The potential roles of sponges in integrated mariculture

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[Correction added on 07 November 2020, after first online publication: The third author's name has been corrected.]

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Abstract

This mini-review evaluates the use of marine sponges in integrated culture systems, two decades after the idea was first proposed. It was predicted that the concept would provide a double benefit: sponges would grow faster under higher organic loadings, and filtration by sponges would improve water quality. It is promising that the growth of some commercially interesting sponges is indeed faster in organically enriched areas. The applicability of sponges as filters for undesired microorganisms has been confirmed in laboratory studies. However, upscaled farming studies need to be done to demonstrate the value of sponges for *in situ* bioremediation of sewage discharge or waste produced by fish cages. In addition, a new idea is presented – the use of sponges as an engine to convert dissolved organic matter (DOM) into particulate organic matter (POM) that can be consumed by deposit feeders through a chain of processes termed the sponge loop. A theoretical design of an integrated culture with seaweeds (*Gracilaria* sp.), sponges (*Halisarca caerulea*) and sea cucumbers (*Apostichopus japonica*) shows that 37% of the part of the primary production that is excreted by the seaweeds as DOM can be directly recovered in sponge biomass and a subsequent 12% in sea cucumber biomass after mediation (conversion of DOM to POM) by sponges. Hence, the total recovery of DOM into (sponge and sea cucumber) biomass within this IMTA is 49%.

Key words: DOM, integrated multitrophic aquaculture, sea cucumbers, seaweeds, sponge loop, sponges.

Introduction

The concept of combining the aquaculture of species from different trophic niches to achieve an ecologically efficient and profitable production dates back to 2200–2100 B.C., when the Chinese applied this concept for the first time (Chopin 2013). In present days, this aquatic polyculture gained renewed attention. Since aquaculture has become the predominant source of seafood for human nutrition (FAO 2014, 2018), management of its associated waste streams (e.g. undigested feed, faeces and inorganic waste) is of increasing concern. As a more sustainable solution to monoculture, the concept of integrated multitrophic aquaculture (IMTA) has been proposed. IMTA is based on the ecological concept of efficient reuse of organic and inorganic waste streams through the application of different trophic levels of the food web within the culture system. Furthermore, by integrating cocultured organisms, IMTA will provide additional harvestable products that have commercial values and/or ecological benefits (waste reduction) as compared to monoculture (Chopin *et al.* 2001). Most IMTA designs combine farming of (i) fed species (e.g. finfish) with (ii) cultures of suspension and/or deposit feeders (e.g. sponges, bivalves, polychaetes, sea cucumbers, sea urchins) that take up organic nutrients and/or with (iii) macroalgae (e.g. kelps, *Gracilaria salicornia*, sea lettuce) that take up inorganic nutrients (Neori *et al.* 2004; Chopin *et al.* 2012; Buck *et al.* 2018). In this way, IMTA aims to mitigate negative effects of fed 'single crop' farming, such as deterioration of water quality through nutrient pollution, pathogen outbreaks, sedimentation of undigested food and faeces particles, and may as such prevent conflicts between stakeholders (e.g.

aquaculture businesses, tourist industry, nature conservation organizations, water quality boards) (Naylor *et al.* 2000). Thus, the sustainability, productivity, profitability and resilience of aquaculture systems are increased by applying the environmental-friendly, product-diversified and socially beneficial concept of integrated farming (Buschmann *et al.* 2001; Troell *et al.* 2003; Chopin *et al.* 2012).

In 1998, Pronzato and co-workers were the first to consider including sponges (phylum Porifera) as an extractive component in IMTA (Pronzato *et al.* 1998). Sponges are ubiquitous benthic marine and freshwater animals that can extract a large amount of waterborne organic substances from extensive amounts of water through very fast and efficient filter–feeding (Weisz *et al.* 2008). The sponge is comprised of a maze of channels and chambers harbouring specialized cells that function in transport of water and efficiently retain a large variety of suspended particles (Reiswig 1971a,b; 1974; Riisgård *et al.* 1993; Vogel 1977), including (pathogenic) bacteria (Zhang *et al.* 2010; Longo *et al.* 2010) and viruses (Hadas *et al.* 2006; Welsh *et al.* 2020). In addition to the capturing of organic particles, sponges also bioaccumulate environmental pollutants, such as surfactants (Pérez *et al.* 2002), polychlorinated biphenyls (PCBs; Pérez *et al.* 2003) and heavy metals (Patel *et al.* 1985; Olesen & Weeks 1994; Hansen *et al.* 1995; Müller *et al.* 1999; Philp 1999; Pérez *et al.* 2005; Cebrian *et al.* 2007). Since these types of pollutants are not commonly associated with aquaculture, we will not discuss this feature of sponges in the current review. The use of sponges to absorb antibiotics from seawater may be of interest to aquaculture, since the use and release of antibiotics in aquaculture is an issue of growing concern (Cabello et al., 2013) . However, no data exist to date on the potential of sponges to bioaccumulate this type of compound.

The efficient filtering of organic particles by sponges coupled with their ability to produce commercially interesting bioproducts, such as biomedical agents, biosilica, biosintering and collagen (Pomponi 1999, 2001; Sipkema *et al.* 2005; Schröder *et al.* 2007; Müller *et al.* 2009; Gokalp et al. 2019), has raised interest in the inclusion of these animals in IMTA applications. Sea-based aquaculture of sponges has successfully been studied for multiple purposes (reviewed by Duckworth 2009; Schippers *et al.* 2012), showing that inclusion of this technique in IMTA systems is nowadays technically feasible (see for example Fig. 1). Nevertheless, sponge farming is a complex process with 235 years of research history (Moore 1910; Duckworth 2009), with many unknowns remaining and with sometimes conflicting results (e.g. about farming protocols, effects of generations, etc.). Examples of commercial application of sponge farming are still scarce (Duckworth 2009), and the inclusion of sponges as an element in IMTA is still at its infancy.

Within the last two decades, evidence has accumulated that the organic diet of many sponges mostly consists of
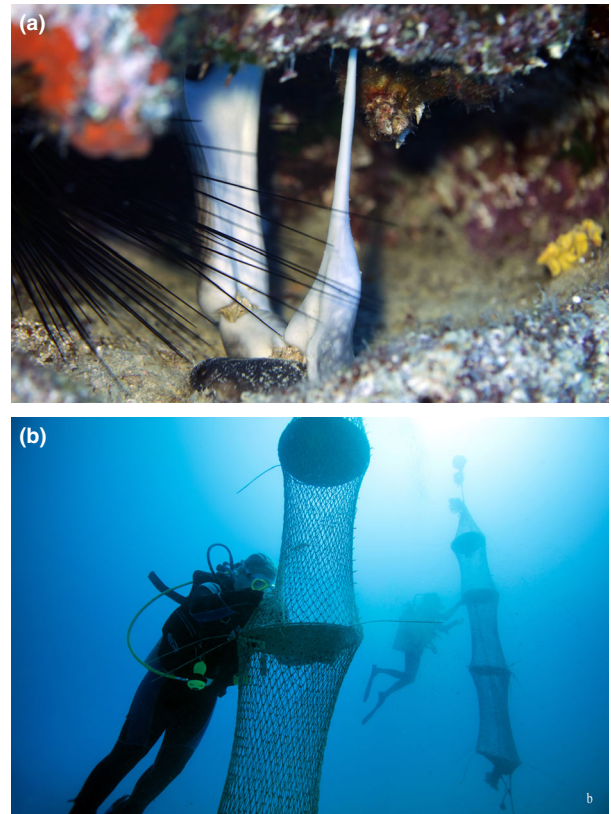
Figure 1 (a) A specimen of *Chondrosia reniformis* (Nardo, 1847) dropping from the ceiling of a rock crevice in order to reach and grow over a new ground. This species is of commercial interest because it is a rich sourceof collagen with biomedical potential (Fassini *et al.* 2017; Gokalp et al. 2019, 2020). (b) Divers cleaning the sponge lanterns designed for IMTA – *C. reniformis* was subjected to a wide range of mariculture applications and IMTA applications due to its collagen-rich cortex and common appearances throughout the Mediterranean coastline.

dissolved organic matter (DOM), operationally defined by all organic matter passing through a 'fine' filter, typically 0.2–0.7 μm (Benner 2002), whereas uptake of particulate organic matter (POM) only represents a minor proportion of total organic intake (see review by de Goeij *et al.* 2017). As DOM is not bioavailable as food source to most other heterotrophic organisms, DOM feeding by sponges provides an additional benefit to their application as extractive IMTA component. Fed aquaculture by itself results in production of DOM (Wang *et al.* 2013) and DOM production is substantially increased when seaweeds are included as IMTA components. Seaweeds and other marine algae release part of their photosynthetic products (sometimes more than 50%) into the surrounding seawater as DOM (Khailov & Burlakova 1969; Haas *et al.* 2011). Hence, a substantial proportion of the primary production of an *in situ* seaweed aquaculture is lost into the environment as DOM, where it may fuel bacteria, including pathogenic

microbes. This, in turn, may add to the proposed 'microbialization' of marine ecosystems (Haas *et al.* 2016). Sponges may potentially buffer against microbialization (de Goeij *et al.* 2017) and use DOM. In an IMTA setting, these features of sponges can be beneficial to reduce organic pollution and to increase their own productivity within the integrated aquafarm. Sponges do not only take up DOM, but can efficiently return the resources stored in DOM into the benthic food chain by converting DOM into particulate organic matter (POM; often referred to as detritus) through a pathway called 'the sponge loop' (de Goeij *et al.* 2013), which may further extend our view on the role of sponges in IMTA. As such, sponges can be net producers of POM instead of being net particle filters. The detritus produced by sponges has been shown to be a food source for detritivores, such as small crustaceans (de Goeij *et al.* 2013; Rix *et al.* 2018). In IMTA systems, sponge detritus production may facilitate the culture and production of commercially attractive detritivores, such as sea cucumbers (Maxwell *et al.* 2009). Sea cucumbers do consume particulate wastes and by-products generated by other trophic levels and have a high economic value (Ahlgren 1998; Yu *et al.* 2012, 2014; MacDonald *et al.* 2013; Yokoyama 2013). Certain sea cucumber species are highly desired by Asian sea product wholesalers, as a result of an escalating demand for their nutritional and medicinal use in, respectively, dietary and pharmaceutical markets (Zamora *et al.* 2018). Moreover, sea cucumbers increase productivity and biodiversity in soft-sediment benthic ecosystems through bioturbation and assimilation of bacterial, fungal and detrital organic matter (MacTavish *et al.* 2012).

Two decades ago, Pronzato *et al.* (1999) predicted a double bonus for integrated farming with sponges: (i) purified water and (ii) an enhanced production of high-quality sponge biomass. In the first part of this review, we will evaluate to what extent this double bonus has been capitalized: to what extent can sponges improve ambient water quality through biofiltration and to what extent has the production of high-quality sponge biomass (e.g. for biotechnological purposes) been achieved in IMTA settings? In the second part of this review, we outline the new potential role of sponges as intermediates between primary producers of dissolved organic matter and consumers of detrital organic matter in an IMTA system, thus capitalizing on the sponge loop. As an example, we present a model calculation of carbon transfer from seaweeds via sponges to sea cucumbers.

The earlier idea: sponges as biofilters for organic particles

The filter-feeding abilities of sponges intrigued several scientists in the last century (Jørgensen, 1949, 1955; Reiswig 1971a,b; 1974; 1975; Riisgård *et al.* 1993). Sponges can have considerable impact on water quality, considering the immense water processing rates of sponges (up to 50 m^3 per dm^3 of sponge tissue per day; Weisz *et al.* 2008), their high particle retention efficiencies (up to 98% (e.g. Reiswig 1971a; Lesser 2006)) and their abundance (in many ecosystems, sponges dominate the benthic community and they have been proposed as potential winners under future climate scenarios; Fabricius *et al.* 2011; Bell *et al.* 2013, 2018; Pawlik *et al.* 2016; de Bakker *et al.* 2018). Sponges are sessile suspension feeders grazing on organic particles within the range of 0.1–50 μm (Reiswig 1971a; Pile *et al.* 1996; Osinga et al., 1999; Ribes *et al.* 1999; Maldonado *et al.* 2010). Carbon uptake rates of sponges were found to be within the same range or even exceed the uptake rates of other, well-established filter feeders, such as bivalves (29–1970 mg C m^{-2} d^{-1} for bivalves vs 9–3621 mg C m^{-2} d^{-1} for sponges; Riisgård & Larsen 2000). This prompted the idea to use sponges for the remediation of organic pollution from aquaculture cages and urban environments (e.g. sewage) (Pronzato *et al.* 1999; Cattaneo-Vietti et al., 2003; Gifford et al., 2007; Stabili *et al.* 2006; Osinga *et al.* 2010; Ledda *et al.* 2014; Gökalp et al., 2019). The wide variety of microorganisms taken up by sponges as revealed in laboratory-based experiments demonstrated the added value of sponges as will be further detailed below.

The Mediterranean sponge species *Chondrilla nucula* was able to retain up to 70 billion *Escherichia coli* cells m^{-2} of sponge surface area, hereby clearing 14 L of water h^{-1} in a laboratory experiment (Milanese *et al.* 2003). A similar study reported remediation of the bacteria *E. coli* and *Vibrio anguillarum* by the sponge *Hymeniacidon perlevis*, filtering up to 8 million *E. coli* cells g^{-1} fresh sponge h^{-1} (Fu *et al.* 2006). The Mediterranean sponge *Spongia officinalis var. adriatica* (i.e. the bath sponge) had a very high efficiency of removing bacteria (12.3 × 10^4 cells ml^{-1} with a maximum retention efficiency of 61%) when used in marine environmental bioremediation (Stabili *et al.* 2006). Similarly, the Mediterranean sponge species *Aplysina aerophoba* exhibited high efficiencies in taking up food microorganisms (bacterial isolates) from environmental water in a flow-through system (Wehrl *et al.* 2007). *Hymeniacidon perlevis* was able to remove pathogenic bacteria, achieving a removal of 60.0–90.2% of faecal coliform bacteria, 37.6–81.6% of pathogenic *Vibrio* spp. and 45.1–83.9% of the total bacteria in a 1.5-m^3 turbot (*Scophthalmus maximus*) aquaculture system (Zhang *et al.* 2010). In a similar study, *H. perlevis* was able to accumulate, remediate, and metabolize halophilic *Vibrio* spp., heterotrophic bacteria, total culturable bacteria, faecal coliforms and faecal *Streptococci* (Longo *et al.* 2010). Algal blooms occurring in central Florida Bay have been suggested to be related to the loss of suspension feeders in the system, implying sponges do not only take up unwanted bacteria, but can

also be used as a tool for mitigating (harmful) algal blooms (Peterson *et al.* 2006; Wall *et al.* 2012).

Although these studies clearly demonstrate the remediation potential of sponges for (unwanted) bacteria and algae, some considerations must be made. First, the reported removal efficiencies for pathogenic bacteria might be deceptive, as most of these studies were done with non-marine microbes and pathogens (e.g. *E. coli*). Second, selective feeding by sponges on nonpathogenic bacteria may lead to sudden proliferation of opportunistic pathogenic microbes, such as *V. anguillarum*, thus increasing the problem (Maldonado *et al.* 2010). Third, there is no consensus on the effect of particle concentration on uptake rates by sponges. The grazing rate of the sponge *H. perlevis* was demonstrated to be dependent on the concentration of the microbes (Fu *et al.* 2006; Maldonado *et al.* 2010). In contrast, in several studies, grazing and retention rates by sponges were independent of the concentration of the food source (Reiswig 1971, 1975; Frost 1978, 1980a,b; Wehrl *et al.* 2007). For larger particles (microalgae), sponge-mediated clearance rates were concentration independent up to a particular threshold concentration, above which clearance rates rapidly decreased (Osinga *et al.* 2001). To further complicate the issue, it is often hard to compare the different studies on sponge feeding efficiency, due to the multitude of sponge size metrics used in scientific literature, which include wet weight (ww), dry weight (dw), ash-free dry weight (afdw), volume and individual. In conclusion, more studies should be done on the density dependency of grazing by sponges, preferably using standardized size metrics. Such studies should address the following questions: (i) What are the optimal food particle densities for different particle sizes and (ii) is there a threshold in densities above which grazing efficiency is seriously compromised? The large variability in feeding dynamics among sponge species shows that candidate sponges for IMTA should be carefully selected to find the species that aligns best with the characteristics of the targeted organic and microbial pollution. Before applying a certain sponge species as biofilter for organic pollutants, repetitive feeding tests on microbial targets should be conducted and the possibility of selective feeding on nonpathogenic bacteria should be excluded (Maldonado *et al.* 2010).

Pilot-scale studies conducted *in situ* have confirmed that sponges can benefit from the increased availability of food in the vicinity of mariculture farms (coculture with sea-bass: Osinga *et al.* 2010; Gokalp et al. 2019; coculture with mussels: Page *et al.* 2011) and in waste-water streams created by urban run-off (Ledda *et al.* 2014). *Dysidea avara* explants (i.e. regrown clones cut from parent sponges) cultured under seabass aquaculture cages in Southwest Turkey exhibited 100% survival and doubled in size within four months, whereas explants cultured under pristine conditions showed lower growth (up to 0–50% per year). *Chondrosia reniformis* explants cultured on suspended PVC plates in the proximity of fish farm effluent (2.4 times difference in TOC levels between the pristine and reference site) achieved a better annual survival and growth rate (86% and 170%, respectively) than explants grown at a pristine site (39% survival and 79% growth) (Gokalp et al. 2019), thus corroborating the earlier findings on *D. avara* (Osinga *et al.* 2010). Mediterranean sponge species *Ircinia variabilis* and *Agelas oroides* showed the highest particle retention and clearance rates at a polluted site (waste water and urban run-off) during a study conducted in the Ligurian Sea, which suggests that these conditions are beneficial for sponges (Ledda *et al.* 2014). There was substantial growth (exceeding 2000% per year) of explants of *Mycale hentscheli* in the vicinity of mussel farms, but in this case, growth was not augmented when compared to cultures at the natural reference site (Page *et al.* 2005). This may relate to the nature of mussel cultures, which are considered as a filter-feeding extractive component of organic matter themselves. The examples above demonstrate that culture of sponges in organically polluted areas can enhance the production of valuable sponge biomass. In fact, the primary motivation behind the integrated mariculture trials described above was to produce sponge biomass with high added value, that is *D. avara* for the production of Avarol (Osinga *et al.* 2010), *M. hentscheli* for the production of Peloruside A (Page *et al.* 2005, 2011) and *C. reniformis* for the production of collagen (Gokalp et al. 2019, 2020).

In addition to the aforementioned studies on bioremediation, potential caveats in sponge farming procedures need to be addressed as well to fully realize the integration of sponge farming in IMTA systems. Potential caveats include (but are not limited to) effects of seasonality, repeated cloning, fouling and predation. Growth rate and filtration activity can vary among seasons (Gokalp et al. 2019; De Caralt *et al.* 2008), which may lead to temporal imbalances between the sponges and the other IMTA components. Effects of repeated cloning have hardly been studied. Repeated cloning led to reduced growth in *Mycale hentscheli* (Page *et al.* 2011), but the effect was confounded by increased fouling and predation as culture trials proceeded. Predation of cultured sponges sometimes occurs unexpectedly. For example, sea turtles removed the majority of *C. reniformis* specimen cultured in open boxes in the East Mediterranean (M. Gokalp, personal observations). However, when fully protecting the sponges with mesh, fouling may become an issue of concern. Fouling of culture systems by algae and invertebrates can compromise the functioning of sponges, for example by blocking water current around the sponges, thus impairing the ability of the sponges to take up food.

In conclusion, two decades after the idea was launched, the proposed double bonus of integrating sponges in maricultures (improved control on organic pollution and enhanced growth of sponges) has been partially confirmed. Enhanced growth of sponges in multitrophic aquaculture settings has been demonstrated. Control on organic pollution has only been confirmed on laboratory-scale and these studies indicated that selective feeding by sponges on non-pathogenic microorganisms is the main risk associated with this idea. To complement these laboratory-scale studies, large-scale studies on the effects of sponge cultures on water quality in *in situ* settings are needed. Whereas positive effects on ambient water quality have been demonstrated for *in situ* shellfish cultures (Handå *et al.* 2012), examples from large-scale integrated maricultures with sponges are currently not available. An additional issue of concern is the production of nutrients by sponges. Sponges are known to produce inorganic nutrients, such as phosphate and dissolved inorganic nitrogen (DIN; Diaz & Ward 1997; Jiménez & Ribes 2007; Southwell *et al.* 2008; Bayer *et al.* 2008). Effects of DIN excretion by sponges on water quality should be included in studies exploring the potential of sponges as extractive components in IMTA.

A new idea: the use of sponges to convert DOM into POM

There has been an increased interest in carbon budgets and energetics of marine benthic fauna (Jørgensen 1955, 1976; Reiswig 1971a;b; Ribes *et al.* 1999; Yahel *et al.* 2003; de Goeij *et al.* 2008a). In the past century, particulate organic matter (POM) was considered as the prime food source for sponges and other filter feeders, whereas dissolved organic matter (DOM) was only hypothesized to be a potential source of food for some marine invertebrates (Jørgensen, 1976). The dogma of sponges being particle feeders was challenged by the suggestion that sponges were not able to balance their demand of organic carbon (i.e. their respiratory demand) by the uptake of POM alone and that uptake of dissolved organic carbon (DOC) could balance their respiratory demand (Reiswig 1981). This nutritional role of DOM in benthic communities was proven only when an accurate methodology to analyse DOC at a sufficiently low detection limit (μmol L^{-1}) had been established (Sharp 2002). Following this advancement, extensive feeding on bulk DOC – representing> 90% of the daily organic carbon uptake – by the sponge *Theonella swinhoei* was reported (Yahel *et al.* 2003). De Goeij and co-workers ignited a renewed attention on DOM studies at ecosystem scale. They found that extensive amounts of DOC were disappearing in coral reef cavities (de Goeij & van Duyl 2007), the largest habitat on coral reef ecosystems, where it was taken up and processed (i.e. respired and assimilated) by

encrusting sponges dominating the cavity walls (de Goeij *et al.* 2008a). Again, DOC represented more than 90% of the daily organic carbon intake, and the uptake rates of DOC by encrusting sponges were found to be in the same order of magnitude as the primary production rates of the entire coral reef ecosystem (de Goeij *et al.* 2008a, 2013). Later studies found a similar dominance of DOC in the diet of excavating sponges (Mueller *et al.* 2014) and massive sponges (McMurray *et al.* 2016; Hoer et al., 2017) (see also review by de Goeij *et al.* 2017). In addition, the encrusting sponges were found to produce large amounts of particulate organic waste (detritus) by massive shedding of rapidly proliferating filter cells (choanocytes) and other cellular waste and undigested food into the ambient water (de Goeij *et al.* 2009, 2013, Alexander *et al.* 2014, Maldonado, 2015, Rix *et al.* 2016). This finding led to the sponge loop hypothesis (de Goeij *et al.* 2013): sponges take up the largest pool of organic energy resources produced on the reef (DOM); they transform the majority of DOM into particulate detritus (i.e. POM), which is then consumed by detritivores and thus returned back into the food web. In this way, sponges play a crucial role in benthic ecosystems; the sponge loop may explain how productive ecosystems such as coral reefs can thrive in nutrient-poor waters (de Goeij *et al.* 2013). The sponge loop pathway has now been established in a Red Sea coral reef ecosystem (Rix *et al.* 2016, 2018) and even in cold-water deep-sea coral reefs (Rix *et al.* 2016).

Based on the increasing body of aforementioned scientific literature, it can be concluded that DOM uptake is a widespread phenomenon among sponges and that DOM is the main source (> 50% of their daily intake) of nutrition for many sponge species. Hence, aquaculture systems that produce large amounts of DOM could benefit from sponges to retain a resource that would otherwise be lost. This idea is particularly relevant for aquaculture systems that include seaweed farming. Seaweeds and other algae release a substantial proportion (up to 56%) of their photosynthetically acquired carbon into the environment in the form of DOM (Khailov & Burlakova 1969; Haas *et al.* 2010b, 2011). This DOM is not only considered as a lost resource, it is also known as a factor that can considerably alter the abundance and composition of microbes of marine ecosystems, such as coral reefs (Haas *et al.* 2016). Algal-derived DOM can promote the occurrence of pathogens that have been associated with coral disease (Smith *et al.* 2006). Consumption of algae-derived DOM by sponges could therefore be considered as a process that is beneficial for the health of reef ecosystems. In fact, sponges may even have a preference for algal-derived DOM over coral-derived DOM. For example, Red Sea sponges *Chondrilla sacciformis*, *Hemimycale arabica* and *Mycale fistulifera* were found to assimilate algal-derived DOM at significantly

higher rates than coral-derived DOM (Rix *et al.* 2017). Interestingly, from a fisheries perspective, the sponge loop pathway has even been proposed to increase local fish production on coral reefs that undergo a shift from coral to algal biomass dominance (Silveira *et al.* 2015).

There is an alternative theory that puts the role of DOM consumption by sponges in coral reef ecosystems into a different perspective. This theory states that sponges and macroalgae enforce each other at the expense of space for corals through a positive feedback loop termed the 'vicious circle' (Pawlik *et al.* 2016): algae promote sponge growth by producing DOM, whereas sponges produce dissolved inorganic nitrogen, which in return fertilizes macroalgae. Effects of such a vicious circle on the environment should be fully understood before implementing integrated seaweed–sponge–fish farms in marine environments.

Also, not all sponges produce detritus in the same quantities as encrusting sponges do (approximately 5–25% of their biomass per day; De Goeij *et al.* 2013; Alexander *et al.* 2014; Rix *et al.* 2016, 2017). Instead of releasing assimilated carbon in the form of detritus, the massive Caribbean sponge species *Xestospongia muta* uses DOM predominantly for somatic growth, thus retaining most of the assimilated DOM as biomass (McMurray *et al.* 2018). The sponge loop can be accomplished not only through the conversion of DOM into POM, but also through predation on sponge biomass, for example by spongivorous fish (McMurray *et al.* 2018). High cell shedding and detritus production may be predominantly associated with encrusting sponges, since these sponges experience high competition for space, which limits their potential to grow (McMurray *et al.* 2018). Kahn and Leys (2016) tested the sponge loop hypothesis on massive, cold-water deep-sea sponge species and did not observe rapid cell cycling and shedding of sponge cells as detritus, which they explained as the consequence of nutrition limitation in these sponges. However, this study was conducted on small tissue fragments (i.e. not on fully functional sponges) and therefore difficult to compare to *in vivo* studies. Another study on massive deep-sea sponges did show extensive deposition of POM (Witte, 1997), thus supporting the existence of the sponge loop pathway in deeper waters. Considering that there are currently more than 9,000 sponge species described and many more expected (World Porifera Database; Van Soest et al., 2012), it can be expected that sponges exhibit a wide variety of traits and functions, which should be considered when choosing a candidate species for an IMTA.

In conclusion, conversion of DOM into edible POM occurs in many, but perhaps not all sponge species, at different rates. Selected sponge species may be used in IMTA to create trophic links between seaweeds and detritivores. Such trophic links have been established for (macro)algae,

sponges and detritivores, such as polychaetes, hermit crabs and ophiuroids (de Goeij *et al.* 2013; Rix *et al.* 2018), but not yet for sea cucumbers (class: *Holothuroidea*), which represent another good candidate detritivore for IMTA applications. Grazing of Holothurian species on sponge-derived POM is likely: there are reported observations of sponge-ophiuroid/holothuroid associations, where ophiuroids feed on the detritus of sponges (Hendler 1984; Hammond & Wilkinson 1985; Rix *et al.* 2018) and there are unpublished observations of Holothurian species that are directly feeding on deposits of sponges in cryptic habitats (M. Gokalp, personal observation). Hence, there is an urgent necessity for research that confirms this trophic link and thus demonstrates that IMTA systems with seaweeds, sponges and sea cucumbers can be established. The IMTA design presented in the next section remains hypothetical until the trophic link between sponges and sea cucumbers has been confirmed. However, it shows a first step in exploring the potential of this type of IMTA.

A case study: IMTA with seaweeds, sponges and sea cucumbers

In this section, we provide a theoretical design for a tropical integrated mariculture that combines the seaweed *Gracilaria* sp., the Caribbean sponge *Halisarca caerulea* and the Asian sea cucumber *Apostichopus japonica*. These species were selected based upon availability of relevant data. As such, they serve as model species to calculate carbon fluxes between these potential IMTA components. The genus *Gracilaria* is of commercial interest as a producer of marine agar (Peng *et al.* 2009), and this seaweed species has been long studied as extractive component in fish–seaweed IMTAs (Troell *et al.* 1997; Halling *et al.* 2005; Hernández *et al.* 2005; Abreu *et al.* 2009). *Apostichopus japonica* is a well-studied, commercially harvested sea cucumber species that has already been tested in IMTA settings (Yokoyama 2013). *H. caerulea* was chosen as a model sponge, because its potential to convert DOM into POM has been well characterized (de Goeij *et al.* 2009, 2013; Alexander *et al.* 2014). Since these individual species occur in distinct geographical areas, we want to stress that this combination of species is purely hypothetical and not intended for implementation in reality.

In the proposed seaweed–sponge–sea cucumber system, the sponges are primarily regarded as an intermediate component, whose role it is to (i) convert organic exudates from seaweed (DOM) into particulate sea cucumber food and to (ii) increase production of the seaweed through sponge inorganic nutrient exudates (e.g. phosphate, ammonium, nitrate). Additionally, as positive side effect, (iii) the sponge is expected to improve the water quality around the IMTA by reducing the microbial load around the farm.

Next to their role as trophic intermediates, sponges in IMTA will also convert part of the ingested DOM and particulate food into sponge biomass. This biomass can be harvested for commercial purposes such as sales as natural bath sponges (Duckworth 2009) or production of collagen (Gokalp et al. 2019, 2020). The extracellular matrix of the chosen model sponge species, H. caerulea, is known to contain large amounts of collagen (de Goeij et al. 2009). Collagen is a key component in sponge tissue regeneration that is helping to rapidly cover up an exposed wound (Alexander et al. 2015). Sponge collagen obtained from maricultures can be applied to promote the regeneration of human tissue and can be used as a scaffold for human bone tissue engineering (Silva et al. 2014). Notwithstanding this, the primary aim of this case study is to explore the dimensions of the different IMTA components needed to obtain an effective trophic connection.

The dimensions of the IMTA (Fig. 2) were calculated using literature data on productivity (e.g. growth, DOM production) and conversion factors (e.g. wet weight to dry weight, dry weight to carbon). First, the sponge biomass needed to take up all DOM excreted daily by 1 kg of Gracilaria dry weight (DW) was calculated (see Box 1). Daily excretion of DOM by 1 kg DW of Gracilaria was estimated at 10.8 g organic carbon (g C; Box 1). To take up 10.8 g C within a day, a H. caerulea sponge biomass of 176 g DW would be needed (Box 1). Second, it was assumed that out of the daily DOM excretion of 10.8 g C by Gracilaria, H. caerulea sponges assimilate 61% or 6.6 g C into biomass, the other 39% (4.2 g C) being used for respiration (de Goeij et al. 2008a). Based on a DOM to cellular detritus conversion factor for H. caerulea of 24% (de Goeij et al. 2013), we calculated that an uptake of 10.8 g C by the sponges would result in a release of 2.6 g C of cellular detritus. Hence, an amount of 2.6 g C d^{-1} would be available for ingestion by sea cucumbers in the form of sponge detritus. According to Gao et al. (2011), 1 kg (WW) of A. japonicus ingests 8.7 g C d^{-1}. This implies that the available amount of sponge detritus of 2.6 g C would be sufficient to feed 299 g WW or 27 g DW of A. japonicus biomass (assuming a 9% DW: WW ratio; Md et al. 2018). We assume an assimilation efficiency for carbon in A. japonicus of 50%, based on the range reported for a related species (Parastichopus californicus: 40–60%; Paltzat et al. 2008; Hannah et al. 2013), which would result in a daily assimilation in biomass of 1.3 g C, that is a recovery of 12% of the DOM that is excreted daily by the seaweeds in sea cucumber biomass (1.3 g C recovered/ 10.8 g C produced * 100%). An additional 4.0 g C (37% of the seaweed-derived DOM) is stored in sponge biomass daily (6.6 g C assimilated - 2.6 g C released as detritus). The total recovery of seaweed-derived DOM into (sponge and sea cucumber) biomass

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Box (1): Excretion of DOM by *Gracilaria* sp. and uptake of DOM by *H. caerulea*:

Five assumptions were used to calculate the daily excretion of DOM per unit of dry weight (DW) of *Gracilaria* and to calculate the amount of *H. caerulea* biomass (DW) needed to take up this amount of DOM:

(1) *Gracilaria* primary production is estimated at 36 g C kg^{-1} DW d^{-1}, which is a conservative estimate within the range 2.7–8.5 g C kg^{-1} WW d^{-1} reported (Orduña-Rojas et al. 2013) and assuming a DW : WW ratio of 10% in *Gracilaria spp.* (McLachlan & Bird 1986; Leedham et al. 2013).

(2) *Gracilaria* excretes 30% of its primary C as DOM. This assumption is based on the median of the range 2.8–56.7% of fixed C as reported for other seaweed species (Khailov and Burlakova, 1969, Brylinsky 1977; Haas et al. 2011), as no data exist for *Gracilaria* sp.

(3) When actively pumping, DOC uptake by *Halisarca caerulea* is 180 µg C cm^{-3} sponge h^{-1}, which is the median of the range of 157–205 µg C cm^{-3} h^{-1} reported (de Goeij et al. 2008a).

(4) The volume : DW ratio of *Halisarca caerulea* is 35 mg DW cm^{-3} (de Goeij et al. 2008b; de Goeij et al. 2013).

(5) *Halisarca caerulea* is conservatively estimated to actively pump during 12 h d^{-1} (de Goeij et al. 2008a).

Under the aforementioned assumptions, 1000 g DW of *Gracilaria* would excrete 10.8 g C d^{-1} as DOM (30% of a primary production of 36 g C kg^{-1} DW d^{-1}). To take up this amount of DOM, 5000 cm^3 *H. caerulea* tissue would be required (10.8 g C / (0.00018 g C cm^{-3} sponge h^{-1} × 12 h)). A volume of 5000 cm^3 *H. caerulea* tissue is equivalent to 176 g DW of sponge tissue (5000 cm^3/35 mg DW cm^{-3}).

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within this IMTA thus adds up to 49% (37% in sponges + 12% in sea cucumbers).

This hypothetical design shows that the standing stock masses of the different culture components are within two orders of magnitude (1000 g of seaweed, 176 g of sponge and 27 g of sea cucumber biomass for a balanced IMTA) and that the gain may be substantial: 49% recovery of a resource that would otherwise have been lost (30% of the primary production of the seaweeds). These outcomes justify further investigations to test this idea. It should be
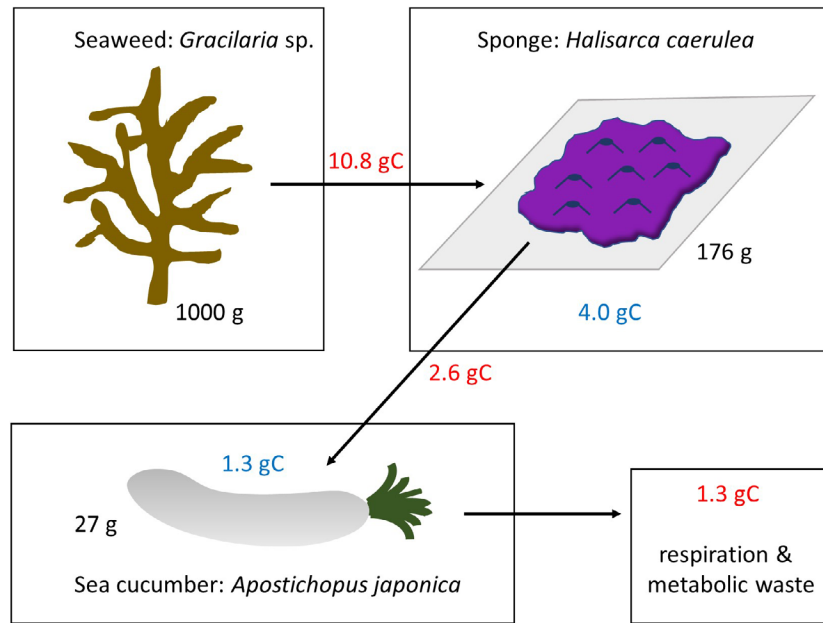
Figure 2 Design of a seaweed–sponge–sea cucumber IMTA. Numbers in black indicate the standing stocks of the three components in g dry weight (DW), numbers in red indicate the daily carbon (C) fluxes between the three components in g C, and blue numbers indicate the daily increase in biomass in g C.

noted, however, that within any IMTA system, the conversion efficiencies of the waste streams depend on the extent to which the produced waste streams can be retained in the system. Hydrodynamics play a crucial role in this respect: a system placed in the open ocean will have a substantially lower conversion efficiency than a fully closed land-based system (Reid *et al.* 2020).

Conclusions

The promises of integrated mariculture with sponges (faster growth of sponges and purified water) have been partially fulfilled. Growth and filtration activity of commercially interesting sponges are enhanced when sponges are cultured in the vicinity of organic waste streams from aquafarms and urban discharges (Osinga *et al.* 2010; Ledda *et al.* 2014; Gokalp et al. 2019). However, to demonstrate the effects of sponges on seawater quality in *in situ* systems, scale-up of integrated sponge farming is needed. Since demonstration scale projects are often expensive and logistically challenging, it is recommended to direct efforts on upscaling of sponge farming within integrated mariculture towards sponge species with an established commercial value, such as bath sponges (Duckworth 2009).

Technology for sponge farming has been established for several species (Duckworth 2009), and some of these techniques have already been applied successfully in IMTA settings (Page *et al.* 2005; Osinga *et al.* 2010). Hence, setting

up a large-scale integrated farm can be considered as technically feasible for some of the previously studied species. Nevertheless, because culture success can vary highly among locations (Duckworth 2009), scale-up efforts should always be preceded by small-scale optimization studies to reconfirm the methodology for the applied settings. Such optimization studies should include assessments of selective feeding and concentration-dependent feeding by the candidate sponges, as candidate sponges for extractive IMTA applications should have filtration characteristics that optimally suit their proposed role in the IMTA system.

Apart from tailored optimization of sponge culture procedures, there are many additional factors to consider before starting an integrated algae–sponge–sea cucumber IMTA system (see reviews by Duckworth 2009 for sponges; Chopin *et al.* 2012 for IMTA; Zamora et al., 2018 for sea cucumbers). Selected sites should have salinity, light and current regimes that are suitable for all IMTA components, and availability of nutrients should be sufficient for each of the components all year around. Safety and suitability of the culture materials and attachment methods must be evaluated with respect to storms, fishing activities, marine traffic, biofouling and predation. The risk for (density-dependent) diseases must be assessed for each of the individual components, and all aspects mentioned must be included in a final estimation of the operational costs.

The ability of sponges to feed on DOM and to convert DOM into POM gives them an added value for use in

IMTA, fulfilling complementary functions to other filter feeders commonly applied in IMTA such as shellfish. The sponges can remove both potentially harmful particles (e.g. bacteria, viruses, faecal pellets) and dissolved organic wastes and convert these into food for deposit feeding animals, including commercially interesting species such as sea cucumbers. An IMTA consisting of seaweeds, sponges and sea cucumbers seems a realistic scenario. To test this idea, the trophic link between sponges and sea cucumbers needs to be confirmed: Do sea cucumbers eat sponge-derived detritus? Once established, the proposed seaweed–sponge–sea cucumber IMTA system can provide valuable plant and animal biomass based solely upon the input of sunlight and a natural supply of inorganic nutrients.

Acknowledgments

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