



PROJECT SEAGRASS

The ecosystem
service role of UK
Seagrass meadows
Project Seagrass – May 2021

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1. Understanding the importance of the UKs Seagrass meadows

Seagrasses (often referred to as eelgrass) are a group of plants adapted to life in the sea, but are distinct from macroalgae (seaweeds). Seagrass meadows in the UK provide a home to around 50 species of fish and they have particular importance as a nursery ground for juvenile cod, pollack, whiting and plaice, as well as herring and sea bass (Bertelli and Unsworth 2014). Despite their high importance recent estimates indicate that the long-term loss of these habitats extends from between 44 and 92% (Green et al. 2021). The reasons for this are complex and range from problems caused by poor water quality (Jones and Unsworth 2016), to impacts from boating and land reclamation (Unsworth et al. 2017). As seagrasses have declined in coverage, so has the appreciation for why these habitats are of importance. There is now a need to fill the charisma gap and provide more detailed information on why these habitats are of value to humans (Unsworth et al. 2019a). Although information on many aspects of the importance of seagrasses in the UK is available, such information has not previously been collated as a summary report. Here we provide a detailed examination of the value of seagrass meadows in the UK through the lens of ecosystem services. This includes a detailed review of local UK information in the context of our global seagrass knowledge, and where gaps in the knowledge are present additional information has been included from beyond the UK. In this present review, particular focus has been given to the role that seagrasses play in supporting birds, previously this topic has received limited attention beyond the links between seagrass and direct grazing birds.

Table 1. EUNIS biotopes listed for UK seagrass meadows. The inclusion of *Z. angustifolia* within this classification remains but requires revision to reflect its taxonomic status as an ecotype of *Z. marina*.

EUNIS Code	MNCR Code	Biotope Description
A2.6	LS.LMp	Littoral sediments dominated by aquatic angiosperms
A2.61	LS.LMp.LSgr	Seagrass beds on littoral sediments
A2.611	-	Mainland Atlantic [<i>Zostera noltii</i>] or [<i>Zostera angustifolia</i>] meadows
A2.6111	LS.LMp.LSgr.Znol	[<i>Zostera noltii</i>] beds in littoral muddy sand
A2.614	-	[<i>Ruppia maritima</i>] on lower shore sediment
A5.53	SS.SMp.SSgr	Sublittoral seagrass beds
A5.533	-	[<i>Zostera</i>] beds in infralittoral sediments
A5.5331	SS.SMp.SSgr.Zmar	[<i>Zostera marina</i>]/[<i>angustifolia</i>] beds on lower shore or infralittoral clean or muddy sand
A5.5343	SS.SMp.SSgr.Rup	[<i>Ruppia maritima</i>] in reduced salinity infralittoral muddy sand

2. Habitat introduction

2.1 Overview

Seagrass beds are biogenic habitats formed by flowering plants (angiosperms) adapted to saline conditions. These plants are rhizomatous in that they have stems that spread horizontally below the sediment surface, and shoots that grow above the surface forming expansive 'meadows' in both the intertidal and shallow subtidal zones. In contrast to other marine vegetation (e.g. macroalgae), seagrasses flower, develop fruit and produce seeds like terrestrial plants. They also have roots and a vascular system that transports gases and nutrients around the plant.

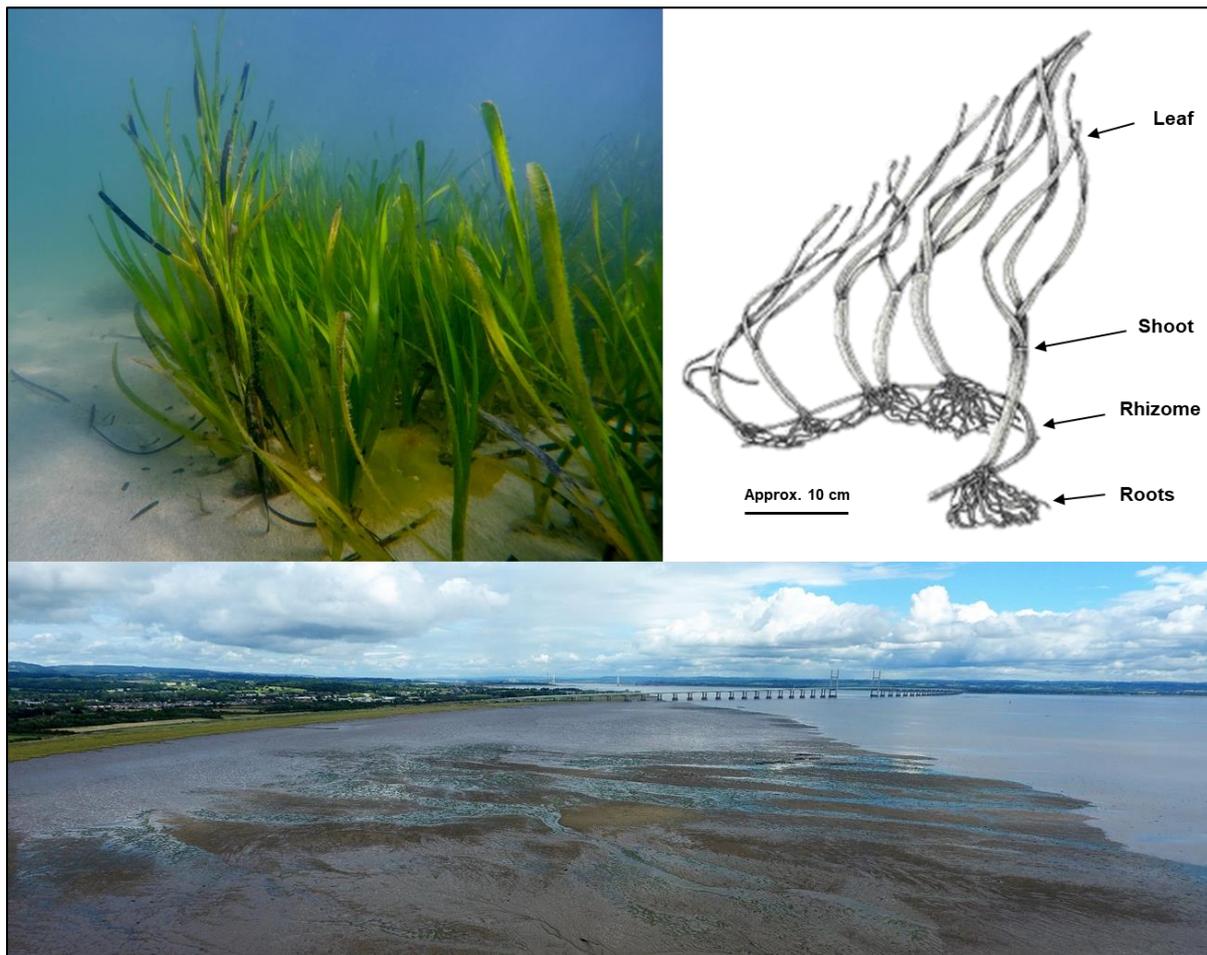


Figure 1 Left: *Zostera marina* at Porthdinllaen © R.K.F Unsworth. Right: Schematic of *Zostera marina* plant (Dawes 1998). Bottom: intertidal *Z. noltii* and *Z. marina* bed in the Severn Estuary, South Wales © Ocean Ecology Limited.

In the UK there are two recognised species of seagrass; eelgrass (*Zostera marina*) and dwarf eelgrass (*Z. noltii*). A third species (narrow-leaved eelgrass *Z. angustifolia*) continues to be recorded in the UK (chiefly during Water Framework Directive (WFD) (2000/60/EC) monitoring) despite genetic evidence indicating that it is an ecotype of *Z. marina* (Becheler et al. 2010). As such, *Z. angustifolia* is not recognised by the international seagrass scientific community and does not appear in major publications about global or European seagrass

(Borum et al. 2004; Short et al. 2011). The use of this species should be discontinued in the UK. *Z. marina* is an intertidal to sublittoral species found in shallow, fully marine conditions on muddy to relatively coarse sediment. When observed intertidally it can sometimes be interspersed with *Z. noltii* in between the mid- and low-tide mark. In these cases it is usually recorded as *Z. marina* var. *angustifolia*, preferring poorly drained muddy sediments, particularly pools, creeks and wet sand ripples that are unlikely to entirely dry out during low tide. *Z. noltii* occurs higher on the shore to the high-tide mark, on mud, sand and muddy sands and, being more tolerant of desiccation, will inhabit areas that entirely dry out at low tide.

The taxonomy of the dwarf eelgrass is also problematic as the World Register of Marine Species (WoRMS) nomenclature does not accept *Z. noltii* and suggests that it should be recorded as *Zostera (Zosterella) noltei*. There is also current discussion as to whether dwarf eelgrass may in fact be of a separate genus, *Nanozostera noltii* (Coyer et al. 2013).

Widgeon grass (*Ruppia* sp.) is a genus of aquatic freshwater plants found in the UK that have similar environmental preferences to *Zostera* spp. i.e. temporarily to permanently flooded mesohaline-hyperhaline estuarine wetlands (Kantrud 1991) brackish waters of lagoonal habitats, lochs and estuaries. The two species of widgeon grass found in the UK (beaked tasselweed, *R. maritima* and spiral tasselweed, *R. cirrhosa*) are not strictly considered as part of the traditional seagrass arrangement (Kuo and den Hartog 2001) but are commonly grouped with *Zostera* spp. as they can occupy a similar niche due to their pronounced salinity tolerance. In this review we focus on the two species of *Zostera*.

2.2 Sub-habitat types

A variety of physical, biochemical and biological factors regulate the colonisation, growth and health of seagrasses. Physical factors include light, substratum and wave exposure. Biological factors include the associated grazing community (controlled through top-down processes of predation) (Reynolds et al. 2018) and the connectivity of the bed with other beds within a wider seascape (Perry et al. 2018). It is the balance of these factors that govern the distribution of the seagrass bed sub-habitat types. These include both mono-specific and two-species strands.

The majority of seagrass beds around the UK are thought to be representative of two intertidal and two subtidal biotopes listed in the European Nature Information System (EUNIS) habitat classification system. These mostly occur on muddy sand sediments: however, some beds have also been recorded on mixed sediments (e.g. the 'Welsh Grounds' bed in the Severn Estuary) that may warrant addition of further mixed sediment biotopes. Biotope mosaics also exist where two or more of the listed biotopes occur over small spatial scales (<25 m²). The most common seagrass mosaic biotope occurs on the lower shore where the lower portions of *Z. noltii* beds merge with the upper portions of *Z. marina* beds or where semi-permanent channels run down the shore. This is represented as either A2.6111 / A5.5331 or A5.5331 / A2.6111 depending on the predominant biotope (Parry 2019).

For WFD monitoring purposes, intertidal seagrass beds are further subdivided into sub-habitats representing >5 % coverage and <5 % coverage, the latter commonly associated with the periphery of the bed (UKTAG 2014).

2.3 Conservation importance

As bioengineers, seagrasses play an important role by establishing positive feedbacks that lead to the local environment becoming more affable for both their own productivity and for that of associated flora and fauna (Maxwell et al. 2017). This trait ultimately leads to seagrass beds being highly valued for the ecosystem services they provide (Costanza et al. 1997; Mtwana Nordlund et al. 2016; Unsworth et al. 2019b). By developing a 3-dimensional structure in an otherwise barren seascape, seagrasses slow the movement of water, resulting in filtration and subsequent trapping of suspended sediments and particles (Maxwell et al. 2017). This also reduces nutrients (McGlathery et al. 2007), bacteria and viruses (Lamb et al. 2017; Reusch et al. 2021). Additionally, the 3-dimensional structure also provides extensive habitat for a range of animals and plants, ultimately leading to seagrass meadows supporting the coastal food web, including providing support for fisheries (Unsworth et al. 2019b). The habitat they create is now becoming increasingly recognised globally for the role it plays in storing and sequestering carbon (Röhr et al. 2018) and for how it helps to reduce coastal erosion (Ondiviela et al. 2014).

In recognition of their ecological and economic importance, seagrass beds are afforded protection by a variety of conservation legislation and policies resulting in their designation as protected features of Marine Protected Areas (MCZs and SACs). They also have protection as habitat in support of seahorses under the Wildlife and Countryside Act 1981. Seagrass beds also qualify as 'higher sensitivity' habitats in the Environment Agency guidance for undertaking WFD assessments in estuarine and coastal waters and represent a sub-element (along with saltmarsh) of the angiosperm Biological Quality Element (BQE), one of the five BQEs used to classify the ecological status of waterbodies.

3. Ecosystem services

3.1 What are Ecosystem Services?

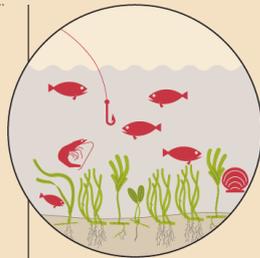
Ecosystem services are defined as the direct and indirect contributions of ecosystems to human wellbeing, and have an impact on our survival and quality of life. There are four types of ecosystem services: provisioning, regulating, cultural and supporting services.

The term "ecosystem services" is relatively new, first used to ascertain the value of nature to bring attention to environmental degradation. In 2011 research estimated that ecosystems provide the equivalent of \$125 trillion in services to our planet per year (Costanza et al. 2014). Our growing understanding of the true worth of nature is worrying when set against the degradation ecosystems face as global loss of ecosystem services due to land use change is \$US 4.3–20.2 trillion/yr (Costanza et al. 2014).

SEAGRASS ECOSYSTEM SERVICES

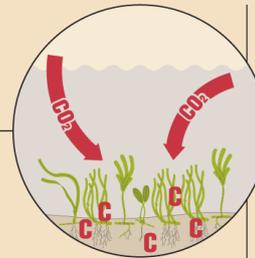
FISHERIES

SEAGRASSES SUPPORT GLOBAL FISHERIES AND PROVIDE NURSERY HABITATS FOR COMMERCIALY TARGETED FISH, BIVALVE AND CRUSTACEAN SPECIES.



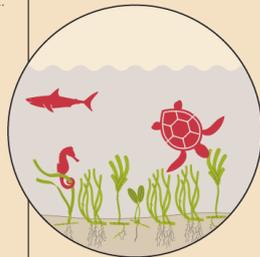
CLIMATE REGULATION

SEAGRASS MEADOWS STORE LARGE AMOUNTS OF CARBON IN THE BIOMASS AND SEDIMENT BELOW, HELPING TO MITIGATE CLIMATE CHANGE.



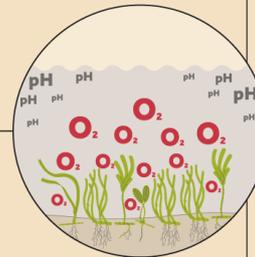
BIODIVERSITY

SEAGRASS MEADOWS ARE HOTSPOTS OF MARINE BIODIVERSITY, INCLUDING PROTECTED AND CHARISMATIC SPECIES SUCH AS DUGONGS, SEA TURTLES, SHARKS AND SEAHORSES.



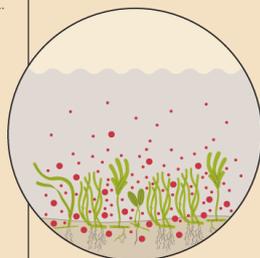
OCEAN ACIDIFICATION BUFFER

SEAGRASS MEADOWS REGULATE THE CHEMICAL COMPOSITION OF SEAWATER BY RELEASING OXYGEN AND REMOVING CARBON DIOXIDE DURING DAYLIGHT, OXYGENATING WATER AND BUFFERING OCEAN ACIDIFICATION.



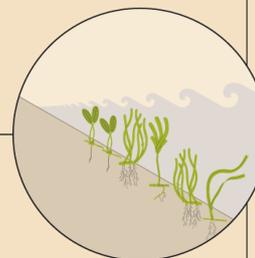
WATER FILTRATION

SEAGRASSES ARE NATURAL FILTERS TRAPPING SEDIMENTS AND EXCESSIVE NUTRIENTS OUT OF THE WATER.



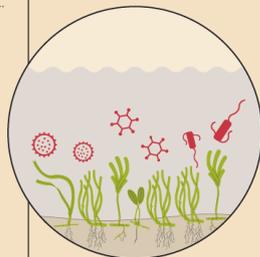
COASTAL PROTECTION

SEAGRASSES PREVENT COASTAL EROSION AND PROTECT FROM FLOODING AND STORM SURGES.



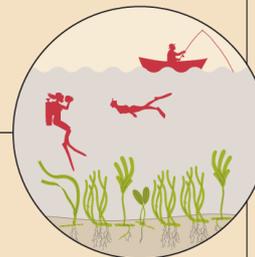
DISEASE CONTROL

SEAGRASSES CONTROL HUMAN, FISH AND CORAL DISEASES BY REDUCING EXPOSURE TO PATHOGENS.



TOURISM

SEAGRASS MEADOWS PROVIDE CULTURAL SERVICES SUCH AS SENSE OF IDENTITY FOR LOCAL COMMUNITIES AND OPPORTUNITIES FOR RECREATIONAL ACTIVITIES (E.G. BIRDWATCHING, DIVING, FISHING).



Source: GRID-Arendal (2020).

Figure 2. Summary figure explaining the breakdown of seagrass ecosystem services into some of the main component services (source: UN Grid Arendal).

3.1.1 Provisioning services

Provisioning services are characterised by the ability of humans to obtain products from ecosystems, such as food, water and resources, including wood, oil and genetic resources and medicines.

3.1.2 Cultural services

Cultural services include non-material benefits that people can obtain from ecosystems. These include spiritual enrichment, intellectual development, recreation, and aesthetic values. These types of services can be hard to monitor, and value compared to regulating and provisioning services, but research in this area is growing. For example, studies have shown that an ability to see or interact with nature, through hospital windows or hospital gardens respectively, increases the speed of patient recovery.

3.1.3 Supporting services

Supporting services are those which relate to habitat functioning themselves, and therefore influence survival. For example, photosynthesis, the water cycle and nutrient cycles are the basis of ecosystems, which in turn allow us to support ourselves. This type of ecosystem service also goes down to the genetic level, such as the maintenance of viable species gene pools.

3.1.4 Regulating services

Regulating services are categorised as any benefit obtained from the natural processes and functioning of ecosystems. Examples include climate regulation, flood regulation and other natural hazard regulation, pollination, water purification and more. For example, natural water purification services in Europe are valued at an estimated €33 billion per year. Further, pollination by wind and insects is a service that would not be possible without nature, particularly bees, as discussed in another one of our articles on the climate crisis and bees.

Table 2. Ecosystem services in the UK NEA classified according to both ecosystem service type (provisioning, regulating, cultural and supporting) and whether or not they are final ecosystem services or intermediate services and/or processes. For each final ecosystem service an example of the good(s) it delivers is provided in italics (Assessment 2011).

Ecosystem processes/intermediate services		Final ecosystem services (<i>example of goods</i>)	
Supporting services	<ul style="list-style-type: none"> • Primary production • Soil formation • Nutrient cycling • Water cycling 	Provisioning services	<ul style="list-style-type: none"> • Crops, livestock, fish (<i>food</i>) • Trees, standing vegetation, peat (<i>fibre, energy, carbon sequestration</i>) • Water supply (<i>domestic and industrial water</i>) • Wild species diversity (<i>bioprospecting, medicinal plants</i>)
	<ul style="list-style-type: none"> • Decomposition • Weathering • Climate regulation • Pollination • Disease and pest regulation • Ecological interactions • Evolutionary processes • Wild species diversity 	Cultural services	<ul style="list-style-type: none"> • Wild species diversity (<i>recreation</i>) • Environmental settings (<i>recreation, tourism, spiritual/religious</i>)
		Regulating services	<ul style="list-style-type: none"> • Climate regulation (<i>equable climate</i>) • Pollination • Detoxification and purification in soils, air and water (<i>pollution control</i>) • Hazard regulation (<i>erosion control, flood control</i>) • Noise regulation (<i>noise control</i>) • Disease and pest regulation (<i>disease and pest control</i>)

The loss, therefore, of ecosystem services is not just an environmental issue, but an economic and social issue as it not only affects the environment, but the economy and individual well-being. However, the holistic nature of ecosystem services and their interactive behaviour means that common anthropogenic pressures often affect more than one service. However, habitat destruction, pollution, and invasive species are among the most prolific threats to ecosystem services.

4. Seagrass supporting ecosystem services

4.1 Seagrass support for Biodiversity

Biodiversity is the biological variety and variability of life on Earth. Biodiversity is typically a measure of variation at the genetic, species, and landscape scales. Biodiversity is important for the functioning of the biosphere, a revelation recognised by the United Nations as leaders pledged to reverse biodiversity loss by 2030 (Vaughan 2020). This is considered to be a supporting service of seagrass meadows. In coastal ecosystems, seagrass beds are some of the most biodiverse habitats (Jackson et al. 2006b) but have suffered dramatic losses due to a multitude of factors (Duarte 2002). Fortunately, seagrass has been subject to conservation legislation by the UK's Biodiversity Action Plan list of priority habitats, the EU Habitats Directive, and in the designation of Marine Conservation Zones (MCZs) (Peters et al. 2014), in hope of improving the status of these systems to support biodiversity.

Seagrass meadows are renowned for their transformative abilities, turning bare homogenised habitats such as sand or mud into structurally complex, productive ecosystems (Bostrom et al. 2006) supporting greater invertebrate (Orth et al. 1984; Tu Do et al. 2012), fish (Zarco-Perello and Enríquez 2019) and bird (Mosbahi et al. 2017) diversity than adjacent sand and mud environments. The increased complexity provides shelter from predation (Whalen et al. 2020), more ecological niches (Boyé et al. 2017) and a wide range of food resources (Heck and Valentine 2006) that enriches faunal species, bolstering the ecosystem against perturbations (Thormar et al. 2016). These ecological advantages make seagrass beds important nursery and feeding habitats for invertebrates and fish (Heck et al. 2003) which support fisheries (Jackson et al. 2001; Lefcheck et al. 2019) and adjacent habitats (Unsworth et al. 2008).

4.1.1 Drivers of seagrass biodiversity

The faunal variability within seagrass beds is driven by increased structural complexity (McCloskey and Unsworth 2015; Smale et al. 2019; Webster et al. 1998), which provides more ecological niches (Mosbahi et al. 2016), refuge from predation (Boyé et al. 2017; Reynolds et al. 2018), more diverse and abundant food sources (Lebreton et al. 2012) and stable hydrological and sedimentary conditions (Boyé et al. 2017) (Figure 3). Seagrass's ability to supply these provisions to a range of different species earns seagrass recognition as an important coastal engineering species (Maxwell et al. 2017).

Seagrasses also alter the biophysical properties of marine sediments. Their high level of primary productivity involving rapid photosynthesis over periods of the day necessitates the exudation of oxygen through their roots as well as their leaf surface. Such oxygen exudation aids with the oxidation of sedimentary sulphides leading to a more affable environment for

invertebrate infauna (Brodersen et al. 2018). The oxidation of these sediments is particularly thought to be increased as a result of a three-way symbiosis of seagrass with Lucinid bivalves and sulphide reducing bacteria (Peterson and Heck 2001; van der Heide et al. 2012).

The diversity of micro-habitats generates a biodiverse invertebrate community (Rueda et al. 2009) with an abundant food supply, as seagrass acts as a sink for organic matter (Janas et al. 2019). However, biodiversity drivers differ amongst infaunal and epifaunal communities.

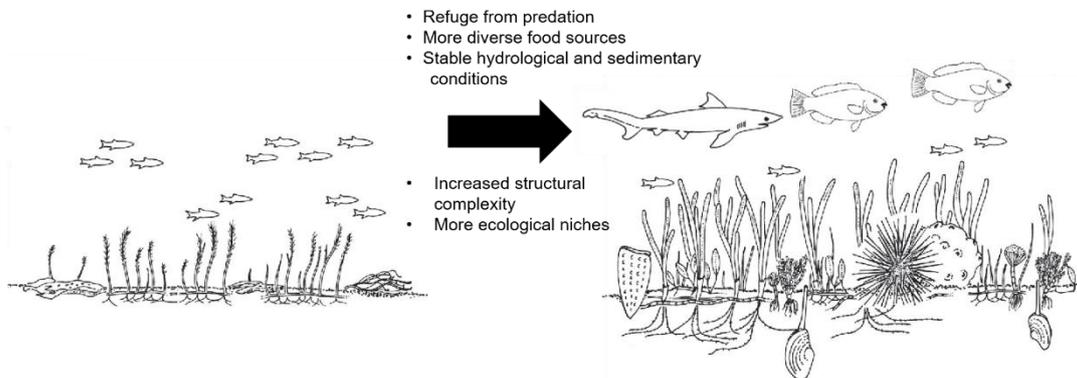


Figure 3. Illustration adapted from Duffy (2006) displaying the increased biodiversity coupled with a more complex seagrass habitat and main drivers labelled.

Infaunal communities are structured by sedimentary conditions and the forces influencing their structure (Gray 1974). Epifaunal communities are instead influenced more strongly by local hydrological conditions (Boyé et al. 2017), directly by currents (Hovel et al. 2002) or indirectly by the interception and retention of nutrients by seagrass's structure and characteristics (Bostrom and Bonsdorff 2000; Moore and Short 2006). Anthropogenic influence has been proven to reduce the invertebrate biodiversity within seagrass beds too (Cullen-Unsworth et al. 2014).

In addition to increased structural complexity and the beneficial drivers that ensue, fish diversity is influenced by invertebrate richness and abundance, due to their trophic significance as prey (Lebreton et al. 2012), and as a result of varying seascape complexity. Less complex seascapes such as large continuous seagrass beds attract juvenile fish assemblages and migrating fish that prey upon them, whilst more complex seascapes such as patchy seagrass beds attract fish taxa known to use multiple habitats (Staveley et al. 2017).

4.1.2 Faunal composition in *Zostera marina* and *Zostera noltii* meadows

Fish communities

Seagrass meadows are known to be one of the most biodiverse subtidal habitats (Jackson et al. 2006b); reflected in their species rich fish assemblages globally. In the Indo-Pacific, 746 species of fish are documented to utilize seagrass meadows, 486 in Australasia, 222 in the North East Pacific, 313 in the Caribbean, and 297 in the North Atlantic. These seagrass associated fish species contribute to both industrial and small-scale fisheries (Unsworth et al. 2019b).

In more temperate regions, the biodiversity is lower in compliance with the latitudinal diversity gradient hypothesis (Hillebrand 2004), nonetheless these habitats are species rich relative to surrounding seascapes (Jackson et al. 2006b). In British and Swedish *Zostera marina* (hereafter, *Z. marina*) beds, 26 and 29 fish species were recorded respectively (Bertelli and Unsworth 2014; Staveley et al. 2017); ten of which were of commercial importance in the British study (Table 3). Juvenile sharks even frequent seagrass beds as nursery areas, such as the dogfish in the UK (Peters et al. 2014). Fish density within temperate *Z. marina* beds is known to be highly variable (Bertelli and Unsworth 2014; Furness and Unsworth 2020; Staveley et al. 2020). In the UK, fish densities have not been quantified spatially across many sites but where data is available this indicates a mean density of $6000 \pm 950 \cdot \text{ha}^{-1}$ (Bertelli and Unsworth 2014). This density was 4.6 times higher than in nearby sand habitats. This density of fish has been shown to be influenced by small and large scale processes within the seascape such as changes in seagrass cover (McCloskey and Unsworth 2015) and landscape patchiness (Jackson et al. 2006b). Comparative analysis of fish assemblages between marine habitat types in the UK using baited video systems reveals that seagrass was amongst the most species rich and contained the most fish (Jones et al. 2021).

Across the wider Northern Atlantic region a range of studies have examined the links between seagrass as a nursery ground and specific species such as the Atlantic Cod (Lilley and Unsworth 2014), with a range of findings indicating some species actively choose seagrass as a nursery habitat and gain clear population level benefits from extended durations using such habitat as a juvenile (Lefcheck et al. 2019; Lilley and Unsworth 2014).

Studies on seagrass fish communities in the UK and northern Europe are dominated by those in *Zostera marina* meadows over those in *Zostera noltii*, with only a handful of studies on the latter species, mostly undertaken in the Wadden Zee (Polte and Asmus 2006a, b; Polte et al. 2005). Although these meadows are transient habitats due to their upper intertidal distribution, the available data indicates that they do remain a key fish nursery habitat, including the provision of substrate for Herring eggs to be laid upon (Polte and Asmus 2006b).

Invertebrate communities

Similarly, invertebrate assemblages are composed of a diverse range of species that are very dense with findings ranging from 5683 to 36,844 ind.m² in European meadows (Mosbahi et al. 2016; Webster et al. 1998). Invertebrate diversity varies spatially; however, composition remains similar even amongst different seagrass types in temperate regions. In *Zostera noltii* (hereafter, *Z. noltii*) beds in the Kneiss Islands (Tunisia), 159 macrobenthic taxa were found, the majority of which were crustaceans (32%), closely followed by molluscs (29%) and annelids (27%) (Mosbahi et al. 2016). Comparably, in Norwegian *Z. marina* beds 127 macrofaunal taxa were found, with crustaceans dominating taxonomic composition, amphipods being the most abundant Crustacea (Fredriksen et al. 2005). In relation to feeding groups, grazers dominate epifaunal taxa (Boyé et al. 2017) and filter feeders dominate infaunal species (Rueda et al. 2009), due to food availability and feeding behaviours. Data on infaunal assemblages from the UK has recorded 5683 ind.m⁻² (Webster et al. 1998). In all, 83 species were collected, representing six phyla, nine classes and over 50 families: most were polychaetes (35 spp.), bivalves (20 spp.) and amphipods (13 spp.) (Webster et al. 1998). Similar densities and species numbers were recorded at other sites in the UK (Hirst and Attrill 2008). Other invertebrate assessments conducted in the UK have examined epifauna

communities on *Zostera marina*, and have recorded 19 species, dominated by an abundance of gastropods, particularly Rissoids. This data collection was part of the ZEB network studies leading to the publication of papers examining large scale processes in *Zostera marina* meadows in the Northern hemisphere (Reynolds et al. 2018). Seagrass density in UK meadows was found to result in increased density of invertebrate infauna (Webster et al. 1998), but this wasn't related to complexity (Attrill et al. 2000).

Faunal composition varies temporally, with meadows experiencing an influx of species in Summer attributed to recruitment (Mosbahi et al. 2016). Spatial variation is documented on a spectrum of scales: within single meadows, on a landscape scale, and among different locations (Boyé et al. 2017). Depth influences invertebrate assemblages too, since within a deep subtidal *Z. marina* bed in the Alboran sea, gastropods dominated taxonomic composition and carnivorous species dominated feeding groups (Rueda et al. 2009), dissimilar to the aforementioned shallower beds (Fredriksen et al. 2005; Mosbahi et al. 2016). In the UK, spatial variation is highlighted by Peters et al. (2015) which found different faunal compositions across three sites, even finding two cephalopods, Common Cuttlefish and Squid.

The attached epifloral communities of seagrass meadows are also known to be biodiverse with the large surface area created by the seagrass shoots and their degradation developing a range of ecological niche. This algal growth is a significant component of the overall meadow productivity contributing to the wider food web (Ouisse et al. 2012). Studies in seagrass communities in West Wales revealed that between 19 and 33 species were recorded on leaves (Johnson et al. 2005). The abundance and richness of these epiphytic communities were not found to be driven by key traits of the seagrass (e.g. shoot density and length).

Table 3. Studies and their key conclusions examining seagrass meadow biodiversity in the UK.

Reference	Seagrass bed species and location	Animal groups assessed	Conclusions
(Bertelli and Unsworth 2014)	<i>Z. marina</i> ; Porth Dinllaen	Fish and motile invertebrates	Supports abundant invertebrate fauna and 10 commercial fish species
(Jones et al. 2021)	<i>UK wide</i>	Fish and motile invertebrates	
(Furness and Unsworth 2020)	<i>UK wide</i>	Fish and motile invertebrates	No difference in abundance and diversity of fish from seagrass to kelp, but assemblages sig change.
(Peters et al. 2014)	<i>Zostera spp.</i> ; Porth Dinllaen, Tremadog Bay & Isle of Wight	Fish and motile invertebrates	Species assemblages were spatially variable but consistently important commercially
(Smale et al. 2019)	<i>Z. marina</i> ; South West UK	Fish and invertebrates	Increased shoot density linked to increased faunal abundance and shifts in assemblage structure
(McCloskey and Unsworth 2015)	<i>Z. marina</i> ; Porth Dinllaen	Fish and motile invertebrates	Decreasing seagrass density negatively influences diversity and abundance
(Hirst and Attrill 2008)	<i>Z. marina</i> ; Torbay	<i>Infauna</i>	Small patches as important for biodiversity as large ones.
(Whalen et al. 2020)	<i>Z. marina</i> ; Global including site in North wales, Porthdinllaen	<i>Predation</i>	Rates of predation peaked at midlatitudes

(Reynolds et al. 2018)	<i>Z. marina</i> ; Global including 2 sites in North Wales, Porthdinllaen and Pen-y-Chain	Epifauna	Local habitat characteristics and latitude influence predation
(Webster et al. 1998)	<i>Z. marina</i> ; Plymouth	Infauna	As seagrass density increased, so did infaunal diversity
(Attrill et al. 2000)	<i>Z. marina</i> ; Plymouth	Infauna	Species abundance and diversity did not relate to habitat complexity
(Jackson et al. 2006a)	<i>Z. marina</i> ; Jersey	Fish and motile invertebrates	fragmented seagrasses support lower species richness
(Jackson et al. 2006b)	<i>Z. marina</i> ; Jersey	Fish and motile invertebrates	Number of species higher in seagrass than sand, but varied with tidal and diel conditions
(Johnson et al. 2005)	<i>Z. marina</i> ; Wales wide	Epiphytes	<i>Zostera</i> canopy variables total leaf length, average leaf length and leaf density per quadrat) were not related to epiphyte species richness nor to the structure of the assemblage

5. Seagrass cultural ecosystem services

5.1 Seagrass support for species cultural importance – birds

5.1.1 Introduction

Seagrass meadows are richly biodiverse ecosystems that occur all over the globe, in both tropical and temperate seas (McKenzie et al. 2020). They are known to be rich in fauna, with complex food systems. Given the wide variety of food sources provided by this environment, it is no surprise that seagrass meadows support this equally wide variety of grazers and predators. Birds however are an often-overlooked part of marine ecosystems yet are crucial to their health (Green and Elmberg 2014).

Here we examine the ecosystem service role of seagrasses in supporting birds. Given the overwhelming evidence of the charitable support provided to bird conservation, the high numbers of birdwatchers interested in observing birds, and some evidence specifying the cultural value of seabirds in the UK (Ainsworth et al. 2019) we've included the links of birds to seagrass as a cultural service. This component of the ecosystem services of seagrass could also be examined as an element of the supporting biodiversity role of seagrasses. We examine how bird species are impacted by seagrass when foraging. This section focuses on bird use ranging from herbivory on seagrass leaf matter to pelagic birds that feed on the fish stocks that the seagrasses support.

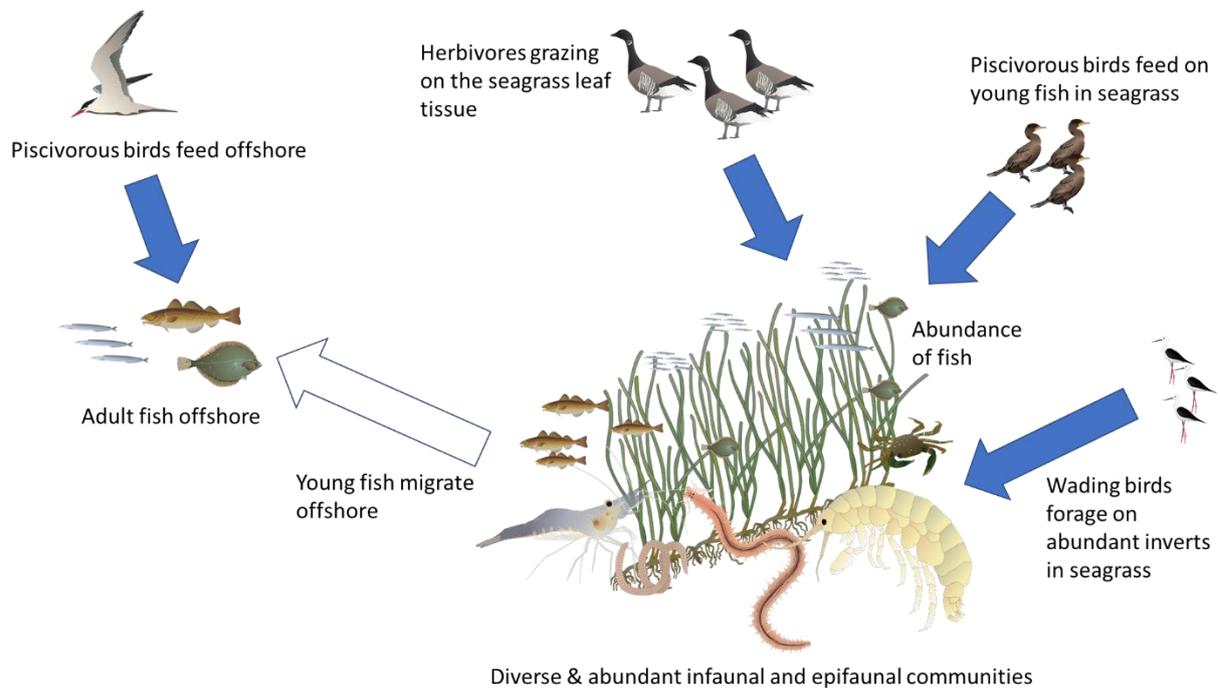


Figure 4. Conceptual diagram examining the potential links between seagrass and seabirds in the UK coastal seas.

5.1.2 Grazing birds

One of the most well-known links between seagrass and avian foraging is when birds graze on the seagrass vegetation. There are several waterfowl species that feed on seagrass worldwide, which have been summarised in literature reviews (Kollars et al. 2017; Valentine and Heck 1999). The paper by Kollars et al. 2017 found that 39 species or subspecies of birds had seagrass as a component of their diet, although it's a dominant or frequent part for just 26 of those species. Studies in the UK have documented that *Zostera* is an important constituent of the diet of two sub-species of Brent geese *Branta bernicla*, wigeon *Anas penelope*, mute swans *Cygnus olor*, and whooper swans *C. cygnus* (Davison and Hughes 1998). Teal *Anas crecca* are also reported to consume eelgrass seeds (Tubbs and Tubbs 1983).

Brent Geese

The Brent goose (*Branta bernicla*) is a small goose which migrates between breeding areas in the Arctic tundra and wintering areas in temperate zones such as North-Western Europe and the coast of the United States of America (Birdlife International, 2021). *Zostera* is a highly dominant component of the Brent goose's diet, in some cases making up 100% of the biomass foraged (Ganter 2000; Harrison and Dunn 2004; Kollars et al. 2017; Moore et al. 2004). It is particularly important during migratory stopovers in spring and autumn, when the birds are expending vast amounts of energy flying long distances (Ganter 2000; Harrison and Dunn 2004). At local levels there is correlation between *Zostera* and Brent goose abundances. Declines in seagrass meadows result in declines in goose abundance (Sedinger et al. 2006). However, Moore et al., 2004, found that while larger seagrass meadows showed higher numbers of geese, a decline in seagrass abundance did not significantly affect the abundance of brent geese within their study area, Humbolt Bay, California. This deviance from the other results is likely due to the isolated nature of the stop-over site limiting the choice of possible locations. However, the decline did appear to effect the success of migration and breeding.

It also appears that Canada geese (*Branta canadensis*) are also affected by declines in *Zostera*, as Seymore et al., 2002, found that Canada geese in Nova Scotia were relying upon seagrass meadows. When those meadows experienced a 95% decline, there was a following 50% reduction in goose abundance. (David and Frederick 2007) also found that over-wintering Canada geese in Maine/New Hampshire fed heavily upon *Zostera*, eating enough to damage the meadow.

In the UK, these links between seagrass and herbivorous birds are well documented, with studies on the Exe, in the Solent and at Lindisfarne, as well as in the estuaries of Essex and at Scolt Head in Norfolk (Burton 1961; Fox 1996; Percival et al. 1996; Percival et al. 1998; Ranwell and Downing 1959; Tubbs and Tubbs 1983).

Swans and other grazers

Swans of various species have also been observed using seagrass as a food source. Black swans in New Zealand rely upon *Zostera* as their main food source, congregating at the largest meadows (Dos Santos et al. 2012). They were found to be most numerous in autumn which is when the plant is at maximum biomass. Though the data in this study only came from one estuary, therefore behaviour could differ elsewhere. Mute swans (*Cygnus olor*) and whooper swans (*Cygnus cygnus*) have also recently been confirmed to use seagrass as a significant part of their diet (Balsby et al. 2017; Kollars et al. 2017; Sato et al. 2020). Widgeon and Teal are also known to graze on UK seagrass (Tubbs and Tubbs 1983).

While these studies show varying degrees of dependence from herbivorous waterfowl upon seagrass, the conclusion one can pull from all of them is that the health and abundance of seagrass meadows has direct effects on the waterfowl which feed on it. Many of these studies take place in an individual location and over the span of only a few years. However, the fact that most have similar conclusions when it comes to seagrass abundance effecting waterfowl foraging, strengthens the argument that they are intricately linked.

5.1.3 Birds feeding on invertebrates

The presence of seagrass increases both the abundance and diversity of the benthic invertebrates that inhabit the sediment it grows in (Attrill et al. 2000; Horn et al. 2020; Lee et al. 2001; Spruzen et al. 2008b). In turn, it would be reasonable to hypothesize that seagrass would indirectly have an effect on the foraging behaviour of bird species that feed on those invertebrates.

The Wadden Sea, one of the largest tidal flats in the world, is recognised as a World Heritage Site in part due to its importance for migratory birds (Boere and Piersma 2012). (Horn et al. 2020), found that the seagrass meadows of the Wadden Sea show significantly higher biomass of the prey species of a number of shorebirds. Within the study, dunlin (*Calidris alpina*), red knots (*Calidris canutus*), and bar-tailed godwits (*Limosa lapponica*) all heavily used the areas of seagrass. Both the red knot and the Eurasian oystercatcher (*Haematopus ostralegus*) showed a marked preference for seagrass meadows over unvegetated areas. Given that their prey was in greater abundance in the seagrass meadows, this is in support of seagrass influencing the shorebirds foraging behaviour. However, it should be noted that this study

only collected data for a single year at each location, therefore there could be other factors involved that were not observed in such a short time frame.



Figure 5. a) Dunlin (*Calidris alpina*) and knots (*Calidris canutus*) are observed in abundance at intertidal seagrass sites in the UK (author: Emma Butterworth). b) Widgeon and Brent Geese grazing on seagrass at Lindisfarne.

The attraction to vegetated habitat may not always hold true, as studies on The Western sandpiper (*Calidris mauri*) indicate a preference for unvegetated areas on exposed tidal flats in the Fraser River Delta, however such congregations align with known areas of high abundance of invertebrates (Harrison and Dunn 2004). This indicates that where seagrass habitat does contain an abundance of invertebrates it may become a more targeted habitat. The Western sandpiper feeds primarily by pecking prey from the surface of the sediment, rather than probing into it for infauna (Sutherland et al. 2000). This may provide an explanation for the preference of unvegetated areas, as seagrass leaf cover would give prey species far more protection and a place to hide from the sandpiper. A similar result was found by (Spruzen et al. 2008a), in Tasmania where shorebirds, such as pied oystercatchers (*Haematopus longirostris*), Red-necked stints (*Calidris ruficollis*), and double-banded plovers (*Charadrius bicinctus*) were studied. On a small scale, the shorebirds showed preference for feeding in areas with less seagrass leaf biomass, as seen with the Western sandpipers in the Fraser River Delta. However, when using a larger scale analysis, the presence of seagrass and associated increased invertebrate biomass correlates with a higher feeding density of shorebirds. When analysed, the larger scale relationship accounted for far more of the variability than on the small scale. Therefore, it can be inferred that while these birds tend to feed in areas with less leaf cover, seagrass meadows are still preferred.

In addition to shorebirds, invertebrate eating waterfowl may also be influenced by seagrass when selecting feeding sites. A 50% reduction in the number of common goldeneyes (*Bucephala clangula*) sighted in the Antigonish Harbour, Canada was observed after the seagrass biomass declined by 95% (Seymour et al. 2002). This species feeds on invertebrates associated with seagrass beds, such as small crustaceans and molluscs (Eadie et al. 1995; Pehrsson 1976).

Understanding of the links between seagrass and the foraging of shore birds for invertebrate prey is far from complete, with studies limited to only a handful and no investigations thought to have previously examined these relationships in UK seagrass.

There is some conflicting evidence available, with some studies finding that the presence of seagrass increases bird abundance (Horn et al. 2020; Seymour et al. 2002) and others finding that shorebirds prefer areas with less seagrass cover but this is a scale dependent relationship (Harrison and Dunn 2004; Spruzen et al. 2008b). While it appears clear that seagrass abundance does influence these birds, it is unlikely to have the same effect across the broad range of species that utilise seagrass meadows worldwide. This area of study reflects a major knowledge gap in our understanding of the support that seagrass provides to seabirds.

5.1.4 Piscivorous birds within the meadow

Many piscivorous birds feed on species of fish that are known to live within UK seagrass meadows. Given that numerous papers exist in the literature documenting the positive relationship between aspects of predatory seabird species condition relative to the availability of forage fish (Campbell et al. 2019) it is reasonable to hypothesise that seagrass meadows do provide a fish foraging ground for seabirds. Seagrass habitats show greater diversity and abundance of fish, particularly juveniles, than unvegetated areas (Bertelli and Unsworth 2014; Lefcheck et al. 2019; Lilley and Unsworth 2014) with the large, healthy, well-connected meadows showing the greatest diversity (Henderson et al. 2017). In North Wales, extensive studies revealed the abundance of fish in seagrass increased by around 4.7 times relative to unvegetated seabed creating an abundant feeding resource for seabirds (Bertelli and Unsworth 2014). Anecdotal evidence indicates cormorants to be regular visitors to the same site, diving for prey within the shallow water seagrass.

Although we hypothesise that the elevated abundance of fish in seagrass would result in piscivorous birds selecting to hunt within it, literature examining such an hypothesis is limited. Significant anecdotal evidence indicates an abundance of potentially piscivorous birds targeting seagrass with searches of images online commonly showing evidence of bird species globally foraging within seagrass.

Great blue herons (*Ardea herodias fannini*) feed on a variety of fish, wading in relatively shallow water to catch their prey (Butler 1991; Hom 1983). (Huang et al. 2015) found that herons hunted within seagrass meadows enough to have a significant impact on the abundance of fish. While this paper does not directly link the presence of seagrass to the herons choice of foraging location, it can be inferred that the species has heavy usage of the meadows. Another factor to be considered however is that herons (*Ardeidae*) are limited in their choice of location by the height of the water (Custer 1978). This means that herons are limited to the use of seagrass meadows that are shallower and more exposed, potentially imposing the time constraints of low tide. It appears that seagrass habitats are selected if the water is low enough for that species. (Butler 1991) found that shallow lagoons with kelp beds or seagrass meadows were a preferred choice for the great blue heron when feeding at the coast.

Phalacrocorax, commonly known as cormorants, are a genus of birds that mainly hunt fish by diving (Dorfman and Kingsford 2001; Grémillet et al. 1998; Heithaus 2005). In Western Australia, pied cormorants (*Phalacrocorax varius*) show strong preference towards seagrass meadows (*Amphibolis antarctica*) over bare sand to hunt in (Heithaus 2005). It was likely not the seagrass itself that caused the birds to choose those locations, rather that cormorants are

able to track prey abundance which is highest within the seagrass. Though the habitat use was also impacted by predators, therefore seagrass is certainly not the only factor. Dorfman and Kingsford, 2001, found a similar preference for seagrass meadows in four cormorant species, great (*Phalacrocorax carbo*), little black (*Phalacrocorax sulcirostris*), pied and little pied (*Microcarbo melanoleucos*). The cormorants appeared to choose to both hunt and roost near seagrass meadows. Unlike herons, who's usage of seagrass beds is limited by water level and diel changes, cormorants showed no trends when it comes to these factors. The implication of this is that the distribution of the birds was determined by characteristics of the locations, for example seagrass abundance, rather than any temporal changes.

As with those species that feed on invertebrates potentially near seagrass, there was limited literature exploring whether seagrass has an influence on the foraging of piscivorous fish. Many seabird species (e.g. Kittiwakes, Guillemots) are known to forage in coastal shallow water areas when nesting (Bugge et al. 2011; Redfern and Bevan 2014) and consume young fish known to be abundant in seagrass such as the Atlantic cod (Bugge et al. 2011; Lilley and Unsworth 2014) (e.g. see Appendix 1 and 2).

With so few species studied with regards to their links to seagrass it would be hard to come to a significant conclusion as to whether this generates impacts on the birds themselves therefore we see this area as a particular knowledge gap.



Figure 6. Significant photographic evidence of the links between bird foraging and seagrass can be found through searching through imagery available on the website flickr.com

5.1.5 Pelagic birds

When looking at the effect seagrass has on birds, it would be an oversight to ignore the link between pelagic birds, their prey species, and seagrass meadows. While these birds often hunt miles away from any seagrass, the species that they prey on, such as Gadoids and Clupeids, often utilise seagrass as nursery habitats (Bertelli and Unsworth, 2014; Lefcheck et al., 2019; Lilley and Unsworth, 2014; McDevitt-Irwin et al., 2016). At ocean basin scales seagrass be incredibly important in supporting fish stocks far from land with 20% of the worlds biggest fisheries supported by seagrass meadows through the provision of a nursery function to juvenile fish (Unsworth et al. 2019b). Where seagrass meadows decline, there is evidence that this has negative effects on the pelagic fish stocks (Kritzer et al. 2016; Seitz et al. 2013). This in turn, may impact the success of the species that feed on them. Given that many fish stocks are overfished already (Einoder, 2009), a reduction in the number of juvenile fish surviving to maturity could severely affect their predators.

A high abundance of juvenile herring (*Clupea harengus*) were found in seagrass in studies that took place in the United Kingdom, Denmark and the Baltic Sea (Bertelli and Unsworth, 2014; Polte and Asmus, 2006; Rönnbäck et al., 2007). Clupeids form a part of the diet of numerous seabirds, notable in the diet of common guillemot (*Uria aalge*) chicks and razorbills (*Alca torda*) (Anderson et al., 2013; Barrett, 2015; Ouwehand et al., 2004; Riordan and Birkhead, 2018). For adult guillemots, capable of catching and eating larger prey, gadoids were a significant prey item (Anderson et al., 2013; Ouwehand et al., 2004).

While some preferences are observed, generally studies have found that many seabirds are relatively flexible with their diet. Larger birds like northern gannets (*Morus bassanus*) and Cory's shearwaters (*Calonectris diomedea*) show particularly great flexibility in prey species (Hamer et al., 2007; Paiva et al., 2010; Pettex et al., 2012) and therefore are less likely to be affected by decreasing of some fish stocks.

Overall seagrass likely may have an indirect effect on pelagic birds by acting as a nursery to their prey items. However there does not appear to be any literature that connects the birds with seagrass. Connections must be made through improved understanding of the diets of pelagic bird species linked to knowledge of how individual fish species utilise seagrass.

5.1.6 Shifting baselines

Conceptions of environmental degradation tend to shift depending on our temporal reference point. In the United Kingdom, this “shifting baseline syndrome” (SBS) (Pauly 1995) occurs when the earliest known data of areal extent of seagrass are assumed as an unaffected baseline condition (Green et al. 2021). This is further exacerbated by data being supported by qualitative accounts that refer to healthier conditions within a scientist’s lifetime. With each generation, the concept of a healthy ecosystem shifts, depending on their perceived baseline. In the UK there is extensive evidence that at least 50% of our seagrass has disappeared., and with it the support it provided for fish stocks and biodiversity (Green et al. 2021). Whilst we cannot for sure understand the pristine state of our coastal seas, we can assume that the contribution from pristine habitats in their support for a more complex and productive food web must have been orders of magnitude higher. In the context of the links between seagrass and seabirds we can only assume that the availability of abundant food

sources for seabirds linked to seagrass would have been historically orders of magnitude higher.

5.2 Other Seagrass cultural services

Seagrass meadows are well known globally to create perfect examples of social-ecological systems and as a result have a strong interaction with human wellbeing at local, regional and global levels that are underpinned by the provision of a range of these ecosystem services examined in this current review (Cullen-Unsworth et al. 2014). A case study of the role of seagrasses in supporting Well Being from North Wales indicates that it does have considerable potential through fishery activity, water filtration and sediment stability to influence peoples livelihoods (Cullen-Unsworth et al. 2014). These roles may have diminished relative to historic levels whereby seagrass formally supported many other cultural services and provision of goods such as stuffing materials, wall insulation and garden fertiliser (REF).

5.3 Seahorses

Seahorses live across a range of habitats, but when in seagrass spend most of their time attached with their tails to the leaves where they hunt for food (UNEP 2020). About 30 per cent of seahorse species, which use seagrass meadows as their main habitat, are included in the IUCN Red List (Hughes et al. 2009). Seahorses are considered a flagship species for the conservation of seagrasses and the associated fauna (Shokri et al. 2009) and considered to have a high cultural value.

In the UK there are two species of seahorse: spiny (*Hippocampus guttulatus*) and short snouted (*H. hippocampus*) (Garrick-Maidment et al. 2010) and although the status of these species are commonly discussed their populations remain unquantified and poorly studied. Significant anecdotal evidence indicates that their distribution has reduced as a result of overfishing throughout the 1970's and as a result their populations are now absent from most UK seagrass meadows. A well known population of seahorses is known to exist in the seagrass at Studland Bay (Garrick-Maidment et al. 2010).

6. Seagrass regulating ecosystem services

6.1 Coastal Defence and Sediment Stabilisation

Seagrasses are often called ecosystem engineers, or foundation species because of the effect they have on their environment (Maxwell et al. 2017; Potouroglou et al. 2017). The ability seagrass has to alter its local environment underpins its position in supplying valuable ecosystems services. Similar to other "blue carbon" habitats like mangroves and saltmarshes, seagrasses are known to serve the ecosystem by means of coastal defence and sediment stabilisation.

6.1.1 Coastal Defence

Existing literature and Intergovernmental Panel on Climate Change (IPCC) scenarios point to an increasing rate of sea level rise (IPCC 2021; Ondiviela et al. 2014) and the frequency/intensity of extreme wave associated events (Koch et al. 2006) resulting in greater

severity of flooding and erosion globally. The UK Climate Change Committee (CCC) states that “Many of the UK’s coastal defences are likely to be at risk of failure as sea levels rise. For example, a sea level rise of 0.5m is projected to make a further 20% of the UKs coastal defences vulnerable to failure” (-Change-Committee 2021). Economic losses from coastal erosion and flooding are already seen today. The CCC claims that damages amount to an average £260m per year with 520,000 properties now in areas of flooding risk and 8,900 in areas at risk of destruction through coastal erosion (-Change-Committee 2021).

Coastal vegetation acts as a buffer, reducing wave and tidal energy (Koch et al. 2006; Ondiviela et al. 2014). It traps sediment and raises sediment profile and through this contributes to coastal protection. In the UK seagrasses from the *Zostera* genus embody an important proportion of the endemic coastal vegetation.

The coastal defence provided by *Zostera* depends on its capacity to dampen and absorb energy from the processes of flooding and coastal erosion –identified as the main natural threat for coasts (Ondiviela et al. 2014). *Zostera* attenuates flooding and coastal erosion by decreasing the intensity of incoming hydrodynamics through three mechanisms:

- 1) In a unidirectional flow (e.g. tides, flooding events) *Zostera* reduces the current velocity as it passes through and over the canopy by **frictional effects of the biomass** causing a loss of momentum.
- 2) In an oscillatory flow (e.g. waves), the circular motion produces periodic movement of *Zostera* leaves, with amplitude strongly dependent on leaf stiffness. The orbital velocity above the canopy is reduced due a drag discontinuity, which propagates in the flow direction **removing wave energy**.
- 3) *Zostera* has an indirect mechanism of coastal defence by **stabilizing and maintaining the sediment, increasing surface elevation**. This reduces water currents and wave energy increasing sedimentation rates within the meadows and reducing potential for resuspension.



Figure 7. Researchers at Plymouth University investigating the effect seagrass has on wave, current and sediment transport processes and to what extent they promote sedimentation and provide natural coastal protection.

The efficiency of seagrass coastal defence in the UK is increasingly becoming a target area for research, however, to date no studies have been published that examine these key ecosystem services of seagrass. Data is expected to emerge from studies in seagrass meadows of the Isles of Scilly conducted during summer 2020. At Project Seagrass coastal communities are increasingly approaching staff to examine the potential for planting seagrass in order to facilitate reduced coastal erosion, particularly sites along the eastern coast of England in Essex and Suffolk where costs are rapidly eroding. It is known that this is a multidimensional area of study that considers site-specific hydrodynamics, the ecosystem involved and the *Zostera* species-specific features (Koch et al. 2006; Ondiviela et al. 2014). There are many factors that impact the efficacy of the plants ability to reduce currents, waves and stabilize sediment. These factors include the depth of the meadow, *Zostera* canopy height, meadow density, meadow extent, annual meadow persistence, wave power and sediment composition (Duarte et al. 2013; Koch et al. 2006; Ondiviela et al. 2014)..

Zostera have been found to be more successful at reducing waves and currents in shallower waters in which they occupy a higher proportion (>50 percent) of the water column (Duarte et al. 2013). More specifically, the degree of wave attenuation is directly related to the fraction of the water column occupied by the vegetation. A laboratory-based flume study measured wave attenuations between 20 and 76 percent over 1 meter length when the plants were occupying the entire water depth and field studies have found values between 1.6 and 80 percent (Koch et al. 2006). This wide data range appears to be related to tidal fluctuations (figure 5). This suggests that seagrass wave attenuation is inversely related to water/tidal level i.e. at high tide, wave attenuation is lower than at low tide.

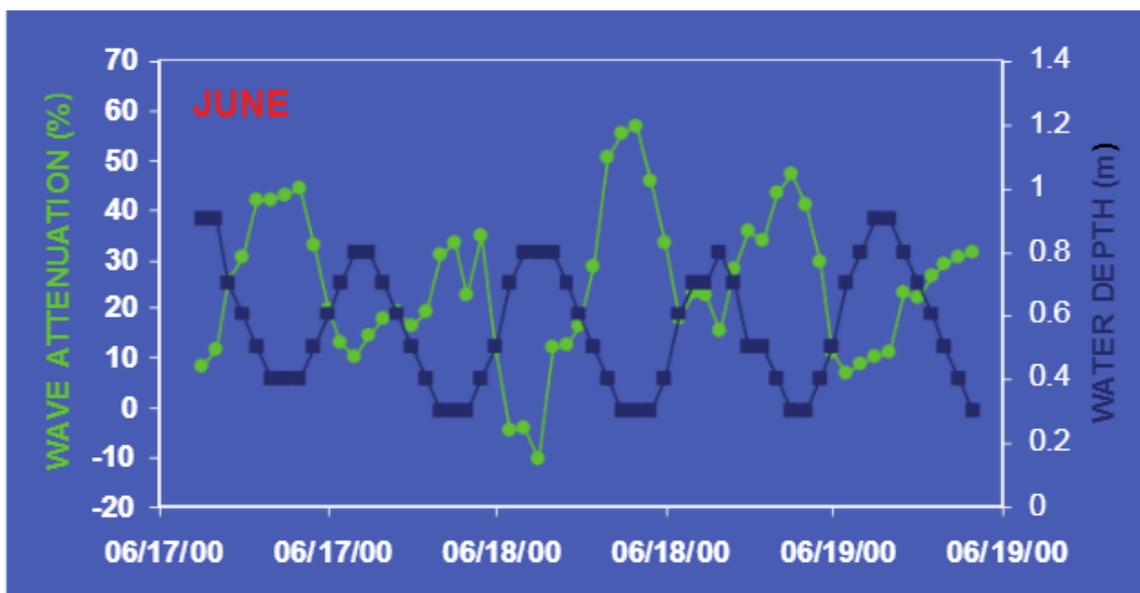


Figure 8. Wave attenuation in a dense *Ruppia maritima* bed off Bishop’s Head Point in Chesapeake Bay, MD. Wave attenuation is inversely related to water/tidal level. Figure obtained from Koch et al. (2006).

6.1.2 Sediment Stabilisation

Zostera meadows retain nutrients (including Nitrogen, Carbon, Phosphorus) directly through assimilation into well-developed root systems, rhizomes and leaves as well as indirectly through trapping allochthonous sestonic particles (Potouroglou et al. 2017). Their root systems secure and consolidate sediment, reducing erosion and water turbidity and thus increasing water transparency (Potouroglou et al. 2017; Wilkie et al. 2012). As aforementioned, *Zostera* canopies reduce ambient current speeds, encouraging particle settlement. These processes result in greater settlement stability and the accumulation of organically rich particles (figure 6).

The amount of sediment accumulation in seagrass meadows is dependent on a balance between deposition of suspended sediment and resuspension. The capacity of UK *Zostera* species for balancing these two processes hinges on the development stage and health of the plants, as well as local hydrological conditions. Sediment stabilisation by *Zostera* is currently believed to be a function of the seagrass canopy properties which reduce physical stress at the sediment surface, creating a stable hydrodynamic state (Potouroglou et al. 2017)

A multi-site study exploring the role of seagrass meadows on surface elevation demonstrated that seagrass meadows significantly stabilise sediment and facilitates elevating the surrounding seabed (Potouroglou et al. 2017). The Scotland site (Firth of Forth, Drum Sands) study found that at plots where *Zostera noltii* was absent, no net annual change in the average height of sand was observed, but with losses in winter, and accumulation in summer (Potouroglou et al. 2017). At plots where *Z. noltii* was present there was a statistically significant increase in sediment elevation. The study concluded that the impact of seagrasses on surface elevation is remarkably strong, with an average difference of 31 mm per year in

elevation between plots with seagrass and plots without (Potouroglou et al. 2017). This average considered all 13 studied species across all four sites (Scotland, Kenya, Tanzania, Saudi Arabia).

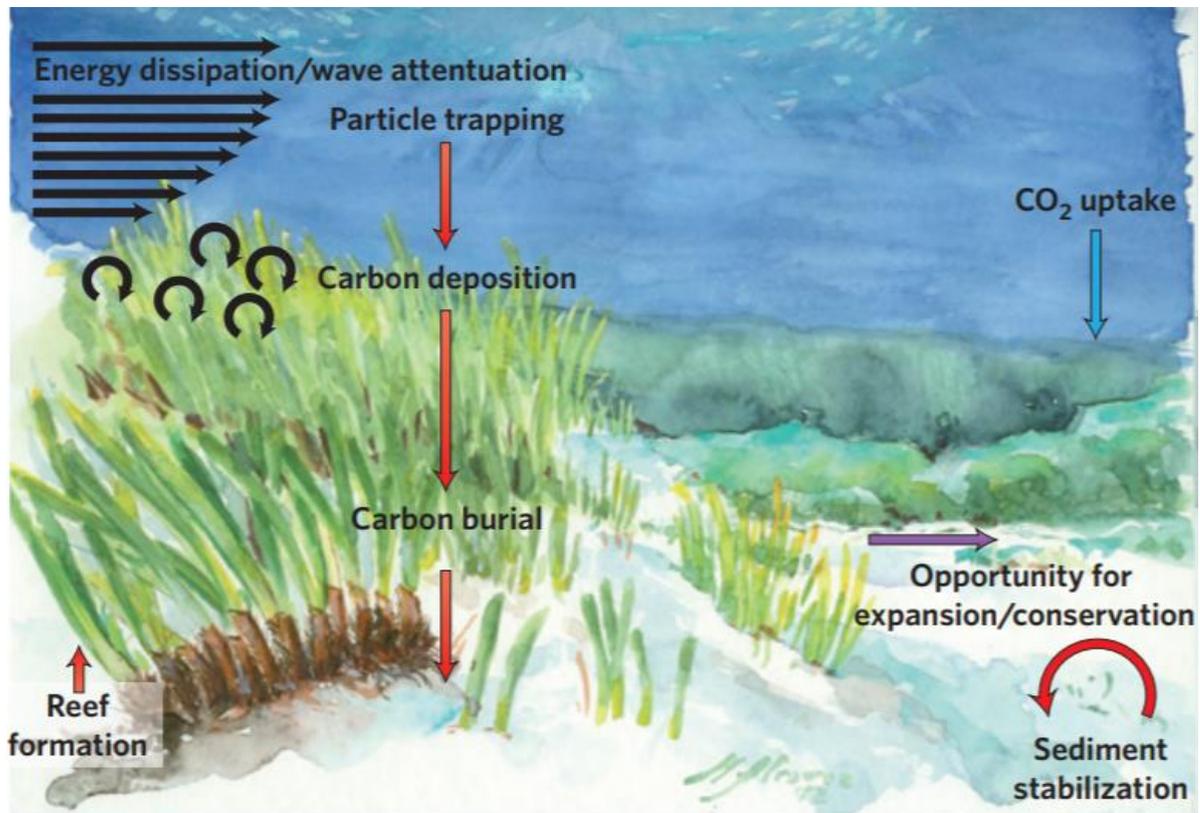


Figure 9. A watercolour painting of a *Posidonia* meadow by Miquel Alcaraz. Shoreline protection and Carbon sink processes. Blue arrows indicate transport of atmospheric or dissolved material, red arrows show transport of particulates and purple arrows indicate vegetative growth Figure obtained from Duarte et al. (2013).

Another study investigating the contribution of annual *Zostera* (Wadden Zee) populations to sediment accretion and grain size modification (Bos et al. 2007) found that during the growing season, *Zostera* patches enhanced sediment accretion and increased the silt content of the sediment (figure 7). Sediment accretion was found again to strongly depend on the density of the *Zostera* bed canopy (Bos et al. 2007). They concluded that during the growing season, *Zostera* beds affect sediment dynamics like perennial seagrass species (Bos et al. 2007), annual populations release the accumulated sediments during winter which can result in an increase in erosion (Bos et al. 2007).



Figure 10. In the Eems Estuary, a *Zostera* planting plot showing the induced sediment accretion. Here the aboveground parts of the *Zostera* have largely disappeared and erosion of previously accreted sediment has started. However, the overall elevation of the patch can still be clearly seen. The silty character of the elevated areas can also still be observed with the lack of ripples in the sediment. Figure obtained from (Bos et al. 2007).

6.2 Carbon storage

The sediments beneath aquatic and terrestrial vegetation provide an efficient means of storing carbon from the atmosphere over long periods, and as such many of the habitats these create are being considered as key potential Nature Based Solutions to climate change. Seagrass meadows (marine vegetation) are one such habitat and the carbon stored in the marine sediments below such habitats is referred to as Blue Carbon.

6.2.1 Global seagrass carbon stores

Seagrass meadows are a functional classification for at least 60 species spanning four families of marine plant that live across a range of different environments and have varied life histories. Some species are analogous to the long lived slow growing Oak Tree whilst others have strategies more analogous to a rapid growing pine. Variation in the ecological functioning of these seagrass meadows within and between species can be vast (Nordlund et al. 2016), and its therefore no surprise that the amount of carbon stored by seagrass meadows and the rate at which this happens varies greatly. Global estimates from the 2012 Nature Geosciences review by James Fourqurean et al (Fourqurean et al. 2012) suggest seagrass stores approximately 139.7 Megagrams (tonnes) of $C_{org} \text{ Ha}^{-1}$, but the values range from 9.1 to 628.1 Megagrams of $C_{org} \text{ Ha}^{-1}$. At a global level these values for seagrass carbon storage are high relative to a range of terrestrial biomes and forest types (see Table 4) (Lal 2005).

6.2.2 UK Seagrass carbon stores

Throughout the Northern Hemisphere, *Zostera marina* is one of the dominant seagrass species, and as such it lives throughout a range of environmental condition. It is one of only 2 species recorded in the UK, the other being *Zostera noltii*. A Northern Hemisphere study on *Zostera marina* meadows found the amount of carbon stored in the top 1m of *Zostera marina* sediments ranges from 23.1 to 351.7 Megagrams of $C_{org} Ha^{-1}$, with a median value of 108 Megagrams of $C_{org} Ha^{-1}$. These ranges are similar to values for various types of forest ecosystem but are less than many mangrove habitats, peatlands and salt marsh on a per unit area (see Table 4). UK specific studies from 27 sites in East Scotland (Potouroglou 2017), Southern England (Green et al. 2018; Lima 2020) and North Wales (Röhr et al. 2018) have recorded a mean storage (extrapolated to 1m) of 124 ± 68.9 Megagrams of $C_{org} Ha^{-1}$, with values ranging from as low as 10 to as high as 380 Megagrams of $C_{org} Ha^{-1}$. The higher values tend to align with the subtidal *Zostera marina* meadows rather than the intertidal *Zostera noltii* meadows. All these values for UK seagrass sit within the expected range of those examined by James Fourqurean et al (Fourqurean et al. 2012), but the smaller intertidal UK species *Zostera noltii* clearly sit at the lower range of global estimates for seagrass carbon storage.

Table 4. Carbon stocks (Megagrams $C_{org} Ha^{-1}$) and accumulation rates (Megagrams $C_{org} Ha^{-1} Yr^{-1}$) in selected biomes, habitats and forests of the world.

	Biome	Vegetation C Store	Soil C Store	Soil C Accumulation	Reference (s)
Whole Biomes	Tundra	9	105	-	(Lal 2005)
	Boreal/Taiga	64	343	-	(Lal 2005)
	Temperate	57	96	-	(Lal 2005)
	Tropical	121	123	-	(Lal 2005)
	Wetlands	20	723	-	(Lal 2005)
Terrestrial habitats	Tropical Forest	157	122	0.04 ± 0.005	(Lal 2005; Mcleod et al. 2011)
	Temperate Forest	96	122	0.05 ± 0.01	(Lal 2005; Mcleod et al. 2011)
	Boreal Forest	53	296	0.05 ± 0.02	(Lal 2005; Mcleod et al. 2011)
	Grasslands	-	-	0.54	(Conant et al. 2001)
	Peatlands	-	180-621	0.38	(Yu 2012)
Aquatic habitats	Global Salt marsh	4.3	330	3.82 ± 0.58	(Alongi 2020)
	Global Mangrove	109.3	738.9	1.62 ± 0.6	(Alongi 2020)
	Global Seagrass (all species)	7.29	139.7	1.38 ± 0.3	(Fourqurean et al. 2012; Mcleod et al. 2011)
	Seagrass (<i>Zostera marina</i>)	0.88	108	0.37 to 0.9 [14]	(Cebrian et al. 1997; Greiner et al. 2013; Miyajima et al. 2015; Poppe and Rybczyk 2018; Röhr et al. 2016; Röhr et al. 2018)
	UK Seagrass (<i>Zostera marina</i>)	-	114±73	0.02	(Green et al. 2018; Lima 2020; Potouroglou 2017)

6.2.3 Seagrass carbon accumulation rates

From a Nature Based Solution habitat restoration perspective what is important is not the total storage, but the amount of carbon that the habitat stores per year in order to help reduce atmospheric CO_2 levels. As a result of the high costs for isotope chemistry, and the difficulty in calculating sediment accretion rates, the amount of data on per year carbon accumulation rates in seagrass (carbon sequestration) is limited. At a global level (across all species) the accumulation of carbon ranges from 0.45 to 1.9 Megagrams of $C_{org} Ha^{-1}.Yr^{-2}$ with a mean value of 138 ± 38 Megagrams of $C_{org} Ha^{-1}.Yr^{-2}$ (Mcleod et al. 2011). It is this figure that has been used to calculate the figure of '35x' referred to by a range of authors (Macreadie et

al. 2015), as the carbon accumulation (for long-term storage) in the soils of many forest ecosystems is quite poor, irrespective of their often-large living carbon biomass.

The only currently available sediment (marine soil) carbon accumulation rates for seagrass in the UK are for mixed *Zostera marina* and *Zostera noltii* meadows around the Solent region and are in the low end of this range at 0.67 ± 0.32 Megagrams of $C_{org} \text{ Ha}^{-1} \cdot \text{Yr}^{-2}$ (Lima 2020). These UK rates are within the range of previous studies on *Zostera* meadows in the northern hemisphere (Greiner et al. 2013; Miyajima et al. 2015; Prentice et al. 2019) and are comparative to values recorded for UK saltmarshes and peatlands (Burden et al. 2019; Yu 2012). Carbon accumulation rates in temperate grasslands have been found to be higher than those in seagrass, however figures are highly variable (Jones and Donnelly 2004). When placed in the context of the comparison of forest soil carbon accumulation used by McLeod et al 2012 (McLeod et al. 2011) UK seagrass stores carbon in its sediment (soils) 16 times faster than tropical forests.

6.3 Mitigating Ocean Acidification

The high productivity of seagrasses affects the carbonate chemistry of the surrounding seawater due to the large quantities of dissolved inorganic carbon taken up during photosynthesis (UNEP 2020; Unsworth et al. 2012). As a result, seagrasses tend to increase seawater pH during the daytime, potentially offsetting the deleterious effects of the increasing anthropogenic CO₂ in the seawater. Marine organisms, particularly calcifying organisms, such as corals (Manzello et al. 2012) and shellfish (Wahl et al. 2018) living within or adjacent to seagrasses, may benefit from this service, since they can find a local refugium from ocean acidification. Although their role in buffering ocean acidification depends on environmental conditions (Koweeck et al. 2018) and temporal cycles (Unsworth et al. 2012), healthy seagrass meadows can contribute to enhancing the resilience of the most vulnerable species to ocean acidification in the short-term (Wahl et al. 2017).

6.4 Nutrient cycling

Seagrass is known to play a crucial role in nutrient cycling by acting as both a sink and a source for nutrients in varying areas of nutrient availability (Connell and Walker 2001). Nitrogen is assimilated in large quantities into the biomass of seagrass where it is temporarily retained for a small period between a few weeks to months (Aoki et al. 2020). Unlike burying or denitrification, the nitrogen that's assimilated is only temporarily held within the seagrass and is subject to be released back into the surrounding environment via decomposition, leaching and grazing (Nils and Lars Ditlev Mørck 2000). As well as assimilating nitrogen in large quantities, seagrass also aids in the burial of nitrogen by increasing the sedimentation as the seagrass canopy can attenuate the waves and current; sediment stabilisation caused by the roots and rhizomes and by the build up of recalcitrant seagrass tissue in the sediment which resists degradation which would release CO₂ (Trevathan-Tackett et al. 2017). Assimilation effects are observed to be much stronger than denitrification, but burial appears to be the most effective way of removing nitrogen from the surrounding environment according to one study by Aoki, 2020 with 85% of nitrogen removal being contributed to burial. Seagrass is viewed as an engineer of its environment often seen to control the amount of nutrients available in its surroundings however the seagrass meadows are subject to seasonal change. They exhibit a much higher rate of growth during spring and summer when seagrass is net O₂

producing where the seagrass bed influx is stronger than the release of nitrogen making them a major sink for Dissolved Inorganic nitrogen (DIN). In Autumn and Winter this will reverse, and seagrass beds will become a moderate source for DIN. There is a large difference between the influx and release of nitrogen with a much larger intake (Table 5) suggesting they may be recycling nitrogen through mineralisation from the sediment and nitrogen reclamation. *Zostera marina* was found to be roughly 20x more effective at N burial and assimilation than bare sediment.

Table 5. Comparison of the amount of nitrogen exchanged via the various nitrogen intake and release methods observed of a *Zostera marina* seabed. Taken from Nils and Lars Ditlev Mørck 2000

	N flux	Mean rate (g N m⁻² yr⁻¹)	95% confidence limits
<i>Seagrass</i>			
	Loading	1.23	0.39
	Fixation	0.93	0.17
	Denitrification	-0.62	0.21
	Burial	-3.52	0.69
	Assimilation	-2.62	0.78

6.4.1 Phosphorus

In low nutrient areas phosphorous is binded to iron oxides in the seagrass roots decreasing its availability in the surroundings (Karen et al. 2007). This phosphorous can be unbound by seagrass facilitation as root respiration and the release of organic acids can lower the pH enough for the dissolution of carbonate minerals in the rhizosphere to release bound Phosphorous (David and Richard 2002). This control of the phosphorous in the environment can reduce the chance of algal bloom growth and appears to take in more phosphorous than released in a year (Table 6).

Table 6. Comparison of the biophysical change caused by a hectare of seagrass on the UK's South Coast of Nitrogen, Phosphorous and carbon. Adapted from Watson et al. 2020.

ELEMENT	BIOPHYSICAL CHANGE (MEDIAN TONNES YR⁻¹)
NITROGEN	127
PHOSPHORUS	-30
CARBON	768

6.4.2 Eutrophication

Eutrophication provides a major issue towards seagrass habitats, Seagrass however can help alleviate these issues. As the population of humans increases along these coastal habitats the chance for nutrients to leach into the environment increases and so does the chance for eutrophication to occur. Seagrass meadows help maintain a high water quality by contributing massively to the benthic-pelagic coupling or the exchange of nutrients from the

benthic to pelagic layer (Griffiths et al. 2017). By large influxes of nitrogen and carbon seagrass can help reduce the chances of algal blooms forming by keeping nutrients out of the water column. In terms of Phosphorus if eutrophication begins to occur this will reduce seagrass metabolisms. Once an area becomes eutrophic the sulfide concentration will increase and begin to compete with phosphorous for the iron oxides in rhizomes meaning the phosphorous concentration will begin to increase causing a positive feedback leading to increased eutrophication. Seagrass acts as a natural buffer so reintroducing it back into the environment can help reduce the stress put on the habitats by eutrophication and human impact.

6.5 Water filtration

Seagrasses can remove microbiological contamination from the water, thus reducing exposure to bacterial pathogens for fish, humans and invertebrates (UNEP 2020). Seagrasses have been recorded to produce a range of bioactive secondary metabolites with antibacterial and antifungal activity. For example, extracts from three tropical seagrass species – *Halophila stipulacea*, *Cymodocea serrulata* and *Halodule pinifolia* – were active against *Staphylococcus aureus*, a bacterium that causes a range of illnesses in humans (Kannan et al. 2010; UNEP 2020). Such anti-panthanogenic properties have been recorded in a high profile paper from Indonesia to reduce the the levels of potentially pathogenic marine bacteria that cause diseases in humans, fish and invertebrates by 50 per cent if seagrass meadows are present compared with sites without seagrasses (Lamb et al. 2017). Coral reefs also benefited from the presence of seagrasses filtering pathogens, with coral disease levels halved when seagrasses are adjacent to reefs (Lamb et al. 2017). A recent pre-press publication from Sweden has revealed this role to also extend to temperate seagrasses with *Zostera marina* reducing the abundance of harmful *Vibrio* bacteria in seawater by up to 63% compared to adjacent sand flats (Reusch et al. 2021). Seagrass meadows can also control harmful algal blooms through algicidal and growth-inhabiting activities against the microalgae causing the blooms (Inaba et al. 2017).

7. Seagrass ecosystem services summary

Seagrasses in the UK provide extensive ecosystem services. A range of global studies have broken these services down to 32 potential contributions to people (McKenzie et al. 2021). Our review indicates that UK seagrasses provide at least 24 of these contributions to people (see Table 7). UK seagrass supports diverse communities of fish, invertebrates, algal epiphytes and birds. It helps keep our coastal waters clean, stripping them of nitrogen, phosphorus and pathogens and stores carbon at rapid rates. The biodiversity in seagrass meadows helps supports productive fisheries and complex food webs.

Whilst we know key elements of these contributions to the lives of people in the UK, many of the details remain missing. Our understanding of the regulating services is limited, especially from the perspective of nutrient cycling and coastal defence. Biological knowledge is also limited with respect to the role that seagrasses play in supporting birds.

Particular wide gaps in knowledge appear to be the reduced focus of work on the intertidal species *Zostera noltii* and the estuarine species of *Ruppia*.

Increased research effort is required to place values on these roles so that their financial contribution to society can be better appreciated.

Table 7. List and description/example of recognized ecosystem contributions by seagrass globally and recommended reporting category for Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) assessments according to the generalizing perspective. Description includes goods, functions, processes, components or life support systems. List modified from de Groot et al. ((2002)), Nakaoka et al. ((2014)), Ramesh et al. ((2019)), Newmaster et al. ((2011)), Nordlund et al. ((2016)) and Díaz et al. ((2018)). Table is adapted to the UK as an abridged version from McKenzie et al 2021.

Seagrass ecosystem contribution (SCP)	IPBES category	Description
Material		
Bioindicator	1	seagrass assessed as an indicator of water quality/ecosystem health through the WFD.
Compost fertilizer	8, 15	wrack historically collected and placed on land crops (unknown whether this still occurs)
Dietary supplement (<i>for humans</i>)	12, 15	No
Genetic resources	14	Includes the genes and genetic information used for animal and plant breeding (<i>including restoration</i>)
Seagrasses as food for detrital and filter feeders	12	food for crabs, <i>etc.</i>
Seagrasses as food for herbivores	12, 15, 17	food for Brent geese.
Source of human food from seagrass gleaning	12, 17	Shrimp gleaned at low tide.
Mariculture (<i>as a substrate</i>)	1, 13	No
Nursery	1, 17	e.g. juvenile habitat for major fish stocks (e.g. Cod)
Ornamental resources	13, 17	No
Pharmaceuticals (<i>incl traditional medicines</i>)	14, 17	No
Fibre/raw materials (<i>e.g. weaving, roof thatch</i>)	13, 17	Historically used but not any longer.
Source of human food from seagrass fishery (<i>net, trap, spear</i>)	12, 13, 17	Spear fishers targeting seagrass
Stock feed supplement	12	No
Trophic subsidy	1	Feeding area for larger fish at night, use by predatory birds

Regulating

Seagrass ecosystem contribution (SCP)	IPBES category	Description
Carbon sequestration (<i>climate regulation</i>)	4	long-term removal or capture of carbon dioxide to slow or reverse atmospheric CO2 pollution and to mitigate or reverse global warming
Regulates ocean acidification	5	increases pH, resulting in higher calcification of molluscs
Sediment stabilization (<i>erosion regulation</i>)	8	Vegetative cover plays an important role in soil retention and the prevention of landslides
Water purification	7	Regulates land based pollution (act as nutrient, sediment, chemical, filter/buffer)
Disease regulation/mitigation	7, 10	Reduces bacteria harmful to humans and corals
Natural hazard regulation/Coastal protection	9	Seagrass presence can reduce the damage caused by storms and waves by dampening
Non-material		
Aesthetic significance	16, 17	Many people find beauty or aesthetic value in various aspects of ecosystems, as reflected in the support for parks. scenic drives. and the selection of housing locations
Bequest benefit	17	Satisfaction of preserving seagrass for enjoyment by future generations (donations to Project Seagrass)
Cultural artifacts	15, 17	No
Education	15, 17	Ecosystems and their components and processes provide the basis for both formal and informal education at Universities and schools.
Inspirational	15	Ecosystems provide a rich source of inspiration for art, folklore, national symbols, architecture, and advertising (in some parts of the UK)
Knowledge systems	15, 17	No
Recreation and ecotourism	16, 17	People often choose where to spend their leisure time based in part on the characteristics of the natural or cultivated landscapes in a particular area. Provide habitat for wildlife viewing opportunities and other recreational opportunities such as swimming through clearer, cleaner water and stable beaches, as well as recreational fishing
Scientific research	15	academic pure and applied
Sense of place	17	Many people value the sense of place that is associated with recognized features of their environment, including aspects of the ecosystem
Social relations	17	Ecosystems influence the types of social relations that are established in particular cultures. Fishing societies, for example. differ in many respects in their social relations from nomadic herding. or agricultural societies
Spiritual & religious	17	No

8. References

- Change-Committee, C., 2021. The UK's independent adviser on tackling climate change. Retrieved 1 March 2021, from <https://www.theccc.org.uk/>.
- Ainsworth, G.B., Kenter, J.O., O'Connor, S., Daunt, F., Young, J.C., 2019. A fulfilled human life: Eliciting sense of place and cultural identity in two UK marine environments through the Community Voice Method. *Ecosystem Services* 39, 100992.
- Alongi, D.M., 2020. Carbon Balance in Salt Marsh and Mangrove Ecosystems: A Global Synthesis. *J. Mar. Sci. Eng* 8.
- Aoki, L.R., McGlathery, K.J., Oreska, M.P.J., 2020. Seagrass restoration reestablishes the coastal nitrogen filter through enhanced burial. *Limnology and oceanography* 65, 1-12.
- Assessment, U.N.E., 2011. The UK National Ecosystem Assessment: Technical Report. UNEP-WCMC, Cambridge.
- Attrill, M.J., Strong, J.A., Rowden, A.A., 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23, 114-121.
- Balsby, T.J.S., Clausen, P., Krause-Jensen, D., Carstensen, J., Madsen, J., 2017. Long-term Patterns of Eelgrass (*Zostera marina*) Occurrence and Associated Herbivorous Waterbirds in a Danish Coastal Inlet. *Frontiers in Marine Science* 3.
- Becheler, R., Diekmann, O., Hily, C., Moalic, Y., Arnaud-Haond, S., 2010. The concept of population in clonal organisms: mosaics of temporally colonized patches are forming highly diverse meadows of *Zostera marina* in Brittany. *Molecular Ecology* 19, 2394-2407.
- Bertelli, C.M., Unsworth, R.K.F., 2014. Protecting the hand that feeds us: Seagrass (*Zostera marina*) serves as commercial juvenile fish habitat. *Marine Pollution Bulletin* 83, 425-429.
- Boere, G.C., Piersma, T., 2012. Flyway protection and the predicament of our migrant birds: A critical look at international conservation policies and the Dutch Wadden Sea. *Ocean & Coastal Management* 68, 157-168.
- Borum, J., Duarte, C.M., Krause-Jensen, D., Greve, T.M., 2004. European seagrasses: an introduction to monitoring and management.
- Bos, A.R., Bouma, T.J., de Kort, G.L.J., van Katwijk, M.M., 2007. Ecosystem engineering by annual intertidal seagrass beds: Sediment accretion and modification. *Estuarine Coastal And Shelf Science* 74, 344-348.
- Bostrom, C., Bonsdorff, E., 2000. Zoobenthic community establishment and habitat complexity - The importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series* 205, 123-138.
- Bostrom, C., Jackson, E.L., Simenstad, C.A., 2006. Seagrass landscapes and their effects on associated fauna: A review. *Estuarine Coastal And Shelf Science* 68, 383-403.
- Boyé, A., Legendre, P., Grall, J., Gauthier, O., 2017. Constancy despite variability: Local and regional macrofaunal diversity in intertidal seagrass beds. *Journal of Sea Research* 130, 107-122.
- Brodersen, K.E., Siboni, N., Nielsen, D.A., Pernice, M., Ralph, P.J., Seymour, J., Kühl, M., 2018. Seagrass rhizosphere microenvironment alters plant-associated microbial community composition. *Environmental Microbiology* 20, 2854-2864.
- Bugge, J., Barrett, R.T., Pedersen, T., 2011. Optimal foraging in chick-raising Common Guillemots (*Uria aalge*). *Journal of Ornithology* 152, 253-259.
- Burden, A., Garbutt, A., Evans, C.D., 2019. Effect of restoration on saltmarsh carbon accumulation in Eastern England. *Biology Letters* 15, 20180773.
- Burton, P.J.K., 1961. The Brent Goose and its food supply in Essex. *Wildfowl Trust Annual Report* 12, 104-112.
- Butler, R.W., 1991. Habitat selection and time of breeding in the Great Blue Heron, (*Ardea herodias*) (T). University of British Columbia. Retrieved from <https://open.library.ubc.ca/collections/ubctheses/831/items/1.0100392>.

Campbell, K.J., Steinfurth, A., Underhill, L.G., Coetzee, J.C., Dyer, B.M., Ludynia, K., Makhado, A.B., Merkle, D., Rademan, J., Upfold, L., Sherley, R.B., 2019. Local forage fish abundance influences foraging effort and offspring condition in an endangered marine predator. *Journal Of Applied Ecology* 56, 1751-1760.

Cebrian, J., Duarte, C.M., Marba, N., Enriquez, S., 1997. Magnitude and fate of the production of four co-occurring western Mediterranean seagrass species. *Marine Ecology-Progress Series* 155, 29-44.

Conant, R.T., Paustian, K., Elliott, E.T., 2001. GRASSLAND MANAGEMENT AND CONVERSION INTO GRASSLAND: EFFECTS ON SOIL CARBON. *Ecological Applications* 11, 343-355.

Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253-260.

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S., Turner, R.K., 2014. Changes in the global value of ecosystem services. *Global Environmental Change* 26, 152-158.

Coyer, J.A., Hoarau, G., Kuo, J., Tronholm, A., Veldsink, J., Olsen, J.L., 2013. Phylogeny and temporal divergence of the seagrass family Zosteraceae using one nuclear and three chloroplast loci. *Systematics and Biodiversity* 11, 271-284.

Cullen-Unsworth, L.C., Mtwana Nordlund, L., Paddock, J., Baker, S., McKenzie, L., Unsworth, R.K.F., 2014. Seagrass meadows globally as a coupled social-ecological system: implications for human wellbeing. *Marine Pollution Bulletin* 83, 10.

Custer, T., 1978. The Use of Feeding Habitat by a Colony of Herons, Egrets, and Ibises near Beaufort, North Carolina. *Proceedings of the Colonial Waterbird Group* 1, 154.

David, J.B., Richard, C.Z., 2002. Impact of Sea Grass Density on Carbonate Dissolution in Bahamian Sediments. *Limnology and oceanography* 47, 1751-1763.

David, O.R., Frederick, T.S., 2007. Effect of grazing by Canada geese *Branta canadensis* on an intertidal eelgrass *Zostera marina* meadow. *Marine Ecology Progress Series* 333, 271-279.

Davison, D.M., Hughes, D.J., 1998. *Zostera Biotopes (volume I). An overview of dynamics and sensitivity characteristics for conservation management of marine SACs.* Scottish Association for Marine Science (UK Marine SACs Project). 95 Pages.

de Groot, R.S., Wilson, M.A., Boumans, R.M.J., 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics* 41, 393-408.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaats, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S., Shirayama, Y., 2018. Assessing nature's contributions to people. *Science* 359, 270-272.

Dorfman, E.J., Kingsford, M.J., 2001. Environmental determinants of distribution and foraging behaviour of cormorants (*Phalacrocorax* spp.) in temperate estuarine habitats. *Marine Biology* 138, 1-10.

Dos Santos, V.M., Matheson, F.E., Pilditch, C.A., Elger, A., 2012. Is black swan grazing a threat to seagrass? Indications from an observational study in New Zealand. *Aquatic Botany* 100, 41-50.

Duarte, C.M., 2002. The future of seagrass meadows. *Environmental Conservation* 29, 192-206.

Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., Marbà, N., 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change* 3, 961.

Eadie, J.M., Mallory, M.L., Lumsden, H.G., 1995. Common Goldeneye (*Bucephala clangula*), version 2.0. In *The Birds of North America* (P. G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA.

Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marba, N., Holmer, M., Mateo, M.A., Apostolaki, E.T., Kendrick, G.A., Krause-Jensen, D., McGlathery, K.J., Serrano, O., 2012. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5, 505-509.

Fox, A.D., 1996. *Zostera* exploitation by Brent Geese and Wigeon on the Exe Estuary, southern England. *Bird Study* 43, 257-268.

Fredriksen, S., Christie, H., Andre Sæthre, B., 2005. Species richness in macroalgae and macrofauna assemblages on *Fucus serratus* L. (Phaeophyceae) and *Zostera marina* L. (Angiospermae) in Skagerrak, Norway. *Marine Biology Research* 1, 2-19.

Furness, E., Unsworth, R.K.F., 2020. Demersal Fish Assemblages in NE Atlantic Seagrass and Kelp. *Diversity* 12, 366.

Ganter, B., 2000. Seagrass (*Zostera* spp.) as food for brent geese (*Branta bernicla*): an overview. *Helgoland Marine Research* 54, 63-70.

Garrick-Maidment, N., Trehwella, S., Hatcher, J., Collins, K.J., Mallinson, J.J., 2010. Seahorse Tagging Project, Studland Bay, Dorset, UK. *Marine Biodiversity Records* 3, e73.

Gray, J.S., 1974. Animal-sediment relationships. *Oceanogr. Mar. Biol. Ann. Rev* 12, 223-261.

Green, A., Chadwick, M.A., Jones, P.J.S., 2018. Variability of UK seagrass sediment carbon: Implications for blue carbon estimates and marine conservation management. *Plos One* 13, e0204431.

Green, A.E., Unsworth, R.K.F., Chadwick, M.A., Jones, P.J., 2021. Historical analysis exposes catastrophic seagrass loss for the United Kingdom. *Frontiers in Plant Science*.

Green, A.J., Elmberg, J., 2014. Ecosystem services provided by waterbirds. *Biological Reviews* 89, 105-122.

Greiner, J.T., McGlathery, K.J., Gunnell, J., McKee, B.A., 2013. Seagrass Restoration Enhances "Blue Carbon" Sequestration in Coastal Waters. *Plos One* 8.

Grémillet, D., Argentin, G., Schulte, B., Culik, B.M., 1998. Flexible foraging techniques in breeding Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? *Ibis* 140, 113-119.

Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S., Winder, M., 2017. The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. *Global change biology* 23, 2179-2196.

Harrison, P.G., Dunn, M., 2004. Fraser River delta seagrass ecosystems, their distributions and importance to migratory birds; in Fraser River Delta, British Columbia, In *Issues of an Urban Estuary*. eds R.I. Groulx, D.C. Mosher, I. Luternauer, D.E. Bilderback. Geological Survey of Canada, Bulletin 567, p. 173-188.

Heck, K., Hays, G., Orth, R., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253, 123-136.

Heck, K.L., Valentine, J.F., 2006. Plant-herbivore interactions in seagrass meadows. *Journal of Experimental Marine Biology and Ecology* 330, 420-436.

Heithaus, M.R., 2005. Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. *Marine Biology* 147, 27-35.

Henderson, C.J., Gilby, B.L., Lee, S.Y., Stevens, T., 2017. Contrasting effects of habitat complexity and connectivity on biodiversity in seagrass meadows. *Marine Biology* 164, 117.

Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. *Am Nat* 163, 192-211.

Hirst, J.A., Attrill, M.J., 2008. Small is beautiful: An inverted view of habitat fragmentation in seagrass beds. *Estuarine Coastal And Shelf Science* 78, 811-818.

Hom, C., 1983. Foraging Ecology of Herons in a Southern San Francisco Bay Salt Marsh. *Colonial Waterbirds* 6, 37.

Horn, S., Schwemmer, P., Mercker, M., Enners, L., Asmus, R., Garthe, S., Asmus, H., 2020. Species composition of foraging birds in association with benthic fauna in four intertidal habitats of the Wadden Sea. *Estuarine, Coastal and Shelf Science* 233, 106537.

Hovel, K.A., Fonseca, M.S., Myer, D.L., Kenworthy, W.J., Whitfield, P.E., 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. *Marine Ecology-Progress Series* 243, 11-24.

Huang, A.C., Essak, M., O'Connor, M.I., 2015. Top-down control by great blue herons *Ardea herodias* regulates seagrass-associated epifauna. *OIKOS* 124, 1492-1501.

Hughes, A.R., Williams, S.L., Duarte, C.M., Heck, K.L., Waycott, M., 2009. Associations of concern: declining seagrasses and threatened dependent species. *Frontiers in Ecology and the Environment* 7, 242-246.

Inaba, N., Trainer, V.L., Onishi, Y., Ishii, K.-I., Wyllie-Echeverria, S., Imai, I., 2017. Algicidal and growth-inhibiting bacteria associated with seagrass and macroalgae beds in Puget Sound, WA, USA. *Harmful Algae* 62, 136-147.

IPCC, 2021. Intergovernmental Panel on Climate Change.
 . Retrieved 1 March 2021, from <https://www.ipcc.ch/>.

Jackson, E.L., Attrill, M.J., Jones, M.B., 2006a. Habitat characteristics and spatial arrangement affecting the diversity of fish and decapod assemblages of seagrass (*Zostera marina*) beds around the coast of Jersey (English Channel). *Estuarine Coastal And Shelf Science* 68, 421-432.

Jackson, E.L., Attrill, M.J., Rowden, A.A., Jones, M.B., 2006b. Seagrass complexity hierarchies: Influence on fish groups around the coast of Jersey (English Channel). *Journal of Experimental Marine Biology and Ecology* 330, 38-54.

Jackson, E.L., Rowden, A.A., Attrill, M.J., Bossey, S., Jones, M., 2001. The importance of seagrass beds as a habitat for fishery species. *Oceanography and Marine Biology* 39, 269-304.

Janas, U., Burska, D., Kendzierska, H., Pryputniewicz-Flis, D., Łukawska-Matuszewska, K., 2019. Importance of benthic macrofauna and coastal biotopes for ecosystem functioning – Oxygen and nutrient fluxes in the coastal zone. *Estuarine, Coastal and Shelf Science* 225, 106238.

Johnson, M.P., Edwards, M., Bunker, F., Maggs, C.A., 2005. Algal epiphytes of *Zostera marina*: Variation in assemblage structure from individual leaves to regional scale. *Aquatic Botany* 82, 12-26.

Jones, B.L., Unsworth, R.K.F., 2016. The perilous state of seagrass in the British Isles. *Royal Society Open Science* 3.

Jones, M.B., Donnelly, A., 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO₂. *New Phytologist* 164, 423-439.

Jones, R.E., Griffin, R.A., Herbert, R.J.H., Unsworth, R.K.F., 2021. Consistency Is Critical for the Effective Use of Baited Remote Video. *Oceans* 2, 215-232.

Kannan, R.R.R., Arumugam, R., Anantharaman, P., 2010. Antibacterial potential of three seagrasses against human pathogens. *Asian Pacific Journal of Tropical Medicine* 3, 890-893.

Kantrud, H.A., 1991. Wigeongrass (*Ruppia maritima*): A literature review. . U. S. Fish and Wildlife Service, Fish and Wildlife Research 10, 58.

Karen, J.M., Kristina, S., Iris, C.A., 2007. Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. *Marine ecology. Progress series (Halstenbek)* 348, 1-18.

Koch, E.W., Sanford, L.P., Chen, S.N., Shafer, D.J., Smith, J.M., 2006. Waves in Seagrass Systems: Review and Technical Recommendations. Report for the US Army Corp of Engineers, ERDC TR-06-15.

Kollars, N.M., Henry, A.K., Whalen, M.A., Boyer, K.E., Cusson, M., Eklöf, J.S., Hereu, C.M., Jorgensen, P., Kiriakopolos, S.L., Reynolds, P.L., Tomas, F., Turner, M.S., Ruesink, J.L., 2017. Meta-Analysis of Reciprocal Linkages between Temperate Seagrasses and Waterfowl with Implications for Conservation. *Frontiers in Plant Science* 8.

Kritzer, J.P., DeLucia, M.-B., Greene, E., Shumway, C., Topolski, M.F., Thomas-Blate, J., Chiarella, L.A., Davy, K.B., Smith, K., 2016. The Importance of Benthic Habitats for Coastal Fisheries. *BioScience* 66, 274-284.

Kuo, J., den Hartog, C., 2001. Chapter 2 - Seagrass taxonomy and identification key, In *Global Seagrass Research Methods*. eds F.T. Short, R.G. Coles, pp. 31-58. Elsevier Science, Amsterdam.

Lal, R., 2005. Forest soils and carbon sequestration. *Forest Ecology and Management* 220, 242-258.

Lamb, J.B., van de Water, J., Bourne, D.G., Altier, C., Hein, M.Y., Fiorenza, E.A., Abu, N., Jompa, J., Harvell, C.D., 2017. Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. *Science* 355, 731-+.

Lebreton, B., Richard, P., Galois, R., Radenac, G., Brahmia, A., Colli, G., Grouazel, M., André, C., Guillou, G., Blanchard, G.F., 2012. Food sources used by sediment meiofauna in an intertidal *Zostera noltii* seagrass bed: a seasonal stable isotope study. *Marine Biology* 159, 1537-1550.

Lee, S.Y., Fong, C.W., Wu, R.S.S., 2001. The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. *Journal of Experimental Marine Biology and Ecology* 259, 23-50.

Lefcheck, J.S., Hughes, B.B., Johnson, A.J., Pfirrmann, B.W., Rasher, D.B., Smyth, A.R., Williams, B.L., Beck, M.W., Orth, R.J., 2019. Are coastal habitats important nurseries? A meta-analysis. *Conservation Letters* 12, e12645.

Lilley, R.J., Unsworth, R.K.F., 2014. Atlantic Cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. *Global Ecology and Conservation* 2, 367-377.

Lima, M.d.A.C., 2020. Assessing the carbon sink potential and impacts of global change on intertidal seagrass meadows in central southern England, In Brighton University.

Macreadie, P.I., Trevathan-Tackett, S.M., Skilbeck, C.G., Sanderman, J., Curlevski, N., Jacobsen, G., Seymour, J.R., 2015. Losses and recovery of organic carbon from a seagrass ecosystem following disturbance. *Proceedings of the Royal Society B: Biological Sciences* 282, 20151537.

Manzello, D.P., Enochs, I.C., Melo, N., Gledhill, D.K., Johns, E.M., 2012. Ocean Acidification Refugia of the Florida Reef Tract. *Plos One* 7, e41715.

Maxwell, P.S., Eklöf, J.S., van Katwijk, M.M., O'Brien, K.R., de la Torre-Castro, M., Boström, C., Bouma, T.J., Krause-Jensen, D., Unsworth, R.K.F., van Tussenbroek, B.I., van der Heide, T., 2017. The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems – a review. *Biological Reviews* 92, 1521-1538.

McCloskey, R.M., Unsworth, R.K.F., 2015. Decreasing seagrass density negatively influences associated fauna. *PeerJ* 3, e1053.

McGlathery, K.J., Sundbäck, K., Anderson, I.C., 2007. Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. *Marine Ecology Progress Series* 348, 1-18.

McKenzie, L.J., Nordlund, L.M., Jones, B.L., Cullen-Unsworth, L.C., Roelfsema, C., Unsworth, R.K.F., 2020. The global distribution of seagrass meadows. *Environmental Research Letters* 15, 074041.

Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment* 9, 552-560.

Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., Adachi, H., Yamano, H., Nakaoka, M., 2015. Geographic variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows. *Global Biogeochemical Cycles* 29, 397-415.

Moore, J.E., Colwell, M.A., Mathis, R.L., Black, J.M., 2004. Staging of Pacific flyway brant in relation to eelgrass abundance and site isolation, with special consideration of Humboldt Bay, California. *Biological Conservation* 115, 475-486.

Moore, K.A., Short, F.T., 2006. *Zostera: Biology, Ecology, and Management*, In *SEAGRASSES: BIOLOGY, ECOLOGY AND CONSERVATION*. pp. 361-386. Springer Netherlands, Dordrecht.

Mosbahi, N., Blanchet, H., Lavesque, N., Montaudouin, X., Dauvin, J.C., Neifar, L., 2017. Main Ecological Features of Benthic Macrofauna in Mediterranean and Atlantic Intertidal Eelgrass Beds: A Comparative Study. *Journal of Marine Biology & Oceanography* 6(2), 100174.

Mosbahi, N., Pezy, J.P., Dauvin, J.C., Neifar, L., 2016. Spatial and Temporal Structures of the Macrozoobenthos from the Intertidal Zone of the Kneiss Islands (Central Mediterranean Sea). *Open Journal of Marine Science* Vol.06No.02, 15.

Mtwana Nordlund, L., Koch, E.W., Barbier, E.B., Creed, J.C., 2016. Seagrass Ecosystem Services and Their Variability across Genera and Geographical Regions. *Plos One* 11, e0163091.

Nakaoka, M., Lee, K.-S., Huang, X., Almonte, T., Bujang, J.S., Kiswara, W., Ambo-Rappe, R., Yaakub, S.M., Prabhakaran, M.P., Abu Hena, M.K., Hori, M., Zhang, P., Prathep, A., Fortes, M.D., 2014. Regional Comparison of the Ecosystem Services from Seagrass Beds in Asia, In Integrative Observations and Assessments. eds S.i. Nakano, T. Yahara, T. Nakashizuka, pp. 367-391. Springer Japan, Tokyo.

Newmaster, A.F., Berg, K.J., Ragupathy, S., Palanisamy, M., Sambandan, K., Newmaster, S.G., 2011. Local Knowledge and Conservation of Seagrasses in the Tamil Nadu State of India. *Journal of Ethnobiology and Ethnomedicine* 7, 37.

Nils, R.-P., Lars Ditlev Mørck, O., 2000. Nitrogen cycling in two temperate *Zostera marina* beds: seasonal variation. *Marine ecology. Progress series (Halstenbek)* 198, 93-107.

Nordlund, L.M., Koch, E.W., Barbier, E.B., Creed, J.C., 2016. Seagrass Ecosystem Services and Their Variability across Genera and Geographical Regions. *Plos One* 11, e0163091.

Ondiviela, B., Losada, I.J., Lara, J.L., Maza, M., Galván, C., Bouma, T.J., van Belzen, J., 2014. The role of seagrasses in coastal protection in a changing climate. *Coastal Engineering* 87, 158-168.

Orth, R.J., Heck, K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7, 339-350.

Ouisse, V., Riera, P., Migné, A., Leroux, C., Davoult, D., 2012. Food web analysis in intertidal *Zostera marina* and *Zostera noltii* communities in winter and summer. *Marine Biology* 159, 165-175.

Parry, M.E.V., 2019. Guidance on Assigning Benthic Biotopes using EUNIS or the Marine Habitat Classification of Britain and Ireland. JNCC Report No. 546, JNCC, Peterborough, ISSN 0963-8091.

Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution* 10, 430.

Pehrsson, O., 1976. Food and Feeding Grounds of the Goldeneye *Bucephala clangula* (L.) on the Swedish West Coast. *Ornis Scandinavica* 7(1), 91.

Percival, S.M., Sutherland, W.J., Evans, P.R., 1996. A Spatial Depletion Model of the Responses of Grazing Wildfowl to the Availability of Intertidal Vegetation. *Journal Of Applied Ecology* 33, 979-992.

Percival, S.M., Sutherland, W.J., Evans, P.R., 1998. Intertidal habitat loss and wildfowl numbers: applications of a spatial depletion model. *Journal Of Applied Ecology* 35, 57-63.

Perry, D., Staveley, T.A.B., Gullström, M., 2018. Habitat Connectivity of Fish in Temperate Shallow-Water Seascapes. *Frontiers in Marine Science* 4.

Peters, J.R., McCloskey, R.M., Hinder, S.L., Unsworth, R.K.F., 2014. Motile fauna of sub-tidal *Zostera marina* meadows in England and Wales. *Marine Biodiversity*, 1-8.

Peterson, B.J., Heck, K.L., 2001. Positive interactions between suspension-feeding bivalves and seagrass - a facultative mutualism. *Marine Ecology-Progress Series* 213, 143-155.

Polte, P., Asmus, H., 2006a. Influence of seagrass beds (*Zostera noltii*) on the species composition of juvenile fishes temporarily visiting the intertidal zone of the Wadden Sea. *Journal of Sea Research* 55, 244-252.

Polte, P., Asmus, H., 2006b. Intertidal seagrass beds (*Zostera noltii*) as spawning grounds for transient fishes in the Wadden Sea. *Marine Ecology-Progress Series* 312, 235-243.

Polte, P., Schanz, A., Asmus, H., 2005. The contribution of seagrass beds (*Zostera noltii*) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. *Marine Biology* 147, 813-822.

Poppe, K.L., Rybczyk, J.M., 2018. Carbon Sequestration in a Pacific Northwest Eelgrass (*Zostera marina*) Meadow. *Northwest Science* 92, 80-91, 12.

Potouroglou, M., 2017. Assessing the Role of Intertidal Seagrasses as Coastal Carbon Sinks in Scotland, In School of Applied Sciences. Edinburgh Napier University.

Potouroglou, M., Bull, J.C., Krauss, K.W., Kennedy, H.A., Fusi, M., Daffonchio, D., Mangora, M.M., Githaiga, M.N., Diele, K., Huxham, M., 2017. Measuring the role of seagrasses in regulating sediment surface elevation. *Scientific Reports* 7, 11917.

Prentice, C., Hessing-Lewis, M., Sanders-Smith, R., Salomon, A.K., 2019. Reduced water motion enhances organic carbon stocks in temperate eelgrass meadows. *Limnology and Oceanography* 64, 2389-2404.

Ramesh, R., Banerjee, K., Paneerselvam, A., Raghuraman, R., Purvaja, R., Lakshmi, A., 2019. Importance of seagrass management for effective mitigation of climate change, In *Coastal Management: Global Challenges and Innovations*. eds R.R. Krishnamurthy, M.P. Jonathan, S. Srinivasalu, B. Glaeser, pp. 283-299. Elsevier, London, UK.

Ranwell, D.S., Downing, B.M., 1959. Brent goose (*Branta bernicla* (L.)) winter feeding pattern and zosteria resources at Scolt Head Island, Norfolk. *Animal Behaviour* 7, 42-56.

Redfern, C.P.F., Bevan, R.M., 2014. A comparison of foraging behaviour in the North Sea by Black-legged Kittiwakes *Rissa tridactyla* from an inland and a maritime colony. *Bird Study* 61, 17-28.

Reusch, T.B.H., Schubert, P.R., Marten, S.-M., Gill, D., Karez, R., Busch, K., Hentschel, U., 2021. Lower *Vibrio* spp. abundances in *Zostera marina* leaf canopies suggest a novel ecosystem function for temperate seagrass beds. *bioRxiv*, 2021.2003.2021.436319.

Reynolds, P.L., Stachowicz, J.J., Hovel, K., Boström, C., Boyer, K., Cusson, M., Eklöf, J.S., Engel, F.G., Engelen, A.H., Eriksson, B.K., Fodrie, F.J., Griffin, J.N., Hereu, C.M., Hori, M., Hanley, T.C., Ivanov, M., Jorgensen, P., Kruschel, C., Lee, K.-S., McGlathery, K., Moksnes, P.-O., Nakaoka, M., O'Connor, M.I., O'Connor, N.E., Orth, R.J., Rossi, F., Ruesink, J., Sotka, E.E., Thormar, J., Tomas, F., Unsworth, R.K.F., Whalen, M.A., Duffy, J.E., 2018. Latitude, temperature, and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere. *Ecology* 99, 29-35.

Röhr, M.E., Boström, C., Canal-Vergés, P., Holmer, M., 2016. Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences* 13, 6139-6153.

Röhr, M.E., Holmer, M., Baum, J.K., Björk, M., Chin, D., Chalifour, L., Cimon, S., Cusson, M., Dahl, M., Deyanova, D., Duffy, J.E., Eklöf, J.S., Geyer, J.K., Griffin, J.N., Gullström, M., Hereu, C.M., Hori, M., Hovel, K.A., Hughes, A.R., Jorgensen, P., Kiriakopolos, S., Moksnes, P.-O., Nakaoka, M., O'Connor, M.I., Peterson, B., Reiss, K., Reynolds, P.L., Rossi, F., Ruesink, J., Santos, R., Stachowicz, J.J., Tomas, F., Lee, K.-S., Unsworth, R.K.F., Boström, C., 2018. Blue Carbon Storage Capacity of Temperate Eelgrass (*Zostera marina*) Meadows. *Global Biogeochemical Cycles* 32, 1457-1475.

Rueda, J.L., Gofas, S., Urrea, J., Salas, C., 2009. A highly diverse molluscan assemblage associated with eelgrass beds (*Zostera marina* L.) in the Alboran Sea: Micro-habitat preference, feeding guilds and biogeographical distribution. *Scientia Marina* 73, 679-700.

Sato, F., Tanaka, S., Kiriwara, S., Tanaka, Y., 2020. The influence of migratory birds on the distribution of the seagrass *Zostera japonica*. *Botanica Marina* 63, 521-525.

Sedinger, J.S., Ward, D.H., Schamber, J.L., Butler, W.I., Eldridge, W.D., Conant, B., Voelzer, J.F., Chelgren, N.D., Herzog, M.P., 2006. EFFECTS OF EL NIÑO ON DISTRIBUTION AND REPRODUCTIVE PERFORMANCE OF BLACK BRANT. *Ecology* 87, 151-159.

Seitz, R.D., Wennhage, H., Bergström, U., Lipcius, R.N., Ysebaert, T., 2013. Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science: Journal du Conseil*.

Seymour, N.R., Miller, A.G., Garbary, D.J., 2002. Decline of Canada geese (*Branta canadensis*) and common goldeneye (*Bucephala clangula*) associated with a collapse of eelgrass (*Zostera marina*) in a Nova Scotia estuary. *Helgoland Marine Research* 56, 198-202.

Shokri, M.R., Gladstone, W., Jelbart, J., 2009. The effectiveness of seahorses and pipefish (Pisces: Syngnathidae) as a flagship group to evaluate the conservation value of estuarine seagrass beds. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19, 588-595.

Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., Calumpong, H.P., Carruthers, T.J.B., Coles, R.G., Dennison, W.C., Erftemeijer, P.L.A., Fortes, M.D., Freeman, A.S., Jagtap, T.G., Kamal, A.H.M., Kendrick, G.A., Judson Kenworthy, W., La Nafie, Y.A., Nasution, I.M., Orth, R.J., Prathep, A., Sanciangco, J.C., Tussenbroek, B.v., Vergara, S.G., Waycott, M., Zieman, J.C., 2011. Extinction risk assessment of the world's seagrass species. *Biological Conservation* 144, 1961-1971.

Smale, D.A., Epstein, G., Parry, M., Attrill, M.J., 2019. Spatiotemporal variability in the structure of seagrass meadows and associated macrofaunal assemblages in southwest England (UK): Using citizen science to benchmark ecological pattern. *Ecology and Evolution* 9, 3958-3972.

Spruzen, F.L., Richardson, A.M.M., Woehler, E.J., 2008a. Influence of environmental and prey variables on low tide shorebird habitat use within the Robbins Passage wetlands, Northwest Tasmania. *Estuarine, Coastal and Shelf Science* 78, 122-134.

Spruzen, F.L., Richardson, A.M.M., Woehler, E.J., 2008b. Spatial variation of intertidal macroinvertebrates and environmental variables in Robbins Passage wetlands, NW Tasmania. *Hydrobiologia* 598, 325-342.

Staveley, T.A.B., Hernvall, P., Stjärnkvist, N., van der Meijs, F., Wikström, S.A., Gullström, M., 2020. Exploring seagrass fish assemblages in relation to the habitat patch mosaic in the brackish Baltic Sea. *Marine Biodiversity* 50, 1.

Staveley, T.A.B., Perry, D., Lindborg, R., Gullström, M., 2017. Seascape structure and complexity influence temperate seagrass fish assemblage composition. *Ecography* 40, 936-946.

Sutherland, T.F., Shepherd, P.C.F., Elner, R.W., 2000. Predation on meiofaunal and macrofaunal invertebrates by western sandpipers (*Calidris mauri*): evidence for dual foraging modes. *Marine Biology* 137, 983-993.

Thormar, J., Hasler-Sheetal, H., Baden, S., Boström, C., Clausen, K.K., Krause-Jensen, D., Olesen, B., Rasmussen, J.R., Svensson, C.J., Holmer, M., 2016. Eelgrass (*Zostera marina*) Food Web Structure in Different Environmental Settings. *Plos One* 11, e0146479.

Trevathan-Tackett, S.M., Macreadie, P.I., Sanderman, J., Baldock, J., Howes, J.M., Ralph, P.J., 2017. A Global Assessment of the Chemical Recalcitrance of Seagrass Tissues: Implications for Long-Term Carbon Sequestration. *Frontiers in plant science* 8, 925-925.

Tu Do, V., de Montaudouin, X., Blanchet, H., Lavesque, N., 2012. Seagrass burial by dredged sediments: Benthic community alteration, secondary production loss, biotic index reaction and recovery possibility. *Marine Pollution Bulletin* 64, 2340-2350.

Tubbs, C.R., Tubbs, J.M., 1983. The distribution of *Zostera* and its exploitation by wildfowl in the solent, Southern England. *Aquatic Botany* 15, 223-239.

UKTAG, 2014. UKTAG Transitional & Coastal Water Assessment Method - Angiosperm: Intertidal Seagrass Tool.

UNEP, 2020. Out of the blue: The value of seagrasses to the environment and to people. UNEP, Nairobi.

Unsworth, R.K.F., Collier, C.J., Henderson, G.M., McKenzie, L.J., 2012. Tropical seagrass meadows modify seawater carbon chemistry: implications for coral reefs impacted by ocean acidification. *Environmental Research Letters* 7.

Unsworth, R.K.F., De Leon, P.S., Garrard, S.L., Jompa, J., Smith, D.J., Bell, J.J., 2008. High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. *Marine Ecology-Progress Series* 353, 213-224.

Unsworth, R.K.F., McKenzie, L.J., Collier, C.J., Cullen-Unsworth, L.C., Duarte, C.M., Eklöf, J.S., Jarvis, J.C., Jones, B.L., Nordlund, L.M., 2019a. Global challenges for seagrass conservation. *Ambio* 48, 801-815.

Unsworth, R.K.F., Nordlund, L.M., Cullen-Unsworth, L.C., 2019b. Seagrass meadows support global fisheries production. *Conservation Letters* e12566.

Unsworth, R.K.F., Williams, B., Jones, B.L., Cullen-Unsworth, L.C., 2017. Rocking the Boat: Damage to Eelgrass by Swinging Boat Moorings. *Frontiers in Plant Science* 8.

Valentine, J.F., Heck, K.L., 1999. Seagrass herbivory: evidence for the continued grazing of marine grasses. *Marine Ecology-Progress Series* 176, 291-302.

van der Heide, T., Govers, L.L., de Fouw, J., Olf, H., van der Geest, M., van Katwijk, M.M., Piersma, T., van de Koppel, J., Silliman, B.R., Smolders, A.J.P., van Gils, J.A., 2012. A Three-Stage Symbiosis Forms the Foundation of Seagrass Ecosystems. *Science* 336, 1432-1434.

Vaughan, A., 2020. Biodiversity summit draws pledges from global leaders. *New Scientist* 248, 18.

- Wahl, M., Schneider Covachã, S., Saderne, V., Hiebenthal, C., Müller, J.D., Pansch, C., Sawall, Y., 2018. Macroalgae may mitigate ocean acidification effects on mussel calcification by increasing pH and its fluctuations. *Limnology and Oceanography* 63, 3-21.
- Webster, P.J., Rowden, A.A., Attrill, M.J., 1998. Effect of shoot density on the infaunal macro-invertebrate community within a *Zostera marina* seagrass bed. *Estuarine Coastal And Shelf Science* 47, 351-357.
- Whalen, M.A., Whippo, R.D.B., Stachowicz, J.J., York, P.H., Aiello, E., Alcoverro, T., Altieri, A.H., Benedetti-Cecchi, L., Bertolini, C., Bresch, M., Bulleri, F., Carnell, P.E., Cimon, S., Connolly, R.M., Cusson, M., Diskin, M.S., D'Souza, E., Flores, A.A.V., Fodrie, F.J., Galloway, A.W.E., Gaskins, L.C., Graham, O.J., Hanley, T.C., Henderson, C.J., Hereu, C.M., Hessing-Lewis, M., Hovel, K.A., Hughes, B.B., Hughes, A.R., Hultgren, K.M., Jänes, H., Janiak, D.S., Johnston, L.N., Jorgensen, P., Kelaher, B.P., Kruschel, C., Lanham, B.S., Lee, K.-S., Lefcheck, J.S., Lozano-Álvarez, E., Macreadie, P.I., Monteith, Z.L., O'Connor, N.E., Olds, A.D., O'Leary, J.K., Patrick, C.J., Pino, O., Poore, A.G.B., Rasheed, M.A., Raymond, W.W., Reiss, K., Rhoades, O.K., Robinson, M.T., Ross, P.G., Rossi, F., Schlacher, T.A., Seemann, J., Silliman, B.R., Smee, D.L., Thiel, M., Unsworth, R.K.F., van Tussenbroek, B.I., Vergés, A., Yeager, M.E., Yednock, B.K., Ziegler, S.L., Duffy, J.E., 2020. Climate drives the geography of marine consumption by changing predator communities. *Proceedings of the National Academy of Sciences* 117, 28160-28166.
- Wilkie, L., O'Hare, M.T., Davidson, I., Dudley, B., Paterson, D.M., 2012. Particle trapping and retention by *Zostera noltii*: A flume and field study. *Aquatic Botany* 102, 15-22.
- Yu, Z.C., 2012. Northern peatland carbon stocks and dynamics: a review. *Biogeosciences* 9, 4071-4085.
- Zarco-Perello, S., Enríquez, S., 2019. Remote underwater video reveals higher fish diversity and abundance in seagrass meadows, and habitat differences in trophic interactions. *Scientific Reports* 9, 6596.