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Positive Indirect Interactions in Marine Herbivores and Algae

Jacqueline E. Bell and Jane E. Williamson

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Abstract

There is an increasing interest in how nested positive indirect interactions involving at least three species maintain community structure. Recent research shows that positive indirect effects can strongly influence community structure, organisation and functioning. It is thus important to understand and identify positive indirect effects for the purpose of predicting system responses to certain perturbations. In order to investigate indirect effects, experimental manipulations must be carried out within the entire framework of the community of interest. Hence, often due to logistical difficulties, indirect effects, especially those that yield positive results, have been less studied. Here we present a synthesis of current information on patterns of positive indirect effects and review and compare recently conducted experimental studies in marine herbivores and algae.

Keywords: indirect, plant, cascade, habitat, facilitation

1. Introduction

In this chapter, we synthesise current information and case examples of defined patterns of positive indirect interactions in marine herbivores. These types of interactions occur when one species causes a change in a second species, which successively affects a third species and where at least one species is benefited and neither is harmed [1]. Herbivores in marine ecosystems have the ability to drastically modify the biogenic structure of habitats. To date, most of the ecological literature on marine herbivory has focused on negative effects arising from the overharvest of predators or shifting environmental conditions, which can lead to a loss of structural habitat. This chapter highlights the diverse roles that herbivorous grazers can play in directly and indirectly enhancing species diversity. The importance of multispecies

interactions involving herbivores has recently been recognised. We highlight that greater survivorship of contributing species inside such associations, as well as behavioural habitat selection, is important in the establishment of such interactions and that food provision is an important driver in their maintenance in marine systems. This chapter concludes with an emphasis on the importance of understanding multispecies interactions in successful management of marine ecosystems. In order to accurately predict the impact of potential perturbations and for mitigation of effects, future research should refocus on the entire ecosystem framework to capture potentially important positive indirect effects that might further define species relationships.

1.1. Positive interactions

The importance of positive interactions between species is increasingly acknowledged in contemporary ecological theory [1–3]. Such interactions occur between two or more species when at least one participant benefits and neither are harmed and take place, simply, as either commensal (+, 0) or mutual effects (+, +) [1, 2, 4, 5]. A species that has a positive effect on another is referred to as a facilitator [2, 6]. Facilitative or positive interactions tend to be most common in environments with high physical stress and/or where strong consumer pressure exists [3, 4]. Here, facilitators play a positive role by ameliorating environmental stress and by creating complex habitat that can lessen the effects of competition and/or predation [1]. Relationships between facilitators and associated organisms may be obligate or facultative, depending on the level of risk to survival for the associated species outside of the relationship [4].

1.2. Direct and indirect interactions

Interactions between species can be both direct and indirect, yielding both positive and negative results [7–9]. A direct effect occurs as a result of a physical interaction between two species [10] and includes processes such as predation, interference competition, inhibition of recruitment, inhibition of feeding, enhancement of recruitment and provision of habitat or shelter [8]. Indirect effects occur in multispecies assemblages when the action of one species causes a change in a second species, subsequently impacting on a third species [11, 12]. This type of interaction includes processes such as keystone predation, tritrophic interactions, exploitation competition, apparent competition, indirect mutualism, indirect commensalism, habitat facilitation and associational resistance [13].

Indirect effects occur when a species is involved in a series of strong pairwise interactions that are not independent of other species [13]. Indirect effects generally occur in a system via two ways [13]. The first is referred to as an interaction chain where species C indirectly changes the abundance of species A by changing the abundance of an intermediary species, species B, which interacts with both [13]. The second is termed either interaction modification or higher order modification and occurs more commonly. It occurs when the abundance of species C changes, causing an indirect effect on the abundance of species A by affecting the interaction between species A and species B [13] (**Figure 1**).

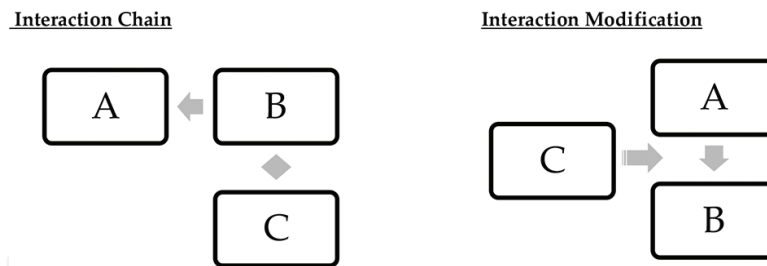


Figure 1. Two fundamental ways in which indirect effects can occur within an ecosystem (adapted from [13]).

Indirect effects also arise through changes in a physical and/or chemical component of the environment, as well as through another species [14]. For example, the effects of nutrient addition to a plant-endophagous-parasitoid trophic chain can result in two types of indirect effects [15]. Fertilised plants (*Chromolaena squalid*) produce larger flower heads that act as a shelter against endophagous insects [15], representing an interaction modification [16]. Concurrently, this fertilisation results in an increase in the nutritional quality of the plant, which in turn increases the quality of the endophages as hosts to parasites [15] representing an interaction chain [16]. A similar example involves fish foraging, which causes a direct increase in sedimentation. This in turn has an effect on the abundance of invertebrates consuming primary producers [17–19]. Chemical cues and chemical communication can also indirectly mediate behaviour and strongly affect community structure [20]. For example, when given a choice between different cue sources, fish (*Lipophrys pholis*) and crabs (*Carcinus maenas*) that consume snails (*Littorina obtusata*) are more attracted to algae (*Ascophyllum nodosum*) that have recently been grazed to algae that have not [21]. It is thought that this indirect effect may have evolved in algae as a mechanism for protection against attacking herbivores [20].

Indirect effects within ecosystems may have important implications. It is thus important to understand and identify such effects for the purpose of predicting system responses to certain perturbations [13]. For example, human-induced perturbations to environments, such as replacement of natural marine habitats with artificial structures such as piling, marinas and seawalls, can have extensive direct and indirect repercussions on the abundances of biota within the ecosystem, and it is important for us to be able to identify such processes [22]. Environmental impacts such the introduction, increase, reduction or extinction of species can have widespread repercussions for the rest of an ecosystem [23]. Categorisation of organisms into separate trophic levels according to their feeding preference provides a useful foundation with which to understand ecological systems [23]. Relationships between producers and consumers can be examined in this way to determine which trophic level, if removed, may control community composition [24].

Detection of indirect effects is, however, sometimes more complex than this, as indirect effects can be masked as direct effects within manipulation experiments. For example, when avian predation pressure was experimentally manipulated within an intertidal community, both direct and indirect effects were found [25]. An increase in predatory gulls reduced the density of the limpet *Lottia digitalis* [10]. The seemingly direct effect of foraging gulls on limpet

abundance was later found to be partial due to an indirect effect involving a change in the abundance of the cryptic goose barnacle (*Pollicipes polymerus*), which comprised the habitat in which the limpet (*L. digitalis*) preferentially colonised [10]. As a direct result of gull predation, the area covered by the cryptic goose barnacle was dramatically reduced, thus increasing the area covered by the habitat-forming mussel, *Mytilus californianus*. A reduction in the preferred cryptic habitat meant an increased risk of predation for *L. digitalis* and thus a reduction in its abundance [6]. This released the limpet *L. strigatella* from exploitative competition with *L. digitalis*, and thus an increase in the abundance of the former was observed [10]. Results of this experiment reveal that gull predation, in fact, indirectly decreases the abundance of the limpet *L. digitalis*, which in turn increases the abundance of the limpet *L. strigatella*, via a decrease in the preferred cryptic habitat of *L. digitalis*, causing a reduction in the strength of exploitative competition between the two species [10]. This example demonstrates the importance of long-term experimental manipulations that consider the full complexities of the community of interest, for the purpose of detecting the underlying indirect effects. It also shows that conclusions from short-term experimental manipulations that simplify systems to direct interactions between species pairs can give questionable results [25].

Many direct effects within marine communities have been investigated in detail. Indirect effects, however, especially those that yield positive results, are less studied [10, 11]. The majority of indirect effects have been inferred from manipulative experiments that were designed to test other interactions rather than having been tested directly (e.g., [8, 26]). This may be due to the logistic difficulties in observing indirect effects within the marine environment or the difficulty in distinguishing between the effects of indirect and direct processes within multispecies interactions [8, 11, 12]. Nevertheless, there is little doubt that positive indirect effects are more common than historically thought and a growing body of work has revealed the importance of such effects within marine communities. Whilst there are almost an infinite number of associations involving indirect interactions between organisms, this chapter focuses on the current trends and significance of positive indirect effects that have shown to be ecologically important within benthic marine communities.

1.3. Patterns of positive indirect interactions associated with marine herbivores within marine communities

1.3.1. Food webs and trophic cascades

Food webs are crucial elements of community ecology as they describe the flow of energy and materials from one trophic (consumer) level to another [7, 8, 24, 27–30]. Species interactions within food webs are important when considering species demography and community structure across different habitats [23, 24]. In several cases, removal or introduction of a predatory trophic level can cause a cascading effect on other trophic levels [7, 10, 24, 31–34]. Such trophic cascades are simple indirect effects that occur as a result of consumer-resource interactions [13]. The most studied and classic marine example is the north-eastern Pacific trophic cascade involving sea otters, sea urchins and kelp [32]. Revival of the sea otter *Enhydra lutris* population had positive indirect effects on the near-shore benthic community structure [32] via a decrease in sea urchin *Strongylocentrotus polyacanthus* herbivory, which in turn

caused an increase in kelp *Laminaria* spp. cover and habitat, as well as changes to the physical parameters of the environment (e.g., water flow, light penetration) [32, 35, 36].

The potential for human-induced trophic cascades has become more apparent in recent years [9, 34]. Introduction of 'no take' marine reserves has reduced the impacts of humans on predatory levels in specific areas, resulting in positive indirect effect within these marine communities than can be observed for the first time [37]. A reversal in community structure was observed within Leigh Marine Reserve in New Zealand as a result of the elimination of fishing since 1976 [37]. Herbivory and the density of sea urchins declined with an increase in predation, which in turn increased the biomass of primary producers and altered seaweed community structure [37]. When comparisons were made between the area within the reserve and the area adjacent to the reserve for the 4–6 m depth zone, a marked distinction could be made between urchin-induced barrens (areas devoid of kelp) as the dominant habitat outside the reserve and the complex kelp habitat that was dominant within the reserve [37].

Predator diversity can strengthen positive trophic cascades by further reducing herbivory and increasing plant biomass [38]. Interspecific competition among predators is considered pivotal in maintaining food web dynamics, community structure and ecosystem functioning within marine systems [38–40]. For instance, an increase in predator diversity is believed to increase the likelihood of keystone predation or facilitation within the predatory assemblage, thus enhancing the efficiency of prey consumption [41]. Predators can affect plant biomass through 'density-mediated indirect interactions' (DMII), by reducing herbivore abundances, or through 'trait-mediated indirect interactions' (TMII) by reducing parameters such as the foraging period of herbivores [42]. Interestingly, Bruno and O'Connor [34] found that inclusion of omnivores in predator assemblages could reverse predicted positive indirect relationships between predator diversity and plant biomass. Through direct consumption of algae, omnivores effectively by-passed the trophic cascade. Thus, the magnitude and direction of changes in this community structure were due to changes in predator diversity. Cascades can sometimes be difficult to predict due to the multiple counteracting interactions that occur, especially when more generalist feeders like omnivores are included [38]. A review by Duffy et al. [31] came to a similar conclusion. Whilst horizontal predator diversity has indirect effects on primary production, the strength and sign of such effects depend on the diversity of prey types consumed (omnivore versus predator) and of course prey behaviour [43].

1.3.2. Indirect mutualisms

Indirect mutualisms can be defined as the shared indirect positive effects that one species has on another [44, 45]. They occur when the benefit exceeds the cost for both participants within an interspecific interaction (+, +) [46]. Positive interactions within the marine environment, especially mutualisms, are surprisingly widespread and play a critical role in shaping ecosystems [5]. Indirect mutualisms can arise through a number of mechanisms but typically involve a consumer-resource interaction linked with competitive interactions and are more likely to occur if the competitive relationship between resource species is strong [13]. In the presence of a competitive hierarchy between resource species, the interaction may become a direct commensalism (+, 0) [47].

Foundation species provide structure to the community and include groups such as kelp, coral and seagrass [5]. Mutualistic interactions frequently occur between foundation species and their residents whereby both resident and foundation species benefit [5]. This process, also known as indirect facilitation [1], will be discussed in more detail later in this chapter. Perhaps the most well-studied mutualistic interaction involving a foundation species within a marine community is that between corals and their photosynthetic dinoflagellate symbionts, zooxanthellae [5]. Photosynthesis by zooxanthellae provides the coral host with carbohydrates, whilst the resident zooxanthellae receive nutrients via nitrogenous waste from the prey of their carnivorous coral host [5]. The carbohydrates are used by the coral for calcification and growth, allowing them to grow at a rapid rate, which is necessary for survival [5]. Whether such rapid growth will be enough to ensure coral survival in many regions under rapid sea level change is still unknown. Survival of one of the most biologically diverse ecosystems in the world would certainly be severely compromised without this mutualistic interaction [5].

Corals persist in tropical environments due, in part, to the efficient grazing activity of herbivores that prevent overgrowth by fouling algae [48]. Within temperate marine communities, however, fewer species of coral survive due to the competitive advantage that algae have over corals, where herbivory is less intense [48]. Contrary to this trend, the coral *Oculina arbuscula* persists in temperate waters off North Carolina despite the prevalence of macroalgae due to a mutualistic relationship with the omnivorous crab *Mithrax forceps* [46]. The coral harbours the crab, which consumes all types of algae and invertebrates inhabiting the coral. The crab uses the coral for protection from predators and gains a dietary advantage from the coral by consuming the lipid-rich coral mucus [48]. This mucus may also attract symbionts that further protect the coral from predation [48].

A negative consumer-resource interaction can flip to a positive interaction through changes to mutualistic effects [43]. Coralline algae, for example, are typically consumed by molluscs that scrape them from the rocks they inhabit with their hardened radulae [49]. Within the Belize Barrier Reef, approximately half of the diet of the herbivorous chiton, *Chonoplax lata*, is made up of its preferred coralline algal host *Porolithon pachydermum* [49]. Feeding by the chiton creates burrows and excavates into the coralline algae, causing damage to the host [49]. When the chitons are experimentally removed, however, the coralline algae become extensively fouled by epiphytic algae, which attract deep biting by powerful herbivorous fish, including parrot fish. This form of herbivory causes substantially more damage to the coralline algae than that caused by the chiton [47]. Thus, removal of the chiton caused an increase in grazing damage rather than a decrease. Herbivorous damselfish can form similar mutualisms with algae. By protecting their food source, less grazing activity occurs to the algal mats on which they feed [50]. As a result, these algal mats are far more species rich and occur in greater biomass than those subjected to all types of grazing [50]. In fact, when damselfish are experimentally removed, these algal mats are consumed entirely within hours [50, 51].

Mutualists in one ecological context may be adversaries in another ecological context [5]. Whilst indirect mutualism yields positive results by definition, this type of effect is often linked with negative interactions, such as exploitative competition [13]. When two competing species are considered in a community context, the effects of a nearby competitor can

sometimes counterbalance the negative effects of competition by lessening physical stresses or preventing attacks by enemies [5]. A classic example is where the addition of a seastar within an intertidal community directly decreases the abundance of the resident mussels (*Mytilus*), which in turn makes space for competitively inferior sessile species [52]. A similar example is described by Wulff [53] whereby particular species of sponges grew better when surrounded by other species of sponges than when grown with conspecifics or when grown alone. This is thought to be due to a nearby competitor lessening the impacts of predation, acting as a positive trade-off to the negative effects of competition [5].

Mutualistic interactions have long been considered a coevolved trait, involving species that are coupled consistently in space and time; however, this is not always the case [5]. Some interactions that appear to have coevolved do not have an obvious coevolutionary history [54, 55], suggesting that their occurrence may have arisen as an incidental benefit [56]. For example, damselfish seek refuge from predators by hiding within branching coral [5]. The damselfish benefits mutualistically the coral by providing nutrients whilst in hiding, via excretion, thus allowing the coral to grow at a faster rate [57]. Extensive branching on this type of coral is thought to have evolved in response to feeding and reproductive needs rather than to take up nutrients provided by the damselfish [5]. Similarly, growth of the brown encrusting alga *Pseudolithoderma* sp. is increased through uptake of ammonium by overlying live honeycomb barnacles (*Chamaesipho columna*) [58]. Occurrence of the alga on the barnacles is most likely due to a refuge from herbivory, and it is thought that the alga reduces the impact of desiccation for the barnacles during low tides [58, 59].

1.3.3. Associational resistance

Associational resistance occurs when an organism takes refuge from predation by associating with a habitat-forming competitor (+, +) or (+, 0) [60]. Palatable marine plants, for example, are more vulnerable to herbivory when occurring alone, but herbivory is reduced and growth enhanced, when the same species grows interspersed with algae that are unpalatable to herbivores [61–63]. This is a facilitative-commensalistic (+, 0) example of associational resistance whereby the palatable plant has a clear benefit by association; however, the unpalatable plant neither benefits nor suffers [1]. Such an interaction can become antagonistic (+, –) if the palatable plant outgrows the unpalatable plant, making the unpalatable plant more attractive to herbivory [1]. In this instance the relationship could also be considered parasitic [1]. When the unpalatable plant remains dominant in the community, however, species growth and diversity can increase significantly by providing a safe haven for the palatable species [63]. This example highlights the transient nature of some associations over time, such that interactions can flip from being positive to negative and potentially back again, given particular biotic and abiotic circumstances [63].

Mobile organisms, often herbivorous, can also take refuge from predation by association with seagrasses, kelps, corals and other sessile or less mobile organisms that provide structural and morphological defences [1]. Smaller marine invertebrates can shelter within the structurally complex habitat formed by seagrass, kelp and corals for protection from predators using their host as both food and habitat [1]. Whilst structural complexity can play a large role in

providing safe havens from predation, the chemical makeup of plants can also deter larger consumers [1]. Some marine invertebrates inhabit plants that contain noxious antipredator chemicals and feed on species other than their host [1]. In such situations the benefit of refuge is thought to outweigh the importance of the quality of the food. For example, the juvenile sea urchin *Holopneustes purpurascens* inhabits the chemically defended foliose red alga *Delisea pulchra* [64]. *H. purpurascens* exhibits a diel pattern of movement on its host plant. It remains wrapped within its host during the day, when predation is greatest, and is more exposed at night, for purposes thought to include nutritional gain, reproduction, avoidance of photo damage and microenvironmental variation associated with the host alga [65]. When *H. purpurascens* reaches a certain size, it moves to a new host plant, the kelp *Ecklonia radiata*, on which it feeds [64]. At this point in its life history, it is thought that the benefit of a more nutritious and easily accessible food source outweighs the benefit of refuge via a chemically noxious host [64].

The decorative behaviour of certain crab species with chemically defended plants is a similar scenario. The decorator crab *Libinia dubia* camouflages itself by covering its carapace with the chemically noxious brown alga *Dictyota menstrualis* [66]. The diterpene alcohol produced by the brown alga deters predators by making the alga unpalatable [66]. The diterpene alcohol also acts as a cue for the crab to commence decorative behaviour [66]. Studies have shown that without this behavioural adaptation, *L. dubia* would most likely become extinct [66]. It is thought that the relationship between the decorator crab *L. dubia* and the brown alga *D. menstrualis* may well be mutualistic, whereby the alga benefits through reduced herbivory via the consumption of amphipods by the crab [66] and gains nutritionally via crab excretion, as in the relationship between the brown alga *Pseudolithoderma* sp. and the barnacle *Chamaesipho columna* [58].

Associational resistance can also occur between invertebrates. For example, less mobile sea urchins (*Parechinus angulosus*) provide a stable habitat for juvenile abalone that are at risk of predation by crayfish [67]. Experimental removal of urchins indirectly affected recruiting abalone by causing an increase in sediment. McClintock and Janssen [68] document a similar occurrence whereby an amphipod increased its chances of survival by capturing a chemically defended pteropod, effectively exploiting the pteropod's chemical defence for its own protection.

Associational resistance is sometimes considered facilitative when the species that provides the associational resistance is facilitated by the association. For example, an Antarctic sea urchin facilitates dispersal of chemically defended seaweeds that have become detached during storms [69]. The sea urchin exhibits a similar decorative behaviour where it collects reproductively viable individuals for camouflage to deter predation whilst also preventing the seaweed from being carried ashore or below the photic zone [69]. This example could also be defined as mutualistic.

1.3.4. Facilitation cascades

Facilitation cascade is another example of a positive indirect effect and is commonly observed in marine herbivores and macroalgae. Within a facilitation cascade, the basal habitat former facilitates an intermediate habitat former, which in turn facilitates a focal species. In marine

environments, where predation is often intense and waves and currents produce abiotically stressful conditions, positive interactions among species, such as facilitation cascades, are expected to play a particularly important role in the structure and organisation of ecological communities [1, 4, 6, 70, 71].

Marine benthic communities inhabit highly dynamic environments [72]. Storm surges, wave action, tides and currents, as well as biotic factors related to food web dynamics; all contribute to the dynamics of this environment [73]. Facilitator species within these systems include benthic species such as kelps [24], seagrasses [74] and mangroves [75]. These mitigate environmental stressors for associated species through substrate formation [76, 77]; enhancement of larval settlement [78]; provision of food [79]; shelter from physical forces such as wave action, tides and currents [80]; and refuge from predation [81]. These species often form large aggregations whereby facilitation of generally smaller species, often herbivores, occurs through the creation of habitat heterogeneity [76].

Herbivores in marine ecosystems have the ability to drastically modify the biogenic structure of habitats. Sea urchins, for example, are major grazers in rocky reef ecosystems, often maintaining areas devoid of macroalgae, namely, 'urchin barrens' [82]. To date, most of the ecological literature has focused on the cascading negative effects of increasing herbivore abundance arising from the overharvest of their predators or shifting environmental conditions, which can lead to a loss of structural habitat [32, 83–87]. However, some herbivores can have positive effects on particular associated species. These positive effects most likely occur at smaller scales than the negative effects associated with large-scale herbivory and often within facilitation cascades, whereby complex systems of direct and indirect pathways make them more difficult to uncover.

Perhaps the most common and simplest way that a herbivore can mediate a facilitation cascade is by providing shelter for other small invertebrates [88–91]. In mangrove forests, for example, marine invertebrates such as sponges and barnacles are directly facilitated by the mangroves in which they inhabit and, in turn, indirectly facilitate the mangroves by providing physical barriers, thus protecting them from wood-boring isopods [92]. Within the lagoons of French Polynesia, gammarid amphipods and chaetopterid polychaetes induce the growth of branch-like 'fingers' on corals through nutrient provisioning, which in turn facilitate the abundance and diversity of fishes [93]. In intertidal cobblestone beaches, cordgrass beds provide habitat for mussels, which in turn create crevice space a shelter to an array of other marine invertebrates [77]. Thomsen [94] conceptualises a specific type of facilitation cascade, described as a 'habitat cascade'. This type of interaction is characterised when a basal habitat former, typically a large primary producer, creates space for an intermediate habitat former to live, that in turn creates habitat for the focal organism.

One example of a habitat cascade mediated by a marine herbivore is that between the common kelp *Ecklonia radiata*, the sea urchin *Holopneustes purpurascens* and the gastropod *Phasianotrochus eximius*. Within this relationship, the intermediary species, the short-spined urchin, *H. purpurascens*, uses its tube feet to wrap itself in the laminae of the kelp [36, 64]. It also preferentially consumes the kelp [95]. The focal organism, the gastropod *P. eximius*, resides with *H. purpurascens* in the temporary shelter the urchin builds within the fronds of

the kelp [65]. The relationship is considered facultative, as *P. eximius* can survive in different types of habitats but is most abundant on *E. radiata* plants with *H. purpurascens* throughout the year [96]. Due to its small size, *P. eximius* is likely to be vulnerable to predation outside of its preferred complex habitat structure. The modified habitat in which both species exist is thought to benefit the sea urchin by providing it with a shelter from predation but also from abrasion by kelps and other objects 'whipping' by in the water due to adverse abiotic factors such as wave action, tides and currents [65].

Covering behaviour in other species of sea urchins has also been considered an adaptation to avoid surge [97]. The sea urchin *Toxopneustes roseus* covers itself in shell fragments and foliose algae in areas of high surge throughout the Gulf of California [97]. It is possible that *H. purpurascens* has adapted in a similar way to *T. roseus* by covering itself to mitigate wave action within the exposed environment in which it inhabits [36]. It is highly likely, therefore, that *P. eximius* also benefits from inhabiting the shelter built by *H. purpurascens*.

Impacts on one species within a facilitation cascade can profoundly change the balance of the relationship. Recently, *H. purpurascens* in this region has been associated with the outbreak of a disease caused by the opportunistic pathogen *Vibrio anguillarum* [98]. The disease reduces the capacity of the urchin to wrap algae around itself and ultimately leads to death of the urchin. The disease is water-borne, and prevalence of the disease is exacerbated by increases in water temperature, such as those associated with climate change [98]. Whilst the impact of the urchin disease on the health and demography of both kelp and gastropod is currently unknown, it is highly likely that both may suffer through prolonged contact with diseased urchins. *P. eximius* may also face reduced availability of habitat formed by *H. purpurascens* should the abundance of urchins be dramatically impacted.

Plants often mediate facilitation cascades. These interactions typically occur in temporally separated, spatially separated or taxonomically distinct species [99–101]. Thomsen [94] investigated one particular example whereby small herbivorous marine invertebrates facilitate habitat for seaweeds, which in turn facilitate habitat for focal species of invertebrates and epiphytes. Other examples involve two levels of plant facilitation. For example, the seaweed *Hormosira banksii* provides habitat for the obligate epiphyte *Notheia anomala*, which in turn facilitates species richness and diversity of mobile invertebrates [102]. Similarly, temperate Australian mangrove forests facilitate free-living algae, which in turn facilitate a dense and diverse assemblage of epifaunal molluscs [103].

For small marine herbivores, associations with larger, habitat-forming herbivores can be driven by a range of environmental obstacles that need to be efficiently overcome to survive [104, 105]. These not only include the need for shelter but also finding a reliable and nutritious food source and access to mates, the former two being generally considered the most important driving factors in habitat and/or host choice [79, 104–106]. Ideally, an individual will choose a habitat or host that provides all of these attributes [16].

By investigating both the direct and indirect effects of species interactions, often a seemingly simple association will be based on more complex foundations. For example, grazing sea urchins and gastropods are directly facilitated by mussel beds by feeding on attached algae;

the mussels are indirectly facilitated by the grazers that keep them free from algal growth and reduce the potential for mussel dislodgement by up to 30-fold [107]. Similarly, juvenile abalone that recruit to the underside of the sea urchin *Parechinus angulosus* [67] receive protection by the urchin but also provision of food via drift algae that the urchin captures on its spines for its own consumption [67]. Another example can be observed between the isopod *Dulichia rhabdoplastis* and sea urchin *Strongylocentrotus franciscanus*, which appears to be indirectly mediated [108]. Within this relationship, the isopod builds strings of detritus made from its own faecal pellets that it connects to the spines of the sea urchin [108]. The strings are colonised by a rich layer of diatoms, which the isopod subsequently consumes [108]. Here, the sea urchin indirectly facilitates the isopod by providing it with a habitat that it uses to capture its prey [108]. This species may also benefit directly by using the spines of the sea urchin as refuge when needed.

Facilitation cascades are not exclusive to herbivores. An invasion by non-native bullfrogs has been facilitated by the coevolved non-native sunfish, where the sunfish increased bullfrog tadpole survival by consuming dragonfly nymphs that preyed on the tadpoles [109]. Such an interaction between two non-native species also has the potential to exacerbate impacts of species invasion [109].

2. Conclusion

Positive interactions involving marine herbivores and algae have been increasingly recognised for their importance in the structure and functioning of ecosystems [94]. However, studies focusing on the role of negative species interactions in shaping ecosystems such as over harvest of predators or shifting environmental conditions, which can lead to loss of structural habitat, still far outweigh those focusing on the importance of positive effects [32, 83–87]. Herbivores in marine ecosystems have the ability to drastically modify the biogenic structure of habitats. Indirect effects add to the complexity with which ecosystems function and are intrinsically difficult to quantify, often requiring long-term and manipulative experiments [101]. Whilst interest in indirect effects has recently grown, there is still a gap in our understanding of the roles that individual indirect effects have and their importance within many systems [16]. An understanding of positive interactions, and both the direct and indirect pathways of occurrence, is essential to predict accurately the impact of potential perturbations for successful management of ecosystems. Greater survivorship of contributing species inside such associations as well as behavioural habitat selection is important in the establishment of such interactions, and food provision is an important driver in their maintenance in marine systems. Whilst difficult, future research should focus on the entire framework of these ecosystems to capture potentially important cascading effects that might further define species relationships. Experiments should centre on the effects of feeding behaviour and the nutritional benefits of association, the role of predation and the risks herbivores face beyond the association as well as environmental stressors such as wave action and climate change on the survival of associates within and outside of preferred habitats.

Throughout the past 50–100 years, human impacts on marine ecosystems (such as overfishing) have resulted in a downturn in the abundance of species that prey on herbivores in some areas [110]. Within such areas this has caused an increase in the abundance of herbivorous species and in turn is likely to have had a positive effect on species that associate with sea urchins [111]. Recently, however, direct threats on herbivores by humans, such as harvesting for food [112], creating suboptimal conditions that, increased sedimentation [113] and ocean acidification [114] on local to regional scales, have increased, which in turn will negatively impact on the species with which the herbivores facilitate. This issue has been identified as particularly relevant to commercially harvested species that rely on herbivore for survival, such as the abalone *H. midae*, which depends on the sea urchin *P. angulosus* throughout its juvenile stage for both food and shelter in South Africa. Depletion of sea urchin stocks in this location has seen a decline in abalone recruits, which have had significant impacts on the abalone industry in this region [67]. This chapter highlights the diverse roles that herbivorous grazers play in directly and indirectly enhancing species diversity. Unfortunately, however, the relatively unstudied nature of many species interactions within the marine environment means that many of these types of associations may disappear before we have the opportunity to understand their importance within ecosystem functioning. With a greater level of understanding of the important roles that herbivores play within various marine ecosystems, the cascading effects as a result of threats to herbivores can be managed appropriately, for the purpose of maintaining future biodiversity.

Author details

Jacqueline E. Bell^{1,2} and Jane E. Williamson^{2*}

*Address all correspondence to: jane.williamson@mq.edu.au

1 Boffa Miskell Ltd., Hamilton, New Zealand

2 Department of Biological Sciences, Macquarie University, Sydney, Australia

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