Chapter 16
The Role of Consumers in Structuring Seagrass Communities: Direct and Indirect Mechanisms

Robert J. Nowicki, James W. Fourqurean and Michael R. Heithaus

Abstract Seagrass ecosystems were traditionally assumed to be structured by competition as well as by “bottom up forces” such as resource availability and disturbance. However, a wealth of new evidence demonstrates that exertion of “top down control” by animals may be widespread. The strength and direction of top down control is context dependent, however, and varies with properties of organisms, the community, and the physical environment. Consumers can facilitate, consume, or destroy primary producers, aid or inhibit seagrass reproduction, or alter bottom up processes with implications for the properties and persistence of seagrass ecosystems. Studies in Australian ecosystems have been critical in helping to elucidate the role of consumers in seagrass ecosystems. Specifically, work investigating the roles of megaherbivores and apex predators and the pioneering of novel experimental approaches which allow for cage-free manipulations of mesograzers have substantially furthered our understanding of top-down control. At the broadest scale, megagrazers are likely to dominate grazing pathways in Australian tropical and subtropical seagrass ecosystems, while macrograzers and mesograzers do so in

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temperate seagrass ecosystems. However, while we have learned much about mechanisms through which top-down control can operate and its effects on seagrass ecosystems, predicting which grazing pathways dominate at smaller spatial scales, and net herbivore effects on seagrasses in specific ecosystems remains challenging due to context dependence and the highly complex nature of species interactions. Anthropogenic impacts further complicate these relationships. Australian seagrass habitats possess unusual properties, including relatively intact populations of megafauna, remote and pristine locations, and distinctive oceanographic features which allow these habitats to provide unique insights of top down control in seagrass ecosystems.

16.1 The Development of Understanding of Top-Down Control on Seagrass Community Structure

One of the central goals of ecology is to understand the forces that structure ecosystems. In pursuing this goal, ecologists have traditionally focused on the roles of physical factors such as light, water and nutrient availability in controlling ecosystems from the "bottom up." This focus on bottom up control was due in part to the ease with which physical variables can be manipulated in controlled experiments. Though ecologists and naturalists had written about the importance of consumers and "top down" forces in ecosystems throughout the field's history (e.g. Elton 1927), it wasn't until a seminal paper published by Hairston et al. (1960) that the role of consumers was brought into the ecological limelight. This paper presented what is known as the "green world hypothesis," and asked a simple question: if herbivores are only limited by resources, then why do plants in terrestrial ecosystems persist? One reason, the authors posited, is that herbivores are not limited from the "bottom up" by plant resources, but from the "top down" by predators—and that this top down control is what allows primary producers to survive. This hypothesis, though remaining far from universally accepted (see Ehrlich and Raven 1964; Murdoch 1966; Strong 1992; Polis and Strong 1996; Polis 1999 for critiques and alternate hypotheses), set the stage for subsequent studies investigating the role of top down control in ecosystems.

Until relatively recently, the importance of top-down control in seagrass ecosystems went largely unrecognized. Indeed, seagrass ecology focused on factors in the physical environment that limited seagrass establishment, growth and distribution—herbivory and predation were considered relatively unimportant (Kirkman and Reid 1979; Klumpp et al 1989). This view began to incrementally change, particularly in the 1980s, when several reviews suggested that the persistence of seagrass ecosystems may be due to herbivore control of algal competitors, which are generally faster growing than seagrasses (Orth and Van Montfrans 1984; van Montfrans et al. 1984). The suggestion that top down control may be important in limiting algal overtake of seagrass ecosystems has since been widely recognized (e.g. Hughes et al. 2004; Heck and Valentine 2007; Verhoeven et al. 2012).

Though there was increasing realization that top down control could play important roles in seagrass-algae dynamics, the paradigm remained that seagrasses *themselves* were only rarely consumed by herbivores and that most seagrass production was probably channeled into the detrital cycle (Kirkman and Reid 1979; Thayer et al. 1984; Klumpp et al 1989). This idea persisted despite the knowledge that sirenians, sea turtles, teleosts and sea urchins that live in seagrass meadows are herbivorous (Klumpp et al. 1989; Lanyon et al. 1989) and that the effects of grazers on the structure of seagrass beds can, in some cases, be readily apparent (Randall 1965). Contributions from historical ecology and contemporary experiments performed over several decades, began to challenge this paradigm.

Taking a historical perspective, some ecologists observed that the seagrass ecosystems of today are rarely intact or natural ecosystems. Modern seagrass ecosystems, they argued, are largely released from top-down control because the marine megaherbivores that roamed such ecosystems centuries or millennia prior had been hunted to functional extinction (Dayton et al. 1995; Domning 2001; Jackson 2001; Heck and Valentine 2007). In a way, this argument echoed that of Hairston et al. (1960)—seagrass ecosystems were green because predators (in this case, humans) were highly effective at exerting top down control on seagrass herbivores such as sea turtles, sirenians, sharks. Thus, ecologist's observations of low rates of herbivory in seagrass ecosystems could in fact be the result of human activity that set an unnatural "baseline" that betrays the truth of the evolutionary and ecological importance of herbivory in these systems.

Other ecologists argued that seagrass herbivory was not only still occurring, but that it could still have strong effects in seagrass ecosystems today. Largely led by the work of ecologists working in the Gulf of Mexico and Northwestern Atlantic, a suite of observations, experiments, reviews, and meta-analyses has built compelling evidence that significant seagrass consumption (and top-down control) continues in contemporary seagrass ecosystems (Valentine and Heck 1991, 1999; Heck and Valentine 1995; Cebrián and Duarte 1998; Rose et al. 1999; Williams and Heck 2001; Kirsch et al. 2002; Hughes et al. 2004; Nakaoka 2005; Valentine and Duffy 2006; Heck and Valentine 2007). Even in the relative absence of marine megafauna, multiple experiments showed how consumer control can still shape seagrass ecosystems at scales from individual plants to the entire community. Partially as a consequence of these and other experiments, the idea that predators play critical roles in controlling herbivory in seagrass ecosystems also gained support (Heck et al. 2000; Williams and Heck 2001; Valentine and Duffy 2006)—something first observed to be important to the formation of the grazing halos described decades before (Randall 1965). Evidence for top down control in seagrass ecosystems (including trophic cascades) continues to accumulate today (Hughes et al. 2004; Burkepile and Hay 2006; Heck and Valentine 2006; Heithaus et al. 2012; Burkholder et al. 2013; Duffy et al. 2013).

By the late 1980s, when the first edition of this book was published, it had begun to become apparent that seagrass herbivory was more important than previously recognized, though most of the focus remained on large bodied consumers like dugongs and green turtles (Lanyon et al. 1989). Now, there is compelling evidence that consumers of varied body size and feeding guild can exert top down control through a variety of mechanism and trophic pathways, sometimes with strong and counterintuitive effects on their ecosystems. The challenge now is not in determining *if* top-down control exists in seagrass ecosystems, but when it is important relative to other forces, by what mechanisms top-down control most commonly operates, and by what pathways it is most likely to dominate. While work to identify mechanisms of top down control has been fruitful, predicting when (and through what avenues) top down control dominates in seagrass ecosystems has proven difficult and remains a key challenge in seagrass ecology.

16.2 The Nature of Top Down Control and the Prevalence of Context Dependence

In order to understand when, where, through which pathways and mechanisms, and how strong top-down influences are, an understanding of the roles of consumers, producers, and their relationships to each other and their environment is necessary. In the most basic sense, the strength and nature of top down control in seagrass ecosystems is a function of the properties of herbivores, predators, and the seagrass, community structure, and features of the physical environment. Seagrasses, and the other primary producers they interact with, have inherently different life histories, chemical compositions, and tolerances to herbivory and environmental conditions. These properties interact with properties of herbivores—their densities, identity, consumption rates, or feeding preferences. Predators in turn influence herbivores or the predators of herbivores—altering their density, traits and behavior—which can generate cascading effects to seagrasses. The strength of these interactions is often linked to food web complexity. Consumers also interact with seagrass directly through nutrient transport and concentration, physical restructuring of habitat, and changes to bottom-up processes. Finally, these interactions occur in the context of the physical environment and are further complicated by anthropogenic impacts such as nutrient pollution, predator removal, and climate change. Below we consider how each of these taxa, guilds, or factors influences the strength and nature of top-down control, providing examples from experiments or observational work to support these considerations.

16.2.1 The Role of Seagrass in Mediating the Strength of Top-Down Processes

Plants are not simply the recipients of consumer effects; they also play an important role in mediating the ultimate effects consumers have on the primary producer community. As one ecologist wrote, “Plants are not passive agents, waiting to be decimated by herbivores” (Polis 1999). Primary producers, including seagrasses, microalgae, and macroalgae, can alter the strength of top down control through their susceptibility and response to herbivory, which may, in turn affect herbivore behavior. Seagrasses exposed to herbivory may decline or die-off, exhibit tolerance through compensatory or super-compensatory growth, or display resistance by altering their physiology or chemistry through methods such as nutrient or carbohydrate re-routing or by producing secondary metabolites (Cebrián et al. 1998; Ricklefs and Miller 1999; Vergés et al. 2008; Burnell et al. 2013a; Steele and Valentine 2015). The tolerance of primary producers to different kinds of herbivory differs by species—though it can also be induced in response to herbivory (e.g. Burnell et al. 2013a; Sanmart et al. 2014)—and this differential tolerance can have implications for seagrass community composition. For example, in mixed species seagrass meadows in Lady Bay, South Australia, overgrazing of seagrasses by sea urchins disproportionately impact *Amphibolis antarctica* compared to *Posidonia* spp., because the leaf cluster meristems of *A. antarctica* are exposed at the surface and therefore are more vulnerable to grazing while the meristems of *Posidonia* species are protected beneath the sediment surface (Burnell et al. 2013a). In this sense, differences in morphology mediate the strength of consumer control of these mixed-species beds.

In general, the life history characteristics of pioneer seagrasses like those in the genera *Halophila*, *Halodule*, *Syringodium*, allow them to grow and expand quickly, giving them generally high grazing tolerance on the level of the meadow, even if their standing biomass is often heavily reduced by regular grazing (e.g. Preen 1995; Masini et al. 2001). Climax seagrasses like those in the Australian genera *Amphibolis*, *Posidonia*, and *Zostera* grow and expand more slowly, but are also less ephemeral, forming dense, thick beds with generally higher stocks of standing biomass. This “climax” life history, however, results in slower responses to large grazing events that can be generated by herbivores like dugongs and urchins (see Preen 1995; Eklöf et al. 2008 for examples). Some climax species, like *Amphibolis antarctica*, do not even generate seeds (Hemminga and Duarte 2000), produce viviparous seedlings to recolonize heavily grazed areas. As we will see, life history characteristics also relate to herbivore feeding preferences.

While primary producers alter how top-down control operates in seagrass ecosystems via their responses to herbivory, they also do so through their properties as a resource. Because seagrasses can act as a different kind of resource (i.e. food, shelter) for different consumers, seagrass properties can influence not only herbivore feeding rates and food preferences, but also habitat use preferences. These preferences can have measurable impacts on seagrass community structure (Preen 1995; Armitage and Fourqurean 2006). Consumer feeding patterns are influenced by variation in primary producer chemical properties (i.e. palatability or food quality), structural properties (i.e. complexity, which provides refuge for predators or herbivores), or through community composition (associations with other producers that may illicit such preferences in herbivores).

From an herbivory perspective, seagrass chemical composition describes the concentration of not only nutrients and soluble carbohydrates which often attract grazing, but also fiber and secondary metabolites, which can deter it. Generalizing the relationship between the seagrass chemical composition and herbivore feeding preference or feeding rate remains surprisingly difficult. For example, some studies find a positive relationship between nutrient content and herbivore feeding preference or consumption rates (ex. McGlathery 1995; Brand-Gardner et al. 1999; Goecker et al. 2005; Prado et al. 2010; Sheppard et al. 2010; Burkholder et al. 2012), while others do not (Cebrián and Duarte 1998; Mariani and Alcoverro 1999; Valentine and Heck 2001; Kirsch et al. 2002; White et al. 2011). This is partially due to the fact that nutrient concentrations as measured in assays may not accurately reflect the actual nutritional content a seagrass presents to herbivores since many nutrients can be bound to indigestible plant tissue that is never assimilated (Cebrián and Duarte 1998). However, some of this complexity is derived from simultaneous variation in defensive compounds which reduce palatability. For example, feeding trials and manipulations using the bucktooth parrotfish *Sparisoma radians* indicate this herbivore prefers macrophytes in inverse relation to their terpene content, even when other factors such as species or biteability are accounted for (Targett et al. 1986). Similarly, in Watamu National Marine Park, Kenya, feeding preferences of the teleost herbivore *Calotomus carolinus* are inversely correlated to the carbon fiber content of primary producer species (Mariani and Alcoverro 1999, Table 16.1). The relationship between nutrient ratios, plant defenses, and herbivore feeding preference is further obscured by the fact that plant characteristics can fluctuate across space, time, species, and individual (e.g. Fourqurean et al. 2005; Hays 2005; Tomas et al. 2011; Steele and Valentine 2015). This complicates drawing patterns because multiple chemical variables can change concurrently, making attribution of herbivory to a single compound or group of compounds difficult. For example, newer seagrass leaves generally have higher nutrient concentrations and fewer structural compounds than older leaves, but may also have higher concentrations of phenolic compounds (Hemminga and Duarte 2000; Agostini et al. 1998; Vergés et al. 2010). Older leaves also tend to have higher epiphyte loads, making them more attractive to grazers targeting epiphytes (Alcoverro et al. 1997; Wressnig and Booth 2007; Vergés et al. 2010), and seagrass leaves have higher N and P content in winter compared to summer in seasonal environments (Fourqurean et al. 1997, 2005, 2007). Finally, different herbivores place varying levels of importance on each of these seagrass qualities (Prado and Heck 2011) meaning that understanding herbivore feeding preference requires not only comprehensive knowledge of seagrass chemical properties, but also insight into which of those properties local herbivores consider most. Despite the complex relationship between chemical properties and herbivory, investigations into a generalizable pattern are important as these chemical properties can significantly influence herbivory rates (e.g. Steele and Valentine 2015).

Though the multitude of factors driving herbivore feeding preferences in seagrass meadows has made generalizing preferences very difficult, one general pattern has emerged. Feeding assays, gut content analysis, and herbivore exclosure experiments indicate that faster growing seagrass species—many of which are of tropical origin—are generally consumed more readily than slower growing climax species (Cebrián and Duarte 1998; Mariani and Alcoverro 1999; Armitage and

Table 16.1 Herbivore seagrass preferences around the world

Consumer	Preferences	Region	Reference
Mostly fish	*Hw* > **Tt**	South Florida, USA	Armitage and Fourqurean (2006)
Three fish species	*Sf* > *Hw* > **Tt**	Caribbean	Prado and Heck (2011)
Sea urchins	*Hw* > *Sf* > **Tt**	Caribbean	Prado and Heck (2011)
Dugongs	*Hu* > *Cr* > **Th**	Indonesia	De Iongh et al. (1995)
Fish (Scaridae)	**Tt** > *Hw* > **Tt**^{E} > *Sf*	Caribbean	Lobel and Ogden (1981)
Fish (probable)	*Hs* = *Hu* = *Ho* > *Ca* > **Aa** = **Pa**	Shark Bay, Western Australia	Burkholder et al. (2012)
Dugongs	*Ho* > *Hu*^{T} > *Hs* > *Si* > *Hu*^{B} > **Zc**	Moreton Bay, Queensland	Preen (1992)
Fish (Scaridae)	*Cr* > *Si* > *Hu* = *Hw* > **Th** > **Cs** = *Hs* > **Tc** > **Ea**	Watamu marine national park, Kenya	Mariani and Alcoverro (1999)
Neritid gastropod	**Zc** > *Ho* > **Cs**	Moreton Bay, Queensland	Rosini et al. (2014)
Green turtle	**Th** > *Cr*	Lakshadweep islands, India	Kelkaret al. (2013)

Studies include feeding preference experiments and observational studies. Observational studies (including diet studies and feeding observation studies) were only included if frequency of occurrence of food items was accounted for in the environment. In some cases herbivore preferences correlate positively to nutrient or soluble carbohydrate content of seagrass tissues, or negatively to fiber content; however, these patterns are not universal. Seagrasses with pioneer life histories are italicized; climax seagrasses are listed in bold. Non-seagrass food items are excluded. *E* epiphytes removed, *T* thin leaf morph, *B* broad leaf morph. Hw = *Halodule wrightii*, Tt = *Thalassia testudinum*, Sf = *Syringodium filiforme*, Hu = *Halodule uninervis*, Cr = *Cymodocea rotundata*, Th = *Thalassia hemprichii*, Hs = *Halophila spinulosa*, Ho = *Halophila ovalis*, Ca = *Cymodocea angustata*, Aa = *Amphibolis antarctica*, Pa = *Posidonia australis*, Si = *Syringodium isotefolium*, Zc = *Zostera muelleri* (formerly *Z. capricorni*), Cs = *Cymodocea serrulata*, Hst = *Halophila stipulacea*, Tc = *Thalassodendron ciliatum*, Ea = *Enhalus acaroides*

Fourqurean 2006; Prado and Heck 2011; Burkholder et al. 2012, Table 16.1). This pattern holds in Australian seagrass ecosystems, where fast-growing seagrasses are more readily consumed than temperate species; the latter are more likely to be targeted for their epiphytes rather than their tissue (Preen 1995; Burkholder et al. 2012). Pioneer-type seagrassess tend to be less structurally complex and higher quality food than climax seagrasses, often due to higher nutritional content, lower mechanical resistance to grazing, or both (i.e. de los Santos et al. 2012).

Seagrass physical structure can also influence top down control by generating refuge or habitat for herbivores or predators, altering habitat use patterns of fauna and, by extension, where and what they consume. For example, amphipods in beds of *Zostera marina* in San Francisco Bay, USA, associate with structurally complex inflorescences over leaves, which may be responsible for increased consumption of inflorescences and associated reduced reproductive potential (Reynolds et al. 2012). Seagrass structural complexity can also affect top down control by mediating predator-prey interactions among smaller-bodied animals. The ability of seagrasses to alter hunting efficiency and, by extension, the degree of predator control of herbivores, is predicted to have implications for mesograzer control of seagrass epiphytes (Duffy et al. 2013). For example, in mesocosm experiments where seagrass habitat complexity was manipulated (using flowering vs. simpler non-flowering shoots of *Zostera marina*), predation rates on the gammarid amphipod *Ampithoe valida* by teleost predators were reduced by half or more in the complex treatments, which was in turn associated with twice as much *Z. marina* biomass lost as in the simpler treatments (Carr and Boyer 2014). However, this relationship is not uniform; instead, the relationship between predation risk and habitat complexity is mediated by both the hunting mode of the predator and the escape mode of the prey (Wirsing et al. 2010). For example, in terrestrial old field ecosystems in New England, USA, spider predators that use a sit-and-wait hunting strategy hide in grasses, reducing grasshopper use of grasses and increasing their use of nearby herbs (Schmitz 2008). As a result, grasshopper herbivores alter the species on which they feed, changing patterns of top-down control (Schmitz 2008).

Because of the diversity of structural and chemical properties of submerged aquatic macrophytes, primary producer community assembly can mediate the effects of top down control. Seagrass that are associated with other primary producers can experience alterations in the intensity and direction of top-down control as herbivores change consumption rates or feeding preference in the context of a more diverse primary producer community. For example, the association between seagrass and seagrass epiphytes is one of the most important associations in seagrass ecosystems. Epiphytes can rapidly overgrow seagrasses, reducing light penetration and nutrient availability to seagrass tissues.. Furthermore, they can reduce seagrass fitness by attracting herbivores to seagrasses and mediating herbivore consumption of seagrass tissue. For example, when given a choice between feeding on *Posidonia australis* blades with or without epiphytes, two species of teleosts (Family *Monocanthidae*) preferentially targeted the heavily epiphytized leaves, resulting in an eightfold increase in percentage of biomass (including seagrass) removed by these herbivores (Wressnig and Booth 2007). Similar feeding preferences are apparent with the sea urchin *Lytechnius variegatus* when feeding on *Thallasia testudinum* (Marco-Mendez et al. 2012). The mediation of grazing effects on one macrophyte by another occurs on larger scales as well; in Moreton bay, Queensland, destructive excavation grazing by dugongs removes not only targeted tropical seagrasses such as *Halophila ovalis* (which quickly recovers), but also the closely associated *Zostera muelleri*, inhibiting the expansion of this climax seagrass (Preen 1995). Associations between two macrophytes may be also detrimental to a seagrass species if the preferred species is overgrazed and herbivores switch grazing to an associated seagrass to compensate, as sometimes occurs when mesograzers eliminate their algal food supply (Duffy et al. 2001, 2003).

The structural complexity created by macrophytes can also alter grazing pressure on surrounding primary producers if they create refuge for herbivores which are unwilling to venture far from the protection of cover, as occurs in the grazing halos of the Caribbean (Randall 1965). This may have positive or negative influences on associated seagrasses, depending on what the feeding preference of the grazer is, and may result in surprising interactions between macrophytes. For example, drift macroalgae in beds of the eelgrass *Zostera marina* in the York River, Virginia, USA, may indirectly reduce epiphyte loads on nearby eelgrass leaves by providing refuge for mesograzers, suggesting that the presence of competitive macroalgae at low densities may actually facilitate eelgrass persistence (Whalen et al. 2013). Seagrasses that are found in association with relatively unpalatable or chemically defended neighbors may also withstand lower rates of direct grazing by creating microsites of reduced herbivory as has been documented with algae (Hay 1986), though we are unaware of similar studies on seagrasses. The potential for this to alter herbivore pressure likely depends heavily on the spatial scales at which herbivores perceive food quality and the spatial arrangement of such an association. While undeniably complex, understanding the drivers of herbivore feeding preference is absolutely critical to predicting the net effects of consumer control in seagrass ecosystems.

16.2.2 The Role of Herbivores

Herbivores in seagrass ecosystems generally adhere to one of three trophic roles—epiphyte consumers, phytoplankton consumers, and macrophyte consumers. However, herbivores vary widely in their individual capacity to mediate the strength of top-down control through these pathways. Australian seagrass ecosystems feature herbivores that range in size by several orders of magnitude, from tiny arthropods and gastropods only a few millimeters across to marine mammals three meters in length.

Seagrass herbivores can be categorized into three categories based on size: mesograzers, macrograzers and megagrazers. Mesograzers are invertebrates, generally arthropods and gastropods, under 2.5 cm across (Fig. 16.1). Though mesograzer densities vary widely with locale, they can be considered cosmopolitan residents of seagrass beds. Many mesograzers facilitate seagrass persistence through the mutualistic mesograzer model, though some consume seagrass tissue (Orth and Van Montfrans 1984; Duffy and Harvilicz 2001; Reynolds et al. 2012; Rossini et al. 2014). Indeed, many invertebrates feed on or bore directly into seagrass tissues or damage them while feeding on associated epiphytes

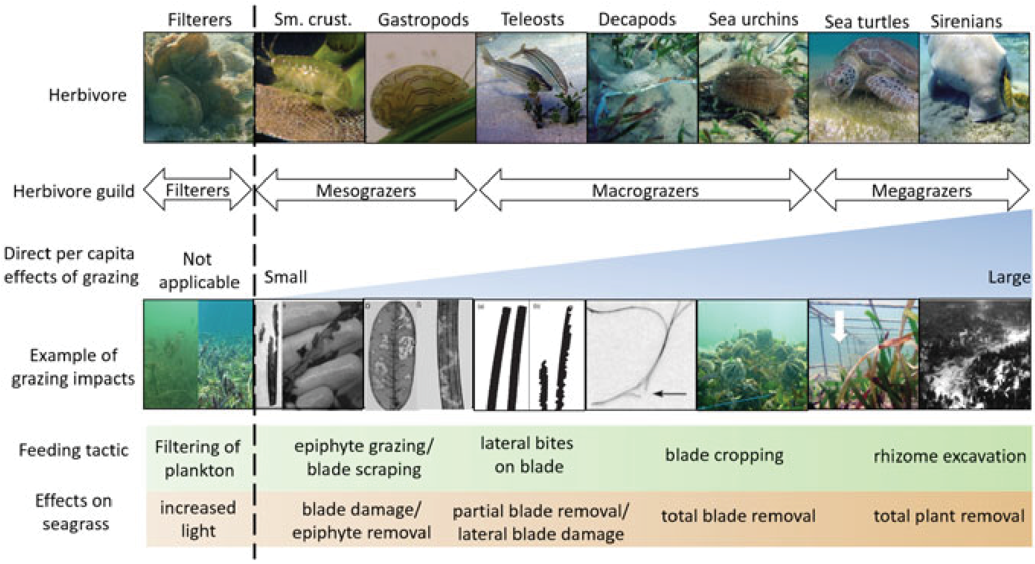

Fig. 16.1 Examples of types of grazers found in Australian seagrass ecosystems, their feeding tactics, and the resulting impact on seagrass tissue. Tactics are listed in order of increasing per-capita effect on seagrass. Filter feeders are included for completeness, though their grazing of phytoplankton only affect seagrasses indirectly. Photos (clockwise from top left): Shark Bay Ecosystem Research Project (SBERP), Duffy et al. (2013), Rossini et al. (2014), SBERP, SBERP, SBERP, Wikimedia commons, Wikimedia commons, Preen (1995), Burkholder et al. (2013), Eklöf et al. (2008), Davis et al. (1998), Goecker et al. (2005), Rossini et al. (2014), Reynolds et al. (2012), SBERP

(e.g. Nienhuis and Groenendijk 1986; Wassenberg 1990; Zimmerman et al. 1996; Brearley and Walker 1995; Rueda and Salas 2007; Brearley et al. 2008; Holzer et al. 2011; Reynolds et al. 2012; Carr and Boyer 2014; Rossini et al. 2014). This herbivory can be widespread with significant implications for seagrass productivity and survival. For example, in the *Zostera marina* beds of San Francisco Bay, USA, consumption by the non-native amphipod *Ampithoe valida* can deplete seed stocks of this seagrass in a matter of weeks, which may reduce the genetic diversity of perennial beds or even jeopardize the persistence of annual seagrass beds which require seeds for their yearly recruitment (Reynolds et al. 2012). Similarly, the isopod *Limnoria agrostisa*, widespread throughout Western Australia, burrows into leaf sheathes of *Amphibolis griffithi* and *Posidonia* spp., consuming seagrass tissue and damaging or destroying leaf clusters (Brearley et al. 2008). The effects of seagrass consumption by *L. agrostisa* are substantial, with 40–70% of leaves being damaged and approximately 40% of leaf clusters destroyed by this species, illustrating that even small grazers can have surprisingly large effects.

Macrograzers include larger herbivores, such as sea urchins, decapod crustaceans, teleosts like parrotfish (Family *Scaridae*) and trumpeters (Genus *Pelates*), and swans (Armitage and Fourqurean 2006; Burkholder et al. 2012; Bessey et al. 2016). These herbivores may target either seagrass tissue or associated epiphytes, though in the case of the latter they still usually remove seagrass tissue in the process, making the impact of seagrass macrograzers generally negative.

For example, along the coast of the Gulf of Mexico, USA, the purple urchin *Lytechinus variegates* is able to consume the majority of aboveground seagrass biomass, sometimes leading to local seagrass extinction (Valentine and Heck 1991; Heck and Valentine 1995; Rose et al. 1999). Similar events have occurred in Australian seagrass meadows and urchin barrens in temperate algal systems are iconic. Multiple instances of overgrazing by sea urchins have contributed to losses of *Posidonia* spp.-dominated seagrass meadows on the scale of hectares in Cockburn Sound, Western Australia since 1980 (Kendrick et al. 2002). Similarly, aggregations of the urchin *Heliocidaris erythrogramma* denuded 45 ha of *Posidonia* habitat in Botany Bay, Australia, between 1979 and 1984 (Larkum and West 1990). In the Torres Straits, reduced seagrass density is correlated with high sea urchin abundance, likely as a result of intense grazing by those urchins (Long and Skewes 1996). Urchins can also overgraze *Amphibolis antarctica*, by targeting leaf meristems (Burnell et al. 2013a). Finally, Australian teleosts like the striped trumpeter *Pelates octolineatus* can be important consumers of seagrass photosynthetic tissue (Bessey and Heithaus 2015).

Though the ranges for individual species differ, mesograzers and macrograzers of some kind can be found in seagrass ecosystems around Australia. Some Australian macrograzers, like the teleosts *Pelates octolineatus*, *Odax acroptilus*, and *Haletta semifasciata*, or the urchin *Heliocidaris erythrogramma*, consume substantial proportions of seagrass and epiphytic algae as part of their diet and can, in the case of *H. erythrogramma*, strip entire areas of seagrass above-ground biomass bare (Eklöf et al. 2008; MacArthur and Hyndes 2007; Bessey et al. 2016). Both macrograzers and mesograzers, however, generally target above-ground leaf tissue and leave below ground biomass intact (Fig. 16.1).

Because of their relatively high populations in Australian coastal ecosystems, megaherbivores play a more important role in these habitats than they do in well studied seagrass ecosystems of Europe and North America (Lanyon et al 1989). Specifically, Australian seagrass ecosystems are home to two species of megaherbivores: green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon*). Though both megaherbivores consume seagrass tissue, their grazing tactics generally differ. When consuming seagrass, green turtles primarily remove above ground biomass by cropping seagrass leaves, though in some areas of the world they will excavate belowground biomass as well (Christianen et al. 2014). Conversely, dugongs commonly excavate seagrass beds, particularly when Australian tropical seagrass such as *Halophila ovalis* and *Halodule uninervis* are present (Anderson 1986; Preen 1995; Masini et al. 2001). During excavation, dugongs dig into the sediment to target seagrass rhizomes, potentially destroying large areas of seagrass beds (e.g. Preen 1995, Fig. 16.1). This grazing tactic, combined with the dugong's large size, relatively high metabolic rate, and obligate seagrass diet, means dugong-seagrass interactions can be very strong. Indeed, in Shark Bay, Western Australia, dugong excavation results in the consumption of approximately 50% of primary production in beds of the pioneer seagrass *Halodule uninervis* (Masini et al. 2001). When such seagrasses are unavailable or when risk of predation makes excavation grazing unappealing, dugongs will instead crop the above ground biomass of temperate seagrasses such as those from the genera *Zostera* or *Amphibolis* (Anderson 1986; Preen 1995; Wirsing et al. 2007a). This has important implications for their impacts on seagrass community structure and ecosystem dynamics (see below).

Finally, suspension feeders play important, if underappreciated, roles in the top down control of seagrass ecosystems. Consisting of a variety of taxa including sponges, bivalves, gastropods, crustaceans, and ascidians, this herbivore group does not actually consume seagrass. Suspension feeders are, however, important herbivores in seagrass ecosystems for a similar reason to facultative mesograzers—they control primary producers (specifically phytoplankton) that compete with seagrasses for light (Peterson and Heck 2001; Newell 2004). The effect of phytoplankton removal on seagrasses is hard to quantify and disentangle from the more general benefit suspension feeders have on water clarity since suspension feeders also remove suspended sediment and particulate organic matter. However, the benefit this herbivore group has on seagrasses can be surprisingly strong due to the high light requirement of seagrasses as a group (Dennison et al. 1993). For example, mathematical models estimate that uniform densities of the Eastern Oyster *Crassostrea virginica* as low as 25 g dry weight m^{-2} reduces suspended sediment concentrations by almost an order of magnitude (Newell and Koch 2004). In areas where phytoplankton loads are high, suspension feeders probably play important, if indirect, roles as seagrass facilitators.

Because the net effects of herbivores in seagrass ecosystems is heavily influenced by which grazing pathways dominate in that system, it is important to understand where specific pathways are most likely to dominate, and by extension, the geographic ranges of important herbivores. Mesograzer control of epiphytes is thought to be widespread and may overshadow the ecological effect of direct seagrass consumption in many places (see Hughes et al. 2004; Valentine and Duffy 2006). However, the dominance of the mesograzer pathway relative to other grazing pathways is likely to be limited to temperate seagrass habitats within Australia. This is due to the presence of megagrazers in tropical and subtropical Australian seagrass ecosystems, as well as the generally pioneer seagrass species that typify tropical Australian waters, the ephemeral nature of which limits the effect of epiphyte colonization. Even within temperate seagrass ecosystems, whether the net effect of herbivores is facultative or destructive towards seagrasses depends on the relative dominance of macrograzers and destructive mesograzers against facultative mesograzers and filter feeders. Indeed, most teleost and urchin macrograzers on which investigations into top down control have been done have subtropical to temperate distributions (Fig. 16.2). This range separation means that in tropical Australian systems, megagrazers should generally have a stronger potential to dominate top-down control than macrograzers or mesograzers, while in temperate habitats clear dominance of herbivore pathways are probably more elusive. All of these herbivore groups overlap in subtropical habitats, however, further complicating predictions about which pathways will dominate the effects of top down control in these habitats. For example, multiple herbivore exclosure studies in Shark Bay suggest that megagrazer and macrograzer pathways may each dominate in different habitats of the same ecosystem (Burkholder et al. 2013; Bessey et al. 2016).

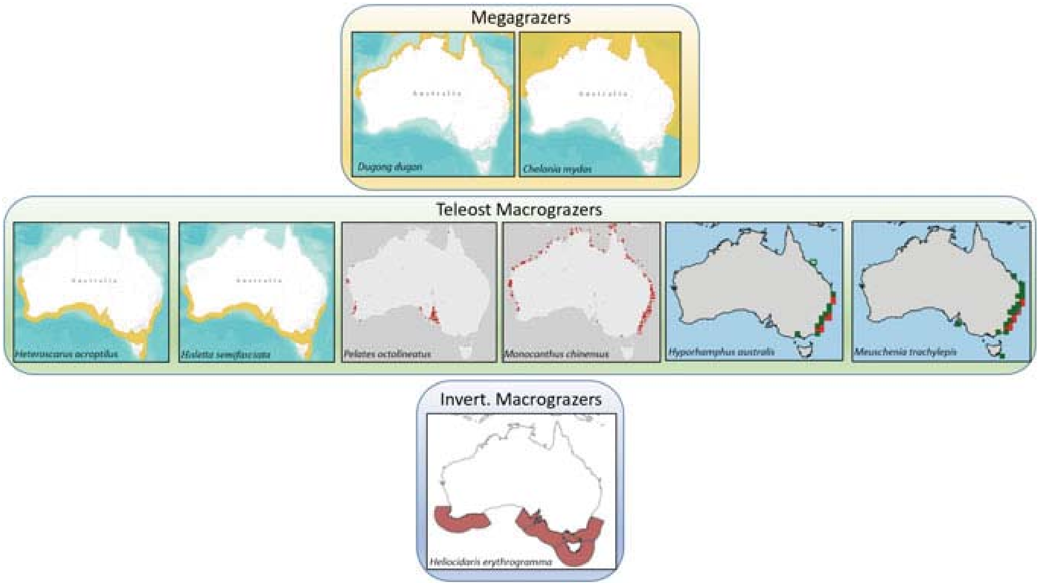

Fig. 16.2 Known distributions of representative Australian seagrass megagrazers and macrograzers. Megagrazers are distributed tropically and subtropically while distributions of well studied macrograzer are largely temperate and subtropical; subtropical areas where ranges between megagrazers and macrograzers interact may exhibit additional complexity because of the co-occurrence of these different guilds. Ranges of macrograzers, however, may reflect geographically restricted research effort rather than true geographic range separations between macrograzers and megagrazers. Map sources by row, left to right: IUCN, IUCN, Encyclopedia of Life, Aquamaps.org, Marinespecies.org

16.2.3 The Role of Predators

Predators exert top-down control in seagrass ecosystems not only by regulating the populations of their prey, but also by altering the intensity, target, and spatiotemporal patterns of herbivory (Heithaus et al. 2008a, b). When this control impacts trophic levels below that of their prey, a trophic cascade occurs (Paine 1980). The potential role of predators in shaping patterns of top-down control by seagrass herbivores has been recognized for decades. As has been mentioned before, for example, Randall (1965) suggested that grazing halos around Caribbean patch reefs were due to reef-associated fishes that targeted seagrass but were unwilling to venture far from the safety of their refuges. Since then, meta-analysis has indicated that trophic cascades tend to be strongest in benthic marine ecosystems (Shurin et al. 2002; Borer et al. 2005).

Traditionally, trophic cascades were thought to operate exclusively through lethal predator effects in which increases in predator abundance reduce mesoconsumer density through predation and, as a result, also reduce pressure on associated resource species (Lima 1998). Predators, however, elicit myriad changes in prey behavior including fear-induced habitat shifts, reduction in foraging rates, or changes in diet (e.g. Randall 1965; Lima 1998; Brown et al. 1999; Peacor and

Werner 2001; Heithaus and Dill 2002, 2006; Brown and Kotler 2004) and traits including morphology and physiology (e.g. Creel et al. 2007). These "risk effects" of predators can initiate or enhance trophic cascades through trait-mediated indirect interactions (i.e. TMIIs, Werner and Peacor 2003; Dill et al. 2003; Schmitz et al. 2004; Preisser et al. 2005).

One type of TMII, a behaviorally mediated indirect species interaction (BMII; sometimes referred to as a behavior-mediated trophic cascade; BMTC), occurs when changes in a property of one species (the "initiator") cause a behavioral shift in a "transmitter" species, which in turn induces a change in a property of a third species (the "receiver") (Schmitz et al. 1997; Dill et al. 2003). BMII have received considerable attention recently in terrestrial, freshwater, and intertidal marine systems and appear to be capable of affecting populations and communities at magnitudes equal to, or greater than, those of lethal effects of predators (e.g. Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005). The power of such non-consumptive predator effects stems from their ability to affect many prey simultaneously, and sometimes through the ability of prey to exhibit compensatory population growth in response to mortality from consumption by predators. Additionally, in some situations BMII can reverse the sign of indirect interactions between top predators and basal resources in food chains with an odd number of trophic levels relative to those predicted by lethal effects of predators alone (Dill et al. 2003; Heithaus and Dill 2006; Wirsing et al 2007c). Importantly, even if predators rarely consume or have minimal effects on the equilibrium population sizes of mesoconsumers, they may still trigger trophic cascades through non-lethal mechanisms by altering where and at what rate mesoconsumers exploit resource species (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005; Heithaus et al. 2008a, b). Finally, the effects of direct predation and risk effects interact with one another to enhance overall predator effects and this interaction may account for the majority of predator impacts (Werner and Peacor 2003; Heithaus et al. 2012).

Most trophic cascades recorded in Australian marine ecosystems have been from temperate and tropical algae reefs (Pinnegar et al. 2000), not seagrass ecosystems. However, this may be due not to a lack of trophic cascades in seagrass ecosystems so much as to a gap in research effort. Indeed, long term studies in Shark Bay, Western Australia, have identified multiple trophic cascades (and BMIIs) in a subtropical seagrass ecosystem. Shark Bay's apex predator, the tiger shark (*Galeocerdo cuvier*) induces habitat shifts at multiple spatial scales in both herbivores and mesopredators. Specifically, dolphins (*Tursiops aduncus*), dugongs, and cormorants (*Phalacrocorax varius*) all shift from foraging primarily in productive shallow seagrass habitats when sharks are scarce to foraging mainly in less productive, but safer, deep habitats when shark densities are high (Heithaus and Dill 2002; Heithaus 2005; Wirsing et al. 2007b). Dolphins and dugongs that continue to forage over shallow habitats when sharks are present largely abandon the highly dangerous interior portions of shallow banks that they used when sharks were scarce, in order to have easy escape options near bank edges (Heithaus and Dill 2006; Wirsing et al. 2007c). Similarly, green turtles in good body condition forage almost exclusively along bank edges, where seagrass quality is lower, when sharks are present but move toward interior microhabitats, with higher seagrass quality, when tiger sharks are scarce (Heithaus et al. 2007). Furthermore, tiger sharks alter dugong foraging tactics, limiting destructive excavation grazing that has been recorded to destroy hectares of seagrass elsewhere (Wirsing et al. 2007a; Preen 1995). None of these spatiotemporal shifts can be explained by variation in food availability, water temperature, or other factors. In the case of megaherbivores, these predator effects cascade down to the seagrass bed, altering which seagrasses dominate on bank edges (Burkholder et al. 2013, Fig. 3).

These studies exemplify the potentially dramatic effects predators can have in seagrass ecosystems through regulating the behavior of their prey, yet the dominant predators and herbivores in Australian seagrass ecosystems differ across the continent. While large-bodied sharks are undoubtedly the largest apex predators commonly found in most seagrass ecosystems, dolphins are also important and widespread upper trophic level predators. Several species of dolphins are found in coastal seagrass ecosystems of Australia–Indo-Pacific bottlenose dolphins (*Tursiops* sp.) and humpback dolphins (*Sousa sahulensis*) being common. Both species are piscivores, and because of high mammalian metabolic rates likely consume a large number of teleosts that may be important in the dynamics of seagrass ecosystems. In the subtropical Shark Bay seagrass ecosystem, *Tursiops* cf. *aduncus* preys upon striped trumpeters (*Pelates octolineatus*) (Heithaus and Dill 2002), the dominant teleost grazers (Heithaus 2004; Burkholder et al. 2012). Given the high population densities of dolphins in Shark Bay (Preen et al. 1997; Heithaus and Dill 2002) it is possible that dolphins could indirectly influence seagrass ecosystems through modifying the population sizes or spatiotemporal patterns of foraging by *P. octolineatus.* Unfortunately, little work has focused on the potential for dolphins to impact the dynamics of fish populations within seagrass ecosystems or how those impacts may cascade to structure seagrass communities.. Similarly, pinnipeds such as Australian sea lions (*Neophoca cinerea*) and fur seals (*Arctocephalus* spp.), may have been important predators in temperate Australian seagrass ecosystems, but their population sizes are much reduced from historical levels and the potential role of pinnipeds in structuring Australian seagrass ecosystems has not been explored. While both pinniped species tend to forage in offshore habitats, using coastal habitats for transit and rest, some individual Australian sea lions do forage consistently in coastal seagrass habitats (Lowther et al. 2011) and could exert top-down impacts on fishes of seagrass beds. This possibility remains largely unexplored, and studies of the potential top-down roles of predatory marine mammals in Australian seagrass ecosystems remains an interesting and potentially significant avenue of inquiry.

Unsurprisingly, many teleosts and smaller elasmobranchs may play important roles in Australian seagrass ecosystems. Indeed, small sharks (<2 m total length), rays, and teleosts can be locally abundant in Australian seagrass communities (e.g. White and Potter 2004; Simpfendorfer and Milward 1993). While some of these predators are actually omnivorous, consuming primary producers in addition to animal matter (e.x. *P. octolineatus*, Belicka et al. 2012; Burkholder et al. 2012;

Bessey and Heithaus 2015), other mesoconsumers feed on a diversity of prey including infauna, cephalopods, crustaceans, and worms, which may initiate trophic cascades. For example, stingrays may initiate three-step trophic cascades under which consumption of filter-feeding bivalves results in increased phytoplankton load, reducing light penetration to seagrass tissues. Indeed, there is strong evidence for the capability of batoids to exert top down control over bivalves when these predators are locally abundant (e.g. Myers et al. 2007), though to our knowledge empirical work on the indirect effects of batoids on seagrass are lacking. Similarly, marine birds have the potential to exert top-down control through direct predation and risk effects (i.e. Bessey and Heithaus 2013). Like predatory marine mammals, marine birds such as cormorants have high metabolic rates and can exist at high densities in seagrass ecosystems (e.g. in Shark Bay, Heithaus 2005; Bessey et al. 2016). Furthermore, the proportion of teleosts in the diets of cormorants in Australia can reach 90% or more (del Hoyo et al. 1992; Blaber and Wassenberg 1989; Humphries et al. 1992), and daily consumption rates can be 15% of body mass or more (Humphries et al. 1992). Interestingly, the role of these mesopredators in generating top-down control (specifically trophic cascades) remains largely unexplored in Australian seagrass ecosystems.

Trophic cascades have been recorded or proposed in seagrass ecosystems at multiple scales and trophic levels worldwide, from control of seagrass associated invertebrates by predatory teleosts (Heck and Valentine 1995; Heck et al. 2000; Lewis and Anderson 2012; Carr and Boyer 2014) to behavioral control of mega-herbivores and secondary predators by tiger sharks (Heithaus et al. 2012; Burkholder et al. 2013). As with herbivores, however, predators do not have equal capacity to exert top-down control or trophic cascades in seagrass ecosystems. Because herbivores influence seagrass communities through two main avenues (direct consumption of seagrass biomass and consumption of seagrass competitors), predators ultimately exert top-down control through these two pathways. In areas where megagrazers are dominant, large sharks are the only apex predators likely to have significant capability to structure seagrass ecosystems through top-down control. Conversely, if smaller teleost herbivores mediate a direct seagrass consumption pathway, intermediate predators such as dolphins, pinnipeds, cormorants and small sharks may all influence the potential for a cascade to occur. Finally, because so many members of the epiphyte-consuming mesograzers are small-bodied invertebrates, myriad intermediate predators may exert top-down control. Though studies evaluating predator control of megagrazers are exceedingly rare, the prominence of megaherbivores in tropical and subtropical Australian seagrass ecosystems means that large-bodied sharks may be, or may have been, disproportionately important to structuring these ecosystems. For example, the loss of large sharks is hypothesized to be important in allowing the release of sea turtles in several seagrass ecosystems that has resulted in considerable declines in seagrass biomass (e.g. Heithaus et al. 2014) and potential ecosystem collapse (Christianen et al. 2014). Conversely, endothermic intermediate predators like dolphins and pinnipeds may be more important to structuring temperate seagrass ecosystems.

16.2.4 The Role of Food Web Structure

To understand the role of top down control, particularly trophic cascades, it is helpful to be able to predict when and where such cascades are most likely to occur. Ecological theory predicts that food web structure, specifically food web length and complexity, will have important effects on the strength and nature of such top down control. In very simple food webs, the number of links between apex predators and primary producers has implications for whether herbivore control on primary producers is strong or weak. Chains with an odd number of linkages should yield weak herbivore control on primary producers and a facultative relationship between apex predators and primary producers through a trophic cascade. Conversely, chains with an even number of levels should yield strong herbivore control of primary producers and an inhibitive effect of apex predators on primary producers as those larger predators regulate intermediate predators, which in turn control herbivores. Assuming that populations are density dependent and limited by food or predation, simple food webs are most sensitive to food chain length because trophic cascades remain strong, having little opportunity to attenuate and diffuse through multiple food web pathways (Strong 1992). Accordingly, ecosystems with simple trophic structure are more likely to suffer from reversals in the "direction" of trophic cascade effects and concomitant changes in the strength of herbivore control on plants if the initiator species (a predator) is removed.

While food chain length influences the net direction of the effect apex predators and herbivores will have on primary producers, food web complexity can often influence how strong those effects can be. This is because the strength of trophic cascades is dependent on the strength of species-species interactions—and the simple construction of food chains leads them to be more likely to have strong species interactions than complex food webs. In simple linear food webs (i.e. food chains), the interaction strengths between predators, herbivores, and resource species is necessarily strong, because consumptive relationships are "unified" (*sensu* Strong 1992) into single species-species interactions (Fig. 16.4). Complex food webs, however, have multiple trophic or interaction pathways from apex predators to primary producers, and these pathways may not have the same number of links. This can diffuse predator effects through many avenues, resulting in fewer of the strong species-species interactions that are typical of linear food webs and attenuating the overall indirect effects of a predator on primary producers (Fig. 16.4). While species diversity increases food web complexity, generalists and omnivores also do so by consuming organisms from multiple trophic levels, creating additional pathways through which predator control can operate. For example, if herbivores are generalists, their negative effects on primary producers may be attenuated through their indiscriminate consumption of resource species, reducing the strength of competitive interactions among seagrasses or between seagrass and epiphytic or benthic algae.

Though increased food web complexity likely reduces the probability of strong species-species interactions (and by extension, strong trophic cascades), they can still occur. But what makes a strong interaction between species? In general, strong interactors are species that are "efficient" (Strong 1992); they may consume more prey per capita, or have strong non-consumptive effects. Most seagrass food webs display some trophic complexity and tend to have multiple trophic channels from apex predators to primary producers—but they can also be dominated by channels with strong interactions that remain undiffused, increasing the likelihood of trophic cascades. This is exemplified in tropical seagrass ecosystems dominated by megagrazers like adult and large juvenile green turtles and dugongs that are almost exclusively at risk from tiger sharks (e.g. Heithaus et al. 2008b; Heithaus 2013; Wirsing et al. 2007a, b, c). The loss of this top predator could not be compensated for by increased predation rates or predation risk from another predator. Megagrazers, in turn, tend to have strong per-capita effects on seagrasses and are thus strong interactors with these primary producers (i.e. Figs. 16.3, 16.4). When this short, three-link chain is the dominant trophic pathway, seagrass ecosystems

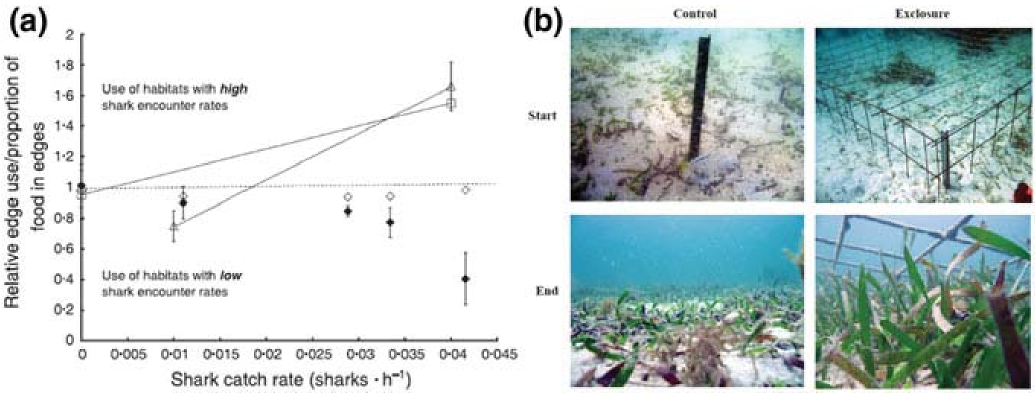

Fig. 16.3 **a** Change in habitat use of dugongs (open triangles), indo-pacific bottlenose dolphins (open squares), and pied cormorants (closed diamonds) associated with changes in abundance of large sharks in Shark Bay, Western Australia. Open diamonds represent the food supply of cormorants. The dashed line represents expected proportion of habitat use if fauna are ideally distributed in relation to their food supply; values above the line represent over-use of seagrass edge habitats, where the chance of tiger shark encounters is highest. Dugongs and dolphins move into edges of seagrass banks when sharks are abundant, choosing to increase predator encounter frequency in exchange for a higher probability of escape to deep water. Cormorants, the escape success of which is independent of benthic terrain, seek to minimize predator encounters and increase use of seagrass meadow interiors when sharks are abundant. This interesting finding illustrates the complex and sometimes counterintuitive nature of predator prey interactions in seagrass ecosystems, and the need to consider properties of predators, prey, and landscape in predicting the effects of antipredator behavior. **b** Megagrazer exclosure experiments in seagrass edges confirm that habitat use patterns of megaherbivores translate to increased top-down control of seagrass edge habitats, signifying a behaviorally mediated trophic cascade from tiger sharks to the seagrass community. Reproduced from Heithaus et al. (2009) and Burkholder et al. (2013)

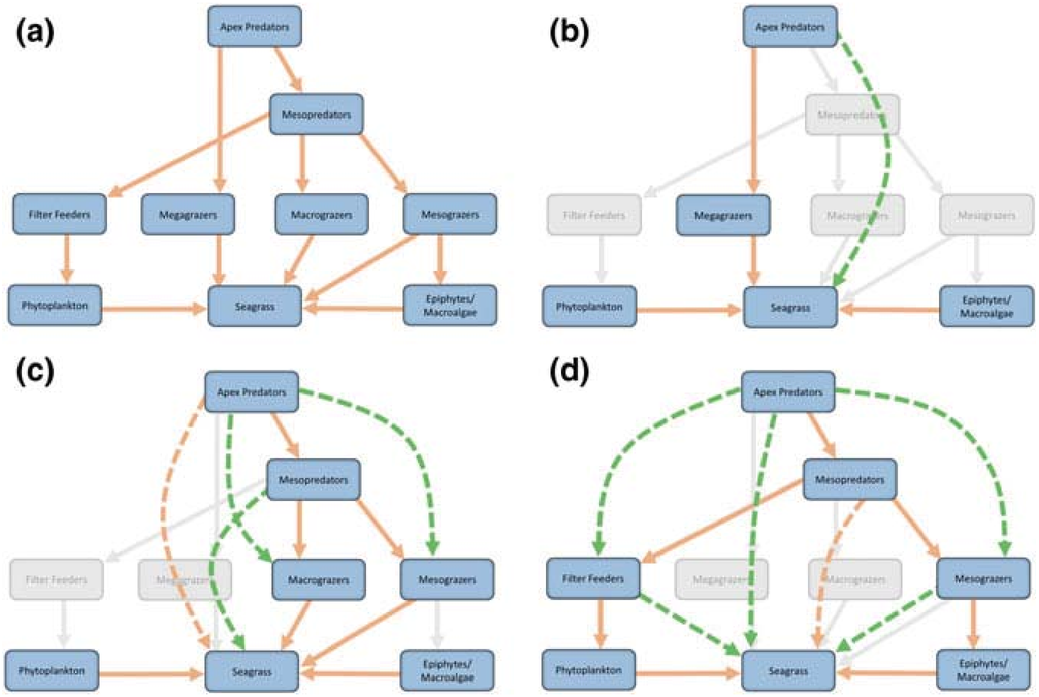

Fig. 16.4 Conceptual food webs illustrating the main direct and indirect pathways through which top-down control operates in seagrass ecosystems. Arrow direction indicates the primary flow of the interaction, while colors indicate positive (green) or negative (orange) effects of one group on another. Solid lines indicate direct effects; dashed lines indicate indirect effects (primarily trophic cascades). Greyed out boxes and lines indicate minor consumers and pathways, depending on the example. An intact seagrass community (**a**) showing direct effects only; the potential for trophic cascades and strong indirect effects depends on which pathways dominate through the strongest interactors. When the megagrazer pathway is dominant (**b**), apex predators can generate trophic cascades that benefit seagrasses by reducing grazing by megagrazers. This pathway has been lost from many tropical and subtropical seagrass ecosystems due to overharvest of these grazers, though it's likely to still dominate throughout much of tropical and subtropical Australia. When smaller seagrass herbivores are the dominant interactors (**c**), mesopredators may initiate a three step trophic cascade that reduces grazing, while mesopredator control by apex predators may initiate a four step cascade that releases grazers and strengthens consumer control of seagrasses. In some ecosystems, mutualistic relationships dominate (**d**), led not only by mesograzers that consume competitive epiphytes and macroalgae, but also by suspension feeders which remove phytoplankton, increasing light penetration to seagrass tissues. Note that indirect interactions tend to be positive when traveling down an odd number of steps, but negative at even numbers of steps

are prone to strong trophic cascades—and by extension, highly vulnerable to predator removal. Consequently, the loss of apex predators like large sharks in these ecosystems may have disproportionate effects on the primary producers of Australian seagrass ecosystems (e.g. Burkholder et al. 2013; Heithaus et al. 2014) (Fig. 16.5).

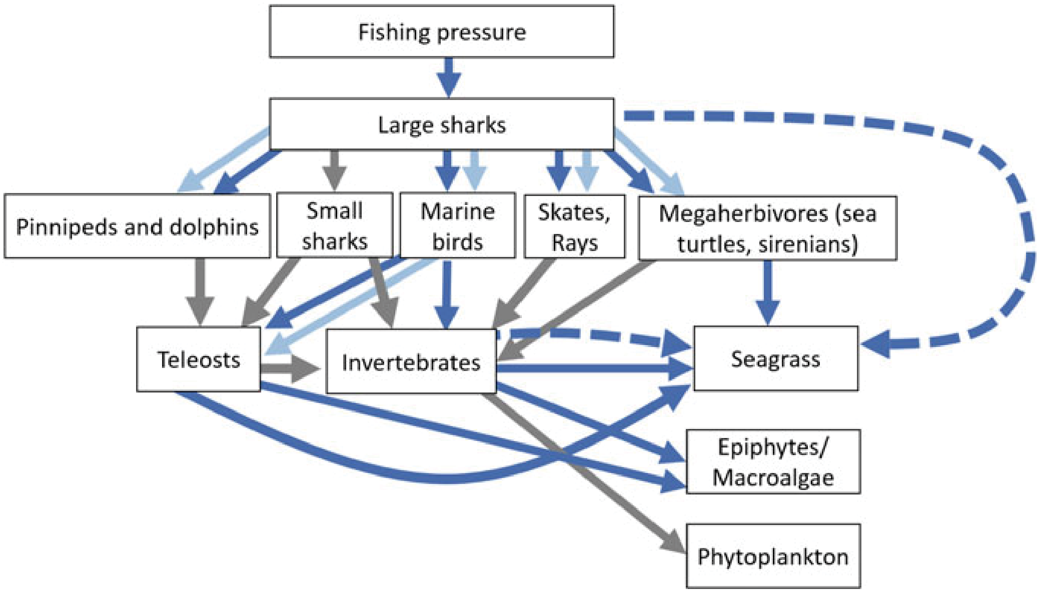

Fig. 16.5 Interaction web highlighting potential connections between large shark removal and lower trophic levels. Individual linkages are denoted by colored arrows; dark arrows indicate consumptive effects while light arrows indicate behavioral effects; dotted lines indicate indirect effects. Only relationships between groups that have been attempted to be quantified have been shown. Interactions which have been observed in Australian seagrass ecosystems are shaded blue. Note a lack of studies on interactions of Australian seagrass-associated teleosts and invertebrates, as well as a general lack of empirical, quantitative estimates of indirect effects, which may be common given the large number of species interactions that typify apex predators. Modified from Ferretti et al. (2010)

16.3 Effects of Consumers on Seagrass Communities

Consumers can structure seagrass communities through consumption or facilitation of primary producers, alteration of community composition, or through influencing bottom-up processes. These forms of top-down control, by altering the properties of seagrass habitats, can drive seagrass ecosystem processes, functions and services at local, regional, and global scales.

16.3.1 Ability of Consumers to Facilitate Seagrasses

Seagrasses provide substrate for epiphytes, which compete with them for resources such as light. High nutrients often increase epiphyte and phytoplankton loads with negative impacts for seagrasses; indeed, eutrophication is one of humanity's most pervasive stressors to seagrass ecosystems (Waycott et al. 2009). By consuming epiphytes and plankton, mesograzers and suspension feeders have the capacity to attenuate the negative effects of eutrophication in seagrass ecosystems (Peterson and Heck 2001; Valentine and Duffy 2006). The role of facultative mesograzers has been particularly well supported with empirical data—historically in the laboratory and mesocosms, but increasingly in the field. Early caging work in Western Australian *Posidonia sinuosa* beds showed that gastropods reduce epiphyte biomass by almost 50%, while amphipods have minimal effects on epiphyte biomass (Jernakoff and Nielsen 1997). Novel cage-free approaches, using slow-release pesticides, have made manipulating invertebrate densities in benthic marine ecosystems easier without introducing caging artifacts (Poore et al. 2009). These experiments, several of which have been conducted in Australian seagrass ecosystems, confirm the importance of invertebrate mesograzers to epiphyte control. For example, exclusion of amphipod mesograzers from seagrass meadows in Cockburn sound,, Western Australia, resulted in significant increases in epiphyte biomass in some seagrass species, though this did not translate to increases in seagrass biomass over the experiment duration (7 weeks) (Cook et al. 2011). Similar cage-less experiments in the *Posidonia angustifolia* beds of Lady Bay, South Australia that manipulated mesograzer densities and nutrient levels showed that such grazers are able to compensate for increased nutrient additions by increasing their per-capita consumption of seagrass epiphytes (McSkimming et al. 2015), mirroring findings elsewhere (i.e. Chesapeake Bay, USA, Reynolds et al. 2014). Indeed, in general, mesograzer presence reduces epiphyte loads approximately as much as nutrient enrichment in the water column increases them: effect sizes are often similar in magnitude but opposite in effect (Hughes et al. 2004; Heck and Valentine 2006).

Mesograzers, and to a lesser degree filter feeders, have received the most attention for their ability to mitigate nutrient enrichment effects, but other consumers are able to do so as well. Larger herbivores, even if they do not target epiphytes, can also be strong controllers of epiphyte biomass in the face of eutrophication (Heck et al. 2000; Goecker et al. 2005; Brodeur et al. 2015; Reynolds et al. 2014). For example, clipping experiments mimicking green turtle grazing in beds of *Halodule uninervis* off of the Derawan Island, Indonesia, almost doubled seagrass production in the face of increased nutrient loads, and may be an important mechanism for exporting excess nutrients from the system, thereby limiting epiphyte overgrowth (Christianen et al. 2012). This top-down facilitation may act as a critical source of resilience for seagrass communities—particularly those near urban centers. Some have even suggested that eutrophication impacts are so large in modern seagrass ecosystems because consumer populations have been largely compromised (Burkepile and Hay 2006; Heck and Valentine 2007). Indeed, factorial experiments in Chesapeake Bay, USA indicated that nutrient additions had minor effects on seagrass productivity when in the presence of grazers, but that grazer exclusion resulted in a sixfold increase in epiphyte biomass and a 65% decrease in seagrass biomass (Reynolds et al. 2014). Perhaps most importantly, these two factors interacted significantly; in the presence of grazers, nutrient additions increased seagrass biomass, while in the absence of grazers, additions reduced biomass (Reynolds et al. 2014). As a result, maintenance of grazer populations has been suggested as a possible tool to combat the negative effects of eutrophication (e.g. Hughes et al. 2004; Reynolds et al. 2014). This suggests that successful seagrass restoration in eutrophic ecosystems will require a combined effort to reduce nutrient loads and maintain healthy populations of epiphyte herbivores (Reynolds et al. 2014). Such facilitation, however, probably has limits (Ghedini et al. 2015); for example, in rocky shore communities of the northwest Atlantic Ocean and Baltic Sea, increased nutrient loads reduce the ability of herbivores to control filamentous algae (Worm and Lotze 2006). Further work is needed to determine when mesograzers are able to control eutrophication derived epiphyte overgrowth, and under what conditions such control results in measureable benefits to seagrass (Cook et al. 2011), as the effects of epiphyte reduction may attenuate at the seagrass-epiphyte interface, and because mesograzers can also have substantial negative effects on seagrass production (e.g. Lewis and Anderson 2012). Lastly, grazers may also facilitate particular seagrass species by removing non-epiphyte competitors such as macroalgae or other seagrasses (see Sect. 3.3, below).

In addition to stimulating seagrass production by inducing compensatory responses to low levels of direct herbivory and through removing competitive epiphytes, consumers can exert top down control by facilitating seagrass reproduction or seed dispersal. Though many organisms are destructive seed predators of seagrass ecosystems, highly mobile seed consumers can also facilitate dispersal and sexual reproduction (Sumoski and Orth 2012). Herbivores may even act as pollinators, as is thought to occur with crustacean and polychaete mesograzers in *Thalassia testudinum* beds (van Tussenbroek et al. 2012). Finally, through active seed dispersal, consumers have the ability to increase genetic connectivity between seagrass communities or promote colonization up currents—something that can be difficult to achieve with passive dispersal alone.

16.3.2 Ability of Consumers to Damage Seagrasses

While top down control can facilitate seagrasses, work over the past few decade has highlighted the detrimental potential of direct seagrass herbivory. Seagrasses generally display a nonlinear response to grazing; low and moderate grazing can stimulate growth and production up to a threshold, while some seagrasses simply resist or tolerate low grazing intensity; however, intense grazing can cross this threshold and jeopardize seagrass persistence (Valentine et al. 1997; Cebrián et al. 1998; Vergés et al. 2008). Concentrated grazing pressure which inhibits seagrass ecosystem function is known as overgrazing (sensu Eklöf et al. 2008). Overgrazing is most common when herbivore densities peak or where herbivore feeding tactics are particularly destructive. These events, though generally rare and usually temporally restricted, can generate strong and lasting detrimental effects on seagrass ecosystems—in extreme cases, even resulting in a complete ecosystem change (see examples in Eklöf et al. 2008). All three main herbivore groups that consume seagrasses (mesograzers, macrograzers, and megagrazers) are capable of overgrazing them (e.g. Nakaoka 2002, 2005; Holzer et al. 2011; Lewis and Anderson 2012; Preen 1995; Eklöf et al. 2008).

In addition to consuming seagrass photosynthetic tissue, herbivores can also impact seagrass communities by reducing seagrass reproductive success. Mesograzers and macrograzers feed on seagrass reproductive tissues such as inflorescences, seeds, and fruits, either directly off of the plant or from the sediment surface (e.g. Wassenberg 1990; Holbrook et al. 2000; Orth et al. 2006b; Vergés et al. 2006; Reynolds et al. 2012). Some species like *Thallasia testudinum* and *Halodule wrightii* appear to be pollen limited—so herbivores may be important in limiting reproduction in these species if consumption rates of male flowers are high (van Tussenbroek and Muhlia-Montero 2012). In some cases, consumptions of flowers, fruits and seeds can result in large reductions in seed populations and thus reproduction via seeds. For example, tanaied crustaceans consume 14–27% of the seeds of *Zostera marina* and *Z. caulescens* in Japanese seagrass beds (Nakaoka 2002), while crustacean seed predators in southern California, USA, consume infloresences and up to half of *Phyllospadix torreyi* seeds (Holbrook et al. 2000). Similarly, in seagrass beds off of Rottnest Island, Western Australia, crustacean seed predators can remove more than half of tethered *Posidonia australis* seeds in a single day (Orth et al. 2006b).

Finally, negative top-down control of seagrasses can occur through non-consumptive means. By using seagrass as shelter, some animals cause damage to seagrass shoots with surprising frequency (e.g. van Tussenbroek and Brearley 1998; Brearley et al. 2008). For example, in a Mexcian Carribbean lagoon, the isopod *Limnoria simulate* burrows into the leaf sheathes of *Thallasia testudinum*, where it reproduces; average infestation rates can approach 50% and cut leaf growth by 30% when infestation rates on an individual ramet are high (van Tussenbroek and Brearley 1998). Instead of burrowing into seagrasses, other invertebrate consumers use seagrass as substrate, inhibiting light penetration to seagrass tissues and reducing growth (e.g. Long and Grosholz 2015). Through excavation of sediment and disturbance of seagrass rhizomes, stingrays can damage, destroy, or inhibit the expansion of seagrass beds while foraging for bivalves (e.g. Orth 1975). These examples illustrate the diversity of non-consumptive avenues through which top down control can inhibit the growth, expansion or persistence of seagrass ecosystems. However, further work is needed to evaluate the capability for such forces to structure seagrass communities relative to consumptive effects, which are better studied.

16.3.3 Alteration of Seagrass Community Composition

In general, the impacts of top down control on seagrasses are not uniform in communities with multiple seagrass species and may result in shifts in community composition and standing biomass. Such impacts are most pronounced in diverse seagrass communities of the subtropics. As previously mentioned, herds of dugongs in subtropical Moreton Bay, Queensland, focus their feeding on mixed species seagrass beds, primarily excavating the nutrient rich tropical seagrass *Halophila ovalis* but incidentally removing the climax species *Zostera muelleri*. Dugongs facilitate *H. ovalis* beds, which are able to recover quickly from grazing. Conversely, grazing prevents the expansion of *Z. muelleri*, which is disturbance-intolerant. Indeed, dugong exclusion over six months resulted in a five-fold increase in the shoot density *Z. muelleri* and a six-fold decrease in the pioneer species *H. ovalis*, while simulated dugong grazing increased shoot densities of *H. ovalis* at a rate five times faster than for *Z. muelleri.* Such feeding behavior can keep seagrass ecosystems in early successional, pioneer states dominated by fast growing, disturbance tolerant species (Preen 1995; Aragones and Marsh 2000).

Green turtles can also shift the species composition of seagrass communities.. In India's Lakshadweep Archipelago, grazing by high densities of green turtles exceeded production of the dominant seagrass species *Thalassia hemprichii* and *Cymodocea rotundata*, and resulted in reduced shoot elongation rates and a community shift from the preferred climax seagrass *Thalassia hemprichii* to a pioneer species *Cymodocea rotundata* (Kelkar et al. 2013). Similarly, a 600-day megagrazer exclusion experiment in seagrass habitats in Shark Bay, Western Australia, resulted in an eightfold decrease in shoot density of the pioneer seagrass *Halodule uninervis* and a concurrent doubling in shoot density of the larger seagrass *Cymodocea angustata* (Burkholder et al. 2013). These cages excluded megagrazers only, reaffirming the strong effects these consumers can have on seagrass community composition and reinforcing their probable general importance to top down control of Australian tropical and subtropical seagrass ecosystems. Teleost grazers can also drive shifts in seagrass community composition; reef fish in south Florida (USA) preferentially consume the pioneer species *Halodule wrightii*, facilitating the dominance of the climax seagrass *Thalassia testudinum* (Armitage and Fourqurean 2006). In each of these cases, knowledge of seagrass life history traits, consumer feeding preferences, and grazing tactics are critical to determining which seagrass species dominate. Since pioneer seagrasses cannot generally match the ecosystem functions of climax species, these shifts in community composition can translate to important changes in the functions of seagrass beds.

16.3.4 Effects of Consumers on Ecosystem Function

As ecosystem engineers, seagrasses serve myriad ecological functions. Seagrasses influence processes such as nutrient cycling, sediment stabilization, and carbon storage (Orth et al. 2006a, b; Fourqurean et al. 2012; McLeod et al. 2011). Seagrasses also act as important habitat and nurseries for fauna (Heck et al. 2003). Many of these functions are much more pronounced in climax seagrasses than smaller, ephemeral species. The effects of top-down control on ecosystem function is dependent on the type and intensity of seagrass herbivory that occurs. For example, moderate levels of grazing by sea urchins grazing can stimulate nutrient recycling, while higher levels of grazing can remove seagrass beds almost entirely (e.g. Eklöf et al. 2008). In seagrass ecosystems in the Gulf of Mexico, sea urchins (*Lytechinus variegatus*) alter the above-ground biomass, shoot architecture, and seagrass density so much through their grazing that they appear to reduce the refuge capabilities of the seagrass beds and facilitate their own predators (Heck and Valentine 1995). Similarly, overgrazing by unusually high densities of *L. variegatus* in Florida Bay, USA resulted in losses of >80% of seagrass biomass over more than 80 ha, altering sediment structure and promoting resuspension of fine sediments (Rose et al. 1999). Such functional alterations can increase light attenuation, reduce the resilience of seagrass beds and promote shifts to alternate, seagrass depauperate states (Orth et al. 2006a, b; Van der Heide et al. 2007, 2011). The associated loss of function from overgrazing can not only affect seagrass habitats, but also nearby habitats which depend on the ecosystem services seagrass ecosystems provide. In fact, loss of seagrass ecosystem function has implications on local to global scales. For example, seagrass loss can affect local faunal communities within and beneath seagrass beds (Heck et al. 2003; Rose et al. 1999; Thompson et al. 2014; Nowicki unpublished data), but also alters the amount of carbon sequestered in seagrass tissues and stored in sediments, influencing the role of seagrass ecosystems in the global carbon cycle (Fourqurean et al. 2012). Even apex predators can influence seagrass ecosystem function, through the trophic cascades they generate. Indeed, seagrass loss through overgrazing and extreme bioturbation have been linked (at least partially) to predator removal in these ecosystems, with implications for carbon sequestration and other functions (Heithaus et al. 2014; Atwood et al. 2015).

16.3.5 Effects of Consumers on Bottom up Processes

The previous example shows how top-down control can alter seagrass ecosystem function indirectly by altering bottom-up processes like sediment stabilization. However, consumers can also alter bottom-up processes directly—a form of top-down control rarely emphasized. Seagrass-associated fauna can do this by acting as nutrient subsidies, altering environmental variables, or changing chemical properties of seagrass ecosystems. For example, avian predators that hunt far from seagrass beds but rest above or adjacent to them can generate nutrient subsidies by transporting nutrient rich guano and concentrating into these habitats, stimulating seagrass productivity and changing seagrass community composition (Powell et al. 1991; Fourqurean et al. 1995). Similarly, the defecation and excretion of fish that seek shelter on coral reefs also provide a nutrient subsidy to nearby seagrass meadows (Dewsbury and Fourqurean 2010; Allgeier et al 2013). On a larger scale, sea lions (*Neophoca cinerea*) and fur seals (*Arctocephalus* spp.) native to temperate Australian waters deposit nutrients near their haul out sites through excretion. In Seal Bay Conservation Park, Kangaroo Island, South Australia, such defecation by the resident population of ~1100 sea lions contributes approximately 3800 kg of nitrogen to the surrounding ecosystem annually (Lavery et al. 2015). This represents a considerable allochthonous source of nutrients which links pelagic productivity to coastal ecosystems, and is likely to be important to the structuring of seagrass ecosystems near pinniped colonies. Sharks may also play a role as nutrient transporters not only by coupling seagrass ecosystems with offshore pelagic ecosystems, but also by linking distant coastal ecosystems. For example, tiger sharks (*Galeocerdo cuvier*) in Australia regularly move hundreds to thousands of kilometers, spending time in both coastal and pelagic zones (Heithaus et al. 2007; Holmes et al. 2014; Ferreira et al. 2015). It should be noted that consumers can, of course, also transport nutrients out of seagrass ecosystems and that the effects of top-down alterations to nutrient cycling ultimately depends on the underlying nutrient characteristics of the surrounding environment. For example, large nutrient subsidies from a local seal colony are likely to exacerbate the effects of nutrient pollution from nearby anthropogenic sources, while consumer driven nutrient export in oligotrophic seagrass ecosystems may intensify nutrient limitation in these habitats, and vice versa.

Consumers can increase nutrient availability to seagrass ecosystems even if they themselves are immobile. For example, sponges can also alter bottom-up processes by processing nutrients in the water column, increasing their bio-availability to seagrasses (Archer et al. 2015). Similarly, bivalves concentrate nutrients in seagrass beds by consuming pelagic plankton and excreting their waste under the canopy (Peterson and Heck 2001). In addition to concentrating nutrients in seagrass beds, bivalves alter bottom-up processes in seagrass beds by altering the chemical and physical environment. Sulfur-oxidizing bivalve-bacteria symbionts are associated with most seagrass species and have been shown to increase seagrass biomass production in the face of sulfide additions (van der Heide et al. 2012). This mutualism is important, because marine sediments are generally anoxic and seagrasses expend large amounts of energy to pump oxygen gained from photosynthesis into below-ground tissues to create an “oxic microshield,” which protect below-ground tissues from chemically reduced toxins (Borum et al. 2007). This need for protective oxygen drives the high light requirements of seagrasses and makes them highly sensitive to disturbance—particularly to reductions in water quality (Borum et al. 2012). Interestingly, a trophic cascade influencing this process have been recorded whereby preferential consumption of the filter feeding bivalve *Dosinia isocardia* by the Red Knot (*Calidris canutus*) reduces competition for particulate organic matter (POM) with a second bivalve *Loripes lucinalis. L. lucinalis* derives energy from both filter feeding and through chemosynthetic bacterial symbionts. Predation on *D. isocardia* may reduce competition for POM and allow *L. lucinalis* to de-emphasize chemosynthetic pathways of energy production, which may result in higher concentrations of toxic porewater sulfide (Van Gils et al. 2012). As can be seen, top-down control through the manipulation of bottom-up processes can be important in structuring the chemical, nutrient, and physical environment in which seagrasses live, with implications for the persistence of seagrass ecosystems.

16.4 Top Down Control and Human Impacts

Humans are altering ecosystems worldwide, and seagrass ecosystems are no exception. All told, there are five major threats to marine biodiversity, all of which occur in seagrass ecosystems: overexploitation, physical habitat modification, sediment and nutrient pollution, invasive species, and climate change (Norse 1993; Waycott et al. 2009). Herbivores can either attenuate or amplify the effects of anthropogenic disturbance, and indirect effects that predators generate can further complicate these relationships. Yet it remains critical to understand how top down control both affects and is affected by human alterations to seagrass ecosystems. We focus here on four of the most pervasive threats to seagrass ecosystems and how they are likely to interact with patterns of top-down control: nutrient pollution, overfishing of marine consumers, invasive species, and climate change.

16.4.1 *Nutrient Pollution and Top Down Control*

While top-down control can attenuate the effects of eutrophication on seagrass ecosystems, nutrient pollution can also influence the strength of top-down control by altering energy distribution in the food web, herbivore feeding patterns, and predator prey dynamics. Eutrophication can increase the strength of top down control either by increasing the actual amount of herbivores or herbivory in seagrass ecosystems, or by reducing the tolerance of seagrasses to such herbivory. For example, as phytoplankton and epiphyte loads increase in response to eutrophication, consumer food supply grows—increasing secondary production in seagrass meadows and energy availability to higher trophic levels. This can lead to increased top down control by herbivores (e.g. Moksnes et al. 2008), which is particularly likely when mesograzers dominate, because their generally short life histories allow for rapid population responses to increased primary production and a potential outpacing of predator control. Because mesograzers and filter feeders generally have a facultative relationship with seagrasses and are capable of consuming large amounts of phytoplankton or epiphytic biomass (e.g. Whalen et al. 2013), this increase in top down control is likely largely facultative. However, in systems where mutualistic mesograzers are rare and most herbivory occurs through larger grazers, eutrophication may still strengthen top down control of these systems even when changes to herbivore population and grazing intensity are minimal. This is because the increased epiphyte loads that generally accompany nutrient pollution increase stress to seagrasses and may reduce their tolerance to direct herbivory. Additionally, increases in secondary production may strengthen non-consumptive predator effects in systems with risk-averse prey and result in less herbivore pressure, as prey in a high energy state are more likely to respond to predation risk (Heithaus et al. 2007). Finally, eutrophication can alter top down control by altering nutrient content or palatability of seagrass and epiphytes. This in turn can influence where, what, and how much herbivores consume.

16.4.2 Overexploitation of Consumers

The most visible effect humanity has on top down control in seagrass ecosystems is actually through removing "the top" of seagrass food webs. Over the past few hundred years, both predators and herbivores have been lost from many coastal ecosystems (Jackson 2001; McCauley et al. 2015). These depletions, which usually target large-bodied consumers like green turtles, sirenians, and large sharks, can eventually lead to depletion of smaller, lower trophic level consumers as old stocks collapse and new target species are harvested (i.e. Pauly et al. 1998). Both depletion of herbivores and predators have important implications for the structure and function of seagrass ecosystems.

Green turtles (*Chelonia mydas*) and dugongs *(Dugong dugon*) have both been subjected to substantial anthropogenic impacts throughout much of their ranges and population sizes are unlikely to approach what they were historically. Industrialized overfishing has also resulted in global population collapse of apex marine predators like large teleosts and sharks, which are disproportionately vulnerable to fishing (Jackson et al. 2001; Myers and Worm 2003; Ferretti et al. 2010). This is of particular concern because of the potential for irreversible losses of apex predator species, as has occurred in earth's terrestrial biomes. The loss of predators large and small alters food web dynamics and can affect herbivore guilds from large bodied megagrazers (Heithaus et al. 2008b, 2014) to amphipod mesograzers (Moksnes et al. 2008) and may alter not only patterns of predation but also reduce important risk effects (e.g. Madin et al. 2016). Shifts in the food web, including species diversity, can also generate or influence trophic cascades that change the strength and direction of top-down control of coastal ecosystems (Jackson 2001; Duffy et al. 2005), leading to overgrazing, increased bioturbation, or plant loss with implications for ecosystem functioning (Atwood et al. 2015). For example, some argue that the ability of mesograzers to facilitate seagrass persistence by consuming harmful epiphytes may been weakened through the loss of apex marine predators, as mesopredators are released from predation and exert further pressure on epiphyte consumers (Williams and Heck 2001), though a trophic cascade may not occur if the mesopredators themselves are omnivores (Heck et al. 2000). Current predator removal studies generally focus on the effects of one or two species interactions, though removal of predators often has cascading effects through multiple pathways simultaneously (Fig. 16.6).

The worldwide plight of shark populations has received considerable attention recently, with population declines estimated to exceed 80–90% in numerous locations (e.g. Baum et al. 2003; Myers et al. 2007; Dulvy et al. 2014; Worm et al. 2013). Although less appreciated, many populations of rays also are threatened (Dulvy et al. 2014), and the potential for rays to generate trophic cascades down the

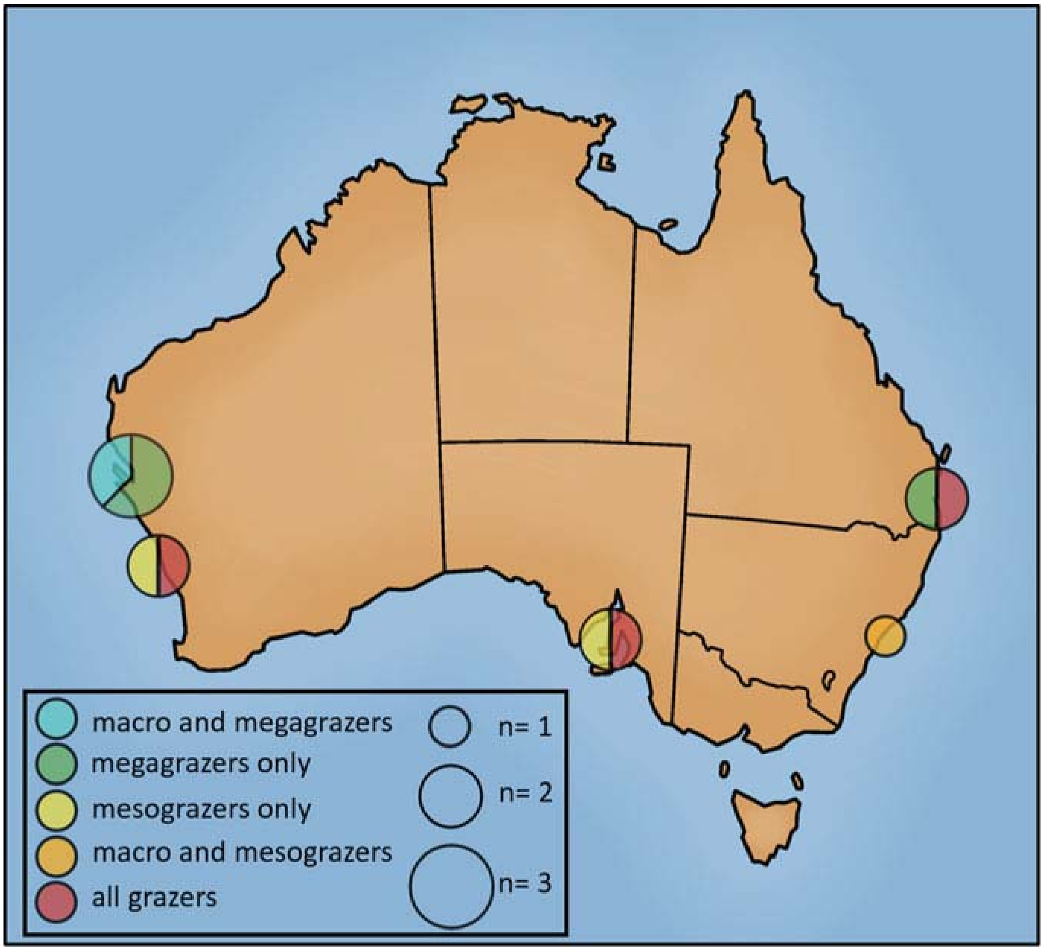

Fig. 16.6 Map indicating sites of herbivore exclosure field experiments in Australian seagrass ecosystems (Total = 10, n indicates number of studies, some of which include multiple experiments). Studies in yellow achieved herbivore exclusion through in situ chemical pesticide deployments; other studies utilized physical cages; Ebrahim et al. (2014) utilized both. Note a complete lack of exclosure studies in tropical Australian ecosystems. Red studies: Jernakoff and Nielsen (1997), Keuskamp (2004), Ebrahim et al. (2014); orange: Garthwin et al. (2014); yellow: Cook et al. (2011), McSkimming et al. (2015); green: Preen (1995), Masini et al. (2001), Burkholder et al. (2013); teal: Bessey et al. (2016). Note that Ebrahim et al. (2014) performed multiple experiments that varied in level of exclusion, from megaherbivore exclusion only to total herbivore exclusion

filter feeder pathway remains untested. These declines in elasmobranch populations have the potential to modify seagrass ecosystems through multiple mechanisms. Surprisingly, despite the ubiquity of marine apex predator declines and the potential for important consequences to these declines, few studies of the effects of such declines in seagrass ecosystems exist (however see Heithaus et al. 2012 and references therein).

16.4.3 Invasive Species

Seagrasses themselves can be invasive species, though records of this occurring are rare. Successful introductions are exemplified by the recent expansions of two small-bodied, fast-growing seagrasses: *Zostera japonica* along the eastern Pacific Ocean (Mach et al 2014) and *Halophila stipulacea* in the Caribbean Sea (Willette et al 2014). Both of these species have weed-like life history characteristics, including high rates of sexual reproduction and seed set and rapid growth rates that predispose them to be successful invaders. While the documentation of invasive populations of seagrasses into the eastern Pacific and Caribbean is recent, it may be that humans have been spreading palatable, weedy seagrasses around the globe for centuries. Phillips and Menez (1988) have suggested that the weedy, fast-growing species *Halophila decipiens*, widely distributed in harbours across the tropical parts of the Atlantic, Pacific and Indian Oceans as well as some extra-topical locales such as Sydney Harbour, could have been spread by shipping activity. Similarly, *Halophila stipulacea*, originally native to the Red Sea and western Indian Ocean, is proposed to have spread to the Mediterranean sea over a century ago with the opening of the Suez canal before spreading to the Caribbean (Lipkin 1975; Willette et al. 2014). As fast-growing seagrasses are preferred as food over more slow-growing ones, and since the species that natural occur in the regions being colonized by these invaders have slower growth, top-down control by seagrass herbivores may prove to be important in regulating the biomass of these invaders.

Most invasive species in seagrass ecosystems are not seagrass, but algae and fauna (Williams 2007). These invasive species usually generate negative effects in the seagrass ecosystems to which they are introduced (Williams 2007). For example, in San Francisco Bay, USA, the invasive amphipod *Amphithoe valida* consumes *Zostrea. marina* tissues directly in its invaded range (Northeastern Pacific), but rarely consumes *Z. marina* in its native range (the north-west Atlantic) (Reynolds et al. 2012). Additionally, teleost predators in *A. valida*'s invaded range are less effective at controlling its population than predators in its natural range (Carr and Boyer 2014). This highlights not only the importance of understanding herbivore feeding preferences, but also the difficulty in using the ecology of invasive species in their native ranges to predict their effects in their invaded ranges.

Invasive species are likely to become more common in seagrass ecosystems with time, as widespread changes in species distributions occur through both traditional human means (i.e. intentional introduction and hitch-hiking on human transport) and through climate change induced range shifts. These range shifts will be largely poleward and may occur gradually (over decades) or rapidly (over months) (Parmesan and Yohe 2003; Fodrie et al. 2010; Last et al. 2011; Poloczanska et al. 2013; Wernberg et al. 2013; Wernberg et al. 2011a, b; Smale and Wernberg 2013; Vergés et al. 2014). Such shifts have the potential to completely re-arrange communities as species migrate at differing rates. The resulting decoupling of some species-species interactions and the formation of novel ones (Walther et al. 2002; Cheung et al. 2009; Kordas et al. 2011) has the potential to alter the strength of top down control in seagrass ecosystems and to destabilize those ecosystems (Vergés et al. 2014). For example, the herbivorous sea urchin *Centrostephanus rodgersii* has shifted poleward along Australia's southeastern coast by more than 600 km in four decades, resulting in its establishment in Tasmanian waters and a concomitant increase in the prevalence of urchin barrens there; exclosure experiments suggest that *C. rodgersii* is responsible for such barrens, and that community diversity at these sites is reduced by $\sim 70\%$ compared to intact kelp beds (Ling 2008). In the subtropical seagrass habitats of the northern Gulf of Mexico, the tropical herbivorous teleost *Nicholsina usta* has increased in abundance almost 25 fold, and is predicted to reduce seagrass cover as warming continues (Heck et al. 2015). Novel associations between herbivores and predators may also alter the direction of effect of top down control. Despite the global scale at which this community mixing is predicted to occur, we have a poor understand of how new species introductions influence seagrass ecosystems, with the effects of most invasive species unassessed (Williams 2007).

The potential for novel species assemblages to completely restructure benthic marine communities is probably not uniform. Seagrasses in temperate ecosystems are likely more vulnerable than those in tropical and subtropical ecosystems to reorganization of the consumer community. This is because of the higher niche diversity of the tropics, which increases the potential for consumers to exploit previously unoccupied niches in temperate systems (Bennett et al. 2015). Furthermore, tropical seagrass ecosystems will experience fewer introductions via range shifts, since temperature induced range shifts are generally poleward. Conversely, temperate seagrass ecosystems may show recalcitrance to range expansions of tropical seagrasses. Indeed, higher latitudes would reduce available light to tropical species, resulting in both reduced growth rates and potentially increased nutrient content and palatability (Fourqurean et al. 2015). In this sense, range shifts may increase the strength of top down control in temperate seagrass habitats, but via different mechanisms for temperate and tropical seagrasses. Australian seagrass ecosystems will be particularly vulnerable to disruptive distribution shifts as Australia is the only continent to have poleward-flowing boundary currents on both coasts, and because its southern coastline occupies only a narrow latitudinal band—meaning changes in ocean temperatures will have very widespread effects on temperate Australian ecosystems (Wernberg et al. 2011b). This poises Australian seagrass ecosystems on the front lines of climate change and provides both a conservation challenge and an opportunity to study how climate change driven species invasions will alter seagrass ecosystems worldwide.

16.4.4 Climate Change

Climate change is probably the single largest avenue through which humans are altering the marine environment. Most effects of climate change are ultimately due to physical forcing of the environment. However, there is increasing evidence that the ecological effects of climate change will be mediated by biotic interactions (Zarnetske et al. 2012). Beyond altering species distributions, climate change will affect the strength of top down control by altering the metabolism, production and consumption rates of organisms, changing stoichiometric ratios of producers, and amplifying climactic extremes, which may reduce the resilience of seagrass ecosystems to herbivory or other means of top-down control. Understanding how these complex interactions will shape seagrass communities is paramount to the management and conservation of these ecosystems in the era of climate change.

As temperature increases, so do the rates of biological processes of ectotherms such as metabolism and consumption (Hillebrand et al. 2009; O'Connor 2009). This ability of temperature to influence metabolic processes and structure ecosystems is the emphasis of the Metabolic Theory of Ecology, or MTE (Brown et al. 2004). Because changes in temperature have the potential to profoundly alter consumption rates, production rates, and the effects consumers have on their ecosystems, MTE has received an explosive surge in attention in the past decade. Since the overwhelming majority of species in seagrass ecosystems are poikilotherms, such changes in temperature can affect entire communities, though different species are likely to react differently. This is because the relationship between metabolic rate and temperature follows a unimodal pattern that peaks at a species-specific thermal optimum, after which physiological stress weakens the relationship, eventually reducing an organism's fitness (Lemoine and Burkepile 2012). Indeed, a central question in MTE is that of metabolic mismatches: what happens when the metabolisms of different organisms scale differently as temperatures rise? Such differential metabolic scaling can have significant ecological consequences for seagrass ecosystems.

The effects of temperature increases on the strength of top-down control will depend largely on how the metabolisms of producers, herbivores, and predators change in relation to one another. For example, if herbivore consumption rates increase faster than primary producer production rates, then top-down control on plant communities is likely to strengthen. Conversely, increases in predator consumption rates or hunting efficiency may increase top-down control on herbivores, releasing resource species from consumption. Furthermore, rates of primary productivity may outstrip the ability of consumers to regulate it, resulting in a weakening of top-down control. Finally, if temperatures surpass the thermal optimum of a species, fitness may suffer, reducing the interaction strength of a consumer with its prey.

Though the topic of differential metabolic scaling in relation to climate change remains fairly young, multiple examples detailing the effects of simulated or real warming on the strength of top-down control in seagrass ecosystems exist. For example, experimental warming of mesocosms containing amphipod grazers and benthic brown algae *Sargassum filipendula* showed that a 4 °C temperature increase resulted in stronger, more negative per-capita interaction strength between the amphipods and algae, indicating stronger consumer control (O'Connor 2009). Similarly, in mesocosms in the Galapagos Islands, green sea urchins (*Lytechinus semituberculatus)* exposed to multi-day warming (28 °C) doubled their oxygen consumption increased their consumption of the green algae *Ulva* sp. by almost

50% compared to urchins kept at cooler temperatures (14 °C) (Carr and Bruno 2013). In South Australia, when the sea urchin *Amblypneustes pallidus* was placed in microcosms mimicking 5 °C of ocean warming and an increase in CO^2 concentrations expected to occur by 2100, urchins increased consumption rates of the Australian endemic seagrass *Amphibolis antarctica* by ~20% (Burnell et al. 2013b). In a predator prey study, experimental warming of a terrestrial old field ecosystem resulted in reduced spatial overlap of spider predators and grasshopper nymph prey, which in turn reduced predator control of herbivores (Barton 2010). In these studies, increases in top-down control were driven primarily by shifts in per-capita effects rather than in consumer densities. This emphasizes the capability of climate change, through physical forcing, to alter the effects of individual consumers on a global scale with potentially significant changes to the strength of top down control at the most basic physiological level.

Climate change may also weaken the potential strength of top-down control by increasing primary productivity. In some cases, this productivity increase can even outpace increased consumption rates of herbivores. For example, experiments in South Australian rocky coastal ecosystems showed that under moderate warming (to 20 °C), the marine gastropod *Turbo undulates* can maintain consumption rates that outpace turf algae production; under conditions predicted by 2100 (24 °C), however, turf algae production outpaced consumption (Mertens et al. 2015). This phenomenon is particularly likely to occur when dominant consumers surpass their thermal optimum and undergo temperature-related physiological stress, reducing their "efficiency" (e.g. Lemoine and Burkepile 2012; Strong 1992), or when grazer control of primary producers is already weak (O'Connor et al. 2009; Eklöf et al. 2012). While compensatory herbivore population growth may dampen runaway productivity effects as consumer populations adjust to reflect the increased food supply, even a temporary loss of consumer control could lead to algal overgrowth of seagrass and increase the likelihood of a regime shift to a seagrass depauperate state, as we will see shortly. Understanding how herbivory, production, predation, and other biological interactions will scale with increases in temperature is critical since seagrass ecosystems are dominated by ectotherms whose metabolism is inherently coupled to ambient temperatures.

While temperature will alter top-down control of consumers, increased CO_2 concentrations are predicted to increase seagrass production, since seagrasses are often light and CO_2-limited (Borum et al. 2015). However, increased production is often paired with reduced proportions of nitrogen and phosphorous in seagrass tissues, reducing their quality as a food source. For example, six-month CO_2 enrichment experiments in South Florida, USA, designed to replicate atmospheric CO_2 concentrations in 2100, increased non-structural carbohydrate content of *Thalassia testudinum* rhizomes by 29% but also reduced nitrogen and phosphorous content of leaves by 11 and 21%, respectively (Campbell and Fourqurean 2013). Differences in stoichiometry may increase herbivore consumption rates to compensate for this lower food quality, or may cause herbivores to avoid lower quality plants and switch to plants of higher food quality (Cruz-Rivera and Hay 2001; Valentine and Heck 2001; Russell and Connell 2007; Hillebrand et al. 2009; Tomas et al. 2011). Changes in temperature and ocean chemistry may also alter plant defensive compounds and secondary metabolites. Since consumer preference is driven by a combination of factors which includes plant defensive compounds (e.g. Steele and Valentine 2015), determining whether (and if so, how) CO_2 concentrations affect plant defenses will also be a key part in understanding the shifting role of herbivores in top-down control. Multi-species CO_2 enrichment experiments should also be undertaken to determine the potential for CO_2 enrichment to majorly alter nutrient concentration hierarchies. These experiments should be paired with simultaneous food choice experiments exploring the potential for this to change consumer preferences or herbivory rates. These investigations would be particularly fruitful for Australia's subtropical ecosystems where species and life history diversity of seagrass is highest.

In addition to range shifts, extreme climactic events can alter seagrass communities and potentially increase the ability of top-down control to generate alternate, seagrass-depauperate ecosystem states. Seagrasses ecosystems are vulnerable to regime shifts, whereby the ecosystem tolerates disturbances to a point before rapidly shifting to an alternate ecosystem state that is often resistant to change. Indeed, environmental stress can increase the vulnerability of seagrass to grazing (e.g. Eklöf et al. 2010), potentially resulting in top-down control exacerbating the effects of disturbances after they occur. Regime shifts, initiated by climactic disturbance and reinforced by herbivore control, have already been recorded in Australian marine ecosystems. On temperate algae reefs in Port Gregory, Western Australia, the loss of the algae canopy associated with a marine heat wave (Pearce and Feng 2013) was reinforced by algivorous teleosts, largely tropical in origin (Bennet et al. 2015). This resulted in shift from an ecosystem state dominated by complex canopy forming algae to one of structurally simple turf algae, which was reinforced by constant herbivory on any remaining kelp (Bennet et al. 2015). Shark Bay's seagrass beds, which were subjected to the same marine heat wave (Thompson et al. 2014; Fraser et al. 2014), may be buffered from similar effects as healthy populations of tiger sharks generate antipredator responses in dugongs, minimizing herbivore control of disturbed seagrass beds (Nowicki et al. unpublished data). Australian seagrass ecosystems are particularly susceptible to these interactive effects of climate disturbance and herbivory because both East and West coasts are home to tropical boundary currents that force tropical waters poleward—and while our oceans are expected to warm globally, these "hotspots" are projected to do so 2–3 times faster than average (Wu et al. 2012; Vergés et al. 2014). Furthermore, these currents are capable of generating rapid and extreme warming events (e.g. Pearce and Feng 2013) such as the aforementioned marine heat wave that struck Western Australia in 2011 and caused widespread ecological changes throughout the coast (Wernberg et al. 2013; Smale and Wernberg 2013; Thompson et al. 2014; Fraser et al. 2014). These examples indicate the potential for climactic disturbance and other anthropogenic stressors to interact to alter the role of top-down control in benthic marine ecosystems and highlight the need for a better understanding of how climate change will interact with anthropogenic stressors at regional and local scales (Wernberg et al. 2011a, b).

As our understanding of individual species relationships under climate change becomes clear, it will be necessary to put them in the context of larger, community scale interaction webs if we are ever to elucidate how top down control will change in our warming oceans. Furthermore, we need to consider the potential for temperature induced metabolism shifts to interact with other ecosystem properties to attenuate or magnify the strength of top-down control, especially since few seagrass ecosystems are subject to isolated anthropogenic impacts. For example, nutrient enrichment of producers can result in increased satiation and decreased per capita grazing sea urchins (Valentine and Heck 2001), suggesting that nutrient enrichment may attenuate some effects of temperature induced increases in consumption rates (Burnell et al. 2013b).

16.5 Conclusions and Future Directions

16.5.1 Progress Since the Last Edition

In the first edition of this volume, published over twenty five years ago, top down control of seagrass ecosystems was given limited attention focusing on the role of grazing by sea turtles and dugongs, and to a lesser degree, teleosts. This emphasis illustrates an important and relatively unique aspect of Australian seagrass ecosystems: many still have ecologically functional populations of megaherbivores and apex predators, particularly in the tropics and subtropics. However, in the past several decades, our view of top-down control in seagrass ecosystems has changed dramatically. Thanks to advances in theory as well as an increasing number of laboratory, mesocosm, and field experiments around the world over the past quarter century, there has been a shift from descriptive studies (Duarte 1999) to a more process oriented approach in seagrass ecology. This shift has led to a much better understanding of how mesograzers, predators, and food web structure interact with each other and with bottom-up factors to structure seagrass ecosystems. We also better understand how human impacts, particularly eutrophication (Hughes et al. 2004) and apex predator removal (Heithaus et al. 2008a, b; Burkholder et al. 2013) are likely to influence seagrass ecosystems. New promising field approaches developed in Australian seagrass habitats, such as cage-less mesograzer exclusions (Poore et al. 2009) and long term multi-trophic level ecosystem research projects (*sensu* Heithaus et al. 2012), have already provided critical insight into top-down control of these seagrass ecosystems and will enable further refinement of our understanding of top down control of seagrass habitats worldwide.

16.5.2 Gaps that Still Remain

Despite the progress made in characterizing top down control in seagrass ecosystems over the last quarter century, many gaps still remain. In particular, the complexity with which top-down control operates in seagrass ecosystems creates new challenges to generalizing top-down control (Valentine and Duffy 2006). We begin with a call to expand the use of manipulative field experiments in Australian seagrass habitats.. This approach is among the most effective in determining how individual or groups of species influence seagrass ecosystems, and when paired with mechanistic studies can provide powerful insight into how top down control operates in these ecosystems. This is particularly true for the dominant and widespread endemic seagrasses in the genera *Posidonia* and *Amphibolis.* Though they are becoming more common, exclosure and enclosure experiments remain under-utilized in testing theory related to top down control, and these experiments remain rare in Australian seagrass habitats when compared to other geographic regions and types of benthic marine ecosystems. For example, out of over 600 herbivore exclusion experiments analyzed by Poore et al. (2012), only 28 studies occurred in seagrass beds, with only 4 of those occurring in Australia (though there have since been others, see Fig. 16.6). All of these studies have occurred in temperate or subtropical seagrass ecosystems. This is probably largely due to the huge logistical challenges associated with completing marine research in these sparsely populated areas. Nonetheless, we believe tropical Australian seagrass ecosystems are understudied and warrant further attention, particularly as seagrass diversity in tropical Australia is high, and our understanding of herbivory in multi-species seagrass beds is still relatively lacking (Lee et al. 2015). Indeed, northern Australia is home to a diverse and expansive tropical seagrass community as well as large populations of macro- and megaherbivores, suggesting herbivory may be an important structuring force in tropical Australian seagrass beds (e.g. Marsh and Lawler 2002; Marsh et al. 2002; Roelofs et al. 2005; André et al. 2005; Sheppard et al. 2008). This is supported by limited evidence from aerial surveys, which indicate that seagrass beds in parts of the Northern Territory and northern Queensland are often heavily scarred from dugong grazing (Roelofs et al. 2005).

As has been emphasized throughout this chapter, understanding herbivore feeding preferences is critical to predicting the nature of top-down control in seagrass ecosystems. A large body of research has investigated relationships between food quality, plant defenses, seagrass structure, and the effects of associated producers, yet these experiments necessarily simplify the number of variables tested due to experimental constraints. We still lack a generalizable mechanistic understanding of how seagrass properties as a whole influence food preferences or consumption rates by herbivores. Instead, we are limited to rough generalizations (such as the previously discussed dichotomy in herbivore feeding preference), which are based on larger patterns from food preference experiments. The relationship between seagrass properties and herbivore feeding behavior is confounded by seagrass properties including palatability (high nutrient, soluble carbohydrate, and lipid content), undesirable traits (defensive phenolic compounds, low nutrient content, and high fiber content), and seagrass structure, which can vary among and within species as well as through space and time. This relationship is further obscured by the variable efficacy of phenolic defenses on different herbivores and the differential perceived value of each of these seagrass properties by different herbivores (e.g. Goecker et al. 2005; Prado and Heck 2011). Because of this it is still difficult to generalize how herbivory influences seagrass community response to anthropogenic stressors like eutrophication and CO_2 enrichment, or how pressures on herbivores (such as predation risk) may alter patterns of top-down control. Given the ubiquity of these stressors and the knowledge that they can interact (e.g. Burnell et al. 2013b), pursuit of a predictive model of how this may occur warrants serious attention. Meta-analyses would be useful to determine how patterns of seagrass nutrient concentration, phenolic compounds, carbohydrate content and other characteristics relate to seagrass consumption rates of different herbivores.

Over the past two decades it has become increasingly apparent that grouping consumers into ecological guilds based on taxonomy or size over-simplifies the diversity of their ecological functions (Duffy et al. 2001, 2003; Valentine and Duffy 2006). This is most true for mesograzers. For example, selective herbivore exclusion experiments in Moreton Bay, Queensland, showed that exclusion of small amphipod mesograzers resulted in a more than doubling of epiphyte biomass while exclusion of larger invertebrate mesograzers resulted in increases in seagrass shoot height, density, and cover (Ebrahim et al. 2014). A similar experiment showed that some mesograzers control epiphyte loads while others do not (Jernakoff and Nielsen 1997). Clearly, these organisms have distinct functional roles in top down control yet are generally grouped simply as "mesograzers." This has been recognized as an oversimplification as ecosystem level impacts are the result of complimentary effects from a diverse range of grazers—not from a single homogenous effect by a uniform herbivore guild (Duffy et al. 2001, 2003; Hughes et al. 2004; Burkepile and Hay 2008; Holzer et al. 2011; Rossini et al. 2014). Yet gaps remain in our understanding of the complimentary roles of sympatric herbivores or the relative strength with which they can exert top-down control (but see Holzer et al. 2011)—often limiting our ability to estimate the net effects of groups of herbivores or herbivores as a whole on seagrass communities. This is an important omission—particularly in regards to differences in interaction strength between major grazer groups and seagrass-because megagrazers, macrograzers and mesograzers are often managed very differently (if at all). Additionally, the effects different grazer groups can generate in seagrass ecosystems can be surprising; for example, herbivores can generate opposite responses in seagrass communities even when they consume the same species of seagrass. Dugongs can facilitate the same seagrass species they target when grazing through destructive and indiscriminant feeding tactics which also remove competitively dominant climax seagrass (Preen 1995). Invertebrate and teleost herbivores, however, are more selective and instead usually suppress the species they target.

Finally, our understanding of how top-down control of seagrass ecosystems will change in the context of human stressors like overfishing and climate change is still in its infancy. Indeed, while there is an increasing focus on how trophic interactions will change as climate change variables continue, few of these studies are in marine ecosystems (Rosenblatt and Schmitz 2014). Furthermore, most of these studies fail to capture the complexity climate change will bring to trophic interactions—often only manipulating two trophic levels and one climate change variable at a time (Rosenblatt and Schmitz 2014). Understanding how climate change, overfishing and other human impacts will alter top down control of seagrass ecosystems will require increasing both the complexity of existing experiments to better understand interactions, and rigorous syntheses of existing experiments to discover general patterns between these factors.

16.5.3 Maximizing Research Potential in Australian Seagrass Habitats

One problem of studying top-down control in coastal ecosystems (including seagrass ecosystems) is that today's seagrass communities have often been fundamentally altered from the conditions under which the ecosystems evolved (Heck and Valentine 2007; Jackson 2001; Dayton et al. 1995). As a result, studies (particularly of predators) in today's seagrass ecosystems probably don't accurately capture the historical importance of top down control. Indeed, while we have a solid understanding of the mechanisms through which trophic cascades can operate, determining the net effects of predator loss on seagrass ecosystems remains difficult because trophic cascades can operate through multiple consumer pathways concurrently (Fig. 16.4) and the relative strength of these pathways remains largely unknown. Many of Australia's seagrass ecosystems, particularly those in the tropical northern and western coasts, remain far from large population centers and provide unique opportunities to study top-down control in relatively pristine seagrass ecosystems. Yet, few of these studies exist. By pursuing the effects of megafauna and apex predators in seagrass ecosystems, focusing on relatively pristine seagrass ecosystems where biodiversity and trophic relationships remain relatively intact, and establishing long-term monitoring projects along the eastern and western coasts where tropical boundary currents will generate "sentinel" ecosystems, in which to study climate change, researchers can leverage the natural capital of Australia's seagrass habitats in ways few other regions can. A better understanding of how predators and megaherbivores structure seagrass ecosystems will become increasingly relevant as populations of megaherbivores like green turtles are restored in regions where they were formally abundant (Heithaus et al. 2014).

The ultimate goal of understanding top down control in seagrass ecosystems is to create a testable framework through which we can make generalizations and predict how top down control will impact those ecosystems. For such a framework to be useful it will have to incorporate theoretical advances as well as a huge compliment of field, laboratory, and observational work to test, validate, and refine it. It will also have to incorporate the role of physical factors (such as temperature and nutrient regimes), species traits (such as species identity and food preferences) and trophic structure (competitive, facilitative, and predator prey relationships) and larger community properties (such as biological and functional diversity). Finally, it will involve understanding the processes that drive the patterns we observe. This is an enormous challenge, but one that will be necessary if we are to effectively generalize patterns we observe in a select few seagrass ecosystems to the many that will need to be managed in the future.

16.6 Final Thoughts

A wide body of work over the past few decades has shown that top-down control can be an important (and even dominant) structuring force in seagrass ecosystems. However, the complexity of these interacting ecosystems continues to make broad generalizations about top-down control difficult. Many Australian seagrass ecosystems have unique qualities, driven by seagrass or megafaunal assemblages not widely found elsewhere. General ecological theory, derived from studied worldwide, will continue to provide hypothesis to test the role of top-down control in seagrass—but an understanding of top-down control in Australian seagrass ecosystems will ultimately have to come from work inside Australia. We have learned much since the original realization of the importance of top-down control in seagrass ecosystems.. The challenge now is to understand when top-down control is important in seagrass ecosystems, what factors control its strength and effects on the seagrass community, where feedbacks or interactions between factors are likely to occur, and what impacts anthropogenic alterations to the local and global environment will have on top-down control. Further research into these areas will aid pursuit of the end goal of a general integrative framework of top-down control in seagrass ecosystems.

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