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Review

A Review of Coastal Anthropogenic Impacts on Mytilid Mussel Beds: Effects on Mussels and Their Associated Assemblages

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Abstract: Mussel beds are an important habitat in many coastal systems, harboring a high diversity of biota. They are threatened by anthropogenic impacts that affect mussels and their associated assemblages. Pollution, harvesting, trampling, dredging and trawling are major threats faced by these communities. Most of the studies on the effects of such impacts on the mussel beds overlook the associated fauna. Since mussels are very resilient, especially to pollution, the associated fauna can provide a better footprint of the impacts' effects. In this review, we looked into the main remarks regarding the effects of anthropogenic impacts in mussel bed communities. Organic pollution was the best studied impact and the Atlantic region was the best studied zone. Low values of abundance, biomass, diversity, evenness and species richness were reported for all categories of impacts, with some studies describing declines in at least three of these descriptors. Among the associated fauna, some tolerant species benefited from the impacts, particularly organic enrichment, and became more abundant, but sensitive species suffered considerable declines in density, mainly in dredging and trawling impacts. Therefore, fauna associated with mussel beds is a suitable indicator of anthropogenic disturbances.

Keywords: Mytilidae; ecosystem engineer; coastal systems; macrobenthos; associated fauna; pollution; harvesting; trampling; dredging; trawling

Citation: Sampaio, L.; Moreira, J.; Rubal, M.; Guerrero-Meseguer, L.; Veiga, P. A Review of Coastal Anthropogenic Impacts on Mytilid Mussel Beds: Effects on Mussels and Their Associated Assemblages. *Diversity* **2022**, *14*, 409. https://doi.org/10.3390/d14050409

Academic Editor: Michael Wink

Received: 16 April 2022
Accepted: 19 May 2022
Published: 22 May 2022

1. Introduction

Anthropogenic disturbances are among the greatest threats for many coastal systems around the world [1–3]. The lack of environmental protecting laws or their effective enforcement prolong this threat [4,5]. Macroinvertebrate communities either have to adapt to the changes, move or perish [6–8].

Mussels of the family Mytilidae are often key species in marine environments and traditionally cluster to form beds on the surface of several substrates. Therefore, mussels provide additional habitat for many other species. Barnacles, algae and other sessile species find an extra substrate on top of the shells of mussels [9]. The byssus that holds bivalves in place creates a very complex habitat forming huge tight clumps [10,11]. This intricate structure easily traps sediment from the water column. The fecal pellets excreted by mussels and other ecosystem engineer bivalves (e.g., oysters, [12]) mix with this sediment creating organic enriched particles that attract many deposit feeders [10,11,13].

The mussel communities supply shelter and food to a rich assemblage of diverse species, making these habitats a good biodiversity hotspot [9,14]. Since mussels are efficient suspension-feeders, they are very important in cleaning the water column of suspended solids and contaminated particles [10]. Mussels have a high resilience to contamination and often bioaccumulate the pollutants extracted from the water column. This bioaccumulation makes them unsafe for consumption but promote the restoration of polluted environments [11,15]. In heavy contaminated sites mussels can die. However, while mussels remain alive, their associated assemblages might change due to pollution [1,2]. By studying the mussel beds' communities, we can look into the health status of the aquatic systems. Since the loss of the mussel beds carries the loss of their associated assemblages [4,6,14,16], it is important to protect them. Protection can be achieved either by creating marine reserves, banning their harvesting or establishing restrictions to safeguard the ecological quality of the aquatic systems [5,17,18].

In order to understand the importance of mussel beds for ecosystem health, we reviewed scientific papers about the biodiversity of fauna associated with mussel beds under different anthropogenic impacts. These papers deal with how the assemblages cope with the impacts and whether the extension or regression of the mussel clumps and their complex structure influences the recovery of impacted ecosystems.

2. Literature Selection

The study of the assemblages associated with mussel beds has been increasingly discussed in the last years, and the existing literature on the subject is still emerging. The literature survey conducted in the present review and the information gathered provide an important insight into the relevance of mussels as ecological engineers that sustain and protect many species and contribute to a better ecological quality of ecosystems. We started with an examination of the literature using SCOPUS and the string search in the title, abstract and keywords: Mussels AND ('Pollution' OR 'Contamination' OR 'Enrichment' OR 'Pollutant*' OR 'Harvesting' OR 'Trampling' OR 'Anthropog*' OR 'Human' OR 'Farm*' OR 'Fisher*') AND ('Assemblages' OR 'Biota' OR 'Communit*' OR '*diversit*').

A large volume of scientific papers was found that met the selected criteria, but we focused our selection on marine environments and considered only the papers that studied the communities associated with mussels in a scenario of anthropogenic impact. By doing so, we further narrowed our results to 68 scientific papers. Then, after a full paper review, we excluded those studies with very limited taxa information, those that used transplanted mussels, those associated with offline platforms or those where mussels did not form relevant clumps, being too scattered and/or scarce, or even those where anthropogenic impacts only referred to adjacent areas and did not affect mussel communities.

The final body of literature was reduced to 31 scientific papers, that were reviewed in the following impact categories: large-scale physical impacts (dredging, trawling), pollution impacts (organic compounds, heavy metals) and small to medium-scale physical impacts (harvesting, trampling). The impact of alien species was not the target of this study, but some papers highlight that the effects of alien species added to those of the considered target impacts. A summary of the studied impacts, target mussel species, main effects and data analysis conducted can be found in Table 1, for each reviewed scientific paper. The location, type of impact and target species is exhibited in Figure 1. Species names were revised using WoRMS [19].

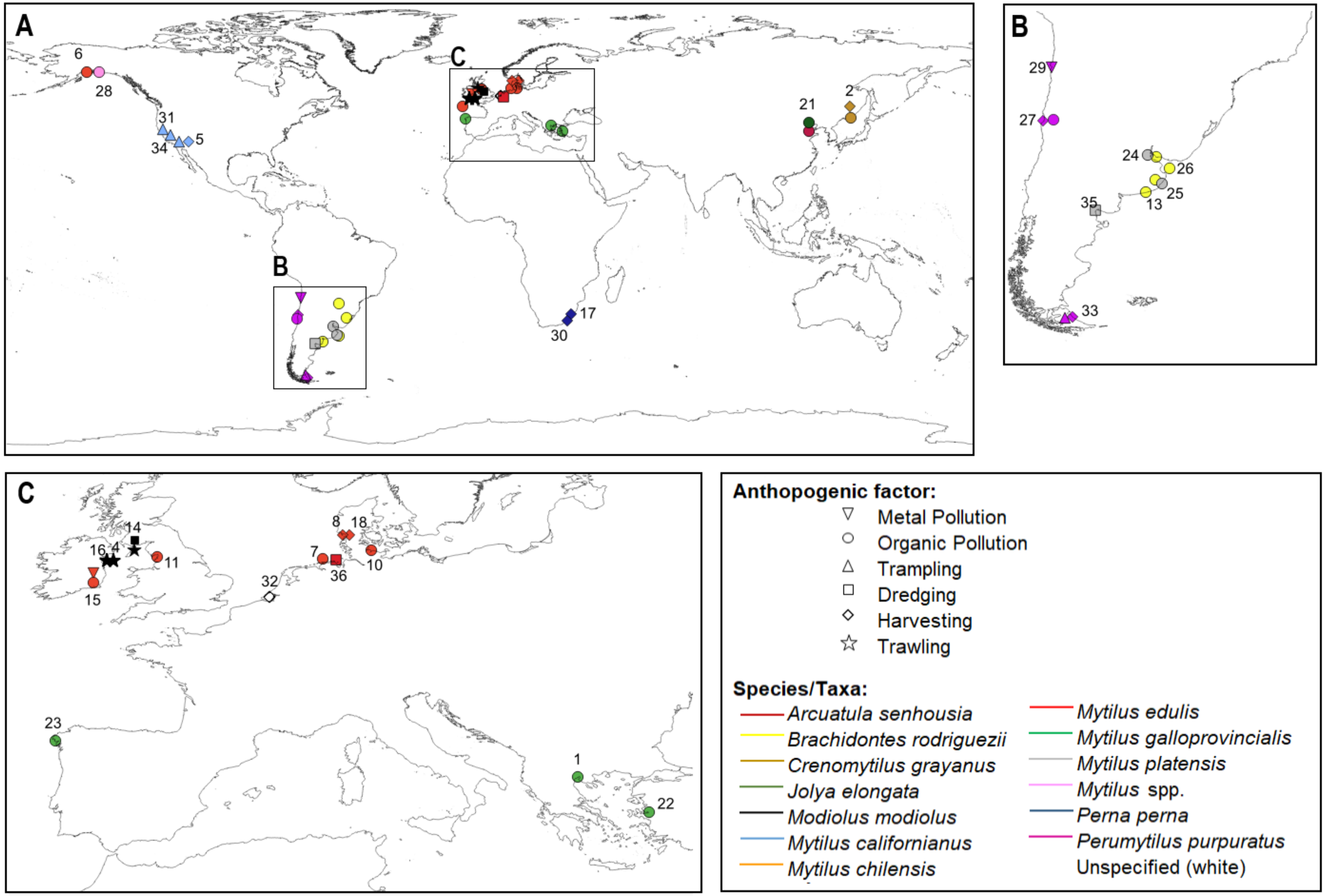

Figure 1. (**A**)—Study distribution around the world with indication of each anthropogenic descriptor and taxa investigated; (**B**)—Detail of studies conducted in South America; (**C**)—Detail of studies held in Europe. Numbers identify the reference studies included in the review.

3. Geographic Area and Taxa

The reviewed scientific papers investigated several anthropogenic impacts (dredging, harvesting, pollution, trampling and trawling) that affected different mussel bed communities around the world (Figure 1, Table 1). More than half of the studies (18, Figure 1, Table 1) were done in the Atlantic region, two thirds at the north (12, Figure 1, Table 1) and one third at the south (6, Figure 1, Table 1). This region was also the best studied concerning the different impacts under review. Organic pollution was the most examined impact here (9, Figure 1, Table 1), while trampling was the least studied (1, Figure 1, Table 1), but all dredging and trawling impacts were investigated in this region (5, Figure 1, Table 1). The Pacific region gathered nine studies, the vast majority at the east (7, Figure 1, Table 1), but a few were done at the west (2, Figure 1, Table 1). At the west, organic pollution and harvesting were the only impacts researched, while at the east, additionally to those, metal pollution and trampling were analyzed (Figure 1, Table 1). Furthermore, this region had more studies concerning trampling effects on mussel beds than anywhere else in the world (3, Figure 1, Table 1). The remaining studies were done in the Indian region (2, Figure 1, Table 1) concerning harvesting impacts, and in the Mediterranean (2, Figure 1, Table 1), investigating organic pollution effects. Until recently there were no mussels in Antarctica, but with the discovery of a first settlement of mussels in this continent one might expect new follow-up studies in the near future in this pristine region [20].

The total number of mussel species considered in the reviewed studies was twelve (sometimes two species were present in a single study), distributed among eight genera: *Arcuatula senhousia* (Benson, 1842), *Brachidontes rodriguezii* (d'Orbigny, 1842), *Crenomytilus grayanus* (Dunker, 1853), *Jolya elongata* (Swainson, 1821), *Modiolus modiolus* (Linnaeus, 1758), *Mytilus californianus* Conrad, 1837, *Mytilus chilensis* Hupé, 1854, *Mytilus edulis* Linnaeus, 1758, *Mytilus galloprovincialis* Lamarck, 1819, *Mytilus platensis* d'Orbigny, 1842, *Perna perna* (Linnaeus, 1758) and *Perumytilus purpuratus* (Lamarck, 1819) (Figure 1, Table 1). Additionally, two studies did not specify the target species, but it could possibly be *M. edulis* mixed with a similar related species (Figure 1, Table 1). Indeed, nearly two thirds of the studies investigated the *Mytilus* species (20, Figure 1, Table 1), while four studies involved a single species of *Brachidontes* (*B. rodriguezii*; Figure 1, Table 1), and three analyzed one *Perumytilus* species (*P. purpuratus*; Figure 1, Table 1) and a *Modiolus* species (*M. modiolus*; Figure 1, Table 1). Moreover, the genus *Mytilus* had by far the highest number of studied taxa, corresponding to five species (*M. californianus*, *M. chilensis*, *M. edulis*, *M. galloprovincialis*, *M. platensis*; Figure 1, Table 1). The other target species, each belonging to a different genus, were researched in four studies (Figure 1, Table 1), among which the genus *Perna* was investigated in two different studies (*P. perna*; Figure 1, Table 1), while two other species (*A. senhousia*, *J. elongata*; Figure 1, Table 1) were investigated in the same study.

The mussels *A. senhousia*, *C. grayanus* and *J. elongata* (Figure 1, Table 1) were only investigated in the west Pacific in areas prone to some degree of organic pollution, although *C. grayanus* (Figure 1, Table 1) was also examined for the impact of harvesting in this region. *M. galloprovincialis* (Figure 1, Table 1) was also employed to observe the effect of organic pollution in mussel beds, both in the northeast Atlantic and in the Mediterranean. *P. perna* (Figure 1, Table 1) was only analyzed in the Indian region in studies that dealt with the effects of harvesting in rocky shores, while *M. modiolus* (Figure 1, Table 1) was only encountered in trawled or dredged areas around the UK. In the southwest Atlantic, *B. rodriguezii* (Figure 1, Table 1) was solely considered in organic pollution studies, alone or in the presence of *M. platensis* (Figure 1, Table 1), while the latter was also examined in a dredging study (Figure 1, Table 1). The other species found in this region, further south, were *M. chilensis* and *P. purpuratus* (Figure 1, Table 1), and were used to investigate harvesting and trampling impacts. Moreover, *P. purpuratus* was also encountered in the east Pacific Chilean coast and employed to study harvesting effects, as well as organic and metal pollution impacts. On the northeast Pacific region, *M. californianus* and *M. edulis* were used in anthropogenic impact studies on mussel bed communities (Figure 1, Table 1). While *M. edulis* was restricted to Alaska, in the Pacific (Figure 1, Table 1), and used to examine the organic pollution impacts there, *M. californianus* was utilized to address the effects of harvesting and trampling further south, in California (Figure 1, Table 1). Moreover, *M. edulis* (Figure 1, Table 1) was the most studied mussel species in the northeast Atlantic and of all the mussel species anywhere else. With the exception of trampling studies, this species was employed as the model to study the effects of every anthropogenic impact dealt with in this review.

4. Anthropogenic Perturbations

4.1. Pollution Impacts

The aquatic environment has been polluted by organic compounds, heavy metals and other pollutants due to anthropogenic activities [1,7,21]. In most cases these compounds bioaccumulate in the food chains, being harmful for some organisms and sometimes leading to indirect effects outside the contaminated areas [1,11].

4.1.1. Organic Compounds

The presence of mussel beds in an area usually mitigates the pollutant effects on the associated community. When their biomass decreases the associated communities are more severely affected [11,22]. We analyzed 16 papers that studied the effects of organic pollution on the mussel beds and their associated fauna.

The studies done in the North Atlantic include the coasts of Ireland, Spain, UK and the North and Baltic Seas. On a shallow soft sediment inshore region in the South of Kiel Bay, Anger [10] found that biomass and the abundance of the macrofauna community increased at short and intermediate distances from a sewage outfall. This enhancement was less pronounced at mussel beds than on adjacent sand bottoms or eelgrass communities. However, the overall diversity and mean species richness was higher in mussel communities. Nevertheless, there was a clear negative effect of pollution on both species' richness and evenness in the mussel beds of the study area [10].

In another pollution study, Crowe and colleagues [11] found a good relationship between hydrocarbon concentration in *M. edulis*, scope for growth (SFG) and the associated assemblages diversity. Fauna associated with mussels had a reduced diversity at sites with low SFG compared with the control sites that had high SFG. Low SFG was due to high hydrocarbon concentrations but also to the high levels of sewage input in one site. According to the authors, the relationship between SFG and diversity was not confounded by environmental factors, but other pollutants could also be at play [11]. Furthermore, experiments with both copper and biocide chlorpyrifos in Ireland, also among *M. edulis* assemblages, revealed consistent plumes of contamination within patches of mussels, but which were not detected in the water outside the patches [15]. Ecotoxicological assays revealed that mussel assemblages exposed to chlorpyrifos had an 81% decrease in amphipod numbers and a 40–70% decrease in annelids when copper was also present. The synergistic effects of the pollutant input, addiction of non-indigenous species and range-related community alterations can produce long-term ecological changes in intertidal mussel bed communities [7]. At Helgoland, North Sea, an invasive alga outcompeted a native alga within the mussel bed in the mid intertidal zone when the study site was revisited 18 years later [7]. Although species richness remained very similar in both surveys, there was a turnover of nearly 60 species, with 27 new records and 32 displacements between surveys. Crustacea had more new records and less species losses compared to annelids and mollusks that lost more species. These community structure changes were the result of combined pollution, alien species and distribution shifts [7].

García-Regueira and colleagues [23] studied oil spilling effects on the diversity and abundance of annelids inhabiting intertidal rocky shores non-impacted and impacted by the Prestige oil spill. The temporal evolution of the annelid assemblage on mussel and algal beds showed positive and negative impacts depending on the tidal level. At the lowest tidal level, the impacted site presented the greatest diversity compared to the control while at higher elevations the control had a higher number of species [23]. However, statistical analyses did not show any clear temporal trend, maybe because other anthropogenic disturbances might overlap with those of the Prestige oil spill [23].

In the South Atlantic, all the studies were done in Argentina in areas with a sewage outfall, using *B. rodriguezii* [13,24–26], although *M. platensis* was also present in two studies [24,25]. The area adjacent to the sewage outfalls was dominated by the opportunistic annelids *Boccardia polybranchia* (Haswell, 1885) and/or *Capitella capitata* (Fabricius, 1780) [13,24–26] that were rarer at other locations [24]. Sometimes their abundance could increase significantly near the outfall in response to temporary increases in sewage discharges [13,26]. Close to the outfall, the mussel abundance was low but at intermediate distances the mussel beds were conspicuous [13], sediments retained by mussels reached their maximum values, and the abundance of other annelids was also high [13] or crustaceans dominated [25]. In this same area, a follow-up research encompassing a 10-year period showed that the impacted sites exhibited significant differences compared to the reference site, and a pattern of increasing disturbance was evident [26].

In the Mediterranean, the studies were focused in the eastern Mediterranean using *M. galloprovincialis*. In a polluted port with high levels of commercial shipment, dense subtidal mussel beds developed at the lower midlittoral. This mussel dominance led to the replacement of an algal-dominated community and its associated fauna [1]. Despite the existence of biogenic mussel structures, the associated fauna diversity decreased due to organic enrichment, and most species were tolerant to pollution and took advantage of the existing enriched conditions [1]. In an area in the Aegean Sea subjected to various pollution discharges since the 1960s, annelids had the highest species richness and abundance within the mussel beds' faunal assemblage [22]. Moreover, there were several invasive species, including the annelid *Hydroides elegans* (Haswell, 1883), that, together with mollusks, had the highest biomass [22]. The less impacted station outside the harbor had the highest species richness and diversity, whereas the abundance and biomass were generally higher inside the harbor [22].

In the Pacific region, in a polluted area of the Vostok Bay where sewage discharges are frequent, Galysheva [2] studied the composition and structure of *C. grayanus* communities impacted since the 1970s. Due to pollution, the diversity and evenness of the mussel communities became lower, and pollution-tolerant species invaded and dominated the assemblages [2]. Further south, in an area impacted for over 20 years through over-fishing and pollution, important changes occurred between two periods of study [21]. The authors found changes in community structure from the 1980s to the 1990s and across geographical regions. The mussel *A. senhousia* disappeared from the surveyed area in the 1990s, while it was abundant in the 1980s at Laizhou Bay, but another mussel, *J. elongata*, replaced *A. senhousia* in the surveyed area. While at Laizhou Bay diversity increased, in the other areas some species dominated and significantly decreased evenness. Annelids and bivalves accounted for over 50% of abundance while crustaceans contributed for a species richness increase between periods [21]. In Chile, Valdivia and Thiel [27] evaluated the effects of direct nutrient addition on the species diversity of the epibenthic assemblage associated with the mussel *P. purpuratus*. However, nutrient addition only had minor effects on diversity compared to another treatment that included mussel removal. The authors concluded that physical and biological stress acting on exposed hard-bottom communities surpasses the possible effects of nutrient addition [27].

Oil spilling can have a low to moderate impact in the intertidal communities of exposed shores [23], but the treatment methods employed to clean a shore can sometimes have a more severe impact [6,28]. For instance, studies at Prince William Sound reported severe impacts to intertidal epibenthos of treatments widely used to remove stranded oil. Moreover, the type and number of significant changes observed varied considerably by elevation and type of treatment, perhaps reflecting the position of the zone relative to washing activities and rigor of washing [6,28]. At upper and mid-levels, where mussels were most abundant, the most significant variations corresponded to abundance declines. Dispersant and beach cleaner treatments had less significant changes in abundance, perhaps due to a less vigorous washing, whereas the hot water treatment was associated with the highest number of negative alterations. In rocky beaches that received no treatment or where the treatment was less severe, the majority of the dominant species, including mussels and associated fauna, survived the oiling [6]. However, the severe effects of hot water treatment remained noticeable three years later. Thus, there were few statistically significant differences between the biota of unoiled rocky shores and those treated with hot water, but a full recovery was still far from being achieved [6,28].

4.1.2. Heavy Metals

The amount of contamination that can be absorbed by an ecosystem before the detection of structural or functional changes can be estimated through manipulative experiments. This information is relevant, in turn, to regulate the use of heavy metals. In situ experimental studies can help manage the dose administrated and the frequency of pollutants to which fauna is exposed [15]. We analyzed one paper reporting an experimental study of the effects of metal pollution on the mussel communities.

In the Pacific, Acevedo and colleagues [29] evaluated the effects of copper on *P. purpuratus* communities using three treatments (continuous, intermittent and no copper administration) on three mussel areas for a short period of time. Here, the effects of copper were less severe than in the Atlantic study. The continuous administration of copper decreased species richness and diversity compared to the other treatments, but only significant effects were found for diversity when analyzing *a priori* orthogonal contrasts between the continuous and intermittent treatments [29]. No significant effects were detected on mussel density, length and number of strata, or faunal species richness, evenness and diversity. Nevertheless, non-metric multidimensional scaling showed a significant effect of the copper treatments compared to the control, suggesting that the associated fauna responds differentially to copper frequency administration [29].

4.2. Small- to Medium-Scale Physical Impacts

Organisms on rocky shores are subjected to physical perturbations when many people visit intertidal zones for recreation, collection of food, fish bait or ornamentation [2,30]. Visitor activities can result in the loss or damage of individuals and cause alterations of the community structure [2,5,31]. We analyzed 11 papers that studied the effects of harvesting and trampling on the mussel beds and their associated assemblages. We found three studies for the North-East Atlantic (North Sea), one study for the South-West Atlantic (Argentina), five studies in the Pacific (SE Russia, USA and Chile) and two studies for the Indian Ocean (South Africa), while other areas remain unstudied.

4.2.1. Harvesting

All the studies aimed at investigating the effects of harvesting impacts in the Atlantic were done in the North Sea using *M. edulis* [8,18,32], except for a study conducted in the Argentinian coast that investigated *M. chilensis* and *P. purpuratus* [33]. No other studies were conducted in the east coast of Brazil, Canada and USA, or in more exposed rocky habitats of the northeast Atlantic coasts. In the North Atlantic, a study in 1980 found major changes in the community of subtidal fauna at the Wadden Sea compared to historical studies of the mid-1920s. These changes were attributed to anthropogenic disturbances and human interference [8]. However, the shell fishery promoted the spread of *M. edulis* across the entire region. Barnacles and many annelids took advantage of the mussel expansion and increased their abundances compared to 1920s, but mollusks and crustaceans decreased in species richness, diversity and evenness. Overall, the total number of species remained approximately the same, but mollusks suffered losses and annelids diversified; nonetheless, the abundance increased with the dominance of a few species (*M. edulis*, *Balanus crenatus* Bruguière, 1789, *Cerastoderma edule* (Linnaeus, 1758), *Scoloplos armiger* (Müller, 1776)) [8]. Twenty years later, Saier [18] studied the epifauna in the same region and found a higher diversity, abundance and species richness in the subtidal zone compared to the intertidal zone. Abundances significantly declined with increasing depth, mainly due to significantly higher densities (97%) of juvenile periwinkles and crabs in intertidal mussel beds [18]. On the other hand, in subtidal mussel beds, species' abundances were more evenly distributed. Therefore, the author suggested an extension of the protective measures against mussel harvesting towards the subtidal zone to keep the high epifaunal diversity and maintain the integrity of the mussel bed communities [18]. High diversity is a common feature among healthy mussel bed communities. For instance, in the Netherlands, unexplored mussel beds had the highest densities and biomass, indicating an unstressed community [32]. When evaluated under the abundance/biomass comparison method, an area with an exploited mussel bed showed moderate stress, and the benthic community had not been able to reach an equilibrium [32].

In the South Atlantic, defaunation was used to simulate a physical disturbance comparable to an extreme harvesting [33]. At the start of the experiment, bivalves appeared in at least two layers with *M. chilensis* over *P. purpuratus*. Beneath the bivalves, there was a variable layer of sediment in which there were mainly annelids, crustaceans and other mollusks. This layer gradually disappeared for reasons still to be investigated but coincided with a massive recruitment of *M. chilensis*. *P. purpuratus* dominated the assemblage in June 2001. However, due to a recruitment event of *M. chilensis* in December 2001, their numbers were higher than those of *P. purpuratus* in the disturbed plots [33]. By February 2002, the proportion of *M. chilensis* in both the disturbed and control plots was over 60% and much higher than at the beginning (about over 20%). Changes in the relative abundance of both mussel species due to disturbance conditioned the presence of the associated fauna. In fact, the diversity, richness and evenness of the associated fauna was significantly lower in the disturbed plots. Moreover, the frequency of some opportunistic annelids and isopods increased, while that of some amphipods and bivalves decreased.

In the Indian region, *P. perna* was the only mussel investigated in the Transkei coast of South Africa. There was a reduction in biomass of the exploited mussels and their associated fauna in both studies considered [17,30]. In some cases, although there were changes in the community structure (e.g., decline in the abundance of certain filter-feeders), they were balanced with an increase in the abundance of some associated seaweeds. Species richness and diversity values were not consistent with the presence or absence of exploitation, but biomass was significantly altered in the exploited sites [30]. The presence of marine reserves safeguarded mussels from harvesting, mollusks increased their densities within reserves, and annelids were more abundant in the exploited sites.

In the Pacific region, three harvesting studies were conducted, each using a different mussel species. At Vostok Bay, in the East Pacific, the biomass of *C. grayanus* declined due to poaching (unselective harvesting, [2]). Since the 1970s, the total biomass of the assemblages and the size–age composition of the population had changed because of poaching effects. At an exposed rocky shore of northern-central Chile, the removal of *P. purpuratus* also had significant and negative effects on the associated assemblages, particularly on species richness, and the abundance of suspension-feeders and sessile organisms. Furthermore, the abundance of top consumers declined significantly with mussel removal in the presence of nutrient addition, but there was no effect on the evenness of the associated fauna [27]. Further north, in California, high human visitation resulted in a significantly lower abundance of *M. californianus* than in less frequented sites. Moreover, the percentage cover, biomass and size measures of mussels were reduced within harvested sites. Nevertheless, the diversity of the fauna associated with the mussel beds was not significantly affected by the level of intertidal use, and neither were the evenness or species richness [5].

4.2.2. Trampling

Studies about the trampling effects on the fauna associated with mussel beds were conducted mainly in the Pacific region with *M. californianus*, except for one study conducted in the Atlantic coast of Argentina, that involved *M. chilensis* and *P. purpuratus*. However, many other areas still lack studies on this subject. In Tierra del Fuego, mussel crushing was done to simulate a physical disturbance comparable to extreme trampling [33]; the diversity of the associated fauna declined in the disturbed plots. Furthermore, sediment trapped among the two mussel species (to less than 5 mm) almost disappeared for unknown reasons, and was not restored until the end of the study period. Species richness and evenness were also significantly lower in the disturbed plots. In general, opportunistic annelids and some isopods endured the disturbance well, while sensitive amphipods and bivalves were more affected. Due to the slow recovery of *P. purpuratus*, the initial structure of multilayers with sand, *P. purpuratus* and *M. chilensis* found at the start of the trial was never completely recovered by the end of the four-year experiment [33].

The remaining studies investigated the human trampling in the Californian coast [5,31,34]. In Santa Cruz, the abundance and diversity among the associated fauna in mussel beds was higher in less trampled sites. However, there was no significant decline of these descriptors in areas subjected to trampling, except at a higher ground [31,34]. At the most trampled site, some small bivalves were less abundant and some algae were absent, compared to less trampled sites. 17 years later, Van de Werfhorst and Pearse [34] employed a different sampling design in their follow-up study. They created a contour map and stratified sampling according to tidal height and found a large variability above the 2 m tidal level. This time, mussel beds and the associated species' richness declined with increased human trampling; they concluded that these differences could be attributed to the sampling strategy and argued that sampling scale and design are important for evaluating and monitoring trampling impacts [34]. In a broader study encompassing ca. 1000 km of the Californian coast, the effect of human visits and trampling impact was evaluated and compared between regulated reserves and unprotected areas [5]. In areas with higher levels of human visits, the mussel cover was significantly lower than in low-use sites, but the diversity of associated species was not affected by the level of use.

4.3. Large-Scale Physical Impacts

Dredging and trawling (where fishing gear is towed near or along the seabed) can physically damage benthic habitats and biota [14,16,35]. These practices can also stir up sediment from the bottom, creating sediment plumes that can impact sensitive species [5,14]. Recovery times for disrupted habitats are usually long and depend on their species sensitivity, the area affected and the intensity of the impact [4,35]. We analyzed five papers that studied the effects of dredging and/or trawling on the mussel communities and adjacent habitats.

4.3.1. Dredging

Among the large-scale physical impacts, dredging seems to be less severe than trawling for the mussel communities [14]. Mussel epifauna is the most affected by dredging, with reductions in abundance of up to 60% following the pass of a dredge [14]. Along the Wadden Sea, the presence of *M. edulis* allowed for a reduction of the impact of dredging, contributing to a higher abundance and diversity than in other mussel-free fishing grounds [36]. Heterogeneous sediments that were inhabited by *M. modiolus* also provided high epifaunal diversity and density. Crustaceans were dominant among the dredged epibenthos, and mussels could provide them with refuge [36].

In the South Atlantic, Morsan [35] (Table 1) observed that dredging causes high disturbance to the whole benthic ecosystem. Multivariate analysis showed that macrofaunal assemblages were altered on each fishing ground between 1987 and 1997, according to fishing intensity and time-lapse, since the last fishing action. However, no significant alterations occurred on the fishing grounds that were not dredged during the 10-year period. In general, the mean density of almost all species declined in dredged fishing grounds. However, in 1997, the abundance of other non-commercial species increased, probably because of the reduction of the commercial target species, that dominated the dredged fishing grounds ten years earlier [35].

Table 1. Reviewed anthropogenic disturbances that impacted mussel beds and associated assemblages. spp. = species; N = abundance; S = species richness; H = Shannon–Wiener's diversity index; J = Pielou's evenness index; ANOSIM = analysis of similarities; ANOVA = analysis of variance; BIOENV = best subset of environmental variables; MANOVA = multivariate analysis of variance; nMDS = non-metric multidimensional scaling; PERMANOVA = permutational analysis of variance; PERMDISP = homogeneity of dispersions; SIMPER = similarity percentage analysis. (+) = Positive impact; (−) = negative impact; null = not mentioned.

Article	Mussel Species	Habitat	Disturbance	Sampling Period	Metazoan Taxa	Mussel Response	Impact on Fauna	Indices and Statistics	Other Measures	Location
[1]	*Mytilus galloprovincialis*	Intertidal, Subtidal: Rock, Sand	Organic pollution (hydrocarbons and sewage)	2004	88 spp. [only mussel beds]: Arthropoda (20.5%); Echinodermata (1.1%), Mollusca (18.2%), Annelida (36.4%), Other (23.8%)	(+)	Moderate impact	N, S, H, J, ANOVA, ANOSIM, nMDS	-	Thermaikos Gulf, Northern Aegean Sea, Greece
[2]	*Crenomytilus grayanus*	Subtidal: Rock, Sand	Organic pollution (sewage), Harvesting	2000–2004	138 spp.: Arthropoda (11.6%), Echinodermata (11.6%), Mollusca (23.2%), Annelida (32.6%), Other (21.0%)	(−)	High impact	N, S, H, J	Biomass, trophic guilds	Vostok Bay, Sea of Japan, Russia
[4]	*Modiolus modiolus*	Subtidal: Mud, Rock, Shells	Trawling	2010	273 spp.: Annelida (34.1%), Arthropoda (17.9%), Echinodermata (6.2%), Mollusca (17.2%), Other (24.6%)	(−)	High impact	N, S, H, J, Margalef, PERMANOVA, PERMDISP, SIMPER	-	Strangford Lough, Ireland
[5]	*Mytilus californianus*	Intertidal: Rock	Harvesting, Trampling	not specified	22 spp. [highest species richness in a site]: not specified	(−)	Low impact	N, S, H, J, *t*-test	Biomass, cover, size, thickness	CA, USA
[6]	*Mytilus edulis*	Intertidal: Rock	Organic pollution (hydrocarbons)	1989	18 spp. [highest species richness in a site]: not specified	(−)	High impact	N, S	Cover	Prince William Sound, AK, USA
[7]	*Mytilus edulis*	Intertidal: Rock	Unspecified pollutants Alien species	2002	154 spp.: Annelida (18.2%), Arthropoda (27.9%), Echinodermata (1.9%), Mollusca (18.2%), Other (33.8%)	-	Moderate impact	S, Conspicuousness, Cluster Analysis, nMDS	-	Helgoland, German Bight, North Sea
[8]	*Mytilus edulis*	Subtidal: Gravel, Mud, Rock, Sand, Shell	Human interference: Harvesting (*Ostrea edulis*),	1980	89 spp.: not specified	(+)	High impact	N, S, Cluster Analysis, Linear Regression	-	Island of Sylt, German Bight, North Sea
[10]	*Mytilus edulis*	Subtidal: Mud, Sand	Organic pollution (sewage)	1971, 1972	38 spp. [only mussel beds]: Annelida (44.7%), Arthropoda (28.9%); Mollusca (21.1%), Echinodermata (2.6%), Other (2.6%)	(-)	Moderate impact	N, S, H, J, Simpson	Biomass	Kiel Bay, Baltic Sea
[11]	*Mytilus edulis*	Intertidal: Rock, Sand, Shells	Organic pollution (hydrocarbons)	1999	57 spp.: Annelida (22.8%), Arthropoda (35.1%), Mollusca (31.6%), Other (10.5%)	(−)	Moderate impact	S, H, BIOENV, MANOVA, nMDS, SIMPER	-	West Coast of UK

Table 1. *Cont.*

Article	Mussel Species	Habitat	Disturbance	Sampling Period	Metazoan Taxa	Mussel Response	Impact on Fauna	Indices and Statistics	Other Measures	Location
[13]	*Brachidontes rodriguezii*	Intertidal: Rock, Sand	Organic pollution (sewage)	1997–2000	12 spp.: only Polychaeta	(−)	Moderate impact	ANOSIM, SIMPER	-	Mar del Plata, Argentina
[14]	*Modiolus modiolus*	Subtidal: Rock	Dredging, Trawling	2007–2009, 2012	29 spp.: not specified	(−)	High impact	N, S, H, J, Margalef, ANOVA, nMDS, PERMANOVA, PERMDISP, SIMPER	-	Isle of Man and Wales, UK
[15]	*Mytilus edulis*	Subtidal: Artificial structures	Metal and Organic pollution (experimental)	2010	not specified	(−)	High impact	ANOVA	-	Malahide Marina, Ireland
[16]	*Modiolus modiolus*	Subtidal: Mud, Rock, Shells	Trawling	not specified	not specified	(−)	High impact	Cluster Analysis, DECORANA	-	Strangford Lough, Ireland
[17]	*Perna perna*	Intertidal: Rock	Harvesting	2008	not specified	(−)	Moderate impact	N, S, PERMANOVA	Cover	Transkei, South Africa
[18]	*Mytilus edulis*	Intertidal, Subtidal: Rock	Harvesting (subtidal)	1997, 1998	19 spp. [Intertidal], 22 spp. [Subtidal]: not specified	(−)	Moderate impact	N, S, H, J, Sørensen's index, Renkon's index, ANOVA, Kruskal-Wallis Test, Mann-Whitney U-Test	-	Island of Sylt, German Bight, North Sea
[21]	*Arcuatula senhousia*, *Jolya elongata*	Subtidal: Mud, Sand	Organic pollution (unspecified),	1985–1987, 1997–1999	460 spp.: not specified	(−)	Moderate impact	N, S, H, J, ANOSIM, nMDS	-	Bohai Sea, China
[22]	*Mytilus galloprovincialis*	Intertidal: Artificial structures	Organic pollution (unspecified)	2004	155 spp.: Annelida (43.2%); Arthropoda (18.1%) Echinodermata (0.6%), Mollusca (9.7%), Other (28.4%)	(+)	Moderate impact	N, S, H, J, Margalef, ANOVA, ANOSIM, BIOENV, nMDS, SIMPER	Biomass	Izmir Bay, Eastern Mediterranean, Turkey
[23]	*Mytilus galloprovincialis*	Intertidal: Rock	Organic pollution (hydrocarbons)	2004, 2005	104 spp.: only Annelida	-	Moderate impact	N, S, H, nMDS	-	Caldebarcos and O Segaño, Galicia, Spain
[24]	*Brachidontes rodriguezii*, *Mytilus platensis*	Intertidal: Rock, Sand	Organic pollution (sewage)	1999, 2000	24 spp.: Annelida (33.3%), Arthropoda (29.2%), Mollusca (20,8%), Other (16.7%)	(+)	Moderate impact	S, H, Margalef, ANOVA, ANOSIM, nMDS	Biomass	Quequén and Necoche, Argentina
[25]	*Brachidontes rodriguezii*, *Mytilus platensis*	Intertidal: Rock, Sand	Organic pollution (sewage)	1997	43 spp.: not specified	(−)	Moderate impact	N, S, H, J, Jack-Knife test	-	Mar del Plata, Argentina

Table 1. *Cont.*

Article	Mussel Species	Habitat	Disturbance	Sampling Period	Metazoan Taxa	Mussel Response	Impact on Fauna	Indices and Statistics	Other Measures	Location
[27]	*Perumytilus purpuratus*	Intertidal: Rock	Harvesting, Organic enrichment (experimental)	2004	45 spp.: Annelida (17.8%), Arthropoda (31.1%), Mollusca (35.6%), Echinodermata (4.4%) Other (11.1%)	-	Moderate impact	N, S, ANOVA, ANOSIM, SIMPER	Trophic guilds	Bahía Totoralillo, Northern-Central Chile
[28]	*Mytilus* sp.	Intertidal: Rock, Heterogenous sediment	Organic pollution (hydrocarbons),	1990, 1991	42 spp. [highest species richness in a site]: not specified	(−)	High impact	N, S, H, ANOVA	Cover	Prince William Sound, AK, USA
[29]	*Perumytilus purpuratus*	Intertidal: Rock	Metal pollution (experimental)	2007	46 spp.: Annelida (30.4%), Arthropoda (19.6%), Echinodermata (8.7%), Mollusca (23.9), Other (17.4%)	null	Moderate impact	S, H, J	-	Bahia San Jorge, Northern Chile
[30]	*Perna perna*	Intertidal: Rock	Harvesting	not specified	not specified	(−)	Low impact	N. S, H, nMDS	Biomass, trophic guilds	Transkei, South Africa
[31]	*Mytilus californianus*	Intertidal: Rock	Trampling	1977, 1978	67 spp.: not specified	null	Low impact	N, S, H, Dominance curves, Kruskall-Wallis Test, Mann-Whitney U-Test	-	Santa Cruz, CA, USA
[32]	unspecified	Intertidal: Mud, Sand	Harvesting	1981–1984, 1987	44 spp. [unpolluted site]: Annelida (50.0%), Arthropoda (20.4%), Echinodermata (3.7%), Mollusca (25.9%)	(−)	Moderate impact	ABC K-Dominance curves	-	Netherlands and Belgium
[33]	*Perumytilus purpuratus*, *Mytilus chilensis*	Intertidal: Mud, Rock, Sand	Harvesting, Trampling (experimental)	2001	not specified	(−)	Moderate impact	ANOVA, Mann-Whitney U-Test	Biomass, cover, size	Rio Grande, Tierra del Fuego, Argentina
[34]	*Mytilus californianus*	Intertidal: Rock	Trampling	1995	20 spp. [highest species richness in a site]: not specified	(−)	Low impact	S, H, ANOVA, ANCOVA, *t*-test	Cover	Santa Cruz, CA, USA
[35]	*Mytilus platensis*	Subtidal: Gravel, Mud, Sand, Shells	Dredging	1986–1997	46 spp. [highest species richness in a site]: not specified	(−)	Moderate impact	S, ANOSIM, MDS	-	Golfo de San Matías, Argentina
[36]	*Mytilus edulis*	Subtidal: Gravel, Sand, Shells	Dredging	1988, 1992	42 spp.: Arthropoda (23.8%), Echinodermata (4.8%), Mollusca (21.4%), Annelida (4.8%), Other (45.2%)	(+)	High impact	Mann-Whitney U-Test	-	Schleswig-Holstein, Wadden Sea, North Sea

The recovery of dredging-impacted areas takes a long time [14]. Comparisons with historical surveys in the Wadden Sea suggested that a decline of nearly 50% of all epifaunal species within the last hundred years could be attributed to fishery impacts [36]. Moreover, the community structure may not return to pre-harvest conditions, but lead instead to new assemblages [14,35].

4.3.2. Trawling

An obvious effect of trawling was the destruction of the mussel clumps, the flattening of the mussel structure and the removing of epifauna [4,16]. In some cases, the substrate was not totally removed, and a few live mussels remained among a noticeable amount of shell debris [16]. Magorrian and Service [16] visually documented the effects of trawling, but their 'Visual Fast Count' approach did not provide as much taxonomic information as traditional methods, mostly due to the difficulty in identifying organisms on video. However, this research could have a potential role in the management of epifaunal communities in future broader assessment studies.

Declines in the abundance of mussels and epifaunal organisms following the passage of a trawl could reach up to 90% of the total fauna abundance [4,14]. Declines in diversity were also observed, mainly for anthozoans, ascidians, bivalves, echinoderms, hydrozoans, sponges or tunicates. A repeated exploitation led to a major reduction in mussel distribution in Northern Ireland since the 1970s, until a fishing ban enforcement was implemented in 2003 [4]. The loss of the structure formed by *M. modiolus* and its role in pelagic-benthic coupling probably accounts for the diversity and abundance declines of most higher taxa [14,16]. Distinct species also respond to the impact in different ways; for instance, the abundance of tunicates or some infaunal annelids increases while vagile taxa or mussel epifauna decline because of the reduction or disappearance of the host [4]. This is reflected in significant decreases of overall values of species richness, diversity and evenness in trawled areas [4,14].

Trawling impacted areas have a very slow recovery, compared to dredging [14]. Therefore, some authors suggest a direct intervention, including habitat restoration, to speed up the process, since the designation of Marine Protected Areas and the introduction of fishing bans alone could not be enough to reverse the negative effects caused by trawling [4].

5. Synthesis and Final Remarks

Mussel beds are very important habitats, forming complex structures and creating niches that harbor a great number of species [9,14]. The biota depends on the mussels' shelter, their water purification abilities or the sediment and fecal pellets trapped amid the byssus, that contribute to the presence of many deposit-feeders and predators [10,11,13]. When the ecosystem is impacted, the assemblages rely on the mussels for protection and/or mitigation. The mussels are capable of bioaccumulating a huge amount of organic and inorganic pollutants, removing them from the water column or making them less available to other species [11,15,27]. Therefore, the removal and killing of mussels by harvesting, trampling, dredging, trawling or pollution threatens the ecological quality of the mussel communities. This is especially prominent when the systems are afflicted by other disturbances and synergistic effects lead to a poor ecological status, reducing biodiversity [2,23,27,33].

Low values of abundance, biomass, diversity, evenness or species richness were reported for all categories of impacts, with some studies describing declines in at least three of these descriptors [2,4,5,8,33]. However, some species, like annelids, opportunistically profited from the perturbations, particularly from organic enrichment, and increased their abundance and biomass [10,22,25]. Regarding the mussel species, some were able to recover faster than others in the same disturbed system [33]. In moderate impacted areas, species tolerant to pollution were thriving, benefiting from the enriched sediments [1,2,13,22,24–26]. Moreover, the presence of heterogenous habitats colonized by mussels also helped to mitigate severe impacts like dredging, since mussels, as ecosystem-engineers, increased biodiversity [36].

Most of the studies here reviewed concern the effects of organic pollution, mainly in the Atlantic–Mediterranean region, and only two discussed the effects of metals in this region. Moreover, organic pollution effects have been less studied in the Pacific region and remain to be studied in the Indian Ocean. In comparison, harvesting or trampling have been less studied but encompass different regions of the world, including the Indian Ocean. However, dredging or trawling have only been studied in the Atlantic region even though trawling, for instance, is a widespread practice in other known mussel regions [37]. The assessment of both impacts in other regions is needed due to their severe effects, particularly trawling. In general, this applies to many areas with mussel beds, regardless of the type of impact, in order to get a better comprehension of their effects on the mussel communities and overall biodiversity.

It is important to protect mussel beds by promoting marine reserves conservation, managing harvesting or establishing limitations to allow for a good restoration [5,17,18]. A direct intervention in the restoration of mussel beds can have a huge impact in habitat degradation reversion and be useful to improve resources and ecosystem function [38]. This should be an approach to follow in the future.

Author Contributions: Conceptualization, P.V., L.G.-M., L.S., J.M. and M.R.; methodology, L.G.-M., L.S., M.R. and P.V.; resources, M.R., and P.V.; writing—original draft preparation, L.S.; writing—review and editing, J.M., L.G.-M., M.R. and P.V.; project administration, P.V.; funding acquisition, P.V. All authors have read and agreed to the published version of the manuscript.

Funding: This research was developed under the Project No. 30181 (PTDC/CTA-AMB/30181/2017), co-financed by COMPETE 2020, Portugal 2020 and the European Union, through the ERDF, and by the FCT (Foundation for Science and Technology) through national funds within the scope of UIDB/04423/2020 and UIDP/04423/2020.

Data Availability Statement: Not applicable.

Acknowledgments: We would like to thank the two reviewers for their constructive comments, which helped to improve the manuscript. Puri Veiga was hired through the Regulamento do Emprego Científico e Tecnológico—RJEC, from the Portuguese Foundation for Science and Technology (FCT) (CEECIND/03893/2018). Laura Guerrero-Meseguer was funded by the "Recovery, Transformation and Resilience Plan of the Ministry of Universities of Spain", "NextGenerationEU" and the University of the Balearic Islands.

Conflicts of Interest: The authors declare no conflict of interest.

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