**ABSTRACT**

The increasing harvesting of low trophic level organisms is raising concern about the possible consequences on the ecosystem functioning. In particular, the continuous demand of sea cucumbers from the international market led to the overexploitation of either traditionally harvested or new target species, including the Mediterranean ones. Sea cucumbers are mostly deposit feeders able to consume sedimentary organic matter and, thus, are ideal candidate for the remediation of eutrophicated sediments, like those beneath aquaculture projects. Breeding and restocking of overexploited sea cucumbers populations are well-established practices for Indo-Pacific species like *Holothuria scabra* and *Apostichopus japonicus*. Some attempts have also been made for the Mediterranean species *Holothuria tubulosa*, but, so far, the adaptation of protocols used for other species has presented several issues. We here summarize narratively the available information about sea cucumbers rearing protocols with the aim of identifying their major flaws and gaps of knowledge and fostering research about new triggers for spawning and feasible protocols to reduce the high mortality of post-settlers.

**HOLOTHURIAN’S EXPLOITATION**

The worldwide consumption of fish food products from 1961 to 2017 increased at an average annual rate of 3.1%, with a consumption per capita of fish food raising from 9.0 kg to 20.5 kg in the same period (FAO, 2020). Although the wild caches have been followed by the development of fish farming, the state of the wild stocks has continued to decline with less than 66% of the stocks harvested in a sustainable way (FAO, 2020). In response to the over-exploitation of wild finfish stocks, the invertebrate fisheries rapidly increased, being a new available source of seafood proteins and socio-economic opportunities (Berkes et al., 2006, Anderson et al., 2008). Many of the new target species now belong to low trophic levels, as a response to the overall down effect of trophic webs caused by top predators (Pauly et al., 2002; Anderson et al., 2008). In many cases, the pressure on stocks within low trophic levels increased faster than their management policies (Anderson et al., 2011a, 2011b), causing the spread of unregulated fishery and raising concerns for the possible consequences on ecosystem functioning and the sustainability of the fishery (Andrew et al., 2002; Leiva and Castilla 2002; Berkes et al., 2006; Anderson et al., 2008; FAO, 2008).

Sea cucumbers, marine invertebrates belonging to the Echinodermata Phylum, include more than 1500 species (Horton et al., 2018) and, mainly being deposit feeders, represent a good example of low trophic level organisms. Their fisheries had rapidly grown and expanded since 1980 as a consequence of the increasing demand from international markets, aquaculture and biomedical research programs (Bordbar et al., 2011).

Holothurians are present in almost all the marine biotopes, from the littoral to hadal depths (Purcell et al., 2012). Holothurians are part of the Chinese culinary tradition, are considered gourmet and luxury seafood and are generally sold as a dried product called bêche-de-mer or trepang (Wen et al., 2010; Yang and Bai, 2015). The market price of this product depends on the quality (grade low, medium, high) (Ram et al., 2014), with some particularly valuable species as *Apostichopus japonicus* Selenga, which holds the highest price of 2950 US$ dried kg⁻¹, followed by *Holothuria scabra* Jaeger, 1833 (115-640 US$ dry kg⁻¹), *Holothuria lessoni* Massin, Uthicke, Purcell, Rowe & Samyn, 2009 (240-790 US$ dry kg⁻¹) (Purcell et al., 2012).

The presence of high-value nutrients such as Vitamin A, Vitamin B1 (thiamine), Vitamin B2 (riboflavin), Vitamin B3 (niacin), and minerals (i.e., calcium, magnesium, iron and zinc) indicate that sea cucumbers are suitable tonic and restorative products, also rich in crude proteins (range 41-63%) (Wen et al., 2010, Bordbar et al., 2011).

Moreover, sea cucumbers, containing a number of biological and pharmacological bioactive compounds, have attracted attention for their potential medical value (Bordbar et al., 2011). Sea cucumbers contain numerous bioactive and anti-age substances that are already exploited in the cosmetic and pharmaceutical industries (Fredalina et al., 1999; Saito et al., 2002; Zhao et al., 2010; Bordbar et al., 2011; Purcell, 2014). All these properties and the high market price led to the overexploitation and decline of sea cucumbers Indo-Pacific populations and the expansion of the fishery to reach new virgin stocks in Galapagos Islands, Mexico, North America and the Mediterranean Sea (Conand, 2006; Purcell et al., 2012; González-Wangüemert et al., 2018). The estimated sea cucumbers harvest, from Asia and Pacific regions, ranges from 20,000 to 40,000 t per year of the dry product (FAO, 2012). Fisheries from African and Indian Ocean regions also contribute to the complex amount with the range of 2000-2500 t per year (FAO, 2012).
Less information are available about sea cucumbers fisheries in the Mediterranean Sea, in particular for *Holothuria tubulosa* Gmelin, 1788, *Holothuria mammata* Grube, 1840, *Holothuria sanctori* Delle Chiaje, 1823, *Holothuria forskali* Delle Chiaje, 1823, *Parastichopus regalis* Cuvier, 1817, and *Holothuria arguinensis* Koehler & Vaney, 1906 (Çakly et al., 2004; Antoniadou and Vafidis, 2011; Sicuro and Levine 2011; González-Wangiémer and Borrero-Perez, 2012; Mezali and Thandar 2014; González-Wangiémer et al., 2014a, 2015). Presently, more than half of global sea cucumber fisheries are considered depleted or overexploited to the extent that governments (including the Italian Government) have banned their harvesting (Anderson et al., 2011; González-Wangiémer et al., 2014, 2018). With the 38% of sea cucumber fisheries currently unregulated and an unknown level of illegal catches, this fishery is considered unsustainable and far from being adequately managed (Anderson et al., 2011; Choo, 2008; Toral-Granda, 2008).

The unregulated exploitation of sea cucumbers is a rising concern for their conservation, with 16 species worldwide now classified as “vulnerable” or “endangered”, according to the IUCN Red list (Conand et al., 2014, Ramirez-González et al., 2020). Concern also raises because most of the harvested sea cucumbers are deposit feeders, thus playing an ecological key role due to their feeding behaviour (Uthicke, 2001; Roberts et al., 2000), their decline could have severe consequences on sedimentary biogeochemistry and benthic ecosystem functioning.

Here we reviewed the available information about the ecological role of sea cucumbers, with a focus on the Mediterranean *H. tubulosa*, their breeding, fishery management issues, main gaps of knowledge and future perspectives for their use as remediation of eutrophicated sediments.

**LIFE HISTORY AND POPULATION DYNAMICS OF SEA CUCUMBERS**

The increasing interest towards sea cucumbers and their use for food, medical and habitat remediation purposes, stimulated exploration about their reproductive cycle and population dynamics, both crucial aspects for the assessment of wild stocks and their eventual management.

Almost all sea cucumbers are broadcast spawners with external fertilization that present an annual or bi-annual maturation season (Mercier and Hamel, 2009; Mohsen and Yang, 2021). With a few exceptions of hermaphrodite species, they are generally gonochoric that leak in sexual dimorphisms (Smiley et al., 1991; Mercier and Hamel, 2009). The life cycle of sea cucumbers is characterised by one or more planktonic larval stages starting with a feeding auricularia (early, mid and late), a non-feeding dolio laria and then a feeding pentactula that settle on the substrate (Strathmann, 1975; Ito and Kitamura, 1997; Yanagisawa, 1998).

Doliolaria actively explore the surrounding environment to identify the best place to settle and made the last metamorphosis into the pentactula. If the conditions are not suitable for settlement, the larvae will keep swimming for several days (Mercier et al., 2000). The pentactula lose the ability to swim but can continue to explore the surrounding environment with the buccal podia, moving by small jumps (Mercier et al., 2000). Although rarely, Evans and Palmer (2003) reported the ability of the pentactula larvae of *Parastichopus californicus* Stimpson, 1857, to clone, forming a bud that, after separation, will normally develop into an auricularia larvae.

The pentactula larvae will start to feed and grow, becoming a juvenile in a variable time lag (Mercier et al., 2000; Agudo, 2006; Mercier and Hamel, 2009; Rakaj et al., 2018, 2019). Information about the mechanisms of settlement, physiology and cue that can stimulate the larvae to settle are poorly explored and understood, so far. Studies conducted in mesocosm investigated the success of the larval settlement, which can strongly depend on the larval nutrition state and the capacity to accumulate lipids (Peters-Didier and Sewell, 2019). In the late auricularia stage of *H. scabra*, the development of the hyaline spheres indicates an adequate feeding, and their size is a reliable indicator for subsequent performance (Duy et al., 2016). The settlement and the last metamorphosis, as for other echinoderms, represents a survivorship bottleneck that can lead to high mortality rates. The early juvenile stage (<5 mm length) is also vulnerable and a critical phase with substantial mortality rates (Agudo, 2006; Rakaj et al., 2018).

The holothurians recruitment has been studied mainly on historically exploited species, and information about post-settlers and juveniles in the field is scarcely recorded in the literature and, even, referred to sporadic occasions. For instance, the recruitment of *H. scabra* has been found to occur on a monthly time scale on seagrasses, with adult specimens mainly observed in sandy sediments and juveniles in organic matter (OM) enriched muddy sediments (Mercier et al., 2000). The lack of other information about holothurians recruitment can also be ascribed to the potential misidentification of the species because they can have a considerably different morphology when compared with that of adults. Besides this, juveniles might occupy different habitats and can be obscured from the researchers’ view because of their cryptic behaviour (Shiell, 2004). *H. scabra* juveniles can also be affected by predation-mediated mortality by fish belonging to the Balistidae, Labri dae, Lethrinidae and Nemipteridae families (Dance et al., 2003), sea stars, and crustaceans (Kinch et al., 2008). Holothurians’ recruitment can also be affected by geographic distances, the duration of the larval period and to
the hydrodynamic retainment in coastal areas (Uthicke, et al., 1998, 1999, 2001; Uthicke and Purcell, 2004).

Most studies about holothurians’ population dynamics explored species with a long history of exploitation, including *A. japonicus*, *Cucumaria frondosa* Gunnerus, 1767, and *Isostichopus fuscus* Ludwig, 1875, (Herrero-Pérezrul et al., 1999; Reyes-Bonilla and Herrero-Pérezrul, 2003; Hamel and Mercier, 2008; Anderson et al., 2011; Purcell et al., 2011; Yang et al., 2015; Glöckner-Fagetti et al., 2016). Unfortunately, the absence of a rigid structure in sea cucumbers and the high plasticity of the body wall make it difficult to investigate the growth rates of holothurians. Alternative methods proposed include marking the calcareous (epi-pharyngeal) ring, chemical marking of spicules, external and internal tagging (Kinch et al., 2008). However, all of these methods are affected by wide methodological biases but also by the bio-ecological traits of holothurians. In fact, the body size of holothurians can vary as a response to changing environmental conditions (Tolon et al., 2017b), the occurrence of asexual reproduction through fission (Purwati and Dwiono, 2005; Uticicce and Conand, 2005; Laxminarayana, 2006; Purwati and Dwiono, 2007; Purcell et al., 2012; Dolmatov, 2014) or the evisceration of their internal organs (intestine, gonads and respiratory trees) through autotomy, in response to predation and other environmental stressors (Shukalyuk and Dolmatov, 2001; Wilkie, 2001; Spirina and Dolmatov, 2003; Zang et al., 2012). The evisceration is a typical behavioral trait of holothurians that does not lead to the death of the organism, rather is followed by the re-growth of the internal organs (Dawbin, 1949; Murray and Garcia-Arrarás, 2004; García-Arrarás et al., 2006; Dolmatov and Ginanova, 2009). Interestingly, after evisceration, the respiratory function shifts to the body wall for the time necessary for the respiratory trees’ regrowth. During this period, sea cucumbers will consume endogenous substances, which causes a significant body weight loss (Zang et al., 2012, Zhang et al., 2017). Because of the multiple factors regulating holothurians body size, small individuals are not necessarily the youngest ones (Kinch et al., 2008).

**FEEDING BEHAVIOR AND ECOLOGICAL ROLE OF SEA CUCUMBERS**

Deposit-feeders holothurians acquire food by swallowing large volumes of sediment (Roberts et al., 2019). They sift through the sediment with tentacles and feed on detritus, organic matter, sand and the relative grown-over biofilm, expelling sandy pellets after digestion (Hartati al., 2020).

The feeding starts with capturing the sedimentary food particles with tentacles and their release into the pharynx through the circum-oral tentacles. Once inside the mouth the particles are mixed with the digestive enzymes and compressed into a plug which moves throughout the gut following a plug-flow reactor model. The plug is then transported by peristalsis along the simple digestive system that ends in the posterior part of the animal (Zamora and Jeffs, 2011).

Sea cucumbers predominantly feed on sedimentary organic detritus associated with micro-organisms and small benthic organisms (Roberts et al., 2000). In the gut mineral and organic particles are found along with fragments of shell, barnacles, seagrasses, echinoderms ossicles, fecal pellets, foraminifera shells, with a highly variable size (Roberts et al., 2000).

Information about the potential selectivity of shallow-water holothurians is controversial. Some holothurians are able to choose OM enriched particles, whereas others appear not to be (Moriarty 1982; Hammond, 1983; Uthicke and Karez, 1999; Battaglene et al., 1999; Slater et al., 2011; Navarro et al., 2013; Sun et al., 2015; Lee et al., 2018; Hartati et al., 2020). The selective ability can be related to how sea cucumbers feed on the sediment, which is highly variable among species, depending on their ten-
tacles dimension, the size and gut morphology (Roberts et al. 2001, Dar and Ahmad, 2006; Ramón et al., 2019). The selection of smaller organic-rich particles might be due to the greater ease of being caught and held by the tentacles, or to the potential chemo-selection ability of holothurians (Schneider et al. 2013; Lee et al., 2018). The presence of a higher OM content in the gut compared to the one present in the sediment can be a consequence of a passive selection of the finest grain size of the particles which can be more easily ingested. This, in turn, can be explained because smaller grain size particles can have a higher OM content due to the wider surface available for the microbial colonization (Hargrave, 1972; Levintson, 1972; Dale, 1974; Yamamoto and Lopez, 1985; Manini and Luna, 2003).

Considering their feeding behaviour, sea cucumbers are great seafloor bioturbators, able to rework large amounts of sediments via ingestion and excretion (9-82 kg ind⁻¹ year⁻¹) which can extensively blend and reform seafloor substrata (Coulon and Jangoux, 1993; Uthicke and Karez, 1999; Mangion et al., 2004). Bioturbation intensity can influence the sediment permeability, oxygen concentration, water content and chemical gradients in pore water, affecting the rate of remineralization and the inorganic nutrient flux and, finally, can redistribute food resources for the other benthos (Reise, 2002; Lohrer et al., 2004; Solan et al., 2004; Meysman, 2006a). Bioturbation carried out by sea cucumbers can be circumscribed to the upper layer of the sediment or reach up to ten centimetres depth based on the habits of the species whether they are fossorial or not (Uthicke and Karez, 1999; Purcell, 2004a; Amaro et al., 2010).

The role of holothurians in recycling the sedimentary OM is considered one of their main ecosystem functions (Purcell et al., 2016). The ability to reduce the OM content in the sediment has been recently investigated (Dar and Ahmad, 2006; İşgören-Emiroğlu and Günyay, 2007; Slater and Carton, 2009; Wolkenhour et al., 2010; Zamora and Jeffs, 2011; Tolon et al., 2017a; Neofitou et al., 2019; Hartati et al., 2020). The sea cucumber *Australostichopus mollis* Hutton, 1872, can significantly reduce total organic carbon (TOC), chlorophyll-a and phaeopigments contents of sediments impacted by green-lipped mussel biodeposits (faeces and pseudofaeces) (Slater and Carton, 2009). MacTavish et al. (2012) reported that *A. mollis* suppressed benthic microalgae and facilitated bacterial activity, causing a shift in the balance of benthic production and decomposition processes. Juveniles of the same species decreased their ingestion rate with the increasing of the total sedimentary organic matter (TOM), showing the ability of this species to use different amounts of TOM, changing their feeding behaviour and digestive physiology (Zamora and Jeffs, 2011). *H. tubulosa* reduced the sedimentary OM and organic carbon (OC) by 31-59%, with an absorption rate of 43 and 55% respectively, both in manipulative laboratory and field experiments (Neofitou et al., 2019).

The functioning of the digestive system of holothurians has been modelled and defined as a sort of ‘bioreactor’, where the ingested nutrients are quickly extracted and assimilated (Penry and Jumars, 1986, 1987; Jumars, 2000; Amaro et al., 2010). The grazing of holothurians could increase the exchange flux of nutrients across the sediment-water interface and promote nutrient regeneration (Zhou et al., 2006; Yuan et al., 2013; Slater and Carton, 2009; Slater et al., 2011; Zamora and Jeffs, 2011, 2012a, b). On the other hand, other species, like *A. japonicus*, could not affect TOC and total nitrogen (TN) sedimentary contents, but can cause OM particles redistribution and inhibit microphytobenthos (Michio et al., 2003).

**THE MEDITERRANEAN SEA CUCUMBER**

**HOLOTHURIA TUBULOSA**

A new target species candidate for sea cucumbers aquaculture is *Holothuria tubulosa* (Gmelin 1788), one of the most common and widespread holothurians in the coastal areas of the Mediterranean Sea and the Eastern Atlantic Ocean (Tortonese, 1965; Koukouras et al., 2007). In the last few years, *H. tubulosa* has been actively harvested in Turkey, Greece, Italy, Spain and the increasing of illegal and unregulated fishing is one of the main issues for its management (Rakaj et al., 2019). Overexploitation of this species led the Italian Ministry of Agriculture, Food and Forestry (MIPAAF) to ban sea cucumbers fishing along the entire national coastline (Ministerial decree 156/2018), as a precaution for the conservation of the species.

*H. tubulosa* is a continuous deposit-feeder, generally encountered in organic matter enriched soft bottoms and seagrass meadows (Bulteel et al., 1992; Gustato et al., 1982). Coulon and Jangoux (1993) reported that large individuals of *H. tubulosa* might ingest up to 17 kg of dry weight sediment ind⁻¹ y⁻¹. Using the data provided by Costa et al. (2014) it can be estimated that the quantity of seagrass detritus potentially ingested by *H. tubulosa* ranges between 12 and 28 g dry weight m⁻² y⁻¹ ind⁻¹.

The reproductive cycle of *H. tubulosa* was studied in specimens from the Adriatic Sea, Oran coast (Algeria) and Dardanelles Strait (Turkey). The development stages of male and female gonads showed a clear annual pattern and all authors agreed that the spawning period was set between June and October with minor local differences, and a resting period from October to January (Despatatovic et al., 2004; Ocaña and Tocino, 2005; Dereli et al., 2015; Tahri et al., 2019). Rakaj et al. (2018) successfully bred and reared *H. tubulosa* in the laboratory, completing the larval development in 27 days, which, however, was followed by high mortality shortly after the settlement. A
recent study reported the use of *H. tubulosa* larvae as new model for embryo-larval bioassays to assess marine pollution (Rakaj et al., 2021), but, to date, rearing techniques of this species remain still not very efficient.

**SEA CUCUMBERS IN INTEGRATED MULTI-TROPHIC AQUACULTURE**

In the last two decades, to satisfy the demand for seafood product, aquaculture activities increased and the need to mitigate its impacts on the environment became an urgent need, especially in the presence of vulnerable habits like seagrass beds (Pusceddu et al., 2007; Holmer et al., 2008). Wastes coming from mariculture plants can affect sediments biochemistry, increasing the organic contents, ultimately exacerbating eutrophication (David et al., 2009; Keeley et al., 2014). In fact, wastes from mariculture can cause benthic hypoxia and anoxia, hydrogen sulfite enrichment and, in extreme cases, also led to rising of methanogenic bacteria populations, which, in turn, can significantly impact the abundance and biodiversity of benthic organisms (Karakassis et al., 2000; Angel et al., 2002; Mirto et al., 2002; Burford et al., 2003; La Rosa et al., 2004; Fodelianakis et al., 2015).

The conceptual approach of integrated multi-trophic aquaculture (IMTA) is to use different trophic-levels organisms in the same system: those belonging to the highest trophic level (generally fish) are fed artificially and those belonging to the lowest trophic level (extractive species) feed on waste released by the specimens of the highest trophic level (Troell, 2009; Granada et al., 2015). The extractive species commonly used in IMTA include molluscs, seaweeds or detritivorous species (Zhou et al., 2006; Slater and Carton, 2007; Yuan et al., 2013; Slater et al., 2009; Zamora and Jeffs, 2011, 2012a, 2012b; Lamprianidou et al., 2015; Shpigel et al., 2018). Among detritivorous species, considering their feeding habits, sea cucumbers appear to be ideal candidates as extractive species for IMTA systems.

Commercially valuable holothurians species most used in IMTA systems include *A. japonicus* (Zhou et al., 2006; Yuan et al., 2013; Kim et al., 2015), *A. mollis* (Slater and Carton, 2007; Slater et al., 2009; Zamora and Jeffs, 2011, 2012a, 2012b), and *P. californicus* (Paltzat et al., 2008), mainly fed with scallops and mussels’ biodeposits alone, or mixed with powdered algae (Yuan et al., 2006). Other small-scale experiments used *Actinopyga bannwarthi* Panning, 1944 (Israel et al., 2019) and *H. scabra* (Mathieu-Resuge et al., 2020).

The IMTA feasibility in the Mediterranean Sea is still in an experimental scale, whereas either pilot or commercial scale activities have been carried out in other regions (MacDonald et al., 2013; Marinho et al., 2013; Lamprianidou et al., 2015). To our best knowledge, only two studies investigated the use of *H. tubulosa* in IMTA systems in the Mediterranean Sea.

Beneath fish cages, Tolon et al. (2017b) observed a biomass increase of holothurians ranging from 9 to 31 g ind⁻¹ in just 90 days and suggested that these animals are ideal candidates to mitigate in IMTA the benthic eutrophication generated by fish farming. Neofitiou et al. (2019) during an experiment carried in the field beneath farming cages of the sea bream *S. aurata* and the sea bass *Dicentrarchus labrax* Linnaeus, 1758, reported that the maximum extractive capacity of holothurians is reached at a density of ca. 10 individuals m⁻². Such a density allowed abating OM and OC contents in sediments beneath the cages by 31 and 59%, respectively. These results, though spatially and temporally fragmented, corroborate the idea of using sea cucumbers beneath fish cages, in IMTA systems, to mitigate the impacts of biodeposition on the sediment, at the same time providing a commercially important by-product, without any additional feed. With these assumptions, it can be envisaged that sea cucumbers in IMTA will increase the environmental sustainability of aquaculture and will also generate an important economic advantage, due to the high value of sea cucumbers.

**HOLOTHURIANS’ MANAGEMENT PERSPECTIVES**

The ecological consequences of holothurians overexploitation include a loss in bioturbation and a consequent reduction of benthic biomass, biodiversity, and ecosystem functioning (Lohrer et al., 2004; Solan et al., 2004; Meysman et al., 2006b). Therefore, sea cucumbers’ over-exploitation claims for urgent measures to preserve natural populations and their ability to provide reproductive adults for either natural or artificial breeding.

On the one hand, the peculiar biological and ecological traits of holothurians and the lack of reliable stock assessments make a scientific based management of this resource still far to be reached. Management and regulation of sea cucumbers fishery are currently being implemented in some countries, using different approaches. Among these, for example, a rotational zone strategy has been applied to the multispecies sea cucumber fishery in Australia’s Great Barrier Reef Marine Park, where this approach led to a substantial reduction of the risk of localized depletion, higher long-term yields, and improved economic performance (Plagányi et al., 2015).

To guarantee significant recruitment in an acceptable timeframe, future management policies of sea cucumbers should set a minimum population density threshold, below which exploitation should be banned (Battaglene and Bell, 2004), also to avoid the Allee effect, which occurrence has been reported for overexploited populations of *H. scabra* in the Warrior Reef, Australia (Skewes et al.,

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