input.

To assess effects of temperature on changes in eelgrass extent, mean and maximum summer temperatures over the entire study period was collected (Fig. 7). Estimates of mean and maximum summer sea surface temperature show a decrease in temperature towards 1960, before it increased toward the early 2000s (Fig. 7). Since early 2000 temperatures have declined slightly again. However, there is a higher frequency of high maximum temperatures towards the end of the century, with maximum temperatures reaching >22°C or higher five times during the last 30 years, compared to only three times in the previous 50 years. Similarly, mean temperatures reached >15°C 15 times during the last 30 years, compared to six times during the previous 50 years.

Effects of nutrient loads in eelgrass extent was assessed by gathering available data on total phosphorus and nitrogen in the inner Oslofjord. Nutrient loads of total nitrogen and total phosphorus have decreased significantly over the last decades (Fig. 7). Nutrient loadings rapidly increased from the early 1900s until 1970. After 1970 phosphorus levels decreased and have remained low until present. Nitrogen levels stagnated in the 70s, and after the slight increase during the 80s, also decreased. Nitrogen levels showed an increase again in the early 2000s, but remain low compared to the peak between 1970-1990.

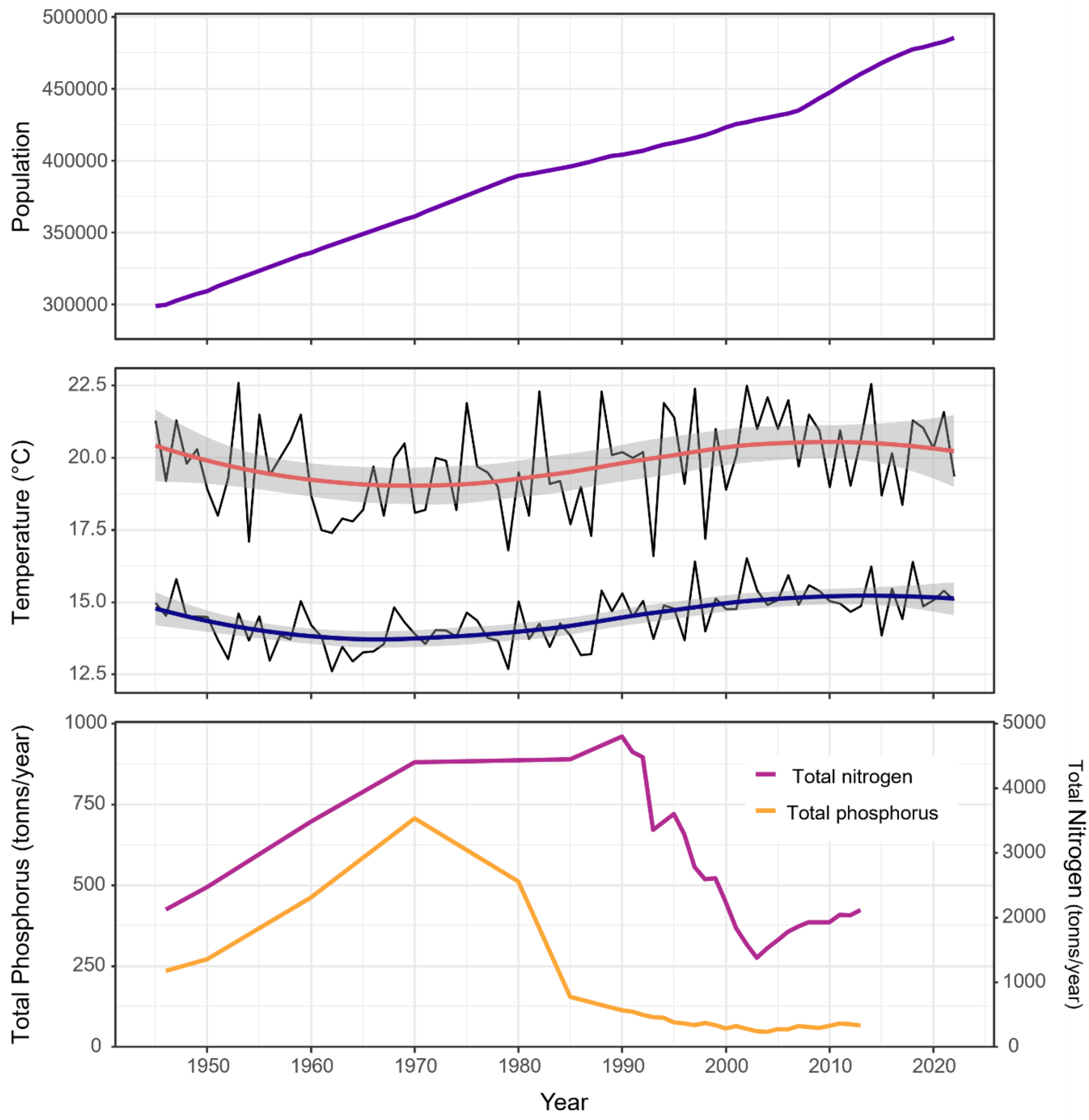

Figure 7: Upper panel shows the population within the catchment area of the southern Norwegian coast. Middle panel show the maximum (upper black line) and mean (lower black line) summer surface temperature at 1 m depth from 1 May-30 Sept. The red and blue line show the maximum and mean summer surface temperature, respectively, with confidence intervals (grey areas). Lower panel shows the yearly estimate of anthropogenic input of total phosphorus (orange line), and total nitrogen (pink line).

4. Discussion

This study is the first to examine to what extent aerial photography can be used as a tool for mapping eelgrass meadows in Norway. We found that aerial photography can be a useful tool for mapping meadow extent and for monitoring, but that the use is applicable only to shallow meadows (<2 m). Using this method, we have assessed the long-term changes in eelgrass meadow extent along the Norwegian Skagerrak coast. These results show that long-term trends are highly variable between sites. However, during the last two decades there seem to be a shift in trajectories, from variability to predominantly expansion.

4.1 Use of Aerial Photography for Mapping Eelgrass Extent

This study shows that aerial photography can serve as a valuable tool for mapping and assessing temporal variation in eelgrass meadow extent in shallow waters (<2). A high median overlap and a low median over- and under-estimation between the analysed aerial photos and the area mapped in field, show that eelgrass area can be identified quite successfully using aerial photography. As the conservatively drawn polygons had the lowest total difference in seagrass area compared to the liberal, the conservative polygons have been used for further assessment of temporal changes in this study.

Some deviation in the registered meadow extent between the field mapping (2022) and the aerial photo (2021) would be expected due to interannual variation. Under-estimating the eelgrass area was more common than over-estimation. When comparing field data with analysed aerial photography, Dolch, Buschbaum and Reise (2013) found that a cover density of about 20% was needed to detect seagrass in aerial photos. However, the photos used for their study was of a lower resolution compared to this study (0.4-0.5 m compared to 0.1-0.25 m), which will likely affect such estimations. Higher density makes for a more defined edge and higher contrast, and a certain density will be needed to detect eelgrass area. This implies that the accuracy of mapping will be lower for sparse meadows, or meadows with sparse edges. It also implies that seagrass area often will be, to some degree, under-estimated. In areas where the vegetation consists of both eelgrass and other submerged aquatic vegetation, other aquatic plants could be mistaken for eelgrass, or the other way around, especially if the nature of the meadow is patchy. Groundtruthing, or knowledge on the presence of other submerged marine vegetation at the mapped area, could reduce uncertainties in mapping. How easily eelgrass area is detected will also rely on the type of substrate the meadow occupies, where light, sandy substrate will make for a stronger contrast than that of a darker, muddy substrate, and thus be easier to detect. Furthermore, the stronger the contrast between substrate and meadow, the deeper it can be while still being able to separate meadow and substrate. However, at a certain depth, it becomes impossible to distinguish regardless, thus this method is mostly applicable in shallow, gently sloping areas along the coast. In study, the largest differences between the mapped area and the area analysed from photos was found for the darkest photos, or stations where the meadow edge was sparse, and vegetation was mixed. In addition, for the Kilen station there was some disturbance to the GPS signal in the beginning of the track. Thus, the overlap is lower, and the under-estimation is greater than would otherwise be expected.

The number of aerial photos available for mapping will be dependent on the timing of the photo (preferably during eelgrass growth season), and environmental conditions including wind and wave condition, reflections from the sun, shading, and water clarity. Geo-referencing methods vary between available photos, and the accuracy of older photos may have a higher standard deviation. However, information on accuracy is often not available. The 2021 photos used in this study have a standard deviation of 1.5 m, but for the other photos it was unknown. Geo-referencing methods differed between aerial photos used in this study, but seemed accurate. The 1975 photo for Sandumkilen, was however off by approximately 2 m. However, it was not distorted to a degree where I would consider it problematic to include in the assessment of temporal changes, but the uncertainty for this exact datapoint may be slightly higher compared to others.

A rapid development in remote sensing technology for mapping shallow water habitats has occurred during the last decade (Hossain et al., 2014; Veettil et al., 2020), but new technology cannot track temporal changes back in time. Present and historic knowledge on eelgrass meadow extent is substantially lacking in Norway. The large database of readily, geo-referenced aerial photos can serve as a cost-effective alternative to field mapping, and one of few sources for historic information for assessing eelgrass extent. We note that when using this method, the first year of available aerial photograph serves as a baseline for all subsequent years, but does not establish the ecological status of this baseline. In this study, we found that mapping was successful down to approximately 2 meters. Thus, mapping eelgrass meadow extent is applicable for meadows in very shallow waters, or for mapping shallow meadow edges. Furthermore, mapping eelgrass extent can serve as a complementary approach to modelling, or as a baseline and tool for further monitoring.

4.2 Temporal Trends in Eelgrass Meadow Extent

Temporal changes in eelgrass meadow extent in southern Norway were considerable, but showed different directions between stations. Trends were especially variable before 2000, but during the last two decades there seem to be a shift in trends. The high variability between stations observed before 2000 did not seem related to a geographical area, but rather to how sheltered the stations are. The largest fluctuations and the most pronounced changes were observed at the most sheltered stations, thus variability between stations seem highly connected to local conditions. Since the early 2000s a more general trend is observed between stations, where meadow extent is predominantly expanding. Still, the greatest change is observed for the sheltered stations, indicating that the response to different stressors may be highly localised. Below, I will explore how these different stressors could have driven the observed trends.

4.3 Possible Drivers of Change

Temporal trends show that eelgrass meadow extent seem highly affected by changes in water quality and seem highly dependent on local conditions such as hydrodynamics, depth and topography. The cumulative effect of deteriorated water quality and heat stress may have contributed to previous decline.

The large retraction observed at some of the stations (Fig. 5) coincided with a time where water quality in the Skagerrak and the surrounding seas were characterized by high levels of eutrophication. In the Oslofjord (Fig. 7) the increase was attributed to the introduction of water closets and a growing coastal population, and later to the use of cleaning agents and industrial wastewater treatment (Bergstøl et al., 1981). Although the nutrient levels in the Oslofjord is not directly transferrable to the Skagerrak, the coastal waters off Agder has likely been affected by the growing human population in a similar manner. While a considerable amount of nutrients also enters the ocean via rivers (Artioli et al., 2008), most of the nitrogen and large amount of phosphorus entering the Skagerrak is advected from the German Bight in the North Sea and the Kattegat (Aure et al., 1998). Similar trends in nutrient levels as those observed in the Oslofjord (Fig. 7) have been reported these surrounding seas, with reported eutrophication from the 50s and a peak in the 90s before nutrient loadings decreased (Carstensen et al., 2006; Vermaat et al., 2008; Voss et al., 2011). Eutrophication, as a result of increased nutrient input from land and surrounding oceans, is likely a main driver of the retractions in meadow extent towards the early 2000s.

In addition to the increase in nutrient input, coastal development became more intense with the growing human population in southern Norway (Fig. 7). The establishment of piers and marinas indicate increased boat traffic and general human activity, and sediment close to such areas tend to contain higher amounts of pollutants (Næs et al., 2002). Furthermore, boat propellers and anchoring can cause mechanical damage to seagrass meadows. All of these pressures are known to negatively impact seagrass meadows (de los Santos et al., 2019; Waycott et al., 2009). Maintenance of marinas can often include dredging, which can cause both physical damages, uprooting and increased sediment resuspension, and the effects of dredging has been identified as a threat to seagrass meadows (Orth et al., 2006; Waycott et al., 2009). However, dredging activities are poorly registered in Norway, and to what extent such events have occurred at the mapped stations is largely unknown. The introduction of piers could have contributed to shading and resuspension during construction, but such effects would likely be contained to a smaller area, considering the relatively small-sized piers at the mapped stations. What seem to be more problematic are the effects of coastal construction, and especially land-claim operations and road development which took place in Alvekilen, Sandumkilen and Båssvika. These events have undoubtably led to increased sediment resuspension and thus increased light attenuation on a local scale.

The temporal trends in eelgrass meadow extent in southern Norway are similar to the trends observed for seagrass meadows across the North Atlantic bioregion during the same period, and particularly other northern eelgrass populations (de los Santos et al., 2019; Dunic et al., 2021). Declines in Europe were mostly attributed to eutrophication, deteriorated water quality, and coastal development (de los Santos et al., 2019; Dunic et al., 2021). Similar to the North Atlantic, deteriorated water quality as a result of increased eutrophication and coastal development, is likely an important driver of the observed retractions in southern Norway towards the end of the century.

Over several decades, high river flow events, driven by rainfall, have been more frequent (Dyrrdal et al., 2018). This development has been especially clear in southern and western Norway (Dyrrdal et al., 2018). In addition, riverine discharge and export of particulate organic matter (POC and PON) and total suspended matter (TSM) into the Skagerrak has increased over the last three decades (Frigstad et al., 2023). As a result, there has been reported an ongoing "coastal darkening" of the Skagerrak, meaning light attenuation has increased as a result of increased turbidity (Frigstad et al., 2023). With the increased riverine input, and the following coastal darkening, one could expect the meadows near rivers to be more responsive to deteriorated water quality. Interestingly, the stations with highest salinity variation (more affected by freshwater discharge and thus turbidity) (Fig. 7) tend to be more stable, with little evidence of retraction during the last three decades. However, as light attenuation increases with depth**,** an increase in turbidity would typically lead to deeper meadows seeking refuge in shallower waters (Lefcheck et al., 2017). Thus, effects of this increase may not be detected at the shallow depths mapped in this study.

Despite the reported coastal darkening during the last three decades, monitoring of eelgrass depth distribution and cover in the Skagerrak show little signs of decreased water clarity. Although there is some variation between the monitored stations, there has been little change in eelgrass depth distribution since 1990 (Dahl et al., 2008; Lundsør et al., 2022). Most monitored stations showed a slight decrease in eelgrass cover in the 1980s and 90s, but increased slightly towards 2005, especially at depths shallower than 6 m (Dahl et al., 2008). Furthermore, Secchi depth measurements from the Skagerrak between 1990-2016 are dome-shaped, with shallowest depth measured around 2000, before returning to 1990 level (Frigstad et al., 2023). Further supporting the argument that conditions may have improved is the emergence of a new meadow at the Kilen station. Despite nutrient reductions and only one coastal development event over more than two decades, no meadow appeared until after 2010. Although the emergence of a meadow at a single station hardly makes a sound basis for drawing any conclusions, it is unlikely that the meadow appeared under worsened condition, which makes the argument that, at least for this station, environmental conditions have likely improved. These results suggest that water clarity may in fact have been lower around 2000, and that light conditions have improved since then.

The shift in trends to predominantly expanding from the early 2000s could be a response to reduced eutrophication. Although nutrient levels have decreased since the 90s (Frigstad et al., 2023), the effect may have had a time-lag response. The coastal zone can efficiently retain nitrogen and phosphorus, especially in shallow coastal systems, thereby reducing eutrophication (Almroth-Rosell et al., 2016; Hayn et al., 2014). However, during times of high nutrient loading the capacity to retain nutrients can be lower, and thereby eutrophication is reduced to a lesser extent. Following nutrient reduction, it may take time to restore the retention capacity, causing a potential years-long time-lag response (Almroth-Rosell et al., 2016). In the Baltic Sea, Andersen *et al.* (2017) found that despite significant reductions in nutrient input along the coast of the southern North Sea and the southwestern Baltic Sea, phytoplankton did not decrease at a similar rate, and signs of improvement in the Kattegat were not observed until

2010 and 2011. Similarly, large reductions of nutrient input into the Skagerrak has been accompanied by a simultaneous decreased in chlorophyll a concentrations and phytoplankton biomass (Frigstad et al., 2017, 2023). However, phytoplankton biomass was still significantly higher in 1994-2001 compared to 2002-2011 (Frigstad et al., 2017). With growing signs of reduced eutrophication, this development may have contributed to the increased water clarity reported since the 2000s, and have likely contributed to the expansion in meadow extent during the last two decades.

Heat stress could have exacerbated effects of deteriorated water quality, especially in the most shallow and sheltered stations. Filbee-Dexter *et al.* (2020) found that both frequency and intensity of marine heatwaves have increased largely in southern Norway over the last 60 years (2020). The intensity of marine heatwaves increased 340% over the past 30 years, compared to the preceding 30, and most MHW categorized as severe and extreme (Hobday et al., 2016) have occurred in the last two decades. These results are similar to the temperature trends registered in Agder (Fig. 6). Eelgrass is known to occupy a wide range of temperature regimes (Lee et al., 2007), and seagrasses have shown a great capacity to acclimate to thermal changes (Zimmerman et al., 1989). However, studies have shown that seagrasses can be sensitive to thermal stress (Stipcich et al., 2022), likely as an effect of increased metabolic rates, which in turn can cause a negative carbon balance (Marsh et al., 1986). Negative effect of thermal stress has been especially clear during short-term exposure (Lefcheck et al., 2017; Marsh et al., 1986; Zimmerman et al., 1989), and there is mounting evidence that the cumulative effect of increased temperatures and decreased light availability can be detrimental to seagrass meadows. Large-scale losses of eelgrass in Chesapeake Bay have been repeatedly attributed to periods of increasing temperatures in combination with increased turbidity (Lefcheck et al., 2017; Moore et al., 2014; Moore & Jarvis, 2008), and a similar effect has been reported for other seagrass species in Australia (Kendrick et al., 2019; Strydom et al., 2020).

Although temperatures observed in Agder are well within the tolerance threshold for eelgrass, and substantially lower than the temperatures associated with the losses in Chesapeake Bay, studies indicate that there are regional differences in temperature tolerance (Bergmann et al., 2010; Winters et al., 2011), and that high-latitude populations tend to be more sensitive to thermal stress compared to low-latitude populations (Winters et al., 2011). Thus, although less extreme than temperatures previously related to eelgrass losses, the observed temperatures in Agder may still be damaging to high latitude eelgrass populations such as those mapped in this study, especially during times of reduced light availability. Although heatwaves have become more frequent also during the last two decades, such effects may have been alleviated by the improved water quality in recent years.

The changes in water quality and thermal stress discussed above fail to explain the large variability observed between stations before the early 2000s. However, there seem to be a connection between differences in trends and how sheltered or enclosed the stations are. Alvekilen, Kilen, Krossvigsundet, Båssvika and Sandumkilen are all very sheltered stations, with Sandumkilen being almost completely enclosed. These stations are also where changes are most pronounced. Waters in sheltered areas tend to have higher water residence times, and are typically characterized by higher temperatures, higher levels of eutrophication, and algal blooms (Lillebø et al., 2005; Maxwell et al., 2017). Furthermore, the effects of thermal stress have been found to be particularly problematic in shallow waters (Krause-Jensen et al., 2021; Lefcheck et al., 2017). This would explain the dramatic retraction observed in Alvekilen and Sandumkilen, where parts of the meadows are located at depths very shallow depths. As sheltered areas can allow for unfavourable conditions to prevail, these meadows are likely more susceptible to the effects of deteriorated water quality and increased temperatures, which could explain the variability in trends between stations. This also implies that changes in meadow extent may be highly localised, and that the effect of stressors could be alleviated or exacerbated, depending on topography and hydrodynamic conditions.

The shifting trends in recent years reported in this study stands in contrast to the initial hypothesis, but is similar to the trend reversal reported for seagrasses in Europe. This trend has mainly been attributed to management action, mostly targeted at reducing nutrient loads and improving coastal water quality, as well as the measures aimed at direct habitat protection (de los Santos *et al.* 2019). Such actions have consisted of regulation of dredging and anchoring, but mostly of water quality improvements. However, despite increased management action and reduced nutrient input in European seas (Carstensen et al., 2006; Vermaat et al., 2008; Voss et al., 2011), 57% of the surveyed European seagrass sites are still in decline (de los Santos et al., 2019). This development is also reflected for seagrass meadows in the nearby regions of Sweden and the Baltics, where despite improvements in water quality, recovery has been mostly absent (Krause-Jensen et al., 2021; Moksnes et al., 2018). In contrast, intertidal *Zostera* meadows in the North Wadden Sea have persisted, following an intermittent decline in the 80s and 90s related to eutrophication (Dolch et al., 2013). In the Baltic Sea, it is suggested that recovery from eutrophication is supressed by increasing temperature and bottom trawling (Krause-Jensen et al., 2021). Along the Swedish Skagerrak coast, almost 60% of eelgrass area was lost between 1980-2000 (Baden et al., 2003). Most of these losses were human induced, with 50% being attributed to reduced water transparency (Baden et al., 2003). Since then, losses have continued, and sediment resuspension and drifting algal mats have acted as hindrances to natural recovery and restauration (Moksnes et al., 2018). In contrast, eelgrass meadows in southern Norway have shown high persistence, and the ability to naturally recover. This study also contrasts the results of the only other study on changes in Norwegian eelgrass from northern Norway (Jørgensen & Bekkby, 2013), highlighting regional differences at multiple scales.

5. Conclusions and Implications for Future Research and Management

This thesis show that aerial photography can serve as a useful tool for mapping eelgrass meadow extent in shallow parts of the meadow, or in areas where the whole meadow is located at very shallow depths (approximately 2 m in this area). Using this method, we revealed great variability in long-term trends in eelgrass meadow extent between stations. However, during the last two decades there seem to be a shift in trajectories from high variability, to predominantly expansion. These results suggest there is an ongoing natural recovery of eelgrass meadows in southern Norway. This stands in stark contrast to the initial hypothesis and the earlier mapping of eelgrass in Troms, highlighting regional differences on multiple scales. The variability between stations indicate that temporal trends are likely a result of local changes in water quality, and that these changes are dependent on local conditions such as hydrodynamics, depth and topography. Furthermore, it seems that thermal stress (repeated heatwaves) may further exacerbate the effects of deteriorated water quality. This study further highlights that potential effects of stressors should be assessed on both a regional and local scale.

Aerial photos from *Norge i bilder* are readily available, geo-referenced, and are among few sources of historic information on eelgrass extent. The method used in this thesis can serve as a cost- and time-efficient alternative to field mapping, and can be used as a complementary approach to modelling. Furthermore, aerial photos could provide a baseline for monitoring, and could be used in combination with historic and future data, gathered through already established monitoring programs covering presence/absence, cover, and depth limit. This method could potentially give further insight into the processes governing eelgrass meadow change along the

Norwegian coast. As repeated thermal stress and degraded water quality are likely important drivers of retractions observed in this study, strengthening the mapping and monitoring effort of eelgrass will be increasingly important with the changing climate. The strongly localised response to stressors also emphasises the important of assessing the potential effect of stressors on both a local and regional scale, and these considerations are important to include in management action. It also calls for a greater monitoring and mapping effort, as there is a need for a larger dataset to conclude on a general trend across the Skagerrak.

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Appendix

Appendix A – Aerial Photos of Mapped Stations

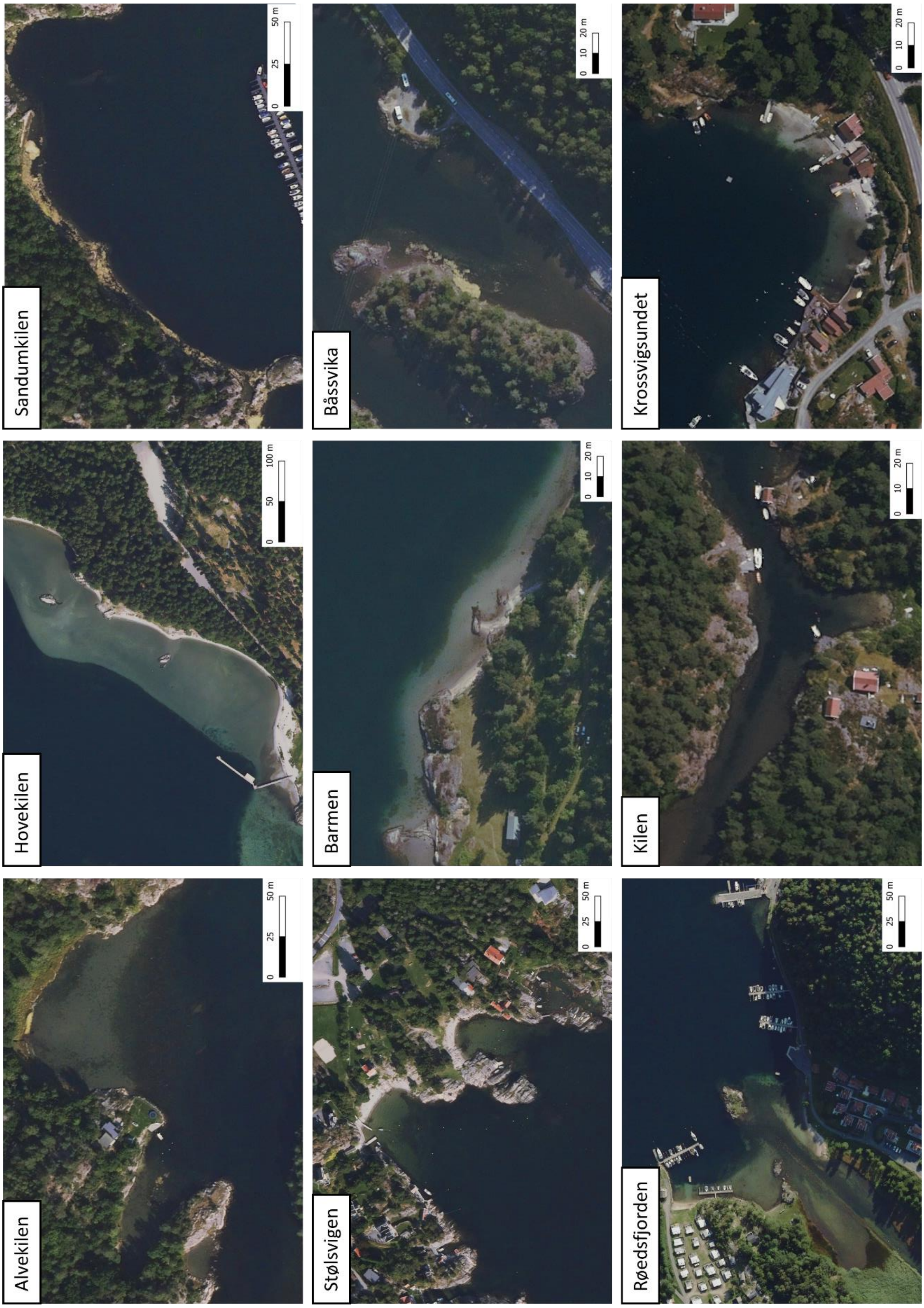

Figure A: Aerial photo showing each of the mapped stations and their station name (see Table 1). For Alvekilen and Stølsvigen, two stations are located right next to each other, Alvekilen West (left) and Alvekilen East (right), and Stølsvigen North (left) and Stølsvigen South (right). All aerial photos are from 2021.

Appendix B – Aerial photo Reference List

© Statens kartverk, Geovekst og kommunene, Agder og Telemark CIR 2021.

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Appendix C – Aerial Photo Selection

Table C: The selection of aerial photos used for mapping eelgrass area extent at the 11 stations, showing the year of the photo, total number of photos per station, and the year span that was mapped for each station. For those station where there were two photos that fit the selection criteria within the same year, both photos were used for mapping.

	Station										
	AW	AE	Ba	Bå	Ho	Ki	Kr	Rø	Sa	SN	SS
Year											
1946	1	1			1				1	1	1
1962								1			
1966						1	1				
1967										1	1
1970			1	1				1			
1975	1								1		
1975											
1999							1				
2001						1					
2003	1	1			1				1	1	1
2004			1	1				1			
2005						1	1				
2010							1				
2011			2	2		2		2			
2012	2	2			2				2	2	2
2014	1	1			1				1	1	1
2021	2	2	2	2	2	2	2	2	2	2	2
Total	8	7	6	6	7	7	6	7	8	8	8
Year span	76	76	52	52	76	56	56	60	76	76	76

Appendix D – Kilen Meadow Area

Table D: Total area (m^2) of the eelgrass meadow at the Kilen station for each mapped year, and the type of photo used for mapping.

Year	Photo type	Eelgrass area (m^2)
2022	Colour	1249
2021	Colour	779
2021	CIR	765
2011	Colour	0
2011	IR	0
2005	Colour	0
2001	Colour	0
1966	Black and white	0