THE H.T. ODUM SYNTHESIS ESSAY

The Dynamics of Seagrass Ecosystems: History, Past Accomplishments, and Future Prospects

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Abstract

The goal of this perspective is to review how seagrass research has evolved over the past half century to our current state of knowledge. We review how our knowledge of seagrass ecosystems changed from the pre-1970s when so little was known about seagrasses and how it progressed during the next 5 decades when seagrass knowledge rapidly expanded. Here, we concentrate on accomplishments in the areas of reproductive biology and ecology, population biology, seagrass-animal relationships, conservation and restoration, and mapping and monitoring. We also look ahead and discuss some areas that are ripe for future research, especially those employing new mapping and monitoring technologies, improved restoration methods that include multiple genetic variants, rhizosphere studies that result in a deeper understanding of microbial effects on nitrogen availability, sulfide levels and carbon sequestration, and how changing climatic regimes and tropicalization will likely affect temperate and tropical seagrass-dominated ecosystems.

Keywords Seagrass · History · Research accomplishments · Climate change

Introduction

Seagrasses are highly productive habitat-forming foundation species that thrive in shallow estuarine and coastal regions throughout the world, with the exception of the most polar seas. The habitats provided by seagrasses are critically important, providing numerous ecosystem services that include serving as nurseries for the juveniles of many economically important fishery species and enhancing local biodiversity (Lefcheck et al. 2019; Unsworth et al. 2022). They also contribute to ecosystem function by sequestering carbon, reducing the abundance of human pathogens, and providing forage for threatened mega-herbivores like dugongs, manatees, and green turtles (Fig. 1 from Orth et al. 2006a; Beck et al. 2001; Barbier et al. 2011; Fourqurean et al. 2012; Lamb et al. 2017; Unsworth et al. 2018, 2022).

Like many other ecosystems, seagrass meadows have been in global decline throughout the twentieth century due to a multitude of factors (Waycott et al. 2009; Dunic et al. 2021) (Fig. 1). Their depth limits are controlled by light (Duarte 1991), and their high light requirements make them particularly sensitive to water quality changes (Dennison et al. 1993), so much so that they often serve as sentinels and harbingers of declining environmental conditions (Orth et al. 2006a, 2017a; Unsworth et al. 2022). However, they now face new challenges associated with accelerating global environmental change, including warming temperatures and associated tropicalization, ocean acidification, increasing coastal eutrophication, and reductions in light and dissolved oxygen concentrations (Short and Neckles 1999; Duarte 2002; Hyndes et al. 2016; Zimmerman 2021; Guerrero-Meseguer et al. 2020; Turschwell et al. 2021).

After five decades of progress in understanding their biology, ecology, and the value of the many services they provide, we have a greater understanding than ever of the continuing threats facing seagrasses worldwide. During these five decades, there have been paradigm shifts in our understanding of seagrass biology and the fundamental processes that underpin the functioning of seagrass meadows. Despite these advances, seagrass science is still a young sub-discipline, with many recent and ongoing discoveries

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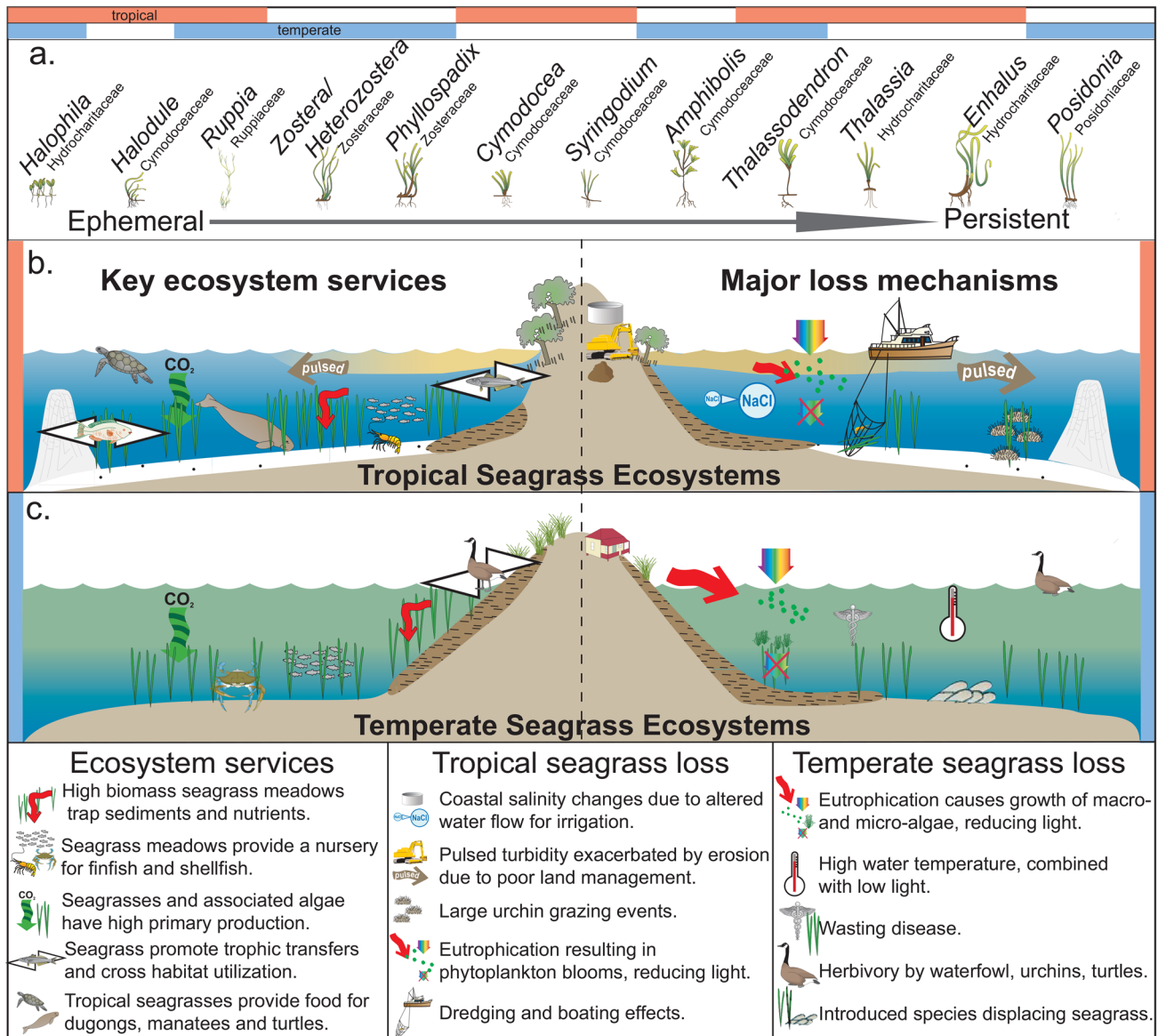
Fig. 1 Conceptual diagrams for (a) tropical and (b) temperate seagrass ecosystems highlighting key ecosystem services and major mechanisms of seagrass loss (from Orth et al. 2006a, b, reprinted with permission from BioScience)

arising from the growing number of researchers now fully engaged in seagrass study, demonstrating that we still have much to learn to properly conserve, manage, and restore these iconic ecosystems.

We review how knowledge of seagrass ecosystems progressed and expanded from the pre-1970s to the present. Next, we describe major accomplishments in seagrass science, concentrating on reproductive biology and ecology, seagrass-animal relationships, conservation and restoration, and mapping and monitoring. Finally, we offer our perspectives on areas that are ripe for future research.

A Short History of Seagrass Science and Conservation

Seagrass Research Prior to 1970

While seagrasses exist in most inhabited coastal areas of the world, peer-reviewed publications on seagrasses were rare prior to 1970 (Fig. 2). Historically, some species of seagrasses had been valued for their uses in weaving hats and baskets, home insulation, fertilizer, and roofing material (Orth et al. 2020). Eelgrass (*Zostera marina*) in northern

Fig. 2 History of seagrass peer-reviewed publications (Digital Science. (2018-) Dimensions available from https://app.dimensions.ai. Accessed on October 10, 2022, under license agreement)
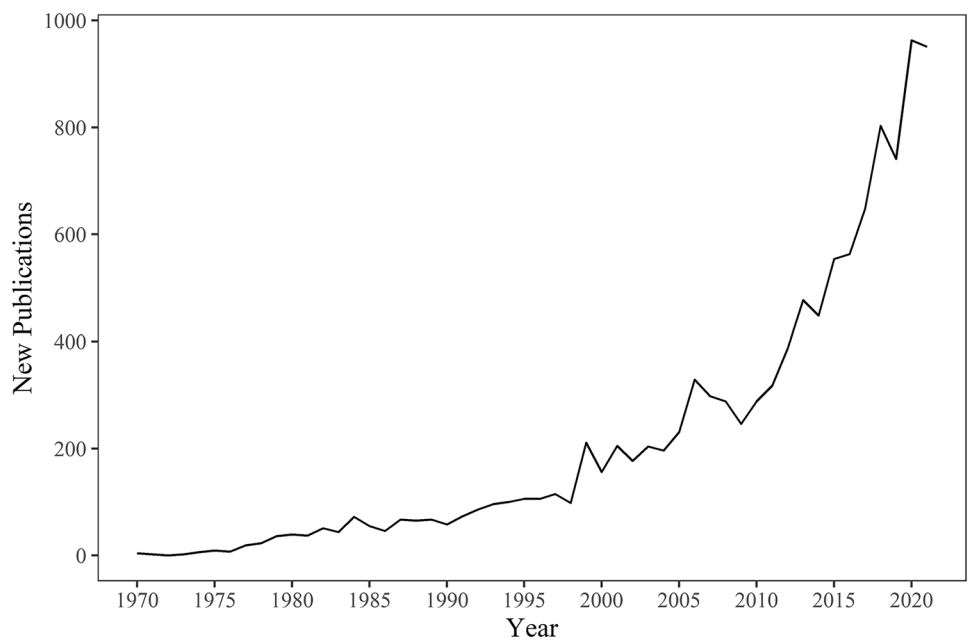
European waters was long valued as habitat for a diverse faunal assemblage, which was thought to contribute to high fish production (Petersen 1918) (Fig. 3a). Although research on the basic biology and ecology of seagrasses in the early

part of the twentieth century was rare, the importance of eelgrass was recognized in the 1930s when it disappeared from most areas in the North Atlantic, presumably from the "wasting disease" caused by the parasitic marine slime mold
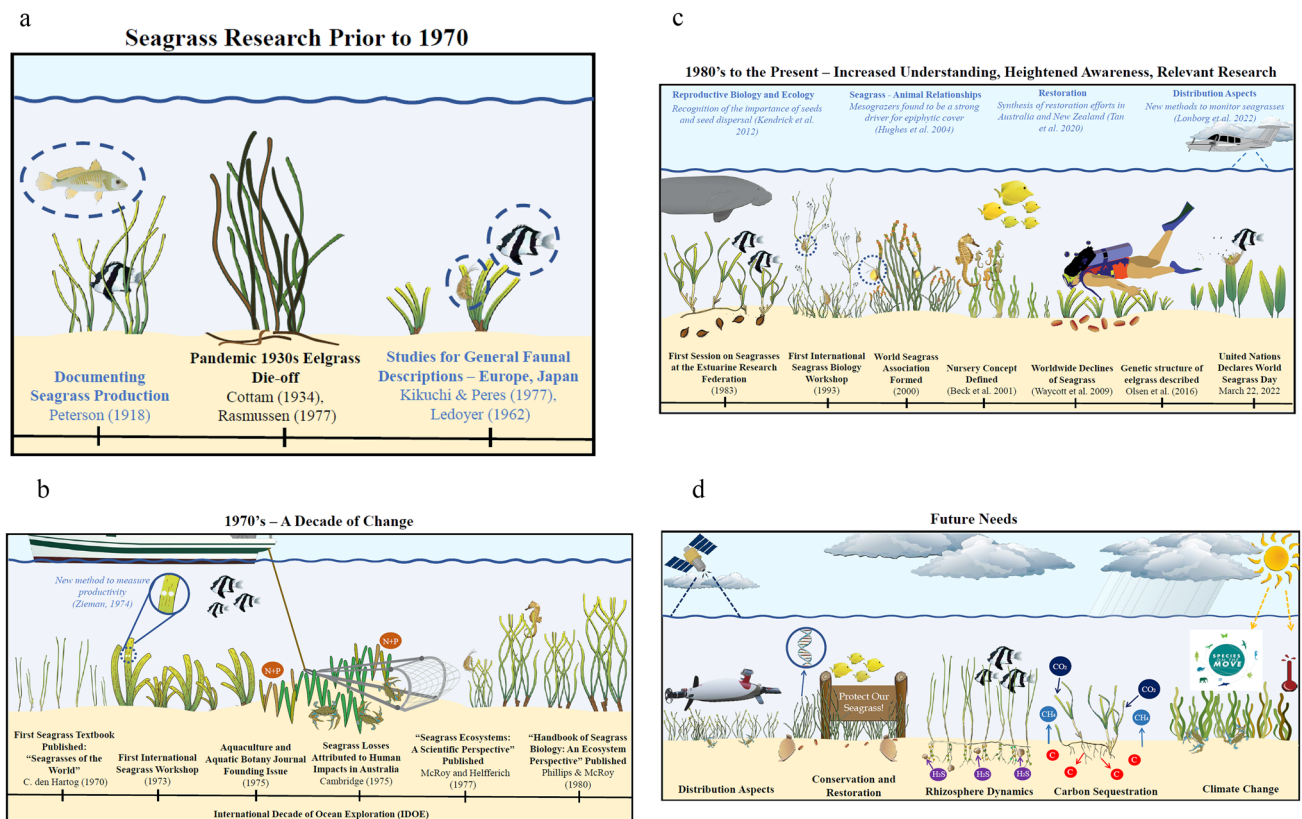

Fig. 3 Timeline of notable events and achievements in the history of seagrasses: **a** prior to 1970, **b** the 1970s, **c** 1980s to the present, and **d** future directions

Labyrinthula sp. (Rasmussen 1977; Muehlstein et al. 1991) (Fig. 3a). Although the effects of eelgrass loss had been considered by Cottam (1934, 1935) and Cottam and Munro (1954), the ecological consequences of this dramatic loss of eelgrass were more thoroughly described and summarized much later by Rasmussen (1973, 1977), including shoreline erosion and faunal disappearance, especially the loss of the commercially important bay scallop that was once common along the east coast of the USA (Rasmussen 1977; Thayer and Stuart 1974; Oreska et al. 2017).

There was early research on seagrass-associated fishes and invertebrates in Japan and southern Europe, mainly in the form of surveys of the many and diverse inhabitants of seagrass meadows (see summaries by Kikuchi and Perez 1977; Kikuchi 1980) (Fig. 3a). Some of this work was published in the 1960s in a series of papers that compared the fauna of French Atlantic eelgrass meadows with that of Mediterranean *Posidonia oceanica* meadows (Ledoyer 1962, 1964, 1966, 1968; Harmelin 1964). In Japan, studies by Kikuchi (1966, 1974) and others (Kita and Harada 1962) documented the diversity of seagrass-associated animals, as well as the role of seagrass as a nursery habitat for juveniles of economically valuable fishes (Kikuchi 1980).

1970s—A Decade of Change

In the 1970s, several notable achievements launched the study of seagrass ecosystems to greater prominence. "Seagrasses of the World" by den Hartog (1970) was published in 1970 with descriptions of the biology, ecology, and systematics of all known species of seagrasses (Fig. 3b). The depth and breadth of this comprehensive, global treatment of seagrasses remain unrivaled today. In 1973, the first International Seagrass Workshop was held in Leiden, The Netherlands, with 37 scientists from 11 countries participating (Fig. 3b). The resulting workshop report served as the nucleus for the first book devoted to seagrasses and their faunal associates (McRoy and Helfferich 1977) (Fig. 3b). A second book (Phillips and McRoy 1980) was also conceived at the Leiden workshop (Fig. 3b). In 1975, the journal *Aquatic Botany* published its first issue, containing 13 papers on seagrass systematics, biology, and ecology contributed by 18 authors from five countries (Fig. 3b). Together, these early volumes marked a turning point for seagrass research.

The *International Decade of Ocean Exploration* was also launched in the 1970s and included studies of seagrasses around the world by researchers from a diversity of disciplines (Fig. 3b). Two issues of the journal *Aquaculture* contributed substantially to the seagrass literature (vol. 4, 1974; vol. 12(3), 1977) (Fig. 3b). During this period, Zieman (1974) described a novel leaf-marking method of measuring seagrass productivity, in which a mark at the base of

seagrass leaves serves to identify new material produced during a growth interval (Fig. 3b). This new approach recognized the inaccuracies caused by storage of oxygen in seagrass leaf lacunae when measuring seagrass production via the "oxygen evolution method" and laid the foundation for decades of seagrass production studies. In addition, during this period, Cambridge (1975) described one of the first widespread losses of seagrass due to human activities in Australia's Cockburn Sound (Fig. 3b). Finally, in 1973, two seagrass papers were presented at the Estuarine Research Federation Conference. This biennial conference (later known as the Coastal and Estuarine Research Federation (CERF) conference) subsequently became a focal point for scientific presentations on seagrasses from North America and around the world. However, despite increasing attention devoted to seagrasses as a result of these seminal studies, there still were very few seagrass research papers being published (Fig. 2).

1980s to the Present—Increased Understanding and Heightened Awareness

Expanding Knowledge

Our understanding of seagrass biology and ecology expanded greatly during the past four decades and moved seagrass studies into the mainstream of marine and estuarine research. There were a number of notable events during this period. The 1983 conference of the Estuarine Research Federation (ERF) contained its first session dedicated solely to seagrasses and resulted in a special issue of the journal *Estuaries* that mainly focused on seagrass faunal relationships (Orth et al. 1984a, b) (Fig. 3c). The International Seagrass Biology Workshop was launched in 1993 and has occurred nearly every 2 years since then at different locations in Asia, Australia, Europe, and North and South America (Fig. 3c). As a result of these successful workshops, the World Seagrass Association was formed in 2000 to facilitate international meetings and provide a forum for the world's seagrass research community to share information (Fig. 3c).

During these decades, several additional books on seagrasses were published (Larkum et al. 1989; Bortone 1999; Hemminga and Duarte 2000; Short and Coles 2001; Green and Short 2003; Larkum et al. 2006, 2018), and the number of papers published on seagrasses increased dramatically (Fig. 2).

Conservation Action

Conservation efforts for seagrasses have lagged behind many other aquatic and terrestrial habitats, but with the landmark publication on the value of ecosystem services by Costanza et al. in (1997), efforts to protect and conserve seagrasses began to emerge regionally and eventually worldwide. And,

as the literature on seagrasses expanded and awareness of their importance increased, governmental and nongovernmental organizations (NGOs) around the world began to focus attention on this important ecosystem and how to protect seagrass (Coles and Fortes 2001). In the USA, the National Estuarine Research Reserve System, a network of sites established to protect and study estuarine systems, includes 17 sites with seagrass present. In these localities, a variety of seagrass parameters are monitored annually using identical methods. Other USA federal programs also include seagrass protection or research (e.g., United States Army Corps of Engineers, United States Fish and Wildlife Service, United States National Park Service, National Oceanographic and Atmospheric Administration, and the United States Environmental Protection Agency), and many states have management agencies and policies designed to protect seagrasses. Furthermore, seagrasses are considered an important "aquatic life use" under the United States Clean Water Act (1972), and thus, federal and state water quality standards and remediation plans (e.g., Total Maximum Daily Load requirements and Watershed Implementation Plans) are specifically designed to maintain or regain this designated use. Similarly, the European Union's Habitats Directive specifically cites seagrass meadows as special areas to preserve; in certain regions in Canada (specifically the Atlantic Coast), eelgrass is designated as an Ecologically Significant Species (DFO 2009); and seagrasses are identified in policy documents currently in place or planned in India, New Zealand, Australia, and Indonesia. In addition, non-governmental agencies around the world focus on seagrass conservation, education, and research, such as Chesapeake Bay Foundation in the USA, and "Seeds for Snapper" in Australia (Sinclair et al. 2021). Finally, many nations are seeking to incorporate seagrasses and their vast stores of sedimentary carbon into their Nationally Determined Contributions to help meet the climate mitigation goals outlined in the 2015 Paris Agreement.

The United States National Science Foundation funded National Center for Ecological Analysis and Synthesis supported two seagrass working groups that produced significant advances in understanding the fundamental importance of seagrass systems (e.g., as nursery habitats, Beck et al. 2001) (Fig. 3c) and their global decline (Waycott et al. 2009) (Fig. 3c). In 2007, the first global assessment of extinction probability of all seagrass species was conducted at three regional workshops, based on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species criteria. Ten of 72 species of seagrass were found to be at elevated risk of extinction, and three species were considered endangered at that time (Short et al. 2011).

The United Nations Environment Program (2020) published a comprehensive report on seagrasses to raise the profile of this "forgotten ecosystem" in the global conservation community. The report recommended developing a seagrass expert group, constructing a world map of seagrasses, and advocating for financial incentives for seagrass conservation and restoration.

On March 23, 2022, the United Nations General Assembly adopted a resolution designating that day as World Seagrass Day (Fig. 3c). In addition, the United Nations included seagrasses in recent proclamations on ecosystem restoration (United Nations 2017) and science-based actions toward resilient and healthy oceans (United Nations 2017). This increasing global awareness of seagrass importance heralds a new era for seagrass research and conservation.

Topics in Seagrass Science, Restoration, and Monitoring

In the following sections, we describe some significant accomplishments in seagrass research, because of, or in fulfillment of, the efforts noted above. We describe how our understanding of certain areas of seagrass science and conservation has changed during the past five decades, including reproductive biology and ecology, plant/animal relationships, trophic ecology and food webs, restoration, and mapping and monitoring. Given the explosive growth of seagrass literature since the 1980s (Fig. 2), we have necessarily drawn from a relatively small group of published papers, and any errors of omission are our own.

Reproductive Biology and Ecology

While seagrasses can grow and spread both asexually via clonal growth and sexually via producing and dispersing seeds, much early work focused solely on clonal growth. Research showed average shoot elongation rates ranging from 2 cm year^{-1} for *Posidonia oceanica* to 356 cm year^{-1} for *Halophila ovalis* (Duarte et al. 2006). The advent of genetic analysis using microsatellites importantly revealed that clones can be large and very old, with one clone of *Posidonia australis*, a slow growing species in Western Australia, estimated to span an extraordinary 200 sq. km and be an astoundingly 4500 years old, making it among the oldest single eukaryotic organisms on the planet (Edgeloe et al. 2022). In the Mediterranean, clones of *P. oceanica*, which covered one to 15 km at different locations, were estimated to be between 80,000 and 200,000 years old (Arnaud-Haond et al. 2012). Additionally, in the Baltic, an eelgrass clone was found to cover 6400 m^2 and was estimated to be more than 1000 years old (Reusch et al. 1999). While clonal growth is advantageous for stable environments and perpetuates genetic uniformity, one limitation is the inability to disperse to new environments should conditions deteriorate. Detached vegetative shoots (with their roots and rhizomes) can disperse long distances, but the extent to which, and for which species, these fragments can actually establish naturally and grow into new colonies (Hall et al. 2006; Thomson et al. 2015) remains unclear (Ewanchuk and Williams 1996). However, it is possible

that the genetic uniformity of large and very old clones described above could be the result of vegetative fragments colonizing nearby locations, thereby facilitating the spread of the single clone.

The dominance of work on clonal growth hindered our understanding of the mechanisms for, extent of, and relative importance of sexual reproduction. However, during the last two decades, we have learned that sexual reproduction and seed production are important in the biology and ecology of seagrass meadows by contributing to seagrass bed establishment and maintenance, with significant achievements in understanding processes influencing successful seed germination in many species (Orth et al. 2000, 2006b; Brodersen and Kuhl 2023). Mechanistically, sexual reproduction was thought to occur primarily through hydrochory, the physical transport of pollen by water movement (see review by Ackerman 2006). However, exciting recent work, first demonstrated in *Thalassia testudinum*, showed that small invertebrates can act as pollinators (van Tussenbroek et al. 2016). Another recent demonstration of the pollination of a red algal species (*Gracilaria gracilis*) by the isopod *Idotea balthica* (Lavaut et al. 2022) suggests that pollination of both seagrasses and algae by animals, something thought to be absent in the world's oceans (Vermeij and Grosberg 2010), may be more common than previously thought, and much remains to be learned.

The importance of sexual reproduction was first shown by early genetic studies that found many areas with higher than expected genetic diversity, suggesting that seeds contributed to meadow development (Waycott 1995; Reusch 2002). Additional evidence came from a number of studies with different seagrass species that found disturbed meadows to recover more rapidly than would be expected from solely clonal growth (*Zostera marina*, Plus et al. 2003; Greve et al. 2005; *Thalassia testudinum*, Whitfield et al. 2004; *Posidonia australis*, Cambridge et al. 2002; and *Halophila ovalis*, Preen 1995), and one study concluded that development of new *Z. marina* patches could have only been established from recruitment of seedlings, rather than entrapment of detached vegetative shoots (Olesen and Sand Jensen 1994). There can also be substantial genetic variability within even small portions of meadows, although the mechanisms responsible for the existence of this variation are incompletely understood (Becheler et al. 2014; Kollars et al. 2022).

Research over the last two decades, notably with *Zostera marina* and *Posidonia australis*, has shown that these two species have a number of dispersal mechanisms that can move seeds 10 to 100 s of kilometer from the parent plant (Fig. 3c), (e.g., floating fruits or intact flowering shoots with viable seeds, Fig. 4 from Kendrick et al. 2012; Orth et al. 2006b). Both biotic (by ingestion and excretion of viable seeds by vertebrates) and abiotic (by wind and currents) processes have been shown to be important for seed dispersal (Fig. 4 from Kendrick et al. 2012; Harwell and Orth 2002: Sumoski and Orth 2012; Ruiz-Montoya et al. 2012, 2015;

Fig. 4 Conceptual diagrams for **a** flower location within seagrass canopies, **b** likelihood of pollen dispersal distance, **c** dispersal distance for positively and negatively buoyant seeds or propagules, and **d** mechanisms of secondary seed dispersal for tropical and temperate seagrass habitats. Abbreviation: m, meters (from Kendrick et al. 2012, reprinted with permission from BioScience)
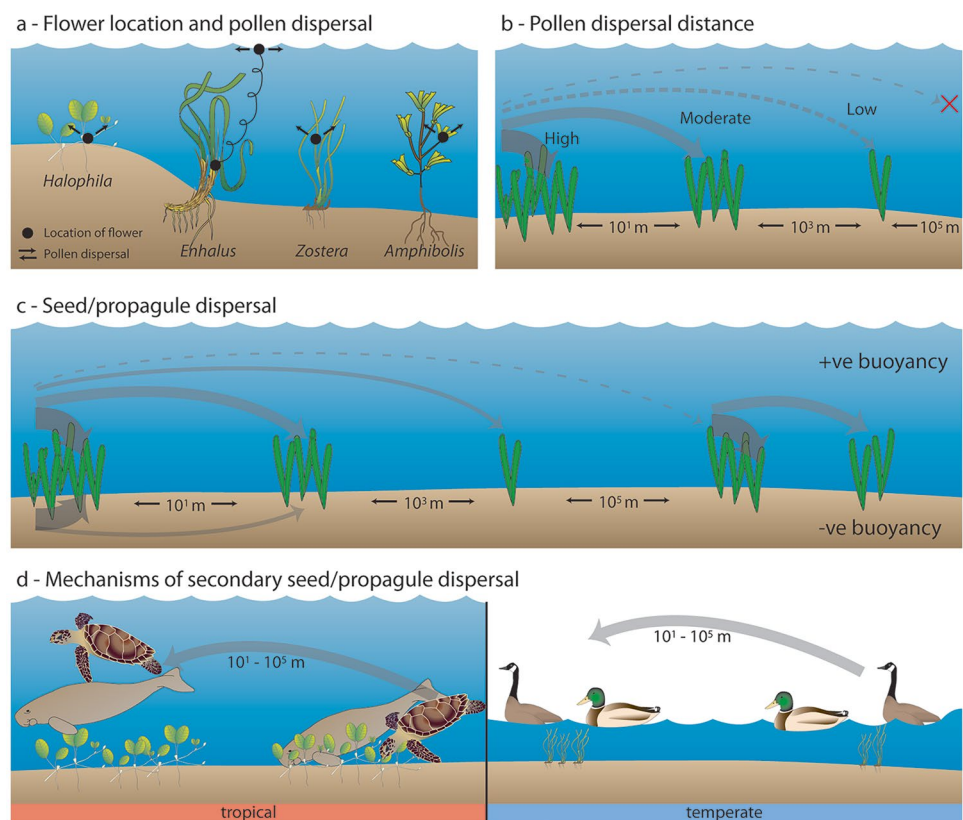
Tol et al. 2017), and in one case with *Halodule wrightii*, a significant distance attributed to active dispersal agents (Tavares et al. 2023). A surprising observation was that some seeds do not move far after settling on the sediment surface, remaining near the parent plant (Orth et al. 1994; Manley et al. 2015; Hosokawa et al. 2015; Li et al. 2018; Kendrick et al. 2019a). Bioturbation and physical processes appear to contribute to seed retention, rapid burial, or loss of settled seeds (Luckenbach and Orth 1999; Delefosse and Kristensen 2012; Blackburn and Orth 2013; Statton et al. 2017). Similar to the fate of seeds in the terrestrial environment (Janzen 1970), predation can result in significant loss of seagrass seeds (Fishman and Orth 1996; Orth et al. 2006c).

Seagrass-Animal Relationships

Animal Communities

Many early studies of seagrass inhabitants in Japan and Europe (see references above) were primarily descriptive, highlighting the richness and abundance of the seagrass-associated faunal community, and demonstrating that seagrasses supported a much more diverse and abundant faunal assemblage than nearby unvegetated habitats (Orth et al. 1984a, b). During the 1970s, many experiments were conducted to attempt to elucidate mechanisms that could explain these differences, such as evaluations of the protection seagrass could provide prey from their predators (Orth et al. 1984a, b). For example, Heck and Orth (1980), building on the experimental results of Nelson (1979) and Stoner (1979), hypothesized that seagrass epifauna density increased with seagrass leaf area by reducing foraging success of larger fish, but only up to the point where shoot densities were so high that meadows became anoxic at night due to increased respiration. At the same time, observational surveys attempted to discern general trends in the macroecology of seagrass and associated fauna over latitudinal scales (Virnstein et al. 1984).

Experiments over the next several decades showed that the relationship between plant cover and animal abundance had been oversimplified by early studies. The large number of manipulative experiments over this time period, both from

PHYSICAL ENVIRONMENT

Salinity, Temperature, Oxygen, Turbidity, Light, Hydrodynamics, Storms, Sediment
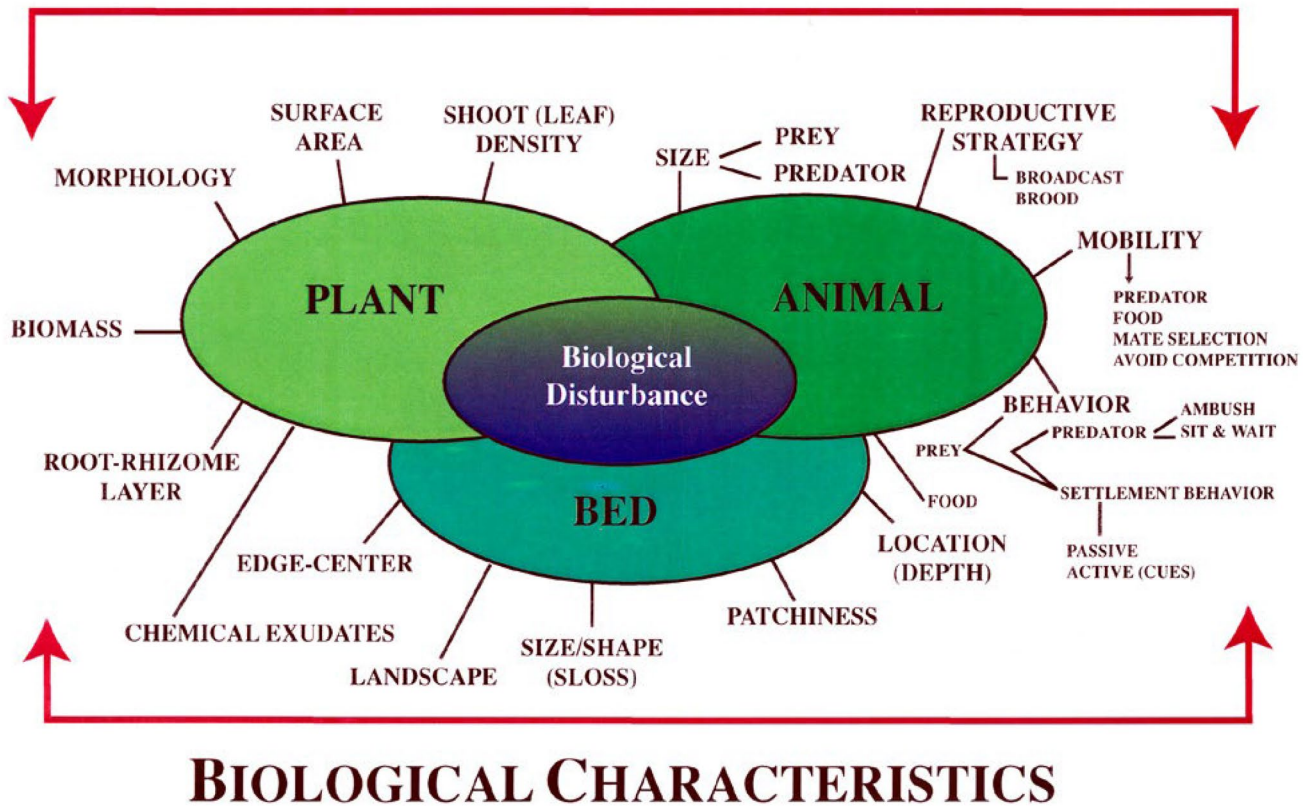

Fig. 5 Factors or processes that can influence the distribution and abundance of animals in seagrass meadows

the field and the laboratory, revealed latitudinally dependent complex interactions that determine animal abundance (Heck and Wilson 1987; Reynolds et al. 2018) (Fig. 5). These interactions involve not just plant characteristics (e.g., surface area, shoot density, biomass, morphology, chemical exudates, or arrangement of shoots; (Heck and Orth 2006)), but also characteristics of the meadow, such as patchiness, size and shapes of patches, edges vs. interiors, and depth (Bologna and Heck 1999; Hovel and Lipcius 2001; Boström et al. 2006; Yeager et al. 2016; Hyndes et al. 2018; Whippo et al. 2018; Stark et al. 2020). In addition, animal characteristics (e.g., behavior, reproductive strategy, size of prey and their coloration, predator foraging behavior, and even larval supply) were found to be important in defining distributional patterns (Orth 1975, 1992; Main 1985, 1987; James and Heck 1994; Yeager et al. 2019). Finally, physical characteristics of the environment can be equally important (e.g., salinity, sediment type, currents, season; Orth 1973; Irlandi and Peterson 1991; Stark et al. 2020).

Heck (2019) summarized how scientific understanding evolved concerning the role of seagrass biomass in protecting small invertebrates from predation. Early experiments documenting positive relationships between seagrass biomass and survivorship of small invertebrate prey were largely carried out in laboratory mesocosms with a single predator present (e.g., Nelson 1979; Heck and Thoman 1984). These lab results were confounded by the decreasing rate that the predator encountered prey as vegetation biomass increased. In nature, as seagrass density increases, so does the abundance of both predators and prey (Heck and Orth 1980; Wyda et al. 2002). Subsequent experiments that allowed numbers of both predators and prey to increase with vegetation density found that although the presence of vegetation improved survival of prey, there was no major effect of the density of the vegetation (Fig. 6; Mattila et al. 2008; Canion and Heck 2009; Scheinin et al. 2011). Therefore, sparse seagrass densities provided the same relative degree of shelter from predation as did high densities, with the consequence that sparse patches of seagrass also deserve protection and preservation. A related conclusion about the value of small, sparse patches of seagrass in supporting diverse animal assemblages has been shown experimentally by both Lefcheck et al. (2016) and Gagnon et al. (2021).

Seagrass Epiphytic Grazers

Another major advance during the past 40 years has been the recognition of the functional importance of epifauna to seagrass meadow health. Historically, while it was recognized that grazing by mobile epifauna regulated abundance of epiphytic organisms, little attention was paid to the possible indirect effects of small mesograzers. However, this changed dramatically following research in the 1980s that
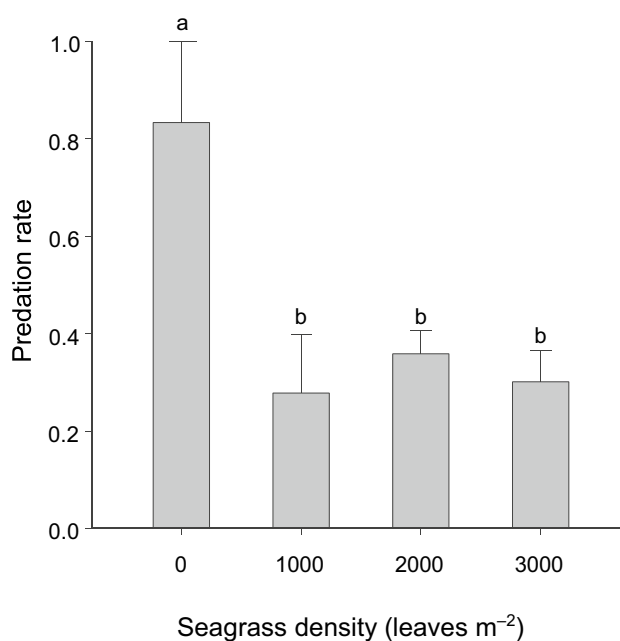

Fig. 6 Predation rate (mean ± SE) of pinfish (*Lagodon rhomboides*) feeding on grass shrimp (*Palaemonetes pugio*) prey in field mesocosm experiments. The predation rate is the percentage of the initial prey number eaten during the experimental period. Treatments with different letters indicate differences at the $p < 0.005$ level. Predator to prey ratios in all seagrass treatments were constant at 1:10 (from Canion and Heck 2009, reprinted with permission from Marine Ecology Progress Series)

suggested that removal of epiphytic cover could have an indirect, positive influences on seagrass growth (van Montfrans et al. 1984; Neckles et al. 1993). This finding led to increasing interest in the role that small grazers played in seagrass meadows around the world (e.g., Duffy et al. 2003; Moksnes et al. 2008; Baden et al. 2010). An important meta-analysis reported that mesograzer abundance explained at least as much, if not more, variance in the abundance of light-blocking epiphytes on seagrass leaves as nutrient concentrations (Fig. 3c; Hughes et al. 2004). This was further rigorously tested in the *Zostera* Experimental Network (ZEN), a global network of researchers studying eelgrass-epifauna (Fig. 3c), (Reynolds et al. 2018; Duffy et al. 2015). These and earlier experiments have consistently shown that food web alterations (e.g., trophic cascades caused by overfishing) can indirectly produce changes in mesograzer abundance that alter the abundance of epiphytes and, ultimately, seagrass health (Douglass et al. 2007; cf Fig. 7, Heck and Valentine 2007; Valentine and Duffy 2006; Valentine and Heck 2020; Gagnon et al. 2021). More diverse seagrass assemblages than those usually occurring in temperate eelgrass meadows also show important top-down effects of food web alterations (Fig. 7), although the food webs of these assemblages can include omnivorous organisms that consume both mesograzers and
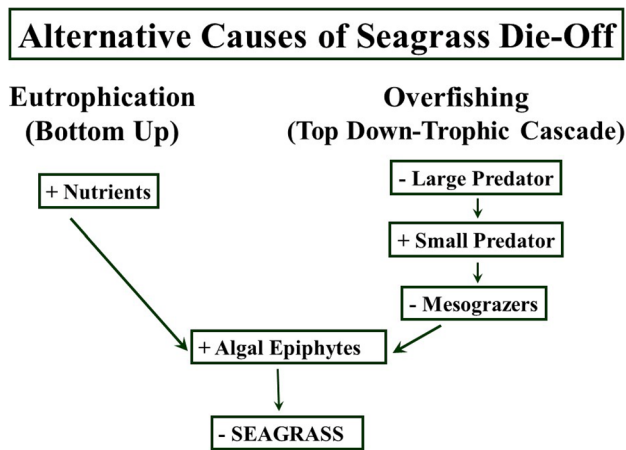
Alternative Causes of Seagrass Die-Off

Eutrophication
(Bottom Up)

Overfishing
(Top Down-Trophic Cascade)

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+ Nutrients                    - Large Predator
                                      ↓
                               + Small Predator
                                      ↓
                               - Mesograzers
        ↓                             ↓
              + Algal Epiphytes ←
                      ↓
                 - SEAGRASS
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Fig. 7 Top-down versus bottom-up alternative explanations for seagrass die-off

epiphytic algae, such as pinfish (*Lagodon rhomboides*), and produce more complicated outcomes (Heck et al. 2000; see review by Duffy et al. 2014).

Seagrasses as Nursery Habitats

The impressive faunal abundance and diversity in seagrass meadows uncovered by initial studies led to the statement in many subsequent papers that seagrass beds were nurseries for a variety of fish and invertebrates with complex life cycles. However, it later became apparent that there was no clear definition of nursery habitat. This issue was resolved by Beck et al. (2001) who defined a nursery as a habitat for juveniles of a particular species if its contribution, per unit area, to the production of individuals that recruit to adult populations is greater, on average, than the production from other habitats in which juveniles occur (Fig. 3c). This definition has not been without its critics (Dahlgren et al. 2006; Sheaves et al. 2006; Fodrie et al. 2009; Sheaves 2009), who proposed the concept of a "seascape nursery," that includes not only one, but several habitats, that are used during different portions of a species' life cycle (Boström et al. 2011; Litvin et al. 2018; Nagelkerken et al. 2015). Most studies of the nursery role in the last two decades have focused on measuring and comparing proxies of production, including density, growth rates, and survivorship, between purported nursery and non-nursery habitats, with literature reviews concluding that structured habitats are crucial to many species of invertebrates and fish, with mangroves and seagrasses emerging as especially important nursery habitats (Heck et al. 2003; Igulu et al. 2014; McDevitt-Irwin et al. 2016; Lefcheck et al. 2019). Documenting the contribution of potential nursery habitats to adult populations remains challenging and usually requires

sustained, complicated efforts, such as those that identify the relative importance of putative nursery habitats by matching the otolith chemistries of adult and juvenile fishes over several years (cf. Fodrie et al. 2020).

Food Webs and Energy Flux

Early studies (e.g., Kikuchi and Peres 1977; Kikuchi 1980) established the commonly held belief that, despite their enormous productivity, little seagrass production was consumed by herbivores. Instead, most seagrass production was thought to enter detrital food webs that formed the energetic base of seagrass ecosystems (see review by Mateo et al. 2006). Stable isotope data later showed that seagrass food webs are supported in large part by the consumption of micro algae growing on seagrass leaves and exposed rhizomes, as well as associated green, brown, and red algae, that are consumed by a variety of invertebrate herbivores, rather than by decaying seagrass biomass (e.g., Kitting et al. 1984). However, in contrast to the belief that living seagrass was not often consumed, as early as 1980, Ogden (1980) described how tropical seagrass was consumed by a variety of urchins, fish, and turtles. Since then, seagrass herbivory has been shown to occur commonly in a variety of locations, including the Mediterranean Sea (Tomas et al. 2005; Vergés et al. 2008; Prado et al. 2007), the Gulf of Mexico (Valentine and Heck 1991, 2020; Rodriguez and Heck 2020), the tropical Pacific (Unsworth et al. 2007; Christianen et al. 2014), and the Indian Ocean (Mariani and Alcoverro 1999; Kelkar et al. 2013a, b; Vanderklift et al. 2021). This work demonstrates that a great deal of energy moves through seagrass meadow food webs via direct consumption of living seagrass leaf tissue, especially in lower latitudes (Valentine and Heck 2020).

Restoration

The science of restoring seagrasses, while a young field of research based on the number of published accounts (Fig. 8; Duarte et al. 2020), apparently had its roots in the late 1930s, after the disappearance of eelgrass in the USA and Europe, and it included some of the first attempts to plant both eelgrass plants and seeds (Addy 1947a, b). Interest in seagrass transplanting occurred in the 1960s and 1970s, with an emphasis on techniques and possible uses for rehabilitating lost or damaged seagrass beds and also as its use as a tool to better understand the biology of seagrasses (Fuss and Kelly 1969; Kelly and Hall 1971; Phillips 1974, 1980; Ranwell et al. 1974; Thorhaug 1974). A significant step in the restoration of seagrasses occurred in 1998 with the publication of the guide for the conservation and restoration of seagrasses in USA (Fonseca et al. 1998) (Fig. 3c). Since that
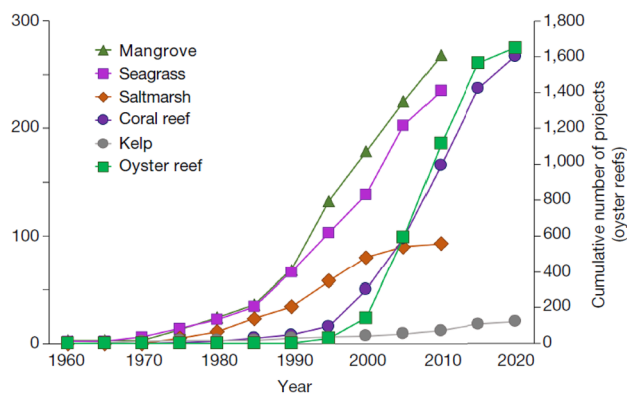
Fig. 8 Changes over time in attempts to restore different marine habitats, including seagrass (from Duarte et al. 2020, reprinted with permission from Nature)

publication appeared, the number of restoration attempts has increased dramatically (Fig. 8; Duarte et al. 2020), as well as a variety of new and innovative methods for transplanting seagrass (Calumpong and Fonseca 2001). These advances include guidelines for seagrass restoration (Short et al. 2002; van Katwijk et al. 2009), incorporating seeds rather than adult plants (Orth et al. 2006b; van Katwijk et al. 2020), positive interactions in restoring seagrasses (Valdez et al. 2020; Zhang et al. 2021), animals to enhance restoration (Sievers et al. 2022), multiple plantings of different species (Williams et al. 2017), or modifying planting designs by clumping plants to ameliorate physical stresses (Temmink et al. 2020).

Restoration efforts have been mainly in the USA (van Katwijk et al. 2016; National Academies of Sciences, Engineering, and Medicine. 2022), Europe (van Katwijk et al. 2016), and Australia (Statton et al. 2018; Tan et al. 2020). However, an analysis of many of these attempts found that most failed to produce significant increases in seagrass coverage. Exceptions occurred for large-scale efforts that incorporated many shoots or propagules (van Katwijk et al. 2016), and suggesting a minimum threshold size was required for successful restoration. This was the case in a large-scale seed-based eelgrass restoration effort in Virginia's coastal lagoons (Orth et al. 2020). There, over two decades, more than 70 million seeds were broadcast into 516 individual plots into four bays, resulting in establishment and subsequent spread of eelgrass to eventually cover nearly 3612 ha of eelgrass. Coupled with this expansion were documented increases in numerous ecosystem services, such as carbon sequestration, animal abundance and biomass, and increased water clarity (Orth et al. 2020). Notable increases in seagrass abundance have resulted from water quality improvements, in numerous locations, such as North America (Greening et al. 2014;

Lefcheck et al. 2018), and in Europe (de Los Santos et al. 2019; Dunic et al. 2021), suggesting that seagrasses have the potential to rebound without active restoration if those negative factors preventing survival can be reversed.

Distribution Aspects

Seagrass beds are now being monitored and mapped throughout the world using both field-based and remotely sensed methodologies. The use of remote sensing tools for mapping and monitoring seagrass was recognized over 40 years ago (Kelly 1980) (Fig. 3c), yet initially remote sensing was rarely used to monitor seagrass populations. However, several long-term aerial monitoring programs in the USA were established during this period, and they have provided a valuable record of changes in seagrass cover over large spatial and temporal scales (in Tampa Bay, Greening et al. 2014; in Chesapeake Bay, Lefcheck et al. 2018; in Indian River Lagoon, Morris et al. 2022; and in Florida Bay, Wilson et al. 2020). The availability of mapped seagrass data at many sites over two or more successive periods was instrumental in documenting the worldwide decline of seagrass (Waycott et al. 2009). Monitoring, especially aerial monitoring, has provided important evidence of direct impacts to seagrass, such as by propellers and anchors, dredging, commercial fishing activities, and vessel groundings (Sargent et al. 1995; Walker et al. 1989; Dunton and Schonberg 2002; Whitfield et al. 2004; Neckles at el. 2005; Orth et al. 2002, 2017a, b), and indirect impacts from aquaculture operations have increased over time (Orth et al. 2017a). Dramatic advances in sensor spectral and spatial resolution technologies, mounted on fixed-wing aircraft and satellites, have increasingly been used to accurately measure seagrass distribution and abundance throughout the world (Hossain et al. 2015; Phinn et al. 2008, 2018; Lyons et al. 2011, 2012; Hill et al. 2014; Zimmerman 2021; Fernandes et al. 2022; Carter et al. 2021; McKenzie et al. 2022; Traganos et al. 2022).

Most field-based and remote-sensing monitoring occurs at local levels, but two long-term studies have unified sites around the world into global monitoring networks involving researchers and community volunteers from around the world: SeagrassNet (https://www.seagrassnet.org/), started in 2001, comprises 126 sites in 36 countries, and Seagrass Watch (https://www.seagrasswatch.org/), started in 1998, comprises 418 sites in 26 countries. Both programs incorporate standardized protocols to make worldwide data comparable. More recently, programs like the Indo-Pacific Seagrass Network (https://indopacificseagrass.network/) seek to expand these efforts to incorporate understudied regions, such as those in Eastern Africa and Indian Ocean.

Future Needs

There remains much to be done to better understand the basic biology and ecology of many seagrass species. Some recent papers have listed priority areas for future research in seagrass meadows (York et al. 2017; Larkum et al. 2018; Unsworth et al. 2019, 2022). Below, we highlight some areas that seem to be especially worthy of future in-depth study.

Conservation and Restoration

The science of seagrass restoration (Fig. 3d) has been rapidly incorporating new technologies and new advances in understanding the genetic diversity of different donor populations and the relevance of phenotypic plasticity in seagrass restoration (Hughes and Stachowicz 2004; Procaccini et al. 2007; Hughes et al. 2008; Sinclair et al. 2014; Evans et al. 2017; Pazzaglia et al. 2021a, b). This has been especially true with efforts to restore seagrasses increasing over the last couple of decades (Saunders et al. 2020; Duarte et al. 2020). Future efforts may entail land or water-based nurseries to minimize impacts to donor populations (e.g., rewilding, van Katwijk et al. 2020). However, this should be approached with caution given the possibility of loss of genetic diversity in successively grown generations in nurseries (Conrady et al. 2023). Restoration efforts may also need to examine the importance of scale as larger planting may be more successful, especially if it involves positive species interactions (van Katwijk et al. 2016; Valdez et al. 2020). Finally, restoration activities need to better understand the role of microbes and stressor dynamics and how they can be used to enhance success and decrease recovery times (Wu et al. 2017; Fuggle et al. 2023).

An emerging worldwide challenge for seagrasses is the rapid expansion of aquaculture of shrimp, bivalves, and fish that require placing cages and other structures in shallow waters often occupied by, or adjacent to, seagrasses (Orth et al. 2017a; Smith et al. 2018; Ferriss et al. 2019; Boudouresque et al. 2020; Herrera et al. 2022; Howarth et al. 2022). These aquaculture activities require an understanding of the levels and severity of disturbances they produce on seagrasses and their ecosystem services, as well as an understanding of the tradeoffs necessary to protect seagrasses while maintaining economically important aquaculture activities, especially in developing countries (Herrerea et al. 2022).

Nursery Role for Fish with Complex Life Histories

Definitive evaluations of the nursery role of seagrass meadows for fish species with complex life cycles remain elusive. The most promising approach involves comparing the otolith chemistry between adult fish in adult habitats and juvenile fishes in putative nursery habitats (Gillanders et al. 2003). If the chemistry of the early otolith growth bands of the adults match one of the potential nursery areas, this indicates from which potential nursery area adult individuals originated. As noted above, this type of study has not often been done, as it is costly and extremely labor intensive. Many species that use nearshore seagrass nursery habitats move offshore as adults and are part of very large, panmictic populations, necessitating enormous sample sizes to assess the isotopic contribution of particular potential nurseries. Additional complications emerge from the potential for water chemistry in nursery areas to vary from year to year, owing to differential inputs of elements from surrounding watersheds that can alter their abundance in otoliths, thereby making it important for studies to last more than one annual cycle (Kraus and Secor 2005; Fodrie et al. 2020). Until simpler methods for quantifying relative nursery values, there remains high value in studies that identify the most productive of the different potential nursery habitats and prioritize their protection and conservation.

Distribution Aspects

The 2020 United Nations Report and several recent review papers (Unsworth et al. 2019, 2022) all stress the need to protect seagrasses, and note that the first step in this process is to understand their distribution and abundance by developing maps of seagrass cover and then, if possible, conducting repeated mapping surveys at different scales to better understand their temporal dynamics (Neckles et al. 2012; Coffer et al. 2023). Current monitoring methods include in situ observations, aerial imagery, and satellite imagery (Hossain et al. 2015; Lønborg et al. 2022). Recent advances in remote sensing include higher resolution sensors and the deployment of multiple relatively inexpensive, small satellites, such as those deployed by Planet Earth (https://www.planet.com/) (Fig. 3d), and automated methods, including machine learning and object-based classification. These advances promise to reduce the need for manual interpretation and improve accuracy, which should have the ability to advance the monitoring of seagrass meadows worldwide (Roelfsema et al. 2014, 2015; Ha et al. 2020; McKenzie et al. 2022; Tahara et al. 2022). While satellites provide coverage for many areas that are otherwise not monitored, they often do not capture data over large swaths of open ocean where many small islands occur that have significant seagrass populations. Recently, drones and autonomous underwater vehicles (AUVs) have been added to the toolbox researchers have as options for monitoring and mapping seagrass (Lønborg et al. 2022). The selection of an appropriate monitoring method is often driven by factors specific to the location being surveyed and the questions being raised by researchers and managers. Machine learning developments are reducing the bottleneck

between the large amount of imagery being collected and its analysis (e.g., for kelps, Mahmood et al. 2020). In addition to these direct monitoring methods, species distribution modeling may be useful as a mapping technique. This modeling approach uses associated data to predict the location of suitable habitat across large spatial scales and has been used to identify potential seagrass habitat (e.g. Bittner et al. 2020). These new tools may provide more efficient means to map and monitor the significant populations of seagrasses that likely exist in relatively unstudied areas around the world, as well as providing new insight in areas where seagrass research is showing significant advances (e.g., China).

Rhizosphere Dynamics

Many studies in the past several decades have demonstrated the negative effects of high sediment sulfide levels on the performance of several temperate and tropical seagrass species (Apostolaki et al. 2018) (Fig. 3d). Sulfide in the rhizosphere can become elevated in association with water column hypoxia, light reduction, sediment organic enrichment, and a variety of other factors (Borum et al. 2005; Holmer et al. 2009, 2014; Kilminster et al. 2014). One mechanism preventing sulfide accumulation in the rhizosphere is the release of oxygen from young root tips, which corresponds with decreased abundance of potential sulphate-reducing bacteria and decreased sulfide concentrations near young roots (Martin et al. 2019; Scholz et al. 2021).

Relevant to rhizosphere sulfide levels, lucinid bivalves, commonly associated with different species of seagrasses since at least the Eocene (Reynolds et al. 2007), contain sulfur oxidizing bacteria that reduce hydrogen sulfide in the rhizosphere and help maintain conditions favorable for seagrass growth and survival (Reynolds et al. 2007; van der Heide et al. 2012). Recent studies have shown that the strength of lucinid–seagrass (*Thalassia testudinum*) facilitation increases under stressful environmental conditions, such as reduced light availability or enhanced porewater sulfide levels, and these results support incorporating interspecific facilitation into seagrass conservation and restoration strategies (e.g., de Fouw et al. 2016; Chin et al. 2021). In addition, a paper by Martin et al. (2020) found lucinid endosymbiotic bacteria associated with seagrass roots in the absence of lucinids, indicating that much remains to be understood about the relationships between sulfur oxidizing bacteria and seagrasses.

Few studies have documented the extent to which seagrasses are able to mobilize their roots to forage for nutrients and use nutrient "hotspots" to develop dense root mats (see Furman et al. 2016 for an example). However, there are several examples of filter feeding bivalve associations with seagrass roots and rhizomes that indicate that bivalve excretory products provide nutrients to seagrass roots, while the roots and rhizomes, in turn, provide protection for the bivalves from crabs and other potential predators (Peterson and Heck 1999, 2001). More studies with additional species of seagrasses are needed to better understand the factors determining root growth and foraging to acquire nutrients.

In addition, a recent experimental study has documented the value of root-associated microbiota in *Zostera muelleri* meadows to alleviate negative effects of nutrient-enriched stress (Fuggle et al. 2023). Functions performed by microbial taxa enriched by nutrients included sulfide oxidation and denitrification, suggesting that seagrass restoration may be improved by enhancing beneficial root-associated assemblages (Fuggle et al. 2023).

Finally, almost completely uninvestigated, with the exception of studies of the consumption of belowground tissues of small seagrasses by mega-herbivorous dugongs (Preen 1995), is the extent to which roots and rhizomes might be fed upon by infaunal invertebrates such as polychaetes. Work on terrestrial grasslands and agricultural fields has shown that belowground consumption of roots and rhizomes is common and can be consequential (e.g., Johnson and Rasmann 2015). To date, the lack of reports of belowground consumption of roots or rhizomes of seagrasses may only reflect a lack of investigation.

Population Biology

Over the years, efforts have been made to study seagrass population biology and make predictions about the growth trajectories of seagrass populations (e.g., the "reconstructive technique" used by Duarte et al. 1994; Durako and Duarte 1997; Short and Duarte 2001; Fourqurean et al. 2003; Marba and Walker 1999), but sufficiently accurate methods remain to be developed. One major unsolved problem in employing modeling to predict seagrass population trajectories is the difficulty in determining the number of individual clones in a given area. In the past few decades, it has become possible to determine both the size and number of clones, but results are dependent on sampling density and distance between replicates (e.g., Sinclair et al. 2014; Edgeloe et al. 2022), and the inability to rapidly identify individual clones in the field remains a significant obstacle.

Carbon Sequestration

Another area of intense investigation and a growing body of literature is the degree to which seagrass meadows sequester carbon, and the likelihood that this carbon will be mobilized or retained when seagrass die-offs occur (Fig. 3d) (Fourqurean et al. 2012; Macreadie et al. 2014). It is clear that healthy seagrass meadows can sequester large amounts of carbon, but the ongoing loss of seagrass meadows globally (Waycott et al. 2009; Rohr et al. 2018; Dunic et al. 2021) raises the

unanswered question of whether, and how quickly, seagrass carbon buried in the rhizosphere might be liberated to the atmosphere and add to the accumulation of greenhouse gasses. Adding complexity to understanding how seagrass meadows factor into the global carbon budget is the recent discovery that seagrass meadows are significant emitters of methane (Schorn et al. 2022), a powerful greenhouse gas that could mitigate some of the benefits that the large amount of organic matter buried in the sediments of seagrass meadows could provide. In addition, ecosystem calcification can result in CO^2 emissions that far exceed organic carbon burial in areas, such as many tropical locations, where calcification rates exceed primary production and burial (Howard et al. 2018; Van Dam et al. 2021). Clearly, work is needed to more fully understand the net effect of seagrass meadows on greenhouse gasses and its relation to our changing climate.

Effects of Climate Change

Climate change has the potential to alter the dynamics of seagrass assemblages worldwide in both negative and positive ways (Short and Neckles 1999; Duarte 2002; Hyndes et al. 2016; Zimmerman et al. 2017; Zimmerman 2021), and there are likely to be winners and losers. The most immediate effects of increasing water temperatures will likely occur at the boundaries of species' distributions and eventually lead to general mortality of temperate species and their replacement by tropical species (Fig. 3d) (Moore and Jarvis 2008; Jorda et al. 2012; Valle et al. 2014; Hyndes et al. 2016; Chefaoui et al. 2018; Duarte et al. 2020; Turschwell et al. 2021). Hyndes et al. (2016) suggest that the new temperate species assemblages will not initially resemble either the original temperate or tropical assemblages, and the biodiversity of seagrass meadows may increase substantially until a new equilibrium in the number of species of plants and animals is reached. We also note that seagrasses have evolved under climatic conditions considerably harsher than those of today, with much higher CO_2 concentrations (Orth et al. 2006a), and thus might benefit from future higher CO_2 levels under certain circumstances (Zimmerman 2021).

Marine heat waves have recently caused massive declines of seagrasses in Shark Bay, Australia, and are likely to become more frequent in the future (Kendrick et al. 2019b). And recent data from Canada suggest that sub-arctic eelgrass populations are not immune to climate warming (Leblanc et al. 2022). In coastal estuaries, additional runoff from increased precipitation has the potential to alter salinities, as well as water clarity, and to negatively influence those seagrass species such as eelgrass that have estuarine populations (Lefcheck et al. 2017). Range expansions and contractions of certain species are certain to occur as evidenced in Florida and Korea (Virnstein and Hall 2009; Kim et al. 2009), although time scales of expansion

may ultimately depend on biotic and abiotic factors that influence propagule dispersal (see above). One potential positive influence seagrass that may have in the climate change scenario is reducing ocean acidification effects on bivalve aquaculture (Garner et al. 2022).

Climate change can also influence faunal species distributions, and such changes may have indirect, but large, effects on seagrass distribution and abundance. For example, herbivory is particularly intense in marine environments, with nearly 70% of benthic production being consumed by grazers (Poore et al. 2012). As tropical herbivores expand their ranges poleward in association with warming temperatures, they can and do impose powerful effects on marine communities (Fourqurean et al. 2019). The disappearance of kelp (*Ecklonia* spp.) and *Sargassum* spp. beds in southern Japan represents one of the best-documented cases of how this can happen. Several thousand hectares of temperate macroalgal-dominated substrate were overgrazed by rabbitfish (*Siganus spp.*) and parrotfish (*Calotomus japonicus*) and converted to rocky barrens, which were subsequently colonized by reef-building corals (Serisawa et al. 2004). Similarly, in southeastern and southwestern Australia, kelp declines, and the appearance of algal turfs followed increased herbivory by tropical fish grazers (Vergés et al. 2016; Wernberg et al. 2016; Zarco-Perello et al. 2019). And in the southern Mediterranean, rabbitfish immigrating from the Red Sea have become increasingly abundant and macroalgae less so (Vergés et al. 2014).

Temperate seagrass meadows are also undergoing tropicalization and experiencing the effects of poleward moving tropical herbivores, although predictions of the expected ecological changes in response to increases in tropically associated herbivores remain to be tested (Heck et al. 2015; Hyndes et al. 2016). Many temperate areas now experience fewer freezes than in the past, and tropical parrot fish and rabbit fish, as well as green turtles, are moving poleward and becoming established in warmer temperate areas (Fodrie et al. 2010; Heck et al. 2015; Rodriguez and Heck 2020, 2021). These herbivores have the potential to reduce the abundance and height of temperate seagrass canopies, reducing formerly lush meadows to the height of freshly mowed lawns, or even to permanently unvegetated substrates (Heck et al. 2015; Hyndes et al. 2016; Rodriguez and Heck 2021; Rodriguez et al. 2022).

Restoration activities will have to be re-evaluated to consider climate change. Locations at the historic latitudinal boundaries of a seagrass species' distribution may no longer support long-term survival of those species (e.g., *Zostera marina* in Chesapeake Bay and North Carolina, USA, *Posidonia oceanica* in the Mediterranean). Alternatively, areas where restoration success was unlikely may become

possible restoration sites, such as northern latitudes that are now free of permanent ice. In some areas, planting genetically distinct genotypes adapted to higher temperatures may become necessary.

Concluding Remarks

Scientific understanding of the biology and ecology of seagrass meadows has advanced tremendously since the pioneering work of researchers in the 1960s and 1970s. We now understand the major role that seagrasses play as foundation habitats in coastal waters and have developed estimates of the value of the services they provide, including those of their nursery habitat role, the provision of habitat for rare and endangered species, and many others. The recognized importance of seagrass-provided services has facilitated the global recognition of the value of seagrasses and the importance of seagrass conservation and restoration.

In addition, we now recognize the importance of sexual reproduction and the role of seed dispersal in the development of new meadows distant from parent populations. We also have evidence that small invertebrate species can pollinate seagrass flowers, something completely unanticipated until recently. The elucidation of the full genomes of *Zostera muelleri* (Lee et al. 2016) and *Z. marina* (Olsen et al. 2016) (Fig. 3c) opened the door to a multitude of new research in seagrass evolutionary biology, and our ability to determine the genetic identities of donor populations (Lee et al. 2018). And the importance of genetic diversity has facilitated the success of seagrass restoration, something necessitated by the massive decline of seagrass meadows during recorded history.

We have also seen a paradigm shift from the understanding that seagrass detritus was the major source of energy for seagrass-inhabiting animals to the recognition that consumption of algae by mesograzers and living seagrass leaves by macrograzers are much larger pathways for energy flux than the detrital one. And we have learned that important rhizosphere interactions between seagrasses and macrofauna, as well as between seagrasses and microbes, occur, even if we have only begun to understand the details of these interactions.

Recognition of the value of seagrass meadows has led to a remarkable increase in mapping and monitoring of seagrass beds worldwide. Advanced technologies, such as the multiple, small satellites from sources such as Planet Earth, and automated mapping and machine learning tools are making it possible to provide accurate maps of seagrass beds for research managers and other conservationists. At small scales, drones are proving invaluable in examining and mapping features of seagrass beds.

Many advancements in seagrass science noted above have come from research in the USA, Europe, Australia, and Japan, likely due to the significant funding available in these countries. But now, we have both increasing capacity and a strong need to investigate seagrasses outside these areas, particularly in places where people rely on seagrass habitats for meeting basic needs, such as for subsistence fishing. The next generation of seagrass science needs to emphasize inclusion of researchers active in these understudied areas, facilitate open data sharing and knowledge transfer at scientific meetings, and develop Communities of Practice (CoP) for mapping and monitoring.

Finally, it has become clear to us over our 50 years as seagrass scientists that there is no substitute for experiencing the natural environment first-hand. Others have explained the critical importance of understanding the natural history of the organisms inhabiting the ecosystems being investigated (Dayton 2003; Able 2016). New technologies and new methods of data analysis are helping to better understand the details of seagrass biology and ecology. However, nothing can replace experience in the field and its value in the formulation of interesting and relevant hypotheses and ways to test them. This has been and continues to be the gold standard for ecological research. It also is important to emphasize that a great deal of important marine and terrestrial ecology has been done in the past, and there is much to learn from this prior work. Currently, obtaining older papers can be difficult, and journals that limit the number of references included in published papers are leading us to waste time relearning lessons from the past. It is good advice for all serious students of marine ecology to thoroughly search the entire body of existing literature before beginning a research project. There is a world of great research that has been done as noted by the number of new publications reported in Fig. 2, and much can be accomplished by building on this foundation.

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