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Impacts of Marine and Lagoon Aquaculture on Macrophytes in Mediterranean Benthic Ecosystems

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The direct and indirect impact of fish farms, shellfish aquaculture, and extensive forms of aquaculture such as seeding of juvenile sea urchins, on macrophytes (seaweeds and seagrasses), is reviewed in Mediterranean benthic ecosystems. Fish farms constitute a source of organic matter and nutrients (food and fecal pellets) that causes the extirpation of *Posidonia oceanica* seagrass meadows beneath and near to farm facilities. In addition to direct effects, the nitrogen enrichment of macrophytes tissues increases the grazing pressure by herbivorous fishes and sea urchins. In some cases, the impact can continue to increase several years after the cessation of farming activities. Natural restoration of extirpated seagrass meadows is generally unlikely at the human time scale. Shellfish aquaculture is the cause of the main flow of introduced macrophytes in the Mediterranean; the main vector is the importation of oyster spat from Japan and Korea. North-eastern Pacific seaweeds are now the dominant biotic component of some Mediterranean lagoons (e.g., Thau, Mar Piccolo, and Venice lagoons). In addition to direct effects, mussel aquaculture can constitute a source of larvae that flow with currents, the adults of which can overwhelm seaweed forests (e.g., *Carpodesmia mediterranea*). Shellfish aquaculture is also a source of fecal pellets, resulting in changes in bottom macrophytes, and a vector of diseases of metazoans, the extirpation of which may change the functioning of recipient macrophyte ecosystems. The edible sea urchin *Paracentrotus lividus* is sometimes erroneously considered as in decline due to over-harvesting. However, its abundance in the second half of the 20th century was probably a consequence of human impact (overfishing of its predatory fish, organic pollution. This man-induced proliferation resulted in the extirpation of seaweed forests (e.g., *Carpodesmia* spp., *Treptacantha* spp. – formerly *Cystoseira* spp. – *Sargassum* spp.; many species are endemic), which play a key role in Mediterranean coastal ecosystems. Therefore, the attempts to restore sea urchin abundance, *via* seeding of juveniles from hatcheries, has further artificialized the habitats rather than contributing to the restoration of natural ecosystems. Good practices guidelines are proposed aimed at minimizing the impact of aquaculture on macrophytes.

Keywords: aquaculture, fish farms, macrophytes, mediterranean, *Paracentrotus lividus*, shellfish culture

INTRODUCTION

The aquaculture of marine organisms has undergone a spectacular development in the Mediterranean since the beginning of the 20th century, particularly since the 1980s, especially shellfish culture in the western basin and fish farming in the eastern basin (Charbonnier, 1990; Belias and Dassenakis, 2002; Basurco and Lovatelli, 2003; Grigorakis and Rigos, 2011; Rountos et al., 2012; Massa et al., 2017).

Until then, it consisted only of very extensive forms of aquaculture, such as valliculture, in the northern Adriatic and Tyrrhenian seas (Italy). Valliculture, the origin of which dates back at least to the 15th century, and is probably even more ancient, is a practice consisting in the exploitation of the natural seasonal migrations of some fish species (mainly gray mullets) from the sea into coastal lagoons, by keeping fish in enclosures ("valli," in Italian), preventing the fish from returning to the sea, then capturing them several years later during their descent to the sea (Lumare, 1983). Aquaculture of brackish species might have been known in the Egypt of the pharaohs, in man-made pools in the Nile Delta (Basurco and Lovatelli, 2003; Soliman and Yacout, 2016).

Modern forms of aquaculture, in the Mediterranean Sea, range from the very extensive ones, such as the seeding of juveniles of the sea urchin *Paracentrotus lividus*, to more intensive methods, such as the fish farms where fish located at a high level in the food webs are reared with artificial food. Here, we review the more or less worrying impact of aquaculture on Mediterranean species of macrophytes and the ecosystems for which they may be an "ordinary" contributor, a key species or an ecosystem engineer. The aim is to present a synthesis of the data dispersed in a large number of publications, by considering both direct and indirect effects of aquaculture, and to propose good practices guidelines aimed at minimizing the impact of aquaculture on macrophytes. In this review, we have taken into all the published references, with the exception of redundant data and gray literature and the Mediterranean Sea. It is important to underline that, despite the peculiarities of the Mediterranean Sea (Lejeusne et al., 2010), the conclusions we draw from the Mediterranean are largely generalizable to the world ocean (e.g., Yokoyama et al., 1997; Boyra et al., 2004; Loya et al., 2004; Hall-Spencer et al., 2006; Weitzman et al., 2019; but see Walls et al., 2017).

The notion of macrophytes actually encompasses a polyphyletic complex (Boudouresque, 2015; Boudouresque et al., 2015a). Macrophytes, or multicellular photosynthetic organisms, belong to both the prokaryotes (namely Cyanobacteria) and the eukaryotes. Within the eukaryotes, macrophytes belong to four taxa, very far apart in the phylogenetic tree of eukaryotes. (i) The Ulvophyceae (phylum Chlorobionta, subkingdom Viridiplantae) are part of what are popularly called "green algae." (ii) The Magnoliophyta (phylum Streptobionta, subkingdom Viridiplantae) are what is popularly called "flowering plants"; some terrestrial flowering plants which had returned to the sea, 100–60 Ma ago, are the ancestors of e.g., modern *Posidonia, Cymodocea,* and *Zostera* (Kuo et al., 2000; Orth et al., 2006). (iii) The Florideophyceae (subkingdom Rhodobionta) are part of what are popularily called "red algae." Ulvophyceae, Magnoliophyta and Florideophyceae belong to the kingdom Archaeplastida. (iv) Finally, the Phaeophyceae belong to the phylum Ochrophyta (= Chromobionta), within the kingdom Stramenopiles (= Heterokonta); they are popularly called "brown algae."

The Mediterranean is a semi-enclosed sea. It is bordered on its southern coast (from Egypt to Morocco) by arid regions and the contribution of its rivers and groundwater discharge does not compensate for evaporation, so that the water deficit is 0.5–1.0 m a^{-1} (Millot and Taupier-Letage, 2005; Rodellas et al., 2015). Last but not least, the construction of the Aswan High Dam in Egypt, completed in 1970, has nearly dried up the Nile River (at its mouth), formerly the most important Mediterranean river, very little of whose waters now reach the Mediterranean Sea (Sharaf and El Din, 1977; Stanley, 1993; Abu-Zeid and El-Shibini, 1997; Khadr, 2003). This deficit in water of the Mediterranean Sea is offset by the entry of Atlantic water through the Straits of Gibraltar (Bethoux, 1979; Farmer and Armi, 1988; Bethoux and Gentili, 1998; Millot and Taupier-Letage, 2005). Despite the relatively nutrient-rich supply of Atlantic water, the low influx of rivers is responsible for the fact that the Mediterranean is an oligotrophic or highly oligotrophic sea; it is also characterized by high environmental variability and by steep gradients, e.g., of salinity, temperature and stratification, which all tend to increase eastwards, within the relatively restricted Mediterranean area (Bethoux et al., 1999; Turley, 1999; Lejeusne et al., 2010; Rodellas et al., 2015; Massa et al., 2017). The Mediterranean Sea has been compared to a giant microcosm of the world's ocean, or to a "miniature ocean" (Bethoux et al., 1999; Lejeusne et al., 2010). Finally, the opening up of the Suez Canal, in 1869, which joins the Red Sea and the Mediterranean, created a real "highway" for the arrival of exotic species in this region, and was the major modern biogeographical event in the world ocean (Por, 1978, 1990; Boudouresque, 1999b).

FISH FARMS

Mediterranean marine fish farming was initially land-based. Since the 1990s, it was transferred to floating cages at sea (Grigorakis and Rigos, 2011; Massa et al., 2017). In 2013, it was dominated by two main species: the European seabass *Dicentrarchus labrax* with ∼161,000 t a^{-1} (tones = metric tons, per year) and the gilthead seabream *Sparus aurata* with ∼135,000 t a^{-1} (Belias and Dassenakis, 2002; Massa et al., 2017). Farming of these species involves a first phase taking place in a land-based hatchery, then the moving of juvenile fish to floating cages at sea. The Atlantic bluefin tuna *Thunnus thynnus* is farmed by a different type of process, as it is based on the capture of wild specimens (8–10 kg) which are then grown in cages to market size of at least 30 kg (Kružić, 2008; Mylonas et al., 2010; Grigorakis and Rigos, 2011). Several other finfish species are reared in the Mediterranean, such as the meager *Argyrosomus regius* and the sharpsnout sea bream *Diplodus puntazzo*, the latter still at an experimental stage (Stipa and Angelini, 2005; Sánchez-García et al., 2014). Although it is a brackish and freshwater form of aquaculture, it is relevant to also mention the most important

Mediterranean aquaculture industry, that of the Nile tilapia *Oreochromis niloticus*; in 2012, for Egypt alone, the production amounted to ~769,000 t (Soliman and Yacout, 2016).

Land-based farm wastewater affects the isotopic composition, and mainly $\delta^{15}N$ values, of benthic macrophytes; the impact of a fairly small farm on the seagrass *Posidonia oceanica* and the red alga *Sphaerococcus coronopifolius* was detected at a distance of 500 m from the outfall (Vizzini and Mazzola, 2004). However, the effects can be easily avoided by using land-based wastewater treatment. Off-shore fish farms are also responsible for elevated $\delta^{15}N$ signature in leaf tissues and epibionts of a deep *P. oceanica* meadow, up to 3 km from the cages (Ruiz et al., 2010).

Offshore fish farms, with fish reared in floating cages, which today represent the bulk of marine fish farming, can affect the marine environment, directly and indirectly, in several ways, through (i) the release of nutrients (nitrogen and phosphorus), (ii) the release of particulate organic carbon (e.g., fecal pellets and uneaten feed) and (iii) chemicals (e.g., copper in antifouling treatments and drugs for disease treatments). The effects vary according to the production system, site characteristics, hydrodynamics and movements at the bottom of the water column, the species farmed, the feed used and the sensitivity of the receiving ecosystem (Sarà et al., 2006; Holmer et al., 2008; Marino, 2011; Massa et al., 2017).

Many environmental requirements for coastal fish farming (e.g., good water quality and water renewal) correspond almost exactly to the habitat preferences of *P. oceanica*; as a result, a number of fish farms are placed over or very near *P. oceanica* meadows (Holmer et al., 2008). Studies on fish cage aquaculture located over *Posidonia oceanica* seagrass meadows have shown a very strong impact on this ecosystem of paramount importance for Mediterranean coastal areas (Pergent-Martini et al., 2006; Boudouresque et al., 2009, 2012, 2016; Grigorakis and Rigos, 2011; Giakoumi et al., 2015; Kletou et al., 2018). The *P. oceanica* ecosystem thrives between the sea level and 30–40 m depth, in the infralittoral zone (Molinier and Picard, 1952; Boudouresque and Meinesz, 1982; Boudouresque et al., 2012); for Mediterranean biotic zones and habitats, see Pérès and Picard (1964) and Pérès (1982). **(i)** There is a decrease in light availability under facilities, due to both increased turbidity (including possible phytoplankton enhancement) and the shadow of the cages: 38% of the bottom light is lost beneath the cages in the Gulf of Ajaccio (Corsica). However, the amount of light is still higher than the compensation irradiance level of *P. oceanica*. Therefore, this factor alone cannot explain the regression of the meadow observed (Verneau et al., 1995; Delgado et al., 1997; Mendez et al., 1997; Pergent et al., 1999; Ruiz and Romero, 2001; Ruiz et al., 2001). This statement may be right for shallow meadows, but not for deeper meadows, which are light limited (Romero et al., 1998). According to Puhr and Pikelj (2012), light availability is the main factor that controls seagrass distribution at fish farm locations. Light available for *P. oceanica* photosynthesis is also reduced by the high epibiont coating caused by nutrient enrichment (Cancemi et al., 2000, 2003; see below). (ii) Because of the input of fecal pellets and uneaten food, the sediment is enriched in organic matter, which alter its physical and chemical characteristics and enhances anoxic conditions and sulfate reduction processes (Pergent et al., 1999; Ruiz et al., 2001; Cancemi et al., 2003; Holmer et al., 2003, 2008; Boudouresque et al., 2012; Weitzman et al., 2019). This factor emerges as one of the main drivers of benthic deterioration, via e.g., sediment anoxia (Holmer et al., 2008). (iii) The water is enriched in nutrients, especially ammonium (Holmer et al., 2008; Grigorakis and Rigos, 2011), which may enhance phytoplankton development but especially fosters the growth of the *P. oceanica* leaves and increases the biomass of their epibionts. It is worth noting that the effect of nutrient enrichment is different according to depth (Romero et al., 1998). The maximum increase in epibiont biomass does not occur beneath the cages, but at a distance of between 20 and 80 m at Figari (Corsica), which may be explained by the large quantities of copper introduced with the fish food and/or antifouling chemicals used for the nets (Mendez et al., 1997; Pergent et al., 1999; Dimech et al., 2000a; Holmer et al., 2003; Pergent-Martini et al., 2006; Kružić, 2008). (iv) In contrast with the increase or decrease in leaf growth and epibiont biomass, the vertical growth of rhizomes abruptly declines by about twofold following the onset of fish farm operations; this decline is perceptible up to 400 m from the farm (Marbà et al., 2006; Holmer et al., 2008). (v) The concentration of trace metals, such as copper and zinc in rhizomes of *P. oceanica,* increases near the facilities. They derive from uneaten feed, fish excreta and antifouling chemicals used to prevent development of fouling organisms on the cages (Pergent et al., 1999; Basaran et al., 2010; Grigorakis and Rigos, 2011). (vi) The epibiontic cover of the leaves, together with the high nitrogen content of leaf tissues and epibionts, are attractive for herbivorous species, such as the teleost *Sarpa salpa* and the sea urchin *Paracentrotus lividus*. Sea urchins are actually more abundant in the vicinity of cages. As a result, the grazing of leaves is higher beneath and near facilities than at control sites (Mendez et al., 1997; Pergent et al., 1999; Ruiz et al., 2001; Pérez et al., 2008; Prado et al., 2008; Balata et al., 2010; Rountos et al., 2012). (vii) Fish populations are increased, both in biomass, number of individuals and sometimes point species diversity (Verneau et al., 1995; Machias et al., 2004, 2005). In the Gulf of Ajaccio, biomass and density of fish are increased four to fivefold (from 54 to 268 g 10 m^{-2} and from 2 to 10 individuals 10 m^{-2}, respectively); the most successful species are e.g., stripped red mullet *Mullus surmuletus*, bogue *Boops boops* and barracuda *Sphyraena sphyraena.* The trophic structure of fish populations is also changed, with fewer invertebrate consumers and more omnivorous species (Verneau et al., 1995). In Malta, benthic invertebrates (decapods, mollusks and echinoderms) also exhibit an increase in abundance of individuals and point species diversity at intermediate distances (40–160 m) from the cages (Dimech et al., 2000b, 2002). (viii) Beneath the cages and in the adjacent area, there is an overall regression of the meadow: the shoot density conspicuously declines and extensive areas of dead *matte* appear (**Figure 1**; Verneau et al., 1995; Delgado et al., 1997; Dimech et al., 2000a; Cancemi et al., 2003; Pergent-Martini et al., 2006; Holmer et al., 2008; Kružić, 2008; Pérez et al., 2008; Boudouresque et al., 2012; Kletou et al., 2018). *Matte* is the structure built by living and dead rhizomes and by the sediment that fills the interstices; because of the very slow or even the absence of degradation of dead rhizomes and roots

FIGURE 1 | A *Posidonia oceanica* meadow severely degraded under and in the vicinity of a fish farm. Bay of Calvi (Corsica). Photo © Gérard Pergent.

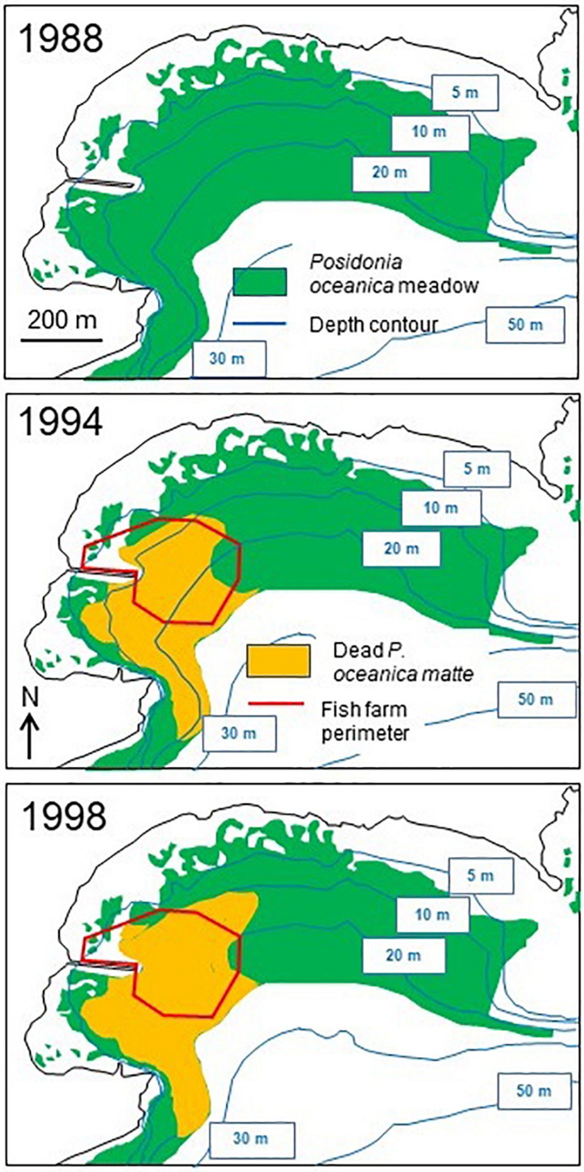

FIGURE 2 | Distribution of *Posidonia oceanica* meadow in 1988, 1994, and 1998 in El Hornillo Bay (Murcia, Spain). Only the complete mortality off (area of dead *matte*) has been mapped. Original drawing, after Ruiz-Fernandez (2000) and Ruiz et al. (2001) data.

within the *matte*, the *matte* can persist for at least millennia (Molinier and Picard, 1952; Boudouresque and Meinesz, 1982; Boudouresque et al., 2012, 2016).

The case of the El Hornillo fish farm (Murcia region, Spain), a medium scale farm (up to 700–800 metric tons of fish per year) is particularly instructive (**Figure 2**). Fish farming began in 1989. Since the onset of fish farming, 11 ha (28%) of the former *P. oceanica* meadow have been rapidly and completely lost and 10 ha (25%) significantly degraded, with a decline in shoot density; the affected area (a radius of 300 m from the fish farm perimeter) therefore amounts to about 53% of the former meadow, and 7 times the fish farm area (Ruiz-Fernandez, 2000; Ruiz et al., 2001).

Another case is also instructive, that of the Fornells Bay (Menorca Island, Spain) fish farm. It was established in 1986, and its activity ceased in 1991. However, the regression of the *P. oceanica* meadow, which quickly began as soon as the farm came into operation, continued for at least three years; the persistence of the seagrass decline could be due to the excess of organic matter remaining in the sediment (Delgado et al., 1999). Interestingly, in Cyprus, close to the upper thermal limit of *P. oceanica*, fish farms initially located over a *P. oceanica* meadow were relocated offshore; three to five years later, not only had the regression ceased, but the margin of the meadow had progressed, which illustrates an important management success story (Kletou et al., 2018).

Similar conclusions can be drawn for coastal detritic bottoms, e.g., maërl beds, which are dominated by calcareous Rhodobionta, in the circalittoral zone, deeper than the infralittoral zone (Sanz-Lázaro et al., 2011; Aguado-Giménez and Ruiz-Fernández, 2012; Massa et al., 2017 and references therein); below experimental fish cages, the maërl community was almost completely buried; dead and blackened rhodoliths were covered by a thin layer of sediment and only a few individuals of *Gracilaria cylindrica, Lithophyllum racemus, Meredithia microphylla* (Rhodobionta) and *Fabellia petiolata* (Ulvophyceae) remained alive (Aguado-Giménez and Ruiz-Fernández, 2012). In a coralligenous ecosystem, from 30 to 40 m of depth, at about 30 m of cages, there is a decrease in β- diversity, encrusting Corallinales, erect Rhodobionta, Dictyotales, Fucales (Phaeophyceae) and *Halimeda tuna* (Ulvophyceae) and an increase in *Peyssonnelia* spp. (Rhodobionta) and algal turfs (Piazzi et al., 2019). Unfortunately, most authors focus on the impact of fish farming on *P. oceanica* meadows, but pay little attention to other macrophyte assemblages. For example, in El Hornillo Bay (Spain), Ruiz et al. (2001) briefly mention other benthic communities, e.g., the presence of the seagrass *Cymodocea nodosa* on shallow sandy bottoms, but the possible impact of the fish farm was not addressed. In Fornells Bay (Menorca Island, Spain), *C. nodosa* was less affected than *P. oceanica* (Delgado et al., 1997). On artificial hard substrate, the fouling community, initially dominated by seaweeds, was transformed, in 6 months, into a community dominated by filter-feeders, probably because of the elevated supply of particulate organic matter (Cook et al., 2006). In Croatia, near fish cages, the proliferation of sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) in rocky reef habitats has been observed, resulting in overgrazing of seaweeds and the occurrence of barren grounds (Kušpilić et al., 2007).

Obviously, as pointed out by Ruiz et al. (2001), the impact resulting from fish farming is highly variable. It depends on water exchange, depth, aquaculture practices (fish feeding, fish yield, etc.) and on the vulnerability of the benthic ecosystem, e.g., the presence of *P. oceanica* meadows or rocky reef seaweed assemblages. Farms may not even have an impact on a given ecosystem; for example, no impact of fish farms on *Carpodesmia amentacea* (= *Cystoseira amentacea*; Ochrophyta) distribution along the French coast has been recorded (Thibaut et al., 2014).

SEA URCHIN SEEDING

The edible sea urchin *Paracentrotus lividus* is, together with the fish *Sarpa salpa*, the main native macro-herbivore in the Mediterranean Sea (Verlaque, 1987; Boudouresque and Verlaque, 2013). Other herbivorous fish, the native parrotfish *Sparisoma cretense* and the introduced (from the Red Sea) rabbitfishes *Siganus luridus* and *S. rivulatus*, are common in the eastern basin and are currently spreading toward the west, because of the warming of the sea surface water (Por, 1978; Astruch et al., 2016; Karachle et al., 2016). *Paracentrotus lividus* is sometimes erroneously considered as in decline, which would have "negative" consequences on the health status of ecosystems; this is due to over-harvesting (see e.g., Guidetti et al., 2004; Couvray, 2014; Couvray et al., 2015; Sartori et al., 2015), as its gonads (roe) are appreciated as a luxury seafood, especially in France, Spain, Italy, and Greece (Ballesteros and Garcia Rubies, 1987; Ledireac'h, 1987; Ledireac'h et al., 1987). However, at least in some Mediterranean areas, e.g., in Corsica, there is no sign of overexploitation, as highlighted by Duchaud et al. (2018). Although the actual baseline of the population density of *P. lividus* in the Mediterranean is unknown, there are reasons to think that its abundance, in the second half of the 20th century, could be, at least partly, a consequence of human impact (overfishing of its predatory fish, organic pollution) (Boudouresque and Verlaque, 2013); it is usually uncommon in No-Take Zones of Marine Protected Areas, i.e., zones where all types of fishing and harvesting (fish, custaceans and echinoderms), both amateur and commercial, are banned (Boudouresque et al., 1992), and proliferates in the vicinity of untreated domestic sewage outfalls (Harmelin et al., 1981; Boudouresque and Verlaque, 2013) and fish farms (Kušpilić et al., 2007). This man-induced proliferation of *P. lividus* has resulted in the extirpation of seaweed forests, e.g., *Carpodesmia* spp., *Treptacantha* spp. (formerly *Cystoseira* spp.), and *Sargassum* spp.; many of them are species endemic to the Mediterranean; they play a key role in Mediterranean coastal ecosystems (Thibaut et al., 2005, 2015; Blanfuné et al., 2016; Thibaut et al., 2016, 2017), and their replacement by barren grounds is a concerning issue (Fraschetti et al., 2011; Agnetta et al., 2015; Ling et al., 2015).

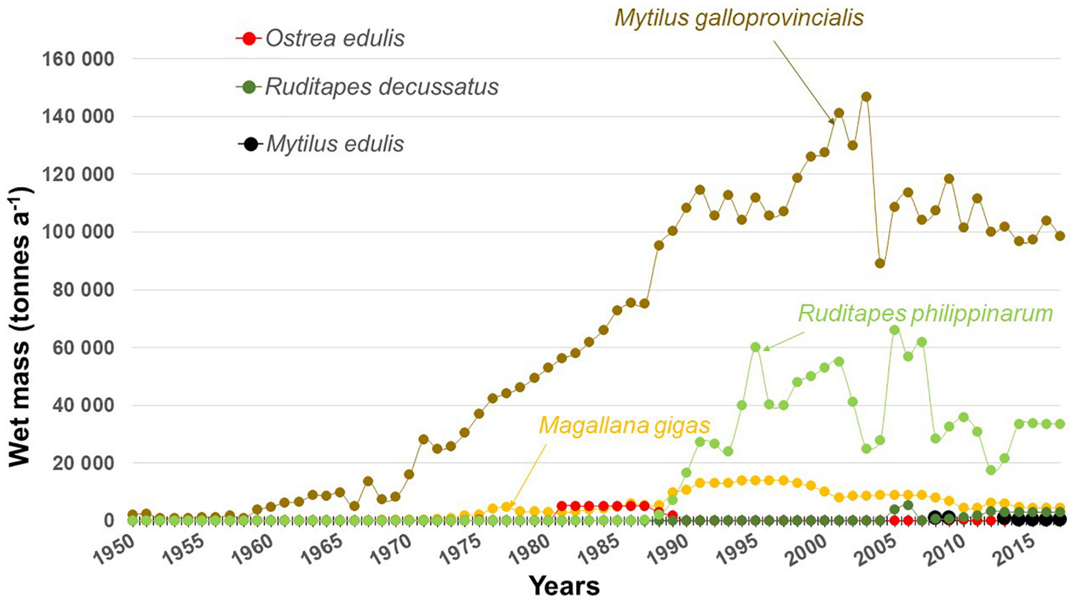

FIGURE 3 | Shellfish production in the Mediterranean. For the countries which have both Atlantic and Mediterranean shores (France and Spain), Atlantic production has been removed from the statistics. Data from FAO (2019).

TABLE 1 | Seaweeds probably non-indigenous to the Mediterranean, of which the vector (or one of multiple vectors) is oyster aquaculture.

Species	Origin	First mediterranean record	Countries of current occurrence	Habitat and status
Rhodobionta (Archaeplastida)				
Aglaothamnion halliae	E Atlantic	Venice (It), 2016	It	Lagoons, Mid
Agardhiella subulata	W Atlantic or NE Pacific	Thau (Fr), 1984	Fr, It	Lagoons, Intro, C
Ahnfeltiopsis flabelliformis	Japan	Thau (Fr), 1984	Fr	Lagoons, Intro, C
Antithamnion nipponicum	Japan	Thau (Fr), 1988	Fr, It	Lagoons, Inv, C
Chondria coerulescens	Atlantic	Thau (Fr), 1995	Al, Cy, Es, Fr, Gr, It, Lb, Ly, Mo, Slo, Tn[a]	Lagoons, shallow reefs, Intro
Chondrus giganteus	Japan	Thau (Fr), 1994	Fr	Lagoons, Intro
Chrysymenia wrightii	Japan	Thau (Fr), 1978	Fr	Lagoons, Intro
Colaconema codicola	Japan ?	French Catalonia, before 1952	Al, Es, Fr, It, Mon, Tn, Tr	Lagoons, shallow reefs, Intro, CC
Dasya sessilis	Japan	Thau (Fr), 1984	Fr	Lagoons, Inv, CC
Dasysiphonia japonica	Japan	Thau (Fr)n 1998	Fr, It	Lagoons, Intro, C
Gracilaria vermiculophylla	Pacific	Adriatic (It), 2008	It	Lagoons, shallow open sea, Intro
Grateloupia asiatica	Japan	Thau (Fr), 1984	Fr	Lagoons, Intro, C
Grateloupia lanceolata	Japan	Thau (Fr), 1982	Fr, It (?)	Lagoons, Intro, CC
Grateloupia minima	NE Atlantic	Thau (Fr), 1998	Fr, It	Lagoons, Intro, C
Grateloupia patens	Japan	Thau (Fr), 1994	Fr	Lagoons, Cas, R
Grateloupia subpectinata	Japan	Thau (Fr), 1990	Fr	Lagoons, Intro, C
Grateloupia turuturu	Japan	Thau (Fr), 1982	Es?, Fr, Is, It	Lagoons, Intro, CC
Grateloupia yinggehaiensis	China		It	Lagoons, R
Griffithsia corallinoides	NE Atlantic and Japan	Sicily (It), 1964	Fr, Al (?), It, Tn, Tr	Lagoons, shallow reefs, Intro, CC
Herposiphonia parca	Japan	Thau (Fr), 1997	Fr	Lagoons, Intro, C
Hypnea valentiae	Japan	Thau (Fr), 1996	Fr, Gr, It, Lb, Mo	Lagoons, shallow reefs, C
Laurencia okamurae	Japan	Thau (Fr), 1984	Fr	Lagoons, Intro, C
Lithophyllum yessoense	Japan	Thau (Fr), 1994	Fr	Lagoons, Intro, C
Lomentaria flaccida	Japan	Thau (Fr), 2002	Fr	Lagoons, Cas
Lomentaria hakodatensis	NE Pacific	Thau (Fr), 1978	Fr, It	Lagoons, Intro, CC
Melanothamnion japonicus	Japan	Venice (It) 2016	It	Lagoons
Nemalion vermiculare	N Pacific	Thau (Fr), 2005	Fr	Lagoons, Intro, C
Neosiphonia harveyi	Japan	Thau (Fr) 1958	Al, Eg, Es, Fr, Gr, It, Mo, Sy	Lagoons, shallow reefs, CC
Nitophyllum stellato-corticatum	Japan	Thau (Fr), 1984?	Fr	Lagoons, Intro, C
Polysiphonia atlantica	Atlantic	Berre lagoon (Fr), 1969–1971	Al (?), Cy, Es, Fr, Gr, It, Lb, Ly, Mo, Tn	Lagoons, shallow reefs, Intro, R
Polysiphonia fucoides	Atlantic	Prevost lagoon (Fr), 1988	Al, Cy, Es, Fr, Gr, Hr, Is, It, Mo, Slo, Tn, Tr[a]	Lagoons, shallow reefs, Intro, R
Polysiphonia morrowii	Japan or Korea	Thau (Fr), 1997	Fr, It, Tr	Lagoons, Intro, C
Pterosiphonia tanakae	Japan	Thau (Fr), 1993	Fr	Lagoons, Intro, CC
Pyropia yezoensis	Eastern Pacific	Thau (Fr), 1975	Fr	Midlittoral lagoons, Intro, CC
Rhodophysema georgii	Japan or NE Atlantic	Thau (Fr), 1978	Fr, Tr	Lagoons, Intro, RR
Solieria filiformis	N Atlantic	Mar Piccolo di Taranto (It), 1922	Fr, Is, It	Lagoons; Intro
Chlorobionta (Archaeplastida)				
Cladophora hutchisioides[b]	Japan or Australia	Thau (Fr), 2002	Fr	Lagoons, Intro, C
Codium fragile	Japan?	Banyuls-sur-Mer (Fr), 1946	Al, Es, Fr, Gr, Hr, It, Ly, Mo, Slo, Tn, Tr	Lagoons, shallow reefs, Intro, CC
Codium taylori	Atlantic or Pacific	Israel, 1955	Eg, Is, Lb, Ly, Sy	Subtidal reefs, Intro
Derbesia rhizophora	Japan?	Thau (Fr), 1984	Fr	Lagoons, Intro, C
Ulva australis (= *U. pertusa*)	Japan ?	Thau (Fr), 1984	Fr, It, Tr	Lagoons, Intro, CC

(Continued)

TABLE 1 | Continued

Species	Origin	First mediterranean record	Countries of current occurrence	Habitat and status
Ulva californica	N Pacific	Venice (It), 2011	It	Lagoons, Cas or Intro?
Ulva lactuca (= *U. fasciata*)[a,c]	Japan	Alexandria (Eg), 1798–1801	Al, Eg, Es, Fr, Gr, Hr, Is, It, Lb, Ly, Mo, Sy, Tn, Tr	Lagoons, subtidal reefs, Intro, C
Ulvaria obscura	NE Atlantic or N Pacific	Thau (Fr), 1985	Fr, It	Lagoons, Intro, CC
Uronema marinum	Australia	Venice and other N Adriatic lagoons	It	Laggons, Intro, C
Ochrophyta (Stramenopiles)				
Acrothrix gracilis	Japan	Thau (Fr), 1998	Fr	Lagoons, Intro, R
Ascophyllum nodosum	NE Atlantic	Mar Piccolo di Taranto (It), 2012	It	Lagoons, Cas
Botrytella parva	Japan	Venice (It), 1996	It, Tr	Lagoons, Cas
Chorda filum?	N Atlantic	Greece, 1899	Fr, Gr?, Tr	Lagoons, Intro, C
Cladosiphon zosterae	NE Atlantic	Venice (It), 1996	Fr, It, Tr	Lagoons, Intro, R
Colpomenia peregrina	NE Pacific	Thau (Fr), 1918	Al, Es, Fr, Gr, It, Mo, Tr	Lagoons, shallow reefs, Intro, CC
Cutleria multifida[d]	Japan	Cannes (2008)	Fr, It, Gr	Subtidal reefs, Intro, C
Desmarestia viridis	NE Atlantic or N Pacific	Thau (Fr), 1978	Fr, It	Lagoons, Intro, CC
Ectocarpus siliculosus var. *hiemalis*	N Atlantic	Turkey, 1986	It, Tr	Shallow reefs, Cas
Halothrix lumbricalis	N Atlantic or N Pacific	Acicastello (It), 1978	Fr, It, Tr	Lagoons, shallow reefs, Intro, C
Leathesia marina (= *L. difformis*)	N Atlantic or N Pacific	Thau (Fr), 1905?	Fr, It	Lagoons, Intro, C
Microspongium stilophorae[a]	N Atlantic	Thau (Fr), 2005	Fr	Lagoons
Punctaria tenuissima	Japan	Jabuka Island (Hr), 1947–1956	Fr, Hr, It, Tr	Lagoons, shallow reefs, Intro, C
Pylaiella littoralis[e]	NE Atlantic or N Pacific	Venice (It), 1962	Es, Fr, Gr, Hr, It, Slo, Tn, Tr	Lagoons, Intro, CC
Rugulopteryx okamurae	Japan	Thau (Fr), 2002	Es, Fr, Gib, Mo	Lagoons, shallow reefs, Inv, CC
Saccharina japonica	Japan	Thau (Fr), 1976	Fr	Lagoons, Cas
Sargassum muticum	Japan	Thau (Fr), 1980	Es, Fr, It	Lagoons, Inv, CC
Scytosiphon dotyi	NE Pacific	Trieste (It), 1960–1977	Es, Fr, It, Tr	Lagoons, Intro, R
Sphaerotrichia firma	Japan	Aegean Sea (Tr), 1970	Fr, Tr	Lagoons, shallow reefs, Intro, C
Undaria pinnatifida	Japan	Thau (Fr), 1971	Fr, It	Lagoons, Intro, CC

The possible area of origin can be only a part of the native range of a species. Data from Verlaque (1994); Ribera and Boudouresque (1995), Boudouresque et al. (2011); Petrocelli et al. (2013), Marchini et al. (2015); Verlaque et al. (2015), Kawai et al. (2016); Ocaña et al. (2016), Wolf et al. (2018), and Sempere-Valverde et al. (2019), updated. Status: Cas, casual; Intro, introduced (established); Inv, Invasive; Mid, midlittoral; RR, very rare; R, rare; C, common; CC, very common. Countries of current occurrence: Al, Algeria; Cy, Cyprus; Eg, Egypt; Es Spain; Fr, France; Gib, Gibraltar; Gr, Greece; Hr, Croatia; Is, Israel; It, Italy; Lb, Lebanon; Ly, Libya;, Mo, Morocco, including Spanish cities), Mon, Monaco; Slo, Slovenia; Sy, Syria; Tn, Tunisia; Tr, Turkey. [a] The species could be native, in some parts of its Mediterranean range. [b] Since the taxonomy of the genus Cladophora is complicated, the confirmation of the identity of this taxon would require further investigation. [c] The European records of Ulva lactuca over the past 200 years correspond to another species than the real U. lactuca Linnaeus (= U. fasciata Delile) which is referred to here (see Butler, 2007 and Verlaque et al., 2015). [d] Cutleria multifida is native to north Atlantic and Japan (Kawai et al., 2016). Molecular analysis of Mediterranean specimens from France, Italy and Greece shows a Japanese origin. The species has been recorded from other Mediterranean countries, but, in the absence of molecular analysis, an Atlantic origin cannot be excluded. [e] Pylaiella littoralis is regarded as introduced only in the northern lagoons of the Mediterranean (Verlaque et al., 2015).

As expected, harvesting results in a decline in density, mean size and percentage of individuals of the largest size classes (Bertocci et al., 2014, 2018). However, the lack of large individuals (the commercial size class) in a highly harvested area of Sardinia does not seem to be alarming for the self-supporting capacity of the population, as the reproductive potential is mainly due to undersized individuals: the amount of released gametes is similar in harvested and non-harvested areas (Loi et al., 2017).

The attempts to restore sea urchin abundance, *via* seeding of juveniles from hatcheries, whether or not effective (see below), and the possible disproportionate financial cost of such operations, cannot be referred to as "ecosystem restoration," but rather as "extensive aquaculture." It is likely that they contribute to further accentuating the artificialization of the environment, for the possible benefit of humans needs, and not to the restoration of its naturalness. In order to mitigate the supposed decline of *P. lividus* populations, and to respond to the growing market demand, land-based and offshore aquaculture, and the reseeding of depleted sites, with juveniles reared in hatcheries, has been considered (e.g., Couvray, 2014; Couvray et al., 2015; Sartori et al., 2015, 2016; Shpigel et al., 2018; Volpe et al., 2018; Zupo et al., 2019). For example, 250,000

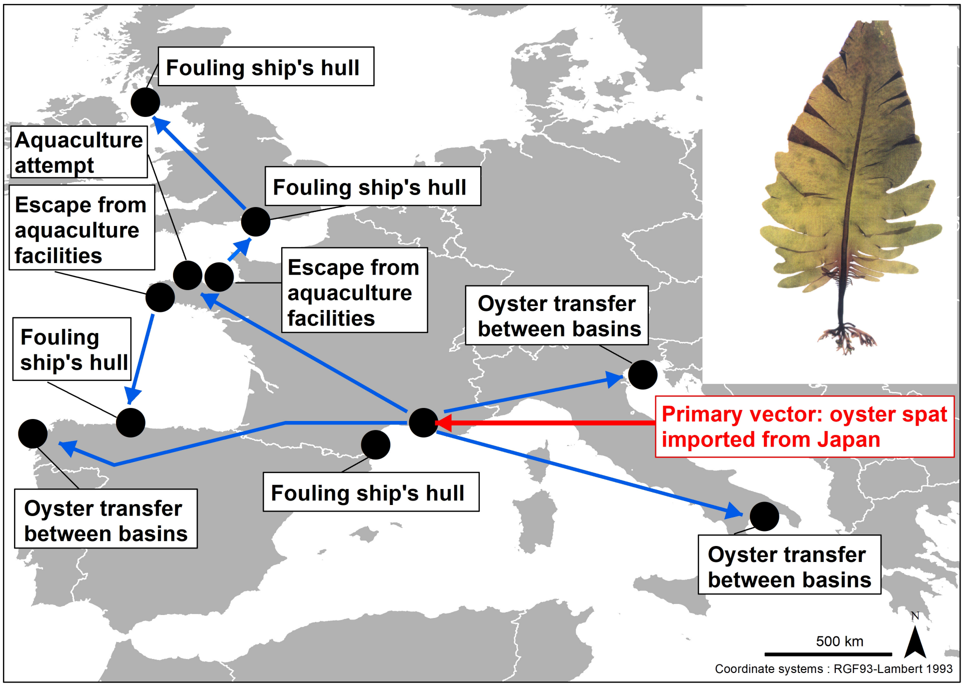

FIGURE 4 | Primary (red arrow) and secondary (blue arrows) vectors of spread of *Undaria pinnatifida* ("brown alga," Stramenopiles) in the Mediterranean and western Europe. Only some of the sites where *U. pinnatifida* occurs, along the western coasts of Europe, have been represented.

hatchery produced juveniles were released in eastern Provence (France); a year after release, they represented 3 and 12% of total recaptured urchins at two experimental sites (Couvray et al., 2015). In Asturias (Atlantic Spain), all small individuals (10–30 mm) released on substrates with burrows did not survive the first few weeks, and only those that were released on substrates with large individuals successfully settled (12%) (de la Uz et al., 2018). This preference of juveniles for habitats with abundant adults could explain the relative failure of some reseeding operations, which for intuitively logical reasons, are carried out in depopulated areas rather than in already densely populated areas. Hatchery rearing of *P. lividus* can cause bottleneck effects (i.e., a substantial reduction in genetic diversity and differentiation from wild populations), as hatchery-reared populations are less diverse than wild populations (Segovia-Viadero et al., 2016). This highlights the need to consider the genetic risks of releasing hatchery-reared juveniles into the wild in the framework of stock enhancement and sea ranching programs (Segovia-Viadero et al., 2016). However, according to Couvray et al. (2015), in eastern Provence, genetic diversity seems not to be affected by introducing juveniles from the hatchery.

FIGURE 5 | Seascape on a shallow rocky substrate near Meze, Thau Lagoon (France). The brown blades: *Undaria pinnatifida*. The yellowish filaments (above, to the left): *Sargassum muticum*. The sketch below (**Figure 6**) shows the rest of the macrophyte stand. Photo: courtesy of Sandrine Ruitton.

SHELLFISH AQUACULTURE

Mediterranean shellfish aquaculture has grown steadily over the years, although with a lower rate of increase than that of fish farming, and a relative plateau or decline since the 1990s: 17 kt in 1970, 56 kt in 1980, 141 kt in 1990, 190 kt in 2000, and 137 kt in 2010; fish production is now higher than that of shellfish (**Figure 3**; Basurco and Lovatelli, 2003; FAO, 2019). Three species of bivalves constitute the bulk of the shellfish aquaculture in the Mediterranean Sea (Basurco and Lovatelli, 2003): the mussel *Mytilus galloprovincialis*, which is native to the Mediterranean (mainly farmed in Italy, Grece and France), the

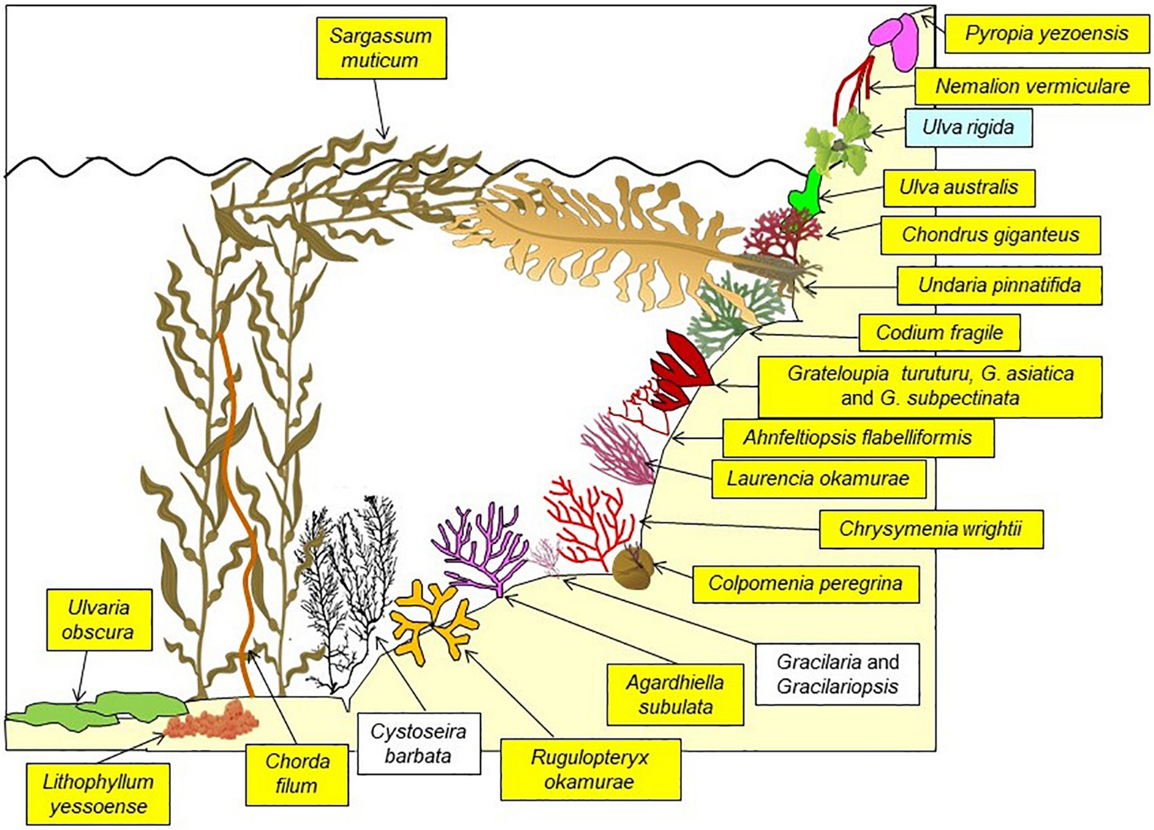

FIGURE 6 | A sketch of the dominant macrophytes on shallow (down to 1 m depth) rocky substrates of the Thau Lagoon in spring. Names on a yellow background: introduced species; blue background: probably cryptogenic introduction; white background: native species. From Boudouresque et al. (2011), modified and updated.

Pacific oyster *Magallana gigas* (= *Crassostrea gigas*) (mainly in France), native to the Pacific coast of Asia (Salvi and Mariottini, 2017), and the Manila clam *Ruditapes philippinarum* (mainly in Italy), native to the coasts of the Indian and Pacific Oceans, from Pakistan to Japan and the Kuril Islands (Goulletquer, 2005). Three other species are bred, but the quantities produced are very limited: the Atlantic mussel *Mytilus edulis*, the flat oyster *Ostrea edulis* and the grooved carpet shell *Ruditapes decussatus* (**Figure 3**) *Magallana gigas* escaped from sea farms and is now introduced (naturalized) in the Mediterranean; in contrast with the European Atlantic coasts, it is not invasive there (Zenetos et al., 2005; Wrange et al., 2010; see Boudouresque and Verlaque, 2002, 2012, for invasion terminology). *Ruditapes philippinarum* escaped from sea farms and was also deliberately introduced, as in the Venice and Berre lagoons; it is locally invasive and its abundance is considered welcome by local fishermen (Mazzola, 1992; Occhipinti Ambroggi, 2001; Pranovi et al., 2003, 2006).

Shellfish aquaculture can affect macrophytes of Mediterranean ecosystems via four processes: a major source of non-indigenous seaweeds, a flow of propagules that can flood macrophyte forests, a vector of diseases of metazoans of which the extirpation changes the functioning of recipient ecosystems, and a change in the functioning of the recipient ecosystem, including a direct effect of the shower of fecal pellets on bottom macrophytes.

A Major Source of Non-indigenous Seaweeds

Oyster culture has been a mass vector for the introduction of macroalgae in the Mediterranean, as in many regions of the earth: "*The greatest agency of all that spreads marine animals* [and plants] *to new quarters of the world must be the business of oyster culture*" (Elton, 1958; Verlaque et al., 2007b; Grigorakis and Rigos, 2011). As many as 65 Non-Indigenous Species (NIS) have been recorded in the Mediterranean (**Table 1**) of which the arrival is linked, directly or indirectly, to shellfish aquaculture, that of the Pacific oyster *Magallana gigas* for the most part, but also the Manila clam *Ruditapes philippinarum* in the case of *Aglaothamnion halliae, Gracilaria vermiculophylla,* and *Uronema marinum* (Sfriso et al., 2014; Verlaque et al., 2015; Wolf et al., 2018). Between 1968 and 1983, large amounts of oyster spat (up to 200 t a^{-1}) were directly imported from Japan (the Bay of Mangoku-Ura, near Sendai) to Thau Lagoon (Occitania, France); in fact, these imports continued well after their official ban in 1983 (Verlaque, 2001). Theoretically, the spat was to be immerged

TABLE 2 | A grid that shows the eligibility of fish farming sites, according to the distance from the nearest *Posidonia oceanica* meadow, the depth, the water movement (openness of the site) and the size of the farm (in wet mass – metric tons – of fish produced per year). Greater distances would of course be welcome.

Depth	Openness	<100 m	100–200 m	200–300 m	300–400 m	>400 m
<5 m	Open	▨	▨	▨	<100 t	<500 t
	Not open	▨	▨	▨		<100 t
5–10 m	Open	▨	▨	<100 t	<500 t	<1 000 t
	Not open	▨	▨	▨	<100 t	<500
10–20	Open	▨	<100 t	<500 t	<1 000 t	<2000 t
	Not open	▨	▨	<100 t	<500 t	<1 000 t
20–40 m	Open	▨	▨	<100 t	<500 t	<1 000 t
	Not open	▨	▨	▨	<100 t	<500 t
>40 m	Open	▨	<500 t	<1000 t	<2 000 t	<5000 t
	Not open	▨	<100 t	<500 t	<1 000 t	<2000 t

In gray, the combination of factors resulting in exclusion. Open sites or not open sites: located outside a bay or within an embayment. After Boudouresque et al. (2012).

for 4 h in fresh water in order to kill exotic epibionts, before immersion in the lagoon (Piquion, 1985), however, this operation was under the sole responsibility of the farmers, who of course did not do it; in addition, freshwater treatment is ineffective in eliminating macroalgae (Verlaque et al., 2007a). Shellfish aquaculture is the main vector of non-indigenous macrophytes in the Mediterranean (42%), ahead of the Suez Canal, fouling, and aquariums. Unsurprisingly, the main region of origin is the North-East Pacific (mainly Japan and Korea) (83% of the taxa) and the main primary recipient area in the Mediterranean is Thau Lagoon (66%).

Most of the known attempts of NIS to become introduced have been successful (89%; **Table 1**). The cases of failure (casual species: recorded once, or for a few years, then apparently extinct) are those of *Grateloupia patens, Lomentaria flaccida, Ulva californica, Botrytella parva, Ascophyllum nodosum, Ectocarpus siliculosus* var. *hiemalis,* and *Saccharina japonica*.

Primary vectors (from the region of origin to the recipient area) can be identical to secondary vectors (from a recipient area acting as a hub to a new recipient area), or different. *Undaria pinnatifida* arrived at Thau Lagoon via a primary vector, i.e., directly from the Bay of Mangoku-Ura (Japan), with imported oyster spat (**Figure 3**; Boudouresque et al., 1985). Subsequently, Thau Lagoon acted as a hub for the dispersal of the species to new areas, via secondary vectors. In some cases, the secondary vector was similar to the primary one, namely the transfer of adult oysters from one aquaculture basin to another (Occhipinti Ambrogi, 2000); adult transfers are common in the oyster business, oysters beginning to grow in one basin (e.g., Thau) and then being transferred to another (e.g., Marennes-Oleron, Atlantic coast of France) for the final *affinage* (refining process). Secondary vectors can also be different: fouling on ship hulls or escape from a seaweed farm (**Figure 4**; Boudouresque et al., 1985; Brault and Briand, 1987; Floc'h et al., 1996; Cecere et al., 2000). *Solieria filiformis* probably arrived in the Mediterranean via shipping (fouling on ships' hulls: primary vector), but was subsequently spread by oyster transfers (secondary vector) (Verlaque et al., 2015).

The impact of invasive species on native species and/or native ecosystems is well known and therefore of major concern: species extinction, e.g., on islands, local extinctions, functional extinctions and disruption of the ecosystem functioning (e.g., Boudouresque, 1997; Schmitz and Simberloff, 1997; Balmford and Bond, 2005; Boudouresque et al., 2005; Clavero and Garcia-Berthou, 2005). However, most studies consider the impact of a given invasive species on native species, rather than the collective impact of a pack of invasive species (Boudouresque, 1999a). In fact, a large number of introduced species can coexist in the same ecosystem, as occurs in e.g., coastal lagoons, along the Tuscany coast (Italy) and in the eastern Mediterranean basin (Piazzi and Cinelli, 2003; Piazzi and Balata, 2009; Boudouresque et al., 2011). Introduced species can of course compete with each other (Piazzi and Ceccherelli, 2002). Thau Lagoon illustrates the disruption of the ecosystems and seascapes by a host of introduced macroalgae, which may outnumber the native species, and represent the bulk of the biomass of primary producers in some habitats. Boudouresque et al. (2011) have even compared Thau Lagoon with a "Japanese botanical garden": overall, 121 putatively native species and 58 introduced species, most of them of Japanese origin, currently occur there (**Figures 5**, **6**). Putatively native species include cryptogenic species (sensu Carlton, 1996), i.e., species which are today more or less cosmopolitan, but were probably introduced in most parts of their current range, before the 18th century and the beginning of the Linnean Era; *Ulva rigida* (**Table 2** and **Figure 6**) is probably a cryptogenic species. On rocky shallow substrates, the seascape is dominated by introduced species, which can account for 97–99% and 48–95% of the biomass in spring and autumn, respectively (**Figures 5**, **6**; Boudouresque et al., 2011). Many introduced macroalgae are also present, although in lesser numbers, in the Lagoon of Venice (28 species) (Occhipinti Ambrogi, 2000; Sfriso et al., 2012, 2014; Marchini et al., 2015; Sfriso et al., 2020) and in the Mar Piccolo di Taranto lagoon (13 species) (Petrocelli et al., 2019).

A Flow of Propagules That Can Flood Macrophyte Forests

The canopy-forming long-lived *Carpodesmia mediterranea* (*Cystoseira mediterranea*; Ochrophyta, Stramenopiles), which forms a dense belt on rocky reefs, at the upper part of the infralittoral zone (sensu Pérès and Picard, 1964), from the mean sea level down to 1 m depth, has experienced marked fluctuation of its abundance since the 1970s in French Catalonia (Gros, 1978; Blanfuné et al., 2019); the most realistic explanation for the episodes of sharp decline of *C. mediterranea* seems to be the invasion of the habitat by dense stands of the mussel *Mytilus galloprovincialis*. Mussels could reduce the survival rate of *C. mediterranea* recruits that settle on its shell because of the vulnerability of this substrate (prone to be pulled out by waves) and the low longevity of the mussels. In addition, there is a light deficit for the recruits of *C. mediterranea* that grow directly on the rocky substrate. Extreme storms are not uncommon in French Catalonia (**Figure 7**; Thibaut et al., 2005; Blanfuné et al., 2019;

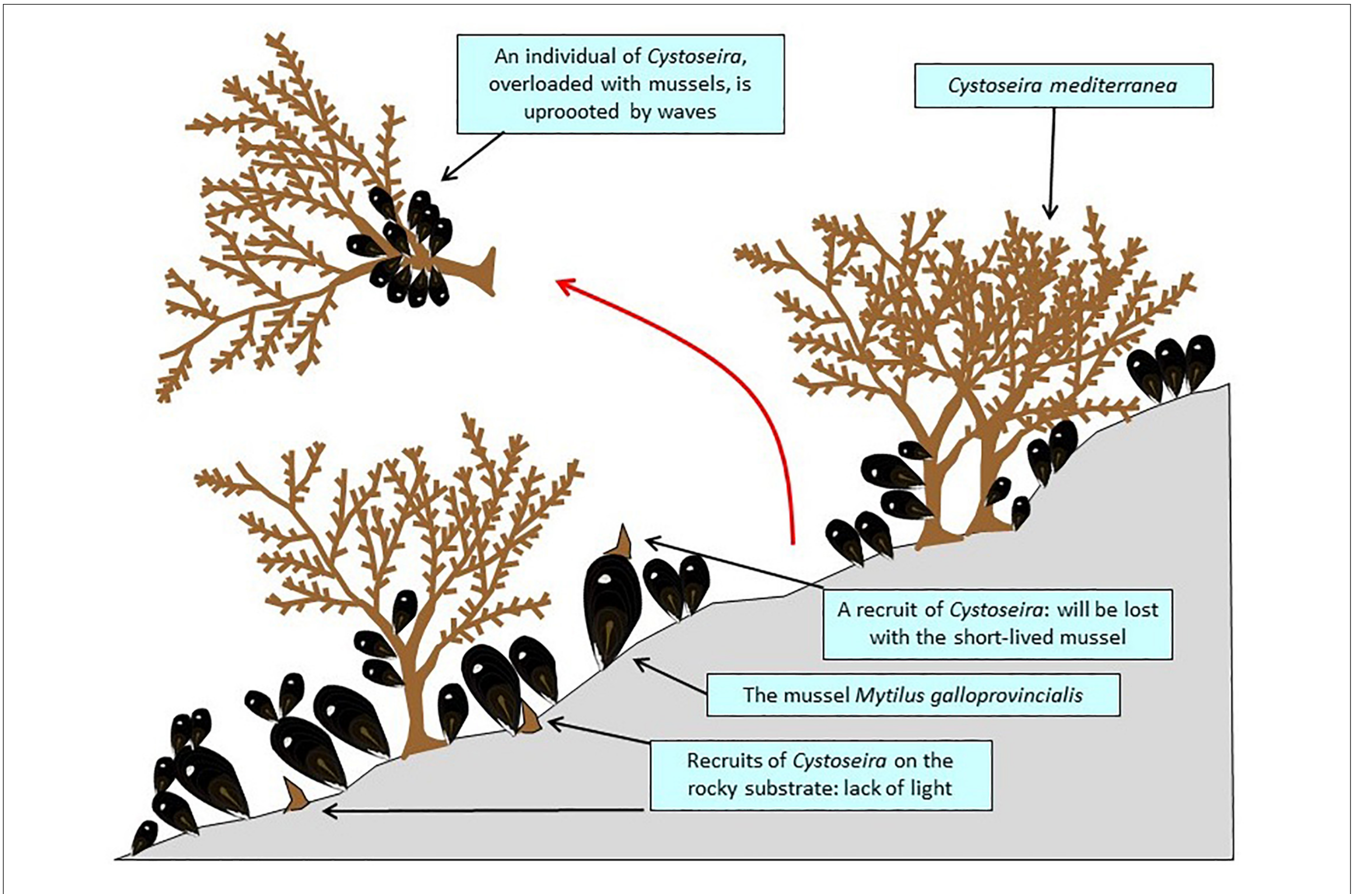

FIGURE 7 | A stand of *Carpodesmia mediterranea* (= *Cystoseira mediterranea*), in French Catalonia, severely disrupted by mussels of which the recruits probably come from offshore mussel farms.

see Navarro et al., 2011, for Spanish Catalonia). The flow of mussel larvae could be due to the development of offshore mussel farms, off Sète, ~100 km upstream, transported by the Northern Mediterranean Current toward Catalonia (Blanfuné et al., 2019). A similar negative impact of mussel proliferation on seaweeds has already been reported, e.g., in Sweden (Lundälv et al., 1986).

A Vector of Diseases of Metazoans of Which the Extirpation Changes the Functioning of Recipient Ecosystems

The transfer of farmed species from one region to another has not only been a vector for accompanying epibionts ("hitch-hikers"), but also for microbial pathogens and for metazoan parasites (Grigorakis and Rigos, 2011; Weitzman et al., 2019). Usually, it is not in the interests of a pathogen or a parasite to kill its host: if the host dies, they will die too. As a result, in the native range, co-evolution has often shaped reciprocal adaptation: an equilibrium between a moderate parasite virulence and a moderate host response (Combes, 1995, 2001). However, especially in marine environment, some pathogens have interest to kill their host to maximize their dissemination using hydrodynamic connectivity (e.g., Fuhrman, 1999; van Kan, 2006; Avrani et al., 2012). In the absence of quarantine, farmed non-indigenous species can transfer their pathogens and parasites to native species (host shift). If their virulence is too high, they extirpate native new hosts. Movements of oysters from California to Maine, Washington and France brought the haplosporidian (kingdom Rhizaria) *Bonamia ostreae*, which caused the severe decline of the flat oyster *Ostrea edulis* (Barber, 1997; Ruesink et al., 2005). The actual origin of a number of parasites and viral diseases which affect marine species is unclear, although some of them could be of Asian origin (e.g., Comps and Duthoit, 1976; Comps et al., 1976; Comps, 1983; Ruesink et al., 2005; Miossec et al., 2009).

In the Mediterranean, the fan mussel *Pinna nobilis*, the largest Mediterranean mollusk (over 1 m tall), is a key species in the *Posidonia oceanica* seagrass ecosystem (Personnic et al., 2014). This long-lived species (over 40 years), endemic to the Mediterranean, is a filter-feeder (Butler et al., 1993; Trigos et al., 2014; Rouanet et al., 2015). A wasting disease (90% to near 100% mortality) occurred in Spain in 2016 (Darriba, 2017; Vázquez-Luis et al., 2017). Subsequently, this mortality spread to the whole of the Mediterranean (González-Wangüemert et al., 2018; Pergent, 2018; Bianchi et al., 2019; Cabanellas-Reboredo et al., 2019). Mortality is caused by a unicellular parasite, *Haplosporidium pinnae*, a species previously undescribed (Catanese et al., 2018). According to Darriba (2017) and Catanese et al. (2018), *H. pinnae* could be either an old symbiont that has changed its relation with the host, due to the environmental changes, or a recently introduced species. The latter hypothesis is by far the most probable: the new parasite presents many of the features that characterize an introduced species (see Ribera and Boudouresque, 1995; Boudouresque, 1999a), e.g., the weak genetic diversity and the pattern of expansion. Many haplosporidans are parasites of bivalves in the north-western Pacific; some of them were introduced to Europe via shellfish transfers, with dire consequences (Sindermann, 1992; Cabanellas-Reboredo et al., 2019). The possible primary vector species of *H. pinnae* (*Magalana gigas*? *Ruditapes philippinarum*?) is still unidentified. Currents and ballast waters seem to have been involved in its spread within the Mediterranean (Cabanellas-Reboredo et al., 2019); in addition, a putative reservoir species (*Mytilus galloprovincialis*?) could account for long-distance dispersal.

A Change in the Functioning of the Recipient Ecosystem

Shellfish aquaculture can profoundly change the functioning of the ecosystems of the recipient lagoon or embayment by (i) removing Particulate Organic Matter (POM; including phytoplankton), via the activity of filter-feeder mollusks, (ii) removing nutrients via the export of farmed shellfish to markets, outside the aquaculture area, and (iii) via the shower of fecal pellets on the bottom compartment (with or without macrophytes), with mineralization which induces anoxy of the sediment, anoxy which can spread to the water column under low wind conditions (Deslous-Paoli et al., 1993; Plus et al., 2003; Gaertner-Mazouni and De Wit, 2012; Boudouresque, 2013; Weitzman et al., 2019).

In Thau Lagoon (Occitania, France), benthic macrophytes are well developed below shellfish facilities: *Zostera marina* (seagrass), *Chaetomorpha linum* (Chlorobionta), *Gracilaria* spp., *Halopitys incurvus,* and *Rytiphloea tinctoria* (Rhodobionta) (Plus et al., 2003). However, the baseline, before the development of shellfish aquaculture, is poorly known. According to De Casabianca et al. (2003), eutrophication, including the effects of shellfish farming, drives the regression of *Zostera* meadows and the expansion of *Gracilaria* and other seaweed stands. In another lagoon, Salses-Leucate (Occitania, France), the isotopic ratio of macrobenthos (including macrophytes) was not modified underneath the oyster facilities (Carlier et al., 2009).

DICUSSION AND CONCLUSION

Global marine captures by fisheries are declining, although this trend is greatly underestimated as small-scale fishery, recreational fishery, discards and of course Illegal, Unreported and Unregulated (IUU) fishery are poorly or not at all taken into account (Zeller et al., 2006; Kaiser and Hiddink, 2007; Pauly et al., 2014; Piroddi et al., 2015; Pauly and Zeller, 2016; but see Hilborn et al., 2020 for an alternative view). This trend is of course dependent upon the nature and extent of fisheries management systems (Hilborn et al., 2020). In the Mediterranean and Black Sea, the production from fisheries declined from about 1.4–1.2 t a^{-1}, from 1993 to 2013, because most fisheries stocks are overfished (Massa et al., 2017). In this context, aquaculture is an important option to feed a growing world population, which is estimated to reach 9 billion people by 2050 (Massa et al., 2017). It is often associated with the concepts of blue growth and blue economy, aiming at providing food and jobs and at the same time limiting the degradation of oceans and revitalizing ecosystems (Le Gouvello and Simard, 2017; Barbesgaard, 2018). This optimistic view of aquaculture should be seen in a more nuanced way by taking into account not only the benefits, but also the costs for natural habitats.

Fish farming is responsible for organic matter and nutrient loads that can be compared to those of small untreated sewage outfalls. At a time when, at least for the EU countries on the northern shore of the Mediterranean, the vast majority of terrestrial wastewater now passes through a sewage treatment plant (Kalavrouziotis et al., 2015), the rapid, strong increase in fish farming, and the resulting untreated loads of organic matter and nutrients, represents a paradox. A number of authors have developed rather optimistic views concerning nutrients, organic matter and trace elements which are released by fish farms and enter the recipient ecosystems. They consider that they are spatially limited, within the range of tolerable levels for the marine ecosystem and that an oligotrophic sea such as the Mediterranean is able to assimilate these loads (Basaran et al., 2010; Puhr and Pikelj, 2012; De Biasi et al., 2016). According to Puhr and Pikelj (2012), when carefully planned, fish farms do not necessarily degrade the health status of *P. oceanica* meadow, but in fact facilitate a transition to an alternative stable state that is "*characterized by a delicate balance between organic input from fish farms and the capacity of the system to process it*"; the difference between a degraded meadow and this "alternative stable state," as Puhr and Pikelj (2012) named it, is however unclear. Whatever the surface area of dead *P. oceanica* meadows resulting from fish farming, its is worth highlighting that seagrass dead *mattes* constitutes a kind of time bomb: the huge amounts of carbon which have been sequestrated within it over millennia can be mineralized into carbon dioxide and returned to the environment, contributing to global warming (Pergent et al., 2012, 2014).

Some authors have rightly pointed out that fish farms cause the increase, by a factor of up to 4, of the overall fish abundance and species diversity, at a spatial scale larger than the immediate vicinity of the fish cages, which constitutes a positive effect on local fisheries (e.g., Machias et al., 2004, 2005). However, it would be naïve, on the basis of a partial and erroneous view of the biodiversity concept, to extend this positive effect to the ecosystem and the environment (see Boudouresque, 2014, for the biodiversity concept). A partial recovery of the annelid fauna of a soft bottom ecosystem, near Murcia (Spain), one year after the cessation of the activities of a fish farm, gives grounds for optimism (Aguado-Giménez et al., 2012), although the annelid assemblage is just a compartment of an ecosystem which also encompasses teleosts, echinoderms, mollusks, etc., compartments which are not addressed by the authors. It has been suggested that multi-trophic aquaculture, i.e., the simultaneous farming of low trophic level organisms, such as bivalves and sea urchins, together with fish, would reduce fish waste impact, while enhancing total productivity (Troell et al., 2003; Israel et al., 2019). However, this optimistic hypothesis has been contradicted by Navarrete-Mier et al. (2011).

With the exception of Egypt, where fish farming is based on the semi-extensive production of mullet, which are omnivorous and opportunistic, most of the farmed fish species are carnivorous (Basurco and Lovatelli, 2003). In aquaculture facilities, they are fed both pelleted and mainly extruded feeds rich in protein (up to 600 g kg^{-1}) and lipids (up to 260 g kg^{-1}) (Kousoulaki et al., 2015). Most farmed fish diets include fishmeal and fish oil; they come from ~14 Mt whole fish and 5 Mt by-products of seafood processing, which produces 4–5 Mt fishmeal and ~1 Mt fish oil. Most of the fishmeal is now used to feed farmed fish (IFFO, 2019). According to Le Gouvello and Simard (2017) and IFFO (2019), the concern that expanding aquaculture would use more and more fishmeal and fish oil, and so would contribute either to fish depletion in the seas, or to the removal of a fish resource for populations of southern countries, is misplaced: the percentage of fishmeal in used fish diet is on the decline. In contrast, other authors accuse farming of carnivorous fish of being "*the aquatic equivalent of robbing Peter to pay Paul*": it transforms small pelagic and other fishes perfectly fit for human consumption into animal feeds the nutritive value of which is lost to humans (Goldburg and Naylor, 2005; Pauly et al., 2005; Jacquet and Pauly, 2008; Grigorakis and Rigos, 2011). It is worth noting that the pilot trial of offshore aquaculture of the sea urchin *Paracentrotus lividus*, on the Italian coast, was based upon anchovy and krill flour (Volpe et al., 2018), although this sea urchin is actually a herbivore (Boudouresque and Verlaque, 2013, 2020).

The recovery times of *Posidonia oceanica* meadows is in the order of at least decades and may be more than a century, so that losses can be considered to be irreversible at human time scales (Molinier and Picard, 1952; Boudouresque and Meinesz, 1982; Holmer et al., 2003; Boudouresque et al., 2009, 2012). According to Holon et al. (2018), the tipping point (shift from a healthy *P. oceanica* meadow to a significantly degraded meadow) is situated, on average, 320 m from a fish farm. A safety distance of 400 m has been suggested between fish farms and the nearest *P. oceanica* meadow (Holmer et al., 2008). Boudouresque et al. (2012) have proposed the following recommendations: (i) No fish farm facilities should be directly established over a *P. oceanica* meadow. In Spain, no fish farm facilities have been directly established over *P. oceanica* meadows, and the existing ones have been moved offshore; however, this is not the case in most other Mediterranean countries. (ii) If there is a meadow nearby, minimum distances from the cages should be respected. They depend upon the depth, the openness of the site (embayment or well-flushed open sea) and the size of the farm (**Table 2**); deep meadows are more sensitive to turbidity and overshadowing, so that farms established above deep bottoms should respect an increased safety distance from the nearest meadow. According to recent literature, these safety distances seem to be under-estimated, as nutrients release by fish farms may reach several kilometers of distance (e.g., Ruiz et al., 2010). (iii) An installation of fish farm facilities on a 45–50 m deep seabed should be given priority, whenever possible. (iv) Permission to set up a fish farm should be reviewed every 4 years for possible extension, on the basis of a demonstration that the *P. oceanica* meadows located nearby have not regressed. In addition, permanent monitoring plots should be established and revisited annually to assess the health of the meadow (Holmer et al., 2008). Physiological parameters of *P. oceanica* leaves and rhizomes (e.g., total nitrogen content, free amino acid concentration and composition, stable nitrogen isotope ratio) are useful indicators of marine environmental degradation (Pérez et al., 2008). For monitoring methods for *P. oceanica* meadows, see Boudouresque et al. (2007, 2012), Personnic et al. (2014), and Boudouresque et al. (2015b). Similar recommendations could apply to coralligenous and coastal detritic ecosystems, although no minimum distance has been proposed for them. Whatever the ecosystem concerned, monitoring programs are of paramount importance (e.g., Borja et al., 2009; De Biasi et al., 2016).

Overall, in the Mediterranean, fish farming can have very negative impact; the impact has mostly been studied on *Posidonia oceanica* seagrass beds, but obviously it also concerns coralligenous and coastal detritic ecosystems. It can be direct (shading, fecal pellets) and indirect (overgrazing). Shellfish aquaculture is the major source (ahead of the Suez Canal and fouling on ship hulls) of the introduction of exotic macrophyte species which deeply disrupt lagoon landscapes and ecosystems. As far as the sea urchin seeding is concerned, fortunately, it is not very effective, which avoids aggravation of the overgrazing of marine forests.

The above conclusions do not call into question marine aquaculture, but underline the importance of taking into account its possible negative effects, in order to avoid them. This requires taking them into account at the very beginning of the project design process. In addition, some knowledge gaps for future research avenue on the thematic deserve to be more developed, e.g., (i) surveillance networks, not only of species, groups of species and functional compartments, but also on the whole ecosystem functioning; (ii) active restoration, after the cessation of aquaculture activities, versus natural restoration (in many cases, nature do things better than humans); (iii) assessing in a less empirical way, using maps of ecosystem distribution and local scale models of currents, the safety distance between aquaculture facilities and high heritage value ecosystems.

AUTHOR CONTRIBUTIONS

All authors equally contributed to the writing of the manuscript.

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