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SEAGRASS ECOSYSTEMS: A CAREER—LONG QUEST TO UNDERSTAND THEIR INNER WORKINGS

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ABSTRACT: Four decades of research findings on the ecology of seagrasses and their animal and plant associates are described here, along with some of the major changes and advances that have taken place in our understanding of the inner workings of these amazingly productive and diverse ecosystems. Of primary importance are shifts in the recognition of: 1) the importance of the nursery role of seagrasses and how it can be quantified; 2) the importance of direct herbivory in the trophic ecology of seagrass-dominated ecosystems; and 3) the primacy of consumer effects in determining the abundance of algal epiphytes that colonize leaves and other aboveground seagrass tissues. Exciting new areas of investigation include elucidating rhizosphere interactions, including developing a deeper understanding of the importance of nutrient foraging by seagrass roots, and of the microbes in the sediments that fix nitrogen and reduce toxic hydrogen sulfide concentrations. Increased understanding of the roles of genetic diversity and the size and integration of seagrass clones, as well as additional and better evaluations of the relative value of different seagrass meadows as fish nurseries are also needed. Of great importance for seagrass researchers of the future is spending large amounts of time in the field developing a thorough understanding of the natural history of the many and varied inhabitants of seagrass meadows. The knowledge gained by this investment of time will be essential for the development of meaningful, new hypotheses and the means for testing them.

KEY WORDS: seagrass, nursery role, herbivory, consumer effects, predator—prey

THE BEGINNING

Two excellent instructors from my undergraduate years at the University of West Florida (UWF), Tom Hopkins and Gerry Moshiri, were most influential in my decision to become a research scientist (Figure 1). Their mentorship, which included supervising my participation in a study of estuarine primary production using light and dark bottles, was complemented by interactions with several other great UWF teachers, including Sneed Collard and Charles D’Asaro. The result at the time of my graduation from UWF was a strong desire for a career in marine ecological research and teaching.

Graduate training had to be postponed because of the arrival of a draft notice from the U.S. Army. This was an invitation that could not be ignored, so I entered the Army the summer after receiving my B.S. degree in Biology. Some 18 months later I was able to receive an early discharge from the Army because I was accepted by the M.S. Program in Biology at Florida State University (FSU). One of my former classmates, Theresa Hooks, was a graduate student of Robert “Skip” Livingston’s (Figure 2A) at FSU and she convinced him to accept me sight unseen. I was ecstatic about leaving the Army and beginning graduate studies, and will be eternally grateful to Skip for taking a chance on me.

My time at FSU was the best graduate experience anyone could have imagined. I immediately began working as a research assistant on a Livingston—led project to evaluate the impact of kraft pulp mill effluents on the seagrass—dominated shallow waters of Apalachee Bay, FL. My first field trip was on a rainy, chilly winter day but the astounding density and diversity of seagrass inhabitants collected by our small shrimp trawls fascinated me. I was hooked, and asked Livingston if I could develop an M.S. project that involved seagrass-associated animals. He agreed to let me take over from Theresa Hooks, who was then finishing her M.S. work (Hooks et al. 1976), and nearly 50 years later I still never tire of sorting the contents of trawls taken in seagrass beds.

At FSU I was able to work with other faculty members who greatly influenced my thinking and stimulated my growing interest in ecology. Larry Abele and Don Strong, along with Dan Simberloff (Figure 2B, C, D), who later agreed to serve as my PhD advisor, led a great group of ecologists who were doing important work and challenging the way ecology was done in the United States. This group became known by
some as the Florida State Mafia, and was characterized by the iconoclastic views of its members.

A biogeography course taught by Simberloff using the seminal papers on island biogeography, along with regular discussions with fellow students Earl McCoy and Ed Connor (Figure 3), broadened my ecological interests to include biogeography (McCoy and Heck 1976), a topic I continued working on after leaving FSU (Heck and McCoy 1978, Abele et al. 1981, Simberloff et al. 1981, Gore and Heck 1986). My own thesis papers were improved immeasurably by Don Strong’s editing, and his impressive editorial skills would later benefit the entire ecological community when he served as the long-time Editor-in-Chief of journals published by the Ecological Society of America.

My regular exchanges about biogeography and ecology with McCoy, now a Professor at the University of South Florida, and Connor, a Professor at San Francisco State University, were an especially noteworthy and valuable part of my training at FSU. Although I remained keenly interested in biogeography, I eventually concluded that many important biogeographical questions were best addressed by genomic comparisons, requiring skills I didn’t possess or intend to acquire. So my interest shifted to focus more fully on marine ecology.

While finishing my M.S. with Skip Livingston, my interests in population and community ecology increasingly drew me toward the ecology group, although my fascination with seagrass meadows remained undiminished. Larry Abele was instrumental in helping me obtain funding for a Pre-Doctoral Fellowship from the Smithsonian Tropical Research Institute and he and his wife Linda helped me get settled when I moved to Panama. This fellowship allowed me to compare faunal assemblages in tropical seagrass meadows with those in the warm temperate northern Gulf of Mexico, and pursue an interest in the origin and maintenance of latitudinal species diversity gradients. Observing the amazing diversity of tropical habitats with Larry Abele’s guidance changed my world view and convinced me of the value of traveling to unfamiliar places for serious students of ecology.

While in Panama an undergraduate I knew at FSU named Greg Wetstone asked if he could come to Panama and work with me in pursuit of his honor’s thesis. Greg and I got along famously, and his ideas led to our paper on the role of habitat complexity as it influenced the species richness of seagrass-associated inhabitants (Heck and Wetstone 1977). Greg also helped me during my regular sampling and we also made a side trip to the San Blas Islands where we observed firsthand the daily foraging by coral reef fishes in the adjacent seagrass meadows. This observation and others collected at my regular sampling locations convinced me of the fundamental differences between the tropical seagrass meadows, whose connectivity with nearby coral reefs was an inherent property of the tropical seascape, and those of the warm temperate meadows I studied in north Florida, which lacked anything similar to interconnected reefs and functioned fundamentally differently (Figure 4; Heck 1976, Heck 1977, Heck 1979, Heck and Orth 1980). This was also made clear by collections of fishes made at night in seagrass meadows that showed the expected presence of fishes in the Haemulidae (grunt family), but also included moray eels and other species I never expected to leave reefs and forage nocturnally in seagrass. The fish work was made possible only by the amazing efforts of my long-term friend and colleague Mike Weinstein, who received the formalin-preserved fishes I sent in paint cans back to FSU monthly, where he counted and identified the species they contained (Weinstein and Heck 1979, Heck and Weinstein 1989).
The Growth of Seagrass Research

The U.S. National Science Foundation’s International Decade of Ocean Exploration in the 1970s contained funding for a significant multi-year seagrass program led primarily by early to mid-career researchers, including Peter McRoy, Gordon Thayer, Jay Zieman, John Ogden and Ron Phillips, who, along with other local and international colleagues, produced 2 seminal volumes that summarized what was known at the time about seagrass meadows (McRoy and Helferich 1977, 1980). Several major findings from these syntheses became part of the conventional wisdom of seagrass ecology, including the belief that despite their enormous productivity, little seagrass production was consumed by herbivores with most of it entering detrital food webs that were the energetic base of seagrass ecosystems. Also reported was the statement that seagrass meadows were important “nursery grounds” for a wide variety of economically important finfish and shellfish species.

Subsequently, stable isotope data conclusively showed that seagrass food webs are supported in large part by the consumption of algae growing on seagrass leaves and exposed rhizomes, as well as associated green, brown and red algae (e.g., Kitting et al. 1984). In addition, it also became clear that direct herbivory of seagrasses is common, especially at warm temperate and tropical locations that contained abundant sea urchins and herbivorous fish species (Valentine et al. 1997, Valentine and Heck 1999). In contrast, areas with low seagrass herbivory are those whose seagrass consumers, such as temperate ducks, geese and swans, and tropical turtles, manatees and dugongs, have been hunted to functional extinction (Valentine and Duffy 2006, Heck and Valentine 2007). It has also long been stated that much, if not most, seagrass loss occurred because of nutrient enrichment that either fueled epiphyte overgrowth of seagrass leaves or plankton blooms that shaded seagrasses (e.g., Kemp et al. 1983, Tomasko and LaPointe 1991, Short and Burdick 1996). While it is undeniable that nutrient enrichment can cause seagrass loss, it is also quite clear that food web alterations resulting in the loss of epiphyte grazers explain as much or more variance in algal biomass in seagrass meadows as nutrient loading does (Hughes et al. 2004, Heck and Valentine 2006, Moksnes and Heck 2006, Baden et al. 2010).

After receiving my Ph.D. in 1976, I left FSU to begin a job as Assistant Curator at the Benedict Estuarine Research
Laboratory (MD), a satellite lab of the Academy of Natural Sciences of Philadelphia. While there I worked on a large investigation of the effects of a nuclear power plant on the Chesapeake Bay. That work culminated in a book I edited that summarized the work of a large group of colleagues (Heck 1987). I also continued investigating how habitat structural complexity influenced the composition and abundance of species in shallow coastal waters. During this time, I also carried out predation experiments with Tim Thoman (Heck and Thoman 1981, 1984), the first technician I was able to hire, with support from the EPA Chesapeake Bay program and my home institution The Academy of Natural Sciences. In addition, I began what would become a career long collaboration with Bob (J.J.) Orth (Figure 5A) that started with descriptive studies of the macrofauna of the meadows of submerged aquatic vegetation in the lower and mid-regions of the Chesapeake Bay (Heck and Orth 1980, Orth and Heck 1980) and continued throughout the next four decades. In 1984, Orth, Mike Weinstein and I co-edited a special issue of *Estuaries* that started with descriptive studies of the macrofauna that brought together work on plant-animal interactions and many other papers on both seagrass and salt marsh ecology. One paper from this special issue has been cited over 1,100 times (Orth et al. 1984).

By the early 1980′s I had moved from Maryland to the Academy of Natural Sciences headquarters in Philadelphia and soon began work in nearby coastal New Jersey in collaboration with Ken Able (Figure 5B) of Rutgers University. This work added to my experience in temperate eelgrass meadows and resulted in several publications with Able and my first (co-advised) Ph.D. student and later post-doc, Kim Wilson (Heck and Wilson 1987, Wilson et al. 1990a, 1990b). I was also invited to join Able and his colleagues Charley Roman and Mike Fahay, along with graduate student Susan Kaiser and technician Mark Lazzari in an effort to document the aquatic resources of the National Park Service’s Cape Cod National Seashore. This work on the outer shores of Cape Cod introduced me to an unfamiliar boreal fauna. Several papers were published from our efforts (Able et al. 1988, Heck et al. 1989, Roman et al. 1990, Heck et al. 1995, Able et al. 2002), all of which broadened my understanding of the way seagrass meadows and salt marshes functioned in New England.

In 1986 I accepted appointments with the Dauphin Island Sea Lab (DISL) and the University of South Alabama and returned to seagrass research in the Gulf of Mexico. This initiated a more than 30 year collaboration with John Valentine (Figure 5C) and allowed me to work with a great group of graduate students, interns, technicians (Figure 6) and post-docs. It was during my years at DISL that Valentine and I documented the importance of herbivory in seagrass meadows of the Gulf and Caribbean, in contrast to the prevailing conventional wisdom that herbivory was unimportant in the trophic dynamics of seagrass meadows (Valentine and Heck 1991, Heck and Valentine 1995, Valentine and Heck 1999). During this time, we also showed how consumer effects were usually more important in determining the amount of algae found growing on seagrass leaves than were nutrients (Heck et al. 2000, Heck et al. 2006, Heck and Valentine 2006, Myers and Heck 2013). Valentine and I continue to work together

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**FIGURE 5.** Influential career-long colleagues. A. Bob (J.J.) Orth with Heck. B. Ken Able with Heck. C. John (Big Daddy) Valentine.

**FIGURE 6.** Graduate students and technicians in the Heck lab. A. Heck and former graduate students Brad Furman (L) and Brad Peterson (R). B. Additional graduate students Dale Booth, Kelly McKay Darnell, Carly Steeves Canon, technician, and students Shana Madsen, Joe Myers, Becky Gericke, Whitney Scheffel and Karen Fisher Stanton. C. Heck with graduate students Maddie Kennedy, Whitney Scheffel, technician Kate Walsh, and graduate students Meg Goeker and Kelly McKay Darnell. D. Dottie Byron David, who started in my lab as an intern and later returned as Lab Manager, a position she has held for 15 years and counting.
and our collaborations have now spanned more than 3 decades. I owe him a great deal and am certain discussions with him inspired some of my best and most interesting work.

During my years at DISL I collaborated with a great group of post-docs on a variety of topics. The first was Loren Coen (Figure 7A), whom I had known since his M.S work on animals associated with seagrass, when I was an external member of his advisory committee (Coen et al. 1981). Coen was involved with numerous projects while working at DISL, including the ecology of filter-feeding bivalves (Coen and Heck 1991) and juvenile blue crabs inhabiting seagrasses (Heck and Coen 1995). Mike Judge also accepted a post-doc position and joined Coen and me as we continued working on bivalve ecology (Judge et al. 1992, 1993). Post-docs arriving later included Johanna Mattila from Finland (Figure 7B; Mattila et al. 1999, 2008) and Per Moksnes from Sweden (Figure 7C), who investigated the role of cannibalism in regulating blue crab populations (Moksnes and Heck 2006). Both Moksnes and Mattila broadened my knowledge by introducing me to Scandinavian thinking about marine and estuarine ecology.

After Johanna returned to Finland to become director of the Huso Biological Station on the Baltic Sea, we began a program of student exchange that lasted some 20 years and led to more than a dozen papers on plant-animal interactions authored by students in the program (e.g., Goecker and Kall 2003, Martin et al. 2010, Scheinen et al. 2011, Nelson et al. 2018). In addition, Silvia Ibarra-Obando obtained a Fulbright Fellowship to work in my laboratory and this collaboration later brought me to Baja California, Mexico, where Silvia’s home institution Centro de Investigacion Cientifica de Educacion Superior de Ensenada (CICESE) was located, and where I gained an understanding of the eelgrass beds that occurred on the Pacific Coast of Mexico. Silvia’s work in the Gulf of Mexico resulted in 2 nice papers (Ibarra-Obando et al. 2004, 2005). The last post-doc who came to DISL and worked with me was Jennifer Hill. Jenn carried out interesting studies of predator-prey behavior (Hill and Heck 2015) and later with Sea Grant support investigated the impact of the non-native tiger shrimp (Penaeus monodon) on the native shrimp species of the Gulf of Mexico (Hill et al. 2017).

I was also fortunate to work with 2 exceptionally hard-working, productive post-docs from Spain, Pat Prado, a student of Teresa Alcoverro’s, a well-known and accomplished Spanish marine ecologist, and Candela Marco-Mendez, whom I first met while she was a graduate student at the University of Alicante (Figure 7D). These two brought a Mediterranean perspective on seagrass research and great energy to my lab. Their impressive work ethic led to sound and productive research (Prado and Heck 2011, Prado et al. 2012, Marco-Mendez et al. 2012, 2015). During this time, I was invited by my colleague Just Cebrian to join him in an exchange program and field course he developed with colleagues at the University of Alicante. This resulted in several class trips and a course co-taught in Spain with Jose Luis Sanchez-Lizaso of the University of Alicante’s Centro de Investigaciones Marinas at Santa Pola. This was where I first met Marco-Mendez and got the opportunity to see Mediterranean seagrass meadows firsthand and later carry out projects with our students (e.g., Schrandt et al. 2016, Marco-Mendez et al. 2016). Just Cebrian and I often worked together at DISL for many years and together with his and my students and other colleagues, published papers on seagrass meadows and oyster reefs (e.g., Anton et al. 2011, McDonald et al. 2016, Heck et al. 2017).

During the 1990’s I made my first trip to Australia to collaborate with colleagues in Western Australia (WA). The first visit in 1997 was facilitated by Peter Jernakoff, then with the Commonwealth Industrial and Scientific Organization (CSIRO). This visit allowed me to see the amazingly diverse seagrass flora that occurs along nearly the entire coastline of WA. Most surprisingly to someone from North America, these seagrass meadows occur in the open ocean and not in protected locations as in most of North America. I would later return to WA where Di Walker, Gary Kendrick, Anne Brearley and Marion Cambridge of the University of Western Australia, along with Hugh Kirkman of CSIRO, introduced me to their incredibly extensive and diverse seagrass meadows and the totally different landscapes of Australia. While in Australia I also met Mat Vanderklift, who was working on a Ph.D. at the University of Western Australia. After finishing his doctoral work, Mat was funded by the Australian Research Committee to carry out post-doctoral work with Valentine and me to compare rates of herbivory and predation intensity on reefs and seagrass meadows in marine reserves and fished
areas of the Florida Keys and Western Australia. This collaboration resulted in several publications (Valentine et al. 2007, Vanderklift et al. 2007).

Follow up visits to Australia found me working there with my old colleague J.J. Orth, who had also been also been working in Western Australia (Orth et al. 2002), and later with Glenn Hyndes and Paul Lavery of Edith Cowan University (Hyndes et al. 2016, 2017), with whom I continue to collaborate. For me, Australia is hands down the most interesting place I ever worked. To a North American, everything in Australia is different, both in the water and on land, and I only wish I had been able to spend more time there.

During the decade of 2001–2010, while Valentine and I still regularly worked together, I collaborated with Mike Beck, then a new employee with The Nature Conservancy, and we developed a working group funded by the National Center for Ecological Analysis and Synthesis (NCEAS). Mike had worked as a technician with Valentine and me before entering a Ph.D. program at FSU, and we had stayed in touch. Our goal was to bring together experienced colleagues who would critically evaluate the information available on the so-called “nursery role” of seagrass meadows, salt marshes and mangrove forests. I was concerned that we were bringing our friends and colleagues to NCEAS in Santa Barbara, CA and if we didn’t really have our act together they would be disappointed in us for wasting their time. However, we had assembled the right people and my fears were unwarranted. Many lively, productive discussions led to several synthesis papers. One, on how to define and measure the nursery role of aquatic habitats (Beck et al. 2001), concepts that had previously remained vague, turned out to be a very popular paper. This was followed by syntheses showing what the literature revealed about the provision of the components of the nursery function by seagrasses (Heck et al. 2003), salt marshes (Minello et al. 2003) and mangroves (Sheridan and Hays 2003). All these papers became highly cited, but none more so than the more than the 2,000–plus citations of the original (Beck et al. 2001). The concepts outlined in that paper have led to a refining of what constitutes a nursery role, as observed in different types of coastal habitats (Kraus and Secor 2004, Nagelkerken et al. 2015, Litvin et al. 2018).

Another NCEAS working group led by J.J. Orth and Bill Denison was funded to better understand the roles and value of seagrass meadows globally. This effort took place in the mid–2000’s and included a number of internationally recognized seagrass researchers. Together this group produced 2 synthesis papers on the global status of seagrass meadows (Orth et al. 2006, Waycott et al. 2009), along with summaries of the literature on different functional aspects of seagrass meadows (e.g., Hughes et al. 2009, Heck et al. 2008). These papers were all well received, but in particular the Orth et al. (2006) and the Waycott et al. (2009) papers have been cited more than 2,000 times.

A RETROSPECTIVE ON STANDOUTS AMONG 40 PLUS YEARS OF SEAGRASS RESEARCH

Among the research efforts in which I’ve participated, I count the findings from 3 of them as among the most important. None was truly original, but then most of what seems new in marine ecological research is built on an existing foundation of knowledge, and this is certainly true of my own work. But among the efforts that stand out are the work done to further document the “nursery role” of seagrasses and its function as essential habitat for a wide variety of animals, a number of which are economically important. This was described in papers resulting from work in the Chesapeake Bay (Heck and Thoman 1981) but it appeared in other papers, including the popular Beck et al. (2001) paper. A second area I rank as among the most important is work led by John Valentine that established herbivory of seagrasses as an on–going process that is an important means of energy transfer in seagrass food webs and which could have large consequences for the structure and productivity of seagrass meadows (Valentine and Heck 1999, 2002). A third area is the demonstration that, as others had suggested, consumer effects were at least as, if not more, important in explaining the abundance of algae growing on seagrass leaves and in seagrass meadows, as was nutrient supply (Heck et al. 2000, 2006, Heck and Valentine 2007). This ran counter to the prevailing view that processes emanating from the bottom, and not the top, of the food web (especially nutrient availability) controlled seagrass ecosystem structure and function.

One topic in seagrass ecology I find to be somewhat overlooked is presented in 3 papers that provided a different take on the conventional wisdom about how the structural complexity of seagrasses provides protection from predation for many small animals living among seagrass leaves. Originally, I had reported, as had several others, a significant positive relationship between seagrass biomass and the survivorship of a variety of small invertebrate prey species (Heck and Orth 1980, Heck and Thoman 1981). However, my work and that of others had been done in the laboratory with a single predator whose prey capture rates varied as vegetation abundance increased (see Nelson 1979 Heck and Thoman 1981). It later occurred to me that these lab experiments were effectively decreasing encounter rate as vegetation biomass increased and this was the very simple explanation for the declining rate of predation success with increasing vegetation abundance. In nature, however, as seagrass density increases, so do the abundance of both predators and prey, in contrast to what had been investigated in and other lab experiments. When later experiments allowed both predator and prey numbers to increase as vegetation density increased, the results showed no important difference between survival rates in low and high densities of vegetation. Survival was clearly higher in all vegetated treatments than in unvegetated conditions, but vegetation density per se did not provide different amounts
of protection when real world conditions were tested (Figure 8; Mattila et al. 2008, Canion and Heck 2009, Scheinen et al. 2011). The main applied conclusion from this work is that sparse densities are of the same relative importance as shelter from predation as are high densities of vegetation, and they deserve protection.

**Future Prospects**

There remains much to be done to better understand the basic biology of many seagrass species, and the many types of plant—animal interactions occurring in seagrass meadows. While we now better understand and appreciate the role of consumers in the ecology of seagrass meadows, including that of seagrass herbivores and the importance of consumers in preventing trophic cascades that result in algal overgrowth of seagrass leaves, several types of plant—animal interactions described below are ripe for future research. Some recent papers have listed priority areas for future research in seagrass meadows (York et al. 2017, Larkum et al. 2018, Unsworth et al. 2018), but below I highlight some areas that seem especially worthy of future in—depth study.

**Plant—Animal Interactions**

**Pollinators of seagrasses**

To date there is only one conclusive demonstration that animals (small invertebrates such as amphipods) can and do pollinate seagrass (Van Tussenbroek et al. 2016). This was shown for tropical turtlegrass (*Thalassia testudinum*), and it remains to be seen if animal—mediated pollination occurs for temperate species such as eelgrass (*Zostera marina*) or other tropical seagrass species. Van Tussenbroek et al.’s (2016) demonstration of pollination of turtlegrass by amphipods required long hours of waiting *in situ* for anthesis of turtlegrass flowers and careful filming of the tiny (<0.5 mm) amphipods as pollen from male flowers accumulated on their bodies and was subsequently transferred to female flowers as they continued foraging among turtlegrass flowers. The well—known difficulty of successfully maintaining seagrasses in aquaria, much less having them flower while under cultivation, means that until seagrasses can be grown and induced to flower in flow—through mesocosms, future observations will need to be made in the field and only in relatively clear water that permits small—scale videography.

**Rhizosphere dynamics**

It has been known for some time that lucinid bivalves are commonly associated with seagrasses, and the fossil record indicates that the longstanding association has existed since at least the Eocene (Reynolds et al. 2007). Lucinids contain sulfur oxidizing bacteria that reduce hydrogen sulfide in the seagrass rhizosphere and help maintain conditions favorable for seagrass growth and survival (Reynolds et al 2007, van der Heide et al. 2012). While studies of the interactions between...
lucinids and seagrasses have recently increased (e.g., de Fouw et al. 2016), more efforts are needed to determine the relative importance of this relationship in additional settings. In addition, there are also nitrogen fixing microbes in the sediments that can provide nitrogen to seagrasses in waters where it is in short supply (Welsh 2000), although there is still little evidence available to judge how important this might be to the nutrient requirements of different seagrass species or how common it is (Petersen et al. 2016). In addition, the filtration of particles from the water column by abundant sponges can benefit seagrasses by improving water clarity. This was demonstrated by Peterson et al. (2006), who attributed seagrass die-off in Florida Bay (USA) to the indirect effect of massive sponge mortality that then resulted in turbid water with negative, lethal effects on seagrasses.

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

Nursery role of seagrass meadows

Definitive evaluations of the nursery role of seagrass meadows for fish species with complex life cycles has yet to be routinely carried out, but such evaluations allow the relative importance of different seagrass meadows as nursery grounds to be assessed quantitatively. The most likely way for this to happen is to compare the chemistry of fish otoliths in adult individuals in the adult habitat with the chemistry of otoliths of 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 would indicate from which nursery area adult individuals originated. This type of study has not been done often, as it is labor intensive. Potentially, water chemistry in nursery areas can vary from year to year, owing to differential inputs of elements from surrounding watersheds, thereby making it important for studies to last more than one annual cycle (Kraus and Secor 2005, Fodrie et al. 2019). However, until simpler methods are developed there is high value in implementing more studies to identify the most productive of the potential nursery habitats and prioritize their protection and conservation.

Seagrass Biology and Ecology

Seagrass Foraging

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 a recent example). However, there are several examples of filter-feeding bivalve associations with seagrass roots and rhizomes that indicate 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).

Population Genetics

Increased ability to genotype seagrasses has led to enhanced understanding of the genetic diversity present in seagrass meadows and to our ability to evaluate the spatial extent of seagrass clones (McMahon et al. 2014). This has enhanced our ability to evaluate the frequency of successful seed dispersal and survival of seedlings and indirectly the relative importance of sexual reproduction in determining the size of seagrass populations. Much still remains to be learned about the average size of clones, especially in the Old World tropics, and the distances that are normally traveled by the seeds of various seagrass species.

Carbon Sequestration

Another area of intense investigation is the degree to which seagrass meadows sequester carbon, and the likelihood that this carbon can be mobilized when seagrass die-offs occur (Fourqurean et al. 2012, MacCreadie et al. 2014). It is clear that healthy seagrass meadows sequester large amounts of blue carbon, but the on-going loss of seagrass meadows globally (Waycott et al. 2009) 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 atmospheric carbon dioxide.

BACK TO THE FUTURE

The successful conservation of seagrass megaherbivores such as green turtles, manatees and dugongs has resulted in a growing number of seagrass overgrazing episodes (Fourqurean et al. 2010, Lal et al. 2010, Christianen et al. 2012, Hernandez and van Tuusbroek 2014). In areas as different as Bermuda, the Indian Ocean and the Caribbean, increased numbers of green turtles have reduced formerly lush seagrass meadows to “mowed lawns” and produced community changes with slower growing large seagrasses replaced by more rapidly growing seagrass of smaller stature (Lal et al. 2010). This “mowed lawn” condition provides greatly reduced shelter and food resources for fish and invertebrates that use seagrasses as nurseries during their first year of life, and can ultimately lead to reduced catches of economically valuable species of fish, shrimp and crabs (Lal et al. 2010, Heck et al. 2015). Greatly reduced densities and lengths of seagrass leaves are the con-
ditions that seagrasses likely experienced for millennia when marine mammals and green turtles were abundant and fed extensively on seagrasses (Domning 2001, Jackson et al. 2001, Velez-Jurabe et al. 2012). If populations of green turtles continue to increase, along with those of manatees and dugongs, there will be a significant question of how to manage their populations along with those of seagrasses in a fashion that is most beneficial to the entire suite of natural resources.

**Concluding comments**

I have found collaborative work to have been the most valuable and enjoyable; indeed, as noted above, some collaborations have existed for decades and continue to this day. I also have found that experiencing new places can dramatically change one’s worldview and I heartily recommend extensive travel for all serious students of ecology. The privilege of working at institutions with supervisors who allowed me the freedom to ask the scientific questions most interesting to me is of paramount importance in my life. The great bosses I have had (Sandy Sage and Clyde Goulden at the Academy of Natural Sciences, and George Crozier, and most recently, John Valentine, at DISL) have my sincere, heartfelt gratitude for allowing me to indulge my unending interest in, and curiosity about, the ecology of seagrass meadows and the animals that inhabit them.

It has also become clear to me over the years that there is no substitute for abundant field work and for experiencing the natural environment first-hand. Others have done a fine job of explaining the critical importance of understanding the natural history of the organisms inhabiting the ecosystems being investigated (Dayton 2003, Able 2016) and I completely agree with them. There is nothing that can replace experience in the field and its value in the formulation of interesting and relevant hypotheses and the proper design of ways to test them. This is and always has been 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 prior work. Currently, obtaining older papers can be difficult, and journals that limit the number of references that can be 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, and much more can be done by building on this foundation.

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