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## 3

# Epibiont-Marine Macrophyte Assemblages

*Carol S. Thornber<sup>1,\*</sup> Emily Jones<sup>2</sup> and Mads S. Thomsen<sup>3,4</sup>*

## Introduction: Ecological importance of basiphyte-epibiont interactions

### *What is epibiont ecology?*

The biology and ecology of marine seagrasses and macroalgae have likely been influenced by the presence of epibionts for millions of years, given the evolutionary history of both groups, and the potential for co-evolution (Taylor and Wilson 2003). Epibionts are ubiquitous in marine environments, span numerous taxonomic divisions and phyla, occur on a wide taxonomic diversity of basiphytes (hosts), and can either be host-specific (obligate) or host non-specific (facultative). Their importance in ecosystem functioning has been well documented in systems ranging from estuaries to subtidal rocky reefs, as well as from tropical to polar regions (Thomsen et al. 2010).

As widely recognized ecosystem engineers and foundation species, seagrasses and their associated epibionts have been widely studied (e.g., Tomas et al. 2005, Cook et al. 2011, York et al. 2012, Lobelle et al. 2013; Fig. 1). While the majority of algal epiphytes are located on older regions of seagrass leaves, epibionts can also occur

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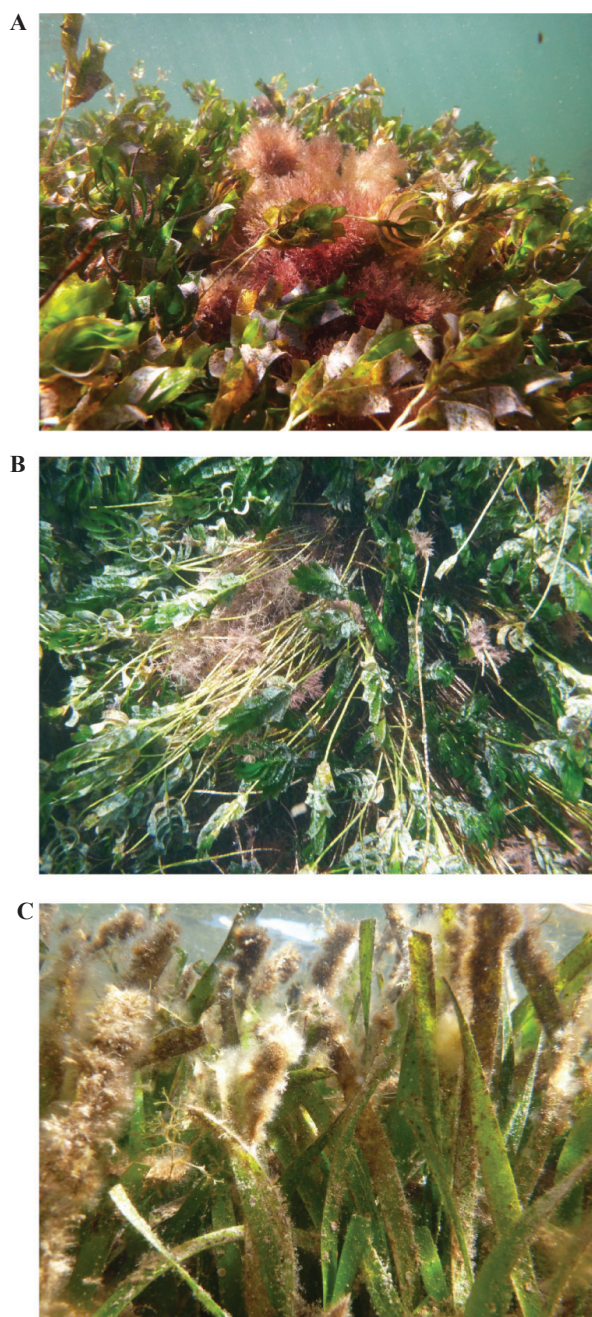
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**Figure 1.** Photos of typical subtidal seagrass beds at Rottnest Island, Western Australia, heavily covered by epibionts. (A) *Amphibolis antarctica* with *Laurencia* sp. epiphyte; (B) *Amphibolis antarctica* with *Metagoniolithon stelliferum* (Lamarck) Ducker (calcareous epiphyte); (C) *Posidonia australis* J.D. Hooker with several epiphytes (including filamentous red algae and *Jania* sp.). *Amphibolis* stems live for over 2 years and are heavily epiphytized, while *Posidonia* leaves are shed in < 100 days.

on seagrass stems and/or rhizomes (Borowitzka et al. 2006). Epibionts can enhance seagrass leaf turnover rates (Cook et al. 2011), occur in dense patches on seagrasses, and have a greater biomass than the seagrasses to which they are attached (Cook et al. 2011). Algal epiphytes can also contribute up to 50–60% of the primary productivity in seagrass meadows (Borowitzka et al. 2006, Cebrian et al. 2013), and play important roles in nutrient cycling (e.g., Pereg-Gerk et al. 2002) and controlling biodiversity of invertebrates (Edgar 1990).

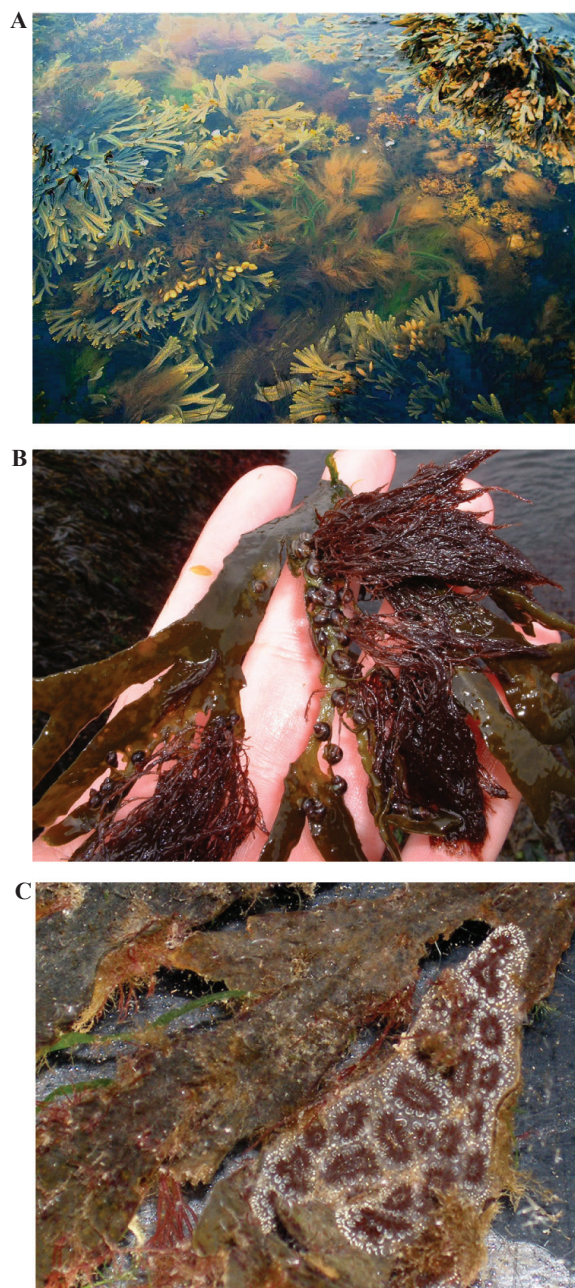
Macroalgal hosts include taxa spanning a wide range of morphological, ecological, and evolutionary diversity (Chlorophyta, Rhodophyta, and Phaeophyceae; Fig. 2). While reports of epibiota on macroalgal taxa are widespread and common (e.g., Jones and Thornber 2010, Kersen et al. 2011, Rohr et al. 2011, Ávila et al. 2012, Engelen et al. 2013), their ecological impacts and interactions are less thoroughly studied than for epibiota on seagrasses (Potin 2012). Like on seagrasses, epibionts on macroalgae are typically more common on older tissues (Arrontes 1990, Pearson and Evans 1990), and can vary in species identity and community across algal thalli (Fricke et al. 2011).

### **Definitions**

For the purposes of this review, we define a basiphyte as a living organism (host) that is typically anchored directly to a (non-living) substrate and is either a seagrass or a macroalga, that has one or more living, attached epibiont species. Non-living substrates can include a variety of habitat types, including sand, shells, pebbles, cobbles, boulders, and rocky reefs. Throughout this review, we follow Wahl (1989) for consistency of epibiont terminology. We therefore use the term epibiosis to refer to a relationship between two organisms, one of which (epibiont) lives on the other (basiphyte), in an interaction that is neither parasitic nor symbiotic. Here, we discuss epibionts (epibiota) that are sessile animals (called epibiotic fauna or epizoans), plants and algae (called epiphytes), while recognizing that epibionts can also include marine bacteria and fungi (e.g., Zhang et al. 2009, Burke et al. 2011, Lachnit et al. 2011) and mobile animals (Wernberg et al. 2004). Epibionts can also live attached to other epibionts, in secondary or tertiary relationships (Wahl 1989, Thomsen et al. 2010). We use the terms epibiotic to describe an epibiont-basiphyte, and epiphytic to describe an epiphyte-basiphyte, relationship. While there is a well-documented gradient across different taxa from purely epiphytic interactions between sessile epibiota and basiphytes to completely parasitic interactions between parasite and basiphytes (e.g., Potin 2012), the focus of this review is on non-parasitic interactions, which may be negative, positive, or neutral.

### **Objectives of this chapter**

In this chapter, we explore the associations between epibionts and their basiphytes through numerous ecological and taxonomic perspectives. We first describe the diversity of key groups and species of epiphytes and epizoans. Next, we explore a suite of documented ecological interactions between epibionts and their hosts, ranging from negative to positive to neutral (e.g., van Montfrans et al. 1984, Leonardi et al.



**Figure 2.** Photos of macroalgae in RI, USA, heavily covered by epibionts. (A) shallow subtidal, Brenton Point, Newport RI algal community including *Fucus vesiculosus* with epiphytic *Ectocarpus* sp., *Codium fragile* subsp. *fragile* with the epiphytes *Ectocarpus*, *Ceramium*, and *Neosiphonia*; (B) rocky intertidal, Fort Wetherill, Jamestown RI—*Fucus vesiculosus* basiphyte, with *Ceramium virgatum* epiphyte and *Lacuna vineta*. (C) subtidal coastal lagoon, Charlestown, RI—*Fucus* sp. with numerous algal epiphytes and the colonial tunicate *Botryllus schlosseri* Pallas.



2006, Jones and Thornber 2010). We then address the cascading impacts of epibiont-basiphyte interactions on community structure of associated mobile animals, with an emphasis on how epiphyte-basiphyte interactions are modified by mobile mesograzers, and finish by investigating the impacts of human-induced stressors on some of these relationships. Our goal in creating this chapter was to provide a thorough (but not exhaustive) review of the existing literature on epibiont-basiphyte ecology, and include both classic and current studies that have illuminated our understanding of these important interactions. Our contribution thereby supplements recent, thorough reviews of epibionts on seagrasses by Borowitzka et al. (2006), of algal epiphytes, endophytes, and parasites on macroalgae by Potin (2012), and on Antarctic endophytes on macroalgae by Amsler et al. (2009). We also hope this chapter will stimulate thought and discussion on this topic by illustrating issues that are in need of further research and critical interpretation.

## **Epibiont diversity**

### ***Epiphytes (plants/algae living on plants)***

Typically, most epiphytes are algae (not vascular plants), including, but not limited to, the Chlorophyta (green algae), Rhodophyta (red algae), Phaeophyceae (brown algae), Dinophyta (dinoflagellates), Bacillariophyceae (diatoms), and Cyanophyta (cyanobacteria). Macroscopic epiphytes can be categorized into different functional groups (*sensu* Littler 1980), including filamentous, foliose, corticated filamentous, corticated foliose, saccate, and coralline groups (Saunders et al. 2003). While macroscopic epiphytes are typically more thoroughly studied and quantified than their microscopic counterparts, microscopic epiphyte assemblages can also be quite diverse (Jernakoff and Nielsen 1997). On seagrass basiphytes, red algal epiphytes typically dominate in terms of biomass, while the presence of mainly cyanobacterial and/or green algal epiphytes frequently indicates eutrophic or other seasonal, high nutrient conditions (Lavery and Vanderklift 2002, Lapointe et al. 2004, Borowitzka et al. 2006).

Epiphytes have a variety of mechanisms they employ to attach to a basiphyte, including via single cells or filamentous/rhizoidal basal structures (e.g., Leonardi et al. 2006), typically at a sporeling or juvenile stage (see **Adaptations** section). Other epiphytes can produce ‘hooks’ to ‘grab’ basiphytes (e.g., *Hypnea musciformis* (Wulfen) J.V. Lamouroux, *Bonnemaisonia hamifera* Hariot), and some epibiotic species produce secondary rhizoids to re-attach, if needed, to new substrates/basiphytes (e.g., Perrone and Cecere 1997).

### ***Epibiotic fauna (epizoans—animals living on plants)***

The taxonomic diversity of sessile faunal epibiota includes groups such as colonial hydroids (Cnidaria: Hydrozoa), encrusting bryozoans (Bryozoa: Gymnolaemata), barnacles (Arthropoda: Cirripedia), sponges (Porifera), ascidians (Chordata: Ascidiacea), and polychaetes (Annelida: Polychaeta). We also include nonmotile sea anemones (Cnidaria: Anthozoa) in this group, while recognizing that some sea

anemones occurring on basiphytes are motile. Sessile epizoans typically settle at the larval stage (Hadfield 1986), via the production of adhesive granules (Stricker 1989) and/or the growth of stolons (Cerrano et al. 2001). Similar to epiphytes, faunal epibiota have distinct zonation patterns on seagrass and macroalgal basiphytes; in some cases, faunal epibiota and epiphytes are inversely correlated in abundance, while on others they are positively correlated (e.g., Trautman and Borowitzka 1999). Individual basiphyte species can harbor a wide richness of sessile epibiotic fauna (e.g., > 20 species; Fredriksen et al. 2007).

One of the most well studied epizoans is the encrusting bryozoan *Membranipora membranacea* Linnaeus, which has been found on kelps such as *Macrocystis pyrifera* (Linnaeus) C. Agardh (Hepburn et al. 2006), *Saccharina longicuris* (Bachelot de la Pylaie) Kuntze (Saunders and Metaxas 2008), and *Laminaria digitata* (Hudson) J.V. Lamouroux and *Laminaria hyperborea* (Gunnerus) Foslie (Schultze et al. 1990), as well as on other large species such as the red alga *Dilsea carnosa* (Schmidel) Kuntze (Nylund and Pavia 2005), the fucoid *Fucus serratus* Linnaeus and the eelgrass *Zostera marina* Linnaeus (Fredriksen et al. 2007). Sessile epizoans such as *Membranipora* can benefit from their association with basiphytes by absorbing supplemental carbon from kelp exudates (De Burgh and Fankboner 1978), while mutualisms have been reported for other epizoan-basiphyte systems (Hepburn and Hurd 2005).

## **Co-existence mechanisms/interactions between basiphytes and epibionts**

### ***Marine macrophytes as secondary substrate***

In marine communities, one of the most limiting resources for both plants and animals is space (Dayton 1971). Many marine macrophytes, including macroalgae, seagrasses, and mangroves, compete for primary substrate such as rock or soft-bottom habitat. However, these organisms also act as foundation species (*sensu* Dayton 1972), increasing substrate heterogeneity and the area available for settlement for smaller algae and invertebrates. These habitat-forming species play critical roles in facilitating epibiota (Stachowicz 2001, Bruno et al. 2003), as shown by the abundance and diversity of organisms that can grow attached to basiphyte hosts. For example, 15 to 30 species of macroalgae grow epiphytically on coralline turf algae in southern California (Stewart 1982), 60% of the macroalgal species in New England have the potential to grow epiphytically (Jones 2007), and over 500 algal species can grow attached to seagrasses (Harlin 1980). The ability for these epibiota and basiphytes to co-exist is based on a variety of mechanisms and interactions, which we will review in this section.

### ***Facultative vs. obligate associations***

Associations between epibiotic organisms can be either facultative, in which epibionts are able to settle and grow on a variety of biotic or abiotic substrates, or obligate, where epibionts depend on one or more specific hosts. The majority of marine

epibiotic organisms are facultative on plant and/or animal basiphytes (Wahl 1989, 2009), with surveys showing that less than 5% of organisms are obligate on a single plant or animal (Wahl 2009). However, several species of obligate epiphytes (e.g., Abbott and Hollenberg 1976, Hallam et al. 1980, Harlin 1980, Gonzalez and Goff 1989, Pearson and Evans 1990) and invertebrates (e.g., Hughes et al. 1991) exist on marine macrophytes, and understanding these obligate interactions is important, as these epibiotic species may be unable to survive in the absence of a specific basiphyte.

Some species that are considered obligate epibionts may be able to settle and grow on other substrates; however, they may grow at very low abundances, be unable to reach full size, or not persist long-term. For example, the filamentous red alga *Smithora naidum* (C.L. Anderson) Hollenberg, an obligate epiphyte on the seagrass genera *Zostera* and *Phyllospadix*, can grow on artificial substrate at lower abundances (Harlin 1973) and on the alga *Plocamium cartilagineum* (Linnaeus) P.S. Dixon at a much smaller size (Hansen 1986). Thus, although *Smithora* may grow on other substrates, it appears to be most productive on its primary seagrass hosts. Because the occurrence of obligate epiphytes on other substrates may be rare, undocumented, or not easily seen (e.g., microscopic life stages) it is difficult to determine how many species are truly obligate on single host species. In addition, the underlying mechanisms causing many of these obligate interactions are not well understood. One of the most well-studied obligate macroalgal interactions is between the red alga *Vertebrata* (*Polysiphonia*) *lanosa* (Linnaeus) T.A. Christensen and the basiphyte *Ascophyllum nodosum* (Linnaeus) Le Jolis (Lobban and Baxter 1983). *Vertebrata* is primarily restricted to the mid-frond, lateral pits of the intertidal canopy-forming brown alga *Ascophyllum* (Lobban and Baxter 1983), as it can only grow on the distal ends of the thallus if wounds are present (Longtin and Scrosati 2009). This epiphyte-host interaction may also be mediated by an obligate fungus on *Ascophyllum*, *Mycophycias ascophylli* (Cotton) Kohlmeyer and Volkmann-Kohlmeyer, which minimizes tissue damage to the host and may aid in nutrient transfer between the two macroalgal species (Garbary et al. 2005). Despite this knowledge, however, we don't know why *Vertebrata* is not found on other macroalgal species or whether *Mycophycias* or other fungi or bacteria must be present for it to persist.

Although some epibiont species are primarily obligate, many species live on a variety of substrate types. The ability of some epiphytic algae to grow on different macrophyte species may depend on attachment mechanisms. In the Northeast Pacific, the red alga *Microcladia californica* Farlow is an obligate epiphyte on the main axis of the brown alga *Egregia menziesii* (Turner) Areschoug, while the closely related congener *Microcladia coulteri* Harvey is able to grow on over 25 genera of macroalgae (Gonzalez and Goff 1989). One reason for these differences is that *M. californica* attaches to substrates via a discoid holdfast, and is sloughed off or dislodged from other basiphytes. In contrast, in addition to discoid attachment, *M. coulteri* also uses rhizoidal attachment, which allows it to resist sloughing (Gonzalez and Goff 1989). Similarly, *Neosiphonia* (*Polysiphonia*) *harveyi* (J.W. Bailey) M.-S. Kim, H.-G. Choi, Guiry, and G.W. Saunders, one of the most abundant epiphytes on a variety of macroalgae in the Northwest Atlantic (Jones and Thornber 2010), shows plasticity for holdfast attachment (Wilson 1978). Wilson (1978) found that when *Neosiphonia* grows on smooth substrata such as *Chondrus crispus* Stackhouse, it uses discoid-like



holdfast attachment, but when it grows on heterogenous substrate such as *Codium fragile* ssp. *tomentosoides* (van Goor) P.C. Silva, it uses rhizoidal attachment. Thus, epibionts may be substratum generalists depending on whether they attach to the surface of other organisms, penetrate into the tissues, or are capable of using both methods. However, despite these early studies, the ecological significance of this holdfast plasticity has largely been ignored; additional studies on what cues elicit these plastic responses and the frequency of this plasticity across species would aid in our understanding of epibiont-basiphyte interactions.

### **Negative vs. positive impacts**

Interactions between epibionts and basiphytes can be negative ([van Montfrans et al. 1984](#), [D'Antonio 1985](#), [Williams and Seed 1992](#)), positive ([Stewart 1982](#), [Norton and Benson 1983](#), [Karez et al. 2000](#)), or neutral ([Cattaneo 1983](#), [Uku 2005](#)), typically depending on environmental conditions ([Bertness and Callaway 1994](#)). The effects of basiphytes on epibionts are generally positive, as they provide substrate for these organisms to grow on when primary substrate is limiting ([Wahl 1989](#)). However, in addition to increasing settlement space, basiphytes raise organisms higher in the water column, increasing flow ([Butman 1987](#)), food and nutrient availability ([Keough 1986](#), [Laihonen and Furman 1986](#)), and light levels for photosynthesis ([Brouns and Heijs 1986](#)). Some species can also act as an associational refuge for epibiotic organisms ([Hay 1986](#)), when consumers avoid unpalatable basiphytes.

Despite these positive impacts, basiphytes can also have negative impacts on their epibionts, especially when basiphyte tissue is removed due to physical stressors, seasonal changes, or consumption. For instance, the tissues of many perennial basiphyte species are shed during winter storms (e.g., [Seed and O'Connor 1981](#)), while many ephemeral macroalgal species that could potentially serve as hosts exist during only parts of the year. Epibionts may also face a "shared doom" ([Wahl and Hay 1995](#)) when epibionts and basiphytes are co-consumed ([Karez et al. 2000](#)). For example, large seagrass herbivores such as dugongs may consume epibionts while feeding on seagrass shoots. In addition to tissue losses of the basiphyte, the macrophyte species can also modify the environment and make it less suitable for epibiont species, relative to other substrate. [Daleo et al. \(2006\)](#) found that *Ulva lactuca* Linnaeus biomass was decreased when growing on the turf-forming alga *Corallina officinalis* Linnaeus compared to growing alone on hard substrate, due to an increase in desiccation stress.

Most research on the interactions between epibionts and basiphytes has focused on the negative impacts epibionts pose to basiphyte species such as decreased growth ([Honkanen and Jormalainen 2005](#)) and reproduction ([Kraberg and Norton 2007](#)) due to increased competition for light and nutrients ([Sand-Jensen 1977](#), [D'Antonio 1985](#), [Cebrian et al. 1999](#)). For instance, in seagrass communities, epibionts can reduce light availability by 10–90% due to shading of basiphyte surfaces ([Sand-Jensen 1977](#), [Borum et al. 1984](#)), and epiphytes may preferentially absorb blue and red light before they reach the seagrass leaves ([Drake et al. 2003](#)). These negative effects may depend on where epibionts grow on the basiphyte. For example [Cancino et al. \(1987\)](#) found that the bryozoan *Jellyella* (*Membranipora*) *tuberculata* Taylor and Monks decreased light

and photosynthesis rates for the alga *Gelidium rex* Santelices and I.A. Abbot, but did not affect net growth rates due to compensatory growth in other parts of the thallus. Epibiotic organisms can also increase physical stressors on basiphytes by increasing drag (D'Antonio 1985, Hemmi et al. 2005) and decreasing elasticity (Dixon et al. 1981), both of which can cause increased mortality. For example, encrusting species such as bryozoans can reduce blade motion and flexibility, increasing breakage in high flow environments (Dixon et al. 1981) and decreasing kelp abundances (Scheibling and Gagnon 2009). Basiphytes may also be damaged by consumers of both invertebrates (Bernstein and Jung 1979) and algae (Karez et al. 2000) if they remove host tissue while feeding on epibiotic organisms.

Although many epibiont effects are negative, epibionts can also benefit basiphyte species. In contrast to epiphytic algae that compete for nutrients, sessile invertebrates may increase nutrient exchange by excreting ammonium. Hepburn and Hurd (2005) found that during times of low nutrient concentrations, *Macrocystis pyrifera* colonized by hydroids actually increased biomass, relative to non-colonized individuals. Epibionts can also decrease physical stress, by retaining water and reducing desiccation during low tide (Stewart 1982). And similarly to unpalatable basiphytes acting as an associational defense for epibionts, epibiont growth can also protect basiphyte species from being consumed by herbivores (Wahl and Hay 1995, Karez et al. 2000). For example, Wahl and Hay (1995) found that urchins fed less on basiphyte species such as *Gracilaria tikvahiae* McLachlan when they were covered by low-palatability epiphytes such as *Ectocarpus* sp. and *Polysiphonia* sp.

## Adaptations

### Basiphyte adaptations

Marine macrophytes have developed a suite of avoidance, tolerance, and defensive traits to prevent colonization and/or overgrowth by epibiotic organisms (Wahl 1989). Some macrophyte species may be able to avoid epibiont settlement either temporally or spatially through rapid or ephemeral growth (den Hartog 1972), high tissue turnover (Bernstein and Jung 1979), or living in locations such as areas with turbulent conditions where epibionts are not able to survive (Seed and O'Connor 1981). Other macrophyte species use mechanical and chemical defenses to remove epibionts or deter them from settling. Sloughing or shedding cuticle and epidermal tissues is a common mechanism for removing epibiotic organisms (Filion-Myklebust and Norton 1981, Sieburth and Tootle 1981, Moss 1982, Russell and Velthkamp 1984, Craigie et al. 1992, Nylund and Pavia 2005). Some macrophyte species may produce mucus or slime that is sloughed off or prevents epibiont settlement (Sieburth and Tootle 1981, Dawes et al. 2000). The effectiveness of these mechanical defenses may be highly variable, however, depending on seasonality of epibiont recruitment and growth rates (Sieburth and Tootle 1981, Wahl 1989, Jones and Thornber 2010) or age of the host (Dawes et al. 2000). Finally, a variety of macrophyte species use chemical defenses to inhibit epibiont growth (e.g., Schmitt et al. 1995, Suzuki et al. 1998, Cho et al. 2001, Hellio et al. 2004, Kim et al. 2004, Wilkström and Pavia 2004, Paul et al. 2006, Nylund et al. 2007). Although many of these studies have used whole tissue extracts

to test for chemical inhibition, [Nylund et al. \(2007\)](#) used more ecologically relevant tissue surface extracts to determine that non-polar metabolites from both *Delisea pulchra* (Greville) Montagne and *Caulerpa filiformis* (Suhr) Herring are capable of inhibiting both sessile invertebrates and epiphytic algae. Basiphytes may also use a combination of these life history, mechanical, or chemical strategies simultaneously, across different tissues of the macrophyte, or over time. For example, *Ulva* species are both ephemeral and are capable of cuticle peeling (Tootle 1974) while *Fucus vesiculosus* Linnaeus exhibits both tissue sloughing (Sieburth and Tootle 1981) and chemical inhibition (Wilkström and Pavia 2004).

### *Epibiont adaptations*

The majority of epibiotic organisms are opportunistic, ephemeral species that have much shorter lifespans than their basiphyte hosts and are poor competitors for primary substrate. As a result of this high competition for space, many species have developed a variety of adaptations at both the settlement and attachment stages so that they can successfully colonize secondary substrata. Settlement of many epibiota is influenced by physical characteristics such as irradiance levels, substrate roughness, and hydrodynamics (reviewed by [Fletcher and Callow 1992](#), [Harder 2008](#)). However, some species are also able to respond to chemical cues released from macroalgae (e.g., [Kato et al. 1975](#), [Bouarab et al. 2001](#)) or surface bacteria ([Joint et al. 2002](#)). By using these abiotic and biotic cues, epibiotic are more likely to settle on favorable substrates.

Once epibiota have settled on a basiphyte, they must successfully attach in order to survive. As mentioned above, the ability of epibionts to attach to different hosts often depends on attachment mechanisms. Linsens (1963) defined holoeipiphytes as algae that attach to the outer layer of a macrophyte, while amphieipiphytes are those that penetrate cell layers. [Leonardi et al. \(2006\)](#) described five different types of epiphyte attachment on the alga *Gracilaria chilensis* C.J. Bird, McLachlan and E.C. Oliveira: (1) weakly attached to surface, (2) strongly attached to surface, (3) penetrating the outer layer of the cell wall, (4) penetrating into the cortical tissue, and (5) penetrating deeply into the cortex. They found that the abundance of epiphytes was greatest for those strongly attached to the surface or penetrating the outer cell layer, while the other attachment types were more seasonal ([Leonardi et al. 2006](#)). This seasonality may be due to the ephemeral nature of the epiphytes themselves, or because there is a tradeoff associated with deeper tissue penetration. However, some of the species that penetrated deep into the cortex, but were only found in the summer (*Ceramium rubrum* C. Agardh, *Neosiphonia harveyi*) can persist throughout the year on other host species ([Jones and Thornber 2010](#)), suggesting that these interactions are variable on different basiphyte substrates or in different geographic locations. Epiphytic macroalgal genera including *Hypnea*, *Bonnemaisonia*, *Cystoclonium*, *Laurencia*, and *Chaetomorpha* can also attach to basiphytes using specialized hooks, tendrils, and/or secondary rhizoids. Not only do these mechanisms allow epiphyte species to attach without directly binding to basiphyte tissue, they also provide a means of reattachment if an epiphyte is dislodged via herbivory or wave action. For example, when severed, the alga *Solieria filiformis* (Kützinger) P.W. Gabrielson produces new rhizoids from the damaged surfaces that

allow it to reattach to secondary substratum (Perrone and Cecere 1997). In addition, if fragmented, *Hypnea musciformis* apical hooks can produce secondary rhizoids to reattach to basiphyte species (Thomsen 2004a). The ability of sessile invertebrates to attach to macrophyte substrates will also be important for epibiont survival, although in contrast to epiphytic algae, some invertebrates such as hydroids on seagrasses can use stolon transfer to “move” between substrates (Hughes et al. 1991).

### **Interaction strengths and community context**

The strength of these basiphyte-epibiont interactions can be highly context dependent, depending on biotic and abiotic conditions. Epibiont communities on the same basiphytes can vary seasonally (Arrontes 1990, Rindi and Guiry 2004, Jones and Thornber 2010), geographically (Rindi and Guiry 2004), and across environmental gradients such as wave exposure (Kersen et al. 2011), salinity (Kendrick et al. 1988), and intertidal height (Longtin and Scrosati 2009, Longtin et al. 2009). This variation in time and space may affect the direction and magnitude of interactions between epibiont and basiphyte species. For example, when epibionts shade seagrass, they decrease the available light and the depth at which seagrasses are able to grow (Borum et al. 1984). However, this interaction may be positive if it allows seagrasses to grow in sunnier locations (Wiencke 1987) or expand into shallower habitats, by reducing photo-inhibition. Epibionts may have varying interactions within an individual basiphyte species as well. The brown alga *Soranthra ulvoidea* Postels and Ruprecht is commonly found attached to the red alga *Odonthalia floccosa* (Esper) Falkenberg in the mid to low intertidal zone from the Bering Sea to California (Abbott and Hollenberg 1976). During low tide, the presence of *Soranthra* can decrease desiccation rates of *Odonthalia* (Anderson 2012). However, when submerged, *Soranthra* increases drag on *Odonthalia* even at low flow, and dislodgment at high flow (Anderson 2012). Thus, the net effect of these interactions may vary with emergence time and flow conditions. However, the majority of research on basiphyte-epibiont interactions has focused on single stressors and response variables (e.g., growth) and additional studies are needed that focus on multiple stressors and response variables (Anderson 2012) to enhance our understanding of how basiphyte and epibiont species are able to co-exist.

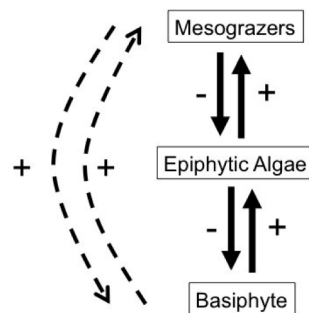
The larger community-context is also important to consider when investigating the consequences of epibiota on basiphyte species. As mentioned previously, consumers may enhance negative effects of epibionts on basiphytes by co-consuming epibiont and basiphyte tissue (Karez et al. 2000). However, consumers can also mediate the interactions between epibionts, reducing epibiont effects. For instance, the removal of epibiota by predatory snails doubled the growth rate of *Fucus vesiculosus* (Honkanen and Jormalainen 2005). In another case, only the combination of two complementary consumers (the snails *Cotonopsis* (*Anachis*) *lafresnayi* P. Fisher and Bernardi and *Astyris* (*Mitrella*) *lunata*) Say successfully removed both solitary ascidians and encrusting bryozoans from the basiphyte *Chondrus crispus*, increasing basiphyte biomass (Stachowicz and Whitlatch 2005). Thus, community interactions among species and trophic levels can play important roles in altering the interactions between epibiota and basiphyte species.

## Cascading effects of basiphyte-epibiont interactions

### *Implications for abundance and diversity of mobile animals*

In the previous sections we discussed basiphyte–epibiont interactions, with an emphasis on how basiphytes increase the abundance and diversity of sessile epibionts by being a host/habitat for these species. Here, we note that the sessile epibiont species themselves also provide and modify habitats for more and/or different sessile and mobile epibionts (we here refer to this second group of epibionts as ‘end-users’). This interaction chain is an example of cascading habitat formation—where indirect positive effects on focal organisms are mediated by successive facilitation in the form of biogenic formation or modification of habitat (Thomsen et al. 2010, Fig. 3). Or, in other words, in this chain reaction basiphytes have indirect positive effects on end-users mediated through positive effect on epibionts.

There are ample data to suggest that cascading habitat formation is common in marine systems dominated by epibiont-basiphyte interactions. For example, numerous studies show that herbivores have positive impacts on basiphytes by preferentially consuming epiphytes (e.g., Howard 1982, Shacklock and Doyle 1983, Orth and Montfrans 1984, Hootsmans and Vermaat 1985, Duffy 1990, Klumpp et al. 1992, Mukai and Iijima 1995, Alcoverro et al. 1997, Boström and Mattila 1999, Pavia et al. 1999, Worm and Sommer 2000, Hily et al. 2004, Tomas et al. 2005, Prado et al. 2007, Jones and Thornber 2010). These studies focus on how herbivores—through keystone consumption (Paine 1966, Thomsen et al. 2010)—control community structure. Thus, in keystone consumption, consumers (here grazers) control abundances and diversity of key species (here basiphytes) by consuming competitive dominants (here epiphytes). Importantly, all of above studies also provide support for cascading habitat formation; reversing focus to the basiphyte suggests that the basiphyte has indirect positive effects on herbivores (and other end-users) by providing high quality food, habitat, and protection from predators. Cascading habitat formation and keystone consumption, are therefore, at least for basiphyte-epiphyte-grazer interactions, ‘mirror-processes’



**Figure 3.** Diagram showing potential basiphyte-epibiont-mesograzers interactions. Arrows go toward the species experiencing the effect from the one causing it. Signs (+/–) indicate the type of effect. Solid lines represent direct effects, while dashed lines represent indirect effects. The solid line pointing away from the mesograzers indicate keystone consumption, while the solid line pointing away from the basiphyte indicates cascading habitat formation.

(Fig. 3). Still, we address keystone consumption, where the main focus is on the pivotal role of herbivores, separately in the next section (as traditionally done). Here we review the relatively few studies that address basiphyte-epiphyte-enduser interactions explicitly as cascading habitat formation, i.e., where research focus is on how basiphytes—through control of epiphytes—control abundances and diversity of end-users. We include a few examples with drift macroalgae entangled around basiphytes, because the main interactors and the type of direct and indirect interactions are conceptually similar to classical basiphyte-epiphyte-end-user interactions. Also, some epiphytes can ‘change’ between attached and drifting states: for example, *Hypnea musciformis* can survive as drift algae, become entangled or re-attach to a basiphyte with hooks and/or secondary rhizoids, and break off and drift around again (Thomsen 2004a).

Cascading habitat formation is well documented from seagrass beds. For example, Hall and Bell (1988) documented positive effects on meiofauna associated with the seagrass *Thalassia testudinum* ex König and its epiphytes. More specifically, surveys and experiments were carried out to examine relationships between the biomass of epiphytic algae on *Thalassia testudinum* blades and density of end-users, in particular copepods, nematodes, amphipods, and crustacean nauplii. Colonization experiments documented a positive relationship between biomass of the epiphytic alga *Giffordia michelliae* (Harvey) G. Hamel and end-users, suggesting that results were density dependent (but length of colonization time did not vary among seagrass blades). Follow up experiments using artificial blades and several densities of artificial epiphytes produced similar results, i.e., with highest densities of end-users on blades in high epiphyte treatments. These results suggested that much of the relationship between these end-users and epiphytes could be attributed to the physical structure—not trophic subsidy—of the epiphyte. In another colonization experiment in a seagrass bed, Schneider and Mann (1991) also used plastic mimics to investigate the relative importance of basiphyte shape and epiphyte cover in determining the distribution of invertebrate end-users. Both epiphyte cover and shape were important, but end-user responses were highly species-specific where some species responded to basiphyte shape while other responded to epiphyte cover. Follow-up laboratory predation experiments suggested that, contrary to expectations, predation by fish and crabs was not affected by the presence of artificial macrophytes. Bologna and Heck (1999b) also used artificial basiphytes and manipulated both epiphytic structure and epiphytic food resources. However, somewhat in contrast to the previous studies, they found that end-user densities and diversity were higher on mimic basiphytes that were covered by live epiphytes, compared to artificial epiphytes. This response to live epiphytes was strong for herbivores and omnivores and weak for filter feeders and predator end-users. Epiphytic structure thereby appeared to play a limited role in determining the density of most mobile end-users, with one exception being the settlement of bivalves. Thus, this study suggested that epiphytes can have a dramatic positive impact on end-users via trophic subsidy (and supported by the extensive literature reviewed in Epibiont-mesograzers interactions section).

Similar general positive effects of epiphytes on invertebrate end-users has also been found in subtropical *Amphibolis* seagrass beds (Edgar and Robertson 1992) where removal of epiphytes resulted in fewer species and lower abundances of focal



organisms. Patches within a mixed bed of the seagrasses *Amphibolis antarctica* (Labillardière) Sonder and Ascherson ex Ascherson and *Amphibolis griffithii* (J.M. Black) den Hartog were manipulated by removing epiphytes, basiphyte leaves, and by reducing basiphyte density. Leaf and epiphyte removal decreased abundances of most end-users dramatically. Follow-up caging experiments showed a reduction in faunal densities on basiphytes both in open plots and enclosed in cages. Hence, predation by fish or decapod predators was unlikely to cause the faunal decline in the open seagrass plots. In this experiment, end-users associated with basiphyte leaves appeared to actively select dense basiphyte habitats, possibly because of evolutionary selection to minimize predation or to avoid high levels of solar radiation. In a somewhat unusual example, it was recently documented that the large invasive macroalga *Codium fragile* (Suringar) Hariot can be an abundant epiphyte on *Zostera marina*, by attaching to the seagrass' rhizomes (Drouin et al. 2011). More specifically, surveys and experiments documented higher abundance and diversity of invertebrates associated with the epiphyte than with the basiphyte alone, i.e., the abundance and taxonomic richness of end-users were positively correlated with the biomass of the epiphyte. Furthermore, experimental manipulation of the epiphyte morphology showed that end-users were not influenced by this factor, indicating that factors other than structural complexity may be important for end-user abundance and diversity.

In addition to seagrass beds, cascading habitat formation is also likely to be important on macroalgal-dominated rocky reefs. For example Martin-Smith (1993) removed epiphytes from two types of *Sargassum* macroalgal mimics in Queensland, Australia. Again, community composition differed between the epiphyte-covered and the clean mimics, leading to higher abundances of crustacean, polychaete and gastropod end-users in the presence of epiphytes. Finally, surveys by Leite and Turra (2003) found significant positive relationships between the combined biomass of the basiphyte *Sargassum cymosum* C. Agardh and epiphyte *Hypnea musciformis*, and the total density of all invertebrate end-users.

Similar to above basiphyte-epiphyte case studies, drift macroalgae that are entangled around seagrass stems and leaves (without being physically attached) provide analogue examples of cascading habitat formations. Thus, invasive (Thomsen 2010) and native (Thomsen et al. 2012a) coarsely branched *Gracilaria*, and a complex of various red algal species (Holmquist 1997) have, just like for typical epiphytic macroalgae, strong positive effects on many invertebrate end-users within seagrass beds. Similar results have also been highlighted in other studies for individual end-user species, showing positive effects of entangled macroalgae within seagrass beds, on the snails *Potamopyrgus antipodarum* J.E. Gray (Cummins et al. 2004) and *Peringia ulvae* Pennant (as *Hydrobia ulva*: Cardoso et al. 2004)—but these studies also report relatively strong negative effects on different invertebrate end-users. Drift seaweeds, like epiphytes, typically have negative impacts on the seagrass itself, competing for light and nutrients and increasing anoxia, sulphide and ammonia levels in the water column or sediment pore-water, and may, in some cases, even kill-off the host (Holmquist 1997, McGlathery 2001, Hauxwell et al. 2003a, Thomsen et al. 2012b), thereby destabilizing the entire habitat cascade.

The above studies suggest that positive effects of epiphytes on mobile animal end-users can be caused by both quantitative and qualitative differences in habitat

attributes and resource provisions between the epiphyte and basiphyte. It is likely that epiphytes simultaneously provide shelter from predators, food for grazers, attachment space for recruits and, potentially, also ameliorate abiotic stress, particularly in the intertidal zone (Norkko et al. 2000, Cardoso et al. 2004, Nyberg et al. 2009a). It is important to note though that the reviewed studies used “addition/removal” (not “substitution”) type experiments and surveys. The combined biomass of the basiphyte and epiphyte is therefore higher than for the basiphyte alone, making it difficult to separate quantitative and qualitative habitat effects. It may therefore be that the increase in total habitat space facilitate mobile animal end-users, irrespective of epiphyte traits. Facilitation could also be caused by qualitative trait differences between epiphytes and basiphytes. For example, the entangled macroalga *Gracilaria* contrasts its host *Zostera*, by being positioned horizontally within the seagrass bed, having cylindrical branching laterals that are not shed and by being more palatable. Thus, there are several co-occurring mechanisms whereby end-users can be facilitated by epiphytes, including stress-reduction from desiccation and extreme temperatures in the intertidal zone, consumer-avoidance and food subsidies. In summary, positive effects of epiphytes on mobile animal end-users are likely large, when the epiphyte is larger, more abundant, and ecologically different from the basiphyte, and when spatial heterogeneity or food web complexity are low and small—because the latter mechanisms represent larger scale alternative pathways for end-users to escape stress and enemies and find resources (Thomsen et al. 2010).

### ***Epibiont-mesograzers interactions***

#### ***Influence of epiphyte-basiphyte associations on mesograzers***

As mentioned above, macrophyte species that support epibiota influence higher trophic levels. In this section, we focus on small herbivores, or mesograzers, which are typically crustaceans and gastropods 0.1 to 2.5 cm in size (Hay et al. 1987, Brawley 1992). These species serve as both a food sources for larger predators (Edgar and Shaw 1995, Taylor 1998, Heck et al. 2000), as well as important consumers of primary producers (Jernakoff et al. 1996, Valentine and Duffy 2006). Because many mesograzers use epiphytic algae for both food and habitat, basiphyte-epiphyte interactions can strongly influence these species and vice versa.

Mesograzers and epiphyte abundances are often strongly correlated, with higher abundances of grazers occurring on epiphytized basiphytes (Pavia et al. 1999, Orav-Kotta and Kotta 2004, Jones and Thornber 2010, Rohr et al. 2011). Large macroalgae and seagrasses are often less accessible and palatable to mesograzers than the small, filamentous epiphyte species (e.g., Steneck and Watling 1982, Chavanich and Harris 2002, Boström and Mattila 2005), so macrophytes with epiphytic algae may provide more suitable food resources compared to areas where epiphyte growth is minimal. In seagrass communities, a large number of organisms feed on epiphytic algae (Jernakoff et al. 1996), and epiphytes are primarily used as food, rather than habitat (Bologna and Heck 1999b; see also **Implications for abundance and diversity of mobile animals**). However, in macroalgal communities, these interactions often vary depending on mesograzers, basiphyte, and epiphyte identity. Pavia et al. (1999) found

that abundances of the amphipod *Gammarus locusta* Linnaeus were five to eight times higher when epiphytes were present on the alga *Ascophyllum nodosum*, while isopod distributions were more variable (*Idotea granulosa* Rathke) or not correlated (*Jaera albifrons* Leach). Small individuals of both *Gammarus* and *Idotea* preferred the epiphytes *Ceramium nodulosum* Ducluzeau and *Pilayella littoralis* (Linnaeus) Kjellman over *Ascophyllum*, while large individuals of *Idotea* also consumed *Ascophyllum*. In contrast to these results, Karez et al. (2000) found that *Gammarus* preferred the tips of the basiphyte *Fucus vesiculosus* over the epiphyte *Elachista fucicola* (Velley) Areschoug, while *Idotea* consumed both *Elachista* and older *Fucus* tissue. Similarly, Orav-Kotta and Kotta (2004) and Kotta et al. (2000) found that the isopod *Idotea baltica* preferentially consumed the epiphyte *Pilayella littoralis* over the basiphyte *Fucus vesiculosus*, while Jormalainen et al. (2001a) found a preference for *Fucus* over these same epiphyte species. These contrasting feeding preferences for epiphytes and basiphytes may be due to structural or palatability differences among the macroalgal species (e.g., *Ascophyllum* may be better habitat and/or tougher than *Fucus*), or due to differences in mesograzers characteristics such as size (Pavia et al. 1999) and sex (Jormalainen et al. 2001b).

In addition to serving as a food source for mesograzers, epibiota can also increase habitat complexity (Hacker and Steneck 1990, Martin-Smith 1993; see also Implications for abundance and diversity of mobile animals), providing protection from predators and buffering abiotic stressors such as desiccation (Salemaa 1987, Boström and Mattila 1999, Williams et al. 2002). This increased habitat structure may be especially important for newly recruited individuals. For instance, recruitment of the snail *Lacuna vincta* Montagu is influenced by epiphyte abundance in the low intertidal zone of New England, with more individuals occurring on macroalgae or mimic substrates where epiphytes are present (Jones and Thornber 2010, Rohr et al. 2011). These snails may also use different epiphyte species for food and habitat, as abundances are positively correlated with *Neosiphonia harveyi* biomass, while they preferentially consume the epiphytic red alga *Ceramium virgatum* Roth (Jones and Thornber 2010). Similarly, using both feeding and habitat preference assays, Kotta et al. (2000) found that *Idotea balthica* Pallas prefers the epiphyte *Pilayella* as food, but the epiphyte *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux as habitat.

### *Influence of mesograzers on basiphytes communities*

A variety of studies have shown that mesograzers can influence primary production, trophic energy transfer, and biogeochemical cycling (Edgar and Aoki 1993, Edgar and Shaw 1995, Heck et al. 2000, Spivak et al. 2009). Mesograzers activity may be especially important in areas dominated by macrophyte foundation species such as macroalgae and seagrasses, as these grazers prevent competition with, or overgrowth by, epibiotic organisms (Duffy 1990, Stachowicz and Hay 1996, Miller 1998, Stachowicz and Hay 1999, Stachowicz and Whitlatch 2005). While mesograzers activity is generally non-lethal to large macroalgae and seagrasses, it can still affect basiphyte fitness and influence community structure, depending on the tissues consumed, grazer feeding rates, macrophyte growth rates, grazer interactions, and abiotic conditions (Arrontes 1990, Ilken 2012). By contrast, via the removal of epiphytes, mesograzers may increase

light availability and nutrient acquisition for basiphytes (Duffy 1990), while providing nutrients via excretion (Fong et al. 1997, Bracken et al. 2007). However, mesocosm experiments clearly support the idea that grazers can control epiphytic algal growth (reviewed by Valentine and Duffy 2006). These effects can vary from strong (Duffy and Hay 2000, Bruno and O'Connor 2005) to weak or undetected (O'Connor and Bruno 2007, Douglass et al. 2008), and the ecological relevance of these studies in field conditions is not well understood.

Most studies investigating mesograzers impacts have manipulated grazer densities and diversity in laboratory mesocosms, or excluded grazers using mesh cages in the field (see review by Poore et al. 2009). Understanding the community-wide effects of these studies is difficult, however, as mesocosm studies fail to incorporate the high spatial and temporal variation of mesograzers densities (Ruesink 2000), species-specificity of feeding preferences for different epiphytes (Duffy and Harvilicz 2001), and consumption of specific basiphyte parts such as meristems (Poore 1994) or reproductive tissues (Nakaoka 2002), while cages present several experimental artifacts (Miller and Gaylord 2007). Two studies, however, have effectively decreased mesograzers abundances in the field using an insecticide, with contrasting results. Poore et al. (2009) found that in a temperate Australian algal bed, mesograzers reductions had no effect on the growth rate of the basiphyte *Sargassum linearifolium* (Turner) C. Agardh, epiphyte cover, or algal community composition. However, using similar techniques, Whalen et al. (2013) found that mesograzers can control seagrass epiphytes in natural seagrass communities, although the dominance of top-down and bottom-up effects shifted with season. During the summer, when mesograzers densities were typically high, removal of grazers led to a significant increase in epiphyte biomass and decrease in eelgrass shoot density. However, during the fall when natural mesograzers densities declined, epiphytes escaped from grazer control, hence removing grazers had no effect on epiphyte abundance. This escape from grazer control occurred at amphipod densities much higher than those found naturally on *Sargassum* by Poore et al. (2009), suggesting that one possible reason for these contrasting results between studies may be due differences in grazing pressure. Further field studies are needed to assess whether there is variation in top-down and bottom-up control between epiphyte-seagrass and epiphyte-macroalgal systems however. In addition, understanding the role in of natural grazer variation may help us predict where or when nutrient enrichment may prevent grazer control of epiphytic algae (e.g., Kotta et al. 2000).

#### *Influence of predators on mesograzers-epiphyte-basiphyte interactions*

In addition to epiphyte abundance and habitat complexity, predation risk can be an important factor in structuring epiphyte communities, although studies on this topic are limited. Predators may influence mesograzers effects on epiphyte species both by direct consumption and by altering mesograzers behavior. For instance, if epiphytes provide a refuge for mesograzers from predators (Williams et al. 2002), predators may have greater effects on mesograzers abundances when epiphyte cover is low. Although empirical evidence for this idea is somewhat lacking, especially from field studies, Russo (1987) found that in the lab, Hawaiian amphipods survived better in more structurally complex mimic habitats in the presence of predators. Predation risk may

also change the behavior of some, but not all mesograzers species. In the absence of predation, the isopods *Idotea balthica* and *Erichsonella attenuata* Harger both select less complex seagrass habitat with epiphytes, their preferred food source (Bologna and Heck 1999a). However, in the presence of a predator, *Idotea* still chose food over shelter, while *Erichsonella* chose the more complex seagrass habitat that provided better protection from predators. These behaviors have the potential to influence both epiphyte abundances and mesograzers mortality, although these effects were not directly measured in this study. One area of research that is lacking in these interactions is how spatial and temporal changes in epiphyte abundances influence mesograzers behavior, indirectly affecting their susceptibility of predation. For example, if mesograzers prefer to feed on epiphyte species, do they increase foraging movement as epiphyte abundance declines, increasing predation risk? More research is needed to understand how these predator-prey interactions change with variation in resources over space and time.

## **Human threats to stable basiphyte-epibiont co-existence**

### ***Human activities modify basiphyte-epibiont interactions***

Human activities have a fundamental influence on almost all aspects of marine ecology. The main human stressors in coastal ecosystems are eutrophication, habitat-alterations, fisheries, invasions, and climate changes (Worm et al. 2006) and the impact of most of these stressors on marine plants (as basiphytes) are described in separate chapters of this book. In this section we briefly outline how these stressors may also modify basiphytes-epibiont interactions. Unfortunately, few studies have specifically tested how human stressors modify basiphyte-epibiont interactions, and much of our discussion below is therefore circumstantial being derived from the more common studies that focus on human impacts on either the basiphyte, the epibiont or on organisms with epibiont-like traits.

### **Eutrophication**

Eutrophication is the ecosystem response to the addition of excessive amounts of nutrients, such as nitrates and phosphates, through fertilizers or sewage, to aquatic systems. Of the different human stressors, eutrophication has the most straightforward-to-predict effects on basiphyte-epiphyte interactions. Large amounts of inorganic nutrients favor plants with high Surface area-to-Volume (SV)-ratios and rapid nutrient uptake and growth more than plants with low SV ratios and slow nutrient uptake and growth (i.e., species with classic r-strategy are favored over species with K-strategy; Duarte 1995, Pedersen and Borum 1996, 1997). Given that many epiphytes (and turf and drift macroalgae) have these r-strategy traits, eutrophication typically favors epiphytes over basiphytes (Lotze et al. 2000, Thomsen et al. 2012b). Indeed, eutrophication can cause population booms of epiphytes (and drift macroalgae) that shade basiphytes and cause low oxygen levels at night or when epiphyte populations decay (Krause-Jensen et al. 1999, Holmer and Nielsen 2007). On longer and larger spatio-temporal scales, epiphytic blooms have caused strong reductions in basiphyte

populations in coastal zones around the world ([Kangas et al. 1982](#), [Cambridge et al. 1986](#), [Kautsky et al. 1986](#), [Valiela et al. 1997](#), [McGlathery 2001](#), [Hauxwell et al. 2003b](#)). These nutrient-driven changes in the relative dominance between basiphytes and epiphytes may ultimately cause strong impacts on the entire ecosystem, which are sometimes referred to as regime shifts ([Troell et al. 2005](#), [Andersen et al. 2009](#)). Typically, most nutrients are derived from diffusive and point sources of the local watershed. This implies that it may be possible to locally manage and rectify problems associated with eutrophication by shifting competitiveness back to the basiphyte, although factors such as ‘hysteresis’ ([Andersen et al. 2009](#)), local extinctions of basiphytes ([Smale and Wernberg 2013](#)), non-local atmospheric pollution ([Paerl 1995](#)), and accumulated nutrient banks in sediments ([Schelske et al. 1986](#), [Reddy et al. 1993](#)) can make this a complicated and slow recovery process.

### **Habitat alterations**

Habitat alterations is probably the most important human stressor in terrestrial ecosystems, but is of less direct importance in marine systems. Direct habitat alterations can be associated with boating activities (e.g., anchoring) and local construction projects, such as building harbours, jetties, groynes, and oil rigs ([Bulleri and Chapman 2010](#)). However, of more general importance for basiphyte-epiphyte interactions are those habitat alterations that occur in adjacent terrestrial drainage basins. Importantly, run-off and sedimentation levels have increased many-fold around the world as coastal forests have been converted to urban centers and agricultural land ([Airoldi 2003](#)). These enhanced sediment levels in coastal systems cause decreased light levels and can smother plants and sessile animals. However, slow growing basiphytes are typically more negatively affected by high sediment loads compared to ephemeral epiphytes that may ‘outgrow’ enhanced sedimentation. Epiphytes typically also have broader habitat requirements than basiphytes, for example typically being able to survive both drifting and attached to man-made structures, and as epiphytes. Indeed, it appears to be a global trend that where sedimentation levels are high, canopy-forming basiphytes are being rapidly replaced with species that have turf and epiphytic algal traits ([Airoldi and Cinelli 1997](#), [Airoldi and Virgilio 1998](#), [Irving and Connell 2002](#), [Eriksson and Johansson 2003](#), 2005, [Balata et al. 2007](#)). Problems associated with enhanced sedimentation can be managed locally by altering those catchment practices that cause increased sediments and by constructing sediment deposition buffer zones to further reduce sedimentation on basiphytes (e.g., by restoring salt-marshes and mangrove forests).

### **Fishing**

Fishing does not appear to affect basiphyte-epiphyte interactions directly, but could cause complex indirect effects. Fishing alters the local communities and abundances of different fish species, typically at first reducing populations of large apex predators, and later, if fishing pressure continues to be intense, also smaller fish lower on the food chain ([Jackson 1997](#), [Caddy et al. 1998](#)). Alteration to the local fish community can be



expected to modify basiphyte-epiphyte relations in complex ways, but in particular, through long and short consumption cascades (Post 2002). For example, removal of big predatory fish may cause population increases of smaller fish which typically consume mesograzers like small crustaceans and gastropods. Given that mesograzers prefer to consume epiphytes over basiphytes (see **Epibiont-mesograzer interactions**), the removal of large predators could indirectly increase epiphytes and thereby increase competitive stress on basiphytes. However, if continued fishing effort subsequently also removes small fish, basiphytes could be indirectly facilitated because predation on mesograzers would thereby be reduced, potentially resulting in less epiphytism. These long and short consumption cascade scenarios are highly simplified, as many fish species are omnivores, can shift diets, and may be replaced by functionally similar species, thereby blurring our ability to predict indirect cascading impacts of fishing on basiphytes and epiphytes (Duffy and Hay 2001, Hay et al. 2004, Burkepile and Hay 2006). Coastal fishing is also a local stressor that, like sedimentation and eutrophication, at least theoretically, can be managed locally.

### **Invasive species**

Invasions by non-native species also modify basiphyte-epiphyte interactions. Invasive species can be both basiphytes and epiphytes, as well as grazers and predators that can affect basiphyte-epiphyte interactions directly (e.g., by consumption) or indirectly (e.g., by altering abiotic environments or consuming grazers). This complexity implies that both basiphytes and epiphytes can be both facilitated and inhibited, and that the net effect on local basiphyte-epiphyte interactions is highly context-dependent (Thomsen et al. 2011). For example, many invasive plants, like *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Nyberg et al. 2009b), *Sargassum muticum* (Yendo) Fensholt (Viejo 1999, Wernberg et al. 2004, Thomsen et al. 2006), *Fucus evanescens* C. Agardh (Wikström and Kautsky 2004), *Grateloupia turuturu* Yamada (Jones and Thornber 2010, Janiak and Whitlatch 2012), and *Codium fragile* (Mathieson et al. 2003, Schmidt and Scheibling 2006, Jones and Thornber 2010) are basiphytes that provide habitat for numerous sessile or mobile organisms. However, although these case studies suggest invaders are common basiphytes—with positive effects on epiphytes—they probably represent rather atypical invasion impacts. Notable, these invasive macrophytes are all relatively large, relatively easy to see and identify, and have conspicuous impacts, and are therefore obvious to study. However, examinations of typical non-native species (and their traits) found on boat hulls, in ballast water, and on aquacultural molluscs, more often points to non-native species being small, inconspicuous, and difficult to detect and identify (small turf and filamentous macroalgae and sessile invertebrates; Carlton 1996, Hewitt et al. 2004). It is therefore possible that many epiphytes are non-native species that have been translocated prior to scientific data collections or remain unrecognized as non-native species, implying that the importance of invasive epiphytic species may be significantly underestimated. Despite a likely underestimation, there are still many case studies on invasive epiphytes, in particular represented by bryozoa (Saunders and Metaxas 2008), tunicates (Dijkstra et al. 2007, McCarthy et al. 2007) and macroalgae (Piazzi et al. 2002, Deudero et al. 2010). Invaders can also be herbivores

that may preferentially graze on habitat forming basiphytes or on epiphytes and other small macroalgae that compete with the basiphytes ([Lubchenco 1978](#), [Eastwood et al. 2007](#)). Finally, many invaders are predators or omnivores, that through their consumption of herbivores further modify basiphyte-epiphyte interactions ([Trussell et al. 2004](#), [Eastwood et al. 2007](#), [Albins and Hixon 2008](#)). Overall, we can therefore, at least not yet, predict simple effects of invasions on basiphyte-epiphyte interactions. Furthermore, the control options for local managers are poor, in part because even extreme border control cannot eliminate invasions (many invasive species arrive by natural dispersal from adjacent less controlled invaded regions), and in part because following a successful establishment, invaders, are extremely difficult to eradicate or even just control.

### Climate change

Finally, climate changes also modify basiphyte-epiphyte interactions. Climate change is a global phenomena with complex and difficult to predict local effects. In marine systems, the main climate changes relate to increased storminess, ocean acidification and warming. Effects associated with increased storminess are difficult to predict in part because effects are expected to be highly localized. However, if increased storminess occurs, both basiphytes and epiphytes could be favored, depending on the specific changes to hydrodynamic regimes. For example, increased storminess could cause increased dislodgement of weakly attached epiphytes ([Schanz et al. 2000](#), [Schanz et al. 2002](#), [Thomsen 2004b](#)) but could alternatively also dislodge or prune the entire basiphyte ([Gaylord et al. 1994](#), [Thomsen and Wernberg 2005](#), [de Bettignies et al. 2012](#)). More complex indirect interactions can also be envisioned because increased storminess may change consumer-basiphyte-epiphyte interactions, as grazers and predators are likely to be dislodged more frequently and their feeding patterns altered ([Schanz et al. 2000](#), [Schanz et al. 2002](#)). Finally, species with high colonization abilities are likely to be favored as storms will increasingly create gaps and open spaces within beds of canopy-forming basiphytes. Importantly, early gap colonizers can reproduce year round and/or can re-attach to substratum from fragments (e.g., [Perrone and Cecere 1997](#)). Many of these species can also exist as epiphytes. As oceans and seas become more acidic, acidification will inhibit calcifying organisms, including calcifying basiphytes ([Martin and Gattuso 2009](#), [Guerra-García et al. 2012](#)), calcifying epiphytes ([Saunders and Metaxas 2008](#)), and calcifying consumers ([Bibby et al. 2007](#)). It is therefore difficult to predict broad acidification effects on basiphyte-epiphyte interactions, being further complicated by recent findings that non-calcified organisms can also be dramatically influenced by acidification ([Russel et al. 2009](#)). Finally, oceans and seas are becoming warmer. Warming is probably the most important driver of climatic changes and will generally favor warm-water species with wide temperature tolerances, and rapid growth. Importantly, these traits are more often associated with epiphytic species (and turf forming and drift macroalgae) than large canopy forming basiphytes. For example, kelp basiphytes are generally adapted to relatively cold waters and can be negatively impacted by warming, particularly near their poleward ranges ([Wernberg et al. 2012](#), [Smale and Wernberg 2013](#)). Similarly,

slow growing seagrass basiphytes may also be more susceptible to heat stress than many epiphytic species ([Short and Neckles 1999](#)) and heating can reduce their resistance to other stressors, such as competition with macroalgae ([Hoeffle et al. 2011](#), [Holmer et al. 2011](#)) or sulphide stress ([Koch et al. 2007](#)). In contrast to the previous stressors, local managers have virtually no options for controlling or rectifying global climate change impacts on basiphyte-epiphyte interactions, but will instead have to focus on adaptations and mitigations to expected changes.

### **Co-occurring stressors**

Most importantly, human stressors do not occur in isolation, and to understand how they modify basiphyte-epiphyte interactions, their combined effects needs to be considered. Unfortunately, relatively few studies have tested for combined effects of multiple human stressors, and we therefore typically have to make simple predictions from their individual effects (but see [Piazzi et al. 2005](#), [Russel et al. 2009](#), [Gennaro and Piazzi 2011](#), [Hoeffle et al. 2011](#), [Holmer et al. 2011](#), [Hoeffle et al. 2012](#)) for examples, suggesting that combined stress effects typically are additive or synergistic). As reviewed above, fishing, invasions, acidification and increased storminess all have complex effects that can both favor and inhibit both basiphytes and epiphytes. However, eutrophication, enhanced sedimentation and warming generally favor epiphytes over basiphytes, suggesting that the net effect from all human stressors combined will be decreased abundances of basiphytes and increased abundances of epiphytes, or species with similar traits and strategies ([Steneck et al. 2002](#), [Orth et al. 2006](#), [Waycott et al. 2009](#), [Wernberg et al. 2012](#)). However, if basiphytes decrease, this may negatively impact species that have adapted to being primarily (or exclusively) epibionts. Furthermore, a simple comparison of attributes associated with epiphytes vs. basiphytes, under increased stress and disturbances, support this notion; typically large basiphytes have, in contrast to epiphytes, relatively slow growth, narrow temperature requirements, are cold-water adapted, perennial, have seasonal recruitment, complex life-history, depend on sexual reproduction, cannot reattach to hard substratum, cannot survive long-term as unattached populations, and have relatively narrow habitat requirements. These traits generally point to basiphytes being less resistant and resilient, compared to epiphytes, to storminess, warming, sedimentation, eutrophication and high water turbidity. Furthermore, epiphytes (including other ephemeral and opportunistic macroalgae) are more speciose compared to large canopy-forming basiphytes being represented by relatively few seagrasses, kelps, fucalean and large red and green algae. This implies that if a basiphytic species is becoming locally extinct, there is relatively little chance it can be replaced by a functionally similar species. By contrast, the more speciose epiphytic species are typically not only better adapted and more resilient to human stressors, but, simply because there are more of them, also have a higher chance that a functionally similar species can replace a lost epiphyte. In conclusion, we suggest that human stressors will continue to favor ephemeral opportunistic epiphytes over perennial slow growing basiphytes, and that an integrated management approach is needed to tackle the many complex direct and indirect effects whereby human stressors can modify basiphyte-epiphyte interactions.

## Conclusions

Epibionts and their basiphyte hosts encompass a wide range of taxonomic diversity and occur in most benthic marine habitats within the photic zone. Epibiont-basiphyte associations are commonplace in marine habitats and impact numerous ecological interactions and processes, from physiology to ecosystem ecology. While their interactions may range from negative to neutral to positive, the consequences of these interactions on the basiphyte are necessarily limited, as extreme epiphyte overgrowth that kills the host can result in host dislodgement, thereby likely causing the death of the epiphytes. In addition, host-epiphyte interactions can impact higher trophic levels.

While the distributions and abundances of epiphytes and basiphytes have been fairly well documented, less is known about the reciprocal impacts of basiphytes and epiphytes on each other—many studies have focused on the impact of epiphytes on a basiphyte, or vice versa. More laboratory and field studies that incorporate this ecological relevance, and/or test for specific interactions (e.g., chemical modifications between epiphytes and basiphytes) are needed. In addition, it is unknown how the species or genetic diversity of epiphytes interacts with the genetic diversity of the host species (Reusch and Hughes 2006). Lastly, epiphytes and basiphytes are not immune to anthropogenic impacts, which may affect them unequally. Understanding how these relationships may be affected as climate change occurs will be of critical importance to preserving these important ecosystem engineers.

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## References

- Abbott, I.A. and G. Hollenberg. 1976. *Marine Algae of California*. Stanford University Press, Stanford, California.
- Airolidi, L. 2003. The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology Annual Review* 41: 161–236.
- Airolidi, L. and F. Cinelli. 1997. Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from mediterranean rocky shore. *J. Exp. Mar. Biol. Ecol.* 215: 269–288.
- Airolidi, L. and M. Virgilio. 1998. Responses of turf-forming algae to spatial variations in the deposition of sediments. *Mar. Ecol. Prog. Ser.* 165: 271–282.
- Albins, M.A. and M.A. Hixon. 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar. Ecol. Prog. Ser.* 367: 233–238.
- Alcoverro, T., C.M. Duarte and J. Romero. 1997. The influence of herbivores on *Posidonia oceanica* epiphytes. *Aquat. Bot.* 56: 93–104.
- Amsler, C.D., M.O. Amsler, J.B. McClintock and B.J. Baker. 2009. Filamentous algal endophytes in macrophytic Antarctic algae: prevalence in hosts and palatability to mesoherbivores. *Phycologia* 48: 324–334.
- Andersen, T., J. Carstensen, E. Hernandez-Garcia and C.M. Duarte. 2009. Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology and Evolution* 24: 49–57.

- Anderson, L. 2012. Cost and benefits of intertidal algal epiphytism. M.S. Thesis. University of British Columbia, Vancouver.
- Arrontes, J. 1990. Composition, distribution on host, and seasonality of epiphytes on three intertidal algae. *Bot. Mar.* 33: 205–211.
- Ávila, E., M. del Carmen Méndez-Trejo, R. Riosmena-Rodríguez, J.M. López-Vivas and A. Senties. 2012. Epibiotic traits of the invasive red seaweed *Acanthophora spicifera* in La Paz Bay, South Baja California (Eastern Pacific). *Mar. Ecol.* 33: 470–480.
- Balata, D., L. Piazzì and F. Cinelli. 2007. Increase of sedimentation in a subtidal system: Effects on the structure and diversity of macroalgal assemblages. *J. Exp. Mar. Biol. Ecol.* 351: 73–82.
- Bernstein, B.B. and N. Jung. 1979. Selective pressures and coevolution in a kelp canopy community in southern California. *Ecol. Monogr.* 49: 335–355.
- Bertness, M.D. and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191–193.
- Bibby, R., P. Cleall-Harding, S. Rundle, S. Widdicombe and J. Spicer. 2007. Ocean acidification disrupts induced defences in the intertidal gastropod *Littorina littorea*. *Biol. Lett.* 3: 699–701.
- Bologna, P.A. and K.L. Heck. 1999a. Macrofaunal associations with seagrass epiphytes—Relative importance of trophic and structural characteristics. *Journal of Experimental Marine Biology and Ecology* 242: 21–39.
- Bologna, P.A.X. and K.L. Heck. 1999b. Macrofaunal associations with seagrass epiphytes: relative importance of trophic and structural characteristics. *J. Exp. Mar. Biol. Ecol.* 242: 21–39.
- Borowitzka, M.A., P.S. Lavery and M. van Keulen. 2006. Epiphytes of seagrasses. pp. 441–461. *In: Larkum, A.W.D., R.J. Orth and C.M. Duarte (eds.). Seagrasses: Biology, Ecology, and Conservation.* Springer, Dordrecht.
- Borum, J., H. Kaas and S. Wium-Anderson. 1984. Biomass variation and autotrophic production of an epiphyte-macrophyte community in a coastal Danish area: II. Epiphyte species composition, biomass and production. *Ophelia* 23: 165–179.
- Boström, C. and J. Mattila. 1999. The relative importance of food and shelter for seagrass-associated invertebrates: a latitudinal comparison of habitat choice by isopod grazers. *Oecologia* 120: 162–170.
- Boström, C. and J. Mattila. 2005. Effects of isopod grazing: an experimental comparison in temperate (*Idotea balthica*, Baltic Sea, Finland) and subtropical (*Erichsonella attenuata*, Gulf of Mexico, USA) ecosystems. *Crustaceana* 78: 185–200.
- Bouarab, K., P. Potin, F. Weinberger, J. Correa and B. Kloareg. 2001. The *Chondrus crispus-Acrochaete operculata* host-pathogen association, a novel model in glycobiology and applied phycopathology. *J. Appl. Phycol.* 13: 185–193.
- Bracken, M.E., C.A. Gonzalez-Dorantes and J.J. Stachowicz. 2007. Whole-community mutualism: associated invertebrates facilitate a dominant habitat-forming seaweed. *Ecology* 88: 2211–2219.
- Brawley, S.H. 1992. Mesoherbivores. Plant-animal interactions in the marine benthos. Clarendon Press, Oxford: 235–263.
- Brouns, J.J.W.M. and F.M.L. Heijs. 1986. Production and biomass of the seagrass *Enhalus acaroides* (Lf) Royle and its epiphytes. *Aquat. Bot.* 25: 21–45.
- Bruno, J.F., J.J. Stachowicz and M.D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18: 119–125.
- Bruno, J.F. and M.I. O'Connor. 2005. Cascading effects of predator diversity and omnivory in a marine food web. *Ecol. Lett.* 8: 1048–1056.
- Bulleri, F. and M.G. Chapman. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *J. Appl. Ecol.* 47: 26–35.
- Burke, C., T. Thomas, M. Lewis, P. Steinberg and S. Kjelleberg. 2011. Composition, uniqueness and variability of the epiphytic bacterial community of the green alga *Ulva australis*. *Isme Journal* 5: 590–600.
- Burkepile, D.E. and M.E. Hay. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* 87: 3128–3139.
- Butman, C.A. 1987. Larval settlement of soft-sediment invertebrates—the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes *Oceanogr. Mar. Biol. Annu. Rev.* 25: 113–165.
- Caddy, J., J. Csirke, S. Garcia and R. Grainger. 1998. How pervasive is “fishing down marine food webs”? *Science* 282: 1383–1383.

- Cambridge, M.L., A.W. Chiffings, C. Brittan, L. Moore and A.J. McComb. 1986. The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. *Aquat. Bot.* 24: 269–285.
- Cancino, J.M., M. Muñoz and M.C. Orellana. 1987. Effects of the bryozoan *Membranipora tuberculata* (Bose) on the photosynthesis and growth of *Gelidium rex* Santelices et Abbott. *J. Exp. Mar. Biol. Ecol.* 113: 105–112.
- Cardoso, P.G., M.A. Pardal, D. Raffaelli, A. Baeta and J.C. Marques. 2004. Macroinvertebrate response to different species of macroalgal mats and the role of disturbance history. *J. Exp. Mar. Biol. Ecol.* 308: 207–220.
- Carlton, J.T. 1996. Biological invasions and cryptogenic species. *Ecology* 77: 1653–1655.
- Cebrian, J., S. Enriquez, M. Fortes, N. Agawin, J.E. Vermaat and C.M. Duarte. 1999. Epiphyte accrual on *Posidonia oceanica* (L.) Delile leaves: implications for light absorption. *Bot. Mar.* 42: 123–128.
- Cebrian, J., J. Stutes and B. Christiaen. 2013. Effects of grazing and fertilization on epiphyte growth dynamics under moderately eutrophic conditions: implications for grazing rate estimates. *Mar. Ecol. Prog. Ser.* 474: 121–133.
- Cerrano, C., S. Puce, M. Chiantore, G. Bavestrello and R. Cattaneo-Vietti. 2001. The influence of the epizoic hydroid *Hydractinia angusta* on the recruitment of the Antarctic scallop *Adamussium colbecki*. *Polar Biol.* 24: 557–581.
- Chavanich, S. and L.G. Harris. 2002. The influence of macroalgae on seasonal abundance and feeding preference of a subtidal snail, *Lacuna vineta* (Montagu) (Littorinidae) in the Gulf of Maine. *J. Molluscan Stud.* 68: 73–78.
- Cho, J.Y., E. Kwon, J. Choi, S. Hong and H. Shin. 2001. Antifouling activity of seaweed extracts on the green alga *Enteromorpha prolifera* and the mussel *Mytilus edulis*. *J. Appl. Phycol.* 13: 117–125.
- Cook, K., M.A. Vanderklift and A.G.B. Poore. 2011. Strong effects of herbivorous amphipods on epiphyte biomass in a temperate seagrass meadow. *Mar. Ecol. Prog. Ser.* 442: 263–269.
- Craigie, J.S., J. Correa and M.E. Gordon. 1992. Cuticles from *Chondrus crispus* (Rhodophyta). *J. Phycol.* 28: 777–786.
- Cummins, S.P., D.E. Roberts and K.D. Zimmerman. 2004. Effects of the green macroalgae *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. *Mar. Ecol. Prog. Ser.* 266: 77–87.
- D'Antonio, C. 1985. Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: Negative effects on the host and food for herbivores? *J. Exp. Mar. Biol. Ecol.* 86: 197–218.
- Daleo, P., M. Escapa, J. Alberti and O. Iribarne. 2006. Negative effects of an autogenic ecosystem engineer: interactions between coralline turf and an ephemeral green alga. *Mar. Ecol. Prog. Ser.* 315: 67–73.
- Dawes, C.J., B.W. Teasdale and M. Friedlander. 2000. Cell wall structure of the agarophytes *Gracilaria tikvahiae* and *G. cornea* (Rhodophyta) and penetration by the epiphyte *Ulva lactuca* (Chlorophyta). *J. Appl. Phycol.* 12: 567–575.
- Dayton, P. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351–389.
- Dayton, P.K. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos of McMurdo Sound, Antarctica. pp. 81–95. *In: Proceedings of the Colloquium on Conservation Problems in Antarctica*. Allen Press, Lawrence, KS.
- de Bettignies, T., M.S. Thomsen and T. Wernberg. 2012. Wounded kelps: patterns and susceptibility to breakage. *Aquatic Botany* 17: 223–233.
- De Burgh, M.E. and P.V. Fankboner. 1978. A nutritional association between the bull kelp *Nereocystis luetkeana* and its epizoic bryozoan. *Oikos* 31: 69–72.
- den Hartog, C. 1972. Substratum: plants-multicellular plants. *Mar. Ecol.* 1: 1277–1289.
- Deudero, S., A. Blanco, A. Box, G. Mateu-Vicens, M. Cabanellas-Reboredo and A. Sureda. 2010. Interaction between the invasive macroalga *Lophocladia lallemandii* and the bryozoan *Reteporella grimaldii* at seagrass meadows: density and physiological responses. *Biol. Invasions* 12: 41–52.
- Dijkstra, J., H. Sherman and L.G. Harris. 2007. The role of colonial ascidians in altering biodiversity in marine fouling communities. *J. Exp. Mar. Biol. Ecol.* 342: 169–171.
- Dixon, J., S.C. Schroeter and J. Kastendiek. 1981. Effects of the encrusting bryozoan, *Membranipora membranacea*, on the loss of blades and fronds by the giant kelp, *Macrocystis pyrifera* (Laminariales). *J. Phycol.* 17: 341–345.
- Douglass, J.G., J.E. Duffy and J.F. Bruno. 2008. Herbivore and predator diversity interactively affect ecosystem properties in an experimental marine community. *Ecol. Lett.* 11: 598–608.



- Drake, L.A., F.C. Dobbs and R.C. Zimmerman. 2003. Effects of epiphyte load on optical properties and photosynthetic potential of the seagrasses *Thalassia testudinum* Banks ex König and *Zostera marina* L. *Limnol. Oceanogr.* 48: 456–463.
- Drouin, A., C.W. McKindsey and L.E. Johnson. 2011. Higher abundance and diversity in faunal assemblages with the invasion of *Codium fragile* ssp. *fragile* in eelgrass meadows. *Mar. Ecol. Prog. Ser.* 424: 105–117.
- Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87–112.
- Duffy, J.E. 1990. Amphipods on seaweeds: partners or pests? *Oecologia* 83: 267–276.
- Duffy, J.E. and M.E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecol. Monogr.* 70: 237–263.
- Duffy, J.E. and A.M. Harvilicz. 2001. Species-specific impacts of grazing amphipods in an eelgrass-bed community. *Mar. Ecol. Prog. Ser.* 223: 201–211.
- Duffy, J.E. and M.E. Hay. 2001. The ecology and evolution of marine consumer-prey interactions. pp. 131–157. *In*: Bertness, M.D., S.D. Gaines and M.E. Hay (eds.). *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Eastwood, M.M., M.J. Donahue and A.E. Fowler. 2007. Reconstructing past biological invasions: niche shifts in response to invasive predators and competitors. *Biol. Invasions* 9: 397–407.
- Edgar, G. and M. Aoki. 1993. Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*. *Oecologia* 95: 122–133.
- Edgar, G.J. 1990. The influence of plant structure on the species richness, biomass, and secondary production of macrofaunal assemblages associated with Western Australia seagrass beds. *J. Exp. Mar. Biol. Ecol.* 137: 215–240.
- Edgar, G.J. and A.I. Robertson. 1992. The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and processes in a Western Australian *Amphibolis* bed. *J. Exp. Mar. Biol. Ecol.* 160: 13–31.
- Edgar, G.J. and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia III. General relationships between sediments, seagrasses, invertebrates and fishes. *J. Exp. Mar. Biol. Ecol.* 194: 107–131.
- Engelen, A.H., A.L. Primo, T. Cruz and R. Santos. 2013. Faunal differences between the invasive brown macroalga *Sargassum muticum* and competing native macroalgae. *Biol. Invasions* 15: 171–183.
- Eriksson, B.K. and G. Johansson. 2003. Sedimentation reduces recruitment success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *Eur. J. Phycol.* 38: 217–222.
- Eriksson, B.K. and G. Johansson. 2005. Effects of sedimentation on macroalgae: species-specific responses are related to reproductive traits. *Oecologia* 143: 438–448.
- Filion-Myklebust, C. and T.A. Norton. 1981. Epidermis shedding in the brown seaweed *Asophyllum nodosum* (L.) Le Jolis and its ecological significance. *Marine Biology Letters* 1981: 45–51.
- Fletcher, R. and M. Callow. 1992. The settlement, attachment, and establishment of marine algal spores. *Eur. J. Phycol.* 27: 303–329.
- Fong, P., J.S. Desmond and J.B. Zedler. 1997. The effect of a horn snail on *Ulva expansa* (Chlorophyta): Consumer or facilitator of growth? *J. Phycol.* 33: 353–359.
- Fredriksen, S., H. Christie and B. Sæthre. 2007. Species richness in macroalgae and macrofauna assemblages on *Fucus serratus* L. (Phaeophyceae) and *Zostera marina* L. (Angiospermae) in Skagerrak, Norway. *Mar. Biol. Res.* 1: 2–19.
- Fricke, A., T.V. Titlyanova, M.M. Nugues and K. Bischof. 2011. Depth-related variation in epiphytic communities growing on the brown alga *Lobophora variegata* in a Caribbean coral reef. *Coral Reefs* 30: 967–973.
- Garbary, D.J., R.J. Deckert and C.B. Hubbard. 2005. *Asophyllum* and its symbionts. VII. Three-way interactions among *Asophyllum nodosum* (Phaeophyceae), *Mycophycias asophylli* (Ascomycetes) and *Vertebrata lanosa* (Rhodophyta). *Algae* 20: 353–361.
- Gaylord, B., C.A. Blanchette and M.W. Denny. 1994. Mechanical consequences of size in wave swept algae. *Ecol. Monogr.* 64: 287–313.
- Gennaro, P. and L. Piazzini. 2011. Synergism between two anthropic impacts: *Caulerpa racemosa* var. *cylindracea* invasion and seawater nutrient enrichment. *Mar. Ecol. Prog. Ser.* 427: 59–70.
- Gonzalez, M.A. and L.J. Goff. 1989. The red algal epiphytes *Microcladia coulterii* and *M. californica* (Rhodophyceae: Ceramiales). II. Basiphyte specificity. *J. Phycol.* 25: 558–567.

- Guerra-García, J.M., M. Ros, D. Izquierdo and M.M. Soler-Hurtado. 2012. The invasive *Asparagopsis armata* versus the native *Corallina elongata*: Differences in associated peracarid assemblages. *J. Exp. Mar. Biol. Ecol.*: 121–128.
- Hacker, S.D. and R.S. Steneck. 1990. Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71: 2269–2285.
- Hadfield, M.G. 1986. Settlement and recruitment of marine invertebrates: A perspective and some proposals. *Bull. Mar. Sci.* 39: 418–425.
- Hall, M. and S. Bell. 1988. Response of small motile epifauna to complexity of epiphytic algae on seagrass blades. *J. Mar. Res.* 46: 613–630.
- Hallam, N.D., M.N. Clayton and D. Parish. 1980. Studies on the association between *Notheia anomala* and *Hormosira banksii* (Phaeophyta). *Aust. J. Bot.* 28: 239–248.
- Hansen, G.I. 1986. A newly discovered host of the seagrass epiphyte *Smithora naiadum* (Bangiophyceae, Rhodophyta). *Canadian Journal of Botany* 64: 900–901.
- Harder, T. 2008. Marine epibiosis: concepts, ecological consequences, and host defence. *Springer Series on Biofilms* 4: 219–231.
- Harlin, M. 1973. 'Obligate' algal epiphyte: *Smithora naiadum* grows on synthetic substrate. *J. Phycol.* 9: 230–232.
- Harlin, M. 1980. Seagrass epiphytes. pp. 117–152. *In*: Phillips R.C. and G.P. McRoy (eds.). *Handbook of Seagrass Biology: An Ecosystem Perspective*. Taylor & Frances, New York.
- Hauxwell, J., J. Cebrian and I. Valiela. 2003a. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Mar. Ecol. Prog. Ser.* 247: 59–73.
- Hauxwell, J., J. Cebrian and I. Valiela. 2003b. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology-Progress Series* 247: 59–73.
- Hay, M.E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *Am. Nat.* 128: 617–641.
- Hay, M.E., J.E. Duffy, C.A. Pfister and W. Fenical. 1987. Chemical defense against different marine herbivores: Are amphipods insect equivalents? *Ecology* 68: 1567–1580.
- Hay, M.E., J.D. Parker, D.E. Burkepile, C.C. Caudill, A.E. Wilson, Z.P. Hallinan and A.D. Chequer. 2004. Mutualisms and aquatic community structure: the enemy of my enemy is my friend. *Annual Review of Ecology, Evolution, and Systematics* 35: 175–197.
- Heck, K.L., J.R. Pennock and J.F. Valentine. 2000. Effects of nutrient enrichment and small predator density on seagrass ecosystems: An experimental assessment. *Limnol. Oceanogr.* 45: 1041–1057.
- Hellio, C., J.-P. Marechal, B. Véron, G. Bremer, A.S. Clare and Y. Le Gal. 2004. Seasonal variation of antifouling activities of marine algae from the Brittany coast (France). *Mar. Biotechnol.* 6: 67–82.
- Hemmi, A., A. Makinen, V. Jormalainen and T. Honkanen. 2005. Responses of growth and phlorotannins in *Fucus vesiculosus* to nutrient enrichment and herbivory. *Aquat. Ecol.* 39: 201–211.
- Hepburn, C. and C. Hurd. 2005. Conditional mutualism between the giant kelp *Macrocystis pyrifera* and colonial epifauna. *Mar. Ecol. Prog. Ser.* 302: 37–48.
- Hepburn, C., C. Hurd and R.D. Frew. 2006. Colony structure and seasonal differences in light and nitrogen modify the impact of sessile epifauna on the giant kelp *Macrocystis pyrifera* (L.) C. Agardh. *Hydrobiologia* 560: 373–384.
- Hewitt, C.L., M.L. Campbell, R.E. Thresher, R.B. Martin, S. Boyd, B.R. Cohen, D.R. Currie, M.F. Gomon, M.J. Keough, J.A. Lewis, M.M. Lockett, N. Mays, M.A. McArthur, T. O'Hara, G.C. Poore, J. Ross, M.J. Storey, J.E. Watson and R.S. Wilson. 2004. Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Mar. Biol.* 144: 183–202.
- Hily, C., S. Connan, C. Raffin and S. Wyllie-Echeverria. 2004. *In vitro* experimental assessment of the grazing pressure of two gastropods on *Zostera marina* L. epiphytic algae. *Aquat. Bot.* 78: 183–195.
- Hoeffle, H., M.S. Thomsen and M. Holmer. 2011. High mortality of *Zostera marina* under high temperature regimes but minor effects of the invasive macroalgae *Gracilaria vermiculophylla*. *Estuar. Coast. Shelf Sci.* 92: 35–46.
- Hoeffle, H., T. Wernberg, M.S. Thomsen and M. Holmer. 2012. Drift algae, an invasive snail and elevated temperature reduces the ecological performance of a warm-temperate seagrass via additive effects. *Mar. Ecol. Prog. Ser.* 450: 67–80.
- Holmer, M. and R.M. Nielsen. 2007. Effects of filamentous algal mats on sulfide invasion in eelgrass (*Zostera marina*). *J. Exp. Mar. Biol. Ecol.* 353: 245–252.

- Holmer, M., P. Wirachwong and M.S. Thomsen. 2011. Negative effects of stress-resistant drift algae and high temperature on a small ephemeral seagrass species. *Mar. Biol.* 158: 297–309.
- Holmquist, J.G. 1997. Disturbance and gap formation in a marine benthic mosaic—influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. *Mar. Ecol. Prog. Ser.* 158: 121–130.
- Honkanen, T. and V. Jormalainen. 2005. Genotypic variation in tolerance and resistance to fouling in the brown alga *Fucus vesiculosus*. *Oecologia* 144: 196–205.
- Hootsmans, M.J.M. and J.E. Vermaat. 1985. The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. *Aquat. Bot.* 22: 83–88.
- Howard, R.K. 1982. Impact of feeding activities of epibenthic amphipods on surface-fouling of eelgrass leaves. *Aquat. Bot.* 14: 91–97.
- Hughes, R.G., S. Johnson and I.D. Smith. 1991. The growth patterns of some hydroids that are obligate epiphytes of seagrass leaves. *Hydrobiologia* 216–217: 205–210.
- Ilken, K. 2012. Grazers on benthic seaweeds. pp. 157–175. *In: Wiencke, C. and K. Bischof (eds.). Seaweed Biology.* Springer, Berlin Heidelberg.
- Irving, A.D. and S.D. Connell. 2002. Interactive effects of sedimentation and microtopography on the abundance of subtidal turf-forming algae. *Phycologia* 41: 517–522.
- Jackson, J.B.C. 1997. Reefs since Columbus. *Coral Reefs* 16: S23–S32.
- Janiak, D.S. and R.B. Whitlatch. 2012. Epifaunal and algal assemblages associated with the native *Chondrus crispus* (Stackhouse) and the non-native *Grateloupia turuturu* (Yamada) in eastern Long Island Sound. *J. Exp. Mar. Biol. Ecol.* 413: 38–44.
- Jernakoff, P. and J. Nielsen. 1997. The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. *Aquat. Bot.* 56: 183–202.
- Jernakoff, P., A. Brearley and J. Nielsen. 1996. Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. *Oceanogr. Mar. Biol. Annu. Rev.* 34.
- Joint, I., K. Tait, M. Callow, J.A. Callow, D. Milton, P. Williams and M. Camara. 2002. Cell-to-cell communication across the prokaryote-eukaryote boundary. *Science* 298: 1207.
- Jones, E. 2007. Impacts of habitat-modifying invasive macroalgae on epiphytic algal communities. M.S. Thesis. University of Rhode Island, Kingston, Rhode Island.
- Jones, E. and C.S. Thornber. 2010. Effects of habitat-modifying invasive macroalgae on epiphytic algal communities. *Mar. Ecol. Prog. Ser.* 400: 87–100.
- Jormalainen, V., T. Honkanen and N. Heikkilä. 2001a. Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. *Mar. Ecol. Prog. Ser.* 220: 219–230.
- Jormalainen, V., T. Honkanen, A. Mäkinen, A. Hemmi and O. Vesakoski. 2001b. Why does herbivore sex matter? Sexual differences in utilization of *Fucus vesiculosus* by the isopod *Idotea baltica*. *Oikos* 93: 77–86.
- Kangas, P., H. Autio, G. Hälfors, H. Luther, Å. Niemi and H. Salemaa. 1982. A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–81. *Acta Bot. Fenn.* 118: 1–27.
- Karez, R., S. Engelbert and U. Sommer. 2000. 'Co-consumption' and 'protective coating': two new proposed effects of epiphytes on their macroalgal hosts in mesograzers-epiphyte-host interactions. *Mar. Ecol. Prog. Ser.* 205: 85–93.
- Kato, T., A.S. Kumanireng, I. Ichinose, Y. Kitahara, Y. Kakinuma, M. Nishihira and M. Kato. 1975. Active components of *Sargassum tortile* effecting the settlement of *Coryne Uchidai*. *Experientia* 31: 433–434.
- Kautsky, N., H. Kautsky, U. Kautsky and M. Waern. 1986. Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940's indicates eutrophication of the Baltic Sea. *Mar. Ecol. Prog. Ser.* 28: 1–8.
- Kendrick, G., D. Walker and J. Arthur. 1988. Changes in distribution of macro-algal epiphytes on stems of the seagrass *Amphibolis antarctica* along a salinity gradient in Shark Bay, Western Australia. *Phycologia* 27: 201–208.
- Keough, M.J. 1986. The distribution of the bryozoan *Bugula neritina* on seagrass blades: settlement, growth, and mortality. *Ecology* 67: 846–857.
- Kersen, P., J. Kotta, M. Bučas, N. Kolesova and Z. Dekere. 2011. Epiphytes and associated fauna on the brown alga *Fucus vesiculosus* in the Baltic and the North Seas in relation to different abiotic and biotic variables. *Mar. Ecol.* 32: 87–95.
- Kim, M.J., J.S. Choi, S.E. Kang, J.Y. Cho, H. Jin, B.S. Chun and Y.K. Hong. 2004. Multiple allelopathic activity of the crustose coralline alga *Lithophyllum yessoense* against settlement and germination of seaweed spores. *J. Appl. Phycol.* 16: 175–179.
- Klumpp, D.W., J.S. Salita-Espinosa and M.D. Fortes. 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aquat. Bot.* 43: 327–349.

- Koch, M.S., S. Schopmeyer, C. Kyhn-Hansen and C.J. Madden. 2007. Synergistic effects of high temperature and sulfide on tropical seagrass. *J. Exp. Mar. Biol. Ecol.* 341: 91–101.
- Kotta, J., T. Paalme, G. Martin and A. Mäkinen. 2000. Major changes in macroalgae community composition affect the food and habitat preference of *Idotea baltica*. *Int. Rev. Hydrobiol.* 85: 697–705.
- Kraberg, A.C. and T.A. Norton. 2007. Effect of epiphytism on reproductive and vegetative lateral formation in the brown, intertidal seaweed *Ascophyllum nodosum* (Phaeophyceae). *Phycol. Res.* 55: 17–24.
- Krause-Jensen, D., P.B. Christensen and S. Rysgaard. 1999. Oxygen and nutrient dynamics within mats of the filamentous macroalgae *Chaetomorpha linum*. *Estuaries* 22: 31–38.
- Lachnit, T., D. Meske, M. Wahl, T. Harder and R. Schmitz. 2011. Epibacterial community patterns on marine macroalgae are host-specific but temporally variable. *Environ. Microbiol.* 13: 655–665.
- Laihonon, P. and E.R. Furman. 1986. The site of settlement indicates commensalism between blue mussel and its epibiont. *Oecologia* 71: 38–40.
- Lapointe, B.E., P.J. Barile and W.R. Matzie. 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: discrimination of local versus regional nitrogen sources. *J. Exp. Mar. Biol. Ecol.* 308: 23–58.
- Lavery, P.S. and M.A. Vanderklift. 2002. A comparison of spatial and temporal patterns in epiphytic macroalgal assemblages of the seagrasses *Amphibolis griffithii* and *Posidonia coriacea*. *Mar. Ecol. Prog. Ser.* 236: 99–112.
- Leite, F.P.P. and A. Turra. 2003. Temporal variation in *Sargassum* biomass, *Hypnea* epiphytism and associated fauna. *Brazilian Archives of Biology and Technology* 46: 665–671.
- Leonardi, P.L., A.B. Miravalles, S. Faugeron, V. Flores, J. Beltrán and J. Correa. 2006. Diversity, phenomenology and epidemiology of epiphytism in farmed *Gracilaria chilensis* (Rhodophyta) in northern Chile. *Eur. J. Phycol.* 41: 247–257.
- Linskens, H.F. 1963. Beitrag zur Frage der Beziehungen zwischen Epiphyte und Basiphyt bei marinen Algen. *Publ. Staz. Zool. Napoli* 33: 274–293.
- Littler, M.M. 1980. Morphological form and photosynthetic performances of marine macroalgae: Tests of a functional form hypothesis. *Bot. Mar.* 23: 161–166.
- Lobban, C.S. and D.M. Baxter. 1983. Distribution of the red algal epiphyte *Polysiphonia lanosa* and its brown algal host *Ascophyllum nodosum* in the Bay of Fundy. *Bot. Mar.* 26: 533–538.
- Lobelle, D., E.J. Kenyon, K. Cook and J.C. Bull. 2013. Local competition and metapopulation processes drive long-term seagrass-epiphyte population dynamics. *PLoS ONE* 8: e57072.
- Longtin, C.M. and R.A. Scrosati. 2009. Role of surface wounds and brown algal epiphytes in the colonization of *Ascophyllum nodosum* (Phaeophyceae) fronds by *Vertebrata lanosa* (Rhodophyta). *J. Phycol.* 45: 535–539.
- Longtin, C.M., R.A. Scrosati, G.B. Whalen and D.J. Garbary. 2009. Distribution of algal epiphytes across environmental gradients at different scales: intertidal elevation, host canopies, and host fronds. *J. Phycol.* 45: 820–827.
- Lotze, H.K., B. Worm and U. Sommer. 2000. Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. *Oikos* 89: 46–58.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *The American Naturalist* 112: 23–39.
- Martin, S. and J.P. Gattuso. 2009. Response of Mediterranean coralline algae to ocean acidification and elevated temperature. *Global Change Biol.* 15: 2089–2100.
- Martin-Smith, K.M. 1993. Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology* 174: 243–260.
- Mathieson, A.C., C.J. Dawes, L.G. Harris and E.J. Hehre. 2003. Expansion of the Asiatic green algal *Codium fragile* ssp. *tomentosoides* in the Gulf of Maine. *Rhodora* 105: 1–53.
- McCarthy, A., R.W. Osman and R.B. Whitlatch. 2007. Effects of temperature on growth rates of colonial ascidians: A comparison of *Didemnum* sp. to *Botryllus schlosseri* and *Botrylloides violaceus*. *J. Exp. Mar. Biol. Ecol.* 342: 172–174.
- McGlathery, K. 2001. Macroalgal blooms contribute to the decline in seagrasses in nutrient-enriched coastal waters. *J. Phycol.* 37: 453–456.
- Miller, L.P. and B. Gaylord. 2007. Barriers to flow: the effects of experimental cage structures on water velocities in high-energy subtidal and intertidal environments. *J. Exp. Mar. Biol. Ecol.* 344: 215–228.
- Miller, M.W. 1998. Coral/seaweed competition and the control of community structure within and between latitudes. *Oceanography and Marine Biology: An Annual Review* 36: 65–96.

- Moss, B.L. 1982. The control of epiphytes by *Halidrys siliquosa* (L.) Lyngb. (Phaeophyta, Cystoseiraceae). *Phycologia* 21: 185–191.
- Mukai, H. and A. Iijima. 1995. Grazing effects of a gammaridean amphipod, *Ampithoe* sp., on the seagrass, *Syringodium isoetifolium*, and epiphytes in a tropical seagrass bed of Fiji. *Ecol. Res.* 10: 243–257.
- Nakaoka, M. 2002. Predation on seeds of seagrasses *Zostera marina* and *Zostera caulescens* by a tanaid crustacean *Zeuxo* sp. *Aquat. Bot.* 72: 99–106.
- Norkko, J., E. Bonsdorff and A. Norkko. 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. *J. Exp. Mar. Biol. Ecol.* 248: 79–104.
- Norton, T.A. and M.R. Benson. 1983. Ecological interactions between the brown seaweed *Sargassum muticum* and its associated fauna. *Mar. Biol.* 75: 169–177.
- Nyberg, C.D., M.S. Thomsen and I. Wallentinus. 2009a. Flora and fauna associated with the introduced red alga *Gracilaria vermiculophylla*. *Eur. J. Phycol.* 44: 395–403.
- Nyberg, C.D., M.S. Thomsen and I. Wallentinus. 2009b. Flora and fauna associated with the introduced red alga *Gracilaria vermiculophylla*. *European Journal of Phycology* 44: 395–403.
- Nylund, G. and H. Pavia. 2005. Chemical versus mechanical inhibition of fouling in the red alga *Dilsea carnosa*. *Mar. Ecol. Prog. Ser.* 299: 111–121.
- Nylund, G., P. Gribben, R. de Nys, P.D. Steinberg and H. Pavia. 2007. Surface chemistry versus whole-cell extracts: antifouling tests with seaweed metabolites. *Mar. Ecol. Prog. Ser.* 329: 73–84.
- O'Connor, N.E. and J.F. Bruno. 2007. Predatory fish loss affects the structure and functioning of a model marine food web. *Oikos* 116: 2027–2038.
- Orav-Kotta, H. and J. Kotta. 2004. Food and habitat choice of the isopod *Idotea baltica* in the northeastern Baltic Sea. *Hydrobiologia* 514: 79–85.
- Orth, R., T.J.B. Carruthers, W.C. Dennison, C.M. Duarte, J.W. Fourqurean, J.K.L. Heck, A.R. Hughes, G. Kendrick, W.J. Kenworthy, S. Olyarnik, F.T. Short, M. Waycott and S.L. Williams. 2006. A global crisis for seagrass ecosystems. *Bioscience* 56: 987–996.
- Orth, R.J. and J.V. Montfrans. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquat. Bot.* 18: 43–69.
- Paerl, H.W. 1995. Coastal eutrophication in relation to atmospheric nitrogen deposition: current perspectives. *Ophelia* 41: 237–259.
- Paine, R.T. 1966. Food web complexity and species diversity. *The American Naturalist* 100: 65–75.
- Paul, V.J., M.P. Puglisi and R. Ritson-Williams. 2006. Marine chemical ecology. *Natural Product Reports* 23: 153–180.
- Pavia, H., H. Carr and P. Åberg. 1999. Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. and its epiphytic macroalgae. *J. Exp. Mar. Biol. Ecol.* 236: 15–32.
- Pearson, G.A. and L.F. Evans. 1990. Settlement and survival of *Polysiphonia lanosa* (Ceramiales) spores on *Ascophyllum nodosum* and *Fucus vesiculosus* (Fuciales). *J. Phycol.* 26: 597–603.
- Pedersen, M.F. and J. Borum. 1996. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar. Ecol. Prog. Ser.* 142: 261–272.
- Pedersen, M.F. and J. Borum. 1997. Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. *Mar. Ecol. Prog. Ser.* 161: 155–163.
- Pereg-Gerk, L., N. Sar and Y. Lipkin. 2002. *In situ* nitrogen fixation associated with seagrasses in the Gulf of Elat (Red Sea). *Aquat. Ecol.* 36: 387–394.
- Perrone, C. and E. Cecere. 1997. Regeneration and mechanisms of secondary attachment in *Solieria filiformis* (Gigartinales, Rhodophyta). *Phycologia* 36: 120–127.
- Piazzi, L., D. Balata and F. Cinelli. 2002. Epiphytic macroalgal assemblages of *Posidonia oceanica* rhizomes in the western Mediterranean. *Eur. J. Phycol.* 37: 69–76.
- Piazzi, L., D. Balata, G. Ceccherelli and F. Cinelli. 2005. Interactive effect of sedimentation and *Caulerpa racemosa* var. *cylindracea* invasion on macroalgal assemblages in the Mediterranean Sea. *Estuar. Coast. Shelf Sci.* 64: 467–474.
- Poore, A.G. 1994. Selective herbivory by amphipods inhabiting the brown alga *Zonaria angustata*. *Mar. Ecol. Prog. Ser.* 107: 113–113.
- Poore, A.G.B., A.H. Campbell and P.D. Steinberg. 2009. Natural densities of mesograzers fail to limit growth of macroalgae or their epiphytes in a temperate algal bed. *J. Ecol.* 97: 164–175.
- Post, D.M. 2002. The long and short of food-chain length. *Trends Ecol. Evol.* 17: 269–277.

- Potin, P. 2012. Intimate associations between epiphytes, endophytes, and parasites of seaweeds. pp. 203–234. In: Wiencke, C. and K. Bischof (eds.). *Seaweed Biology*. Springer-Verlag, Berlin.
- Prado, P., T. Alcoverro, B. Martínez-Crego, A. Vergés, M. Pérez and J. Romero. 2007. Macrograzers strongly influence patterns of epiphytic assemblages in seagrass meadows. *J. Exp. Mar. Biol. Ecol.* 350: 130–143.
- Reddy, K., W. DeBusk, R. DeLaune and M. Koch. 1993. Long-term nutrient accumulation rates in the Everglades. *Soil Sci. Soc. Am. J.* 57: 1147–1155.
- Reusch, T.B.H. and A.R. Hughes. 2006. The emerging role of genetic diversity for ecosystem functioning: Estuarine macrophytes as models. *Estuaries and Coasts* 29: 159–164.
- Rindi, F. and M.D. Guiry. 2004. Composition and spatio-temporal variability of the epiphytic macroalgal assemblage of *Fucus vesiculosus* Linnaeus at Clare Island, Mayo, western Ireland. *J. Exp. Mar. Biol. Ecol.* 311: 233–252.
- Rohr, N.E., C.S. Thornber and E. Jones. 2011. Epiphyte and herbivore interactions impact recruitment in a marine subtidal system. *Aquat. Ecol.* 45: 213–219.
- Ruesink, J.L. 2000. Intertidal mesograzers in field microcosms: linking laboratory feeding rates to community dynamics. *J. Exp. Mar. Biol. Ecol.* 248: 163–176.
- Russel, B.D., J.A. Thompson, L.J. Falkenberg and S.D. Connell. 2009. Synergistic effects of climate change and local stressors: CO<sub>2</sub> and nutrient driven change in subtidal rocky habitats. *Global Change Biol.*
- Russell, G. and C. Veltkamp. 1984. Epiphyte survival on skin-shedding macrophytes. *Mar. Ecol. Prog. Ser.* 18: 149–153.
- Salemaa, H. 1987. Herbivory and microhabitat preferences of *Idotea* spp. (Isopoda) in the northern Baltic Sea. *Ophelia* 27: 1–15.
- Sand-Jensen, K.A. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3: 55–63.
- Saunders, J.E., M.J. Attrill, S.M. Shaw and A.A. Rowden. 2003. Spatial variability in the epiphytic algal assemblages of *Zostera marina* seagrass beds. *Mar. Ecol. Prog. Ser.* 249: 107–115.
- Saunders, M. and A. Metaxas. 2008. High recruitment of the introduced bryozoan *Membranipora membranacea* is associated with kelp bed defoliation in Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.* 369: 139–151.
- Schanz, A., P. Polte, H. Asmus and R. Asmus. 2000. Currents and turbulence as a top-down regulator in intertidal seagrass communities. *Biol. Mar. Medit.* 7: 278–281.
- Schanz, A., P. Polte and H. Asmus. 2002. Cascading effects of hydrodynamics on an epiphyte-grazer system in intertidal seagrass beds of the Wadden Sea. *Mar. Biol.* 141: 287–297.
- Scheibling, R.E. and P. Gagnon. 2009. Temperature-mediated outbreak dynamics of the invasive bryozoan *Membranipora membranacea* in Nova Scotian kelp beds. *Mar. Ecol. Prog. Ser.* 390: 1–13.
- Schelske, C.L., D.J. Conley, E.F. Stoermer, T.L. Newberry and C. Campbell. 1986. Biogenic silica and phosphorus accumulation in sediments as indices of eutrophication in the Laurentian Great Lakes. *Hydrobiologia* 143: 79–86.
- Schmidt, A.L. and R.E. Scheibling. 2006. A comparison of epifauna and epiphytes on native kelps (*Laminaria* species) and an invasive alga (*Codium fragile* ssp. *tomentosoides*) in Nova Scotia, Canada. *Bot. Mar.* 49: 315–330.
- Schmitt, T.M., M. Hay and N. Lindquist. 1995. Constraints on chemically mediated coevolution: multiple functions for seaweed ecology metabolites. *Ecology* 76: 107–123.
- Schneider, F.I. and K.H. Mann. 1991. Species specific relationships of invertebrates to vegetation in a seagrass bed. II, Experiments on the importance of macrophyte shape, epiphyte cover and predation. *J. Exp. Mar. Biol. Ecol.* 145: 119–139.
- Schultze, K., K. Janke, A. Krüß and W. Weidemann. 1990. The macrofauna and macroflora associated with *Laminaria digitata* and *Laminaria hyperborea* at the island of Helgoland (German Bight, North Sea). *Helgolander Meeresuntersuchungen* 44: 39–51.
- Seed, R. and R.J. O'Connor. 1981. Community organization in marine algal epifaunas. *Annu. Rev. Ecol. Syst.* 12: 49–74.
- Shacklock, P.F. and R.W. Doyle. 1983. Control of epiphytes in seaweed cultures using grazers. *Aquaculture* 31: 141–151.
- Short, F.T. and H.A. Neckles. 1999. The effects of global climate change on seagrasses. *Aquat. Bot.* 63: 169–196.
- Sieburth, J.M. and J.L. Tootle. 1981. Seasonality of microbial fouling on *Asophyllum nodosum* (L.) Lejol., *Fucus vesiculosus* L., *Polysiphonia lanosa* (L.) Tandy and *Chondrus crispus* Stackh. *J. Phycol.* 17: 57–64.



- Smale, D.A. and T. Wernberg. 2013. Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B: Biological Sciences* 280: 2012–2829.
- Spivak, A.C., E.A. Canuel, J.E. Duffy and J.P. Richardson. 2009. Nutrient enrichment and food web composition affect ecosystem metabolism in an experimental seagrass habitat. *PloS ONE* 4: e7473.
- Stachowicz, J.J. 2001. Mutualism, facilitation, and the structure of ecological communities. *BioScience* 51: 235–246.
- Stachowicz, J.J. and M.E. Hay. 1996. Facultative mutualism between an herbivorous crab and a coralline alga: advantages of eating noxious seaweeds. *Oecologia* 105: 377–387.
- Stachowicz, J.J. and M.E. Hay. 1999. Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense. *Ecology* 80: 2085–2101.
- Stachowicz, J.J. and R.B. Whitlatch. 2005. Multiple mutualists provide complementary benefits to their seaweed host. *Ecology* 86: 2418–2427.
- Steneck, R.S. and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.* 68: 299–319.
- Steneck, R.S., M.H. Graham, B.J. Bourque, D. Corbett, J.M. Erlandson, J.A. Estes and M.J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* 29: 436–459.
- Stewart, J.G. 1982. Anchor species and epiphytes in intertidal algal turf. *Pac. Sci.* 36: 45–60.
- Stricker, S.A. 1989. Settlement and metamorphosis of the marine bryozoan *Membranipora membranacea*. *Bull. Mar. Sci.* 45: 387–405.
- Suzuki, Y., T. Takabayashi, T. Kawaguchi and K. Matsunaga. 1998. Isolation of an allelopathic substance from the crustose coralline algae, *Lithophyllum* spp., and its effect on the brown alga *Laminaria religiosa* Miyabe (Phaeophyta). *J. Exp. Mar. Biol. Ecol.* 225: 69–77.
- Taylor, P.D. and M.A. Wilson. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Sci. Rev.* 62: 1–103.
- Taylor, R.B. 1998. Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Mar. Ecol. Prog. Ser.* 172: 37–51.
- Thomsen, M. 2004a. Macroalgal distribution patterns and ecological performances in a tidal coastal lagoon, with emphasis on the non-indigenous *Codium fragile* ssp. *tomentosoides*. Ph.D. Thesis. University of Virginia, Charlottesville, Virginia.
- Thomsen, M.S. 2004b. Species, thallus size and substrate determine macroalgal break forces and break places in a low-energy soft-bottom lagoon. *Aquat. Bot.* 80: 153–161.
- Thomsen, M.S. 2010. Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. *Aquatic Invasions* 5: 341–346.
- Thomsen, M.S. and T. Wernberg. 2005. What affects the forces required to break or dislodge macroalgae? A minireview. *Eur. J. Phycol.* 40: 1–10.
- Thomsen, M.S., T. Wernberg, P.A. Stæhr and M.F. Pedersen. 2006. Spatio-temporal distribution patterns of the invasive macroalga *Sargassum muticum* within a Danish *Sargassum*-bed. *Helgol. Mar. Res.* 60: 50–58.
- Thomsen, M.S., T. Wernberg, A.H. Altieri, F. Tuya, D. Gulbrandsen, K.J. McGlathery, M. Holmer and B.R. Silliman. 2010. Habitat cascades: The conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integr. Comp. Biol.* 50: 158–175.
- Thomsen, M.S., J.D. Olden, T. Wernberg, J.N. Griffin and B.R. Silliman. 2011. A broad framework to organize and compare ecological invasion impacts. *Environ. Res.* 111: 899–908.
- Thomsen, M.S., T. de Bettignies, T. Wernberg, M. Holmer and B. Debeuf. 2012a. Harmful algae are not harmful to everyone. *Harmful Algae* 16: 74–80.
- Thomsen, M.S., T. Wernberg, A.H. Engelen, F. Tuya, M.A. Vanderklift, M. Holmer, K.J. McGlathery, F. Arenas, J. Kotta and B.R. Silliman. 2012b. A meta-analysis of seaweed impacts on seagrasses: generalities and knowledge gaps. *PLoS ONE* 7: e28595.
- Tomas, F., X. Turon and J. Romero. 2005. Effects of herbivores on a *Posidonia oceanica* seagrass meadow: importance of epiphytes. *Mar. Ecol. Prog. Ser.* 287: 115–125.
- Tootle, J.L. 1974. The fouling of intertidal seaweeds: Seasonal species and cuticular regulation. M.S. Thesis. University of Rhode Island, Kingston.
- Trautman, D.A. and M.A. Borowitzka. 1999. The distribution of the epiphytic organisms on *Posidonia australis* and *P. sinuosa*, two seagrasses with differing leaf morphology. *Mar. Ecol. Prog. Ser.* 179: 215–229.

- Troell, M., L. Pihl, P. Roenbaek, H. Wennhage, T. Soederquist and N. Kautsky. 2005. Regime shifts and ecosystem services in Swedish coastal soft bottom habitats: when resilience is undesirable. *Ecol. Soc.* 10: 13 pp., online journal.
- Trussell, G., P. Ewanchuk, M.D. Bertness and B.R. Silliman. 2004. Trophic cascades in rocky shore tide pools: distinguishing lethal and non-lethal effects. *Oecologia* 139: 427–432.
- Valentine, J.F. and J.E. Duffy. 2006. The central role of grazing in seagrass ecology. pp. 463–501. In: Larkum, A.W.D., R.J. Orth and C.M. Duarte (eds.). *Seagrasses: Biology, Ecology, and Conservation*. Springer, Dordrecht, The Netherlands.
- Valiela, I., J. McClelland, J. Hauxwell, P.J. Behr, D. Hersh and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.* 42: 1105–1118.
- van Montfrans, J., R.L. Wetzel and R.J. Orth. 1984. Epiphyte-grazer relationships in seagrass meadows: consequences for seagrass growth and production. *Estuaries* 7: 289–309.
- Viejo, R.M. 1999. Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquat. Bot.* 64: 131–149.
- Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar. Ecol. Prog. Ser.* 58: 175–189.
- Wahl, M. 2009. Epibiosis: Ecology, effects, and defences. pp. 61–72. In: Wahl, M. (ed.). *Marine Hard Bottom Communities*. Springer-Verlag, Berlin.
- Wahl, M. and M. Hay. 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. *Oecologia* 102: 329–240.
- Waycott, M., C.M. Duarte, T.J.B. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, J.K.L. Heck, A.R. Hughes, G.A. Kendrick, K.W.J., F.T. Short and S.L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106: 12377–12381.
- Wernberg, T., M.S. Thomsen, P.A. Staerh and M.F. Pedersen. 2004. Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark). *Helgol. Mar. Res.* 58: 154–161.
- Wernberg, T., D.A. Smale, F. Tuya, M.S. Thomsen, T.J. Langlois, T. de Bettignies, S. Bennett and C.S. Rousseaux. 2012. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change* 3: 78–82.
- Whalen, M.A., J.E. Duffy and J.B. Grace. 2013. Temporal shifts in top-down versus bottom-up control of epiphytic algae in a seagrass ecosystem. *Ecology* 94: 510–520.
- Wiencke, C. 1987. Respiration and photosynthesis in the intertidal alga *Cladophora rupestris* (L.) Kütz under fluctuating salinity regimes. *J. Exp. Mar. Biol. Ecol.* 114: 183–197.
- Wikström, S.A. and L. Kautsky. 2004. Invasion of a habitat-forming seaweed: effects on associated biota. *Biol. Invasions* 6: 141–150.
- Wikström, S.A. and H. Pavia. 2004. Chemical settlement inhibition versus post-settlement mortality as an explanation for differential fouling of two congeneric seaweeds. *Oecologia* 138: 223–230.
- Williams, B.S., J.E. Hughes and K. Hunter-Thomson. 2002. Influence of epiphytic algal coverage on fish predation rates in simulated eelgrass habitats. *Biological Bulletin* 203: 248–249.
- Williams, G.A. and R. Seed. 1992. Interactions between macrofaunal epiphytes and their host algae. pp. 189–211. In: John, D.M., S.J. Hawkins and J.H. Price (eds.). *Plant-animal Interactions in the Marine Benthos*. Clarendon Press, Oxford.
- Wilson, L. 1978. Epiphytes on *Codium fragile* (Chlorophyceae). M.S. Thesis. University of Rhode Island, Kingston, RI.
- Worm, B. and U. Sommer. 2000. Rapid direct and indirect effects of a single nutrient pulse in a seaweed-epiphyte-grazer system. *Mar. Ecol. Prog. Ser.* 202: 283–288.
- Worm, B., E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern, J.B.C. Jackson, H.K. Lotze, F. Micheli, S.R. Palumbi, E. Sala, K.A. Selkoe, J.J. Stachowicz and R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787–790.
- York, P.H., B.P. Kelaher, D.J. Booth and M.J. Bishop. 2012. Trophic responses to nutrient enrichment in a temperate seagrass food chain. *Mar. Ecol. Prog. Ser.* 449: 291–296.
- Zhang, Y., J. Mu, Y. Feng, J. Zhang, P.-J. Gu, Y. Wang, L.-F. Ma and Y.-H. Zhu. 2009. Broad-spectrum antimicrobial epiphytic and endophytic fungi from marine organisms: Isolation, bioassay, and taxonomy. *Mar. Drugs* 7: 97–112.