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ANOTHER BRICK IN THE RESTORATION OF GORGONIANS: Assessment of Coral Bycatch in Artisanal Fisheries and its Potential for Restoration Actions

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Declaração de autoria de trabalho

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Declaro ser o(a) autor(a) deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

Vítor Dias

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Resumo

Os jardins de coral e corais de águas frias (CWCs) são definidos como agregados relativamente densos de uma ou de várias espécies de coral que fazem parte de vários grupos taxonómicos, incluindo escleractínios (Scleractinia), corais negros (Antipatharia), corais moles (Alcyonacea) e penas-do-mar (Pennatulacea). Muitas destas espécies são engenheiros de ecossistemas, pois para além de criarem habitat, tais organismos também são capazes de alterar fatores bióticos e abióticos, possibilitando assim a colonização dos habitats bentónicos por outros organismos o que faz com que sejam muito importantes. Os corais também representam habitat essencial para muitas espécies de peixes e crustáceos que, em alguns casos, são explorados comercialmente. Outro dos serviços que estes habitats nos dão é relativo a materiais, para joias como é o caso do coral vermelho (*Corallium rubrum*) ou mesmo a nível da medicinal como a espécie *Sarcodictyon roseum*, em que alguns dos seus compostos estão a ser usados em ensaios clínicos para combater o cancro. Infelizmente, estes magníficos ecossistemas enfrentam imensas ameaças associadas às atividades humanas. Desde 2004, os jardins de coral e CWCs são considerados ecossistemas marinhos vulneráveis (VMEs). Os VMEs são definidos como espécies ou habitats que são raros ou únicos e que apresentam uma complexidade estrutural e funcional significativa, enquanto apresentam uma probabilidade limitada de recuperação aos impactos a que estão sujeitos. Tais atividades humanas incluem derrames de petróleo, acidificação dos oceanos e o impacto causado pelas pescas. Este último é, sem dúvida, o impacto mais preocupante e mais devastador principalmente por causa dos arrastos de fundo. Apesar de já existirem muitos estudos efetuados sobre os impactos da pesca em jardins de coral e CWCs, a sua maioria foca-se na pesca industrial como o caso dos arrastos. Como resultado, sabe-se muito pouco sobre os impactos causados pelas pescas artesanais (i.e. armadilhas, covos e redes de tresmalho e de emalhar) nestes habitats, apesar de representar 84% e 90% da frota pesqueira na Europa e mundo, respetivamente. Para combater os diversos impactos que afetam os ecossistemas de coral, já foram implementadas várias medidas, tais como criação de áreas marinhas protegidas (MPAs), o fecho temporário da pesca em algumas zonas e outras medidas relacionadas com as pescas, como a proibição de arrastos a profundidades inferiores a 800m instituída na Europa. Visto que os jardins de coral e CWCs são tão importantes ecologicamente e são *hotspots* de biodiversidade, o interesse em implementar medidas de conservação e recuperação de habitats têm crescido nos últimos tempos. No entanto, o número de trabalhos desenvolvidos até ao momento com o objetivo de restaurar habitats de corais circalitorais e profundos é limitado, pois este tipo de restauração é monetariamente dispendioso uma vez que

no geral requer o uso de tecnologia subaquática especializada visto que estes habitats ocorrem maioritariamente a profundidades abaixo dos 50m de profundidade. Como tal, os objetivos deste trabalho são: 1) documentar o impacto causado por redes de emalhar usadas pela pesca artesanal nos jardins de coral e CWCs ao largo de Sagres (Portugal); 2) identificar *hotspots* de biodiversidade de corais e de capturas acidentais pela pesca artesanal que possam constituir áreas de gestão prioritárias, assim como melhorar o conhecimento sobre a biodiversidade de corais que existem ao largo de Sagres; 3) testar a viabilidade de usar corais de zonas profundas apanhadas acidentalmente pela pesca artesanal para ações de recuperação de habitats pouco profundos; e 4) testar o efeito da densidade e da composição de espécies em transplantes de corais de modo a fornecer indicações para projetos de recuperação de corais futuros. Este estudo foi dividido em duas componentes científicas: a documentação do impacto causado por redes de emalhar ao largo da costa de Sagres (Capítulo 2) e o estudo piloto de recuperação de habitats de corais usando biomassa apanhada nas redes de emalhar (Capítulo 3). Para o Capítulo 2, foi seguida a atividade de uma embarcação pesqueira durante 42 dias, onde foi documentado todos os corais recolhidos, assim como os seus tamanhos e algumas variáveis adicionais como a profundidade, malhagem, localização das redes lançadas, espécie alvo e número de indivíduos capturados. Em 118 redes documentadas, foram recolhidos 4,326 fragmentos/colónias de coral pertencentes a 22 espécies, o que representa 13% das espécies conhecidas para esta área. Em média, foram recolhidos 31.1 (±2.7) corais em cada rede, onde o máximo observado foi de 144 corais numa única rede. Adicionalmente, em média foram recolhidas 4.31 (±0.2) espécies de coral em cada rede, atingindo um máximo de 10 espécies numa só rede. Os resultados, mostram que as comunidades de corais recolhidas, tal como as suas quantidades, estão relacionadas com a profundidade a que as redes foram lançadas. Foram ainda identificadas 4 áreas com grande biodiversidade e abundância de corais e que foram designadas de *hotspots*. Os resultados deste estudo indicam que o impacto causado por redes de emalhar em jardins de coral e CWCs é muito superior ao que se pensava anteriormente, e revela a necessidade de novas medidas de conservação e o uso de artes de pesca alternativas. Além destas medidas, o desenvolvimento de protocolos de captura acidental excessiva de corais em águas nacionais que imponha a obrigatoriedade de pescar noutra zona pode também ser uma alternativa de gestão viável. Globalmente, este estudo revela a grande biodiversidade de espécies de coral que existe nos jardins de coral e CWCs ao largo de Sagres, bem como o impacto potencialmente significativo que a pesca artesanal pode ter em certas áreas. Para o Capítulo 3 de recuperação de habitats de coral, foram utilizados 12 recifes artificias construídos com blocos de alvenaria para replantar um total de 90 colónias de coral provenientes de descartes da pesca artesanal e que foram instala

20m de profundidade. O desenho experimental incluiu 4 tratamentos diferentes, de acordo com os dois fatores definidos para o estudo, nomeadamente a densidade dos transplantes (10 colónias por m^2 *vs.* 20 colónias por m^2) e composição de espécies (mono-específico *vs.* multi-específico). A espécie *Eunicella verrucosa* foi usada para os tratamentos mono- e multi-específico e as espécies *Leptogorgia sarmentosa* e *Paramuricea grayi* para o tratamento multi-específico. Em média 78% (±4%) dos corais transplantados sobreviveram até 8 meses pós-transplantação. Os resultados mostraram que o tratamento multi-específico de baixa densidade teve a melhor taxa de sobrevivência (87%) apesar do efeito dos tratamentos experimentais não ter sido estatisticamente significativo. No geral, as taxas de sobrevivência para cada tratamento experimental diferiram entre espécies. A espécie com maior taxa de sobrevivência foi a *E. verrucosa* (82%), enquanto que a *P. grayi* e *L. sarmentosa* tiveram a mesma taxa de sobrevivência (67%). A níveis de crescimento, o estudo demonstra que em média não houve crescimento efetivo do comprimento total dos ramos dos corais (-0.32cm±5.97cm) durante os 8 meses de monitorização. Contudo, o potencial de crescimento é bastante elevado em todas as espécies estudadas com a observação de um aumento máximo do comprimento total dos ramos das colónias de 72.61cm, 21.90cm e 113.42cm para a *E. verrucosa*, *P. grayi* e *L. sarmentosa*, respetivamente. Estes resultados, demostram o elevado grau de dinamismo do crescimento das colónias de octocorais, que se partem e voltam a crescer com frequência e rapidez, visto que muitos dos transplantes deste estudo tiveram tal dinâmica. Os resultados também mostraram que o uso da métrica do tamanho total dos ramos parece ser melhor do que a altura máxima das colónias para detetar variações no crescimento de espécies com morfologia ramificada como é o caso dos octocorais. No geral, a metodologia usada neste estudo foi bem-sucedida, sendo que apenas 10% das colónias morreram nos primeiros 3 meses de monitorização, o que indica que a fixação das colónias não constitui uma limitação. No entanto, são necessários estudos adicionais para se perceber se o uso de recifes artificiais poderá ser usado com outras espécies, visto que a sensibilidade a manipulação e características biológicas varia de espécie para espécie. Os dois estudos apresentados aqui demonstram também a importância de colaborar com as comunidades pesqueiras, quer para melhorar o conhecimento sobre a distribuição das espécies de coral e os impactos a que estão sujeitas, quer para juntos proteger estas espécies vulneráveis.

Palavras chave: pesca acidental de coral, pescas artesanais, restauração ecológica, medidas de conservação, redes de emalhar, corais de águas frias, jardins de coral**.**

Abstract

Coral gardens and cold-water corals are key habitats for many marine organisms, providing several goods and services. Because of their ecological importance and susceptibility to degradation caused by human activities, these habitats are considered vulnerable marine ecosystems. Fisheries are likely the most destructive threat affecting these habitats and there is an urgent need to understand how different fishing gear affects them, as well as how to implement effective conservation and protection measures that mitigate these impacts. This study aims to provide baseline information on the impact of fisheries using bottom-set gillnet locally on coral assemblages, and to develop a time-effective and low-cost restoration pipeline for both deep- and shallow-water populations using coral bycatch. In order to assess the impact of bottom-set gillnet fisheries on coral assemblages, the fishing activity and coral bycatch of one vessel were documented over 42 days, determining coral composition, specimen size, fishing depth, location, number of fish caught, mesh size and soaking time for each net deployed. In total, 4,326 specimens of corals belonging to 22 different species of corals were collected from 118 bottom-set gillnets. Additionally, we report 4 hotspots of coral biodiversity. This study confirms anecdotal evidence on the destructive impact of bottom-set gillnets on benthic ecosystems, demonstrating that the impact is greater than previously observed. For the restoration component of the study, twelve artificial reefs were used to transplant 90 corals obtained from bycatch, which were divided in 4 treatments varying transplant density and species composition. On average, 78% of the colonies transplanted survived after 8 months. The results show that total branch length metric can detect the changes in growth of branching organisms better than maximum height metric. Additionally, this study demonstrates that octocorals grow much faster than generally assumed, but the constant dynamic of breakage and recovery that these species cope with maintains their net growth relatively low.

Keywords: coral bycatch, artisanal fisheries impact, ecological restoration, conservation measures, bottom-set gillnets, cold-water corals, coral garden.

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List of abbreviations and acronyms

CPUE- Catch Per Unit of Effort

CWC- Cold-water Corals

db-RDA- Distance-based Redundancy Analysis

EFH- Essential Fish Habitat

GAM- Generalized Additive Model

GCV- Generalized Cross-Validation Statistic

MAF- Marine Animal Forests

MPA- Marine Protected Area

NAFO- Northwest Atlantic Fisheries Organization

NEAFC- North East Atlantic Fisheries Commission

PCoA- Principal Coordinates Analysis

RFMO- Regional Fisheries Management Organizations

SAIs- Significant Adverse Impacts

SSF- Small-Scale Fisheries

UNGA- United Nations General Assembly

VME- Vulnerable Marine Ecosystem

1. Chapter 1: Introduction

1.1. Circalittoral/deep coral communities and their ecosystem services

In the marine environment, suspension feeders like sponges, bivalves and corals function frequently as ecosystem engineer species, forming complex megabenthic assemblages. Ecosystem engineers are defined as species that sustain or form habitats for other species and regulate the availability of food and other resources by physically changing biotic and abiotic factors (Jones et al., 1994). Moreover, these species are able to increase structural complexity, increasing accumulation of suspended particles (Gacia and Duarte, 2001), as well as changing current flow velocity (i.e. reducing current flow) and stabilizing the substrate (Eckman et al., 1989). These megabenthic assemblages have been termed marine animal forests (MAF) and compared with forests in terrestrial systems (Rossi et al., 2017a). Similar to their terrestrial counterparts, marine animal “forests” may be composed of one or several species, providing high habitat heterogeneity, including in environmental conditions, thereby functioning as hotspots of biodiversity (Rossi et al., 2017a). Tropical coral reefs (<50m depth), for instance, are one of the most iconic type of coral dominated MAF. However, more than 3000 coral species are known to occur at depths below 50m (Cairns, 2007), corresponding to 65% of the total number of corals known worldwide (Roberts, 2006).

Circalittoral and deep coral communities (i.e. corals that occur at depths below 50m, henceforth referred to as “deep”) such as coral gardens and cold-water corals (CWCs) are defined as habitats formed by relatively dense aggregations of corals that belong to several taxonomical groups including stony corals (Scleractinia), black corals (Antipatharia), soft corals (Alcyonacea) and sea pens (Pennatulacea; Roberts, 2006; Cairns, 2007). These occur in several environments worldwide, including continental shelves, island slopes, mounds, seamounts, canyons and fjords (Watling et al., 2011), but are generally confined to waters with average temperatures between 4ºC and 14ºC (Roberts, 2006). These communities are key habitats in the deep-sea, constituting one of the most dominant ecosystem engineers.

Coral gardens and CWCs are known as some of the most biodiverse ecosystems in the deep-sea (Freiwald and Roberts, 2005), providing a wealth of economic and ecological goods and services that directly or indirectly affect human well-being (Rogers, 1999; Millennium Ecosystem Assessment, 2005; Beaumont et al., 2007; Foley et al., 2010). Ecosystem services can be classified into provisioning services, regulating services and cultural services that directly affect people, and supporting services that indirectly affect people by providing services needed to produce the other services (i.e. habitat and nutrient cycling; Capezzuto et al., 2018). Supporting services include, the ability of corals to increase structural complexity, providing habitats for other species (e.g., crabs, fish and shrimp), as well as feeding ground for many species such as basket stars and snails (Roberts and Hirshfield, 2004). Although it is controversial whether or not these habitats are in fact essential fish habitat (i.e. habitat necessary for fish to breed, feed, spawn or grow to maturity; EFH; Foley et al., 2010), corals are undoubtedly the preferred habitats for several fish life processes, including feeding, spawning and breeding, as well as for some life stages (Fosså et al., 2002; Costello et al., 2005). Additionally, coral habitats have the ability to sequester and store carbon, through calcification and formation of biogenic reefs, which contributes to the carbon cycling system by acting as carbon sinks (Mallo et al., 2019).

Provision services refer to goods that are exploitable by humans, directly from the ecosystem (i.e. food and primary materials). For example, corals provide food to humans by supporting species which are commercially exploited by fisheries (e.g., redfish, monkfish, shrimp and rockfish). Additionally, coral ecosystems are also frequently associated with higher fish abundance than surrounding areas (Freiwald and Roberts, 2005), which indirectly contributes to higher fishing catches. Another example of provision services is associated with the exploitation of primary materials for several products, including jewellery, as is the case of the Mediterranean precious red coral (*Coralium rubrum*) and *Primnoa* sp. Other uses of primary materials include utilizing chemical compounds towards pharmaceutical, medical, engineering and food applications, such as extracts of *Sarcodictyon roseum*, which have been used in clinical trials against cancer (Beaumont et al., 2007; Foley et al., 2010), and extracts of the Caribbean gorgonian *Antillogorgia elisabethae* which has been exploited for over 20 years for their pseudopterosins, which are used for anti-inflammatory and analgesic products (Goffredo and Lasker, 2008).

Regulating services are the processes that regulate the ecosystem processes, such as, natural hazard regulation (Millennium Ecosystem Assessment, 2005). Coral ecosystems, principally coastal coral reefs, can decrease water flow and high wave power, which decreases the damage caused by hurricanes and waves (Millennium Ecosystem Assessment, 2005). Cultural services are the non-materialistic services that humans exploit, such recreation, spirituality, religion and employment. For example, recreational diving in coral reefs is a 35.8 billion dollar industry worldwide (Spalding et al., 2017). In southern Kenya, people developed spiritual rituals around reefs to appease spirits (Moberg and Folke, 1999).

1.2. Threats to circalittoral/deep coral communities

Coral gardens and CWCs face innumerous threats mainly associated with human activities (Orejas and Jiménez, 2019). Fisheries are one of the activities that most heavily impact these coral communities through biomass removal and partial damage to coral colonies, particularly fisheries using bottom-contact gear such as trawling and bottom-set longlines and nets (Pham et al., 2015). Fisheries' bycatch (species caught that are not targeted and when are not commercially valuable, have illegal size or the total caught is above the total allowable catch or are protected, can be discarded) in the continental shelf and slopes is mainly composed of sea birds, marine turtles, marine mammals, fish and habitat-forming organisms, including corals, kelp, seagrass, mussels beds and sponges (Dayton et al., 1995; Althaus et al., 2009; Bo et al., 2014). The morphology and 3-D structure of habitat-forming organisms, in particular, make them prone to entanglement in fishing gear (Bo et al., 2014), with coral gardens and cold-water corals (CWC) among those most affected (Althaus et al., 2009). Fisheries also have indirect impacts on these habitats, mostly through littering and lost fishing gear. For instance, lost fishing gear can become entangled on deep-sea organisms, which contributes to a phenomenon known as "ghost fishing", being the specific case of corals, which continues to impact colonies through friction, abrading and entanglement (Saldanha et al., 2003; Brown and Macfadyen, 2007; Bo et al., 2014).

Although bottom-contact fisheries are the activity with the highest direct impact on coral ecosystems, there are several other human activities that pose a threat to these habitats (Hall–Spencer et al., 2002; Bo et al., 2014; Pham et al., 2015; Clark et al., 2016). These include littering (Brown and Macfadyen, 2007; Bo et al., 2014), oil spills, mineral extraction (Secretariat of the Convention on Biological Diversity, 2014), and ocean acidification as a result of climate change (Rossi et al., 2017b). Litter produced by humans are entering our ocean at a rate of 4.8 to 12.7 million metric tons per year (Jambeck et al., 2015). In most cases, marine debris marine debris sinks to the sea floor (Pham et al., 2014), which can entangle or cover sessile organisms such as corals. For instance, Sheehan et al. (2017) reported that from the hundreds of pink sea fans found stranded in southwest England, more than 83% of them were entangled in marine debris from different sources. This study showed that marine debris interacts with sessile organisms and may cause the removal of entire colonies from the seafloor as most of the individuals collected by the authors had a holdfast (Sheehan et al. 2017).

Oils spills can severely impact the function and resilience of coral gardens and CWCs. For example, White et al. (2012) reported that 3 to 4 months after an oil spill in the Gulf of

Mexico, gorgonians located 11km away from the oil spill site presented several signs of stress, namely tissue loss, sclerite enlargement and excess mucous production, and were covered by brown material from the oil spill. Stress signs were also visible in the associated fauna (i.e. ophiuroids) which presented anomalies in their coloration (White et al., 2012).

Ocean acidification can also impact coral gardens and CWCs. These organisms are biocalcifiers (i.e. organisms that produce and subsequently accumulate calcium carbonate morphotypes) which live at depths characterized by a very low calcium carbonate saturation state (Thresher et al., 2011). Atmospheric CO_2 when dissolved in seawater dissociates into carbonate and bicarbonate, with release of H^+ ions, thereby decreasing pH. The increase of atmospheric CO_2 dissolution in the seawater and consequent decrease in pH drives the conversion of carbonate to bicarbonate, which lowers the calcium carbonate morphotypes (i.e. aragonite and calcite) saturation state in seawater (Lunden et al., 2013; Movilla et al., 2014). Since coral gardens and cold-water corals inhabit areas with low carbonate saturation state, with the decrease of this saturation they may decrease calcification (Movilla et al., 2014). For instance, Morato et al. (2020) predicted that deep-sea coral species in the North Atlantic would face a loss of suitable habitat by 2100 caused by the ocean acidification.

1.3. Conservation and restoration measures for circalittoral/deep coral communities

The terms “conservation” and “restoration” are frequently associated with actions that aim to maintain/recover the original state of habitats (i.e. protect) or an equivalent habitat state that has been lost or destroyed, respectively (Rinkevich, 2005). Conservation is defined as any preservation and protection actions (e.g., vulnerable status, creation of marine protected areas-MPAs and temporary fisheries closure) that mitigate impacts with minimal manipulation (Rinkevich, 2008). On the other hand, ecological restoration is defined as the procedure of actively assisting the recovery of a habitat in order to revert the habitat sustainability, health and integrity to a previous state (Rinkevich, 2005).

Therefore, the historical condition of the habitat is a good source of information for restoration actions, although this state may be difficult or near impossible to achieve as habitats face new threats and different conditions (SER and Policy Working Group, 2004).

In the last several decades, the knowledge about coral gardens and CWCs, and the threats they face have increased gradually. As result, several measures of conservation have been implemented. For instance, these habitats have been listed as vulnerable marine ecosystems (VMEs) since 2004 by the United Nations General Assembly (UNGA, 2004; FAO, 2009). VMEs are defined based on multiple criteria, namely: 1) uniqueness and rarity- habitats that contain endemic, threatened or endangered species or constitute essential fish habitats (EFH); 2) structural complexity- complex structures created by numerous concentrations of biotic and abiotic features; 3) functional significance- areas with importance for life stages of important fish stocks or endangered species; and 4) life-history traits- habitats that are composed of species characterized by slow growth rates, late maturity, low recruitment and long-lived that makes them fragile and with limited probability of recovery (FAO, 2009; Auster et al., 2011; Aguilar et al., 2017; Davies et al., 2017). The most vulnerable ecosystems are those that are frequently and easily disrupted, and their recovery is extremely slow or impossible (given the ongoing pressures), as is the case of coral gardens and CWC communities (Fuller, 2008; Miller et al., 2009; Ardron et al., 2014; Davies et al., 2017). Following the various UNGA resolutions, local governments and Regional Fisheries Management Organizations (RFMO) adopted measures to reduce impacts on these habitats (UNGA, 2019). Some of these measures included the implementation of MPAs, temporary and permanent closure of fisheries, and fisheries management rules that reduce significant adverse impacts (SAIs) (Aguilar et al., 2017).

With regard to MPAs, only a small percentage of our seas is protected (3.7%; Morgan et al., 2018). Deep-sea MPAs, in particular, are still scarce because of the difficulties of accessing deep-sea habitats and the costs to implement such measures, which are much higher compared to shallow-water MPAs (Huvenne et al., 2016). Deep-sea MPAs have, however, proven to mitigate fishing pressures on CWCs (Huvenne et al., 2016). For instance, Huvenne et al. (2016) reported that after 8 years of the MPA designation and bottom trawling fisheries closure in the Darwin Mounds (west of Scotland), the protection of this ecosystem was successful as fishing impacts were avoided (i.e. the proportions of CWCs were the same as 8 years before). The authors also recognized that areas with high fishing impacts pre-closure did not show any signs of coral recolonization and showed little regrowth of the damaged colonies, suggesting that CWCs have low resilience and slow recovery time. Additionally, temporary closures to fisheries have been suggested as an effective measure to mitigate fishing impacts on coral gardens and CWCs (Wright et al., 2015), with model prediction indicating a reduction of coral bycatch by 80% after 9 months of the closure in some cases (Grantham et al. 2008). This measure is also be considered more flexible and easily accepted by stakeholders (Grantham et al., 2008). One example of temporary closure for bottom-contact fisheries is the case of the seamount Condor de Terra in Azores, which was closed in 2010 with the purpose of becoming a scientific observatory, as the seamount hosts a rich assemblages of CWCs and commercial fish species (Morato et al., 2010).

Ecological restoration of coral habitats has been based on multiple approaches, although most of them focused on tropical coral reefs. Historically, coral restoration consisted of using the technique of assisted colonization (i.e. direct transplantation), where small fragments of corals were harvested from donor populations in order to be transplanted to a damaged area (Plucer-Rosario and Randall, 1987; Thornton et al., 2000). Transplant methods included explanting or attaching fragments or whole colonies with epoxy, cement and even cable ties to the degraded area (Jaap, 2000). This method has the advantage of being low-tech and low-cost, which can ease the collaboration with local communities to protect reef habitats (Young et al., 2012). Another advantage of the method is that it allows to salvage corals from sites with, for example, construction activities planned that would disturb or destroy the reefs (Boström-Einarsson et al., 2020). However, the direct transplantation of corals has the disadvantages of potentially causing negative impacts on the donor populations, as well as being time-consuming methodology as it requires the corals to be transplanted one by one (Boström-Einarsson et al., 2020).

More recently, new methods have been developed based on the terrestrial concepts such as silviculture, which gave rise to the method most frequently used, which is based on the gardening concept (Rinkevich, 2005, 2015). This technique comprise of two steps, the first of which consists of stocking coral recruits *in situ* or *ex situ* (i.e. nubbins, fragments, and small colonies of coral) in nurseries (i.e. aquaculture of marine organism) in order to protect them from damage until they reach the adequate size (i.e. when the survival is higher) for transplantation (Rinkevich, 2005; Boström-Einarsson et al., 2020). The second step consists of transplanting the corals to the damaged area using many of the same attachment methodologies described above (Rinkevich, 2005). The gardening method is a promising method that has the advantage of producing many more fragments of the corals maintained in the nursery, thus increasing the biomass available to outplant instead of further damaging donor population (Boström-Einarsson et al., 2020).

Even though this method is employed worldwide, it still requires improvement, particularly with regard to scaling up the transplantation step to large areas (Rinkevich, 2008), which remains extremely costly. The costs associated with maintaining nurseries is also a critical argument (Edwards et al., 2007).

The gardening method gave rise to other techniques such as micro-fragmentation and larval enhancement (Boström-Einarsson et al., 2020). The micro-fragmentation method was developed to fragment encrusting and massive corals, which normally are less susceptible to fragmentation, as these species have a thicker skeleton. This method consists in cutting small fragments of ~1cm^2 using a diamond blade saw and attaching the fragments to tiles (Forsman et al., 2015). This method allows for certain species to increase the biomass available for transplants by producing multiple micro-fragments from one coral, which grow relatively fast to the adequate size needed to be transplanted to the damage areas. However, this method as the disadvantage of all transplants having the same genotype. Larval enhancement consists in settling larvae onto natural or artificial substrates. This method uses harvested gametes and generates embryos ex-situ or on the reef that are thereafter settled in the natural reef or artificial structures. This method has the advantages of increasing the genetic diversity by obtaining larvae from different sources and the ability to produce corals from the first stages of their life, using embryos that generally have high mortality rates for growth and transplantation by maintaining them in nursery conditions (Chamberland et al., 2017; Cruz and Harrison, 2017). The problem related to this method is that larvae and newly settled recruits are extremely sensitive to adverse environmental conditions, which means that early life stages have higher mortality rates that decrease with size and age. For this reason, larval settlement and rearing face an important bottleneck (Edwards et al., 2015). Another method to obtain coral biomass for transplantation is using fragments of "opportunity" such as storm-generated coral fragments (Garrison and Ward, 2008) or fisheries' coral bycatch (Montseny et al., 2019, 2020). This methodology has the advantage that with minimal effort and cost, large quantities of corals can be collected without causing further damage to donor populations, using coral biomass that would otherwise be lost.

A substantially lower number of studies have been conducted on temperate and cold-water coral restoration compared to tropical counterparts (Rinkevich, 2005; Young et al., 2012). This is primarily due to the difficulties of accessing intermediate depths and deep-sea corals, demanding the use of underwater technology with high economic costs (Montseny et al., 2019). Nevertheless, restoration efforts on coral gardens and CWCs have provided encouraging results (Linares et al., 2008; Montseny et al., 2019, 2020), although there is space for improvement. For instance, Linares et al. (2008) reported a 40% attachment failure for colonies of the Mediterranean red gorgonian (*Paramuricea clavata*), despite a 80% survival of the colonies that were successfully attached, which is higher than most studies in tropical environments (66%; Boström-Einarsson et al., 2020). More recently, Montseny et al. (2019) transplanted corals obtained as fishing bycatch onto stainless steel structures that had a grid with fiberglass conical supports which were deployed at 85m depth. This method proved to be successful, as

98.8% of the colonies were still in place after 6 months. The disadvantage of this method is that it is costly, and it demands underwater technology in order to monitor the transplanted corals. This study also demonstrates that using coral bycatch for restoration purposes is feasible.

1.4. Objectives of the thesis

The overall aims of this study are to provide A) baseline information on the impact of bottom-set gillnets used by artisanal fisheries on deep coral habitats in Sagres (Portugal) and B) to assess the utility of the incidental coral catches generated by these fisheries in actions of habitat restoration. Specific objectives of the project are to: 1) estimate the coral bycatch frequency and species affected by artisanal fisheries using gillnets; 2) improve the knowledge of the distribution of coral species and biodiversity in the study area; 3) identify potential areas of high coral biodiversity and bycatch pressure that may warrant protection measures; 4) develop a time-effective and low-cost restoration pipeline for both deep- and shallow-water populations that uses coral bycatch; and 5) test the effect of coral transplant density and species composition (monospecific vs. multi-specific) on the survival and growth of transplanted corals.

1.5. References

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2. Chapter 2: High Coral Bycatch in Bottom-set Gillnet Coastal Fisheries Reveals Rich Coral Habitats in Southern Portugal[1]

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Keywords: benthic invertebrate bycatch, bottom fisheries impact, cold-water corals, coral gardens, vulnerable marine ecosystems, biodiversity conservation, marine animal forests.

2.1. Abstract

Bottom-contact fisheries are unquestionably one of the main threats to the ecological integrity and functioning of deep-sea and circalittoral ecosystems, notably cold-water corals (CWC) and coral gardens. Lessons from the destructive impact of bottom trawling highlight the urgent need to understand how fisheries affect these vulnerable marine ecosystems. At the same time, the impact of other fishing gear and Small-Scale Fisheries (SSF) remains sparsely known despite anecdotal evidence suggesting their impact may be significant. This study aims to provide baseline information on coral bycatch by bottom-set gillnets used by artisanal fisheries in Sagres (Algarve, southwestern Portugal), thereby contributing to understand the impact of the activity but also the diversity and abundance of corals in this region. Coral bycatch frequency and species composition were quantified over two fishing seasons (summer-autumn and spring) for 42 days. The relationship with fishing effort was characterized according to métiers (n = 6), and corals were identified to the maximum possible taxonomical level. The results showed that 85% of the gillnet deployments caught corals. The maximum number of coral specimens per net was observed in a deployment targeting Lophius budegassa (n = 144). In total, 4,326 coral fragments and colonies of 23 different species were captured (fishing depth range of 57-510 m, mean 139±8m). The most affected species were Eunicella verrucosa (32%), Paramuricea grayi (29%), Dendrophyllia cornigera (12%) and Dendrophyllia ramea (6%). The variables found to

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significantly influence the amount of corals caught were the target species, net length, depth and mesh size. The 22 species of corals caught as bycatch belong to Orders Alcyonacea (80%), Scleractinia (18%), Zoantharia (1%) and Antipatharia (1%), corresponding to around 13% of the coral species known for the Portuguese mainland coast. These results show that the impact of artisanal fisheries on circalittoral coral gardens and CWC is potentially greater than previously appreciated, which underscores the need for new conservation measures and alternative fishing practices. Measures such as closure of fishing areas (definitive or temporary), frequent monitoring onboard of fishing vessels or the development of encounter protocols in national waters is a good course of action. This study highlights the rich coral gardens and CWCs of Sagres and how artisanal fisheries can pose significant threat to corals habitats in certain areas.

2.2. Introduction

The impact of human activities on marine life is a global crisis that has left virtually no area of the ocean unaffected, with benthic habitats like coral-dominated ecosystems among those most strongly impacted (Halpern et al., 2008). There are many stressors threatening the ecological integrity and functioning of coral ecosystems, including pollution (Ragnarsson et al., 2017; Consoli et al., 2020), overfishing (Hughes, 1994; Jackson, 2001), oil and gas extraction (Glover and Smith, 2003; Purser and Thomsen, 2012; Cordes et al., 2016), ocean acidification (Bramanti et al., 2013; Movilla et al., 2014; Albright et al., 2018) and global warming (Hughes et al., 2017, 2018). However, the direct impact of fisheries using bottom-contact gear remains the primary cause of habitat destruction and biomass removal (Hall-Spencer et al., 2002; Glover and Smith, 2003; Hourigan, 2009). This is of special concern for circalittoral and deep coral communities (i.e. those below 50 m depth, henceforth referred to as “deep”) such as coral gardens and cold-water corals (CWC), which have life-history traits (e.g., slow growth rates and late age at maturity) that make recovery from physical damage especially difficult, if even possible.

Coral gardens and CWC reefs are key ecosystems in the marine realm. The three-dimensional complex species that build these habitats, known as engineers, create high structural complexity that provides shelter, feeding and nursery grounds for many organisms, including many species of commercial value (Buhl-Mortensen et al., 2010; Ashford et al., 2019), supporting levels of biodiversity comparable to those found in tropical coral reefs and terrestrial forests (Rossi, 2013; Rossi et al., 2017). These habitats include coral species from several taxonomical groups (Orders Scleractinia, Zoantharia, Antipatharia, Corallimorpharia, Alcyonacea and Pennatulacea), representing nearly 65% of all known coral species (Roberts, 2006; Cairns, 2007). In 2004, the United Nations General Assembly (UNGA) drew attention to the susceptibility of deep coral communities and other habitats to the impacts of deep-sea fisheries, designating them as vulnerable marine ecosystems (VMEs) that required urgent conservation and protection actions (UNGA, 2004; Fuller, 2008). As a result of several resolutions of the UNGA, Regional Fisheries Management Organizations (RFMO) and local governments adopted several measures to protect VMEs (UNGA, 2019), including the reduction of the frequency of significant adverse impacts by bottom-contact fisheries like trawling (e.g., encounter or "move-on" rule triggered by a bycatch threshold) (Parker et al., 2009; Aguilar et al., 2017; Davies et al., 2017) and the creation of Marine Protected Areas (MPA) in areas where VMEs occur (Armstrong and Hove, 2008; Huvenne et al., 2016).

Among the various types of gear used by deep-sea fisheries, bottom trawling is notorious for being the most destructive and has received increasing pressure for legislation banning its use worldwide. Indeed, in 2018 the European Parliament instituted a ban on trawling below 800 m depth in European waters (Clark et al., 2016; EU Council, 2016; Victorero et al., 2018). Other fishing techniques used in the deep-sea, such as longline, have been shown to have a much smaller impact on coral communities (Pham et al., 2015). However, some studies suggest that the extensive use and often considerable long configuration of this gear may also pose a threat to complex deep-sea benthic habitats, including coral communities. For instance, Mytilineou et al. (2014) have found that during experimental longline fishing in the Ionian Sea, 72% of the longline sets used in hake and blackspot seabream fisheries captured corals. In the Azores, Sampaio et al., (2012) reported that 15.2% (n = 45 out of 297) of the fishing trips of the longline fleet surveyed landed corals, with at least 205 specimens caught.

Although there are several studies on the impact of fishing gear on deep-sea ecosystems, most studies focused on large scale industrial fisheries, which represent a very small fraction of the fishing work force (Shester and Micheli, 2011). Worldwide, artisanal fisheries employ over 20 million workers, both directly and indirectly through processing, marketing and distributing (McGoodwin, 2001; Teh and Sumaila, 2013). In the EU, artisanal fisheries represent 84% of the fishing fleet and employ around 100,000 workers (Garcia et al., 2008; Guyader et al., 2013; Lloret et al., 2018). Yet, studies documenting the impact of artisanal fisheries on deep coral communities and other benthic ecosystems are still scarce when compared to large-scale fisheries (Guyader et al., 2013; Lloret et al., 2018). Generally, artisanal fisheries are considered to have a lower impact on benthic communities. The actual effect, however, may be largely obscured and much greater than assumed due to the lack of reliable data for this sector and because some of the gears used are not selective (Lloret et al., 2018). For example, Shester and Micheli (2011) demonstrated experimentally that for bottom-set gillnets deployed over rocky reefs, ca. 77% of the interactions between nets and corals caused the removal or partial damage of the colonies. While that study focused on shallow-water communities, the results suggest that bottom-set gillnets represent a critical conservation concern that extends to deep coral communities as artisanal fisheries also operate over deep habitats.

This study investigates the impact of bottom-set gillnets used by artisanal fisheries on deep coral communities in Sagres, Algarve, southern Portugal. The aims of the study are to 1) better understand the biodiversity of corals in the area; 2) provide a baseline quantitative assessment of coral bycatch frequency and of the species affected by different types of bottom-set gillnets used in local fisheries; and 3) identify coral bycatch and diversity "hotspots" that could constitute priority management areas.

2.3. Materials and methods

2.3.1. Study Area and Data Collection

To assess the impact of bottom-set gillnets on circalittoral and deep coral habitats, the coral bycatch of a fishing vessel operating in Sagres, southern Portugal (Figure 2.1), was documented over 42 workdays during the summer-autumn of 2019 (September 1st to October 16st) and spring of 2020 (May 11th to June 5th). Coastal fisheries in Portugal are predominantly small-scale operations (~ 91% of the fleet has <12m hull length; DGRM, 2019) that can be categorized into different métiers, i.e. a group of fishing activities that targets a specific assemblage of species, using one kind of fishing gear, in a particular period of the year within the same area (EC, 2008; Deporte et al., 2012). In Sagres, the fishing fleet is mostly composed of small vessels (<12m hull length) that operate locally and use multiple artisanal gear such as traps, pots, bottom longlines, trotlines, jigs, trammel nets and small bottom-set gillnets. A few larger coastal multigear vessels (12-15m hull length) use trammel nets and bottom-set gillnets to fish demersal and benthic species. We documented coral bycatch in a vessel belonging to the latter group, which mainly operates using bottom-set gillnets with different mesh sizes to fish several target species year-round (Table 2.1). The vessel mainly targets Black-bellied angler (*Lophius budegassa*) and John dory (*Zeus faber*). Several secondary species, including European spiny lobster (*Palinurus elephas*), pink spiny lobster (*Palinurus mauritanicus*), Atlantic wreckfish (*Polyprion americanus*) and blonde ray (*Raja brachyura*), are also targeted for their high commercial value. In this study, the métiers were defined according to the hierarchy presented in decision 2008/949/EC from the European Commission (EC, 2008), all of which are part of the category "set of gillnets", differing at the levels of target assemblage (i.e. target species) and mesh size used (Table 2.1). For target species in which more than one mesh size was used (i.e. European spiny lobster and pink spiny lobster), we defined one métier per target species as few deployments used a smaller mesh size (1 out of 2 in *P. mauritanicus* and 3 out of 9 in *P. elephas*). To simplify the results, our treatments were divided according to métier and the periods over which coral bycatch was monitored (i.e. "seasons"). These were chosen as a function of regulatory fishery closures for the target species and weather conditions, as some of the rocky-bottom-dwelling targeted species are not fished during winter to prevent damage or loss of the nets (Table 2.1). Coral bycatch and the amount of target species caught were quantified individually for each set of gillnets deployed. The geographic positions and depth at the start and endpoints of the nets, as well as the soaking time (in days) were also recorded.

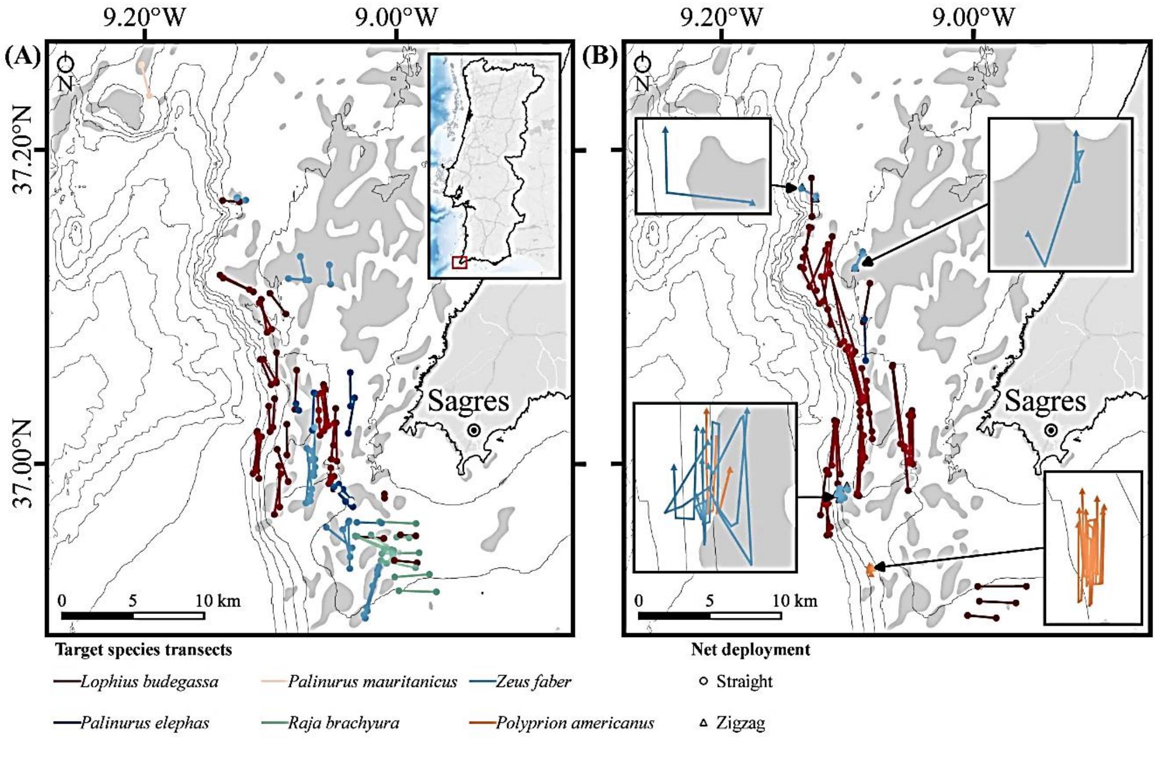

Figure 2.1. Map of the study area off the coast of Sagres (southern Portugal) showing the transects of bottom-set gillnets used to document coral bycatch in circalittoral and deep-sea habitats. (A) Summer-autumn sampling season (September 1st to October 31st) with inset showing the location of the study area in Portugal; (B) Spring sampling season (May 11th- to June 5th) with insets zooming on nets deployed following a zigzag course. Sets of gillnets are shown by target species (colours). Bathymetric isobaths are as follows: 50m, 100-500m (increments of 100m) and > 500m (increment of 200m).

Table 2.1. Features of the target species métier (average ± standard error) of the bottom-set gillnets deployed during the documentation of coral bycatch in Sagres (southern Portugal) during the two seasons studied.

Season	Target species	Closure of fisheries (months)	Net length (km)	Depth (m)	Soaking time (d)	Mesh size (mm)	No of nets deployed
Summer -autumn	*Lophius budegassa*	01-02 (>3%)	2.07±0.11	148±15	4.6±0.3	240	38
	Palinurus elephas	10-12	1.70±0.26	83±4	8.4±1.3	110/200	8
	Palinurus mauritanicus	10-12	1.75±0.51	225±67	10.0±4.0	200/240	2
	Raja brachyura	05-06 (>5%)	2.11±0.23	97±2	2.8±0.3	240	10
	Zeus faber	NA	1.94±0.24	101±5	1.0±0.0	200	20
Spring	*Lophius budegassa*	01-02 (>3%)	3.25±0.13	157±14	4.1±0.3	240	47
	Palinurus elephas	10-12	2.91±0.00	96±0	7.0±0.0	200	1
	Polyprion americanus	NA	3.24±0.07	135±6	0.9±0.4	200	7
	Zeus faber	NA	3.12±0.63	124±14	1.0±0.0	200	6

The average depth of each net set was calculated using the start and endpoint depths for deployments that followed a straight line, and the depth of each vertex point for deployments following a zigzag course (see Figure 2.1). Collected corals were preserved and identified to the maximum taxonomical level using available guides (e.g., Carpine and Grasshoff, 1975; Grasshoff, 1992; Cairns and Kitahara, 2012) and expert opinion. For the purpose of this study, the coral fauna assessed included members of the subclasses Octocorallia and Hexacorallia (orders Antipatharia, Zoantharia and Scleractinia). For specimens in which species could not be identified based on visual inspection of colony alone, the morphology of skeletal sclerites (octocorals) and corallites (scleractinians) were analysed. The maximum height and width of each specimen (orientation inferred from the presence of a holdfast or from the branching pattern characteristic to each species; Figure S2.1-supplementary material) were measured in the lab. The specimens were classified as fragments or whole colony depending on the presence of holdfast (e.g., Octocorallia) or presence of substrate attached to the colony (Scleractinia). Additionally, the dry weight of *Dendrophyllia* spp. were also measured in order to estimate bycatch biomass.

2.3.2. Data Analysis

In order to understand the relationship between target species landings and coral bycatch, the fishing and bycatch data were standardized as catch per unit of effort (CPUE). CPUE represents the number of specimens caught (N of fish or lobster *vs.* coral) as a function of the product of the soaking time (T in days) per 100m of net (L) (Equation 2.1). The analysis of the spatial distribution of the CPUEs did not include 4 of the 139 nets documented for which only one GPS coordinate was available, or the soaking time was not determined.

The effect of different métiers on bycatch was tested with a general addictive model (GAM) using a Poisson distribution and a log-link function. We modelled the number of corals caught per net (response variable) as a function of target species, mesh size, depth, net length and soaking time (fixed factors). Model selection was based on generalized cross-validation criterion (GCV) and adjusted R^2. Because overdispersion was detected, the standard errors were corrected using a quasi-GAM model with the variance given by 2.06 x 1.04, where 2.06 represents the mean and 1.04 the dispersion parameter (ϕ). Backwards selection and *F*-test were used to determine statistical significance of the variables and interaction terms. Model validation was performed through visual inspection of the residuals (quantile-quantile plot, histogram of residuals, residuals *vs*. predictors plot, and observed *vs*. fitted values plot) to detect any violation of the assumptions (Figure S2.2-supplementary material). The analyses were performed using the MGCV package (Wood, 2017) in R version 3.6.2 (R Core Team, 2019).

The resemblance of the coral communities (species composition and abundance) caught by the different métiers was evaluated using principal coordinates analysis (PCoA). Because the GAM analysis did not show any relationship between coral bycatch and sampling season, the data was pooled. Coral species data for each net was used to calculate a dissimilarity matrix using Hellinger distance (Kindt and Coe, 2005). The resulting dissimilarity matrix was then used as input for the PCoA. Important contributions to the overall ordination along the first two PCoA axes were evaluated using Pearson correlation between the descriptors (coral species) and PCoA1 and PCoA2. To further analyse the results of the PCoA, the influence of depth on differences in species composition between métiers was evaluated with a distance-based redundancy analysis (db-RDA). In this technique, the ordination is constrained by the environmental variable. The species matrix was transformed using the Hellinger transformation (Kindt and Coe, 2005), which together with the environmental matrix (i.e. depth matrix) was used as input for the db-RDA. The significance of the constraint imposed by depth was tested with an ANOVA like permutation test (9999 permutations).

$$\boldsymbol{CPUE = \frac{N}{L \times T}}$$

Equation 2.1. Fishing effort calculated as catch per unit of effort (CPUE) for each bottom-set gillnet in Sagres (Portugal) during the two sampling seasons documented. CPUE represents the number of specimens (fish/lobster or coral) caught (N) as a function of the product of the soaking time (T in days) per 100m of net (L).

Furthermore, scaling method 2 was used to represent db-RDA with the position of the species vectors representing the correlation between species. The PCoA and db-RDA analyses were performed using the BiodiversityR package (Kindt and Coe, 2005) in R version 3.6.2.

2.4. Results

Coral bycatch was documented for a total of 139 net deployments: 78 in the summer-autumn and 61 in the spring sampling seasons. Coral specimens were caught in 118 of the nets (85%), covering a total length of 300.32km. A total of 4,326 specimens were collected (45% of which entire colonies) over the 42-day survey period: 2,404 specimens over 22 days in the summer-autumn season and 1,922 specimens over 20 days in the spring season. On average (±SE), we recovered 31.1 (±2.7) corals from each net, with a maximum of 144 corals caught in a single net (target species: Black-bellied angler). The maximum number of coral species found in a single net was 10 species, with an average (±SE) of 4.31 (±0.2) coral species per net.

2.4.1. Coral bycatch biodiversity and bathymetric distribution

The diversity of coral species captured as bycatch in the study area was high. A total of 22 different taxa were identified: 17 from the Order Alcyonacea (*Acanthogorgia armata*, *A. hirsuta*, *Callogorgia verticillata*, *Corallium rubrum*, *Ellisella paraplexauroides*, *Eunicella verrucosa*, *E. labiata*, *E. gazella*, *Isidella elongata*, *Leptogorgia sarmentosa*, *Paramuricea clavata*, *P. grayi*, *Spinimuricea atlantica*, *Viminella flagellum*, (Octocorallia) sp.1, (Octocorallia) sp.2 and (Octocorallia) sp.3), 3 from the Order Scleractinia (*Dendrophyllia cornigera*, *D. ramea* and *Pourtalosmilia anthophyllites*, 1 from the Order Zoantharia (*Savalia savaglia*) and 1 from the Order Antipatharia (*Antipathella subpinnata*). The gorgonians *E. verrucosa* (1380 specimens), *P. grayi* (1271 specimens) and *C. verticillata* (247), and the scleractinians *D. cornigera* (522 specimens) and *D. ramea* (249 specimens) were the most frequent species, making up 85% of the total amount of coral bycatch (Figure 2.2). It is worth noting that most *C. verticillata* specimens were caught in the spring sampling season in 12 net sets targeting *Z. faber* (4 nets) and *P. americanus* (8 nets) deployed at 99-170m depth. Overall, the diversity found in both sampling seasons was similar in terms of species composition and abundance. Exceptions include the species *A. armata*. *I. elongata*, (Octocorallia) sp.3, *V. flagellum* and *Pourtalosmilia anthophyllites*, which were only caught during the spring sampling season, and species (Octocorallia) sp.1 and (Octocorallia) sp.2 during the summer-autumn.

The size of the specimens collected varied considerably reflecting species-specific differences in growth form and size (Table 2.2). For instance, colonies of *E. verrucosa* had an average height and width of 22.9cm (±0.3) and 15.5cm (±0.2), respectively (Figure S2.3A-supplementary material), whereas *P. grayi* colonies were on average 17.6cm (±0.3) long and 11.9cm (±0.2) wide (Figure S2.3B-supplementary material). *Callogorgia verticillata* was the species with the largest fan area, with an average width of 32.6cm (±5.5) for whole colonies and 23.2cm (±0.8) for fragments (Table 2.2). The giant gorgonian *E. paraplexauroides* with candelabrum-shaped colonies was the tallest coral species collected: average height of 70.4cm (±5.5) for whole colonies and 55.7cm (±2.0) for fragments. From the three scleractinian species caught as bycatch, *D. ramea* was the largest species with an average colony weight of 331.4g (±95.1) and 38.1 (±8.9) polyps per colony, and average fragment weight of 87.1g (±18.7) with 20.1 (±1.8) polyps.

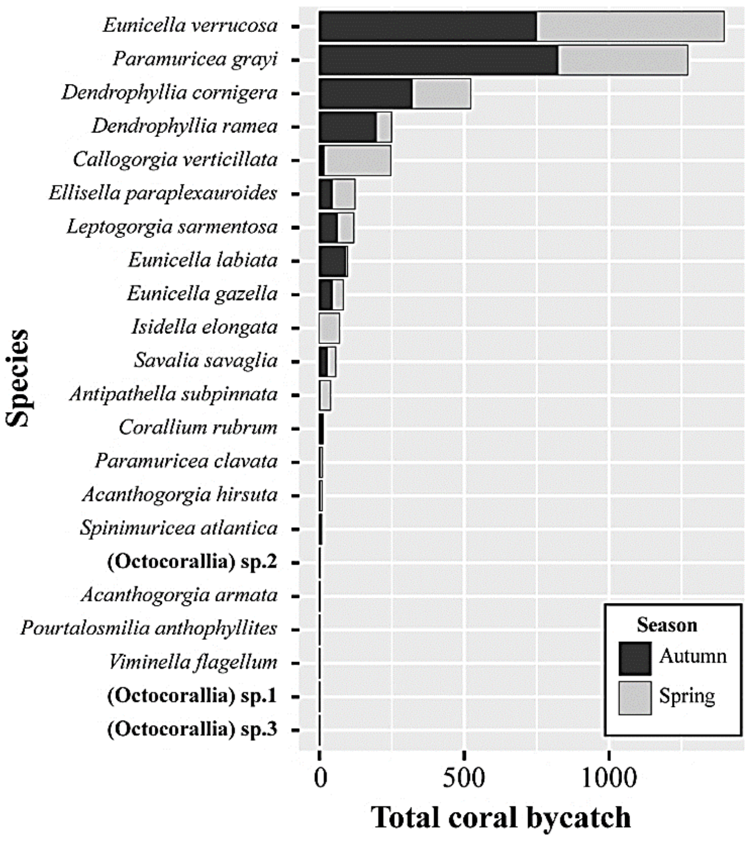

Figure 2.2. Species composition and total amount of the corals caught as bycatch in bottom-set gillnets during the two sampling seasons in Sagres (southern Portugal). In total, 4326 specimens (branch fragments or entire colonies) were collected from 118 gillnet deployments.

Dendrophyllia cornigera had an average weight of 72.4g (±3.7) with 7.2 (±0.4) polyps for whole colonies, and 59.4g (±3.9) with 5.6 (±0.2) polyps for fragments.

The majority of specimens and species were caught at locations shallower than 120m depth (90% and 68%, respectively), where most fishing effort occurred (Figures 2.3 and 2.4). Notable exceptions include the deep-water species *Isidella elongata* (296-510m), *Antipathella subpinnata* (85-510m) and *C. verticillata* (99-293m), which were caught at average depths of 417m, 169m and 141m, respectively. The octocorals *P. grayi* (85-97m), *L. sarmentosa* (57-124m) and *Corallium rubrum* (73-134m) were the species collected at shallower areas, with average depths of 89m, 92m and 97m, respectively (Figure 2.3). Interestingly, several specimens of *E. labiata* and *E. gazella* were caught deeper than the bathymetric ranges reported in the literature (Figure 2.3).

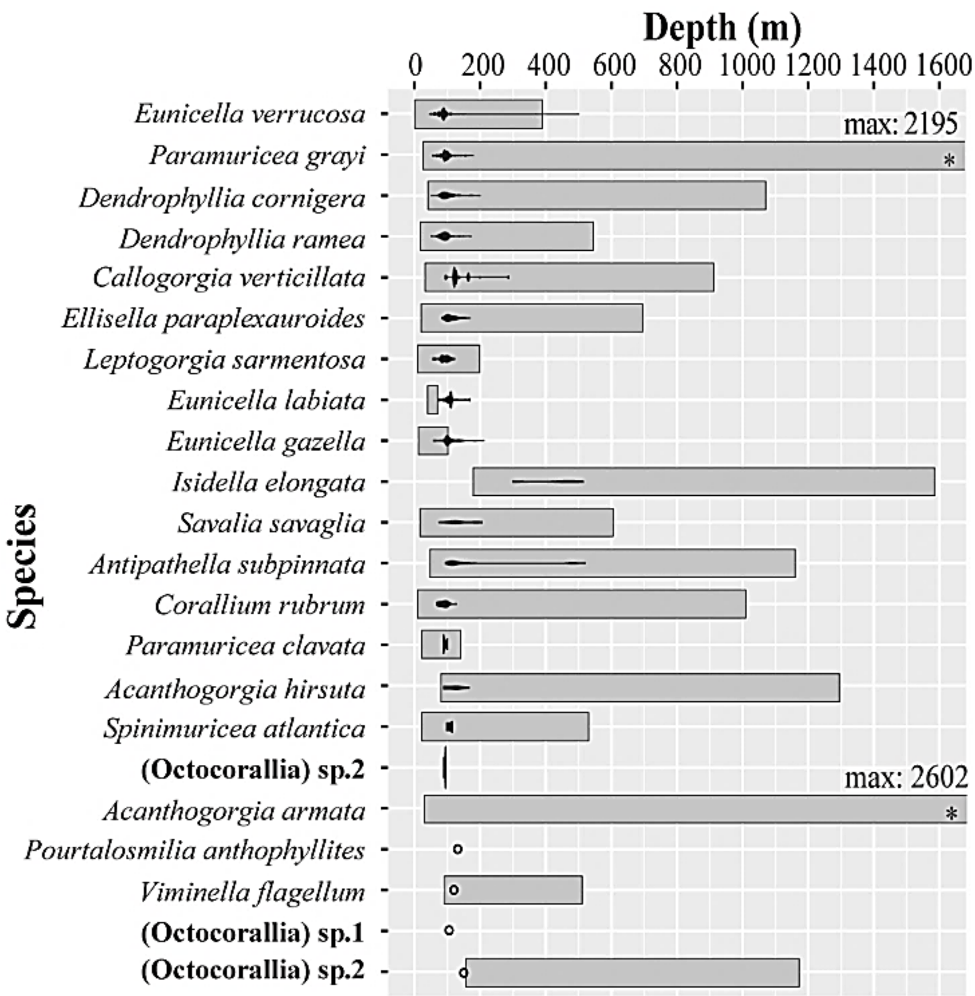

Figure 2.3. Collection depth ranges of the coral species caught as coral bycatch by bottom-set gillnets in Sages (southern Portugal) during the two seasons studied. The bathymetric distribution recorded in the literature for each species is shown as grey band. The abundance of each species at each depth is also shown with the width of each plot.

Table 2.2. Species composition and description of the variability between colonies and fragments of the number of specimens (No) and sizes (height and width) of all specimens collected as bycatch in bottom-set gillnets during the two sampling seasons in Sagres (southern Portugal).

Species	Colony			Fragment		
	No	Height (cm) average (min-max)	Width (cm) average (min-max)	No	Height (cm) average (min-max)	Width (cm) average (min-max)
Eunicella verrucosa	746	22.9 (6.3-41.5)	15.5 (2.5-41.5)	634	15.3 (3.5-38.9)	11.9 (2.0-32.7)
Paramuricea grayi	667	17.6 (3.0-40.5)	11.6 (2.2-36.5)	604	12.3 (3.2-42.4)	8.2 (1.7-10.2)
Dendrophyllia cornigera	241	8.4 (4.2-20.0)	8.6 (2.2-90.5)	281	7.8 (2.7-19.7)	7.5 (1.0-23.0)
Dendrophyllia ramea	36	14.7 (5.0-38.8)	11.9 (2.9-39.5)	213	10.8 (3.2-88.0)	8.2 (1.3-32.5)
Callogorgia verticillata	8	34.3 (20.5-49.8)	32.6 (8.8-57.1)	239	29.4 (8.7-63.4)	23.2 (2.8-109.3)
Ellisella paraplexauroides	17	70.4 (35.0-107.7)	15.1 (6.6-33.0)	106	55.7 (15.9-104.1)	11.0 (1.4-50.0)
Leptogorgia sarmentosa	32	28.9 (6.2-64.3)	26.7 (5.0-61.9)	87	23.6 (9.2-53.7)	19.8 (5.7-62.1)
Eunicella labiata	56	23.7 (13.1-41.5)	15.7 (4.2-33.5)	59	14.9 (6.0-34.8)	11.3 (3.0-26.0)
Eunicella gazella	39	14.1 (7.4-25.3)	11.7 (4.8-20.7)	43	13.4 (6.4-30.5)	10.6 (3.5-19.7)
Isidella elongata	49	13.2 (4.5-22.4)	8.3 (3.0-23.0)	21	11.1 (7.8-16.8)	6.9 (3.1-10.4)
Savalia savaglia	4	39.0 (26.2-68.0)	19.5 (12.9-31.3	53	22.5 (3.9-80.4)	14.2 (2.3-48.0)
Antipathella subpinnata	19	35.1 (16.0-67.5)	24.8 (8.0-44.3)	20	22.0 (8.7-57.9)	19.3 (5.8-49.3)
Corallium rubrum	1	5.0	7.3	12	6.8 (4.8-10.2)	4.2 (1.5-8.5)
Paramuricea clavata	4	12.6 (9.1-18.3)	9.1 (1.8-13.0)	7	11.0 (5.7-17.2)	8.2 (5.8-12.3)
Acanthogorgia hirsuta	7	18.0 (8.3-28.0)	18.2 (10.4-21.7)	3	9.1 (7.7-11.2)	8.0 (5.7-11.0)
Spinimuricea atlantica	6	27.8 (21.7-37.5)		2	20.25 (15.5-25.0)	
(Octocorallia) sp. 2	2	21.5 (20.7-22.2)	6.7 (2.1-11.3)	1	23.6	3.5
Acanthogorgia armata	1	17.4	17.2	1	11.9	12.2
Pourtalosmilia anthophyllites	1	4.0	4.0	0		
Viminella flagellum	0			1	72.7	13.0
(Octocorallia) sp. 1	0			1	26.0	
(Octocorallia) sp. 3	1	8.7	4.3	0		

2.4.2. Spatial patterns of fishing effort and bycatch

Consistent with the expectations, total coral bycatch was generally higher when the nets were deployed on or nearby areas where rocky substrate is known to occur (Figure 2.4). When examining the CPUEs for the pooled dataset (i.e. irrespective of coral or target species), the mismatch between the amounts of coral and target species caught is evident, particularly in the summer-autumn for which the nets captured substantially more coral than fish or lobster (Figure 2.4A). For instance, 6 of the nets deployed in the summer-autumn sampling season had a CPUE for coral specimens higher than 3.40 (n/day.100m; Figure 2.4A), which had an average net length of 1.99km thus corresponding to more than 60 corals per net. In contrast, for the spring survey season there is a better correspondence between the amount of coral and fish caught, with areas where coral bycatch was high, generally matching those with high fish or lobster catches (Figure 2.4B).

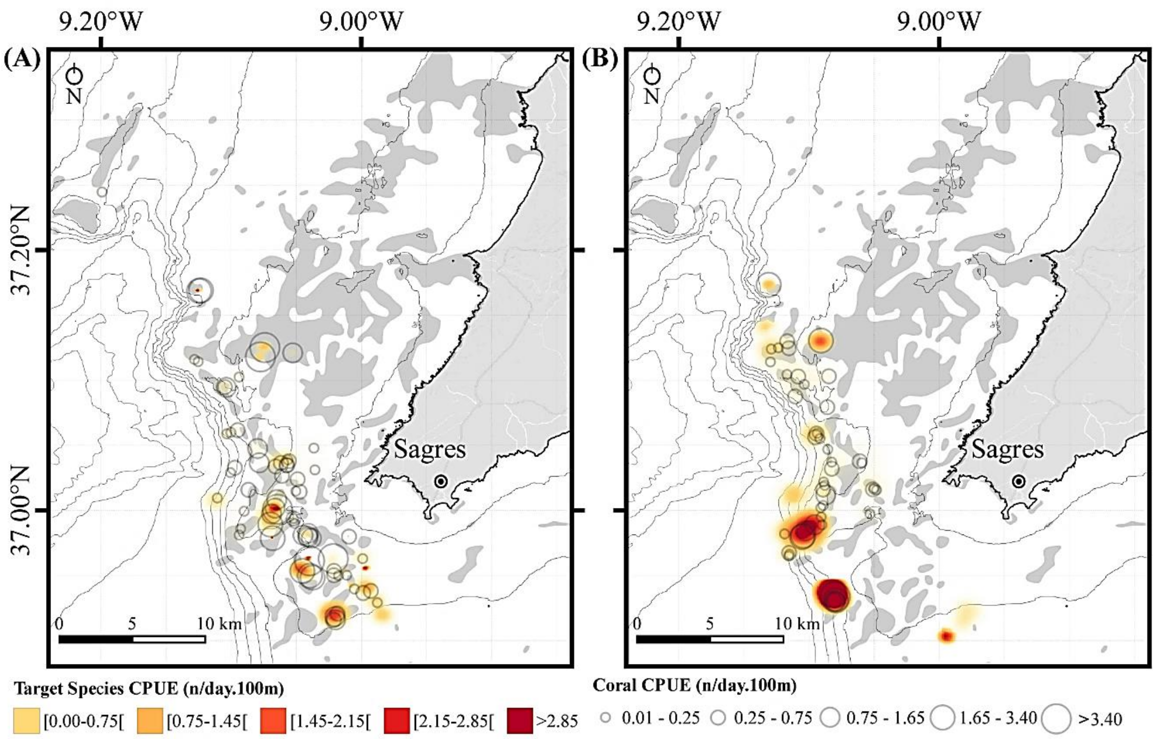

Figure 2.4. Spatial distribution of the total fishing effort for target species and coral bycatch in bottom-set gillnets off the coast of Sagres (southern Portugal). Fishing effort was calculated as the catch per unit effort (CPUE) and represents the number of specimens (fish/lobster or coral) as a function of the product of the net soaking time (days) per 100m of net. (A) Summer-autumn sampling season (period); (B) Spring sampling season (period). CPUEs for the target species are displayed as heatmaps generated using triweight kernel density and corals displayed as bubbles. Bathymetric isobaths are as follows: 50m, 100-500m (increments of 100m) and > 500m (increment of 200m). Rocky substrate is represented as grey shadow.

Only 3 of the 61 nets deployed in the spring sampling season had a coral CPUE higher than 3.40 (n/day.100m; Figure 2.4B).

The preferred Poisson GAM model (Table S2.1-supplementary material) for the amount of coral caught as bycatch, supported by both the GCV and adjusted R^2, included 4 significant factors: target species, depth, net length and mesh size without any interaction term. The total deviance explained by the model was 40.3%. Overall, all variables have a strong effect on the amount of incidental coral catches (GCV=21.53; R^2=0.379): target species (df=5, F=6.049, P<.01), mesh size (df=2, F=4.910, P<.01), net length (df=1, F=15.820, P<.01) and depth (df=1, F=15.198, P<.01). The coral CPUE (n/day.100m) was generally higher than that of the target species for the métiers documented, except for fishing activities targeting pink spiny lobster (*P. mauritanicus*) and blonde ray (*R. brachyura*; Figure S2.4-supplementary material, Figure 2.5). The spatial analysis of CPUEs by target species shows that the métiers targeting John dory and Atlantic wreckfish have the highest CPUEs, but also the highest removal rates of corals (Figure 2.5, Figure S2.4). In the case of the John dory fishery, the pattern is only evident at a few locations during the summer-autumn sampling season, with most net deployments capturing comparatively few fish (Figure 2.5C). Conversely, and despite being the dominant fishery of the vessel that we followed in this study, the métier used to fish black-bellied angler showed the lowest overall coral removal rates, with the exception of a single set that removed 144 coral specimens (Figure 2.5AB).

For the 5 coral species most often caught as bycatch, the spatial segregation of fishing effort across the 2 sampling seasons is evident, with most incidental captures during the spring season occurring further offshore. Additionally, for *P. grayi* (Figure 2.6A), *E. verrucosa* (Figure 2.6B) and the two *Dendrophyllia* species (Figure 2.6C-D), more specimens were caught in the nets deployed in the summer-autumn sampling season (i.e. higher CPUEs). In contrast, *C. verticillata* (Figure 2.6E) was mainly caught during the spring sampling season with CPUE values being higher for this season.

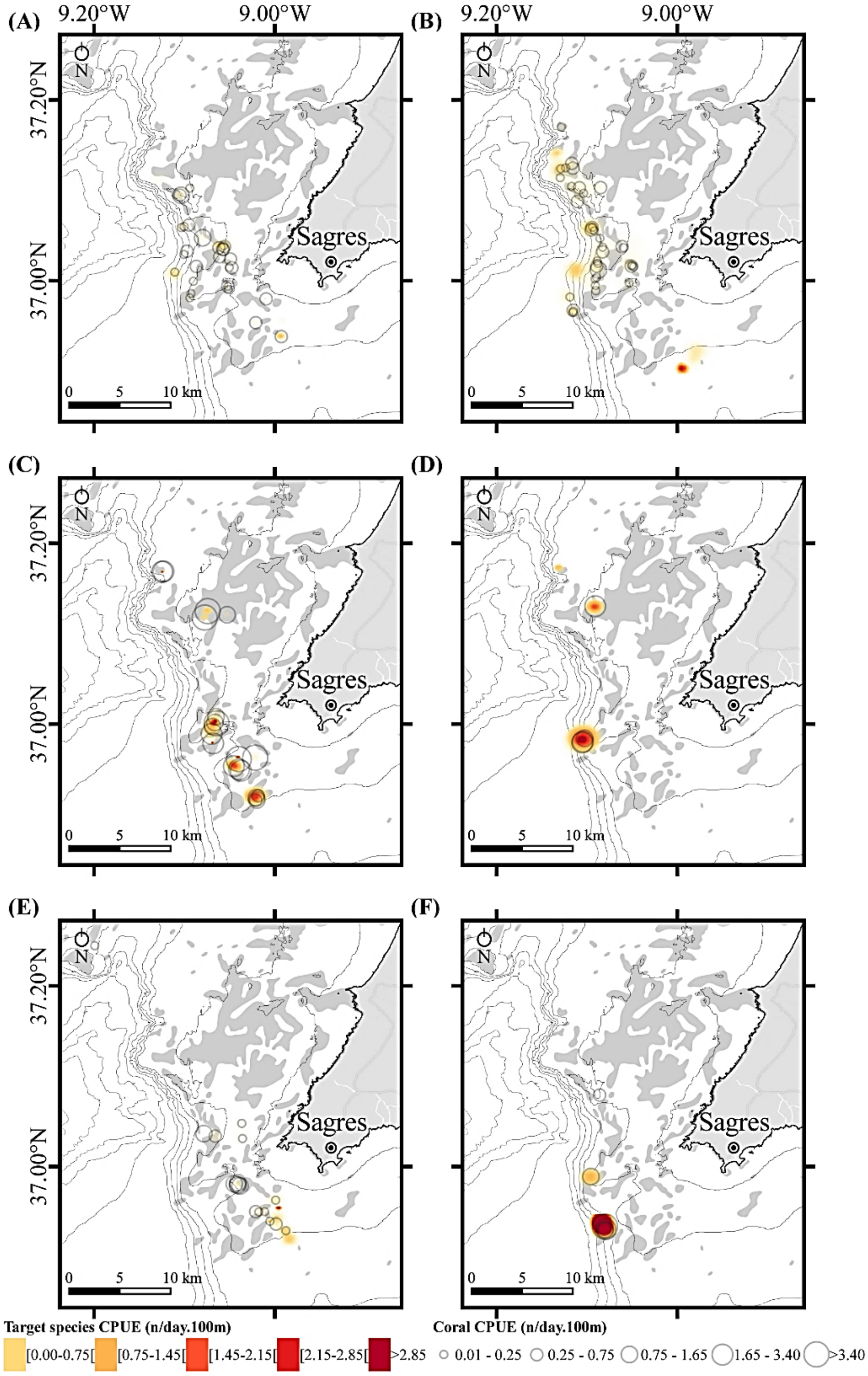

Figure 2.5. Spatial distribution of the fishing effort for target species and coral bycatch in bottom-set gillnets off the coast of Sagres (Portugal) during the summer-autumn (left panels) and spring (right panels) sampling seasons. Fishing effort was calculated as the catch per unit of effort (CPUE) and represents the number of specimens (fish/lobster or coral) as a function of the product of the net soaking time (days) per 100m of net. (AB) Lophius budegassa; (CD) Zeus faber; (E) Raja brachyura, Palinurus elephas, Palinurus mauritanicus pooled; and (F) Palinurus elephas and Polyprion americanus pooled. The maps in (E) and (F) show seasonally deployed nets for target species that are targeted over specific periods of the year. CPUEs for the target species are displayed as heatmaps generated using triweight kernel density and corals displayed as bubbles. Bathymetric isobaths are as follows: 50m, 100-500m (increments of 100m) and > 500m (increment of 200m). Rocky substrate is represented as grey shadow.

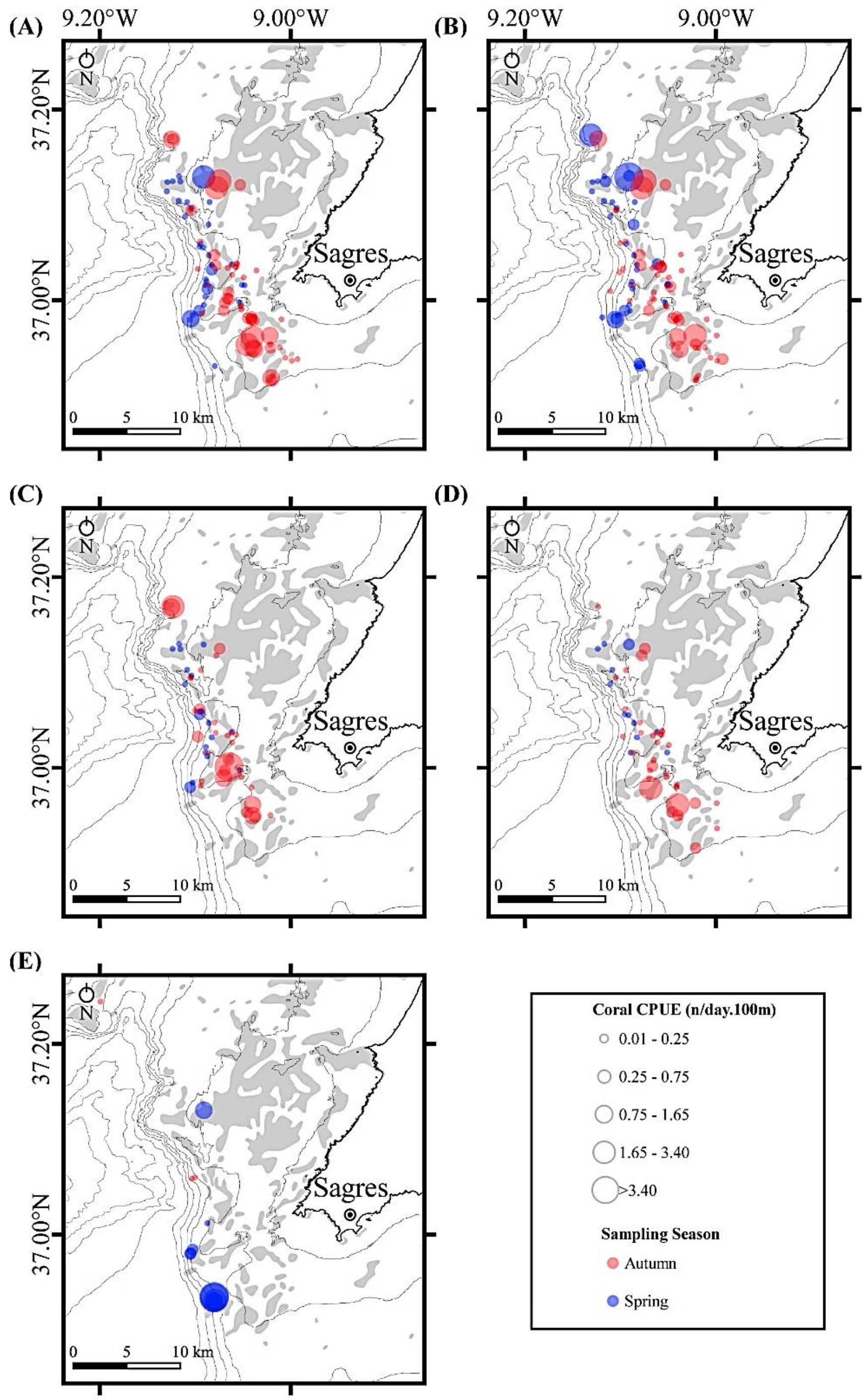

Figure 2.6. Spatial distribution of the fishing effort for the 5 specimens of coral caught as bycatch in bottom-set-gillnets off the coast of Sagres (Portugal) during summer-autumn (blue colour) and spring (red colour) sampling seasons. Fishing effort was calculated as the catch per unit of effort (CPUE) and represents the number of specimens (coral) as a function of the product of the net soaking time (days) per 100m of net. (A) Paramuricea grayi; (B) Eunicella verrucosa; (C) Dendrophyllia cornigera; (D) Dendrophyllia ramea and (E) Callogorgia verticillata. CPUEs for the corals are displayed as bubbles. Bathymetric isobaths are as follows: 50m, 100-500m (increments of 100m) and > 500m (increment of 200m). Rocky substrate is represented as grey shadow.

2.4.3. Coral bycatch community structure and biodiversity hotspots

The variation in coral community structure per gillnet set is illustrated in the PCoA analysis for the entire dataset, with the two axes capturing 43.59% of the variation in the ecological distances. The analysis shows weak separation in species composition and abundance between the majority of the métiers documented, with the exception of the métier for *P. americanus*, which is clearly segregated from the remaining métiers (Figure 2.7). This separation is strongly correlated with the coral species *C. verticillata* for which a high number of colonies was caught during the spring sampling season (the only season in which the métier was used; Figure 2.7). As expected, the depth at which the nets were deployed was found to significantly affect coral bycatch species composition and abundance (df=1, F=11.861, P<.01). The variation in coral community structure per net set could be partially explained by differences in the depth of deployment, with the constrained ordination axis (i.e. that defined by depth) accounting for 9.42% of the total variation in the distance matrix.

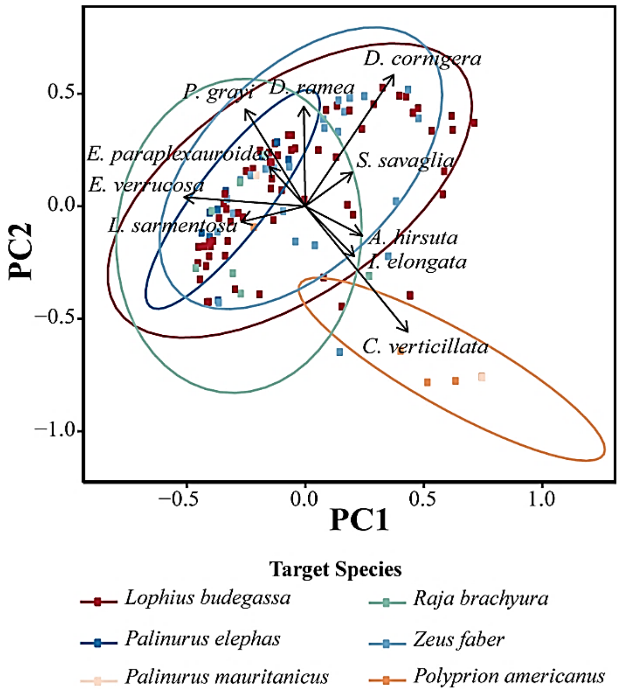

Figure 2.7. Principal Coordinate Analysis (PCoA) showing the variation in the coral species community structure from bycatch using bottom-set gillnets during two sampling seasons off the coast of Sagres (Portugal). PCoA plot based on species composition per net deployed and métier. The species matrix describing the ecological resemblance per net was calculated using the Hellinger distance. The vectors display the Pearson correlations (p-value<0.05) between the descriptors (i.e., coral species captures per net) and the PCo1 and PCo2. PCoA biplot of the métier documented in both sampling seasons. Significant groupings defined by métier are shown in colour. For more information concerning the PCoA refer to the Methods section.

Overall, the constrained ordination axis and the first residual axis of the db-RDA contributed to explain 33.29% of the variation found in the distance matrix (Figure 2.8). The depth vector in the db-RDA indicates the direction in the graph for which net sets were deployed at deeper depths (right-hand side of Figure 2.8). This shows that deeper deployments contained more *C. verticillata*, *I. elongata*, *A. subpinnata* and *S. savaglia*, whereas shallow deployments contained more *P. grayi*, *E. verrucosa*, *D. ramea*, *D. cornigera* and *L. sarmentosa* (Figure 2.8). Additionally, the db-RDA analyses show that the species *D. cornigera*, *D. ramea* and *P. grayi* are more correlated with each other, as their vector directions create small angles between them, implying that these species tend to appear in the same nets. The same pattern occurs for the pair of species *C. verticillata* with *S. savaglia* and *I. elongata* with *A. subpinnata*. Conversely, species like *P. grayi* and *I. elongata* or *E. verrucosa* and *S. savaglia* are negatively correlated (i.e. with opposite vector directions) and are not generally recovered in the same net.

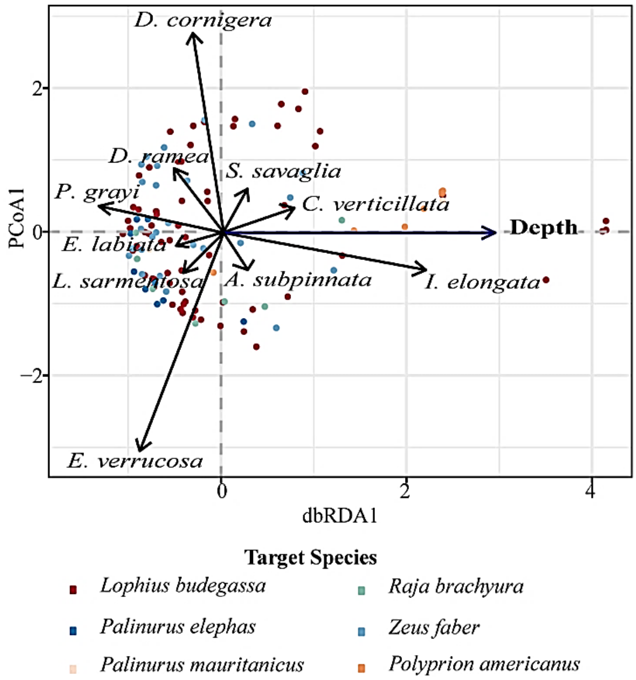

Figure 2.8. Variation of the coral community according to the depth (db-RDA), from the assessment of coral bycatch using bottom-set gillnets during two sampling seasons off the coast of Sagres (Portugal). Species composition per net was converted to a resemblance matrix using Hellinger distance and the variable depth described as constrained ordination axis. The vectors display the Pearson correlations (p-value<0.05) between the descriptors (i.e., coral species captures per net) and the dbRDA1 and PCo1. Db-RDA biplot shows the variation of the coral community according to the depth at which nets were deployed. The depth vector indicates the trend from shallow (left) to deep (right). Significant groupings defined by métier are shown in colour. For more information concerning the db-RDA refer to the Methods section.

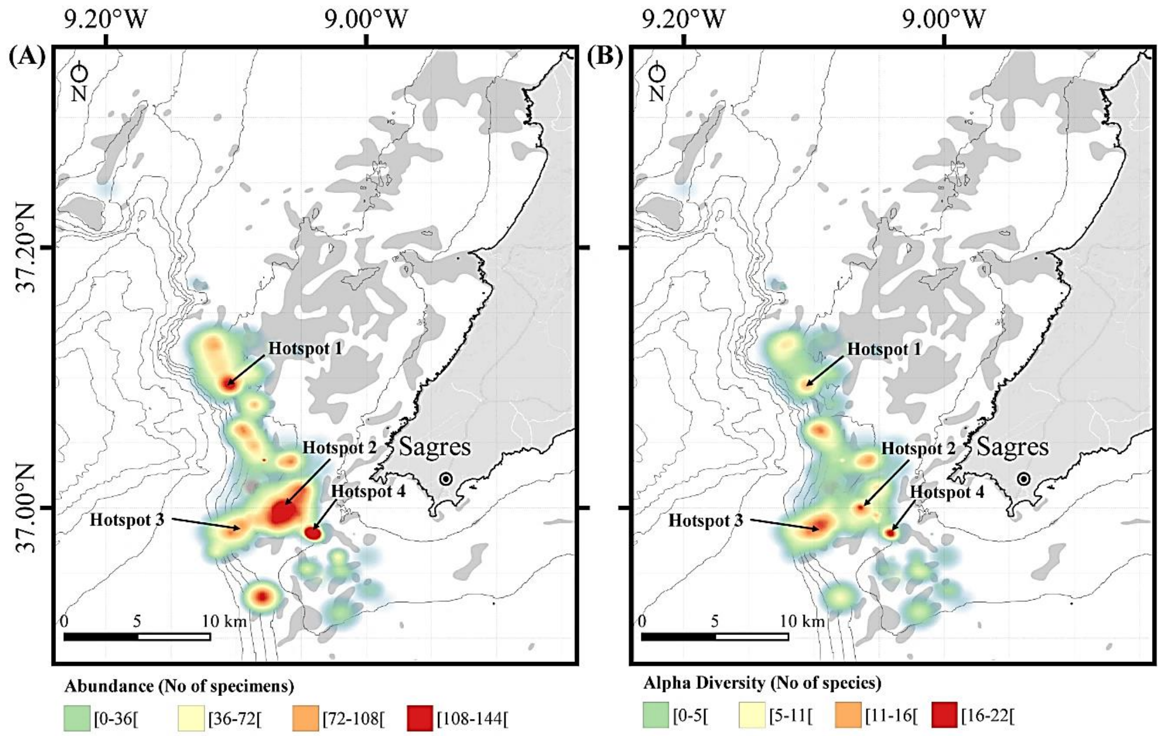

Figure 2.9. Spatial distribution of coral bycatch and biodiversity (no. of species) caught as incidental catches in bottom-set gillnets in Sagres (southern Portugal). Identification of possible hotspots of coral gardens and CWCs that should be protected from significant adverse impacts. (A) Density map of corals showing the hotspots based on the number of corals collected in each net deployed; (B) Diversity map of corals showing hotspots based on the diversity of corals collected in each net deployed. Coral diversity and abundance are displayed as heatmaps generated using triangular kernel density. Bathymetric isobaths are as follows: 50m, 100-500m (increments of 100m) and > 500m (increment of 200m).

The spatial abundance and alpha diversity found in each net allowed us to identify 4 main areas where the diversity and abundance are highest, which we classified as coral *hotspots* (Figure 2.9). In the hotspot areas, coral diversity was up to 22 species and 144 specimens. Other areas displayed lower but still relatively high diversity (11-16 species) and abundance (72-108 specimens) (Figure 2.9).

2.5. Discussion

This study confirms anecdotal evidence suggesting that the impact of bottom-set gillnets on deep-sea coral communities in Portugal, and on marine animal forests in general, is greater than previously appreciated. The coral removal rates reported here, while far lower than those reported for bottom trawling (Clark et al., 2016; Victorero et al., 2018), are substantially higher than what has been described for other fishing gears such as longlines and traps (Mytilineou et al., 2014; Pham et al., 2015). Overall, our findings highlight the urgent need to better understand the large-scale impacts of artisanal and other coastal multifleet and multispecific fisheries, as well as the urgent need for appropriate management policies to conserve and protect existing coral gardens and CWCs.

2.5.1. Impact of bottom-set gillnets on coral communities

Similar to previous studies conducted in other regions, bottom-set gillnets had a substantial impact on coral gardens and CWC reefs in Sagres with high levels of coral removal (Shester and Micheli 2011). In total, 4,326 coral specimens, a large proportion of which entire colonies (45%), were caught as bycatch in the 118 nets deployed over the 42-day period of our survey, corresponding to an average (±SE) of 31.1 (±2.7) corals per net. When considering each net's length and soaking time, the removal rates become less pronounced (average coral CPUE of 0.92/day.100m), although in some areas, particularly those for which the nets were deployed over rocky-bottom habitat, the CPUE was as high as 13.02/day.100m (top 5% of 4.14-13.02/day.100m). Based on the average of coral bycatch per net and daily number of nets recovered, a single fishing vessel using bottom-set gillnet can catch between 26,421-27,902 corals as bycatch per year (extrapolated to 214-226 fishing days to discounting 27-39 days of bad weather). Such high levels of coral bycatch, although based on a different metric, are in line with the findings of Shester and Micheli (2011) for Small-scale fisheries (SSF) in Baja California (Mexico), where gillnet sets had the highest removal rate (0.37 gorgonians per m^2) when compared with fish and lobster traps. In that study, the authors report that only 21.7% of the gillnet sets interacted with gorgonians, which is much lower than what we observed here (85%), though it is possible this disparity reflects site-specific differences in coral density. While not unexpected, our analysis indicates that the type of substrate over which the nets are deployed strongly influences coral bycatch, as the amount of coral caught in rocky-bottom areas was generally higher than in areas where hard seabed does not occur. Most coral species are found on hard substrate where they can form dense aggregations with complex architecture, which substantially increases the probability of corals becoming snagged or entangled in the nets, thus causing damage or detachment of the colonies. This association is well correlated with the ecology of the target species, which is particularly evident in the amount of coral caught when fisherman deploy sets for John Dory, a species that typically is associated with rocky habitats. In contrast, the fishery of Black-bellied angler, a species which lives on sandy or gravel-covered sea bottom (Maravelias and Papaconstantinou, 2003), had lower impact, except for deployments that crossed (or were very close to) rocky substrate. Unsurprisingly, our study also showed that coral community composition and species abundance vary significantly with depth. For instance, *P. grayi* and *Dendrophyllia* spp. are distributed in shallower habitats, while *I. elongata*, *S. savaglia*, *C. verticillata* and *A. subpinnata* occur at greater depths. Different depths are normally associated with different environmental factors (i.e. sea bottom temperature, bottom current velocity and chlorophyll-a concentration), which contribute to differences in community stratification as different species can have different optimal environments (Stone, 2006).

The magnitude of disturbance observed here is still considerably lower than that documented for trawlers. For example, in seamounts off the coast of Australia, it has been estimated that only 10 deep-sea trawlers passes would be required to completely decimate an area with 15-20% coral cover (Pitcher, 2000; Burridge et al., 2003; Clark et al., 2010). Although we did not attempt to quantify actual removal rates (i.e. amount removed according to the abundance *in situ*), our results suggest that it is likely that the community structure (i.e. size of colonies and species diversity) in the study area was different in the past. Deep-water coral species have slow growth rates and as such population recovery and reestablishment (Bavestrello et al., 1997) in the face of constant partial and total damage can be very slow (if possible at all), especially after decades of fishing. For instance, the recovery time of *E. verrucosa* has been estimated to range between 17 and 20 years, which can lead to the replacement of *E. verrucosa* colonies by shorter-lived species with quicker recovery rates (e.g., *Alcyonium digitatum*; Kaiser et al., 2018). This recovery times may be substantial longer for scleractinian, and possible, for anthipatharian species that grow much slower.

Other fishing gears for which data is available like longlines and traps appear to have a much lower impact on coral communities compared to that caused by bottom-set gillnets. For instance, Pham et al. (2015) reported removal rates of 0.32 corals per 1000 hooks (1.15 corals per set) for deep-sea longline fishing in the Azores. For the vessel we followed in Sagres, the average coral CPUE for bottom-set gillnets was 0.92 per day.100m (31.1 corals per set). These observations indicate that bottom-set gillnets have a higher removal rate, as we report 27 times the average coral removal per set of fishing gear. Additionally, Shester and Micheli (2011) did not report any coral bycatch from fish and lobster traps, suggesting that traps have the lowest overall impact on benthic communities.

In addition to complete removal of benthic habitat-formers, set gillnets can cause other types of physical damage, including abrasion, breakage and partial mortality (Shester and Micheli, 2011; Bo et al., 2014). In the particular case of corals, the colonies are expected to survive and recover from partial mortality, as natural breakage is part of their population dynamics and evolutionary ecology (Hughes and Jackson, 1980; Hughes et al., 1992). However, partial colony mortality is known to have profound effects on fitness by reducing fecundity and resource availability (Wahle, 1985; Page and Lasker, 2012). Moreover, the damage caused by abrasion and breakage can promote the development of disease and necrosis points, which can further increase mortality (Bavestrello et al., 1997). While we did not evaluate the effect of these processes (beyond the biomass of fragments removed) on surviving colonies, it is expected that the extent of coral mortality caused by gillnets in Sagres, and globally, is an underestimation of the real impact (Sampaio et al., 2012). More broadly, decades of unchecked damage to these habitats, as is likely the case in Sagres, can result in long-term (potentially permanent) changes in community composition and structure, which can reduce local biodiversity and the associated fishing catches (Cryer et al., 2002; Clark and Rowden, 2009; Atkinson et al., 2011; Clark et al., 2016).

Overall, the gorgonians *E. verrucosa* (the pink sea fan) and *P. grayi* and the scleractinians *Dendrophyllia* spp. were the most severely impacted species, making up nearly 80% of the total bycatch. *Eunicella verrucosa*, in particular, is listed as a species of principal importance in the UK and vulnerable in the IUCN Red List and may warrant protection. For instance, our results indicate that the colonies of *E. verrucosa* colonies caught as bycatch in Sagres were generally small (average height: 22.9 ±0.3cm; average width 15.5 ±0.2cm) considering the species can reach 25 to 50cm in height and a similar width (Grasshoff, 1992). Similarly, the scleractinian *D. cornigera* (12% of total bycatch) can reach a height of 60cm, yet the maximum height of the colonies collected in this study was 20cm (Brito and Ocaña, 2004). These observations suggest that decades of accidental captures these coral species by artisanal fisheries is taking a toll on the populations, as their recovery is too slow (Kaiser et al., 2018) to recover from such fishing pressures.

2.5.2. Coral biodiversity

The diversity of coral species recovered as bycatch from bottom-set gillnets in Sagres was surprisingly high given the relatively small-scale and geographic coverage of our study. Previous assessments of deep-sea (<200m depth) coral diversity for the Northeast Atlantic listed 173 species of corals, including antipatharians, gorgonians and scleractinians (Hall-Spencer et al., 2007), with a total of 174 species known to occur in the exclusive economic zone (EEZ) of mainland Portugal (i.e. excluding Madeira and the Azores; Horton et al., 2020). We found a total of 22 species of corals belonging to the anthozoan Subclasses Octocorallia (n = 17) and Hexacorallia (n = 5), which corresponds to 13% of the species known to occur in mainland Portugal and more than previous recorded in the OCEANA/MeshAtlantic ROV campaign for circalittoral off Sagres (Monteiro et al., 2013; Nestorowicz, 2020). Despite the high number of species identified, this is likely an underestimation of the diversity of coral garden and CWC reef forming species in Sagres as our survey was limited to a 57-510m depth range, and mostly to the upper 120m (67% of the nets). Interestingly, the collection depths of the three species of *Eunicella* was higher than the bathymetric range documented in the literature.

Our analysis of the spatial distribution of coral bycatch alpha diversity and captures identified 4 main biodiversity hotspots in the study area with up to 22 species and 144 specimens. These findings are in accordance with recent recommendations put forward by OCEANA, which urged Portugal to expand the Natura 2000 Network to incorporate seamounts and other coral garden areas around Cape St. Vincent (OCEANA, 2005, 2011). The unique richness of this area warrants a special status of protection, especially given the high direct impact of fisheries through coral removal (as documented here), as well as by lost and discarded fishing gear, a secondary effect of commercial fishing activities on benthic communities that has also been documented (Oliveira et al., 2015; Vieira et al., 2015).

2.5.3. Conservation and management implications

This study shows that the impact of bottom-set gillnets on coral gardens and CWC reefs seems to be significant, underlining the conservation concern that fishing operations using this type of gear creates. Reducing the impact of gillnets on these habitats requires active measures that fall within one of several categories (not mutually exclusive), including measures of spatial management (i.e. MPAs), environmental legislation (i.e. list habitats as VMEs or Essential Fish Habitat-EFH) and fisheries management (i.e. temporary closures and other restrictions, and the use of different fishing gear). The creation of MPAs, eventually associated with VMEs and/or EFH effective measure to protect slow-growing benthic communities (and the biodiversity associated) such as coral gardens and CWCs. Only a few studies have attempted to assess the impact of deep water MPAs, as MPA placement in deep waters is still in its infancy (Huvenne et al., 2016). Additionally, closure of certain areas to bottom trawling has been modelled and found to be potentially effective in the protection of coral gardens and CWCs, with negligible losses for bottom trawlers (Lagasse et al., 2015).

With regard to fisheries management, some of the strategies that have been adopted include frequent monitoring onboard of fishing vessels (i.e. in order to reinforce bycatch and landing laws), temporary closure of certain areas where the fishing effort is very low and coral bycatch very high (e.g., Hattonand Rockall Banks; Wright et al., 2015), and development of protocols for encounters such as move-on rules in national waters (UNGA, 2009). The move-on protocol, in particular, currently applies solely to areas beyond national jurisdiction and it mandates that when the catch of a fishing vessel (i.e. single trawl tow or set of static fishing gear) reaches a bycatch threshold of a VME indicator species, the vessel has to stop its fishing activity and move two nautical miles (NM) away from the site (Rogers and Gianni, 2010). In the Northwest Atlantic Fisheries Organization area, the thresholds were defined by weight and largely without scientific basis despite widespread advice of the scientific community for lower thresholds (Aguilar et al., 2017). In the North East Atlantic Fisheries Commission (NEAFC) area, the protocol defines that a temporary closure with 2NM on each side of the trawler track or a 2NM-radius from the most likely position of the encounters should be applied when encounters surpass a threshold of 30kg of live coral or 400kg of live sponges for trawler tows and other gear like gillnets, and 10 specimens per 1000 hooks or 1200m of longline gear (FAO, 2016). If the NEAFC VME threshold for gillnets (30kg of coral) was to be applied to the métiers studied, at least 10,345 colonies of *Eunicella verrucosa* (average dry weight of colonies 2.901g ± 0.078g, n = 988) or 350 colonies of *Dendrophyllia* spp. (average dry weight of colonies 85.49g ± 7.45g, n=819) would have to be caught in a single set to trigger the move-on rule, a value 67 and 2 times higher than the highest bycatch value documented in this study for a single set, respectively. Even though this estimates are based on weight data for entire colonies only (i.e. excluding fragments) and dry weight (as opposed to wet weight), a capture of more than 10,000 colonies to trigger the move-on rule would constitute a profound impact on coral communities studied here.

Such protocols can be improved by lowering or adapting (i.e. account for the life-history traits of the dominant VME species) the thresholds based on bycatch data (as provided in this study), and by increasing the move-on and closure distances (Rogers and Gianni, 2010; Aguilar et al., 2017). These measures could also be adopted in waters of national jurisdiction, since many VME indicator species are found throughout these areas and have long been impacted by fisheries. For instance, in national waters it may be advisable that each gear type have its own threshold and move-on distance. As an example for fishing activities using similar métiers to those documented in Sagres, the vessels could move at least 1.0NM from the middle point of the most likely position of encounters (e.g., biodiversity hotspots identified in Figure 2.9) because the average length of each net was 1.99km for our study. Caution should be taken in setting distance that could be used as move-on, as information about coral gardens distribution in scares. In areas where gorgonians are common, fisheries regulators may consider instituting a threshold based on the number and size of specimens instead of weight, as it is easy to overlook the scale of the impact on the ecosystem when simply measuring the weight of a gorgonian colony (just a few grams for potentially quite old individuals). Counting specimens in these métiers is also simpler to implement.

Frequent monitoring onboard of fishing vessels, although expensive, can be a valuable management tool as well given that it can contribute to effectively implement and enforce fishing regulations (both proposed and existing), thereby reducing coral bycatch (Boenish et al., 2020). Using different fishing gear that cause substantially lower impacts, while not a panacea, can help reducing the impacs on coral gardens and CWC reefs. In that regard, a potential alternative is the use of bottom longlines or traps, as these gear cause substantially lower impacts to benthic ecosystems (Shester and Micheli, 2011).

2.5.4. Final remarks

This study is a pioneer assessment of the interaction between artisanal fisheries using bottom-set static gear and coral communities in mainland Portugal. Additional research will be required to fully understand the extent of the damage caused by these activities. SSF constitute more than 90% of the Portuguese fishing fleet and our findings may only show the "tip of the iceberg" of the potentially irreversible crippling of deep-sea coral habitats. Studies of this type provide essential contributions to the knowledge of the distribution and abundance of corals in southwestern Portugal, and worldwide in general. We have identified a number of important biodiversity hotspots for which habitat mapping using newer technologies like ROVs will prove essential to confirm the presence of VMEs and evaluate the scale of fishing impacts. Our findings also highlight the importance of stricter control measures onboard of fishing vessels and draws attention to the fact that artisanal fisheries as a whole pose a serious threat to the ecological functioning and integrity of coral gardens and CWC reefs in certain areas. Nevertheless, this study highlights the importance of collaborating with fishermen in order to better understand deep-sea coral biodiversity, as well as of how scientists and fishermen can work together to protect such vulnerable species. In that regard, recent efforts, including work led by our team (in prep), have shown that the tremendous amount of coral biomass generated in fishing vessels using bottom-contact gear constitutes a major resource for restoration ecology (Montseny et al., 2019, 2020).

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3. Chapter 3: The utility of incidental coral catches from artisanal fisheries in restoration measures of coral gardens: The effect of density and species composition on coral transplants

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3.1. Abstract

The high structural complexity created by coral garden species provides nursery grounds, shelter and relevant habitat for numerous species, including commercially important species. These habitats are considered vulnerable marine ecosystems, as they are susceptible to degradation by human activities. Because of their vulnerability and low recovery rates, attention has been drawn to the need to actively protect and restore such habitats. This study aims to assess the feasibility of using coral bycatch and artificial reef structures in actions of habitat restoration, testing the potential of using coral biomass from deeper environment to restore shallow-water populations, as well as the effect of coral transplant density and species composition on the survival and growth of the transplanted corals. To this purpose, 12 artificial reefs made of clay bricks were deployed at 20m depth for 8 months with a total of 90 specimens of corals obtained from fisheries' bycatch. Three species were chosen based on the natural assemblage in the study area and the abundance as bycatch in artisanal fisheries (*Eunicella verrucosa*, *Leptogorgia sarmentosa* and *Paramuricea grayi*). Four treatments were defined based on two factors (density and species composition): monospecific low-density, monospecific high-density, multispecific low-density and multispecific high-density treatment. The results of the study show that on average 78% (±4%) of the transplants survived until 8 months. While the transplants in multispecific low-density treatment presented higher survival (87%±9%), no statistical significance between treatments was found. The results show that, on average, the variation in total branch length was -0.32cm (±5.97cm). Additionally, this study shows that octocorals have greater growth than reported in the literature (up to 1.37cm/day). This occurs mainly due to continuous dynamic of breakage of branches with subsequent

recovery. Even though the species used in this study showed high growth between monitoring, the yearly net growth was relatively low. This study demonstrates that *Eunicella verrucosa* is an ideal candidate for actions of transplantation, and shows the feasibility of using artificial reefs together with coral bycatch in order to restore damaged coral gardens without the possible limitations that methods using donor population fragments face, circumventing the negative impacts to the donor reefs.

3.2. Introduction

In the last few decades, technological advances in the exploration of the deep-sea and the increase in fishing of deeper commercial species have been revealing the scale of the impacts caused by human activities on these ecosystems (Althaus et al., 2009), including by mineral extraction (Glover and Smith, 2003; Cordes et al., 2016), littering (Ragnarsson et al., 2017; Consoli et al., 2020), oil spills (White et al., 2012) and fishing activities (Bo et al., 2014; Angiolillo et al., 2015). Fishing and, in particular, bottom-contact fishing activities (i.e. trawling and bottom-set longlines and nets) are considered highly destructive as these activities damage and remove species that are structurally important, while overexploit deep-sea resources (Bo et al., 2014; Angiolillo et al., 2015). For instance, the decline of the bamboo coral (*Isidella elongata*) in the Mediterranean Sea has been linked to the activity of bottom trawlers targeting red shrimp, causing the species to become critically endangered (Maynou and Cartes, 2011; Bo et al., 2017). The high susceptibility of these habitats to impacts by human activities and the important ecosystem services they provide has triggered the urgent need for active interventions to preserve and restore these ecosystems (Davies et al., 2017).

Ecological restoration of marine habitats consists of supporting the recovery of a degraded (i.e. long-term impact that affect the loss of biodiversity and structural integrity), damaged (i.e. impact that partially destroy the ecosystem, as trawling) or entirely destroyed ecosystems to its historical conditions (SER and Policy Working Group, 2004; Van Dover et al., 2014). On the other hand, ecological conservation includes all measures to remove or mitigate environmental stressors in an attempt to promote natural recovery of the system. This includes increasing water quality, closure of areas to fisheries and creation of marine protected areas (MPAs), where no interactions between humans and the system occur (Basconi et al., 2020). Even though conservation can help the natural recovery of degraded ecosystems, there is growing concern that coral gardens and CWC reefs may not recover naturally because of their slow growth rates (Dayton, 2003) and because the efforts to reduce these threats and allow for recovery may be too little. Therefore, active restoration involving direct interventions to accelerate habitat recovery and restore ecosystem functioning is necessary. Such measures include interventions such as coral transplantation, deployment of artificial substrates (i.e. to increase reef fauna, to prevent trawling or to combine with transplantation methods) and active removal of invasive species (Rinkevich, 2005, 2008; Elliott et al., 2007; Jungblut et al., 2019).

Coral restoration efforts have mostly focused on shallow-water tropical coral reefs (Rinkevich, 2005; Young et al., 2012), with comparatively few studies on temperate and cold-water coral habitats. As with their tropical counterparts, restoration of coral garden and CWC habitats predominantly consists of direct transplants from donor populations or from naturally and artificially detached colonies. For instance, Linares et al., (2008) used detached coral fragments to test transplantation success using 3 different attachment techniques, namely raw (i.e. gluing the fragments directly to the epoxy putty), tube (i.e. using a plastic tube to attach the fragments avoiding direct contact of the living tissue with the epoxy) and stick (i.e. using a PVC stick to support the fragment attached to the epoxy). Although the authors reported a survival of 70% beyond 1 year after transplantation for the stick method, the authors also assumed technique failure, as 40% of the colonies got detached across treatments. In another study, Montero-Serra et al. (2018) used epoxy putty to directly fix fragments of the precious red coral (*Corallium rubrum*) recovered from illegal poaching, reporting 99.1% of survival after 4 years. Even though some studies reported survival of more than 90% (Clark and Edwards, 1995), such studies were not time-effective, as transplantation was performed fragment by fragment or was dependent on donor populations (Weinberg, 1979; Brooke et al., 2006). Additionally, restoring deeper habitats can be substantially more expensive than shallow-water habitats as deep-sea habitats are remote and often require advanced underwater technology, which is likely to increase the price of restoration (i.e. two or three times higher than shallow-water restoration; Van Dover et al., 2014).

The use of artificial reefs can circumvent the problem of time efficiency by providing surface for multiple transplants at once (Montseny et al., 2019), which are subsequently deployed in the field. In addition to providing suitable habitat for the transplanted corals, artificial reefs also provide hard substrate for larval settlement of numerous invertebrate species and shelter and spawning grounds for fish (Macreadie et al., 2011), thereby increasing local biodiversity (Santos and Monteiro, 1997; Sherman, 2002). Even though artificial substrates can be a useful tool in coral restoration projects by providing a large area of transplants with minimal effort, many challenges still need to be overcome, including the choice of transplant density, the number of species, the selection of species to be used, the development of techniques to ease the deployment of such structures, the design of the artificial reefs and the materials to build them. For instance, while some restoration efforts have attempted to reproduce the natural densities of corals (Montseny et al., 2019), most studies do not consider the effect of coral density (strongly location-dependent) on growth and survival of the transplants, nor the potentially negative interactions between transplanted species in multi-specific treatments. Instead, most coral transplantation actions target the dominant habitat-structuring species (e.g. Linares et al., 2008 and Montero-Serra et al., 2018). In a natural environment, coral gardens are generally composed of several species (Cairns, 2007). As a result, multi-specific assemblages may be preferable, even though interspecific competition may occur. The choice of species and the size of the fragments to use is indeed crucial, as different species present different life traits and different stress resistance (i.e. resistance to manipulation and changes in environmental conditions; Montero-Serra et al., 2018; Montseny et al., 2019, 2020). For instance, *Paramuricea clavata* shows low survival in aquaria and is sensitive to manipulation and change of conditions (Montseny et al., 2019). Consequently, the survival of such species tends to be lower following transplantation (Montseny et al., 2019). Another challenge to take into consideration is transplantation failure, which may occur as a result of poor attachment of the transplants to the substrate that facilitates subsequent coral dislodgement, or post-attachment failure due to maladaptation of the transplants to local environmental conditions (Linares et al., 2008).

More recently, Montseny et al. (2019) used artificial substrates to transplant colonies of gorgonians from fisheries´ bycatch. The gorgonians were attached to stainless-steel structures and had a survival of more than 87% after 10 months. In another study, Montseny et al. (2020), attached gorgonian colonies to cobble supports (i.e. both natural and man-made) and deployed them from the surface to test the best type of support and if the colonies correctly landed on the bottom (termed 'badminton' method). The authors reported a landing success of more than 90% (Montseny et al., 2020). Coral discards from incidental catches by commercial fisheries (i.e. coral bycatch) represent a largely untapped asset for restoration actions, as fisheries generate a large amount of unused biological material (Sampaio et al., 2012; Chapter 2 of this study). For example, Mytilineou et al. (2014) reported that 72% of longline sets used in hake and blackspot seabream fishery in the Ionian Sea captured corals. Moreover, using coral bycatch to restore coral gardens is a more environmentally responsible method as no added impact to healthy donor population is created and it is easier to collect detached fragments (Montseny et al., 2019).

In general, this study aims to explore the sustainability of using coral bycatch and artificial reef structures in actions of habitat restoration, thereby developing a time-effective and low-cost restoration pipeline for both deep- and shallow-water populations that uses coral bycatch. More specifically, it aims to test the viability of using corals from deeper environment to restore shallower environment and to test the effect of coral transplant density and species composition (monospecific vs. multi-specific) on the survival and growth of the transplanted corals.

3.3. Materials and methods

3.3.1. Study site and experimental design

A pilot study of habitat restoration using coral biomass from incidental catches by bottom-set gillnets was conducted in Sagres, southwestern Portugal (Figure 3.1). The biomass was obtained from one fishing vessel targeting several commercial species of fish and lobster (see Chapter 2). In order to test if and how coral biomass from deep origin (i.e. average depth of 99m and range of 57m-380m) can be used in restoration actions of shallow-water depths (<30m depth), the effect of coral transplant density and species composition on coral survival and growth was evaluated for transplants deployed at 20m depth. We used a nested design with two levels for each of the two factors: density (low vs. high) and species composition (monospecific vs. multispecific). The final densities of colonies transplanted onto each artificial reef was 10 colonies/m^2 and 20 colonies/m^2 for the low- and high-density treatments, respectively. These densities were selected in order to represent the natural abundances of gorgonian assemblages reported for the Mediterranean and south of Portugal (Bo et al., 2009; Bullimore et al., 2013; Cúrdia et al., 2013; Grinyó et al., 2016). According to the literature, the density and species composition of gorgonians in coral gardens can vary considerably from region to region. For instance, in the Mediterranean sea, *Paramuricea clavata* can be found at maximum densities of 18.5 colonies per square meter (colonies/m^2) (Gori et al., 2011), while *Eunicella verrucosa* in the coast of Algarve can have a density of 8.8±2.19 colonies per 5m^2, reaching a maximum of 39 colonies per 5m^2 at depths between 20 to 25m (Cúrdia et al., 2013). In total, we deployed 12 artificial reefs (3 for each treatment) with a total of 90 corals. Originally, this study intended to include an additional experimental factor (depth level) with the deployment of an additional 12 artificial reefs at 50m depth as the deep treatment. However, due to time and logistical constraints it was not possible to achieve this goal within the time frame of the MSc project. Nevertheless, the deployment of the deep treatment is scheduled to be carried out in the last weeks of October 2020.

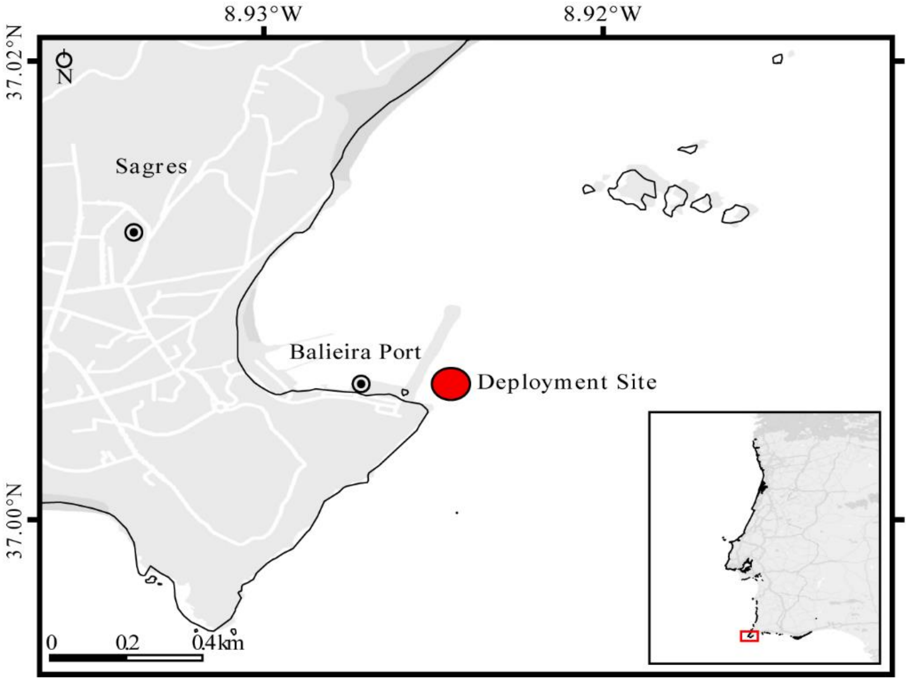

Figure 3.1. Geographic area showing the deployment site of the pilot study of restoration using coral bycatch obtained from bottom-set gillnets in Sagres (southern Portugal). In total, 12 artificial reefs were deployed at 20 m depth (for more details refer to methods).

3.3.2. Species used

Preliminary data on coral bycatch species composition and frequency showed that *E. verrucosa* was the most abundant species caught by the vessel that was followed in Sagres (see Chapter 2). Due to the abundance of bycatch biomass and given that the species is listed as vulnerable in the IUCN Red list (IUCN, 1996), *E. verrucosa* was used in the monospecific treatments.

In the multi-specific treatment, the species *Paramuricea grayi* and *Leptogorgia sarmentosa* were also selected (in addition to *E. verrucosa*), as these were also commonly caught as bycatch and naturally occur in the same coral assemblages (Boavida et al., 2015, 2016). Although the species chosen for the transplantation were some of the most abundant species, other species such as *Acanthogorgia* spp., *Callogorgia verticillata*, *Ellisella paraplexauroides*, *Corallium rubrum*, *Eunicella labiata*, *Dendrophyllia ramea* and *Dendrophyllia cornigera* could be used for coral transplantation to deep sites as they are frequently collected as bycatch by fisheries (Chapter 2).

3.3.3. Coral collection and maintenance

Colonies of *E. verrucosa*, *P. grayi* and *L. sarmentosa* were obtained from the fishing activity of one boat using bottom-set gillnets during the autumn of 2019. The corals were maintained on board of the fishing vessel in a 60-L tank with continuous seawater flow from the sea surface. Once on land, the corals were transferred to two 600-L tanks filled with sea water in a DOCAPESCA warehouse at the Baleeira port (Sagres) until further processing (see below). A total of 120 corals were maintained in the tanks with a closed seawater system, in the dark, fed four times a week with a mix of frozen rotifer and copepods (*Calanus finmarchicus*). Submersible pumps were used to provide continuous water flow, with the seawater replaced each week. The fragments collected were maintain in the tanks until transplantation to the study site (between three weeks to a maximum of six weeks depending on collection date).

3.3.4. Artificial reefs and transplant preparation

In this study, coral specimens were attached to artificial reefs that were subsequently deployed in the study area (Figure 3.1) in order to facilitate the deployments and the transplantation process, thus making it time effective. The artificial reefs were pyramid-shaped structures, made of clay bricks, with a height of 0.21m and a basal area of 0.55m^2 (Figure 3.2). Each artificial reef weighed approximately 50kg. The rectangular hollow bricks used were made of clay, which is a natural, non-toxic material that has the advantage of having a porous structure which promotes larval settlement (Hoog Antink et al., 2018). The robustness of the artificial reef was improved by gluing the bricks together with adhesive cement and further reinforced with metal rods and cement across its length (i.e. through the brick holes). Two metal rods were hammered trough each artificial reef and into the substrate to stabilize it *in situ*.

Figure 3.2. Artificial reef built and used in this pilot study of restoration using coral bycatch originated from gillnets in Sagres (southern Portugal).

To facilitate manipulation and improve the attachment success of the coral fragments, the specimens were fixed to PVC plugs pre-filled with calcium carbonate using marine epoxy (Reefers epoxy putty). This was done *ex situ* in the holding tanks. The fragments were prepared following a modified version of the methodology used by Brinkhuis (2009). Briefly, the first 2cm of the basal branch of whole colonies was stripped, removing any living tissue and exposing the skeleton (Figure 3.3A). The exposed skeleton was then inserted and fixed into the plugs using marine epoxy (Figure 3.3.B). The height of each transplant was standardized in order to minimize the size-dependent effects on survival and growth. The specimens were selected based on size classes (10-20cm) defined to prevent the need to cut branches.

On the deployment day, the artificial reefs were transported and deployed from a vessel, with the corals maintained in a small tank filled with seawater until the moment of deployment. The transplants were fixed in pre-made boreholes on the artificial reefs (33mm in diameter) and sealed with marine epoxy at the surface, and immediately lowered to the sea floor. While being glued, the fragments already fixed to the plugs, to the artificial reef were constantly wetted with seawater. The transplants' arrangement within the artificial reef was standardized, with each fragment fixed to the centre of each brick, in order to ensure equal distancing between transplants (Figure 3.2). Additionally, the transplants of each species in the multispecific treatments were distributed randomly. Once on the sea floor, scuba divers used a lifting bag to rearrange the position of the artificial reefs. In total, 90 coral fragments were deployed, including 66 fragments of *E. verrucosa* (5 and 10 for the monospecific low- and high-density treatments, respectively; and 3 and 6 for the multispecific low- and high-density treatments, respectively), 12 fragments of *P. grayi* (1 and 3 for the low- and high-density treatments, respectively) and 12 fragments of *L. sarmentosa* (1 and 3 for the low- and high-density treatments, respectively).

3.3.5. Monitoring of coral transplants survival and growth

The monitoring was conducted by scuba diving 1, 3, 6 and 8 months after deployment. The survival of the transplants, attachment status (attached, loose or missing), condition (alive or dead), feeding status (polyps extended or retracted) and necrosis (present or absent) were recorded *in situ*. Coral growth was estimated from photographs, which were taken *in situ* using a black or white PVC slate marked with a ruler to provide a background contrast. Changes in total branch length, maximum height were quantified for each transplant.

(A) (B)

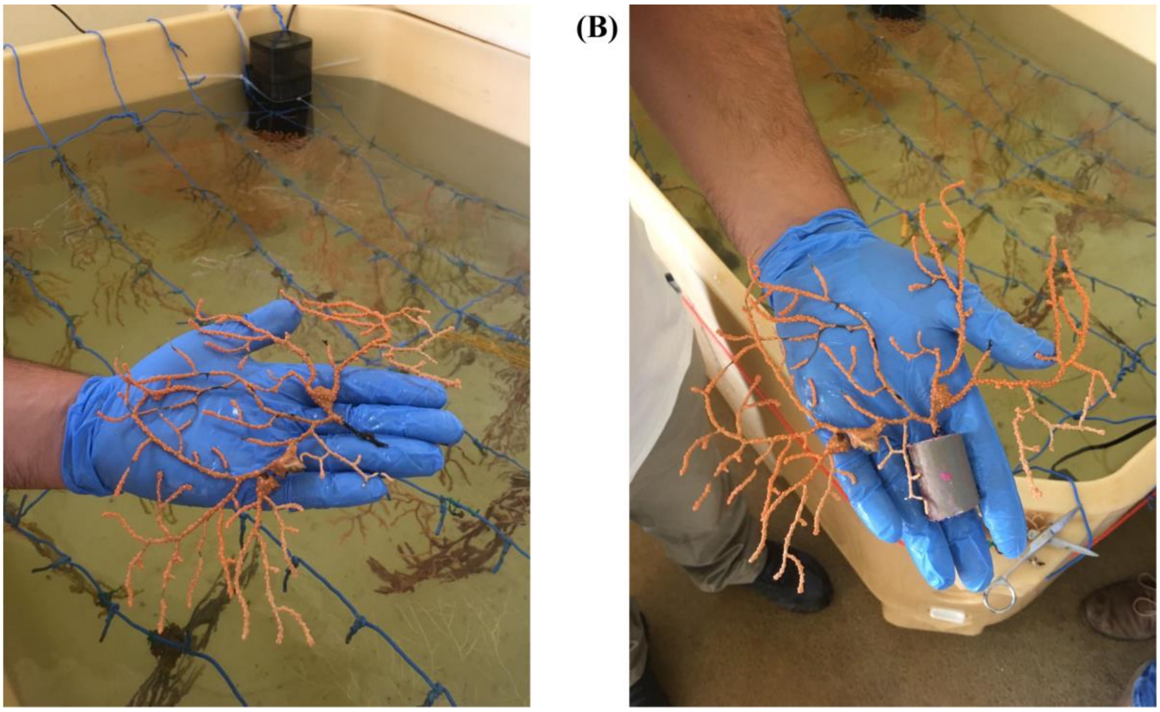

Figure 3.3. Methodology to attach the colonies to the PVC plugs in the pilot study of restoration using coral bycatch originated from gillnet sin Sagres (southern Portugal). (A) coral colony with the 2cm of the base stripped, before being fixed; (B) colony fixed to the plug using marine epoxy (Reefers epoxy putty).

All pictures were analysed using ImageJ software v. 1.8.0 (Rueden et al., 2017; see Figure S3.1- supplementary material for more details).

3.3.6. Data analysis

To analyse the differences in coral survival and growth between the 4 treatments over time, a two-way repeated measures analyses of variance (ANOVA) was performed for the survivorship and variation of total branch length (i.e. response variables) as a function of transplant density and species composition (explanatory variables). This analysis was performed as the variables recorded were dependent over time (i.e. the same transplants were followed over time). The proportion of transplants alive on each structure (i.e. survivorship) was logit transformed. Pairwise *t*-test was used as post-hoc test. The assumption of normality was checked using the Shapiro-Wilk test. The data was also inspected for sphericity (i.e. differences in variance over time) using Mauchly's test (η_p^2). The presence of outliers was accessed through visual analysis (Figure S3.2 and S3.3- supplementary materials). The analysis were performed using rstatix package in R version 3.6.2 (Kassambara, 2020).

3.4. Results

3.4.1. Coral transplant attachment

Overall, the results indicate an average (±SE) attachment success of 72% (±5%) after 8 months. The monospecific high-density treatment had the highest attachment (83%±7%), followed by the multispecific low-density treatment (80%±10%) when analysed across species.

On the other hand, the monospecific low-density treatment had the lowest attachment (67%±13%; Table 3.1). The average attachment success of the transplants across treatments was different between species, with *E. verrucosa* having the highest values (82%±5%) on average and *P. grayi* the lowest (25% ±13%). Additionally, *E. verrucosa* had the highest attachment success in the multispecific low-density treatment (100%±0%) and the lowest in the monospecific low-density treatment (67%±13%) (Table 3.1). For the multispecific treatments, *P. grayi* had an average attachment success of 33% (±33%) and 22% (15%) for the low- and high-density treatments, respectively, whereas *L. sarmentosa* had the same attachment success in both treatments (67%) (Table 3.1).

3.4.2. Coral transplant necrosis

The average (±SE) percentage of colonies with tissue necrosis across all treatments and monitoring times was 32% (±6%). Colonies in the monospecific low-density treatment had the highest tissue necrosis after the 8 months (50%±17%), followed by those in the multispecific high-density treatment (43%±12%). Colonies in the monospecific high-density treatment presented the lowest overall tissue necrosis (21%±8%). The variation in necrosis over time differed between treatments (Figure 3.4). For the monospecific low-density treatment, the percentage of colonies with tissue necrosis decreased throughout the 8 months of monitoring from 80% at the moment of transplant to 50% at 8 months, while for the monospecific high-density and multispecific low-density treatments it remained around ~25%, though there was a drop to ~12.5% at 3 months following transplantation in the later (Figure 3.4BC). Additionally, the necrosis presence in the multispecific high-density treatment varied over time peaking at 24 and 193 days (~44%). It is important to note that the presence of tissue necrosis was considerably higher in *P. grayi* for which all the transplanted colonies that survived had tissue necrosis (n=8). In contrast, colonies of *E. verrucosa* (n=54) presented the lowest percentage of tissue necrosis across treatments with an average of 27% (±6%; Table 3.1).

Table 3.1. Percentage of coral transplants attached and colonies with tissue necrosis after 8 months of deployment in the study area of the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as average ± standard error percentage of attached colonies and percentage of colonies with tissue necrosis.

Species	**Monospecific Treatment**		**Multispecific Treatment**		**Metric**
	Low-density	High-density	Low-density	High-density	
Eunicella verrucosa	67%±13%	83%±7%	100%±0%	83%±11%	
Leptogorgia sarmentosa			67%±33%	67%±17%	Attachment
Paramuricea grayi			33%±33%	22%±15%	
Eunicella verrucosa	50%±17%	21%±8%	22%±15%	25%±15%	
Leptogorgia sarmentosa			0%±0%	50%±24%	Tissue necrosis
Paramuricea grayi			100%±0%	100%±0%	

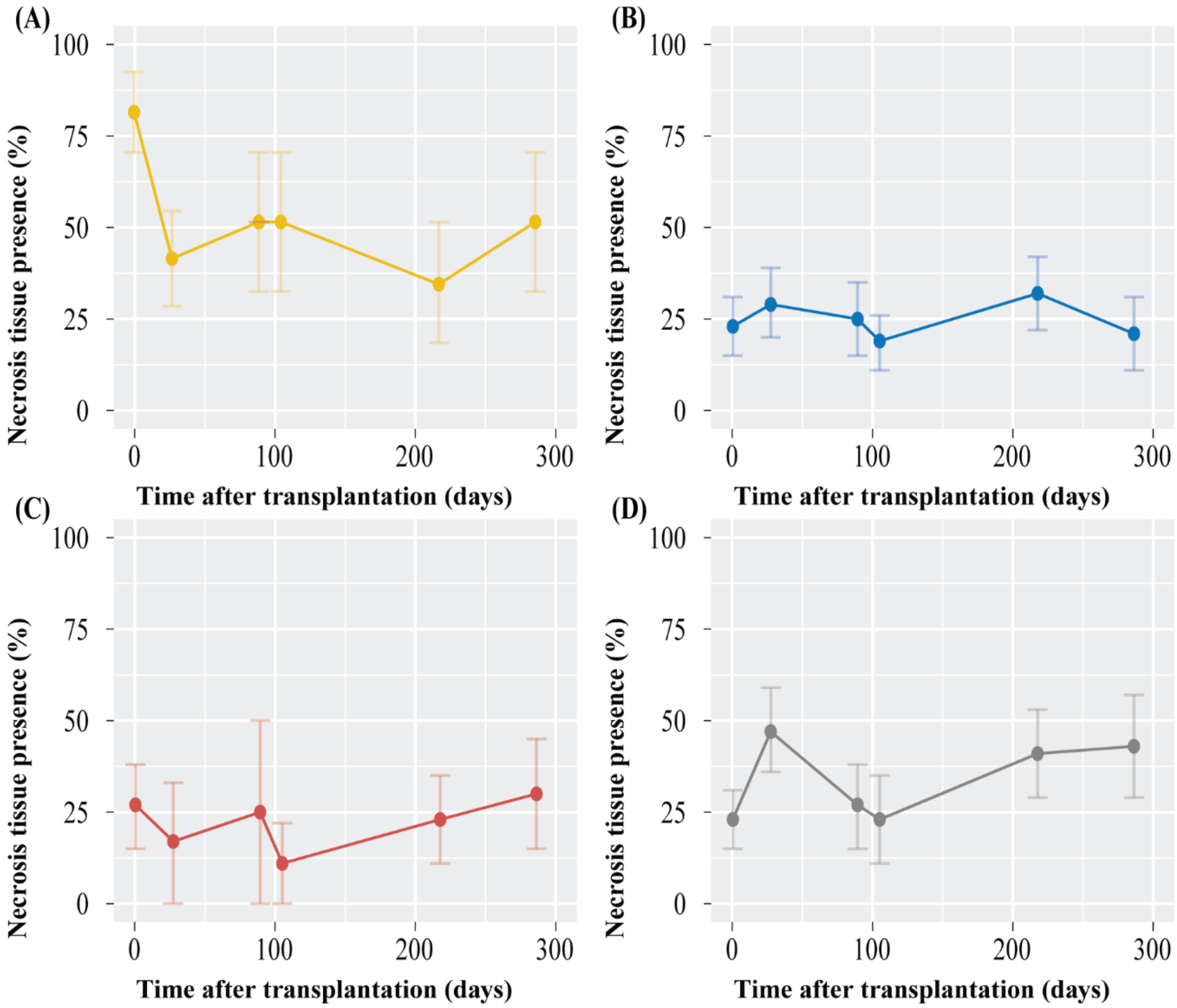

Figure 3.4. Variation in colony tissue necrosis throughout the 8 months after the deployment in the study area of a pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as average of colonies with presence of tissue necrosis and error bars for the standard error. (A) Monospecific low-density treatment; (B) Monospecific high-density treatment; (C) Multispecific low-density treatment and (D) Multispecific high-density treatment.

3.4.3. Coral transplant survival

Overall, 70 of the 90 corals transplanted survived until 8 months after transplantation, corresponding to an average (±SE) survival of 78% (±4%). The multispecific low-density treatment presented the highest survival (87%±9%; Figure 3.5C), followed by the monospecific high-density (80%±7%; Figure 3.5B) and by the multispecific high-density treatment (77%±8%; Figure 3.5D). Colony mortality was the highest for the monospecific low-density treatment (67%±13% survivorship; Figure 3.5A). The two-way repeated measures ANOVA test showed that there was no significant main effect of the treatments on the survival of coral transplants over time (df=3,6; F=0.690, *P*=.059, η_p^2=0.159).

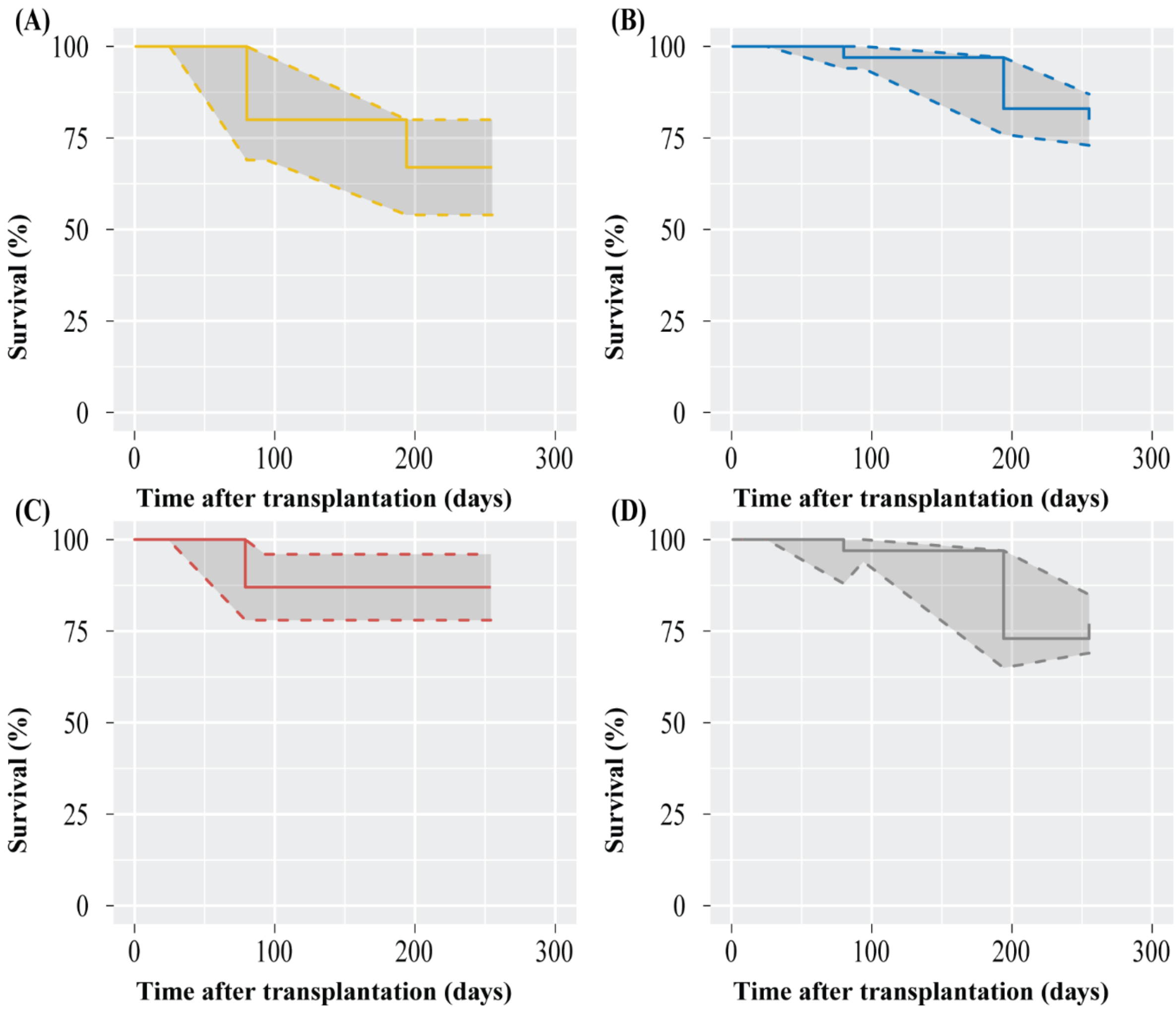

Figure 3.5. Variation in coral transplant survival throughout the 8 months after deployment in the study area of a pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as average of colonies surviving to each time point (irrespective of species) in each artificial reef, with the maximum and minimum values delimited by dashed lines (area shaded in grey). (A) Monospecific low-density treatment; (B) Monospecific high-density treatment; (C) Multispecific low-density treatment and (D) Multispecific high-density treatment.

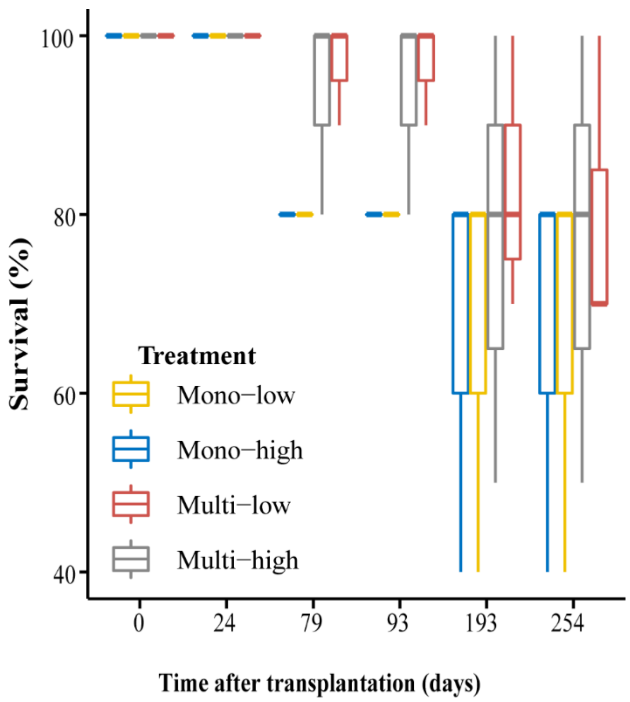

Figure 3.6. Boxplot comparing colony survival in each treatment at each monitoring time of the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as average percentage of colonies surviving to each time point.

Additionally, the interaction between treatment and time was not significant (df=15,30, F=1.266, *P*=.282, η_p^2=0.190). Even though no statistically significant differences were found between treatments, it is important to note that at 79 and 93 days after transplantation, the monospecific treatments differed considerably from the multispecific treatments (Figure 3.6).

Of the 70 corals that survived, 54 were *E. verrucosa*, 8 *L. sarmentosa* and 8 *P. grayi*, representing an overall average survival per species of 82%, 67% and 67%, respectively. *E. verrucosa* was the species that presented the highest overall survival average (82%±5%). This species had an average survival of 100% (±0%) in the multispecific low-density treatment and the lowest survival in the monospecific low-density treatment (67%± 12%; Figure S3.4A-suplementary material). *P. grayi* and *L. sarmentosa* had the same average survival in both, low- (67%±33%) and high-density treatments (67%±17%; Figure S3.4C-D-suplementary material).

3.4.4. Coral transplant growth

Overall, the average (±SE) variation in total branch length (i.e. final total branch length subtracted the initial total branch length) of the colonies was -0.32cm (±5.97cm) across treatments and independent of the species after 8 months. Colonies in the monospecific high-density treatment presented the highest positive variation in total branch length (6.04cm±9.82cm; Figure 3.7B) after the 8 months, followed by those in the monospecific low-density treatment (3.23cm±6.34cm; Figure 3.7A). For the multispecific treatments (Figure 3.7C-D), the average net colony growth after 8 months was negative in both densities tested, with colonies in the low-density having the highest negative variation in total branch length (-6.40cm±5.97cm; Figure 3.7C). The two-way repeated measures ANOVA test showed that there was no significant main effect of the treatments on the variation in the total branch length of the colonies (df=3,6; F=0.682, P=.595, η_p^2=0.118; Figure 3.8). The interaction between time and treatment was also not significant (df=12,24; F=1.175, P=.353, η_p^2=0.207). Despite no statistically significant differences found between treatments, it is worth to notice that at 93 days after transplantation, the monospecific high-density treatment differed considerably from the multispecific low-density treatment (Figure 3.8).

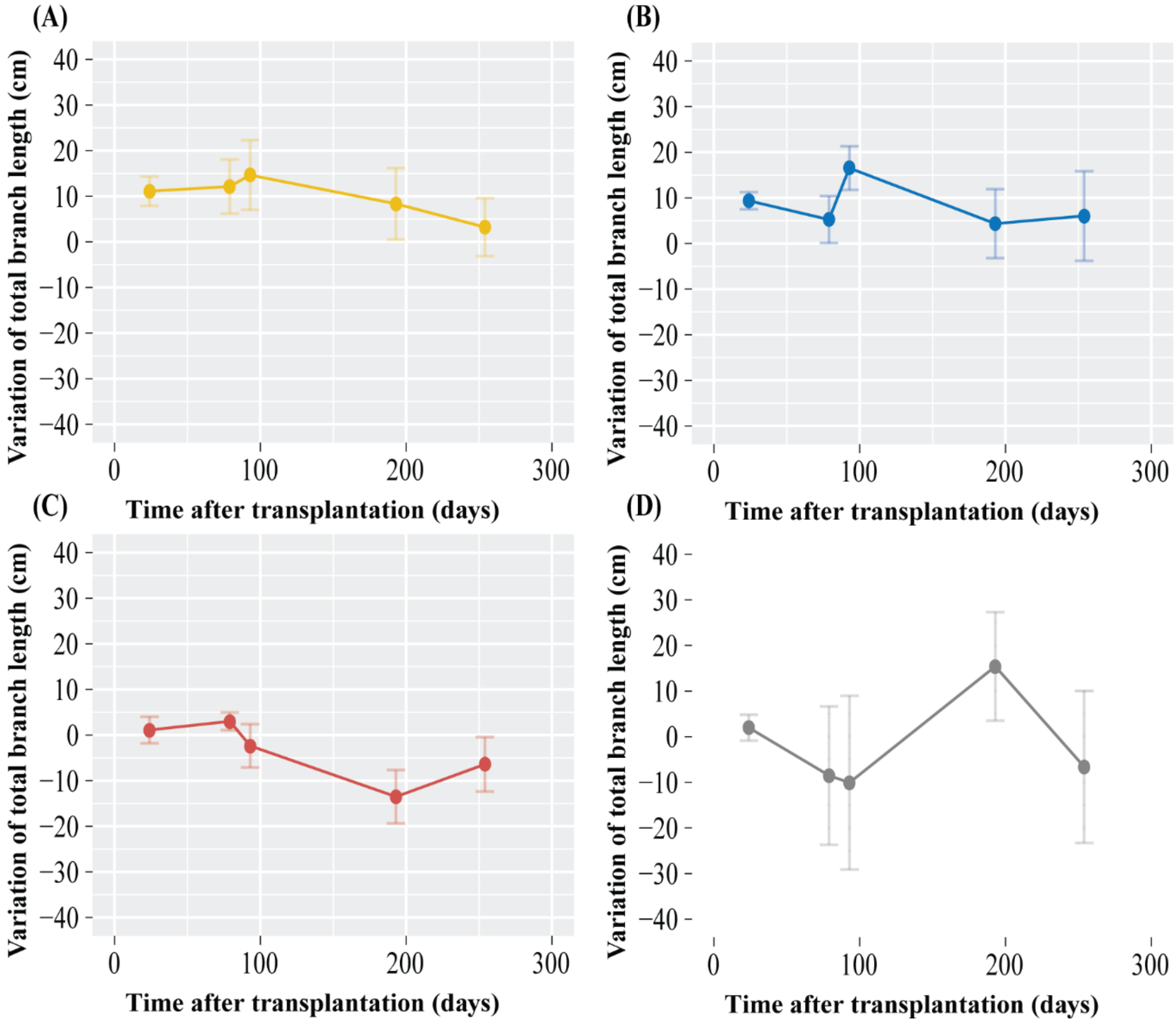

Figure 3.7. Variation in colonies total branching length throughout the 8 months after deployment in the study area of the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as colonies variation of total branch length (cm) to each time point (irrespective of species) in each artificial reef, with standard error showed as error bars. (A) Monospecific low-density treatment; (B) Monospecific high-density treatment; (C) Multispecific low-density treatment and (D) Multispecific high-density treatment.

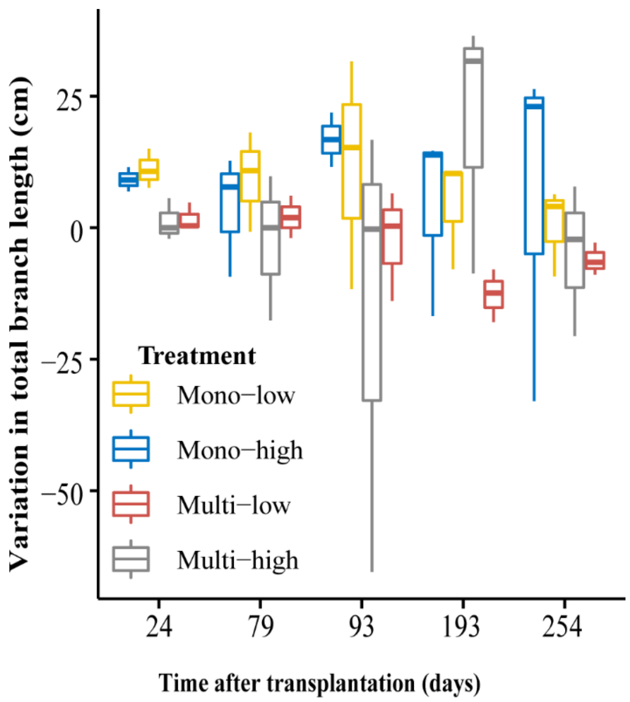

Figure 3.8. Boxplot comparing colony variation in total branch length in each treatment at each monitoring time of the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as variation in total branch length of the colonies (cm).

When examining coral net growth at the species level, *E. verrucosa* was the only species with a positive increase in total branch length 8 months after transplantation, with higher overall colony growth in the multispecific high-density (6.18cm±4.86cm) and monospecific high-density treatments (6.04cm±9.82cm; Table 3.2). For this species, colonies in the multispecific low-density treatment had a negative variation in total branch length (-4.63cm±6.38cm). Colony net growth for the species *P. grayi* and *L. sarmentosa* after 8 months was depressed, with negative variation in total branch length for both density treatments, a pattern that was particularly strong for *P. grayi* (~-22cm for both density treatments), despite of *L. sarmentosa* having the highest net negative growth (-24.65cm±61.77cm in the multispecific high-density treatment; Table 3.2).

Table 3.2. Variation of total branching length of the transplanted corals after 8 months of deployment in the study area of the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as average (cm) ± standard error (cm) of the variation in total branching length of the colonies.

Species	Monospecific Treatment		Multispecific Treatment	
	Low-density	High-density	Low-density	High-density
Eunicella verrucosa	3.23±6.34	6.04±9.82	-4.63±6.38	6.18±4.86
Leptogorgia sarmentosa			-1.12±3.53	-24.65±61.77
Paramuricea grayi			-22.33±0.00	-21.80±13.81

The results show that coral growth over time in the species used in this study is highly dynamic, with multiple increases in total branch length followed by negative growth (Figure 3.9). This observation is clearer for the species *E. verrucosa* and *L. sarmentosa* (Figure 3.9A-B), whereas *P. grayi* seem to decrease in total branch length (Figure 3.9C). The maximum variation (i.e. maximum growth) in total branch length of the species *E. verrucosa* was obtained for the monospecific high-density treatment at 93 days after deployment (72.61cm total variation, 0.78cm/day). The species *L. sarmentosa* was the species that had the highest maximum variation in total branch length in the multispecific high-density treatment at 193 days after deployment (113.42cm total variation, 0.59cm/day).

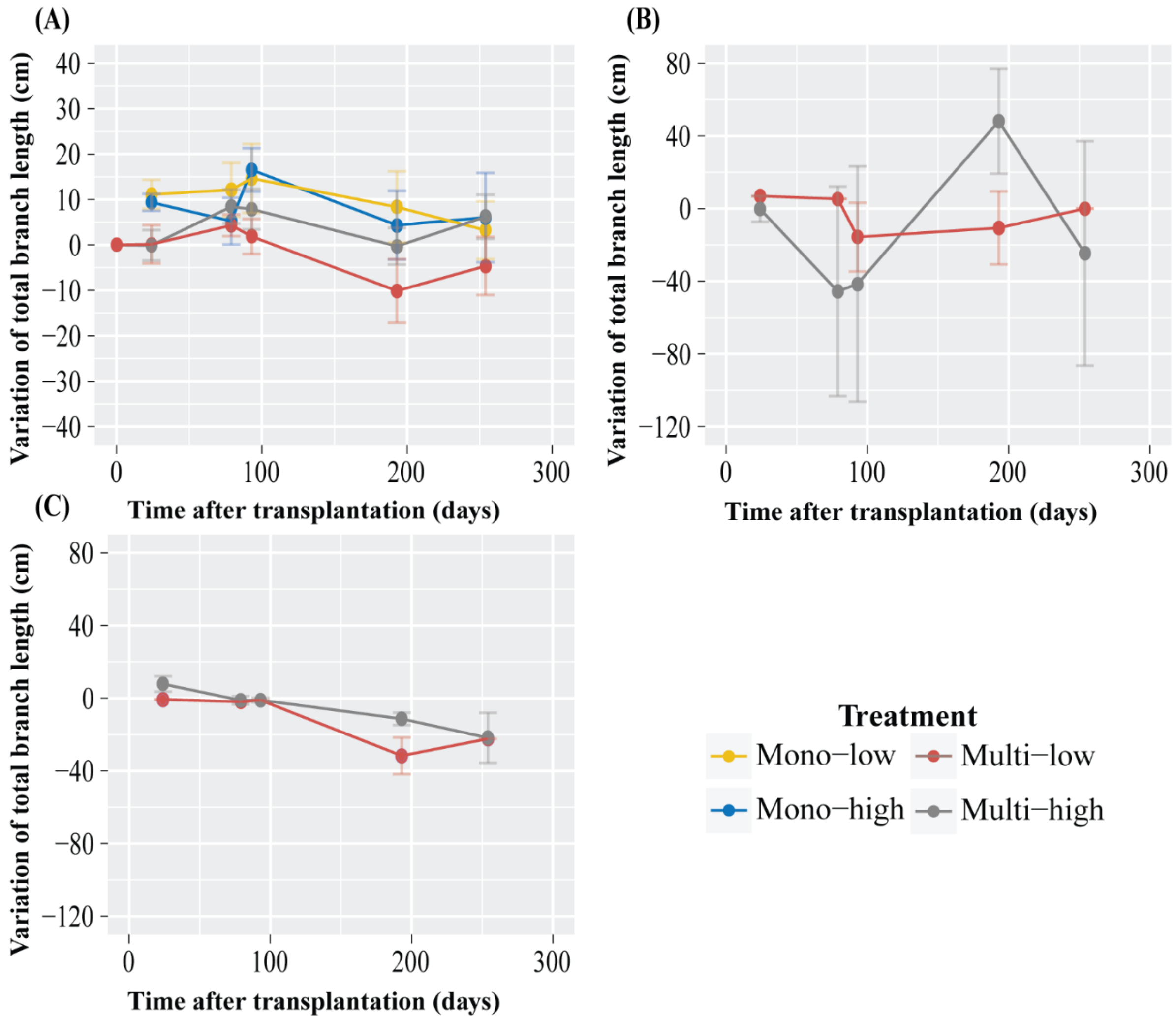

Figure 3.9. Variation in colonies total branching length throughout the 8 months after deployment in the study area of the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as colonies variation of total branch length (cm) to each time point in each artificial reef, with standard error showed as error bars. (A) *E. verrucosa*; (B) *L.* sarmentosa and (C) *P. grayi*.

On the other hand, the species *P. grayi* show the lowest maximum variation in total branch length in the multispecific low-density treatment at 193 days after deployment (-7.99cm total variation). *Eunicella verrucosa* increased total branch length in the first 2 monitoring followed by a decrease in the winter months followed by a new increase. The pattern for *L. sarmentosa* seems more complex, where for the low-density treatment this species decreased in total branch length in the first 3 monitoring followed by an increase. For the high-density treatment this species decreased in total branch length in the first 2 monitoring followed by an increase until the 4th monitoring followed by a new decrease.

Compared to the total branch length, the magnitude of variation in colonies maximum height was much smaller, although with the same patterns as total branch length (Figure S3.6- supplementary materials). The average (±SE) maximum height variation (i.e. final maximum height subtracted the initial maximum height) of the transplants after 8 months was -0.52cm (±0.39cm) independent on the treatment and of species (Table S3.1- supplementary materials).

3.5. Discussion

The results of this study show that 90% of the corals transplanted were still attached after the first 3 months and 72% after 8 months. In general, the restoration failure can be due to two main factors: attachment failure and environmental factors (Linares et al., 2008; Montseny et al., 2019). In this study, ~10% of the colonies transplanted were detached from the artificial reefs, while the remaining colonies survived and were attached after the first 3 months, indicating that the technique used in this study was successful. The principal decrease in attachment of the transplants occurred during the winter period (January to March). The artificial reefs were deployed at a relatively shallow depth (20m) in an area characterized by its exposure to North Atlantic swells and storms that cause high-energy waves (Pacheco et al., 2017), which could explain the decrease in attachment success that occurred during the first months of the year. Edwards and Clark (1999), in their review, reported that a significant proportion of transplants can be lost, even when apparently well secured, when transplantation sites are exposed to extreme weather conditions. Additionally, some colonies may have been detached due to interactions with anthropogenic activities, particularly recreational and professional fishing, as several types of gear were found near or on the artificial reefs deployed (S 3.7- supplementary material).

In general, the attachment success of *P. grayi* colonies was lower than that of the other study species in both multispecific treatments (low- and high-density). Such attachment failure can be partially explained by the percentage of colonies with tissue necrosis present after the 8 months (100%), which could weaken the supporting axis of the colonies resulting in breakage. For instance, Hall-Spencer et al. (2007) reported that necrotic tissue of *E. verrucosa* presented a shrinking of the mesoglea and loosely packed sclerites (microscopic calcareous elements conferring colony stiffness) in areas with necrotic tissue, making the coenchyme fragile. At the moment of deployment, an average 33% of the colonies already presented necrotic tissue. This was mainly due to the origin of the colonies (i.e. incidental catches from fishing) and the prolonged exposure to sub-optimal aquaria conditions in which the colonies were maintained until transplantation (i.e. no control in water temperature and closed seawater system). Yet, after 8 months, we report the same overall percentage of colonies presenting necrotic tissue (33%). The proportion of colonies with necrotic tissue decreased over time in the monospecific low-density treatment, remained somewhat constant for the monospecific high-density and multispecific low-density treatments, and increased over time. for the multispecific high-density treatment. This increase can be explained by the increase of colonies of *L. sarmentosa* (50%) and *P. grayi* (100%) with necrotic tissue in this treatment, which suggests these species are more sensitive to contact with the fishing gear and manipulation.

3.5.1. Coral transplant survival

Although the time frame of this study included only 8 months of monitoring, which is a short period of time to evaluate the survival of the transplants, it still gives a strong indication of what the survival will be 1 year after transplantation. The results of this study showed that colonies in the monospecific low-density treatment had lower survival over the 8 months of monitoring, although not statistically significant. However, due to the overall low number of replicate artificial reefs (n=3), the lack of a balanced experimental design (i.e. same number of transplants from each species in the multispecific treatments) and the lack of monospecific treatments for the two species used in the multispecific treatments (i.e. *L. sarmentosa* and *P. grayi*) it is difficult to draw definitive conclusions about the treatments effect. Consequently, additional research would be needed to test the presence of real treatment effect.

For all treatments presented here coral survival was higher than 75%, which shows that, independently of the treatment, species survival was considerably good compared with previous studies. For instance, we report an 82% survival for *E. verrucosa* and 67% survival for *P. grayi* and *L. sarmentosa* after 8 months. In their review, Montero-Serra et al. (2018) reported an annual mean survival of transplants of 60% ranging from 30% to 100% for the species *Eunicella* *singularis*, *E. verrucosa*, *Paramuricea clavata* and *Corallium rubrum* in the Mediterranean sea. In that study, *C. rubrum* was the species that showed the highest survival (100%) and *E. verrucosa* the lowest (30%). In addition, Fava et al. (2010) reported an average survival of 40% and 30% for transplants of *E. verrucosa* in the Mediterranean sea, 8 months and one year after of transplantation, respectively. Comparing the results obtained in this study with the results obtained by Fava et al. (2010), we report a 2-fold increase in survival of the species *E. verrucosa* after 8 months. The success of this species can be associated with its broader depth distribution and subsequent adaptability to different environmental conditions, when compared with the other two species.

The survivorship of the *Paramuricea grayi* transplants was expected to be lower than the other species used as this species, having more defined deep waters affinities, presented high tissue oxidation when momentarily exposed to air (i.e. 1-3 minutes when removing colonies from the nets) and aquaria condition (e.g. high temperature and low water flow), which indicates the species is less resilient to manipulation and environmental variability. The tissue oxidation could have influenced the survival in this species as 50% of the colonies had already developed tissue necrosis at the time of transplantation and only a few colonies remained attached after 8 months of monitoring (25%). Such tissue degradation could be explained mainly due to temporary air exposure and poorly aquaria conditions, which appears to stress the colonies, causing tissue degradation when enduring prolonged exposure. Montseny et al. (2019) made similar observations for the sister species *Paramuricea clavata*, which showed rapid degradation of the living tissue and high mortality when kept in culture. Our study corroborates the observations made by Montseny et al. (2019) for the few specimens of *P. clavata* that we maintained in the tanks. Biological interactions in the field such as entanglement of drifting seaweeds may have further reduced survival of *P. grayi* as seaweeds prevent colonies from opening the polyps and this effect can be more severe in already debilitated transplants (Weinberg, 1979).

3.5.2. Coral transplant growth

This study provides support for the complex dynamics of growth in gorgonian corals, showing that breakage of branches is a frequent process as evidenced by the high variability in total branch length over time. Indeed, breakage of colony fragments between monitoring times was obvious for multiple colonies when analysing the photographs. The high breakage that was observed in this study could be explained by water turbulence and flow, which are generally more pronounced at lower depths, especially during storms and strong current conditions (Linares et al., 2008) as is often the case in Sagres. Additionally, negative growth due to colony breakage has been previously recognized in several other gorgonian species, including *E. verrucosa* (Coz et al., 2012) and *P. clavata* (Coma et al., 1998). Fava et al. (2010) also reported a similar growth pattern, where colonies under stressful conditions exhibited negative growth followed by positive growth when such conditions were mitigated.

On average, most colonies did not increase their total branch length (-0.32±5.97cm) over the 8 months of monitoring despite the potential to grow quite significantly. For instance, the maximum total branch length rate (i.e. growth in total branch length divided by the number of days) observed for *E. verrucosa* was 1.37cm/day over 24 days after transplantation. For *L. sarmentosa*, a maximum total branch length rate of 0.73cm/day was observed after 193 days after transplantation, corresponding to a growth of 113.42cm, whereas *P. grayi* attained a maximum increase in total branch length of 21.90cm with an estimated growth rate of 0.91cm/day after 24 days after transplantation. Clearly, all three species studied can grow new tissue fairly rapidly, in particular *E. verrucosa* in high densities, alone or in the presence of other species.

Comparing the results of total branch length and maximum height, it is clear that the growth dynamics of the colonies were better captured by the variation in total branch length. This is in accordance with Weinbauer and Velimirov (1996), Lasker et al. (2003) and Coz et al. (2012), which defend that the height of the colonies is a poor descriptor of growth in gorgonians and that total branch length is a better option.

The latter better captures the small changes in growth of branching organisms resulting from partial mortality due to processes such as breakage and predation. Despite the metric total branch length being more reliable to describe the growth patterns in branching structures, it is only possible to capture the previous mentioned pattern using photographic records and frequent monitoring.

3.5.3. Final remarks

While the timeline of this study was short (8 months) and long-term monitoring is required to fully understand the success of the transplantation strategy adopted here, this study supports the feasibility of using coral biomass from deep origin in restoration actions at shallow depths for species that have a broad bathymetric range. However, it will be crucial to evaluate the role of other processes such as local adaptation to depth on transplantation of coral biomass from deep to shallow environments. Additionally, as previous studies in the Mediterranean (Montseny et al., 2019, 2020), this study confirms that a large number of coral species captured as bycatch by artisanal fisheries can be successfully rescued and used to develop restoration actions of coral gardens and CWCs.

Although the species chosen were based on the natural assemblage present at the deployment area, *P. grayi* had a lower tolerance to stress resulting from contact with the nets and air, as well as from being kept at suboptimal aquaria conditions. While the magnitude of stress can be significantly reduced by improving the *ex situ* culture conditions and reducing the time until transplantation (21-42 days in this study), more resilient species like *E. verrucosa* may prove a better candidate for transplantation actions, as this species did not show signs of stress in aquaria conditions and had the highest attachment success and survival. This species is also listed as vulnerable in the IUCN Red List since 1996 (IUCN, 1996) due to the multiple threats it faces, including fisheries impact. More actions of habitat restoration focused on this species should be developed, as this species is commonly caught as bycatch in fisheries (Chapter 2) and it is an ideal candidate for restoration actions.

This study proved that coral bycatch can be used in restoration actions without the possible limitations and pitfalls that methods using donor population fragments face, as it circumvents the negative impacts to the donor reefs (Rinkevich, 2014). However, because transplants are from deep origin, genetic differences between transplants and shallow natural occurring colonies may occur, which can cause an overall reduction in fitness of the restored population (reviewed in Baums, 2008). For instance, Costantini et al. (2016) reported genetic divergence of colonies above and below 40m for the species *Eunicella singularis*. This could be a pitfall, as colonies at shallow depths can be adapted to the high light intensity and high-energy wave climate, while the transplants of deep origin are not, influencing the survival and growth of the transplants. Additionally, as transplants come from different origin than the natural populations in the restoration site, other genetic problems can occur, namely genetic sweeps, founder effect and inbreeding (Baums, 2008).

While using artificial reefs like those built here was time- and cost-effective for transplanting many coral colonies, the durability of such reefs can be a pitfall as storms and high-energy waves may easily destroy these structures, potentially damaging or killing the transplants. Building more robust structures (e.g. solid cement blocks) can be a significant improvement as such structures would be more durable. Additionally, the deployment method could be improved in order to be able to restore deeper environments, as the deployment was achieved using ropes to lower the artificial reefs and divers were required to position them in the desired area. For instance, trigger mechanisms to release structures from the ropes together with ROVs could improve the deployment of such structures.

Overall, the multispecific assemblage did not seem to affect the survival of *Eunicella verrucosa*, suggesting that other species can be used in restoration actions together with *E. verrucosa*. In addition, increasing the density of colonies appears possible as no significant differences in survival and growth between the different densities were detected. This study highlights that the 3 species used have greater growth than previously appreciated as gorgonians species are often considered slow-growing species with an overall growth rate of only a few cm per year when considering colony height (Coma et al., 1998). In this study, we show that these species can grow considerably in one month, but due to environmental factors and anthropogenic impact which cause branches to break, the species have an overall low colony net growth over the course of a year.

This study contributed to the development of alternative restoration actions, as well as the general knowledge of growth dynamics of octocorals. Additional research is needed to evaluate the potential of using artificial reefs with different species as different species have different life traits. Nevertheless, the collaboration with fishermen proved once more to be useful to increase knowledge of coral species biological functions and how scientists and fishermen can work together to protect such vulnerable species.

Acknowledgment

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4. Supplementary materials

Chapter 2: High Coral Bycatch in Bottom-set Gillnet Coastal Fisheries Reveals Rich Coral Habitats in Southern Portugal

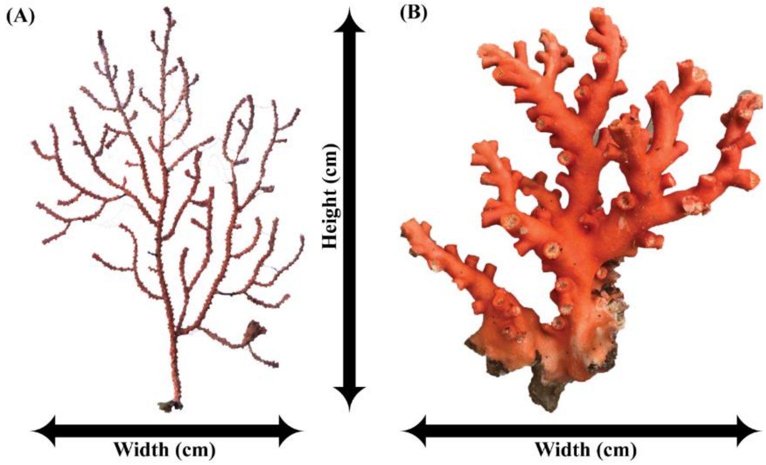

Figure S2.1. Size orientation (height and width) for the specimens caught as bycatch in bottom-set gillnets during the two sampling seasons in Sagres (southern Portugal). (A) Gorgonians orientation. (B) Scleractinians orientation.

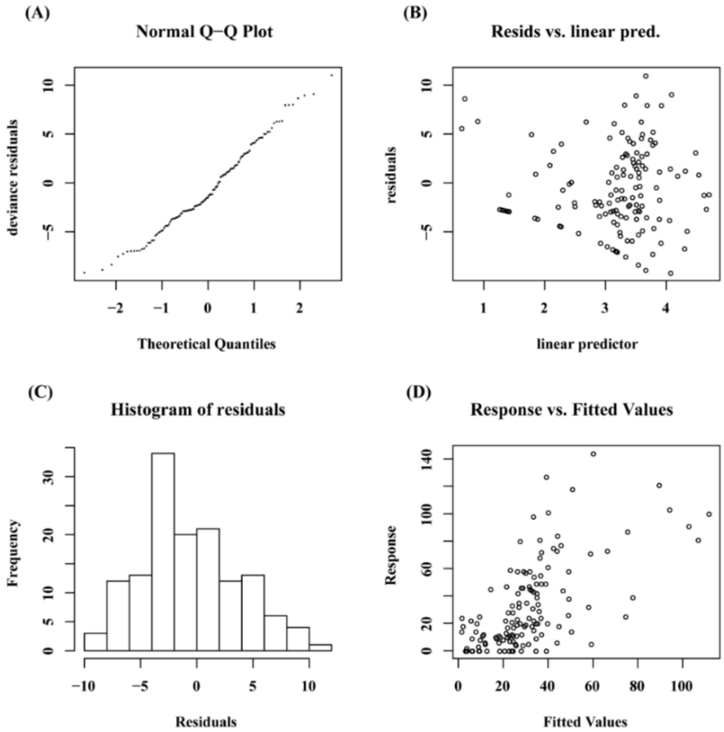

Figure S2.2. Poisson generalized additive model (GAM) residuals distribution of the model with 4 variables: depth, target species, net length and mesh size and no interaction to explain the amount of corals caught as bycatch from bottom-set gillnets during two sampling seasons in Sagres (southern Portugal). (A) QQplot of deviance residuals vs. theorical quantiles. (B) Scatter plot of residuals vs. linear predictor. (C) Residual distribution in histogram with frequencies associated. (D) Scatterplot with response vs. fitted values.

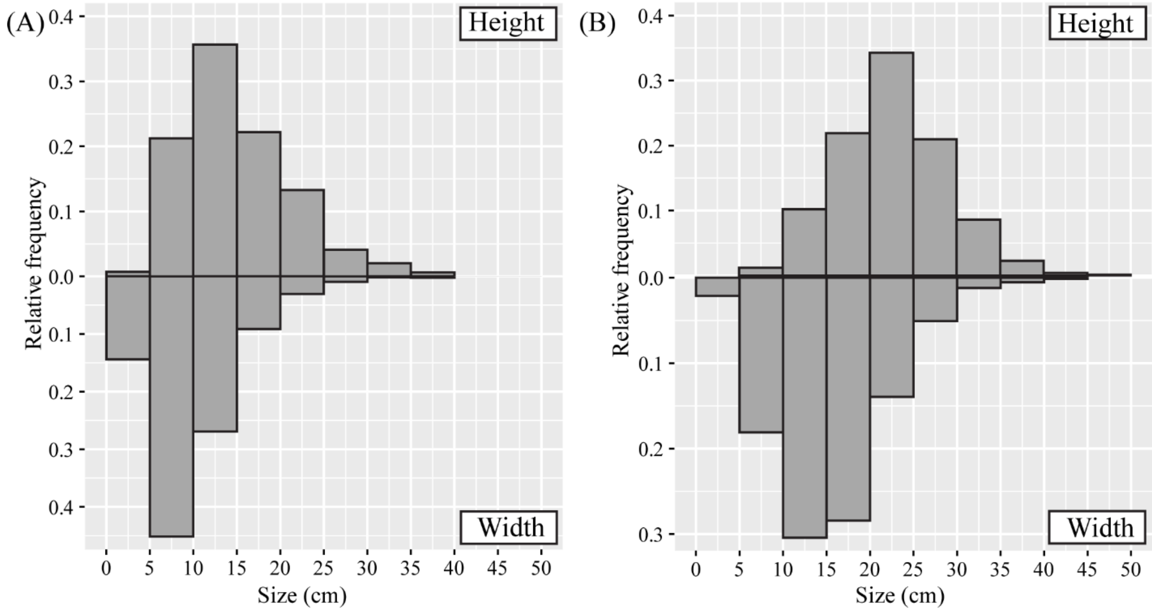

Figure S2.3. Size distribution (height and width) of the whole colonies of the species most affected: Paramuricea grayi and Eunicella verrucosa caught as bycatch in bottom-set gillnets during the two sampling seasons in Sagres (southern Portugal). (A) Height (cm) and width (cm) distribution of P. grayi whole colonies. (B) Height (cm) and width (cm) distribution of E. verrucosa whole colonies.

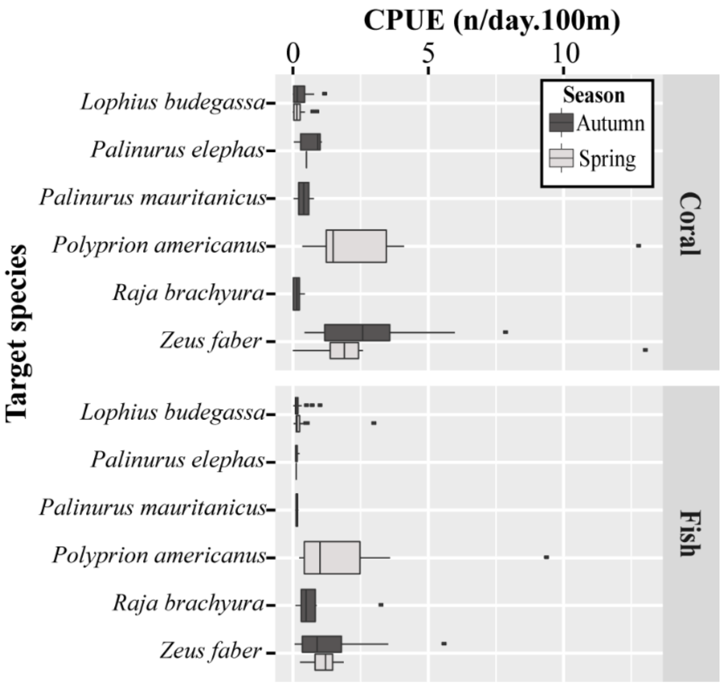

Figure S2.4. Coral and target species fishing effort distribution according to target species and sampling season for the study of coral bycatch of bottom-set gillnets documentation during two sampling seasons in Sagres (southern Portugal). Fishing effort was calculated as the catch per unit effort (CPUE) and represents the number of specimens (fish/lobster or coral) as a function of the product of the net soaking time (days) per 100m of net.

Table S2.1. Poisson generalized additive model (GAM) output of the model with 4 variables: depth, target species, net length and mesh size and no interaction to explain the amount of corals caught as bycatch from bottom-set gillnets during two sampling seasons in Sagres (southern Portugal).

Family: Quasi-Poisson
Link function: Log
Formula: No of Corals ~ Target Species + Net length + Mesh Size + Depth

Parametric coefficients:	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2.06E+00	7.23E-01	2.845	0.0052
Target Species *Palinurus elephas*	1.03E+00	4.31E-01	2.397	0.0180
Target Species *Palinurus mauritanicus*	8.89E-01	6.61E-01	1.345	0.1810
Target Species *Polyprion americanus*	-1.31E-01	5.60E-01	-0.234	0.8152
Target Species *Raja brachyura*	-1.13E+00	4.72E-01	-2.391	0.0182
Target Species *Zeus faber*	4.73E-02	4.87E-01	0.097	0.9227
Net length	2.39E-04	6.01E-05	3.977	0.0001
Mesh size 200	1.78E+00	5.71E-01	3.124	0.0022
Mesh size 240	1.45E+00	6.80E-01	2.125	0.0355
Depth	-7.08E-03	1.82E-03	-3.898	0.0002

R-sq.(adj) = 0.379 **Deviance explained** = 40.3%
GCV = 21.532 **Scale est.** = 18.932 **n** = 139

Chapter 3: The utility of incidental coral catches from artisanal fisheries in restoration measures of coral gardens: The effect of density and species composition on coral transplants

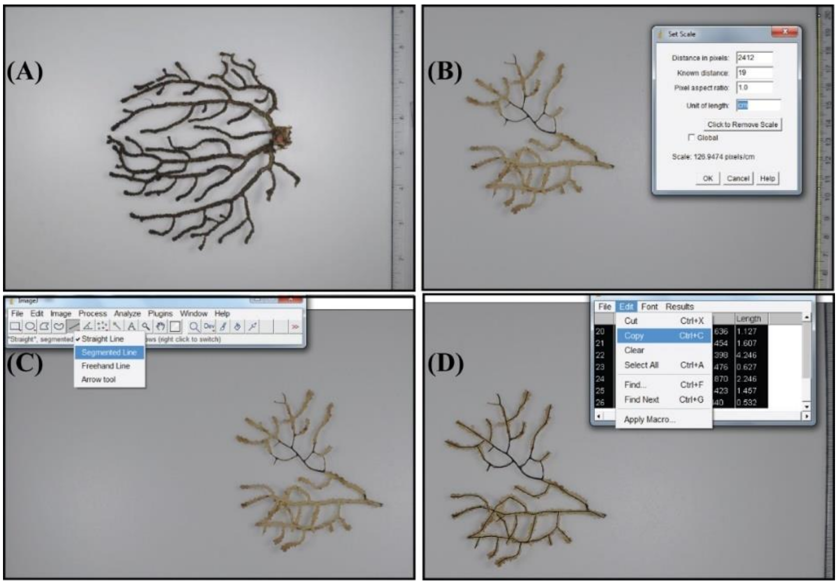

Figure S3.1. Method used to measure total branch length, maximum height and maximum width in Image J software v1.8.0 in the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). (A) raw image of the coral; (B) Calibration of the image; (C) Selection of segmented line to measure each branch and (D) All branches measured and final data table.

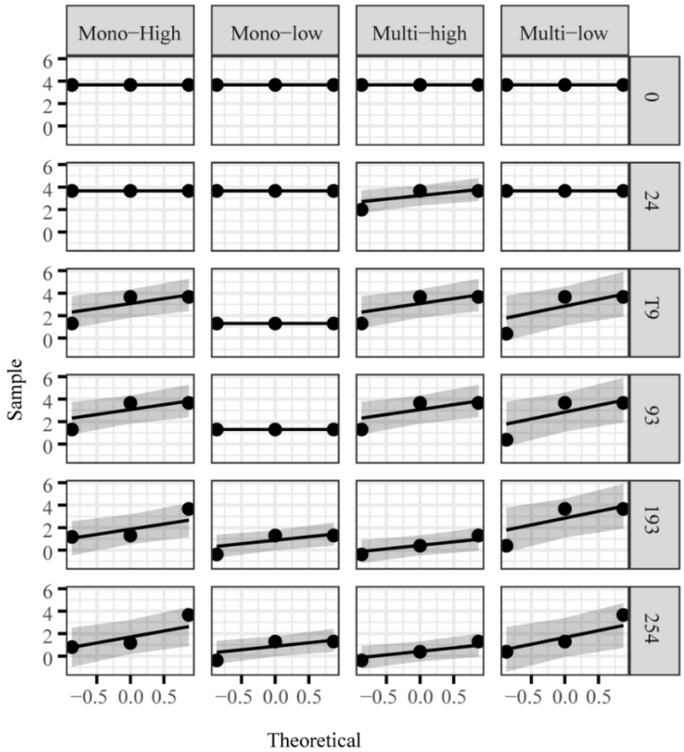

Figure S3.2. Residuals output of the two-way repeated measures ANOVA test for the survival (i.e. percentage of colonies alive) of each treatment throughout monitoring time in the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal).

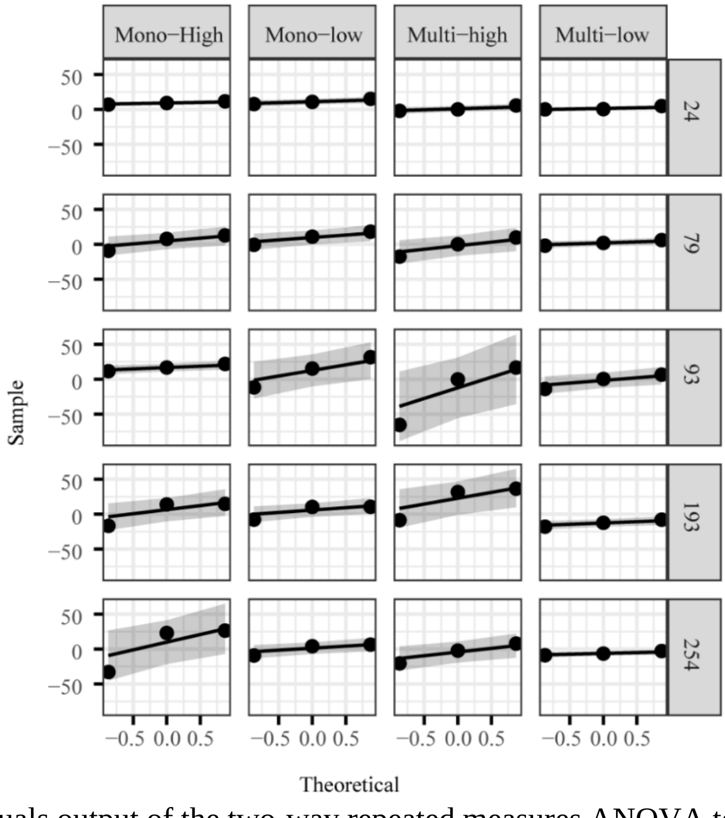

Figure S3.3. Residuals output of the two-way repeated measures ANOVA test for the variation in total branch length of each treatment throughout monitoring time in the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal).

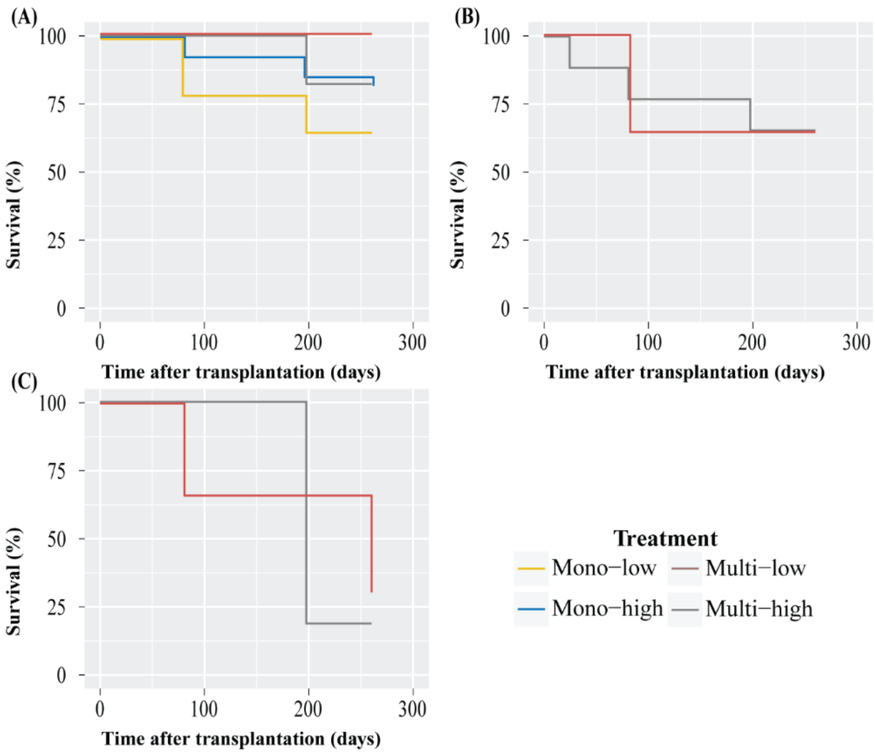

Figure S3.4. Average survival (i.e. colonies alive) of the 3 species over time in the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). (A) *Eunicella verrucosa*; (B) *Leptogorgia sarmentosa* and (C) *Paramuricea grayi*.

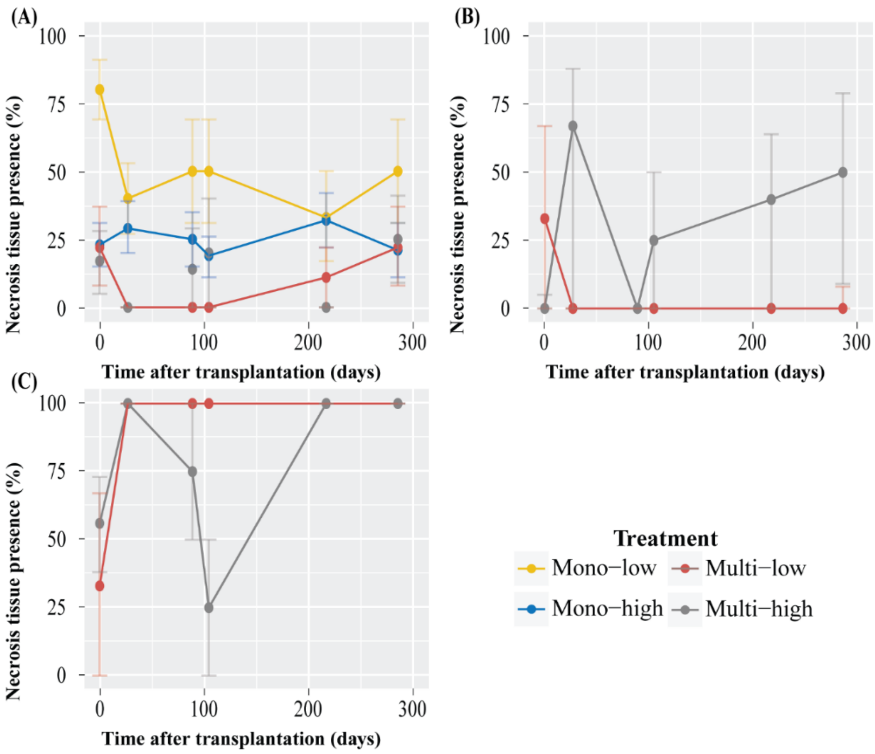

Figure S3.5. Variation in colony tissue necrosis throughout the 8 months after deployment in the study area for the pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as percentage of colonies with tissue necrosis and error bar for the standard error. (A) irrespective of species; (B) *Eunicella verrucosa*; (C) *Leptogorgia sarmentosa* and (C) *Paramuricea grayi*.

Table S3.1. Variation in maximum height growth of the transplanted corals after 8 months of deployment in the study area of a pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as average (cm) ± standard error (cm) of the variation of growth in maximum height after 8 months of monitoring.

Species	Monospecific Treatment		Multispecific Treatment	
	Low-density	High-density	Low-density	High-density
Eunicella verrucosa	-0.99±0.73	0.91± 0.59	-1.33±0.79	-0.64±0.48
Leptogorgia sarmentosa			-2.40±0.78	-2.80±2.28
Paramuricea grayi			-2.24±0.00	-2.60±4.29

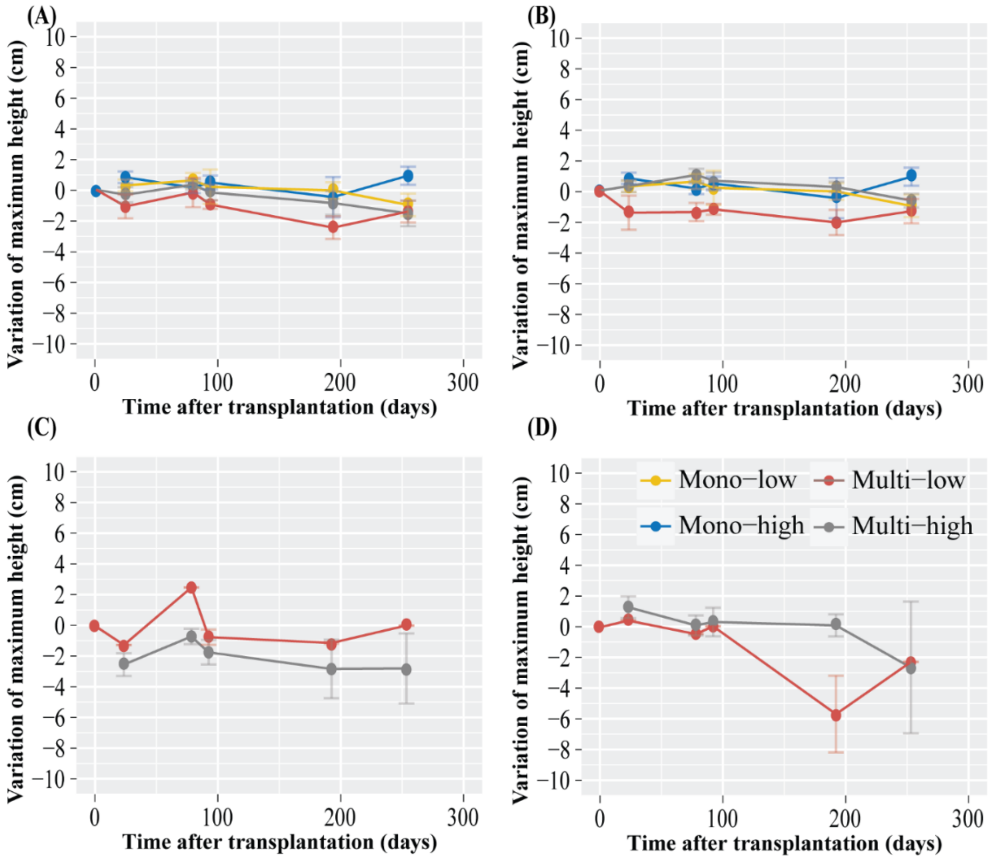

Figure S3.6. Variation in maximum height throughout the 8 months after deployment in the study area for a pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). Values presented as colonies variation of maximum height (cm) to each time point in each artificial reef, with standard error showed as error bars. (A) irrespective of species; (B) *Eunicella verrucosa*; (C) *Leptogorgia sarmentosa* and (C) *Paramuricea grayi*. Values presented as colonies variation of total branch length (cm) to each time point (irrespective of species) in each artificial reef, with standard error showed as error bars.

(A) (B)

Figure S3.7. Anthropogenic impact visible on or near by the restoration site of a pilot study of restoration using coral bycatch originating from gillnets in Sagres (southern Portugal). (A) Trap at 2 meters from the artificial reefs; (B) Fishing gear entangled on the artificial reef.