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Assessing the effect of temperate MPAs on elasmobranch communities

By

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ABSTRACT

Global chondrichthyan (sharks, skates, rays and chimaeras) populations are experiencing alarming declines, driven by intense targeted and incidental extraction. Marine Protected Areas (MPAs) represent one potential solution, which has gained traction in recent years. When implemented effectively, MPAs demonstrate potential to rebuild populations and enable ecosystem recovery. However, their value as an elasmobranch conservation tool remains contested, particularly in temperate waters such as the UK. One essential component of MPA efficacy is the implementation of robust ecological monitoring regimes that allow species trajectories to be characterised and responded to, in real-time. However, several challenges, inherent to both elasmobranchs and temperate marine environments, currently impede adequate elasmobranch surveillance inside MPAs. This thesis addressed these two interlinked components of elasmobranch conservation by 1) exploring the drivers of temperate MPA success and 2) investigating opportunities for elasmobranch monitoring advancements. A literature review was conducted to explore the determinants of MPA success for temperate elasmobranch conservation. Meanwhile, novel monitoring opportunities presented by technological developments were explored, in relation to current method limitations. This was aided by an in-depth field study exploring the impact of Lyme Bay MPA on the elasmobranch community, using a 12-year BRUV dataset. Finally, a drifting pelagic BRUV was developed to address specific difficulties associated with surveying pelagic sharks and their wider food webs. This thesis found that MPAs exhibit potential to benefit temperate elasmobranchs, but their success varies vastly between contexts depending on a variety of social and biophysical factors. Furthermore, studying Lyme Bay MPA identified minimal robust evidence of benefits on the elasmobranch community, and these were mainly afforded to a small-bodied, fast-growing shark (*Scyliorhinus canicula*). Finally, the pelagic drifting BRUV failed to detect pelagic sharks, but demonstrated value for characterising spatial variation in the wider pelagic food web. Overall, this work indicates that temperate elasmobranch MPAs can represent an effective elasmobranch conservation tool when the necessary guardrails are in place. Furthermore, to guarantee comprehensive elasmobranch protection, MPA establishment should be supported by robust ecological monitoring and a wider network of target and limit-based conservation strategies.

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Introduction

Elasmobranchs (sharks, skates and rays) represent a highly successful and ancient taxon of cartilaginous fishes, with an expansive history tracing back to their divergence from actinopterygians (ray-finned fishes) 400 – 450 million years ago (Long, 1995; Nelson, 2006; Stein et al., 2018). Their diversification throughout the marine realm often positioned them near the top of marine food webs (Stevens, 2000; Heupel et al., 2014; Roff et al., 2016) where they have remained for millions of years, exerting top-down control on lower trophic levels (Ferretti et al., 2010; Heithaus et al., 2012). Elasmobranchs remarkably persisted through four of the "big five" mass extinction events, including the end-Cretaceous extinction (Bazzi et al., 2021) which eradicated 76% of all species on Earth (Jablonski, 1991). However, their evolutionary prosperity has presented no barrier to human exploitation, which has decimated global populations in a matter of centuries (Dulvy et al., 2008; Dulvy et al., 2021). Elasmobranchs continue to be subject to intensive commercial extraction, driven by both targeted efforts to obtain lucrative elasmobranch products (e.g. meat, fins, squalene) and retention as a valuable bycatch species in other fisheries (e.g. billfish, tuna and prawn fisheries (Stobutzki et al., 2000; Molina & Cooke, 2012; Worm et al., 2013)). Consequently, current estimates indicate that 32.6% of all Chondrichthyan (elasmobranchs and chimeras) species are approaching extinction according to IUCN Red List criteria (Dulvy et al., 2021) signifying the onset of a global crisis.

Equipped with this understanding, marine resource managers have reached a crossroads, whereby the interventions chosen in the coming decade will define the capacity for elasmobranch species recovery. An array of potential conservation strategies exist, from fishing restrictions (e.g. quotas, landing size limits) to market regulations (e.g. fin trade bans, CITES appendices) and these have been adopted at various scales and with differing degrees of success (Tolotti et al., 2015; Simpfendorfer & Dulvy, 2017; Ferretti et al., 2020; Jorgensen et al., 2022). While there is consensus that integrated implementation of multiple strategies is required for optimal protection, much remains unknown about the specific value of marine protected areas (MPAs) as an elasmobranch management tool (Jorgensen et al., 2022).

MPAs can be used to limit or exclude fishing activity from a discrete area of marine habitat, both for the benefit of marine populations and to reverse habitat degradation (Gell & Roberts, 2003; Duarte et al., 2020). However, their appropriateness for protecting highly mobile species has triggered considerable debate (Roberts, 2000; Game et al., 2009; Breen et al., 2015) and their success is contingent on a range of factors (Edgar et al., 2014; MacKeracher et al., 2019). Despite this, considerable growth in MPA establishment over the past decade has been driven explicitly by elasmobranch conservation (MPA Atlas, 2016; Davidson & Dulvy, 2017) representing a substantial investment of conservation resources. To improve the management of existing MPAs and optimise designation of new MPAs, a range of evidence gaps must first be populated. Firstly, elasmobranch research has disproportionately focussed on large, apex predatory sharks (particularly Sphyrnidae and Carcharhinidae (e.g. Hayes et al., 2009; Curtis et al., 2014; Pacoureau et al., 2021)), leading to a greater understanding of these populations relative to smaller sharks and batoids (skates and rays). Meanwhile, our current knowledge of MPA performance is based predominantly on tropical case studies (MacKeracher et al., 2019), whilst temperate MPA examples, particularly in the Northern Hemisphere, are scarce and their efficacy remains comparatively inconclusive (Breen et al., 2015). Of particular priority is determining the underlying conditions (e.g. MPA management style, size, location) of MPA success, and identifying the elasmobranch species that may benefit from their establishment.

Furthermore, inextricably linked to MPA effectiveness is the ability to monitor population responses following their initiation (Fox et al., 2014; Ahmadia et al., 2015). Without adequate monitoring, conservation outcomes cannot be evaluated relative to objectives, which impedes the adaptive management necessary to protect spatiotemporally dynamic populations (Haney & Power, 1996; Rouphael, 2020). However, accurate assessment of elasmobranch populations is complicated by their scarcity as depleted apex and mesopredators (Dulvy et al., 2021), and by method limitations which make in-situ observation logistically challenging, costly and often destructive (Port et al., 2016; Talwar et al., 2020). Challenges are exacerbated further for: 1) pelagic species, due to even lower abundances, patchy distributions, and less accessible habitats (Letessier et al., 2017) and 2) in temperate waters where water visibility often represents a constraint for visual methods (Unsworth et al., 2014). Resultantly, elasmobranch populations assessments have historically depended on fishery landings data and fishery-independent extractive surveys (Clarke et al., 2008; Letessier et al., 2017). However, these too are constrained by low taxonomic resolution (Dulvy et al., 2000; Clarke et al., 2008), underreporting of catch (Worm et al., 2013) and are inappropriate for study of vulnerable populations in MPAs. Overall, less than 5% of elasmobranch species have been directly or indirectly assessed with fisheries stock assessments (Cortés et al., 2012; Simpfendorfer & Dulvy 2017) and 12.9% of Chondrichthyans remain Data Deficient (DD) meaning their conservation status cannot be evaluated (Dulvy et al., 2021).

There is a clear need for novel methodologies to advance the monitoring of elasmobranch populations, including those inside MPAs and facilitate a move away from reliance on fishery-dependent and extractive surveillance. Several technologies offer encouraging alternatives, ranging from molecular tools such as eDNA (Boussarie et al., 2018) and visual methods (e.g. drones (Butcher et al., 2021)). While many of these tools have not been fully evaluated in the specific context of elasmobranch monitoring in temperate MPAs, their use in various contexts has demonstrated potential to revolutionise elasmobranch monitoring. Particularly encouraging, is the emergence of pelagic video monitoring methods (e.g. pelagic (BRUVs), animal borne video systems (ABVSs)), which may overcome the magnified challenges associated with monitoring pelagic elasmobranchs (Letessier et al., 2017; Chapple et al., 2021). Pelagic BRUVs have demonstrated capacity to non-invasively characterise pelagic communities in tropical waters (Santana-Garcon et al., 2014a; Bouchet & Meeuwig, 2015), however, there is not yet any published literature employing this method in the UK.

This thesis aims to address several of the knowledge gaps formerly highlighted to optimise the future use of temperate elasmobranch MPAs and their monitoring. The thesis is structured in the following way:

Chapter 1 aims to explore how MPA design, management and monitoring could be optimised to benefit temperate elasmobranchs. This was achieved by conducting a literature review with the following objectives:

- Determine the major drivers of MPA success in the specific context of temperate elasmobranch conservation.
- Characterise the challenges associated with monitoring elasmobranchs in temperate MPAs and identify opportunities for advancement.
- Recommend a best practice protocol to improve the future adoption of temperate elasmobranch MPAs.

The aim of **Chapter 2** was to characterise the effect of Lyme Bay MPA on the elasmobranch community in order to understand the value of partially-protected, non-elasmobranch focussed MPAs to elasmobranch conservation. Home to a range of priority species (e.g. Tope, Rajidae Skates, Smoothounds), this study set out to determine which elasmobranch species, if any, were afforded benefits and to characterise potential underlying drivers. A secondary goal was to take advantage of the extensive BRUV survey dataset to provide a detailed fishery-independent account of the overlooked elasmobranch community. This was broken down into the following objectives:

- Determine the effect of Lyme Bay MPA on elasmobranch abundance.
- Determine the effect of Lyme Bay MPA on elasmobranch diversity.
- Explore the role of elasmobranch exploitation and habitat associations in driving MPA efficacy.
- Examine the significance of the Lyme Bay elasmobranch community in relation to wider research

Finally, **Chapter 3** honed-in on the specific challenges related to surveying both pelagic elasmobranchs and the pelagic component of temperate MPAs. This chapter set out to develop and test a drifting pelagic BRUV, highlighting advantages and limitations to guide its future use. The following objectives were achieved:

- Design and build six pelagic BRUV units.
- Design and deliver a pilot study to demonstrate the potential of pelagic BRUVs as a temperate research tool.
- Quantify spatial (horizontal and vertical) variation in pelagic communities inside Lyme Bay MPA.

Chapter 1: How can MPA design, management and monitoring be optimised for temperate elasmobranch conservation?

1.1. Introduction

Elasmobranchs (sharks, skates and rays) are confronted with a multitude of threats, from anthropogenic pollution to habitat destruction (Dulvy et al., 2014). However, overfishing, driven by high demand for elasmobranch products (e.g. fins and meat) (Worm et al., 2013) and exacerbated by substantial bycatch rates (Molina & Cooke, 2012) has had the most detrimental impact on elasmobranchs globally (Dulvy et al., 2021). Fishing has caused over one third of chondrichthyans (elasmobranchs and chimeras) to be considered threatened globally (Dulvy et al., 2021) and depleted several UK elasmobranch populations, including large-bodied skates, and pelagic sharks (Walker and Heessen, 1996; Rogers et al., 1999; Ellis et al., 2005; Clarke et al., 2008). Furthermore, elasmobranchs generally exhibit K-selected life history strategies (e.g. slow growth and low fecundity (Cortés, 2000)) which inhibit their recovery, making them extremely vulnerable to overexploitation (Dulvy et al., 2008; Worm et al., 2013). This is especially alarming considering the crucial role elasmobranchs play in maintaining ecosystem health, structure and function (Myers et al., 2007; Ruppert et al., 2013; Roff et al., 2016). In particular, the removal of elasmobranchs at apex predator level can trigger knock-on impacts throughout the food web (e.g. trophic cascades) due to the deregulation of lower trophic levels (Heithaus et al., 2007; Ruppert et al., 2013).

The many conservation strategies proposed to tackle elasmobranch declines can be broadly condensed into: target-based and limit-based strategies (Shiffman & Hammerschlag, 2016). Target-based strategies (e.g. catch and size limits) aim to facilitate sustainable exploitation of elasmobranch populations by regulating landings with quotas and limits (Walker, 1998; Worm et al., 2014). Unfortunately, these policies are difficult to enforce, require detailed prior knowledge of the target species and rely on considerable supervision and fishery management infrastructure (Shiffman & Hammerschlag, 2016). Consequently, only 9% of global elasmobranch catch is considered biologically sustainable (Simpfendorfer & Dulvy, 2017), and these fisheries are typified by exploitation of relatively productive, small-bodied elasmobranchs such as the Gummy Shark *(Mustelus antarcticus* (Walker, 1998; Shiffman & Hammerschlag, 2016)).

Alternatively, limit-based strategies employ spatial management to exclude elasmobranch threats from a clearly defined area. These include marine protected areas (MPAs) which may (e.g. shark sanctuaries) or may not be designated specifically for elasmobranchs. These can be easier to manage than nuanced, context specific quotas and limits, since any fishing activity can be clearly identified as illegal (Shiffman & Hammerschlag, 2016), however they too require considerable management infrastructure (MacKeracher et al., 2019). Evidence is mounting to support the use of MPAs for elasmobranch conservation, despite doubts over their efficacy for protecting highly mobile species (Shipp, 2003; White et al., 2013; Thorburn et al., 2015; Oh et al., 2017). Whilst the performance of MPAs in tropical regions and for a select number of species (e.g. tiger sharks (*Galeocerdo cuvier)* and blacktip reef sharks (*Carcharhinus melanopterus*)) is relatively well-documented (Acuna-Marrero et al., 2017; Daly et al., 2018; Speed et al., 2018; Gallagher et al., 2021), fewer studies have investigated the value of temperate MPAs. Therefore, before MPAs can be implemented as a core elasmobranch conservation method, the true value of temperate MPAs should be further investigated and crucial knowledge gaps must be addressed. These include identifying the specific conditions under which MPAs are successful and for which species benefits can be afforded (De Santo, 2013; Pala, 2013; Davidson & Dulvy, 2017).

Furthermore, it is becoming widely agreed that no conservation strategy should be considered complete without the establishment of a complementary monitoring regime. In the absence of adequate surveillance, neither target nor limit-based strategies can be appropriately evaluated or adapted, and the status of target populations cannot be determined (Leverington et al., 2010; Ahmadia et al., 2015). Unfortunately, a lack of effective monitoring methods and regimes has led to overdependence on fishery landings data for characterising elasmobranch population trends (Letessier et al., 2017) which are often incomplete and display low taxonomic resolution (Clarke et al., 2008; Griffiths et al., 2013). Meanwhile, existing fishery-independent survey techniques exhibit inherent limitations and biases (Stat et al., 2018), particularly in temperate waters where water turbidity often represents a barrier for visual methods. Monitoring of elasmobranchs is further impeded by their mobile and often elusive nature (Letessier et al., 2017; Pikitch, 2018) which makes observation in-situ challenging. Together, these roadblocks have allowed elasmobranch declines in the UK to go largely unnoticed or be detected retrospectively with little opportunity for intervention (Ellis et al., 2005; Port et al., 2016; Hiddink et al., 2019; Wall & Dulvy, 2021). There is therefore a clear need to explore alternative, real-time monitoring strategies and optimise existing methods for use on elasmobranchs to better support elasmobranch conservation efforts.

This paper aims to contribute to enhanced temperate elasmobranch conservation by exploring two key and complementary aspects of elasmobranch management. Firstly, the determinants of MPA success for temperate elasmobranchs will be investigated and summarised. Secondly, in order to advance elasmobranch MPA research, the key limitations of current elasmobranch monitoring methods will be analysed alongside opportunities presented by novel methods and technological innovations (e.g. eDNA and machine learning). Examples from the literature will be used to address these points and determine key avenues for future research, focussing wherever possible on temperate water examples. Finally, the findings of this review will be condensed into key ‘guardrails’ to guide and enhance the future use of temperate elasmobranch MPAs.

1.2. The drivers of MPA efficacy for temperate elasmobranch conservation

There is increasing evidence that MPAs can be highly effective for elasmobranch conservation under certain conditions. These can be categorised into: 1) biophysical drivers (natural factors intrinsic to focal species ecology and environment) and 2) social drivers (human-influenced factors) of MPA success (MacKeracher et al., 2019).

1.2.1. Biophysical drivers of temperate elasmobranch MPA success

Firstly, the ecology and behaviour of the focal elasmobranch species plays a crucial role in the success of MPAs. In particular, species mobility and spatial range relative to MPA size and location have received considerable attention in the literature (Table 1.1.) since this determines the amount of time the target species is exposed to and protected from fishing (Murawski et al., 2000). It is generally agreed that species exhibiting a high degree of site fidelity will benefit more from spatial protection than highly mobile species (Shipp, 2003; White et al., 2013; Thorburn et al., 2015; Oh et al., 2017). However, even highly mobile elasmobranch species can exhibit strong associations with small-scale habitats, either for feeding or for specific life-history stages (Lascelles et al., 2014; Doherty et al., 2017). Meaning that migratory species can be afforded MPA benefits when critical habitats are protected (Casselberry et al., 2020). For instance, migratory Tiger sharks (*Galeocerdo cuvier*) within the Bahamian shark sanctuary were found to spend 71% of their time in protected waters due to their strong associations with protected seagrass habitats for feeding (Gallagher et al., 2021). Similar findings were demonstrated in the Galapagos Marine Reserve, where *G. cuvier* exhibited a high degree of philopatry with areas of predictable and high prey availability (Acuña-Marrero et al., 2018). Site associations have also been identified in some highly mobile temperate species such as the Spiny spurdog (*S. acanthias* (Vince, 1991; Thorburn et al., 2015)) which may justify their potential suitability for spatial protection in certain areas (e.g. Loch Etive, Scotland).

Whilst it is well-established that spatial range varies between elasmobranch species, different populations of the same species can also exhibit varying degrees of site residency depending on; sex (Vince, 1991; Mucientes et al., 2009; Quieroz et al., 2010), ontogenetic stage (Thorburn et al., 2019) and in response to various abiotic factors (Schlaff et al., 2014). Meanwhile, advancements in telemetry-based research have revealed individual-level variability in movement behaviours. For instance, porbeagle sharks (*Lamna nasus)* tagged off the Southwest UK coast, displayed distinct individual departures in their use of vertical habitat. In shallower coastal waters (< 80m), some sharks exhibited no depth preference, whilst another displayed an association with surface waters during the day and moved into deeper water (> 20m) at night (Pade et al., 2009). Intraspecific variation in movement patterns, has been raised as a potential issue for the designation of MPAs, as spatial management may disproportionately increase the survival of less mobile individuals, ontogenetic stages or sexes (Stehfest et al., 2014) and may select for lower mobility over time (Dawson et al., 2006). Furthermore, the presence of inter and intraspecific variation in mobility highlights the danger of generalising movement behaviours at a species-level and the importance of using population-specific knowledge to evaluate the suitability of MPAs in each unique circumstance.

The value of MPAs can also be enhanced if critical habitats associated with key ontogenetic stages (e.g. parturition, mating) and important behaviours (e.g. feeding) are encompassed (Le Port et al., 2012; Albano et al., 2021; da Silva et al., 2021). In particular, discrete elasmobranch nursery areas are often advocated as ideal MPA locations, which if protected adequately could result in significant population growth (Murawski et al., 2000; Heupel et al. 2007; Heupel et al., 2018). For instance, the discovery of high densities of flapper skate (*Dipturus intermedius)* egg-cases, justified the recent (March 2021) establishment of the UKs first skate-focussed MPA in Scotland (Marine Scotland, 2021; The Red Rocks and Longay Nature Conservation Marine Protected Area (No. 2) Order 2021). Meanwhile, several studies have deemed MPAs to be successful based on their inclusion of nursery habitats (as defined in Heupel et al. (2007)), amongst other factors (Le Port et al., 2012; Oh et al., 2017). For example, a small (34 km^2) no-take MPA in South Africa considered highly valuable for the encompassed Smoothound (*Mustelus mustelus*) population, since it incorporates a pupping, nursery and feeding ground (da Silva et al., 2021). In contrast, Wiegand et al. (2011) argue that the optimum way to ensure population growth is to protect subadult and adult populations (particularly for k-selected species with late-age maturity and long lifespans (Cortés, 2002; Kinney & Simpfendorfer, 2009) since their relative contribution to population growth is greater than that of younger individuals. For this reason, conducting a comprehensive population viability analysis (PVA) for target species to determine the relative contribution of each size class to population growth, would aid the optimal protection of habitats.

Table 1.1. A summary of studies analysing the efficacy of temperate MPAs for elasmobranch conservation, including: the species studied, outcomes measured, survey method and evaluation of the MPA's success according to the author(s).

Study	Location	Elasmobranch(s) studied	Outcome(s) Measured	Survey Method	Evaluation of MPA Success according to Author(s)
Albano et al., 2021	South Africa	11 Elasmobranch Species	Assemblage Composition, Frequency of Occurrence and Relative Abundance	Baited Remote Underwater Video (BRUVs)	MPA deemed **successful** because relative abundance and frequency of occurrence of elasmobranchs was higher inside the MPA compared to control sites.
da Silva et al., 2013	South Africa	*Mustelus mustelus* (Smoothound)	Movement of sharks in and around MPA	Acoustic Telemetry	MPA deemed **partially successful** because sharks exhibited a high degree of residency within MPA boundaries. Furthermore, sharks spent more time inside the MPA during peak fishing months, but were still exposed to commercial and recreational fishing when traversing MPA boundaries.
da Silva et al., 2021	South Africa	*Mustelus mustelus* (Smoothound)	Reproductive biology, diet, growth and maturity	Fishery-independent lethal capture	MPA was considered **highly successful** because it protected a critical pupping/ nursery area and feeding ground, and sharks were larger and older here than any other location.
Le Port et al., 2012	North Island, New Zealand	*Dasyatis brevicaudata* (Short-tailed stingray)	Abundance, sex, size class, mating wounds inside the MPA.	Diver Visual Surveys	MPA deemed **successful** because it encompassed a breeding aggregation and nursery site, and rays exhibited predictable site residency within the MPA.
Link et al., 2005	Georges Bank and in Southern New England	*Raja erinacea* (Little skate) *Leucoraja ocellata* (Winter skate)	Inside vs outside MPA comparison of several biotic (abundance, biomass, size, stomach contents, species richness of benthos and nekton)	Seabed Observation and Sampling System (SEABOSS) and Otter Trawl	MPA deemed **partially successful** because individual skates were generally bigger inside than outside the MPA. However, substrate type was a stronger factor in the level of recovery/ species abundance because some habitats were far more vulnerable to fishery impact than others.
Morel et al., 2013	Jersey, English Channel	*Raja brachyura* (Blonde ray) *Raja microcellata* (Small-eyed ray)	Time spent within and spatial use of MPA	Acoustic Telemetry	MPA was considered **unsuccessful** because the MPA was too small and skates were not spending enough time here for it to offer any real protection.
Murawski et al., 2000	Georges Bank, New England	*Raja erinacea* (Little Skate) *Raja ocellata* (Winter skate)	Temporal abundance changes	Evaluation of historical fishery closures and landings data	MPA deemed **successful** because skates increased in abundance over time in closed areas and experienced reduced exploitation. However, several factors contributed to the level of success including: degree of fish movement in and out of the area, amount of fishing effort in adjacent areas and proportion of stock encompassed.

Study	Location	Elasmobranch(s) studied	Outcome(s) Measured	Survey Method	Evaluation of MPA Success according to Author(s)
Rodriguez-cabello et al., 2008	Cantabrian Sea, Bay of Biscay, Spain	*Scyliorhinus canicula* (Small-spotted catshark) and several skates	Abundance, catch length composition, changes in species community and biomass	Bottom-trawl survey	MPA deemed **partially successful** because it increased *S. canicula* biomass, however no benefits were received by the target teleost species (Hake, Megrim and Monkfish) or by skates.
Wiegand et al., 2011	Thames Estuary, England	*Raja clavata* (Thornback ray)	Theoretical efficacy of MPA vs size limits for *R. clavata* population recovery	Four-season deterministic age-based matrix population model	MPA was deemed the more **successful** option for *R. clavata* recovery than maximum size catch limits however, sole fishery yields would be more impacted by the MPA than size limits.

In some cases, the resilience of the habitat to fishing damage can greatly influence the value of a protected area (Link et al., 2005). For instance, protecting a sandy or gravel habitat from fishing gear may have less impact on species recovery than protecting a structurally complex habitat (e.g. biogenic reef) because fishing does not dramatically alter dynamic sandy and gravel habitats, whilst a biogenic reef could take years to recover after just a single trawling event. Link et al. (2005) found that substrate type was more important than the level of protection in driving groundfish species recovery in Georges Bank, New England, since less vulnerable habitats could tolerate exploitation and recovered even in unprotected sites. This suggests that MPAs are likely to be of increased value for species associated with discrete, sensitive habitats.

1.2.2. Social drivers of temperate elasmobranch MPA Success

Decisions made during the design stage of MPA establishment greatly influence outcomes for focal species (Rudd, 2015). Ideally, prior knowledge of the target elasmobranch species, their life-history strategies and their unique interactions with local habitats should be used to guide the design (e.g. site selection and size) of MPAs to maximise their value for target species. Since, even relatively small MPAs can have positive impacts on elasmobranch populations when designed effectively (Heupel et al., 2007; Albano et al., 2021). Unfortunately, major knowledge gaps exist surrounding elasmobranch ecology and research and conservation efforts have predominantly overlooked temperate, non-charismatic, benthic and batoid elasmobranchs (Dulvy et al., 2014; Momigliano & Harcourt, 2014). Resultantly, most MPAs are designed with little prior knowledge or planning and are established opportunistically with vague objectives (Hearn et al., 2010; da Silva et al., 2013). This can lead to the establishment of unsuccessful MPAs, due to inappropriate placement and size, even for species with restricted ranges and exhibiting strong philopatry. For instance, whilst Rajidae species have demonstrated predictable movement and significant site fidelity, an MPA designated in Jersey (English Channel) was found to be ineffective for Rajidae skates which only sporadically entered the MPA due to its small (0.5km^2) size (Morel et al., 2013). Similarly, an analysis of MPAs in Mozambique and South Africa found that only 5.97% of *G. cuvier* hotspots overlapped with MPAs (Daly et al., 2018). It is generally believed that marine reserves should ideally be at least double the size of the home range of target species to be beneficial (Green et al., 2015). Therefore, prior knowledge of species ranges would greatly improve MPA design and ultimate success level.

Furthermore, the specific focus of the MPA is thought to influence conservation success (MacKeracher et al., 2019), since non-elasmobranch focussed MPAs are theoretically less likely to encompass critical elasmobranch habitats (e.g. mating or nursery grounds) or be established at relevant spatial scales. But whilst MPAs designated specifically for elasmobranchs (namely ‘Shark Sanctuaries’) are becoming increasingly popular, most are designated without a robust understanding of the target species and habitats (Gallagher et al., 2021). Resultantly, elasmobranch focussed MPAs are generally perceived to be only slightly more effective than more non-elasmobranch focussed MPAs (MacKeracher et al., 2019).

When MPAs are established, fishing effort is often displaced which can lead to high levels of fishing pressure directly outside MPA perimeters if left unchecked (Leurs et al., 2021). For instance, destructive fishing methods were eliminated from two MPAs in West Africa but more than 70% of surrounding buffer zones were impacted by destructive fishing gears (e.g. trawling and longlines), which were associated with increased elasmobranch landings (Leurs et al., 2021). Similarly, the extent and distribution of displaced fishing around MPA perimeters in Georges Bank limited the recovery of some groundfish species (Murawski et al., 2000). In this way, displaced fishing can negate MPA benefits, particularly if focal species are frequently traversing MPA boundaries (Murawski et al., 2000; Leurs et al., 2021) and may therefore disproportionately affect highly mobile and migratory species. Alternatively, actively involving fisher communities with MPA management can have a significant positive effect on MPA success by increasing compliance (Pollnac et al., 2010; Woodhouse et al., 2015). In fact, 'support and buy-in' related factors are perceived as the most important determinants of MPA success for elasmobranch conservation, even more so than ecological and environmental factors (MacKeracher et al., 2019).

Increasing evidence demonstrates that limiting destructive fishing activities is essential to allow elasmobranch populations to recover (Murawski et al., 2000; Pondella & Allen, 2008; Ward-Paige et al., 2010). Unfortunately, most MPAs permit even the most destructive fishing methods making them ecologically meaningless (Vianna et al., 2016; Dureuil et al., 2018; Collins et al., 2021). Some MPAs theoretically prevent fishing through legislation, but a lack of management and enforcement facilitates illegal fishing and undermines the ecological benefits of spatial protection (White et al., 2015). For example, although the CoCos Island MPA in Costa Rica is touted as a landmark conservation success story, diver surveys discovered declines in the relative abundances of six elasmobranch species including: scalloped hammerhead sharks (*Sphyrna lewini*) (−45%), whitetip reef sharks (*Triaenodon obesus*) (−77%), mobula rays (*Mobula spp.)* (−78%) and manta rays (Manta birostris) (−89%), meanwhile two further species were less likely to occur (White et al., 2015). This was due to a lack of enforcement which facilitated illegal fishing within the MPA but was also influenced by ineffective MPA design (White et al., 2015). However, increased enforcement can lead to rapid and meaningful changes in species protection and ultimately recovery. In Cape Byron Marine Park, Australia, improved management and enforcement of an under-performing MPA lead to a 201% increase in fines (Kelaher et al., 2015) which was associated with a significant increase in elasmobranch abundance and occurrences of critically endangered grey nurse sharks (*Carcharias taurus*). Furthermore, to achieve holistic protection of elasmobranch populations, all potential threats must be managed (not just commercial extraction), since the presence of additional threats (e.g. boat strikes or recreational angling) can have adverse impacts on elasmobranch populations in MPAs (da Silva et al., 2013; Allen et al., 2021).

Finally, whilst social factors (e.g. buy-in and enforcement) are generally perceived to be more important to MPA success than biophysical factors (MacKeracher et al., 2019) the relative importance of factors generally seems to vary based on the specific context of the MPA. Furthermore, factors may interact uniquely in each setting to influence MPA success in different ways. For instance, Murawski et al. (2000) discussed that when a species range is not entirely encompassed by an MPA, the overall conservation success depends on fishery effort in adjacent regions. Furthermore, strong habitat associations can increase the benefits of MPAs for species that would otherwise not receive benefits from spatial protection (Gallagher et al., 2021). Overall, whilst biophysical factors determine the ideal ecological outcome, in actuality, MPA establishment involves a wide range of stakeholders and is constrained by social limitations (e.g. limited money or resources for management). For instance, whilst larger MPAs are generally desirable for increased protection of highly mobile elasmobranchs (White et al., 2017) these require considerable enforcement and monitoring which is often unfeasible (MacKeracher et al., 2019). Therefore, enhanced understanding of the target species, environment and stakeholder conflicts would help govern trade-offs to reach the best possible ‘middle-ground’, which achieves ecological outcomes whilst meeting the needs of involved stakeholders, with the most effective use of available resources (Jones, 2002).

1.3. Monitoring as an essential component of Temperate Elasmobranch MPAs

1.3.1. The importance of adequate MPA monitoring

Whilst monitoring does not directly influence MPA outcomes for elasmobranchs, well-designed long-term monitoring is an essential aspect of MPA management (Santana-garcon et al., 2014b; Rees et al., 2020; White et al., 2015; MacKeracher et al., 2019). Without adequate monitoring, MPA performance cannot be evaluated in relation to objectives, which prevents the continual adaptation and improvement (adaptive management) necessary for long-term protection of dynamic populations (Oh et al., 2017; Rouphael, 2020). Unfortunately, although MPAs are being established at increasing frequency for elasmobranch conservation (Gallagher et al., 2021), few have been implemented alongside appropriate monitoring schemes, making it unclear whether target species are effectively protected (White et al., 2015; Letessier et al., 2017). Furthermore, it is crucial that monitoring is conducted at adequate frequency to detect population declines with enough time for a proactive response (Parry et al., 2012). However, since population trend data is often noisy, analysis over long periods is normally necessary to confidently identify declines, particularly for rare and depleted species and when data are incomplete (Ellis et al., 2005; IUCN, 2022). According to the IUCN, declines (in either extent or abundance) should be assessed over periods of 'ten years or three generations, whichever is the longer' (IUCN, 2022). These factors mean that declines in rare species are often only detected in hindsight (Ellis et al., 2005; Taylor et al., 2007). Therefore, since MPAs are used to protect depleted populations, integration of high-quality monitoring schemes should be a priority to allow species declines to be detected and responded to in real-time.

1.3.2. How is MPA performance measured?

MPA performance can be measured using an array of different indicators and methods (as demonstrated in Table 1.1), reflecting changes at individual, species or community level. Commonly measured indicators and their associated survey strategies are summarised in Table 1.2.

Table 1.2. Typical measurable indicators used to evaluate the efficacy of MPAs for elasmobranch conservation, and their associated monitoring methods.

Measurable Indicator	Survey Method (s)
Species movement in relation to MPA	Telemetry (satellite or acoustic), photo identification, mark-recapture, Drones/ Aerial Surveys
Relative abundance (inside vs outside the MPA and changes over time since MPA establishment)	Fishery landings data, fishery-independent surveys, BRUVs, UVC, Drones/ Aerial surveys
Elasmobranch diversity (inside vs outside the MPA and changes over time since MPA establishment)	Fishery landings data, fishery-independent surveys, BRUVs
Population size structure (inside vs outside the MPA and changes over time since MPA establishment)	Fishery landings data, fishery-independent surveys, BRUVs
Condition/ Health of individuals (inside vs outside the MPA and changes over time since MPA establishment)	Fishery-independent surveys
Presence of critical habitats or important reproductive events inside MPAs	Telemetry (satellite or acoustic), Fishery landings data, fishery-independent surveys, BRUVs, UVC
Diet analyses (inside vs outside the MPA and changes over time since MPA establishment)	Stereo-Isotope Analysis, Stomach Contents Analysis

At an individual level, the extent to which an elasmobranch remains within MPA boundaries can be studied using traditional mark-recapture methods (Simpson et al., 2020) or satellite or acoustic telemetry (Morel et al., 2013; da Silva et al., 2013). If conducted for a representative sample size, this can provide a useful indication of the appropriateness of MPA design for the focal population. Alternatively, analysing spatiotemporal changes in elasmobranch abundance can reveal the role of MPAs in aiding population recovery (Murawski et al., 2000; Le Port et al., 2012). Although an increase in abundance is often used to signify a successful MPA (Speed et al., 2018), elasmobranch populations may take years to fully recover from overexploitation due to K-selected life-history strategies (Cortés, 2000). Therefore, MPA success may be more realistically represented by a stable population size or a halting or slowing of declines, particularly in the short-term (MacKeracher et al., 2019). Similarly, population recovery can be measured by examining population size structure (da Silva et al., 2021). Since fishing can disproportionately remove larger individuals from a population and reduce the average size of species (Myers & Worm, 2003; McClenachan, 2009), an increase in average size may represent a stabilisation of population structure as a result of MPA protection (Rodriguez-cabello et al., 2008; Le Port et al., 2012). Alternatively, MPA success may be signified by a high abundance of small size classes or neonates, indicating the protection of an important nursery site (da Silva et al., 2021). More specific aspects such as growth rate or 'condition' can also demonstrate the value of MPAs as elasmobranch conservation strategies in improving population health (Henderson et al., 2016; da Silva et al., 2021).

At a community-level, changes in assemblage structure such as biodiversity and community biomass can be explored to examine the extent of community recovery (Link et al., 2005; Rodriguez-cabello et al., 2008). Additionally, since removal of large apex predators can trigger trophic cascades, MPA performance may be explored by investigating the proportion of apex predators in relation to other trophic levels (Speed et al., 2018). Increasing numbers of apex predators could signify a rebalancing of the food web therefore representing community recovery and MPA success. Finally, since social factors such as compliance and support are crucial for MPA success, measuring social indicators is becoming increasingly important for analysing MPA performance on a holistic level (Wiegand et al., 2011; MacKeracher et al., 2019).

1.3.3. Challenges and limitations associated with monitoring temperate elasmobranch MPAs

Several options exist for monitoring elasmobranch populations within and around MPAs (Table 1.2.). However, most traditional methods exhibit limitations when applied to temperate elasmobranch conservation research. Firstly, lethal and non-lethal capture of individuals (e.g. fishery-independent surveys) is valuable for investigating crucial life history knowledge gaps (e.g. reproduction, growth, diet) which ultimately enhance conservation

(Heupel & Simpfendorfer, 2010). However, there is growing debate surrounding the justification of using lethal sampling to obtain elasmobranch conservation data, since it depletes already suffering populations (Hammerschlag & Sulikowski, 2011). Utilising fishery landings data takes advantage of an existing data source, without further damaging populations and is useful for characterising large-scale trends in abundance (Letessier et al., 2017). However, many elasmobranchs have been historically recorded under blanket terms (e.g. Skates and Rays (UK)), impeding the investigation of species-specific trends (Dulvy et al., 2000). Furthermore, fisheries data is biased towards locations of high-species abundance, whereas absence data is also necessary to determine the true extent of a species range (Abel & Grubbs, 2020). Overall, this has resulted in a paucity of reliable baseline data against which to evaluate the impacts of MPA establishment.

Visual methods such as BRUVs, submersibles and UVC (Underwater visual census) address the need for non-invasive fishery-independent methods (Abel & Grubbs, 2020), appropriate for recovering ecosystems (Sheehan et al., 2013). However, these require considerable survey effort and can therefore be relatively costly and time-consuming. Furthermore, visual methods require relatively clear waters and can be biased towards conspicuous species whilst overlooking smaller, more cryptic species (Stobart et al., 2007; Harvey et al., 2018; Albano et al., 2021). Furthermore, the efficacy of UVC is reliant on the focal species being easy to locate and approach (Le Port et al., 2012) and can therefore overlook timid-natured species.

Survey limitations are further exacerbated by inherent challenges associated with monitoring temperate elasmobranchs. Firstly, in-situ observation of elasmobranchs is difficult since many species are highly mobile and often patchily distributed (Letessier et al., 2017; Pikitch et al., 2018). Apex predators in any ecosystem are naturally found in low densities (Abel & Grubbs, 2020) and overexploitation has confounded this problem by further depleting populations (Dulvy et al., 2014; Dulvy et al., 2021). Therefore, obtaining appropriate sample sizes to accurately infer population trends is extremely challenging and statistical assessment of MPA effects is often impossible without significant replication (Blampied et al., 2022). These challenges are further exaggerated in temperate waters where adverse weather conditions and reduced water visibility can make visual strategies less effective (Port et al., 2016; Tang et al., 2019). Meanwhile, the monitoring of pelagic species introduces a unique set of difficulties related to expansive home ranges, migratory behaviours, and the relative inaccessibility of oceanic ecosystems compared to coastal and benthic habitats.

Finally, the robust interpretation of MPA effects on elasmobranchs is often limited by inadequate experimental design of monitoring schemes (Leverington et al., 2010; Ahmadia et al., 2015) which are frequently restricted to spatial comparisons at discrete timepoints, sometimes several years after initiation (Link et al., 2005; Albano et al., 2021). Although these experiments are valuable descriptors of relative habitat importance, a higher abundance (or other indicator outlined in Table 1.2.) of elasmobranchs inside the MPA compared to control sites cannot be interpreted as a direct result of MPA designation, without the inclusion of baseline data and temporal analyses (Link et al., 2005; Bond et al., 2012). Inferring MPA benefits from spatial comparisons alone disregards the possibility of pre-existing natural differences (Lester et al., 2009), which are often introduced by strategic placement of MPAs in particularly diverse locations. Furthermore, spatial comparisons may even mask negative population trends that can only be detected by surveying populations at multiple timepoints. Baseline population data obtained either prior to or in the initial phases of MPA establishment, complete with ecologically analogous control sites, are critical to confidently disentangle the effects of MPA establishment from natural variation and environmental changes (Ahmadia et al., 2015). In older MPAs where early monitoring was not conducted, historical ecology and local ecological knowledge approaches (Moore & Hiddink, 2022) could be employed to reconstruct baseline communities and gain a better understanding of contemporary MPA effects. Unfortunately, monitoring at sufficient frequency and spatial coverage requires significant and consistent economic investment, which is often severely limited in the conservation sector (Bohorquez et al., 2019).

1.3.4. Monitoring opportunities offered by technological advancements

Due to the aforementioned challenges, current temperate monitoring efforts are generally inadequate, allowing elasmobranch declines to frequently go unnoticed and unaddressed (Ellis et al., 2005; Port et al., 2016). Therefore, to prevent further avoidable species declines, current monitoring approaches require a transformation. Monitoring must move away from overdependence on landings data and towards targeted and systematic surveillance. Recent technological advancements present several opportunities to overcome method limitations and potentially revolutionise elasmobranch monitoring.

Firstly, video methods are rapidly becoming an integral component of elasmobranch monitoring. Mono and stereo-BRUVs offer cost-effective, non-extractive approaches to measuring elasmobranch diversity and relative abundance. A major advantage of these methods is their high repeatability which increases potential for inter-study comparisons by standardising methodologies across a range of habitats and locations (Whitmarsh et al., 2017). This enhances the interpretation of results and allows each study to contribute to a broader knowledge network. Additionally, video methods have great potential for diversification, as the individual components of the design can be adapted for specific purposes. For instance, the addition of a clear liquid optical chamber (CLOC) to BRUV systems has been shown to increase their efficacy in low water visibility (Jones et al., 2019) expanding their potential application in temperate waters.

Additionally, pelagic BRUVs, consisting of a baited camera rig suspended beneath surface buoys and anchored to the seabed, are emerging as a tool to survey discrete areas of oceanic habitat (Heagney et al., 2007; Letessier et al., 2013; Santana-Garcon et al., 2014a). While these static pelagic BRUVs have proven successful for detecting spatial differences in mid-water species assemblages (Sanatana-Garcon et al., 2014a) and offer an effective method for populating pelagic elasmobranch evidence gaps, the emergence of drifting pelagic BRUVs brings further advantages. Without the constraints of a mooring system, pelagic drifting BRUVs could shed light on the oceanic elasmobranchs utilising deep-water habitats beyond the continental shelf, including those residing in large and 'blue water' MPAs (Bouchet & Meeuwig, 2015; Gilman et al., 2020; Meeuwig et al., 2021). Meanwhile, the lack of contact with the benthos make un-moored BRUVS well-suited for use above fragile or recovering seabed habitats, such as those inside MPAs.

Video methods are also diverging in more creative ways. The advancement of animal borne video systems (ABVSs) has displayed encouraging capacity to characterise inaccessible marine habitats and communities (Chapple et al., 2021). For example, a camera mounted on a white shark (*Carcharodon carcharias)* was able to quantify the spatial density of kelp holdfasts in a Giant kelp forest ecosystem in Gansbaai, South Africa (Chapple et al., 2021). Furthermore, when employed as part of a multi-sensor package and in combination with telemetry methods, ABVSs can illustrate habitat-use and behaviour of focal species (Moll et al., 2007) at higher spatial resolution than acoustic and satellite tags alone (Papastamatiou et al., 2015; Nakamura et al., 2015) which are typically accurate to tens of meters maximum (depending on tag type, e.g. SPOT vs PAT (Heithaus et al., 2001; Hammerschlag et al., 2011)). Meanwhile their capacity to illustrate the role of prey-interactions in driving habitat-use (Ryan et al., 2022), could be particularly valuable since prey distributions are often missing from studies of predator spatial ecology, despite their unequivocal importance in driving movement (Heithaus, 2001; Torres et al., 2006). Their suitability has also been demonstrated for pelagic sharks (e.g. Oceanic whitetips (*Carcharhinus longimanus*)) indicating potential for this method to overcome pelagic-specific monitoring challenges (Papastamatiou et al., 2018). Finally, both ABVSs and telemetry have exhibited potential for observing reproductive events *in situ*, for instance, Basking shark *(Cetorhinus maximus)* courtship behaviours (e.g close following and parallel swimming) were observed using ABVSs in Scotland (Rudd et al., 2021), meanwhile egg-laying behaviour in small-spotted catsharks (*S. canicula)* was detected with archival tagging (Wearmouth et al., 2012). Given our understanding of the significance of habitat associations and reproductive events in driving temperate MPA performance, ABVSs integrated with telemetry present many opportunities to advance monitoring of elasmobranchs in MPAs.

A major bottleneck in the application of video methods to elasmobranch monitoring is the time-consuming and costly nature of manual video analysis. Advancements in artificial intelligence (AI), however, may overcome some of these barriers (Goodwin et al., 2022). The application of AI to underwater video analysis is rapidly expanding, offering potential to automate: species identification, species quantification, individual identification and behaviour classification (Brewster et al., 2018; Schneider et al., 2019; Jenrette et al., 2022). Deep learning (DL), as a subdivision of both AI and machine learning, facilitates the automation of human-performed tasks using complex machine learning algorithms called 'neural networks'. The early integration of DL with BRUV research has already resulted in 7.1 % more accurate fish abundance estimates than manual video analysis by experts (Ditria et al., 2020) and the process was more cost-effective and quicker. Furthermore, machine learning is likely to be disproportionately valuable to the study of rare and highly mobile species, such as elasmobranchs, since such vast quantities of footage are required to gain sufficient species observations for statistical analyses (Blampied et al., 2022).

Aerial surveillance of elasmobranchs represents a monitoring opportunity for species residing in surface waters. Historically conducted with a manned aircraft (Squire, 1990) the improvement of batteries and wireless communication in advancing unoccupied aerial vehicles (UAVs) has made aerial surveillance an increasingly feasible elasmobranch research method (Butcher et al., 2021). UAVs have elucidated habitat-use patterns of a range of tropical sharks in MPAs (Ayres et al., 2021) but have not yet been applied to elasmobranchs in temperate MPAs. However, UAVs have revealed insights into the behaviour of various temperate shark species, including the significance of "torus" or circling behaviour in aiding basking shark *(C. maximus)* courtship which facilitate multiple intra-specific interactions over a short period (Sims et al., 2022). This ability to characterise behaviour and movements of surface-swimming temperate species exemplifies the suitability of UAVs for surveying temperate MPAs.

Novel molecular tools are also emerging with potential to advance the study of elasmobranchs in temperate MPAs. One such tool may offer a particularly revolutionary approach (Poulakis & Grubbs, 2019) by detecting species through discarded genetic material (e.g. waste products) in the water column known as environmental DNA (eDNA). eDNA is typically applied to elasmobranch research through two main avenues. The first: eDNA barcoding, identifies the presence of a target species using a species-specific primer and has been principally used to study rare and threatened species (Simpfendorfer et al., 2016; Weltz et al., 2017). The second method: eDNA metabarcoding, facilitates community-level exploration by simultaneously identifying multiple species from a single water sample using a primer-set (Boussarie et al., 2018; Lui et al., 2022).

Studies comparing eDNA with traditional elasmobranch monitoring methods (Table 1.3) have identified several key strengths. Firstly, eDNA requires substantially less survey effort and time to achieve similar results to other methods (Table 1.3.). Boussarie et al. (2018) found that the collection of 22 eDNA samples detected more shark species than 2,758 underwater visual census (UVC) surveys (over 20+ years) and 385 baited remote underwater video (BRUV) deployments (over three years). Secondly, eDNA requires no observation or capture of elasmobranchs, making it particularly suited to the study of MPAs, threatened species and turbid waters. Importantly, studies concurrently implementing extractive and eDNA methods have revealed eDNA to be of equal or greater efficacy (Thomsen et al., 2016). Furthermore, eDNA may exceed the ability of bottom trawls to detect large mobile species (such as the Greenland shark, *Somniosus microcephalus)* which are able to evade the net (Thomsen et al., 2016). Since eDNA does not rely on visual cues, it yields greater species detection in low visibility environments (e.g. temperate waters) and more readily detects visually inconspicuous or cryptic species (Port et al., 2016; Tang et al., 2019). Meanwhile, it is extremely sensitive and is therefore particularly suited to the study of threatened species (Simpfendorfer et al., 2016; Weltz et al., 2017). Finally, whilst waste genetic material can be transported over large distances by ocean currents, eDNA metabarcoding is able to identify distinct assemblages over small spatial scales (Port et al., 2016; Stoeckle et al., 2017; Yamamoto et al., 2017) possibly resultant of the rapid degradation of eDNA (0 – 6 days) in seawater (Dell'Anno and Corinaldesi, 2004; Thomsen et al., 2012).

Table 1.3. A summary of studies comparing the ability, in terms of survey effort and detection efficiency, of eDNA and traditional survey methods to monitor elasmobranchs.

Study	eDNA			Comparative Method		
	Method	Survey Effort	Species Detections	Method	Survey Effort	Species Detections
Boussarie et al., 2018	Metabarcoding	22 samples	13 shark species	BRUV & UVC	385 BRUV surveys 3 years 2758 UVC surveys 28 years	9 shark species each
Gargan et al., 2017	Barcoding	31 samples	Devil rays detected at 5 sites	Visual Surveys	31 visual surveys	Devil rays detected at 5 sites
Port et al., 2016	Metabarcoding	12 samples	29 taxa	UVC	12 surveys (10 minutes)	12 taxa
Stat et al., 2019	Metabarcoding	41 samples	55 taxa	BRUVs	41 BRUV surveys (1 hour each)	73 taxa
Thomsen et al., 2012	Metabarcoding	3 samples 1-day collection	15 fish species	9 different methods (extractive and non-extractive)	Several different surveys 3 years	Average of 4.3 - 14.7 species per survey event
Thomsen et al., 2016	Metabarcoding	21 samples	29 fish families	Bottom Trawl	21 trawls (~30 minutes tow time)	28 fish families
Yamamoto et al., 2017	Metabarcoding	282 samples 6 hr-collection	112 fish species	UVC	140 surveys 14 years	80 fish species

However, because eDNA methods are still in their infancy, several method limitations must be addressed to facilitate their adoption as a core research tool for elasmobranchs in MPAs. Firstly, without adequate sample replication it is possible for the presence of a species to go undetected (false negative) (Kelly et al., 2014a; Gargan et al., 2017). This is because eDNA is rapidly dispersed in the ocean, resulting in dilution and a heterogenous distribution (Takahara et al., 2012). False negatives may also be attributed to primer design (Kelly et al., 2017) whereby primers may possess a greater affinity to target DNA of certain taxa, leading to preferential amplification and representation of these taxa in the dataset. For example, a vertebrate-specific primer set used in the Monterey Bay aquarium was biased towards teleost fish DNA and unable to detect cartilaginous fish (Kelly et al., 2014b). eDNA may also detect a species without it actually being present (false positive). This can occur at assignment stage, if a sequence is misidentified when compared to the species database (Andruszkiewicz et al., 2017). Alternatively, due to the sensitivity of eDNA there is a significant risk of contamination (Goldberg et al., 2016). Allochthonous DNA may enter samples from positive controls, via cross-contamination between samples or eDNA may be transported in currents from non-local areas (Poulakis & Grubbs, 2019). Due to these limitations, it is generally agreed that eDNA should be considered a supplementary rather than stand-alone survey tool. Equally, each monitoring method considered prior exhibits unique advantages and limitations, therefore, a multimethod-monitoring approach is recommended to achieve a holistic and robust understanding of temperate MPA performance.

1.4. Temperate Elasmobranch MPA Guardrails

The findings of this review demonstrate that temperate elasmobranch MPAs are only successful under specific biophysical and social conditions, and when employed in tandem with effective monitoring. Whilst MPA establishment in reality, is constrained by resources and complicated by stakeholder objective trade-offs, the following section synthesises the findings of this study into a series of practical guardrails, representing the ideal temperate elasmobranch MPA, intended to serve as a guide for the optimal implementation of temperate elasmobranch MPAs. Illustrated in Figure 1.1., the guardrails fall into four main categories: 1) building a detailed prior knowledge base 2) integrating social and ecological goals 3) striving for legitimate governance and 4) implementing effective monitoring.

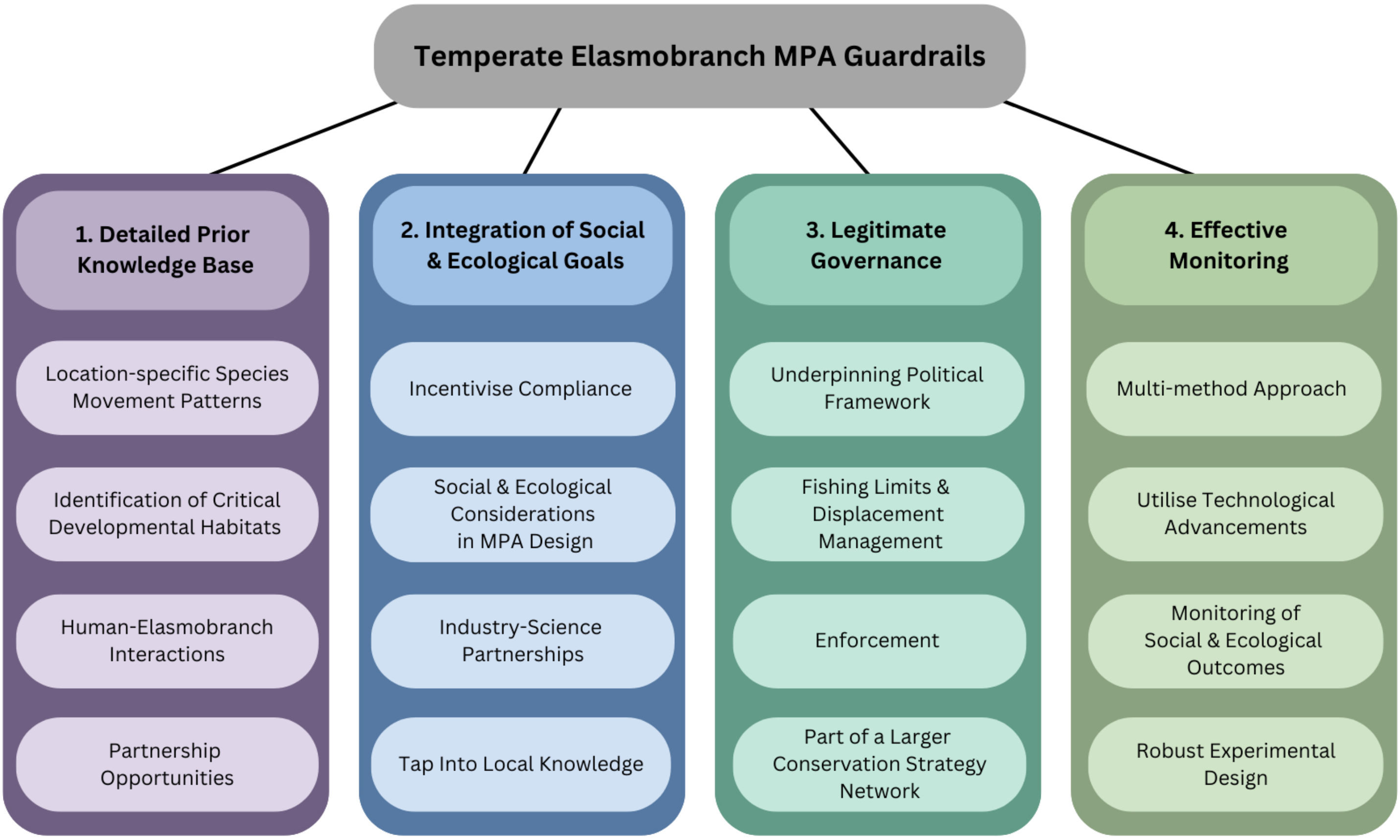

Figure 1.1. A summary of the guardrails identified to guide the ideal use of temperate MPAs for elasmobranch conservation.

The aim of guardrail 1, obtaining **Detailed Prior Knowledge Base**, is to develop a context specific understanding of the target elasmobranch species in the target location to determine whether an MPA would be an effective use of conservation resources and inform effective MPA design. This is crucial considering the extensive potential for variation in movement behaviours between and within populations. This stage should focus not only on gaining a comprehensive ecological evidence base but developing an in-depth understanding of the local socio-economic context. Particular attention should be given to the identification of critical habitats, determining the ontogenetic stages contributing most to population growth and identifying opportunities for industry-science collaboration.

Guardrail 2**, Integration of Social and Ecological Goals,** aims to raise the profile of social outcomes throughout the entire process of: MPA design, implementation, and management. Fishing industry-science partnerships will be crucial for building relationships to ultimately enhance support, buy-in and compliance. Meanwhile, these partnerships will feed into the growing knowledge base, by acknowledging and tapping into the body of information held in local communities.

Guardrail 3 strives for **Legitimate Governance**, which addresses the lack of ecologically meaningful protective measures in most established MPAs. For elasmobranch MPAs to be successful, damaging fishing activities must be limited if not entirely prohibited, since fishing is unequivocally implicated in elasmobranch declines (Dulvy et al., 2021). For fishing limits to be legally enforceable, a legitimate political framework is necessary, preferably complete with an objective external watchdog to uphold consequences. However, due to the nuanced nature of MPA success, MPAs should be incorporated as part of a larger elasmobranch conservation network including both limit-based and target-based strategies.

Finally, guardrail 4 recognises the importance of **Effective Monitoring**, in the success of temperate MPAs and their adaptive management. It encourages the integrated use of a combination of monitoring tools, including novel technologies, to overcome individual method limitations and develop a comprehensive understanding of MPA performance. Robust experimental design should underpin monitoring regimes to allow confident attribution of population responses to MPA effects. Early monitoring should be included where possible and when missing, reconstruction of past communities should be pursued with historical ecology and local ecological knowledge approaches. Finally, social outcomes (such as fishery displacement and stakeholder support) should be frequently assessed and managed, as essential components of success.

1.5. Conclusions

Several factors influence the efficacy of MPAs for conserving temperate elasmobranchs, these include biophysical drivers (e.g. species mobility and habitat association) and social drivers (e.g. fishing displacement and compliance). Factors can interact uniquely in each location and the importance of factors can change (even for the same species) depending on the specific context of the MPA and focal population. Therefore, research into the specific target population in terms of life-history strategies, habitat-use and mobility would greatly enhance the value of MPAs and advance our understanding the species that may benefit from MPA establishment.

Biophysical factors limit the theoretical efficacy of an optimum MPA with unlimited research and management resources. However, in reality, MPAs involve a wide range of stakeholders with diverging needs and ideas of success. Resultantly, overall MPA success is typically determined by a trade-off between ecological and social goals. Therefore, striving to adopt a 'middle-ground' approach is perhaps more achievable. Nevertheless, a greater understanding of displaced fishing effort, additional local elasmobranch threats, enforcement and compliance levels will help guide management (e.g. increased stakeholder engagement) or MPA design modifications (e.g. MPA expansion or inclusion of buffer zones) to optimise existing opportunities.

Since MPAs are only effective under specific conditions, it is alarming that very few are established with sufficient monitoring schemes to evaluate performance and detect changes in target species. For temperate MPAs to be effective for elasmobranchs, not only must systematic long-term monitoring be established with ecologically analogous control sites, but challenges associated with studying highly mobile, endangered species in low visibility and adverse weather conditions must be overcome. Exploration of novel survey techniques such as eDNA and ABVSs may address some of these limitations, and automation of video analysis through AI, has potential to greatly advance video monitoring efficiency. However, a transformation of current elasmobranch monitoring will likely require the integrated adoption of various research tools, to overcome individual limitations associated with each method.

This review demonstrates that MPAs can be highly effective for temperate elasmobranch protection under the correct conditions, however, they are not always appropriate, and should therefore not be regarded a panacea. Instead, they should be considered one option in the elasmobranch conservation arsenal and their implementation should be complemented by a wider network of well-connected MPAs, fishing restrictions and market regulations. MPA use should be tailored specifically to focal species in local contexts and established in conjunction with experimentally robust monitoring schemes. It is hoped that the guardrails outlined in section 1.4. will help guide the optimal use and modification of MPAs to contribute to the holistic protection of elasmobranchs.

Chapter 2: Abundance and diversity of Elasmobranchs in and around Lyme Bay MPA

2.1. Introduction

Chondrichthyan populations are in a global state of crisis with over a third of all species threatened with extinction according to IUCN red list criteria (Dulvy et al., 2021). Although several management interventions exist, including both fishing restrictions (e.g. species quotas, landing size limits) and spatial management strategies (Caddy & McGarvey 1996; Shiffman & Hammerschlag, 2016), these have not yet been implemented sufficiently to prevent significant overextraction and alarming biodiversity loss (Davidson et al., 2015; Simpfendorfer & Dulvy, 2017; Dulvy et al., 2021; Juan-Jorda et al., 2022).

MPAs represent a promising strategy to combat declines, whilst providing additional ecosystem-wide benefits through improved habitat quality (Davidson & Dulvy, 2017; MacKeracher et al., 2019). Elasmobranch-specific MPAs (e.g. 'Shark Sanctuaries') have surged in recent years (Ward-Paige, 2017), and designation of the first elasmobranch-focussed MPA in Scotland for Flapper skate (*Dipturus intermedius* (The Red Rocks and Longay Nature Conservation Marine Protected Area (No. 2) Order 2021) signifies a growing appetite for elasmobranch-focussed spatial protection in the UK. Since MPAs are set to further proliferate both globally, with the '30 by 30' initiative, and in the UK, with the imminent establishment of Highly Protected Marine Areas, HMPAs (Defra, 2019), timely population of crucial evidence gaps is critical to guide the effective use of limited conservation resources.

Optimal establishment of MPAs is currently limited by a lack of understanding around the specific conditions under which MPAs can successfully conserve elasmobranchs. Firstly, knowledge gaps surrounding the specific value of different types of MPAs (e.g. partially-protected compared to no-take zones) and for various species in alternative contexts exist. MPAs have demonstrated success in tropical regions (Speed et al., 2018; Gallagher et al., 2021) for protecting species such as Caribbean reef sharks (*Carcharhinus perezi)* and Tiger sharks (*Galeocerdo cuvier*), however the efficacy of temperate MPAs has received less attention (Breen et al., 2015). Furthermore, elasmobranchs exhibit substantial interspecific variability in life-history strategies and behaviours (Cortés, 2000), suggesting they may receive differing degrees of protection from MPAs. However, there remains a paucity of knowledge on this subject, particularly in temperate and UK waters.

Synthesis of existing case studies has identified various biophysical and social drivers of MPA success (MacKeracher et al., 2019). Whilst social determinants such as stakeholder engagement and fishing restrictions are perceived by experts as particularly important for driving MPA success, specific ecological factors can also greatly influence MPA efficacy. In particular, strong habitat associations (e.g. for feeding or reproductive activity) can facilitate MPA benefits even in highly mobile elasmobranchs, since they increase the time spent within MPA boundaries (Gallagher et al., 2021). However, the role of these drivers has been disproportionately overlooked in temperate and Northern hemisphere locations.

Unfortunately, few MPAs are established with adequate monitoring regimes, complete with baseline data and analogous control sites, so opportunities to experimentally test MPA effects are scarce (Sciberras et al., 2013) and many depend solely on spatial comparisons of abundance or habitat-use (Link et al., 2005; Bond et al., 2012). This has potential to mask temporal population responses and falsely conclude that an MPA is achieving positive conservation outcomes. In contrast, Lyme Bay MPA, a partially-protected area on the Southwest UK coast, has been the focus of extensive BRUV surveys, conducted annually since MPA establishment in 2008 (Davies et al., 2021; Davies et al., 2022). The resultant long-term video dataset, complete with controls, presents a unique opportunity to experimentally test the effect of a temperate MPA on elasmobranch populations and determine which species, if any, are afforded benefits. Meanwhile, as a partially-protected area, Lyme Bay may shed light on the appropriateness of middle-ground approaches to concurrently achieve elasmobranch conservation and social goals.

Lyme Bay MPA was designated to protect a nationally important and biodiverse rocky-reef habitat (Sheehan et al., 2013) and was therefore not strategically designed for elasmobranchs. However, its effective management, including continuous engagement with stakeholders and a politically enforced demersal fishing ban (Singer & Jones, 2021), has potential to provide opportunistic benefits to the local elasmobranch community. The primary focus of this study is to assess the effect of Lyme Bay MPA on elasmobranchs, determining: 1) the impact on the community as a whole, 2) inter-specific differences in population responses and 3) the influence of two potential underlying drivers: elasmobranch exploitation and habitat associations with protected rocky reef features. However, 12 years of monitoring with BRUVs in Lyme Bay has created one of the most comprehensive temperate BRUV datasets to date. Therefore, as a secondary goal, this study takes this unique opportunity to create a detailed fishery-independent account of a priorly overlooked elasmobranch community. MPA effects and their underlying drivers will be explored with the following hypotheses:

1. The elasmobranch community inside the MPA will become increasingly different from the elasmobranch community in control sites over time since MPA initiation.
2. Individual elasmobranch species will become more abundant inside the MPA, compared to controls over time since MPA initiation.
3. Elasmobranch exploitation will decrease over time in Lyme Bay following MPA initiation.
4. Elasmobranchs will be significantly associated with protected rocky reef habitats.

2.2. Methods

2.2.1. Study site and Background

Located on the Southwest coast of the UK, Lyme Bay MPA (Figure 2.1) encompasses ecologically important rocky reef habitat which is protected by a combination of spatial management strategies. A statutory instrument (SI), established in 2008, prohibits the use of demersal towed fishing gears from a 206km^2 section of seabed (Defra, 2008; Mangi et al., 2011). The statutory instrument employs a whole-site approach whereby towed fishing gears are banned from the entire area. An overlapping Special Area of Conservation (SAC) and associated byelaws were later introduced in 2011, partially protecting 236 km^2 of reef (Rees et al., 2016). The SAC constitutes feature-based protection and only prohibits demersal fishing from specific rocky reef habitats. The MPA was specifically designated to protect the biodiverse rocky reef features which are listed under Annex 1 of the EU Habitats Directive (Council Directive 92/43/EEC) and are home to fragile habitat-forming species such as *Eunicella verrucosa* (pink sea fan) and *Pentapora fascialis* (ross coral). Static fishing gears (e.g. nets, pots) are still permitted throughout the reserve, classifying the MPA as partially protected.

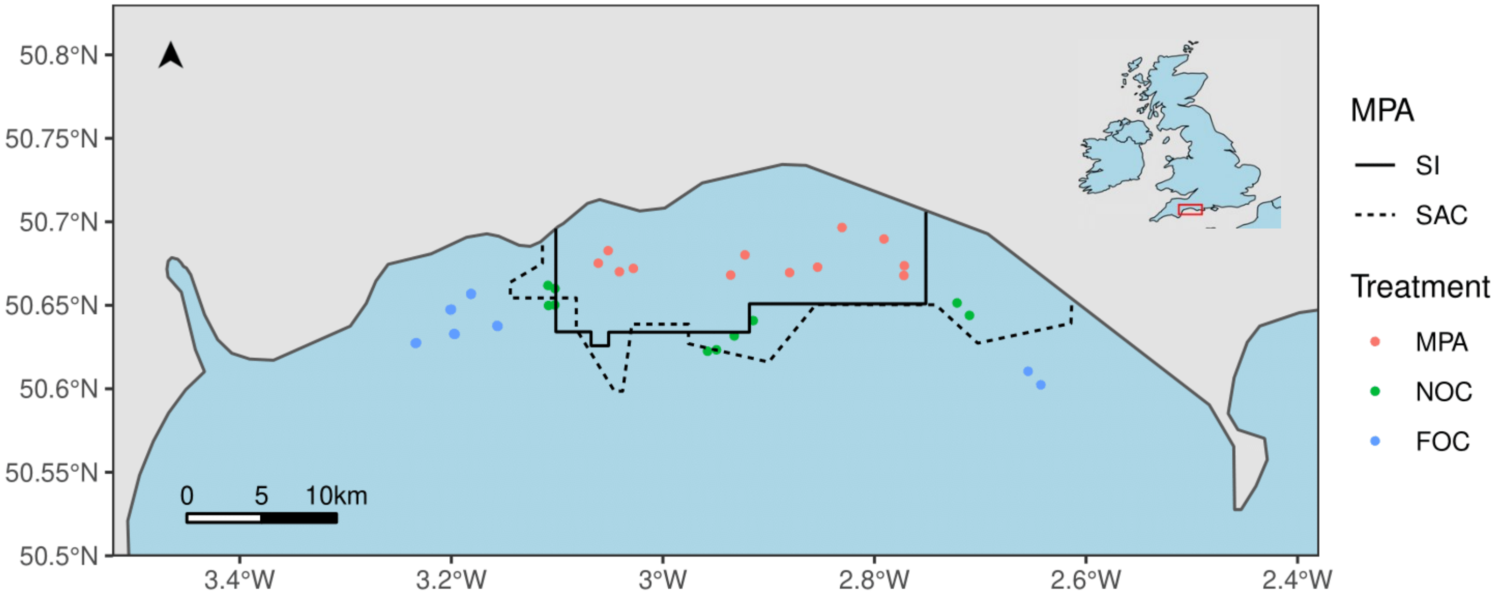

Figure 2.1. Map of Lyme Bay MPA, including the two overlapping MPA boundaries (SI = Statutory Instrument, SAC = Special Area of Conservation). Points represent BRUV deployment sites (MPA = Marine Protected Area, NOC = Near Open Control, FOC = Far Open Control).

2.2.2. Study design

To determine the effect of Lyme Bay MPA on the elasmobranch community, this study analysed footage from a 12-year BRUV survey, conducted in the summer months of 2009 – 2020. Survey sites were selected to include protected sites (MPA treatment) and ecologically analogous control sites (Near & Far Open Controls; Figure 2.1). Site selection was based on habitat data (Stevens et al., 2014) to encompass a variety of rocky reef habitats (including cobbles, boulders and bedrock), but also included adjacent patches of mobile substrates (e.g. sand and gravel). The survey was not initially designed to document the recovery of highly mobile species, therefore most control sites selected were in close proximity to the MPA boundary (herein named Near Open Controls: NOCs) to reduce the impact of confounding environmental variation. However, the highly mobile nature of elasmobranchs, means changes in community are more likely to be detected over broader spatial scales. Therefore, additional control sites (Far Open Controls: FOCs) were added from 2010 onwards to expand the spatial coverage of the study and reduce the influence of elasmobranch movement between treatments. FOCs therefore represent control sites > 3.5km from the SI boundary meanwhile, control sites < 3.5km from the boundary represent NOCs. This study only analysed MPA sites situated within the statutory instrument (excluding those only encompassed by the SAC) as it offers the highest level of protection (following a whole-site approach) whereas the feature-based protection within the SAC was not expected to have a detectable effect on highly mobile elasmobranchs and inclusion of these sites was expected to reduce the strength of perceivable effects. Furthermore, the establishment of the SAC engulfed many of the NOC sites and these were resultantly excluded from analysis beyond 2011.

2.2.3. BRUV system and Deployment

BRUV rigs (as described in Bicknell et al., 2019) consisted of a single horizontally orientated camera (Panasonic HDC- SD60 and HDC- SD80) and an LED light, mounted upon a metal frame with lead weights (approximately 30kg). Bait boxes filled with 100g of Atlantic mackerel (*Scomber scombrus*), were suspended 1m in front of the camera on a bait arm and were restocked before each new deployment. For each site, three BRUV replicates of 45 minutes were deployed and distributed at least 100m apart to minimise duplicate detections of the same individual within simultaneous deployments.

2.2.4. Video Analysis

Videos underwent quality assurance checks (outlined in Davies et al., 2021) to ensure that replicates were only analysed when footage was clear, unobstructed, correctly oriented and these conditions were sustained for at least 30 minutes. For analysis, videos were played at normal speed and after a settling period of 5 minutes (to allow water visibility to return), the presence of any elasmobranchs was recorded alongside the time of occurrence over a 30-minute period. Elasmobranchs were identified to highest possible taxonomic resolution and MaxN was obtained as a conservative estimate of relative abundance, whereby the maximum number of individuals of a species within a single frame was recorded for each replicate.

2.2.5. Potential Drivers of MPA effects

2.2.5.1. Fishery Landings Data

To explore elasmobranch exploitation in Lyme Bay, publicly available landings data were obtained from the Marine Management Organisation (MMO) website (https://www.gov.uk/government/organisations/marine-management-organisation, accessed: 15/02/2022). Data were available at relatively low spatial resolution, provided as landings per ICES rectangle. Therefore, landings could not be directly apportioned to either inside or outside the MPA, but rather represent an overview of the wider Lyme Bay area. Lyme Bay MPA spans the boundaries of two ICES rectangles: 30E6 and 30E7, so data from both these rectangles were downloaded and combined. No measure of catch effort was available for landings; therefore, they cannot be interpreted as a measure of population change. Furthermore, it is possible that landings reporting was inconsistent throughout, and therefore, it cannot be inferred that changes in reported landings represent an actual changes elasmobranch exploitation. Instead, these data should be interpreted as a proxy for fishing effort in Lyme Bay across the study period.

2.2.5.2. Relationship between habitat and elasmobranch abundance

To elucidate the influence of habitat type on elasmobranch abundance inside the MPA, the substrate type at each site was classified for a subsample of videos. The year 2016 was selected as a subsample for analysis due to the enhanced water visibility, and habitats were only classified inside the MPA. Substrate type was broadly categorised into Mobile or Reef substrate. Whilst Mobile substrates included: sand, gravel, mud, loose rocks or any combination of these, Reef substrate comprised any habitat where cobbles, boulders or bedrock were present, or clearly dominated by biogenic reef species. Since the same sites were sampled each year, it was assumed that the substrate type remained constant over time. Therefore, substrate data were extrapolated across the full survey to enhance the power of statistical analysis. Since three replicate BRUVs were deployed at each site, the most common substrate type from the 3 replicates was applied to all other years. If there was no agreement between replicates, an additional year was analysed, and the most common substrate was recorded. An additional measure of habitat (Biogenic Reef Species % Cover) and its relationship with elasmobranch abundance is presented in the appendices (Appendix 1).

2.2.6. Data analysis

2.2.6.1. *Elasmobranch abundance*

To explore taxon-specific patterns in relative abundance (MaxN) over time (2009 – 2020) and among experimental treatments (MPA, NOC and FOC), mean relative abundance was visualised (using the package "ggplot2" in R (Wickham, 2016)) for less common elasmobranch taxa across the survey period, to allow descriptive interpretation of species trends. With the exception of highly abundant *S. canicula,* the effects of Year and MPA treatment could not be statistically analysed for each elasmobranch species in isolation, due to low abundances. Instead, the relative abundances for all shark species (excluding *S. canicula*) and all skate species respectively were aggregated and analysed together. *Scyliorhinus canicula* was abundant enough to be statistically evaluated separately. Prior to statistical analysis, all data were explored following the protocol from Smith et al. (2020) based on Zuur et al. (2010), to investigate: presence of outliers, distribution of response variables, multicollinearity between covariates and independence of response variables. Survey effort was imbalanced over time, with the first two years of the survey (2009 and 2010) exhibiting significantly lower sampling effort (and lacking the FOC treatment), therefore, these two years were not included in statistical analyses.

Generalised linear mixed models (GLMMs) were used to test statistical relationships between variables due to the non-independence of response variables introduced by repeated sampling of specific sites over time (characteristic of 'repeated measures design'). GLMMs included the random effect of Site and the fixed effects of and interaction between MPA treatment and Year. Their effects on the relative abundance of Skates, Sharks (excluding *S. canicula)* and *S. canicula* were individually assessed. Since the response variables comprised abundance data, GLMMs were fitted with a poisson distribution and log link function (using the "lme4" package in R (Bates et al., 2015)), due to the non-normality of count data. Poisson GLMMs assume that the mean and variance of the response variable increase at the same rate. To check this assumption, residual deviance of fitted models was compared with the residual degrees of freedom. When this assumption was violated and overdispersion was detected, GLMMs were fitted with a negative binomial distribution and log link function (using the "MASS" package in R (Venables & Ripley, 2002)). Final models were chosen using stepwise selection during which both Maximum Likelihood tests and Akaike's Information Criterion (AIC) were used to compare model performance and guide the deletion of non-significant terms. Model misfit was assessed by plotting pearson residuals vs fitted values for each covariate. Pairwise post hoc comparisons were conducted with estimated marginal means (using the package "emmeans" version 1.5.1. (Lenth, 2020)) when a significant effect of MPA treatment or interaction was identified, to determine which treatments were significantly distinct.

2.2.6.2. *Elasmobranch diversity*

Changes in univariate elasmobranch diversity over time since MPA establishment were investigated by assessing the random effect of Site and fixed effects of Year, MPA Treatment and their interaction on elasmobranch taxon richness. This was conducted following the same data exploration and GLMM model selection approach outlined prior for elasmobranch abundance assessments. Taxon richness exhibited a right-skewed distribution and was therefore fitted with poisson GLMM and log link function.

Changes in multivariate diversity in response to MPA establishment were also assessed whereby species assemblages were visualised across years and MPA treatments with a non-metric Multidimentional Scaling (nMDS) plot. To assess the effect of MPA establishment on elasmobranch assemblage composition, PERMANOVA was used to statistically analyse differences in multivariate diversity over time and across the experimental treatments. Since PERMANOVA is robust to unbalanced survey designs, all years (2009 – 2020) were included in the analysis. Prior to analysis, a bray-curtis transformation was applied to relative abundance data.

2.2.6.3. *Elasmobranch exploitation*

To explore changes in elasmobranch exploitation over time since MPA initiation, public landings data were aggregated for all sharks and all skate species and visualised as total landings per year per species groups. Landings were categorised into mobile (exclusively used outside the MPA) and static gears to allow some interpretation of the location of landings.

2.2.6.4. *Habitat Associations*

Habitat associations were investigated by statistically assessing the relationship between substrate type and elasmobranch abundance. Habitat data could not be included as a factor in the larger GLMM analysis outlined prior, because data were only obtained for sites in the MPA treatment. Instead, separate GLMM analyses were conducted to explore the effect of substrate type on the abundance of the main elasmobranch groups (skates, sharks (excluding *S. canicula)* and *S. canicula*). Model selection was not warranted due to the presence of only a single fixed factor (substrate type). Assumptions and model misfit were tested following the same approach outlined above. All statistical analyses were conducted using the statistical programme R (R Core Team, 2021).

2.3. Results

A total of 827 BRUV deployment videos were analysed, conducted over the summers of 2009 – 2020 resulting in 413.5 hours of footage, with 1355 shark observations (of which *S.*

canicula represented 1307 occurrences) and 45 skate observations (Table 2.1). From these, three shark and four skate taxa were identified to species level from the families Scyliorhinidae, Triakidae and Rajidae. A further shark taxon was identified to genus level (*Mustelus sp.)* with the possibility of being two closely-related Smoothound species: *Mustelus mustelus* and *Mustelus asterias* (difficult to visually distinguish).

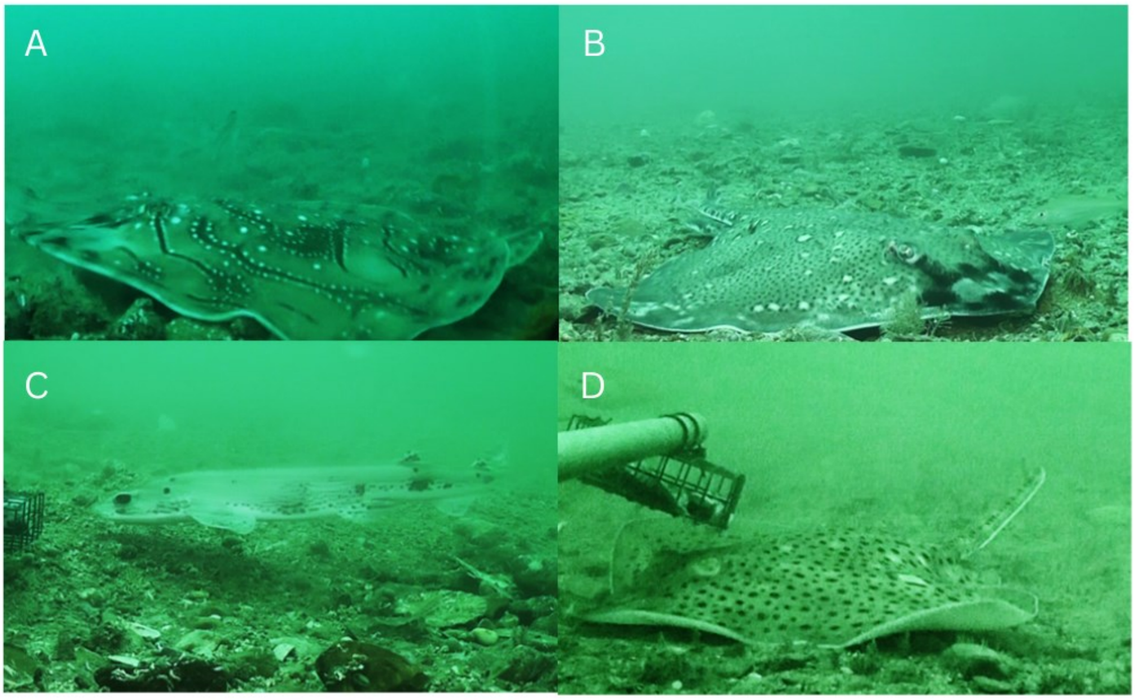

Figure 2.2. Some of the elasmobranch species detected in BRUV surveys and around Lyme Bay MPA (2009 – 2020). A) *Raja undulata*, B) *Raja clavata,* C) *Scyliorhinus canicula* and D) *Raja montagui.*

Table 2.1. All species observed from BRUV deployments (2009 – 2020) in and around Lyme Bay MPA, their IUCN red list statuses and total MaxN values.

Species Group	**Family**	**Species Name**	**Common Name**	**ICUN Red List Status (Europe)**	**ICUN Red List Status (Global)**	**∑MaxN MPA**	**∑MaxN Controls**	**Overall ∑MaxN**	**Proportion of Overall Observations**
SHARKS	Scyliorhinidae	*Scyliorhinus canicula*	Small-Spotted Catshark/ Lesser dogfish	Least Concern	Least Concern	653	654	1307	93.4%
	Scyliorhinidae	*Scyliorhinus stellaris*	Bull Huss/ Nursehound	Near Threatened	Vulnerable	30	3	33	2.4%
	Triakidae	Triakidae sp.	Houndsharks	-	-	5	3	8	0.6%
	Triakidae	*Galeus galeorhinus*	Tope	Vulnerable	Critically Endangered	4	0	4	0.3%
	Triakidae	*Mustelus sp.*	Smoothounds	Vulnerable	Endangered	2	1	3	0.2%
Total Sharks		**3 Species**				**694**	**661**	**1355**	**96.8%**
SKATES	Rajidae	Rajidae sp.	Skates	-	-	8	4	12	0.9%
	Rajidae	*Raja clavata*	Thornback Ray	Near Threatened	Near Threatened	27	1	28	2%
	Rajidae	*Raja undulata*	Undulate Ray	Near Threatened	Endangered	0	1	1	0.1%
	Rajidae	*Raja microocellata*	Small-eyed Ray	Near Threatened	Near Threatened	2	0	2	0.1%
	Rajidae	*Raja montagui*	Spotted Ray	Least Concern	Least Concern	2	0	2	0.1%
Total Skates		**4 Species**				**39**	**6**	**45**	**3.2%**
Total Elasmobranchs		**7 Species**						**1400**	

2.3.1. Species-specific Elasmobranch abundance

2.3.1.1. *Species-specific Skate Abundance Trends*

Skate species were not observed frequently enough to allow statistical assessment of individual abundance trends in response to MPA establishment. However, presenting species-specific relative abundance (MaxN) data (Figure 2.3) allowed low-level, descriptive interpretation of species differences. *Raja clavata* (thornback ray) was the most abundant skate species in Lyme Bay, with a total of 28 observations over the entire survey. *R. clavata* relative abundance exhibited a general increase over time (excluding the years 2014 and 2018) in the MPA, with the greatest abundance (0.25 skates per deployment) observed in the MPA treatment in 2020 (Figure 2.3a). *R. clavata* were only present in the NOC in 2012, and in the FOC in 2016 with respective relative abundances of 0.083 and 0.027 skates per deployment. Only two *Raja microocellata* (small-eyed ray) individuals were observed in this study, and they were only found inside the MPA treatment towards the end of the survey. This resulted in two relative abundance peaks of 0.027 skates per deployment in 2018 and 2020 (Figure 2.3b). *Raja undulata* (undulate ray) was observed only once in the survey in the FOC treatment. This resulted in a single relative abundance peak of 0.027 in 2016 (Figure 2.3c). *Raja montagui* (spotted ray) was documented twice in 2016 inside the MPA (with a relative abundance of 0.058 per deployment) but was not identified in either of the control treatments (Figure 2.3d). Meanwhile, a total of 12 Rajidae skates (MPA = 8; FOC = 2; NOC = 2) could not be identified to species level due to low visibility and remaining at distance from the camera. Most of these observations took place in the second half of the survey, from 2014 onwards (Figure 2.3e). The highest relative abundance of Rajidae spp. (0.083) skates per deployment) was observed in the NOC treatment in 2016 and in the MPA treatment in 2018.

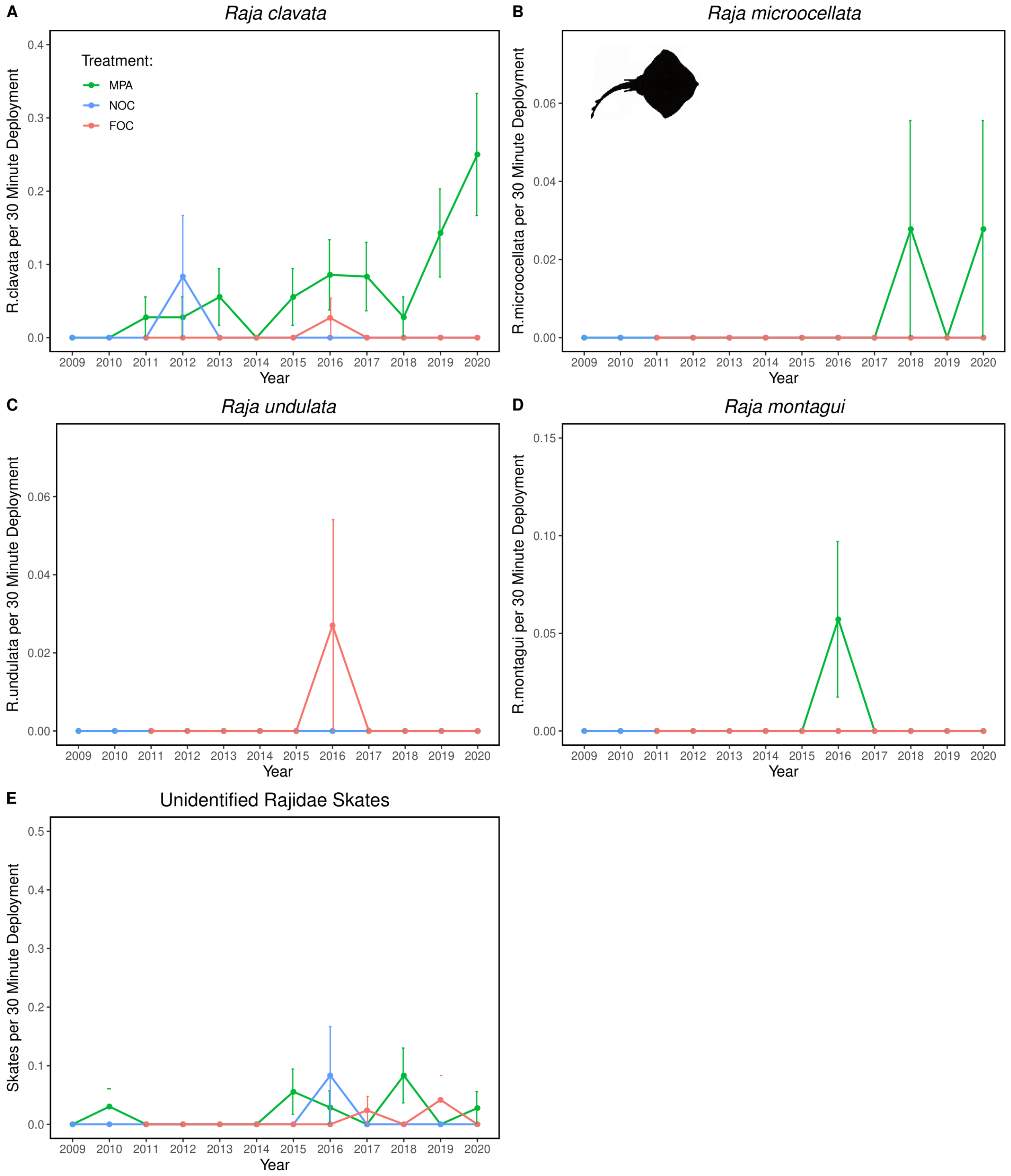

Figure 2.3. Mean relative abundance (MaxN (+/- SE)) of Rajidae skate species detected in BRUV surveys in Lyme Bay across different experimental treatments (MPA = Marine Protected Area (2009 – 2020), NOC = Near Open Control (2009 – 2020), FOC = Far Open Control (2011 – 2020)). Points represent mean relative abundance per treatment year. Note the differing scales on the Y axes.[1]

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[1] Spatiotemporal differences were not statistically analysed and therefore represent descriptive trends only.

2.3.1.2. *Species-specific Shark Abundance Trends*

Most shark species were also observed too infrequently to enable statistical assessment of abundance trends following MPA initiation. Therefore, interpretation of species-specific relative abundance (MaxN) data was once again restricted to descriptive trends (Figure 2.4). *Scyliorhinus stellaris* was the second most abundant shark species (following *S. canicula*), representing 33 of the shark observations over the survey period (Figure 2.4a). Sightings were higher inside the MPA than in controls and abundance fluctuated greatly across the survey period. Observations peaked inside the MPA in 2012 at 0.25 sharks per deployment. Two lower peaks were observed later in 2016 and 2020, but abundance generally declined over the survey period in the MPA. No *S. stellaris* individuals were observed in the FOC treatment, and they were only observed in the NOC treatment in 2012, with a relative abundance of 0.17 sharks per deployment. Four sightings of *Galeorhinus galeus* (tope) were observed during the study and they were exclusively found in the MPA treatment and only in the second half of the survey period from 2015 onwards (Figure 2.4b). Peak relative abundance was detected in 2015 at 0.06 sharks per deployment. Of similar abundance were *Mustelus sp.* (smoothounds) which were detected on three occasions, two of which were observed inside the MPA in 2016 and 2020 (Figure 2.4c). The final *Mustelus sp.* shark was present in the FOC treatment in 2016. Eight Triakidae sharks were not identified to species-level and these were spread across all treatments (Figure 2.4d). Unidentified Triakidae sharks were only documented in 2011 and 2013, with the highest relative abundance (0.17 sharks per deployment) detected in the NOC treatment in 2011.

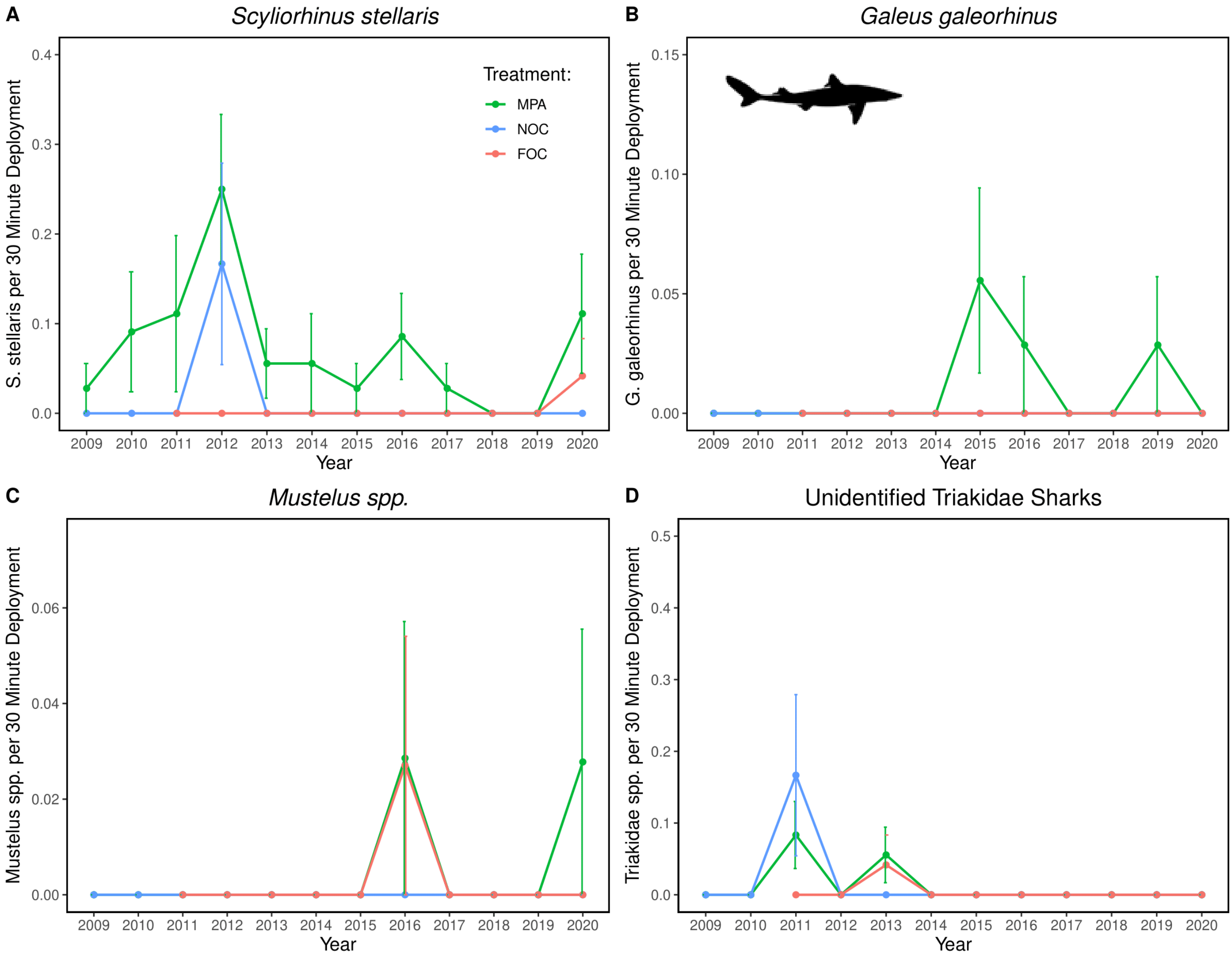

Figure 2.4. Mean relative abundance (MaxN (+/- SE)) of uncommon shark species detected in BRUV surveys in Lyme Bay across different experimental treatments (MPA = Marine Protected Area (2009 – 2020), NOC = Near Open Control (2009 – 2020), FOC = Far Open Control (2011 – 2020)). Points represent mean relative abundance per year. Note the differing scales on the Y axes.[2]

Scyliorhinus canicula (small-spotted Catshark) was the most abundant elasmobranch in the survey and was considerably more prevalent than any other species, with a total of 1307 observations, accounting for 93.4% of all elasmobranch encounters. As a result, abundance was sufficient to analyse statistically (Table 2.2, Figure 2.5). *S. canicula* relative abundance declined in all treatments over time since early MPA establishment (2011). However, GLMM model selection found that the interaction between Year and MPA treatment was significant (Table 2.2, $p < 0.01$), confirming that the scale of declines differed significantly across treatments. Post-hoc tests identified the significant difference between MPA:Year and FOC:Year ($p < 0.01$, Table 2.3), confirming that declines were significantly greater in the FOC sites than in the MPA treatment (Figure 2.5). Meanwhile the difference between MPA:Year and NOC:Year ($p = 0.07$, Table 2.3) was almost significant. A particular drop in mean relative

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[2] Spatiotemporal differences were not statistically analysed and therefore represent descriptive trends only.

abundance was evident across all treatments from 2016 – 2018, with the greatest reduction was displayed in the FOC treatment (Figure 2.5).

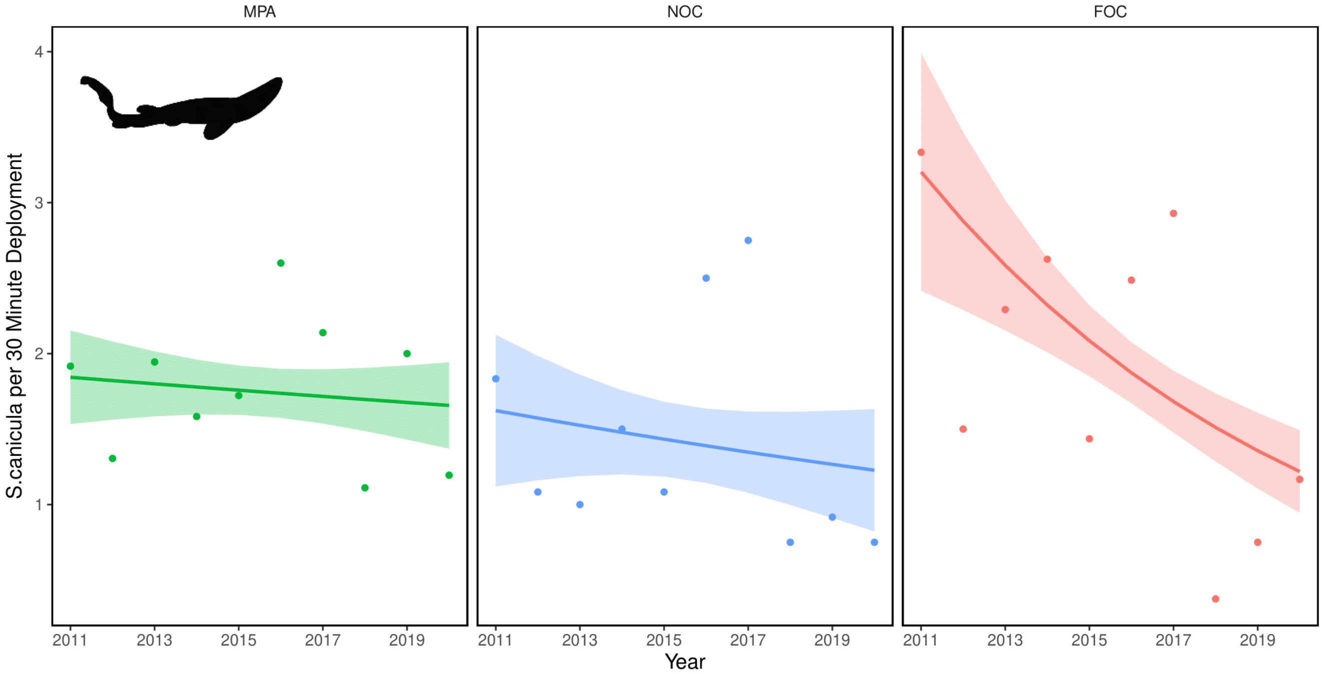


Figure 2.5. *Scyliorhinus canicula* relative abundance and over time (2011 – 2020) in and around Lyme Bay MPA across the treatments (MPA = Marine Protected Area, NOC = Near Open Control, FOC = Far Open Control). Points represent mean relative abundance (MaxN) per year, whilst the solid line represents modelled trends (Binomial GLMM) and 95% confidence intervals are represented by the shaded area.

Table 2.2. Generalised linear model analysis of variance among MPA treatments (M) and years (Y) (with Site and Year|Site as random effects) in the abundance of elasmobranchs in Lyme Bay (UK).

Species	**Response variable**	**Final Model Type**	**Full model**	**Dropped Term**	**AIC$_{full}$**	**ΔAIC**	***p*-value**
Sharks (excluding *S. canicula)*	Total Relative Abundance (A)	Poisson GLMM	A = M + Y + MY + (1|Site) + (Year|Site)	(Year|Site)	310	0	0.12
			A = M + Y + MY + (1|Site)	(1|Site)	311	1	**0.055**
			A = M + Y + MY + (1|Site)	MY	310	2	**0.031**
Skates	Total Relative Abundance (A)	Poisson GLMM	A = M + Y + MY + (1|Site) + (Year|Site)	(Year|Site)	304	-6	1
			A = M + Y + MY + (1|Site)	(1|Site)	298	5	**0.010**
			A = M + Y + MY + (1|Site)	MY	298	-1	0.22
			A = M + Y + (1|Site)	Y	297	14	**0.000077**
			A = M + Y + (1|Site)	M	250	11	**0.00055**
All	Taxon Richness	Poisson GLM	A = M + Y + MY + (1|Site) + (Year|Site)	(Year|Site)	1543	-6	1
			A = M + Y + MY + (1|Site)	(1|Site)	1537	-2	1
			A = M + Y + MY	MY	1535	1	0.064
			A = M + Y	Y	1536	0	0.22
			A = M + Y	M	1536	13	**0.00022**
Scyliorhinus canicula	Relative Abundance (A)	Negative Binomial GLMM	A = M + Y + MY + (1|Site) + (Year|Site)	(Year|Site)	2480	-4	0.61
			A = M + Y + MY + (1|Site)	(1|Site)	2476	11	**0.00034**
			A = M + Y + MY + (1|Site)	MY	2476	8	**0.0023**

Table 2.3. Generalised Linear Mixed Effects Model outputs for the final models chosen through stepwise selection. Representing the fixed effects (only) of Year and MPA treatment and their effect on elasmobranch relative abundance and taxon richness. All models included site as a random effect.

Response variable	Final Model Type	Terms	Estimate	SE	*p*
Skate Relative Abundance	Poisson GLMM	Intercept	-4.734	0.622	**<0.001**
		FOC – MPA	-2.099	0.636	**<0.01**
		MPA – NOC	1.83	0.856	0.083
		FOC – NOC	-0.269	0.987	0.96
		Year	0.604	0.162	**<0.001**
Shark Relative Abundance (Excl. *S. canicula*)	Poisson GLMM	Intercept	-4.655	0.648	**<0.001**
		FOC : Year – MPA : Year	-2.08	0.679	**<0.01**
		MPA : Year – NOC : Year	4.29	2.528	0.2056
		FOC : Year – NOC : Year	2.22	2.590	0.6684
Taxon Richness	Poisson GLM	Intercept	-0.3453	0.0752	**<0.001**
		FOC – MPA	-0.365	0.0916	**<0.001**
		MPA – NOC	0.274	0.1281	**<0.05**
		FOC – NOC	-0.090	0.1162	0.76
***S. canicula* Relative Abundance**	Negative Binomial GLMM	Intercept	0.5536	0.0519	**<0.001**
		FOC : Year – MPA : Year	9.02e-15	2.68e-15	**<0.01**
		MPA : Year – NOC : Year	7.75e-15	3.49e-15	0.068
		FOC : Year – NOC : Year	-1.27e-15	3.02e-15	0.91

2.3.2. Aggregated Elasmobranch Abundance

When aggregated, mean relative abundance (MaxN) of elasmobranchs (excluding *S. canicula*) per BRUV deployment remained low across the entire survey period, with < 0.4 elasmobranch observations per 30-minute deployment. However, abundance exhibited distinct relationships with MPA treatment and year for skates and sharks respectively (Figures 2.6 & 2.7).

The interaction between Year and MPA treatment did not significantly affect aggregated skate relative abundance (Table 2.2, $p = 0.22$). However, the main effects of MPA treatment and Year and the random effect of Site all significantly influenced skate relative abundance ($p < 0.05$, Table 2.2). The relative abundance of skates significantly increased over time since early MPA initiation (2011) across all treatments (Figure 2.6a). Meanwhile, post-hoc analysis of the main effect of MPA treatment found that skates were significantly more abundant in the MPA compared to the FOC ($p < 0.01$; Table 2.3) however, the abundance of skates in the NOC treatment was not significantly different to the other treatments (Table 2.3, $p > 0.05$, Figure 2.6b).

Statistical assessment of the relationships between aggregated shark (excluding *S. canicula*) relative abundance, MPA treatment and year identified a significant interaction between Year and MPA treatment (Table 2.2, $p < 0.05$). Post-hoc tests identified that the changes in shark abundance over time were significantly different between the MPA and FOC treatments (Table 2.3, $p < 0.05$), but no significant difference was found between NOC and the other treatments (Table 2.3, $p > 0.05$).

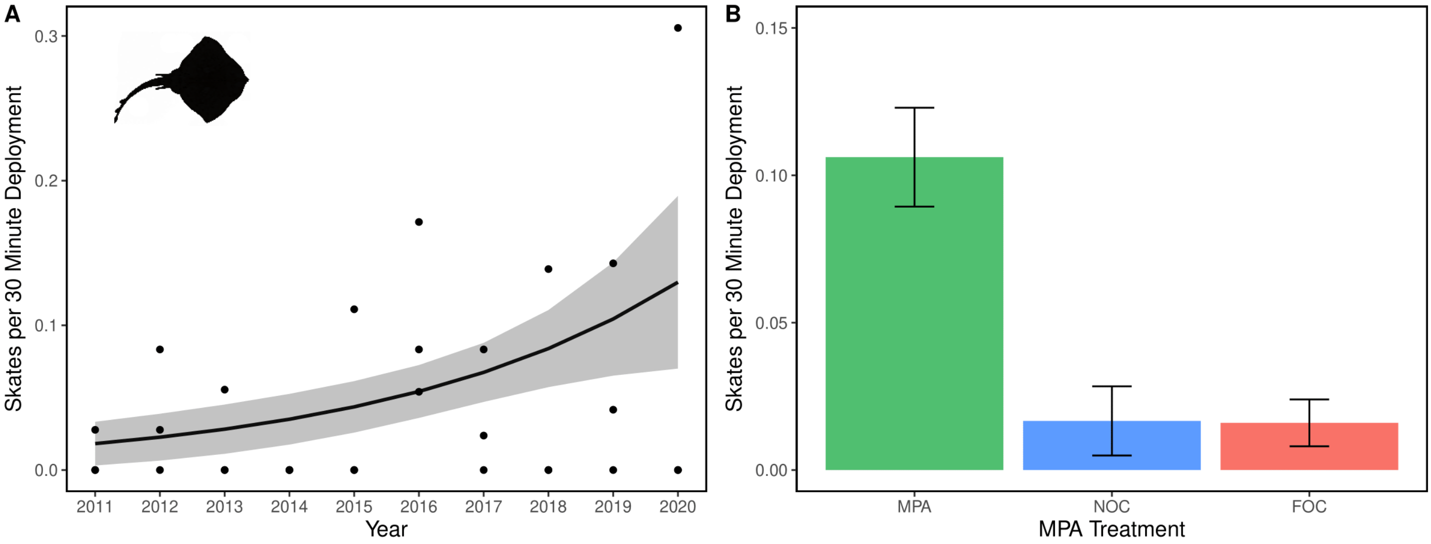


Figure 2.6. Rajidae skate relative abundance (MaxN) A) over time (2011 – 2020) points represent mean relative abundance (MaxN) per year, whilst the solid line and shaded area represent modelled data (Poisson GLMM) and 95% confidence intervals) and B) across experimental treatments (MPA = Marine Protected Area, NOC = Near Open Control, FOC = Far Open Control) in and around Lyme Bay MPA. Bars represent mean skate abundance per deployment per treatment (+/- SE).

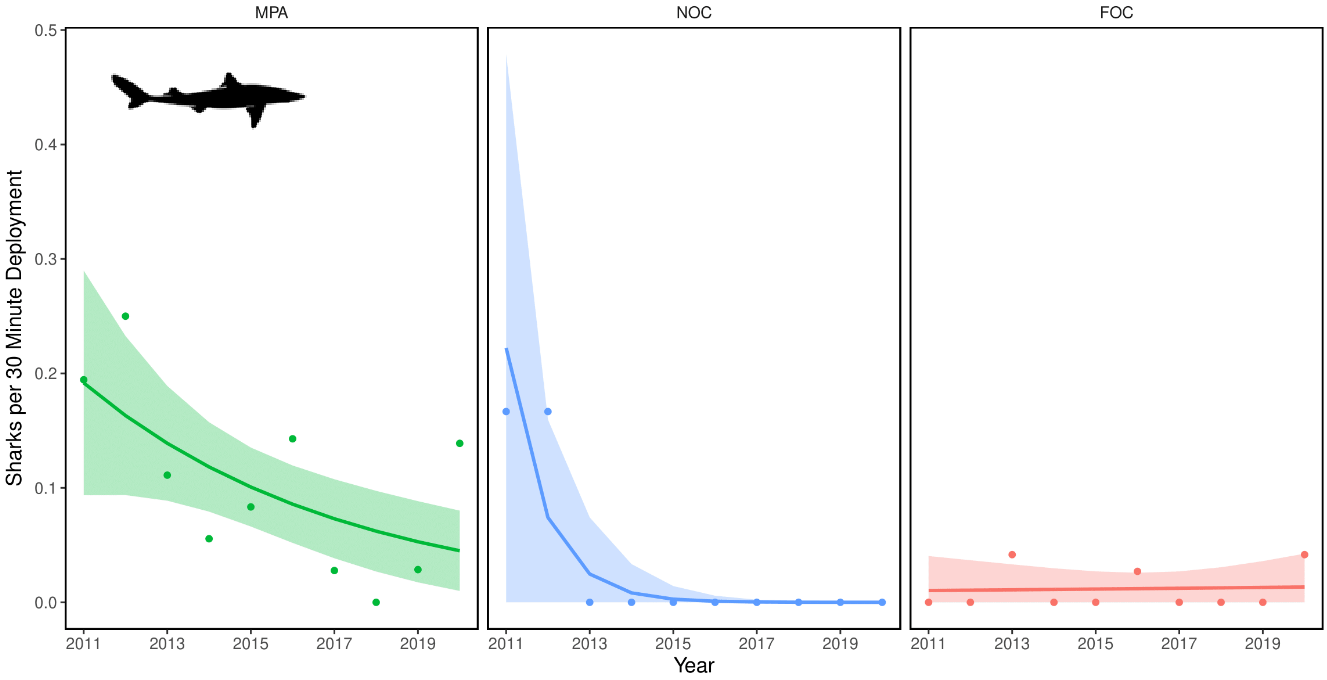


Figure 2.7. Shark (excluding *S. canicula*) relative abundance (MaxN) over time (2011 – 2020) in and around Lyme Bay MPA across the treatments (MPA = Marine Protected Area, NOC = Near Open Control, FOC = Far Open Control). Points represent mean relative abundance (MaxN) per year, whilst the solid line represents modelled trends (Poisson GLMM) and 95% confidence intervals are represented by the shaded area.

2.3.3. Elasmobranch community

2.3.3.1. Taxon Richness

Taxon richness varied from 0 – 3 elasmobranch species per 30 minute BRUV deployment. When statistically assessed, temporal changes in taxon richness were not significantly different between MPA treatments ($p = 0.06$, Table 2.2, Appendix 2). Furthermore, taxon richness did not significantly change over time from 2011 to 2020 ($p = 0.22$, Table 2.2). However, the main effect of MPA treatment was significant ($p < 0.001$, Figure 2.8, Table 2.2), and post-hoc tests revealed that the MPA exhibited significantly higher taxon richness than both the control treatments (MPA vs NOC, $p < 0.05$; MPA vs FOC $p < 0.001$, Table 2.3).

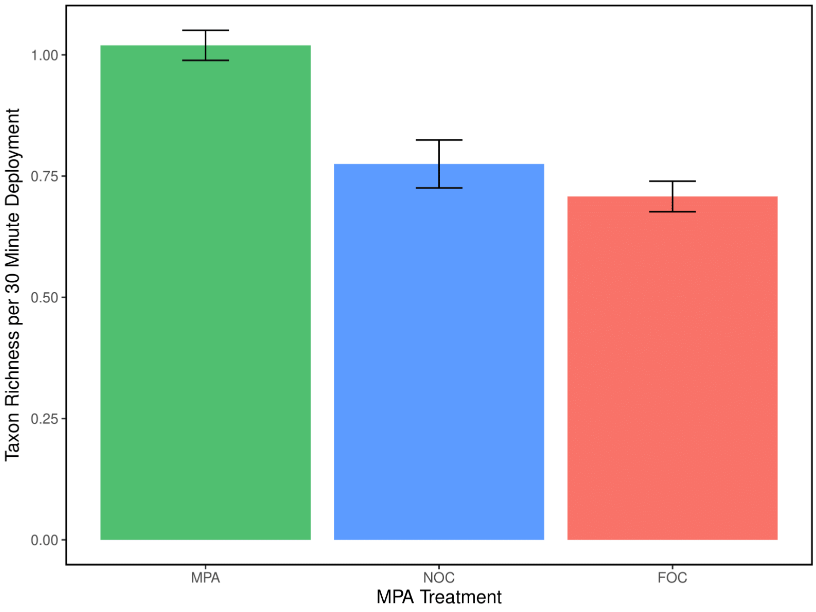


Figure 2.8. Mean taxon richness (+/- SE) of elasmobranchs per 30 minute BRUV deployment across experimental treatments (MPA = Marine Protected Area, NOC = Near Open Control, FOC = Far Open Control) in and around Lyme Bay MPA.

2.3.3.2. Multivariate Assemblage Composition

The nMDS plot (Figure 2.9) had a stress value of 0.03 (< 0.2) indicating that it accurately represented the multivariate distance among samples (Clarke & Gorley, 2006). MPA treatment clusters exhibited substantial overlap, particularly for the NOC and FOC treatments. However, whilst the MPA exhibited considerable similarity and overlap with the other treatments, it displayed noticeable departure from controls in the years (2009 and 2012) and to a lesser extent in (2011, 2019 and 2020). Results of the PERMANOVA analysis (Table 2.4) revealed a significant difference between MPA treatments ($p < 0.05$) but no significant effect of Year ($p = 0.085$) nor a significant interaction between MPA treatment and Year ($p = 0.075$) though these were not far from the significance threshold.

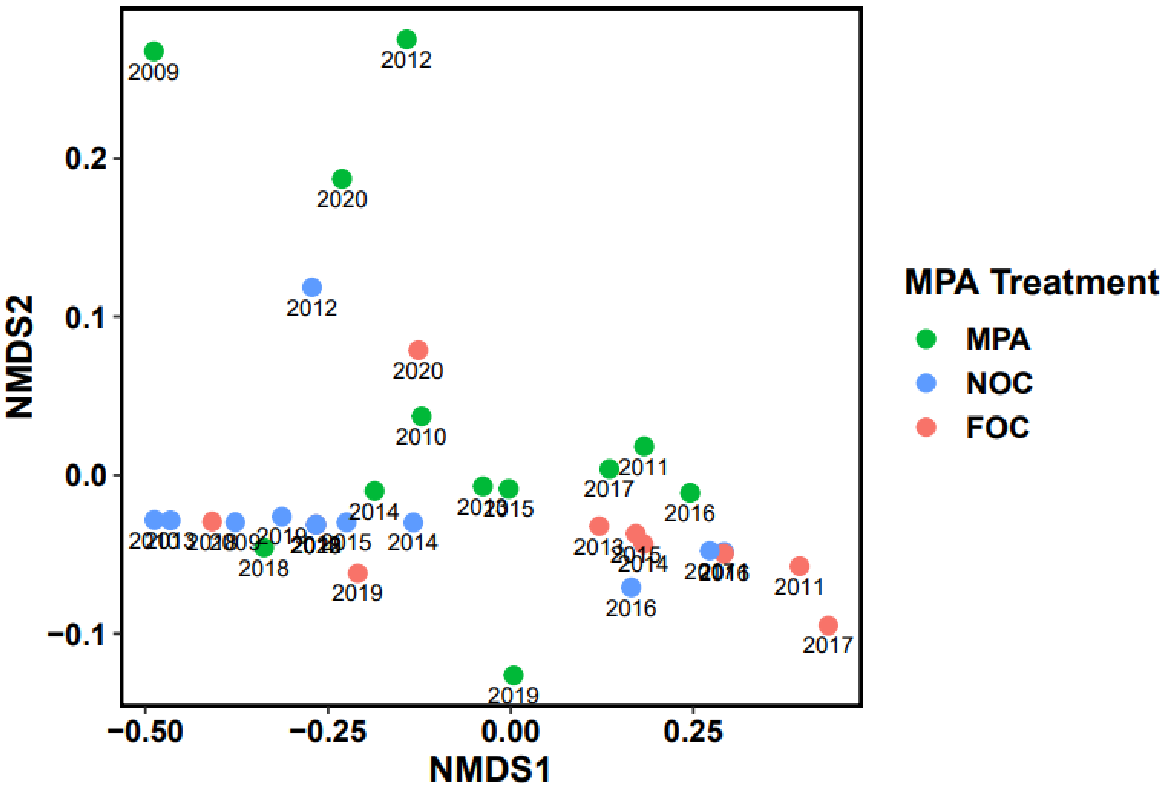


Figure 2.9. Multivariate diversity representing the elasmobranch community across different experimental treatments (Marine Protected Area (MPA), Near Open Control (NOC) and Far Open Control (FOC)) and over time (MPA and NOC, 2009 – 2020; FOC, 2011 – 2020).

Table 2.4. Results from PERMANOVA analysis, exploring the effects of MPA treatment, Year and their interaction on multivariate diversity of elasmobranchs in and around Lyme Bay MPA (2009 – 2020).

Terms	**R^2**	**F**	***p***
MPA Treatment	0.032	9.70	**<0.01**
Year	0.0041	2.47	0.085
MPA Treatment : Year	0.0066	2.00	0.075

2.3.4. Potential drivers of MPA effects

2.3.4.1. Elasmobranch Exploitation

Neither shark nor skate landings decreased over the survey period following MPA initiation (Figure 2.10). Documented shark landings remained relatively low and stable for the first five years after MPA establishment at a mean of ~ 9 T y^{-1}, however, beyond 2014, shark landings increased, reaching 118 T y^{-1} in 2016 (Figure 2.10a). Mobile gear landings, caught outside MPA boundaries, were responsible for most of this increase in shark exploitation. Beyond 2015, overall shark landings were sustained at much higher levels than the first half of the survey, with mobile gears responsible for a significant majority of the catch. Meanwhile, skate catch was higher in the first 4 years than shark catch during the same period, with an average catch of ~ 35 T y^{-1} (Figure 2.10b). Skate landings also increased over time, but not to the same extent as shark landings, reaching their highest level in 2015 at ~ 70 T y^{-1}. Similar to sharks, skate landings remained higher in the second half of the survey period compared to the first.

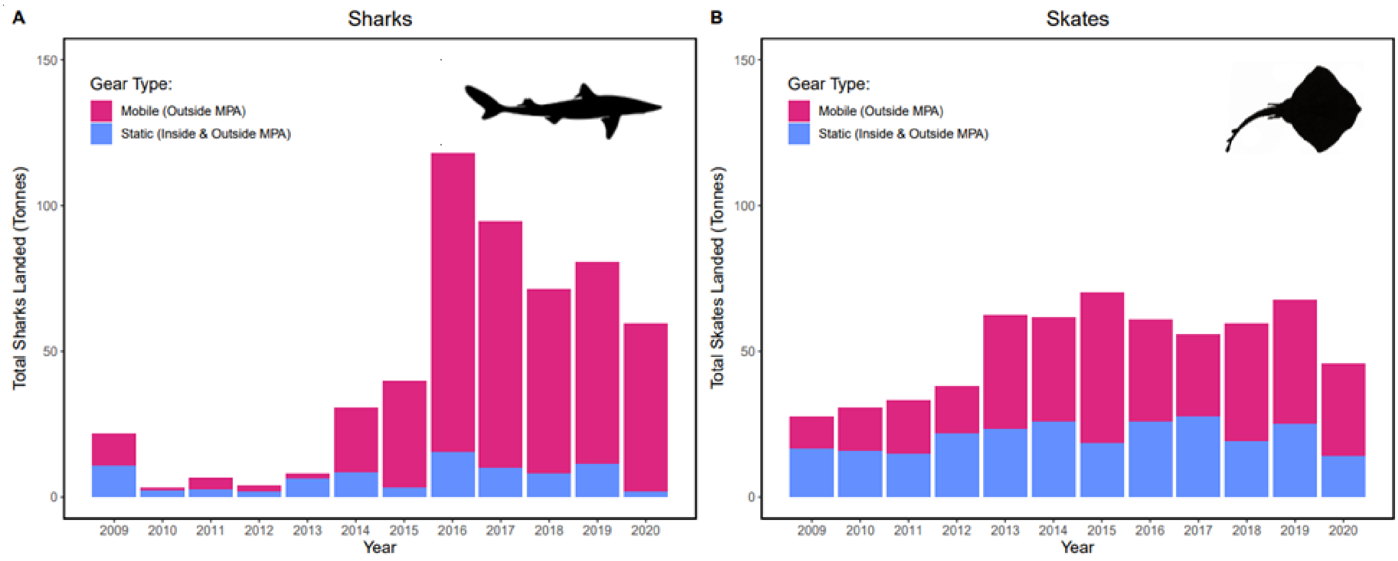


Figure 2.10. Publicly available landings data (https://www.gov.uk/government/organisations/marine-management-organisation, accessed: 15/02/2022) representing a proxy for the total weight (T) of landed A) sharks and B) skates in the wider Lyme Bay region (ICES rectangles: 30E6 & 30E7). Landings are apportioned to those landed by mobile (prohibited inside the MPA) and static gears and represent the sum of all reported landings per year.

2.3.4.2. Habitat Associations

There was no significant relationship between shark (excluding *S. canicula*) relative abundance and substrate type (Figure 2.11a, Table 2.5, p = 0.24) or between *S. canicula* relative abundance and substrate type (Figure 2.11c, Table 2.5, p = 0.84). However, a significant relationship was identified between Rajidae skate abundance and substrate type (Table 2.5, $p < 0.05$) with skates occurring predominantly in mobile sediment substrates (Figure 2.11b).

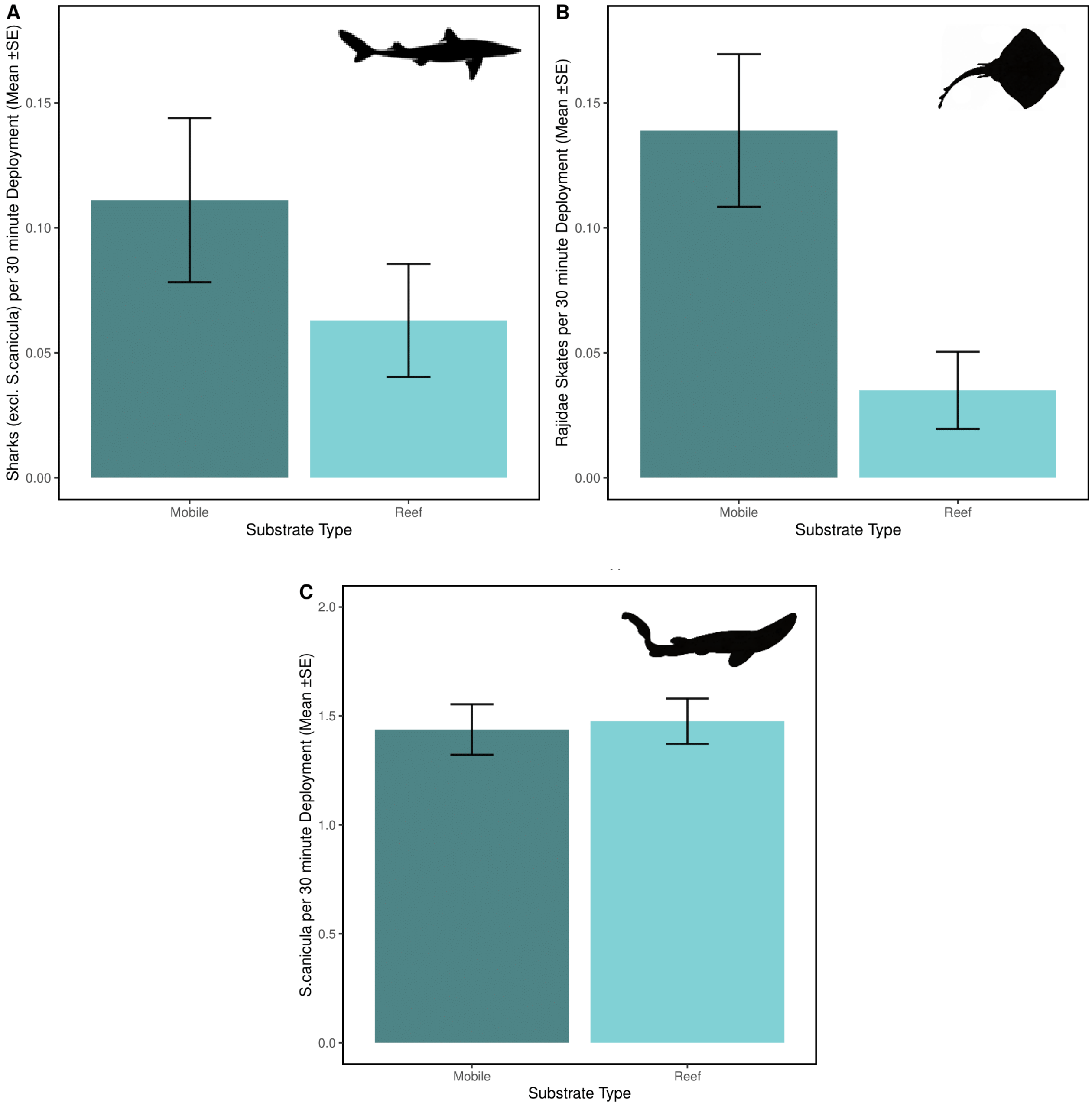


Figure 2.11: The relationship between substrate type and relative abundance (Mean ± SE) of A) sharks (excluding *S. canicula*), B) Rajidae skates and C) *S. canicular* sharks inside Lyme Bay MPA.

Table 2.5. Generalised Linear Mixed Effects Model outputs representing the fixed effect of substrate type and its effect on elasmobranch relative abundance inside the MPA. All models included site as a random effect.

Response variable	**Model Type**	**Terms**	**Estimate**	**SE**	***p***
Skate Relative Abundance	Poisson GLMM	Intercept	-2.0896	0.3544	**<0.001**
		Reef - Mobile	1.43	0.614	**<0.05**
Shark Relative Abundance (Excl. *S. canicula*)	Negative Binomial GLMM	Intercept	-2.2125	0.3235	**<0.001**
		Reef - Mobile	0.57	0.483	0.24
***S. canicula* Relative Abundance**	Poisson GLMM	Intercept	0.38074	0.14961	**<0.05**
		Reef – Mobile	0.042	0.206	0.84

2.4. Discussion

This study set out to determine the effect of Lyme Bay MPA on the elasmobranch community and explore the potential role of fishing and habitat associations in driving these trends. Overall, evidence for MPA benefits was equivocal. Elasmobranch (skates and sharks (excluding *S. canicula*)) abundance tended to be higher inside the MPA compared to controls. However, for skates, population increases could not be robustly attributed to MPA benefits, because abundance increases were not significantly greater inside the MPA relative to control sites. Meanwhile, for sharks (excluding *S. canicula*), abundance declined significantly over time inside the MPA. Furthermore, although MPA sites harboured significantly higher univariate and multivariate diversity than control sites, the MPA did not become significantly more diverse over time relative to controls. The only clear MPA benefit was demonstrated for *S. canicula* abundance which declined less over time inside the MPA relative to steep declines evident in control sites.

Exploring elasmobranch landings data supported these findings, indicating that the initiation of the MPA did not trigger a reduction in elasmobranch exploitation, and instead, elasmobranch fishing increased in Lyme Bay over the survey period. Meanwhile, an investigation of habitat associations demonstrated that neither sharks nor skates were significantly associated with reef habitats, suggesting that the MPA design is not particularly appropriate for the protection of these species. These effects are discussed in more detail in the following sections.

Secondary to assessing MPA effects, this study aimed to take advantage of the extensive BRUV survey to provide an in-depth, fishery-independent account of the elasmobranch community in Lyme Bay. To achieve this, the findings of this study are discussed in the broader context of Lyme Bay landings data and comparable BRUV surveys in other temperate areas.

2.4.1. The effect of Lyme Bay on Elasmobranch Abundance

2.4.1.1. Skate Abundance

Firstly, aggregated skate abundance increased significantly over time in all treatments, however, population benefits could not be convincingly attributed to MPA establishment alone, because increases in abundance over time were not significantly greater inside the MPA relative to controls. Two potential explanations for this exist. Firstly, the population increase could be explained by an external factor (e.g. improved fisheries management or a positive response to climate change) which is positively influencing the wider skate community as a whole, including those in control sites. Notable skate management interventions were introduced in 2009 in the Western English Channel (ICES division VIIe), including a total allowable catch (TAC), species-specific reporting for skate and ray landings (Ellis et al., 2010) and temporary (2009 - 2014) prohibition of *R. undulata* landings (Small, 2021a; ICES, 2018) meanwhile local byelaws now enforce minimum landing sizes for several Rajidae species in the East of Lyme Bay (Small, 2021a-c). These management strategies could be responsible for wide-scale skate population benefits, however, analysis of skate landings in this study indicated an increase in both mobile and static skate exploitation since 2009, making this explanation less compelling.

Alternatively, mobility of skates between treatments may have diluted spatially distinct population responses, meaning the bay-wide population increase could represent a large spill-over effect from population benefits within the MPA. This could also explain the significantly higher abundance of skates inside the MPA compared to FOC sites (but not NOC sites), whereby the MPA could be acting as a source population for the surrounding waters. Mark-recapture studies in the UK demonstrate that Rajidae skates are typically recaptured around 20 - 30 km (maximum 61 – 82.6km) from release locations (Ellis et al., 2010; Simpson et al., 2020), making movement across the 206km^2 MPA boundary highly plausible. Meanwhile, long-term analysis of trawl data at multiple locations around Plymouth, observed a general decline in *R. clavata* CPUE over the past century in response to ocean warming and exploitation (Genner et al., 2009) suggesting that skate population increases may be localised to Lyme Bay, and therefore, potentially caused by the MPA. Furthermore, wider research in Lyme Bay has documented significant increases in the abundance and diversity of both invertebrates and fish inside the MPA (Davies et al., 2020), possibly affording skate population benefits through increased prey availability, despite no clear reduction in exploitation.

Unfortunately, the results from this study alone cannot conclusively assign Lyme Bay MPA as the main driver of skate population increases, but future studies employing telemetry or mark-recapture methods could be particularly helpful for investigating potential spill-over effects. Meanwhile comparison with temporal abundance trends across wider locations could help determine the spatial extent of skate population increases. Interestingly, analysis of skate habitat associations inside the MPA indicated that skates were significantly associated with mobile substrates rather than reef habitats which may further explain the inconclusive population benefits detected. MPA design has been identified as a key driver of MPA efficacy (Edgar et al., 2014; MacKeracher et al., 2019), and since Lyme Bay MPA was predominantly designed to protect rocky reef features, conservation benefits offered to inhabitants of mobile substrates may be limited. This finding does however emphasise the importance of the whole-site approach for delivering greater conservation benefits, particularly beyond target species, ensuring that the entire matrix of interacting and important habitats receive protection.

2.4.1.2. Shark Abundance

When aggregated and statistically assessed, shark abundance (excluding *S. canicula*) declined over time in the MPA treatment, whilst abundance in the FOC treatment remained stable at near zero for the entire survey. This indicates that Lyme Bay MPA is not currently providing adequate protection for uncommon shark species. Presenting total landings across the survey revealed a substantial increase in reported shark exploitation in Lyme Bay since MPA initiation, particularly from 2016 onwards. Mobile fishing gears (e.g. trawls, dredges) acting outside MPA boundaries accounted for most of this increase, perhaps resulting from displacement into nearby waters. Displacement of demersal fishing outside Lyme Bay MPA, has been implicated in increased Lemon Sole, Scallops and Cuttlefish landings following MPA establishment (Rees et al., 2021) and therefore represents a viable explanation for increased shark landings. This is also supported by the literature which demonstrates that when species frequently traverse MPA boundaries, MPA efficacy relies, not only on fishery management within protected areas, but also in adjacent waters (Murawski et al., 2000; Leurs et al., 2021). Therefore, additional fishery management within the MPA (such as shark specific quotas and limits) and in a 'buffer zone' around the MPA perimeter may improve the efficacy of Lyme Bay for sharks. Once again, elucidating species-specific movement patterns through telemetry could help inform these management modifications.

Moreover, evidence suggests that for MPAs to successfully protect highly mobile species, critical habitats such as feeding or nursery areas, should be encompassed (da Silva et al., 2021; Gallagher et al., 2021). Triakidae sharks are highly mobile, exhibiting complex migratory behaviours, such as triennial migration in the US (Nosal et al., 2021) and movement from the UK to the Mediterranean (Thorburn et al., 2019). The lack of affinity between sharks and protected reef habitats observed in this study, may therefore further explain the decline in shark abundance, by reducing the time sharks spent inside the MPA and protected from demersal fishing. This also likely signifies a mismatch between MPA design and shark ecology, which is unsurprising considering the MPA was designed for sessile reef species (Council Directive 92/43/EEC). Nevertheless, rare sharks were more commonly observed in the MPA relative to control sites suggesting that Lyme Bay MPA may represent an important shark habitat, relative to surrounding waters, providing further incentive for increased conservation measures.

Conversely, when analysed alone, the most abundant shark species, *S. canicula,* demonstrated the only convincing evidence of an MPA population benefit. Whilst *S. canicula* relative abundance decreased in all treatments over time, the decline in the MPA treatment was significantly smaller than the FOC treatment. This indicates that the MPA may have provided sufficient benefit to *S. canicula* sharks to slow population declines. Whilst the aspiration of elasmobranch MPAs is generally to provide complete protection from threats and encourage population increases, some argue that slowing declines or stabilising populations represents a more realistic benchmark of success considering the intrinsic slow reproduction and growth rates of most elasmobranch species (MacKeracher et al., 2019). However, the fast-growing nature and high reproductive output of *S. canicula,* facilitate rapid recovery and therefore, population increases could realistically be achieved for this species. The overall significant decline in this species across all treatments (potentially a result of rising catshark landings (Appendix 3)) indicates that extraction rates have exceeded the rate of population replenishment. This is concerning given the apparent resilience of this species to extraction and makes declines in more sensitive shark species unsurprising. Once again, *S. canicula* was not significantly associated with reef habitats. However, unlike Triakidae sharks and Rajidae skates, *S. canicula* is considered a generalist scavenger (Lyle, 1983), meaning it may more opportunistically utilise the greater quality and quantity of resources (e.g. prey and hard features for egg-laying) offered by the recovering ecosystem in the MPA (Sheehan et al., 2013; Davies et al., 2020). Overall, the slowing of *S. canicula* declines inside the MPA is evidence that partially-protected MPAs can effectively contribute to population stability, particularly for faster growing species.

2.4.1.3. Elasmobranch diversity

Exploring the response of univariate (taxon richness) and multivariate elasmobranch diversity to MPA establishment revealed no significant effect of Year, nor a significant interaction between Year and MPA treatments. Indicating that elasmobranch diversity has not been clearly altered or improved by the establishment of the MPA and associated management. This may once again be explained by a general lack of adequate protection from fishing in the wider area and a lack of associations between elasmobranch species and protected reef habitats. However, the MPA exhibited significantly greater multivariate and univariate diversity than the far control sites providing further evidence that Lyme Bay MPA encompasses critical elasmobranch habitat and may meet some criteria for an 'Important Shark and Ray Area' (ISRA, Hyde et al., 2022). Firstly, the MPA encompasses a range of threatened species (e.g. *Mustelus sp.),* with tope (*G. galeus*) being exclusively detected within the MPA and not in surrounding waters (Criterion A). Secondly, significantly higher elasmobranch diversity and abundance is supported by the MPA compared to nearby waters (Sub-criterion D2). Further study into specific elasmobranch behaviours and habitat-use in Lyme Bay at various ontogenetic stages could confirm whether additional criteria are met. However, this evidence alone warrants an investigation into potential MPA modifications or supplementary fishery restrictions to enhance the conservation outcomes of Lyme Bay MPA for elasmobranchs.

2.4.2. Detailed, Fishery-independent Account of Lyme Bay Elasmobranch Community

Overall, this survey identified seven elasmobranch taxa to species-level from 503 hours of BRUV deployments in Lyme Bay. Elasmobranchs spanned various morphologies, ranging from highly mobile migratory pelagic sharks (e.g. *G. galeus*) to small, benthic sharks (e.g. *S. stellaris)* and skates (e.g. *R. clavata)*. To place findings in a wider context, a handful of temperate BRUV studies were identified with comparable methodologies (< 100 – 500g of bait, < 30 – 60 minute soak times) and full species lists. Most were conducted in temperate Australia (Broad et al., 2010; Colton & Swearer, 2012; Hardinge et al., 2013; Wraith et al., 2013) and the remainders were in the UK (Griffin et al., 2016; Blampied et al., 2022). In the UK, Griffin et al. (2016) documented just two elasmobranch species around windfarms, from 40 hours of footage, whilst Blampied et al. (2022) identified six species from 67 hours of footage in Jersey. Meanwhile, studies in Australia identified similar numbers of elasmobranch species (n = 6 – 9) to this study (n = 7), but with markedly less survey effort (20 – 78 hours). When considering disparities in survey effort, the elasmobranch species richness per unit effort in Lyme Bay is lower than all other studies, including those in the UK. However, this may be partly explained by reduced species accumulation at higher sampling efforts (likely in Lyme Bay) when communities have been adequately sampled and remaining unsampled species are increasingly rare. Nevertheless, these comparisons are consistent with global patterns of elasmobranch diversity which place the UK among the least diverse temperate regions and markedly more species-poor than Australia (Tittensor et al., 2010; Lucifora et al., 2011; Dulvy et al., 2014).

Low diversity in Lyme Bay and in the UK generally may be influenced by various factors. Firstly, method inadequacies may have led to underreporting by BRUVs. This is supported by a comparison with elasmobranch diversity observed in landings data over the same period (Appendix 4) which indicated that BRUVs detected 35% of all species (n = 20) present in fishery landings data in Lyme Bay over the same period. BRUV surveys frequently underestimate elasmobranch diversity compared to fishery landings for multiple reasons (Jabado et al., 2018). Firstly, low water visibility or individuals remaining at distance from the camera inhibits species-level identification (Rees et al., 2015; Port et al., 2016; Tang et al., 2019), particularly affecting the detection of cryptic species whose distinction requires examination of fine-scale visual features (e.g. Rajidae skates) (Stobart et al., 2007; Colton & Swearer, 2010). Similarly, BRUVS cannot distinguish closely related species groups whose differentiation requires analysis of genetic markers (e.g. *Mustelus spp.,* Farrell et al., 2009). Accordingly, *Mustelus spp.* and Rajidae skates comprised ≥ 65% (n ≥ 15) of individuals not identified to species-level in this study. BRUVs will also fail to detect species whose ecological niches do not overlap with the spatiotemporal sampling regime of the study (De Vos et al., 2015). This likely explains the absence of pelagic sharks (e.g. *Prionace glauca* (Blue sharks), Rigby et al., 2019), and deep-water species (e.g. *Centroscyllium fabricii* (Black dogfish), Ebert et al., 2013) residing beyond the shallow (~30m) coastal waters under study.

Method limitations cannot fully explain the absence of other species present in landings data, such as *Raja brachyura* and *Squalus acanthias*, whose habitat preferences were adequately sampled by this survey and have been successfully detected by previous BRUV surveys (Blampied et al., 2022; Ovegård et al., 2022; Simpson et al., 2020). Instead, these absences likely indicate low abundance, which reduces the probability of individuals encountering bait plumes and interacting with BRUVs (Jabado et al., 2018), a barrier overcome by landings data with vastly greater “effort” (e.g. longer soak times, high boat trip frequency, multi-seasonal, targeting high abundance areas, Jabado et al., 2018). Recent documented declines of > 90% in NE Atlantic *S. acanthias* populations (Hammond & Ellis, 2005) and marked reductions in *R. brachyura* relative abundance (Roger & Ellis, 2000; Ellis et al., 2005) due to significant fishery exploitation support this theory. Similarly, population declines likely also account for the absence of other intermediate and large-bodied skates which were historically present (*Leucoraja fullonica*) or common *(Dipturus batis*) in inshore habitats (Roger & Ellis, 2000; McHugh et al., 2011).

Elasmobranch abundance varied between species. Whilst overall relative abundance was low for most species, the community was dominated by *S. canicula* catsharks which constituted 93.4% of all elasmobranch observations and equated to a mean CPUE of 2.59 catsharks per hour of BRUV survey effort. This aligns with the wider literature which highlights the ubiquity of *S. canicula* throughout UK inshore habitats (McHugh et al., 2011; Griffin et al., 2016; Blampied et al., 2022). Most *S. canicula* subpopulations in the NE Atlantic are stable or increasing (Ellis et al., 2009) and a clear increase has been documented specifically in the Western English Channel (Rogers & Ellis, 2000; McHugh et a., 2011). Increasing Scyliorhinidae populations have been attributed to several factors, including: high discard (due to low commercial value) and survival rates (Revill et al., 2005), tolerance to exploitation (owed to r-selected life history traits (Ellis et al., 2009)), mesopredator-release (due to declines in higher trophic-level elasmobranchs (Fogarty & Murawski, 1998)) and a positive response to rising sea temperatures under climate change (Genner et al., 2004; Genner et al., 2009; Simpson et al., 2011). These explanations therefore suggest that the *S. canicula* dominance in Lyme Bay and the wider UK, rather than a natural phenomenon, may be an artefact of an exploited and impacted system.

The remaining six elasmobranchs detected were present at considerably lower abundances, with a mean CPUE of 0.18 individuals per hour of BRUV survey effort, aligning closer with the relative abundance of elasmobranchs in temperate Australia (Hardinge at al., 2013). Wider comparisons were challenging, because studies targeting elasmobranchs tend to use greater volumes of bait (Whitmarsh et al., 2017), and reporting on elasmobranchs was limited in non-elasmobranch specific studies (Whitmarsh et al., 2017). While some evidence suggests that bait quantity has no significant effect on elasmobranch relative abundance (Hardinge et al., 2013) which would justify wider study comparisons, this may vary contextually and has not yet been tested in Lyme Bay. Nevertheless, when compared to Jabado et al. (2018) which presented average CPUE of elasmobranchs recorded by BRUVs around the globe, the CPUE in Lyme Bay observed in this study is markedly lower than almost all locations excluding the UAE. This may be resultant of the long history of exploitation in UK waters, the naturally lower abundance of species in temperate climates compared to the tropics or could be a product of methodological differences. To disentangle these drivers, future studies determining the effect of greater bait quantities on elasmobranch detection specifically in the UK would enable more confident global comparisons. Meanwhile historical ecology could help reconstruct a baseline for past elasmobranch communities to aid a deeper understanding of natural vs unnatural abundance and diversity patterns.

2.4.3. Study Limitations

Finally, a common theme throughout this discussion was the low detection of elasmobranchs which obstructed the statistical assessment of species-specific population trends. This is a well-documented challenge for predatory species, naturally present in low abundances (Hardinge et al., 2013). Studies exploring method optimisations could improve the detection of elasmobranchs and the statistical power of resultant datasets, without relying solely on increasing survey effort. For instance, exploring the rate of elasmobranch detection with longer soak times and greater bait quantities, may increase the likelihood of rarer species encountering bait plumes (Hardinge et al., 2013; Currey-Randall et al., 2020). Alternatively, changing the time of deployment to target periods of high activity (e.g. during crepuscular periods, or at night) could increase the effectiveness of BRUV surveys for certain species (Kelly et al., 2020). However, to facilitate inter-study comparisons, minimum reporting guidelines should be adhered to (Whitmarsh et al., 2017), since wider comparisons were limited in this discussion by a general lack of reporting of full species lists. Furthermore, species-level identification was often limited by species remaining far from the camera, therefore, future efforts to entice elasmobranch closer to bait boxes, perhaps through use of multiple attractants, may aid greater detection of species, particularly in temperate waters. Finally, survey design was not tailored specifically to elasmobranchs, which motivated the selection of control sites near MPA boundaries. Whilst the survey was expanded to include more far controls (FOCs) in 2011, there was a lack of data in the first two years of the study which may have impeded the detection of interactions between Year X MPA Treatment in some cases. This seems particularly likely for taxon richness, which was similar across treatments in the first 3 years and departed considerably after this time (Appendix 2), and the interaction effect was almost significant ($p = 0.06$).

2.5. Conclusion

To conclude, this study found minimal evidence of robust MPA benefits for the elasmobranch community in Lyme Bay. Whilst the diversity and abundance of skates was higher inside the MPA compared to control sites, this could not be convincingly attributed to MPA establishment as changes over time were not significantly different between experimental treatments. Meanwhile, the case for sharks (excluding *S. canicula*) demonstrated a clear lack of protection, with dramatic declines in both the NOC and MPA treatments and almost no sightings in FOC sites. The lack of MPA benefits was supported by an exploration of elasmobranch exploitation, which found increased elasmobranch fishing in Lyme Bay following MPA establishment. Meanwhile, a lack of habitat associations between elasmobranchs and protected reef habitats likely reduced their time spent inside the MPA, protected from demersal fishing. The only robust evidence of an MPA benefit was identified for *S. canicula,* which declined less inside the MPA relative to controls. This effect may be explained by the generalist nature of this species, which likely allowed it to opportunistically exploit the increased habitat quality and resources, made available through ecosystem recovery. Overall, these results support the importance of appropriate MPA design and limiting fishing pressure inside MPAs and in surrounding waters to ensure adequate protection of elasmobranchs. However, since Lyme Bay MPA appears to harbour greater elasmobranch diversity than surrounding waters, it is recommended that Lyme Bay MPA management is adapted to improve conservation outcomes for this threatened species group.

Furthermore, when considering the community as a whole, Lyme Bay exhibited lower elasmobranch diversity, but equal species abundances when compared other temperate locations (e.g. Southwest Australia). However, the abundance of *S. canicula* was considerably higher than most elasmobranch species in this and other studies and may be indicative of significant historic exploitation and changing climatic conditions in UK waters. Finally, water turbidity represented a barrier to species-level identification, on some occasions. Finally, since low detection of elasmobranchs significantly limited statistical assessments, method optimisation (e.g. increased soak times) should be explored for increasing detection-rates.

Chapter 3: Developing and testing a drifting pelagic BRUV

3.1. Introduction

Determining spatial patterns in species abundance and diversity underpins our ability to answer a variety of ecological questions. From characterising the extent of anthropogenic impacts on the environment, to identifying critical habitats to inform appropriate conservation measures. However, characterising spatial variation in pelagic communities poses significant challenges, associated with the heterogenous spatiotemporal distribution of species and relative inaccessibility of habitats (Barnes et al., 2006; Murphy & Jenkins, 2010). This is exacerbated for apex predator populations which are present in naturally low abundances and depleted further by overexploitation (Dulvy et al., 2008; Letessier et al., 2017; Dulvy et al., 2021). As a result, the surveillance of pelagic populations has historically depended on analysing fishery landings data, which exhibits severe limitations (e.g. non-specific landings categories, targeting areas of high abundance, underreporting) that ultimately misrepresent the true status of many populations (Stevens et al., 2000; Clarke et al., 2008; Mucientes et al., 2022). For instance, population assessments for porbeagle sharks (*Lamna nasus)* and shortfin mako sharks (*Isurus oxyrinchus*) in the Northeast Atlantic have been impeded by a historic lack of species-specific population data resulting from non-specific catch reporting under the blanket term “Sharks” (Clarke et al., 2008). This lack of effective monitoring is particularly concerning considering the widespread declines in pelagic fish populations (Cheung et al., 2012; Christensen et al., 2014) and oceanic predators (Dulvy et al., 2008; Pacoureau et al., 2021; Juan-Jorda et al., 2022). Whilst technological advances have facilitated the proliferation of telemetry research for elucidating movement patterns (Hussey et al., 2015), and the emergence of promising new methods such as eDNA (Bohmann et al., 2014; Boussarie et al., 2018), these remain costly, and are not yet able to reliably quantify patterns in relative abundance. Therefore, there is an imperative to develop novel, cost-effective and non-destructive pelagic survey methods.

Video-based survey methods offer non-invasive, cost-effective approaches to marine ecological monitoring, which can be creatively tailored to specific research questions. These vary from exciting frontiers in animal borne video systems (ABVSs; Chapple et al., 2021) to more traditional application of remotely operated and autonomous video systems (ROVs and AUVs, Sward et al., 2019; Di Ciaccio & Triosi, 2021). Baited Remote Underwater Video (BRUV) surveys have demonstrated particular promise for quantifying patterns in benthic marine species abundance and diversity, including elusive and highly mobile species such as tiger sharks (*Galeocerdo cuvier*) and requiem (*Carcharhinus spp*.) sharks (Bond et al., 2012, Espinoza et al., 2014; Goetze et al., 2018). Resultantly, BRUVs have become embedded in benthic ecological research across the globe. The use of BRUVs in the pelagic realm remains far less common (Whitmarsh et al., 2017). Many pelagic BRUV surveys to date have employed static camera rigs, anchored to the seabed and suspended in the water column beneath a surface buoy (e.g. Santana-Garcon et al., 2014a; Santana-Garcon et al., 2014b). However, the emergence of un-moored, drifting BRUV rigs may offer multiple advantages. The most intuitive benefit is the greater spatial coverage achieved through a mobile unit, offering potential to remotely sample a transect of pelagic habitat rather than a single discrete point (Bouchet & Meeuwig, 2015). Furthermore, drifting BRUVs are not constrained by seafloor depth facilitating their use in deep oceanic waters beyond the continental shelf. Meanwhile, their lack of mooring systems or contact with the seabed makes them well-placed to survey the water column above fragile benthic habitats (e.g. seagrass, maerl, coral).

Before drifting BRUVs can be adopted as a core monitoring tool, they must first be validated in a range of environmental contexts. To date, research employing drifting pelagic BRUVs has been predominantly spatially restricted to tropical waters (Bouchet & Meeuwig, 2015; Cambra et al., 2021) therefore, their performance in temperate waters is less understood. Lyme Bay spans the Devon and Dorset coasts on the Southwest UK and is the focus of a comprehensive, multi-method annual monitoring scheme to observe the effects of its unique spatial management strategies (Stevens et al., 2014; Davies et al., 2021) and large-scale, offshore mussel farm (Bridger et al., 2022). Whilst pelagic assemblages in and around the Mussel Farm are documented annually with un-baited camera deployments, the pelagic community encompassed by the combination of MPAs (collectively referred to as Lyme Bay Marine Reserve for the purpose of this study) has been comparatively neglected. Of particular interest are a range of oceanic predators known to occur in the waters around Lyme Bay (e.g. *Lamna nasus* (porbeagle shark) and *Alopias vulpinus* (common thresher shark)*),* but their presence has not yet been detected by the existing monitoring programme.

This study aimed to contribute to a greater understanding of the pelagic community in Lyme Bay Marine Reserve as a currently overlooked aspect of the wider ecosystem, whilst validating the use of drifting BRUVs as a survey tool in temperate waters. More specifically, this research explores the extent to which the pelagic community in Lyme Bay varies spatially, by investigating changes in community over the vertical (depth from sea surface) and horizontal planes (Northing and Easting).

3.2. Methods

3.2.1. Method Development: Pelagic BRUV design

An un-moored pelagic BRUV was designed to be deployed and drift with the prevailing current at a constant depth (Figure 3.1). The design was inspired by and builds on moored and un-moored designs presented in earlier studies (Heagney et al., 2007; Santana-Garcon et al., 2014a; Bouchet & Meeuwig, 2015) and consists of an aluminium frame suspended by a rope beneath a surface marker buoy. 0.7 m of shock cord was used to minimise vertical movement of the rig and stabilise camera footage. The marker buoy was ballasted with lead dive weights (3 kg) to support a 2m tall flagpole. A GPS tracker (at the top of the flagpole) aided reconstruction of rig deployment tracks and allowed rigs to be deployed and relocated 3 hours later with real-time tracking. While the aluminium frame has capacity for stereo-videography, for the purpose of this study, each rig was mounted with a single GoPro Hero 4 and battery extender. The bait canister, made from a plastic tub perforated with 6mm diameter holes, was positioned in front of the camera by a 1m aluminium bait arm.

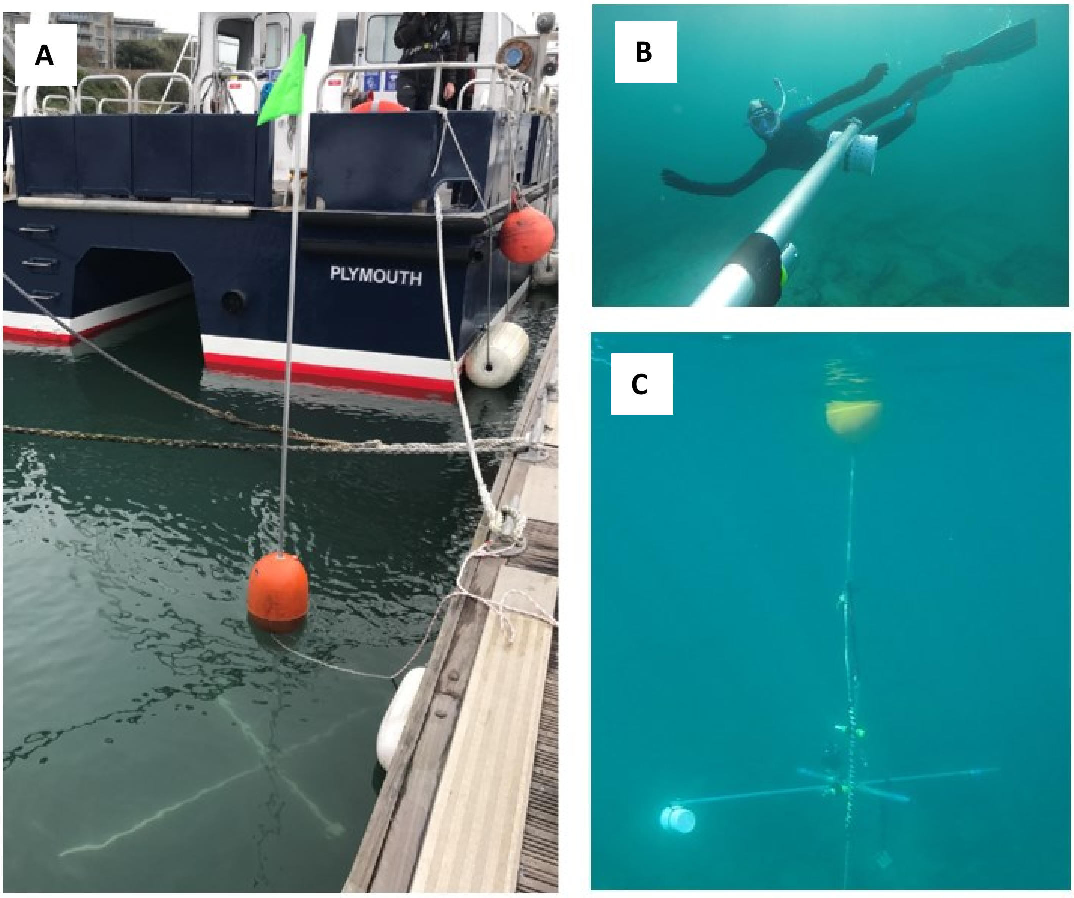


Figure 3.1. Images of the final pelagic BRUV design from various perspectives.

3.2.2. Study Site and Survey Design

The experiment tested the effect of suspension depth (two levels: 3m and 15m) below the sea surface on pelagic species abundance and diversity, at various locations (predominantly within the marine reserve) in Lyme Bay (Figure 3.2). BRUVs were deployed 10 times per depth treatment over 3 days (25th, 26th and 29th April 2022) with a total of 20 deployments and a soak-time of 3 hours per replicate. Bait composition was based on typical shark chum recipes, and consisted of: 400g of minced mackerel, 400g of chopped mackerel (*Scomber scombrus*), 200ml of sardine oil and 200g of bran. An additional visual attractant (mirror ball) was attached to the bait canister to enhance attraction of species, since Rees et al. (2015) recommend combined use of attractants in the pelagic realm. A buffer period of 1 hour before and after sunrise and sunset was implemented to negate the influence of crepuscular activity on species assemblages. Deployment sites were selected at random from a range of potential starting points based on the predicted trajectory of the BRUV (estimated by tidal flow forecasting) with the aim of sampling a range of locations across an environmental gradient. However, as the first study conducted with this method, uncertainty over retrieval difficulty meant BRUVs were deployed in clusters of six to reduce the risk of losing equipment (Figure 3.2). BRUVs deployed simultaneously were distributed at least 300m apart to minimise bait plume overlap and repeated observations of the same species, and bait was replenished prior to each new deployment. Both depth treatments were sampled concurrently in similar areas to reduce the confounding influence of temporal variability.

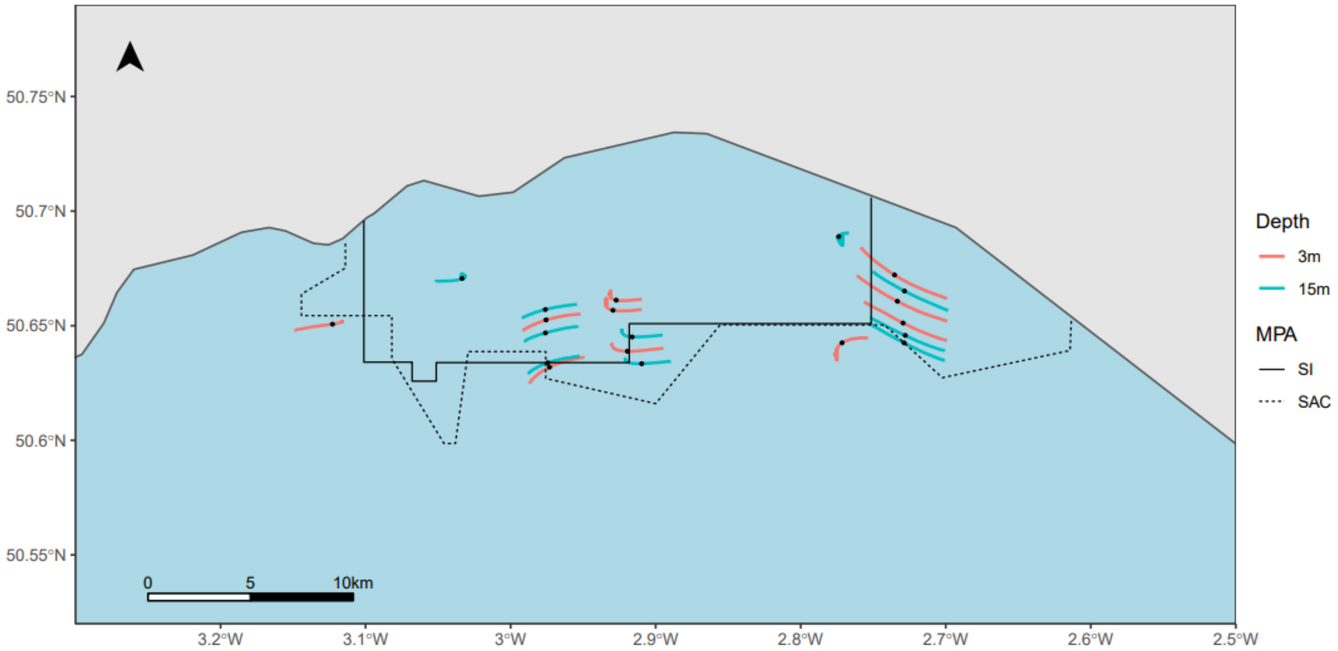


Figure 3.2. Map of pelagic BRUV deployment tracks, displaying the distance travelled during 3-hour deployments. Colours represent suspension depth below the sea surface (Red = 3m, Blue = 15m). The two MPA boundaries (Statutory Instrument = SI, Special Area of Conservation = SAC), are represented by black lines. Black points indicate BRUV locations halfway through their deployments and the Northing/Easting data incorporated into Generalised Linear Models.

3.2.3. Video Analysis

Videos were watched from start to finish at 4 X speed. When an animal was detected, the footage was paused and re-watched at normal speed. All species present in the videos were identified to highest possible taxonomic resolution and recorded alongside their time of occurrence. For each species, MaxN was obtained as a conservative estimate of relative abundance, whereby the maximum number of individuals of a species within a single frame was recorded for each replicate. A subsample of the videos (5%, 3 hours) was watched at normal speed to ensure that watching videos at faster speeds did not result in a loss of information.

3.2.4. GPS Track Construction

GPS data were downloaded from trackers and used to reconstruct the paths of all successful (those resulting in a full 3 hours of footage) camera deployments. Maps and BRUV tracks were created using the packages “rworldmap” and “rnaturalearthhire” (South, 2011; South, 2022) in the statistical software, R (R Core team, 2021) and the distance travelled was calculated using the “geodist” package (Padgham et al., 2021).

3.2.5. Data Analysis

Generalised linear mixed models (GLMMs) were used to test statistical relationships between explanatory variables and univariate data to account for potential similarity among deployments sampled on the same day. GLMMs included the fixed effects of: 1) suspension depth below sea surface, 2) depth of seafloor, 3) Northing and 4) Easting and the random effect of day. Northing and Easting were documented for BRUV locations halfway through each deployment (at 1.5 hours). The effects of these factors on the response variables: 1) taxon richness, 2) total abundance (MaxN per deployment) of all taxa, 3) juvenile fish abundance and 4) ctenophore abundance were tested using step-wise model simplification. With the exception of taxon richness, all univariate response variables exhibited non-normal distributions and significant overdispersion, therefore, GLMMs were fitted with a negative binomial distribution and a log link function (using the “MASS” package in R (Venables & Ripley, 2002)). Conversely, changes in taxon richness were assessed using a Gaussian GLMM (using the “lme4” package in R (Bates et al., 2015)). Maximal models underwent step-wise selection, during which both Maximum Likelihood tests and Akaike’s Information Criterion (AIC) were used to justify model simplifications, whereby a *p*-value of > 0.05 of and a decrease in AIC value indicated no significant loss of explanatory power. Relative abundance (MaxN) data underwent a bray-curtis transformation prior to visualisation of multivariate assemblage data with a non-metric multidimensional scaling (nMDS) plot. PERMANOVA was then used to statistically test the influence of: 1) depth below sea surface, 2) depth of seafloor, 3) Northing and 4) Easting and 5) day on multivariate species assemblage data. Finally, the effect of suspension depth on distance travelled by BRUVs was assessed with a T-Test after assumptions of homogeneity of variance and normal distribution were confirmed. All statistical analyses were conducted using the statistical programme R (R Core Team, 2021) and the package “ggplot2” (Wickham, 2016) was used to visualise data.

3.3. Results

A total of 20 pelagic BRUV deployments were conducted over three days for the full soak time of 3 hours, resulting in 60 hours of footage. No sharks were observed, but analysis of footage documented 141 individuals from 3 different phyla and 8 families, ranging from small ctenophores to large fish and a diving bird (Figure 3.3, Table 3.1).

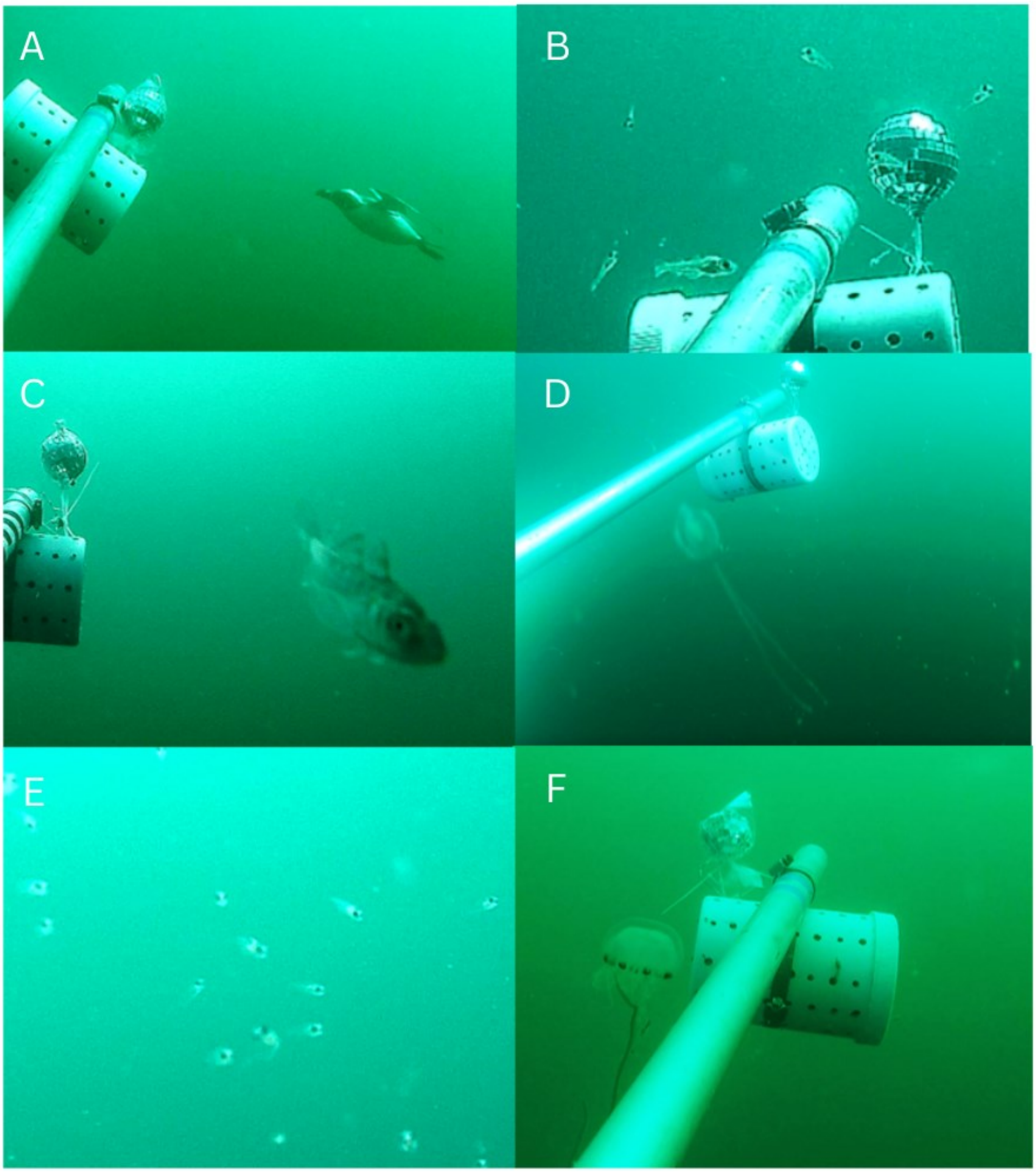


Figure 3.3. Various species observed by pelagic BRUVS: (A) *Alca torda,* (B, C and E) Juvenile and larval fish, D) *Pileus pleurobranchia* and F) *Chrysaora hysoscella.*

Table 3.1. All taxa and their relative abundances documented by pelagic BRUV deployments (n = 20) at two different suspension depths (3m and 15m) below the sea surface.

Phylum	Family	Species Name	Common Name	∑MaxN Deep	∑MaxN Shallow	Overall ∑MaxN	Proportion of Overall Observations
CNIDARIA	Pleurobrachiidae	*Pleurobranchia pileus*	Sea Gooseberry	3	51	54	37.7%
	Beroidae	*Beroe cucumis*	Melon Comb Jelly	2	7	9	6.3%
	Bolinopsidae	*Bolinopsis infundibulum*	Northern Comb Jelly	0	4	4	2.8%
	Cyaneidae	*Cyanea lamarckii*	Blue Jellyfish	2	4	6	4.2%
	-	-	Unidentified Jellyfish	2	2	4	2.8%
	-	-	Unidentified Ctenophore	1	1	2	1.4%
	Pelagiidae	*Chrysaora hysoscella*	Compass Jellyfish	1	0	1	0.70%
Total Cnidaria		**7 Taxa**		**11**	**68**	**79**	**55.6%**
CHORDATA	Gadidae	*Pollachius pollachius*	Pollack	5	0	5	3.5%
	-	-	Unidentified juvenile fish	8	48	56	39.2%
	Alcidae	*Alca torda*	Razorbill	0	1	1	0.70%
Total Chordata		**3 Taxa**		**13**	**49**	**62**	**43.7%**
ARTHROPODA	Caridea	-	Unidentified shrimp	0	1	1	0.70%
Total Arthropoda		**1 Taxon**		0	1	**1**	**0.7%**

3.3.1. GPS Tracks

The distance travelled by BRUVs ranged from 1.16 km to 4.97 km (Figure 3.4), and distance was not significantly influenced by the depth of suspension below the sea surface (T-test, p = 0.45).

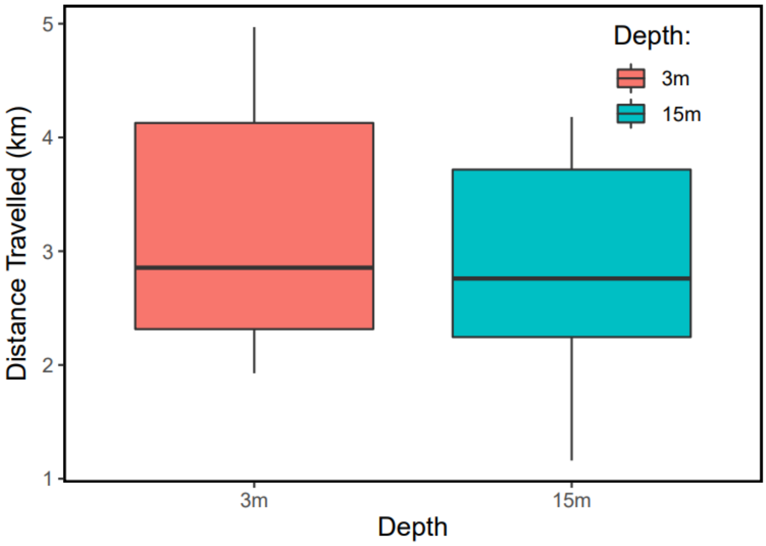


Figure 3.4. Distance travelled by pelagic BRUVs (n = 20) during 3-hour deployments, grouped by Depth of suspension below the sea surface.

3.3.2. Univariate Abundance and Diversity Metrics

Taxon richness per deployment ranged from 0 to 7 and differed significantly across treatments. Taxon richness was significantly lower in the deeper (15m) deployments (p < 0.01, Table 3.1, Figure 3.5a) than shallow (3m) deployments and was significantly associated with Northing (p < 0.05, Table 3.1, Figure 3.5b), with generally higher numbers of taxa detected further South. However, seafloor depth (p = 0.49, Table 3.2) and Easting (p = 0.26, Table 3.2) had no significant effect on taxon richness. When all taxa were aggregated, total relative abundance (MaxN) ranged from 0 to 39 individuals per deployment. When statistically analysed, total abundance was significantly negatively associated with Depth (p < 0.0001, Table 3.3, Figure 3.6a). Easting also significantly influenced total abundance (p < 0.0001, Table 3.3, Figure 3.6b), with generally higher abundances documented towards the West. No significant effect was detected for Seafloor Depth (p = 0.55, Table 3.2) or Northing (p = 0.43, Table 3.2).

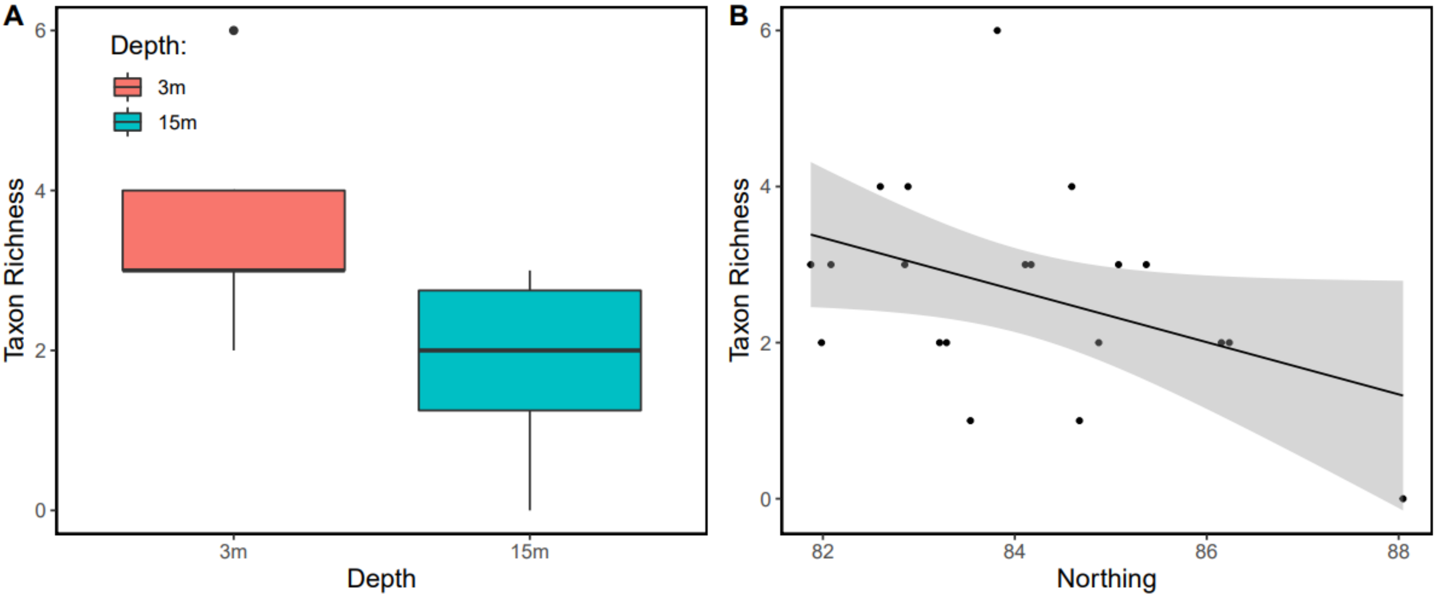


Figure 3.5. Taxon richness per pelagic BRUV deployment (3 hours) and relationship with A) Depth below sea surface (3m or 15m) and B) Northing.

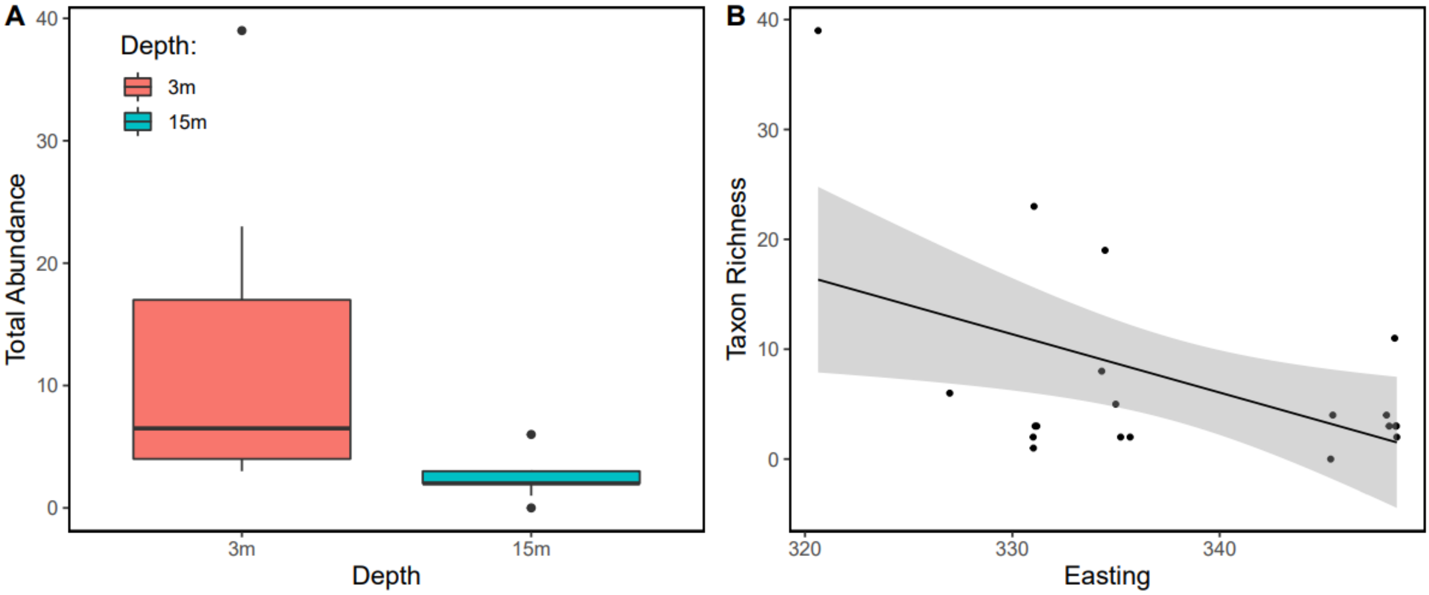


Figure 3.6. Total abundance of all taxa detected per pelagic BRUV deployment (3 hours) and relationship with A) Depth below sea surface (3m or 15m) and B) Easting.

Table 3.2. Generalised linear model (GLM) model selection of factors the abundance and diversity of pelagic species in Lyme Bay (UK). Models included the fixed effects: Suspension Depth (D), Northing (N), Easting (E) and Seafloor Depth (S) and the random effect of Day (1|Day).

Focal Taxa	Response variable	Final Model Type	Full model	Dropped Term	AIC$_{full}$	ΔAIC	*p*-value
All Taxa	Total Relative Abundance (A)	Negative Binomial GLM	A = D + N + E + S + (1|Day)	(1|Day)	113	-2	1
			A = D + N + E + S	SF	111	-2	0.55
			A = D + N + E	E	109	7	**0.0032**
			A = D + N + E	N	109	-1	0.43
			A = D + E	D	108	13	**0.0001**
All Taxa	Taxon Richness (TR)	Gaussian GLM	TR = D + N + E + S + (1|Day)	(1|Day)	76	-13	1
			TR = D + N + E + S	SF	63	-2	0.49
			TR = D + N + E	E	61	0	0.26
			TR = D + N	N	61	3	**0.024**
			TR = D + N	D	61	8	**0.00087**
Juvenile Fish	Relative Abundance (A)	Negative Binomial GLM	A = D + N + E + S + (1|Day)	(1|Day)	81	-2	1
			A = D + N + E + S	SF	80	-2	0.75
			A = D + N + E	E	78	5	**0.0095**
			A = D + N + E	N	78	-2	0.68
			A = D + E	D	76	0	0.15
Ctenophores	Relative Abundance (A)	Negative Binomial GLM	A = D + N + E + S + (1|Day)	(1|Day)	86	-2	1
			A = D + N + E + S	SF	84	-1	0.42
			A = D + N + E	E	83	1	0.063
			A = D + N	N	83	-1	0.58
			A = D + N	D	83	16	**0.0000029**

Table 3.3. Outputs of final GLMs selected through step-wise model selection. Demonstrating the role of spatial variables (Suspension Depth, Northing & Easting) in influencing the abundance and diversity of pelagic species in Lyme Bay (UK).

Response variable	Final Model Type	Terms	Estimate	SE	*p*
All Taxa Relative Abundance	Negative Binomial GLM	Intercept	19.01	5.89	**<0.01**
		Suspension Depth	1.46	0.32	**<0.0001**
		Easting	-0.054	0.018	**<0.01**
Taxon Richness	Gaussian GLM	Intercept	28.59	11.86	**<0.05**
		Suspension Depth	1.46	0.44	**<0.01**
		Northing	-0.32	0.14	**<0.05**
Juvenile Fish Relative Abundance	Negative Binomial GLM	Intercept	45.51	14.06	**<0.01**
		Easting	-0.12	0.042	**<0.01**
Ctenophore Relative Abundance	Negative Binomial GLM	Intercept	-0.51	0.45	0.26
		Suspension Depth	2.35	0.51	**<0.0001**

Juvenile fish were relatively abundant in comparison to most other species groups, occurring in both depth treatments, but in higher numbers at 3m (Table 3.1). 56 individual juvenile fish were documented in total, accounting for 41% of all species observations (Table 3.1). When analysed statistically the effect of depth was not significant ($p = 0.15$, Table 3.2), nor were the effects of Northing ($p = 0.68$, Table 3.2) or Seafloor Depth ($p = 0.75$, Table 3.2). However, Juvenile fish abundance was significantly associated with Easting ($p < 0.01$, Table 3.3, Figure 3.7), with generally higher abundances towards the West of Lyme Bay.

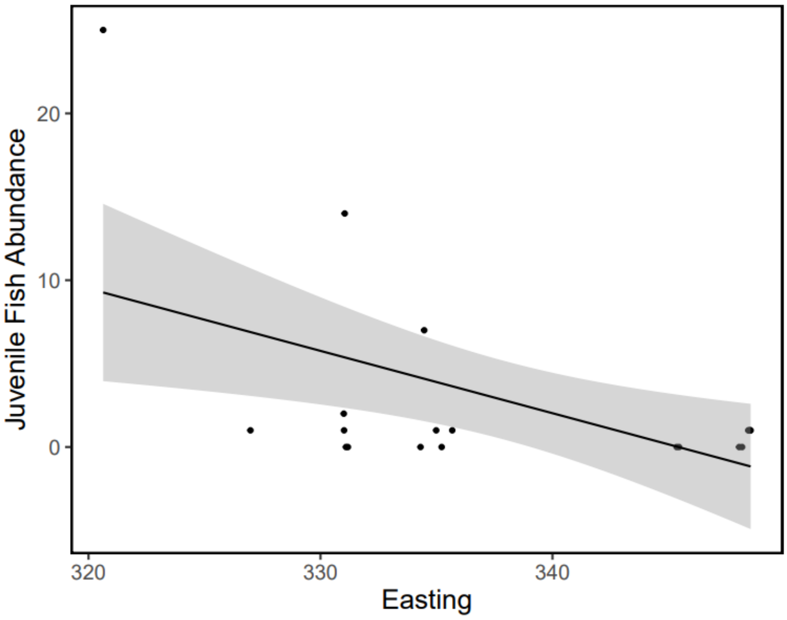


Figure 3.7. Abundance (MaxN) or Juvenile Fish detected per pelagic BRUV deployment (3 hours) and relationship with Easting.

When all ctenophore species were aggregated, they accounted for 49.6% of all species observations (Table 3.1) making them the single most abundant taxon. In total, 3 ctenophore taxa were identified to species level (Table 3.1). One species, *Pleurobranchia pileus* was particularly common, accounting for 38% of all species observations. When grouped and analysed statistically, Ctenophore relative abundance was significantly associated with the Shallow (3m) treatment rather than the Deep (15m) treatment ($p < 0.0001$, Table 3.3). Meanwhile, the variables: Seafloor Depth ($p = 0.42$, Table 3.2), Northing ($p = 0.58$, Table 3.2) and Easting ($p = 0.063$, Table 3.2) had no significant impact on ctenophore abundance.

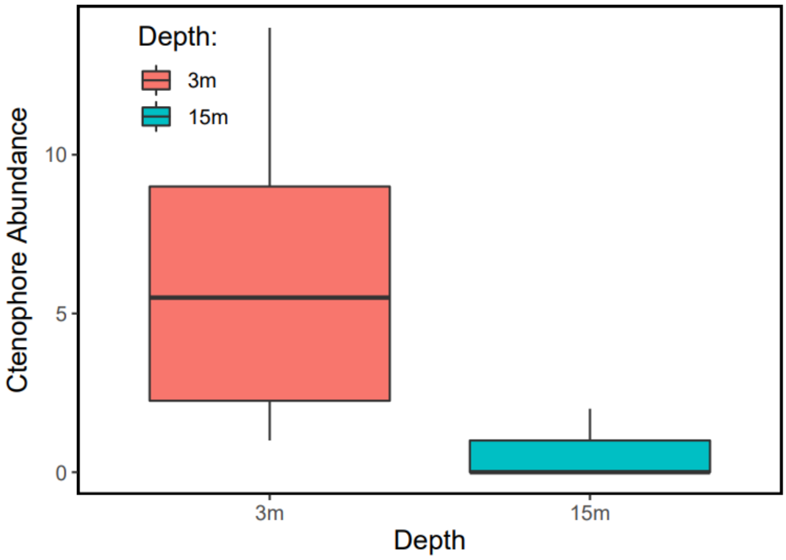


Figure 3.8. Abundance (MaxN) of Ctenophores detected per pelagic BRUV deployment (3 hours) and relationship with Depth (3m or 15m) below the sea surface.

3.3.3. Multivariate Diversity

A stress value of 0.15 (< 0.2) was calculated for the nMDS plot, suggesting that it accurately reflected the multivariate distance among replicates (Clarke & Gorley, 2006). Depth treatment clusters exhibited considerable overlap, however, PERMANOVA analysis (Table 3.4) identified that the 3 variables: Depth ($p < 0.01$, Figure 3.9, Table 3.4), Northing ($p < 0.05$, Table 3.4) and Easting ($p < 0.05$, Table 3.4) all significantly influenced multivariate diversity. Conversely, no significant effect was identified for Seafloor Depth ($p = 0.67$, Table 3.4) or Day ($p = 0.50$, Table 3.4).

Table 3.4. Results from PERMANOVA analysis, exploring the effects of: Suspension Depth, Northing, Easting, Seafloor Depth and Day, on multivariate diversity detected by pelagic BRUVs.

Terms	**R^2**	**F**	***p***
Suspension Depth	0.21	5.55	**<0.01**
Northing	0.11	2.97	**<0.05**
Easting	0.11	2.81	**<0.05**
Seafloor Depth	0.025	0.67	0.67
Day	0.035	0.92	0.50

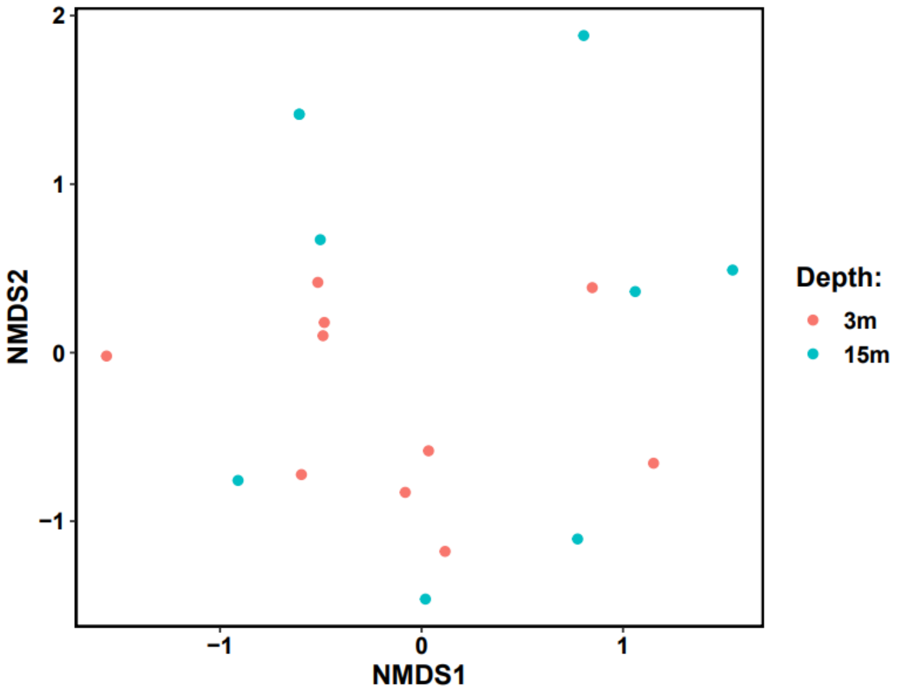


Figure 3.9. Non-metric multidimensional scaling plot displaying multivariate at two different depths (3m = Red, 15m = Blue) below the water surface measured by pelagic drifting BRUVs.

3.4. Discussion

The findings of this study shed light on the unique community supported by the pelagic environment in Lyme Bay and reveal some of the underlying drivers of assemblage variation. Results indicated that, when considered as a whole, the pelagic community in Lyme Bay showed distinct spatial differences both vertically, in terms of depth below the sea surface and horizontally in terms of Nothing and Easting. However, when broken down into the different univariate components, spatial variables influenced each measure of abundance and diversity to varying degrees. Whilst depth was an important driver of differences in both total abundance and taxon richness, Northing was associated with changes in taxon richness and Easting was more influential for total abundance. Furthermore, the two most abundant taxa; Juvenile Fish and Ctenophores, were each only significantly associated with Easting and Depth respectively. These findings alone demonstrate considerable potential for pelagic drifting BRUVs to characterise the relationships between pelagic species and environmental drivers and detect variation over short spatial scales.

Species detected by drifting BRUVs exhibited significant variation in morphologies, sizes and trophic levels, indicating the value of this method for providing a holistic view of the ecosystem. However, none of the pelagic or benthopelagic shark species known to occur in Lyme Bay were detected in this survey. This may in part be explained by the seasonal mobility of sharks in combination with the temporal constraints of this experiment which took place over just 3 days in April. Although some benthopelagic shark species appear to exhibit year-round residency in UK waters (Thorburn et al., 2015) most pelagic shark species undertake seasonal migrations making them uncommon in UK waters in early spring. For instance, blue sharks (*Prionace glauca*) have been found to move from the English Channel into the Bay of Biscay in the late summer and early autumn (Quieroz et al., 2010), which is thought to indicate a larger Southerly migration in response to cooling surface waters (Stevens, 1976; Stevens, 1990). Similar behaviour has been documented in porbeagle sharks (*Lamna nasus*) which tend to move offshore or further South from coastal waters around the British Isles over the Autmn and Winter (Saunders et al., 2011). Although, behaviour varies considerably between individuals, and accounts also exist of *L. nasus* migrating northwards in Autumn months (Pade et al., 2009) and even undertaking transatlantic movements (Cameron et al., 2017). Therefore, taking the behaviour of pelagic sharks into account, repeating this experiment in the late Spring or Summer may result in greater detection success of large pelagic sharks.

Alternatively, the lack of pelagic shark observations could be explained by the restricted spatial coverage of the survey. Whilst the drifting component of the BRUVs increased the spatial coverage of individual deployments, the total area sampled remained limited relative to the scale of shark movements. This is particularly noteworthy since the pelagic realm exhibits considerable vertical and horizontal heterogeneity in environmental variables (e.g. salinity, temperature, dissolved oxygen, chlorophyll), and most pelagic species are associated with specific oceanographic characteristics driven by physiological limits, bioenergetic demands and prey distributions (Sims et al., 2006; Quieroz et al., 2010; Scales et al., 2014). For instance, movement of blue sharks (*P. glauca)* tagged in the English Channel exhibited significant site fidelity associated with productive oceanographic fronts and in inshore regions, meanwhile vertical movement was generally related to thermal habitat preferences (Quieroz et al., 2012). Therefore, designing pelagic BRUV studies to target specific oceanographic features and known hotspots may yield greater encounter success of large pelagic species with low abundances and patchy distributions. In Lyme Bay, a deep channel of fast flowing water runs past Portland Bill, locally known as ‘the Race’, resulting in the formation of ephemeral eddies and a potential frontal system inside Lyme Bay (Pingree, 1983). This area is often targeted by recreational shark anglers; however, the unique oceanography has not yet been characterised in association with shark distributions and could present an interesting avenue for future research.

A final potential explanation for the pelagic shark absence may be that the bait quantity used was insufficient. Whilst the bait composition was based on shark chum recipes used by recreational anglers, the amount (1kg) was considerably lower than that typically used to attract sharks towards fishing vessels. Therefore, exploring the effect of increasing bait quantities may help optimise this method for attracting large pelagic predators. However, increasing bait quantities expands the size of bait plumes, thereby reducing the spatial resolution of deployments. Therefore, this trade-off between greater species attraction and lower spatial resolution must be considered when tailoring this method to specific ecological questions. Overall, the value of drifting BRUVs for studying large pelagic species in UK waters remains uncertain from this study alone.

Despite a lack of large pelagic species observations, this pilot study demonstrated the capability of pelagic drifting BRUVs to characterise the wider pelagic food web and detect patterns of spatial variation, even at relatively low sampling effort and over short spatial scales. This was particularly notable since primary productivity is highest in April in the Northeast Atlantic (Edwards et al., 2022) which generally limits water visibility over this period. In terms of species diversity, pelagic BRUVs successfully detected species at the base of the food web (ctenophores and fish larvae) up to larger juvenile fish and mesopredators (pollack, *Pollachius pollachius* and a razorbill, *Alca torda*) demonstrating suitability for a wide range of applications. For example, the detection of *Bolinopsis infundibulum* and simultaneous observation of one of its predators, *Beroe cucumis* (Greve, 1975) demonstrates potential to apply this method to the study of trophic interactions. Meanwhile, the observation of a diverse array of cnidarians and ctenophores indicates the potential for pelagic BRUVS to overcome inherent challenges associated with non-destructively sampling fragile-bodied organisms with plankton nets. An issue which has previously led to the underrepresentation of ctenophores in traditional planktonic studies (Dennis, 2003; Haddock, 2004).

This study found that overall taxon richness and total abundance were significantly higher in the 3m treatment than in the 15m treatment and were associated with Northing and Easting respectively. This agrees with the wider consensus that pelagic communities are highly variable across vertical and horizontal space (Gluchowska et al., 2017; Edwards et al., 2022). Although the oceanographic drivers of diversity were not explored in this study, the majority of species observations represented zooplankton, including: juvenile fish, ctenophores and jellyfish. Zooplankton are known to exhibit significant spatial segregation in assemblage composition, exhibiting sensitivity to various environmental (e.g. temperature, salinity, time of day) and biological drivers (e.g. predation, competition), varying by context (Hays et al., 2005; Steinberg & Landry, 2017; Drago et al., 2022). Future studies could therefore employ this method in combination with oceanographic instruments to elucidate the chemical and physical drivers underpinning the bottom-up structuring of pelagic communities. However, it should be noted that the drifting aspect of this method may obscure actual abundance estimates, particularly for planktonic species as these may drift with the camera. Therefore, future efforts to calibrate this method with traditional methods (e.g. plankton nets) or static pelagic BRUVs may increase the accuracy of relative abundance interpretation.

Deconstructing the pelagic community into two major taxonomic groups aided finer interpretation of assemblage differences. When analysed alone, ctenophores were significantly more abundant in shallow waters, than at 15m below the surface. The wider literature indicates that ctenophore abundance differs with depth (Youngbluth et al., 2008), although this study appears to be one of few revealing community differences over such short vertical distances (12m). Evidence demonstrates that vertical distribution of ctenophores can be influenced by an array of factors including distribution of predators and prey (Esser et al., 2004). They are also inextricably linked to the spatiotemporal dynamism of water column stratification (Youngbluth et al., 2008). Preferences for specific light profiles along with the aggregating or segregating effects of pycnoclines and mixing are all likely to influence the distribution of these species at any given time (Graham et al., 2001). The use of this method over broader spatiotemporal gradients and in combination with oceanographic instruments and plankton nets (to explore lower trophic levels) may help disentangle the relative importance of drivers. Nevertheless, the most abundant species was *P. pileus;* a carnivorous ctenophore which feeds on smaller zooplankton, particularly copepods (Greve, 1975; Neal, 2005). Previous studies have demonstrated that *P. pileus* alters its vertical distribution in response to presence of benthic predators (Esser et al., 2004), some of which include lumpfish, *Pagurus spp.*, *Carcinus maenas*, *Crangon spp.* and Gadidae fish (Eriksen et al., 2018). This could be a plausible explanation for the trends seen in this study, whereby ctenophores were less common lower down in the water column, particularly given the recovery of many benthic crustaceans and benthopelagic fish (Davies et al., 2021). However, this cannot be concluded from this study alone due to the limited vertical gradient sampled. Bentho-pelagic linkages such as these remain predominantly un-explored in the discourse surrounding MPA recovery and may represent another opportunity for the future application of pelagic BRUV research.

Juvenile fish, were the single most abundant taxon observed in this survey, agreeing with broader studies in the NE Atlantic which observed high abundances of larval fish in coastal waters over the continental shelf (Harith et al., 2021). Juvenile fish were not significantly associated with Depth, which was unexpected considering the vastly greater overall abundance of juvenile fish observed at 3m than at 15m. This lack of effect may be explained by apparent vertical segregation of behaviour between the two different depths. While juvenile fish were detected more consistently at 15m compared to 3m, when observed in the 3m treatment, juvenile fish tended to be more abundant (n = 1 – 25) due to clear schooling behaviour. Meanwhile, at 15m, juvenile fish were only ever observed in isolation. The distinct behaviours observed may suggest that fish occurring at these two depths are of different species or developmental stages. Conversely, juvenile fish abundance was significantly negatively associated with Easting, supporting the current consensus that larval fish assemblages are highly spatially variable (Gray & Miskiewicz, 2000; Harith et al., 2021). Spatial variation in juvenile fish abundance is influenced by a range of biophysical factors, from adult spawning seasons and locations (Doyle et al., 1993; Harris et al., 2001) to prevailing oceanographic conditions and water mass properties (Muhling et al., 2008). Since this study exhibited low replication and was conducted over a short time-period, further investigation is warranted to determine whether the West of Lyme Bay MPA encompasses essential juvenile fish habitat and illustrate the role of potential structuring factors.

3.5. Conclusions

To summarise, whilst this study demonstrated the potential for pelagic BRUVs to characterise spatial variation in pelagic assemblages, a lack of elasmobranch observations leaves doubts surrounding the application of this method to quantifying rare and highly mobile species. Furthermore, considering the general scarcity of pelagic elasmobranchs and their affinity for specific oceanographic features and conditions, this method may be better suited for use in combination with oceanographic instruments to characterise the bottom-up drivers (e.g. prey abundances) of shark distribution in formerly identified shark hotspots. This was further supported by the successful identification and relative quantification of several species across a range of trophic levels, demonstrating potential to provide a snapshot of the wider pelagic food-web. Pelagic BRUVs were able to detect statistically distinct assemblages over short vertical and horizontal scales indicating considerable value as a non-destructive survey tool and application to a variety of ecological questions.

General Conclusions

To summarise, this thesis set out to address several evidence and methodological gaps surrounding the value of temperate MPAs as an elasmobranch conservation tool. Overall, this thesis found that MPAs exhibit potential to benefit temperate elasmobranch populations, but the in-depth appraisal of existing case studies (Chapter 1) found that MPA success was equivocal and context-specific. Accordingly, further exploration into the underlying drivers of MPA performance uncovered the role of several biophysical and social factors in driving MPA benefits. These included the size of a species' home range, the intrinsic vulnerability of the protected habitat to fishing and the extent of stakeholder support. Furthermore, factors were found to interact and vary in significance depending on the specific location and focal elasmobranch population. It was concluded that, biophysical factors (e.g. species mobility, habitat type, site associations) set the theoretical limits on MPA efficacy, if resources were unlimited. Yet, in reality, MPA performance is generally governed by a trade-off between ecological and social outcomes, since the implementation of MPAs involves a wide range of stakeholders with diverging needs and ideas of success.

Studying the partially-protected MPA in Lyme Bay revealed more about the conditions necessary for MPA success (Chapter 2). As a non-elasmobranch focussed MPA, designated specifically to protect rocky-reef habitat and sessile bioconstructors (e.g. Ross Coral, *P. foliacea*), Lyme Bay MPA demonstrates the potential for MPAs to provide opportunistic benefits to some elasmobranch species. Since Lyme Bay was not strategically designed for elasmobranchs, the benefits detected are likely attributed to the achievement of many key social criteria (e.g. long-term monitoring, stakeholder engagement, buy-in and, compliance). However, benefits were limited predominantly to the small-spotted catshark (*S. canicula*) a small-bodied shark with r-selected life history traits and of low conservation priority. Contrastingly, benefits in priority species (*G. galeus, Mustelus spp.* and Rajidae skates), were less evident. This likely reflected the lack of fishing limits, beyond the prohibition of demersal fishing inside the MPA, which enabled the continual extraction of these species and included significant fishing effort in adjacent waters. Furthermore, a lack of habitat associations between elasmobranchs and protected reef habitats likely reduced the time spent inside the MPA.

This interspecific variability in MPA benefits was thought to be explained by a range of factors. Firstly, while the generalist scavenger foraging behaviour of *S. canicula* likely enabled this species to take advantage of the increased food sources available in the recovering reef habitats, the more specialist feeding strategies of Triakidae sharks and Rajidae skates likely limited the benefits they received. Meanwhile, *S. canicula* exhibits r-selected life-history strategies and therefore exhibits greater reproductive output, potentially allowing it to compensate for significant extraction rates. In comparison, Rajidae skates and Triakidae sharks are less productive, making them more intrinsically vulnerable to overextraction. Overall, the findings of this chapter supported those in Chapter 1, which demonstrated the nuanced nature of MPA success.

All three chapters revealed insights into the inherent challenges associated with temperate elasmobranch monitoring in MPAs. Meanwhile, the two BRUV studies (Chapter 2 & 3) revealed specific limitations surrounding the application of BRUVs to elasmobranch monitoring in UK waters. Chapter 2 found that low water visibility impeded species-level identification in some instances, particularly for cryptic species (e.g. Triakidae sharks). Meanwhile, both Chapters 2 and 3 demonstrated the necessity for large quantities of footage in order to achieve sufficient species observations for statistical analysis. This issue appeared to be magnified in the pelagic study, during which no sharks were detected despite obtaining 60 hours of footage and using large quantities (1kg) of bait. It was suggested that this tool may be best suited to exploring known pelagic shark hotspots where detection probability would be higher. Alternatively, since Chapter 3 demonstrated the capacity for drifting pelagic BRUVS to characterise spatial variation in pelagic communities, this method may prove useful as a complement to telemetry or visual encounter surveys, for determining the role of wider pelagic food web (e.g. prey distributions) in driving pelagic shark distributions. Regardless, further study to optimise BRUV methodologies (e.g. soak time, bait type, bait amount, time of deployment) for detecting elasmobranchs in UK waters would greatly benefit the future application of these methods.

Overall, this work supports the notion that MPAs should play a key role in the conservation of temperate elasmobranchs. However, they should not be considered a panacea and serious consideration should be given to the exact conditions under which they are established. It is recommended that MPAs should be one part of a larger network of conservation strategies, including an interconnected network of MPAs, complementary fishing limits and market-based interventions. Whilst non-elasmobranch focussed MPAs may inadvertently provide benefits to generalist and fast-growing elasmobranch species, minor MPA modifications could opportunistically maximise conservation outcomes for rarer and more mobile species. However, this should not negate the pursuit of ‘gold-standard’, elasmobranch-focussed MPAs, designed according to the guardrails outlined in Chapter 1. Finally, holistic protection of elasmobranchs will not be achieved without a transformation of current monitoring approaches, both in MPA research and more widely, to facilitate real-time detection and response to elasmobranch declines. This will benefit considerably from the further optimisation and adoption of novel technologies.

References:

Abel, D.C. and Grubbs, R.D. 2020. *Shark Biology and Conservation: Essentials for Educators, Students, and Enthusiasts*. Johns Hopkins University Press.

Acuña-Marrero, D., Smith, A.N.H., Hammerschlag, N., Hearn, A., Anderson, M.J., Calich, H., Pawley, M.D.M., Fischer, C., Salinas-De-León, P., 2017. Residency and movement patterns of an apex predatory shark (Galeocerdo cuvier) at the Galapagos Marine Reserve. PLoS ONE 12, 1–20. https://doi.org/10.1371/journal.pone.0183669

Acuña-Marrero, D., Smith, A.N.H., Salinas-De-León, P., Harvey, E.S., Pawley, M.D.M., Anderson, M.J., 2018. Spatial patterns of distribution and relative abundance of coastal shark species in the Galapagos Marine Reserve. Mar. Ecol. Prog. Ser. 593, 73–95. https://doi.org/10.3354/meps12505

Ahmadia, G.N., Glew, L., Provost, M., Gill, D., Hidayat, N.I., Mangubhai, S., Purwanto,., Fox, H.E., 2015. Integrating impact evaluation in the design and implementation of monitoring marine protected areas. Philos. Trans. R. Soc. B Biol. Sci. 370, 20140275. https://doi.org/10.1098/rstb.2014.0275

Albano, P.S., Fallows, C., Fallows, M., Schuitema, O., Bernard, A.T.F., Sedgwick, O., Hammerschlag, N., 2021. Successful parks for sharks: No-take marine reserve provides conservation benefits to endemic and threatened sharks off South Africa. Biol. Conserv. 261, 109302. https://doi.org/10.1016/j.biocon.2021.109302

Allen, H. L., Stewart, B. D., McClean, C. J., Hancock, J., Rees, R. 2021. Anthropogenic injury and site fidelity in Maldivian whale sharks (*Rhincodon typu*s). Aquatic Conservation: Marine and Freshwater Ecosystems, 31, 1429–1442. https://doi.org/10.1002/aqc.3524

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Barnes, P.B., Davis, A.R., Roberts, D.E., 2006. Sampling patchily distributed taxa: A case study using cost-benefit analyses for sponges and ascidians in coastal lakes of New South Wales, Australia. Handb. Environ. Chem. Vol. 5 Water Pollut. 319, 55–64. https://doi.org/10.3354/meps319055

Bazzi, M., Campione, N.E., Ahlberg, P.E., Blom, H., Kear, B.P., 2021. Tooth morphology elucidates shark evolution across the end-Cretaceous mass extinction. PLoS Biol. 19, e3001108. https://doi.org/10.1371/journal.pbio.3001108

Bicknell, A.W.J., Sheehan, E.V., Godley, B.J., Doherty, P.D., Witt, M.J., 2019. Assessing the impact of introduced infrastructure at sea with cameras: A case study for spatial scale, time and statistical power. Mar. Environ. Res. 147, 126–137. https://doi.org/10.1016/j.marenvres.2019.04.007

Blampied, S.R., Rees, S.E., Attrill, M.J., Binney, F.C.T., Sheehan, E.V., 2022. Removal of bottom-towed fishing from whole-site Marine Protected Areas promotes mobile species biodiversity. Estuar. Coast. Shelf Sci. 276, 108033. https://doi.org/10.1016/j.ecss.2022.108033

Bohmann, K., Evans, A., Gilbert, M.T.P., Carvalho, G.R., Creer, S., Knapp, M., Yu, D.W., de Bruyn, M., 2014. Environmental DNA for wildlife biology and biodiversity monitoring. Trends Ecol. Evol. 29, 358–367. https://doi.org/10.1016/j.tree.2014.04.003

Bohorquez, J.J., Dvarskas, A., Pikitch, E.K., 2019. Filling the Data Gap – A Pressing Need for Advancing MPA Sustainable Finance. Front. Mar. Sci. 6.

Bond, M.E., Babcock, E.A., Pikitch, E.K., Abercrombie, D.L., Lamb, N.F., Chapman, D.D., 2012. Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier reef. PLoS ONE 7, 1–14. https://doi.org/10.1371/journal.pone.0032983

Bouchet, P.J., Meeuwig, J.J., 2015. Drifting baited stereo-videography: A novel sampling tool for surveying pelagic wildlife in offshore marine reserves. Ecosphere 6. https://doi.org/10.1890/ES14-00380.1

Boussarie, G., Bakker, J., Wangensteen, O.S., Mariani, S., Bonnin, L., Juhel, J., Kiszka, J.J., Kulbicki, M., Manel, S., Robbins, W.D., Vigliola, L., Mouillot, D., 2018. Environmental DNA illuminates the dark diversity of sharks. Sci. Adv. 4, 1–8.

Breen, P., Posen, P., & Righton, D. (2015). Temperate marine protected areas and highly mobile fish: A review. Ocean and Coastal Management, 105, 75–83. https://doi.org/10.1016/j.ocecoaman.2014.12.021

Brewster, L.R., Dale, J.J., Guttridge, T.L., Gruber, S.H., Hansell, A.C., Elliott, M., Cowx, I.G., Whitney, N.M., Gleiss, A.C., 2018. Development and application of a machine learning algorithm for classification of elasmobranch behaviour from accelerometry data. Mar. Biol. 165, 62. https://doi.org/10.1007/s00227-018-3318-y

Bridger, D., Attrill, M.J., Davies, B.F.R., Holmes, L.A., Cartwright, A., Rees, S.E., Cabre, L.M., Sheehan, E.V., 2022. The restoration potential of offshore mussel farming on degraded seabed habitat. Aquac. Fish Fish. 00, 1–13. https://doi.org/10.1002/aff2.77

Broad, A., Knott, N., Turon, X., Davis, A.R., 2010. Effects of a shark repulsion device on rocky reef fishes: No shocking outcomes. Mar. Ecol. Prog. Ser. 408, 295–298. https://doi.org/10.3354/meps08591

Butcher, P., Colefax, A., Gorkin, R., Kajiura, S., López, N., Mourier, J., Purcell, C., Skomal, G., Tucker, J., Walsh, A., Williamson, J., Raoult, V., 2021. The Drone Revolution of Shark Science: A Review. Drones 5, 8. https://doi.org/10.3390/drones5010008

Caddy, J.F., McGarvey, R., 1996. Targets or Limits for Management of Fisheries? North Am. J. Fish. Manag. 16, 479–487. https://doi.org/10.1577/1548-8675(1996)016<0479:TOLFMO>2.3.CO;2

Cambra, M., Lara-Lizardi, F., Peñaherrera-Palma, C., Hearn, A., Ketchum, J.T., Zarate, P., Chacón, C., Suárez-Moncada, J., Herrera, E., Espinoza, M., 2021. A first assessment of the distribution and abundance of large pelagic species at Cocos Ridge seamounts (Eastern Tropical Pacific) using drifting pelagic baited remote cameras. PLOS ONE 16, e0244343. https://doi.org/10.1371/journal.pone.0244343

Cameron, L.W.J., Roche, W., Green, P., Houghton, J.D.R., Mensink, P.J., 2018. Transatlantic movement in porbeagle sharks, Lamna nasus. Fish. Res. 207, 25–27. https://doi.org/10.1016/j.fishres.2018.05.014

Casselberry, G.A., Danylchuk, A.J., Finn, J.T., DeAngelis, B.M., Jordaan, A., Pollock, C.G., Lundgren, I., Hillis-Starr, Z., Skomal, G.B., 2020. Network analysis reveals multispecies spatial associations in the shark community of a Caribbean marine protected area. Mar. Ecol. Prog. Ser. 633, 105–126. https://doi.org/10.3354/meps13158

Chapple, T.K., Tickler, D., Roche, R.C., Bayley, D.T.I., Gleiss, A.C., Kanive, P.E., Jewell, O.J.D., Jorgensen, S.J., Schallert, R., Carlisle, A.B., Pilly, J.S., Andrzejaczek, S., Wikelski, M., Hussey, N.E., Block, B.A., 2021. Ancillary data from animal-borne cameras as an ecological survey tool for marine communities. Mar. Biol. 168, 1–13. https://doi.org/10.1007/s00227-021-03916-w

Cheung, W.W.L., Pinnegar, J., Merino, G., Jones, M.C., Barange, M., 2012. Review of climate change impacts on marine fisheries in the UK and Ireland. Aquat. Conserv. Mar. Freshw. Ecosyst. 22, 368–388. https://doi.org/10.1002/aqc.2248

Christensen, V., Coll, M., Piroddi, C., Steenbeek, J., Buszowski, J., Pauly, D., 2014. A century of fish biomass decline in the ocean. Mar. Ecol. Prog. Ser. 512, 155–166. https://doi.org/10.3354/meps10946

Clarke, K.R., Gorley, R.N. 2006. User manual/tutorial. PRIMER-E Ltd, Plymouth

Clarke, M., Guzman, D., Ellis, J., 2008. An overview of pelagic shark fisheries in the Northeast Atlantic. … Collect. Vol. … 62, 1483–1493.

Collins, C., Nuno, A., Broderick, A., Curnick, D.J., de Vos., A., Franklin, T., Jacoby, D.M.P., Mees, C., Moir-Clark, J., Pearce, J., Bech Letessier, T., 2021. Understanding persistent non-compliance in a remote, large-scale marine protected area. Front. Mar. Sci. 8, 1–13. https://doi.org/10.3389/fmars.2021.650276

Colton, M., Swearer, S., 2010. A comparison of two survey methods: differences between underwater visual census and baited remote underwater video. Mar. Ecol. Prog. Ser. 400, 19–36. https://doi.org/10.3354/meps08377

Colton, M.A., Swearer, S.E., 2012. Locating faunal breaks in the nearshore fish assemblage of Victoria, Australia. Mar. Freshw. Res. 63, 218–231. https://doi.org/10.1071/MF10322

Cortés, E., 2002. Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. Conserv. Biol. 16, 1048–1062. https://doi.org/10.1046/j.1523-1739.2002.00423.x

Cortés, E., 2000. Life History Patterns and Correlations in Sharks. Rev. Fish. Sci. 8, 299–344. https://doi.org/10.1080/10408340308951115

Cortés, E., Brooks, E.N., Gedamke, T.D., 2012. Population dynamics, demography, and stock assessment. In: Carrier JC, Musick JA, Heithaus MR (eds) *Biology of sharks and their relatives, 2nd edn.* CRC Press, Boca Raton, FL, p 453−486

Curtis, T.H., McCandless, C.T., Carlson, J.K., Skomal, G.B., Kohler, N.E., Natanson, L.J., Burgess, G.H., Hoey, J.J., Jr, H.L.P., 2014. Seasonal Distribution and Historic Trends in Abundance of White Sharks, Carcharodon carcharias, in the Western North Atlantic Ocean. PLOS ONE 9, e99240. https://doi.org/10.1371/journal.pone.0099240

Da Silva, C., Attwood, C.G., Wintner, S.P., Wilke, C.G., Winker, H., Smale, M.J., Kerwath, S.E., 2021. Life history of Mustelus mustelus in the Langebaan Lagoon marine protected area. Mar. Freshw. Res. https://doi.org/10.1071/MF20277

da Silva, C., Kerwath, S., Attwood, C., Thorstad, E., Cowley, P., Økland, F., Wilke, C., Næsje, T., 2013. Quantifying the degree of protection afforded by a no-take marine reserve on an exploited shark. Afr. J. Mar. Sci. 35, 57–66. https://doi.org/10.2989/1814232X.2013.769911

Daan, N., Heessen, H., ter Hofstede, R., 2005. North Sea Elasmobranchs: distribution, abundance and biodiversity. ICES Committee Meetings Documents 2005 (N:06). ICES, Copenhagen, Denmark 1–15.

Daly, R., Smale, M.J., Singh, S., Anders, D., Shivji, M., Clare, C.A., Lea, J.S.E., Sousa, L.L., Wetherbee, B.M., Fitzpatrick, R., Clarke, C.R., Sheaves, M., Barnett, A., 2018. Refuges and risks: Evaluating the benefits of an expanded MPA network for mobile apex predators. Divers. Distrib. 24, 1217–1230. https://doi.org/10.1111/ddi.12758

Davidson, L.N.K., Dulvy, N.K., 2017. Global marine protected areas to prevent extinctions. Nat. Ecol. Evol. 1, 1–6. https://doi.org/10.1038/s41559-016-0040

Davidson, L.N.K., Krawchuk, M.A., Dulvy, N.K., 2016. Why have global shark and ray landings declined: Improved management or overfishing? Fish Fish. 17, 438–458. https://doi.org/10.1111/faf.12119

Davies, B.F.R., Attrill, M.J., Holmes, L., Rees, A., Witt, M.J., Sheehan, E.V., 2020. Acoustic Complexity Index to assess benthic biodiversity of a partially protected area in the southwest of the UK. Ecol. Indic. 111, 106019. https://doi.org/10.1016/j.ecolind.2019.106019

Davies, B.F.R., Holmes, L., Rees, A., Attrill, M.J., Cartwright, A.Y., Sheehan, E.V., 2021a. Ecosystem Approach to Fisheries Management works—How switching from mobile to static fishing gear improves populations of fished and non-fished species inside a marine-protected area. J. Appl. Ecol. 1–16. https://doi.org/10.1111/1365-2664.13986

Davies, B.F.R., Holmes, L., Rees, A., Attrill, M.J., Cartwright, A.Y., Sheehan, E.V., 2021b. Ecosystem Approach to Fisheries Management works—How switching from mobile to static fishing gear improves populations of fished and non-fished species inside a marine-protected area. J. Appl. Ecol. 58, 2463–2478. https://doi.org/10.1111/1365-2664.13986

Dawson, M.N., Grosberg, R.K., Botsford, L.W., Steneck, R.S., Cowen, R.K., Paris, C.B., Srinivasan, A., 2006. Connectivity in Marine Protected Areas. Science 313, 43–45.

Defra. 2008. Explanatory memorandum to the Lyme Bay designated area. Fishing Restrictions Order 2008 No. 1584. London: Defra.

Defra. 2019. Benyon Review into Highly Protected Marine Areas - Final Report

De Santo, E.M., 2013. Missing marine protected area (MPA) targets: How the push for quantity over quality undermines sustainability and social justice. J. Environ. Manage. 124, 137–146. https://doi.org/10.1016/j.jenvman.2013.01.033

De Vos, L., Watson, R.G.A., Götz, A., Attwood, C.G., 2015. Baited remote underwater video system (BRUVs) survey of chondrichthyan diversity in False Bay, South Africa. Afr. J. Mar. Sci. 37, 209–218. https://doi.org/10.2989/1814232X.2015.1036119

Dell'Anno, A., Corinaldesi, C., 2004. Degradation and Turnover of Extracellular DNA in Marine Sediments: Ecological and Methodological Considerations. Appl. Environ. Microbiol. 70, 4384–4386. https://doi.org/10.1128/AEM.70.7.4384

Dennis, C., 2003. Close encounters of the jelly kind. Nature 426, 12–14. https://doi.org/10.1038/426012a

Di Ciaccio, F., Troisi, S., 2021. Monitoring marine environments with Autonomous Underwater Vehicles: A bibliometric analysis. Results Eng. 9, 100205. https://doi.org/10.1016/j.rineng.2021.100205

Ditria, E.M., Lopez-Marcano, S., Sievers, M., Jinks, E.L., Brown, C.J., Connolly, R.M., 2020. Automating the Analysis of Fish Abundance Using Object Detection: Optimizing Animal Ecology With Deep Learning. Front. Mar. Sci. 7, 429. https://doi.org/10.3389/fmars.2020.00429

Doherty, P.D., Baxter, J.M., Godley, B.J., Graham, R.T., Hall, G., Hall, J., Hawkes, L.A., Henderson, S.M., Johnson, L., Speedie, C., Witt, M.J., 2017. Testing the boundaries: Seasonal residency and inter-annual site fidelity of basking sharks in a proposed Marine Protected Area. Biol. Conserv. 209, 68–75. https://doi.org/10.1016/j.biocon.2017.01.018

Doyle, M. J., Morse, W. W., Kendall, A. W. 1993. A comparison of larval fish assemblages in the temperate zone of the northeast Pacific and northwest Atlantic Oceans. Bulletin of Marine Science, 53, 588–644.

Drago, L., Panaïotis, T., Irisson, J.O., Babin, M., Biard, T., Carlotti, F., Coppola, L., Guidi, L., Hauss, H., Karp-Boss, L., Lombard, F., McDonnell, A.M.P., Picheral, M., Rogge, A., Waite, A.M., Stemmann, L., Kiko, R., 2022. Global Distribution of Zooplankton Biomass Estimated by In Situ Imaging and Machine Learning. Front. Mar. Sci. 9, 1–22. https://doi.org/10.3389/fmars.2022.894372

Duarte, C.M., Agusti, S., Barbier, E., Britten, G.L., Castilla, J.C., Gattuso, J.P., Fulweiler, R.W., Hughes, T.P., Knowlton, N., Lovelock, C.E., Lotze, H.K., Predragovic, M., Poloczanska, E., Roberts, C., Worm, B., 2020. Rebuilding marine life. Nature 580, 39–51. https://doi.org/10.1038/s41586-020-2146-7

Dulvy, N.K., Baum, J.K., Clark, S., Compagno, L.J.V., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martinez, J.J., Musick, J.A., Soldoi, A., Stevens, J.D., Valenti, S., 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquat. Conserv. Mar. Freshw. Ecosyst. 18, 459–482. https://doi.org/10.1002/aqc

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, M., Harrison, L.R., Carlson, J.K., Davidson, L.N.K., Sonja, V., 2014a. Extinction risk and conservation of the world's sharks and rays. eLife 3, 1–34. https://doi.org/10.7554/eLife.00590

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, M., Harrison, L.R., Carlson, J.K., Davidson, L.N.K., Sonja, V., 2014b. Extinction risk and conservation of the world's sharks and rays. eLife 3, 1–34. https://doi.org/10.7554/eLife.00590

Dulvy, N.K., Metcalfe, J.D., Glanville, J., Pawson, M.G., Reynolds, J.D., 2000. Fishery Stability, Local Extinctions, and Shifts in Community Structure in Skates. Conserv. Biol. 14, 283–293. https://doi.org/10.1046/j.1523-1739.2000.98540.x

Dulvy, N.K., Pacoureau, N., Rigby, C.L., Pollom, R.A., Jabado, R.W., Ebert, D.A., Finucci, B., Pollock, C.M., Cheok, J., Derrick, D.H., Herman, K.B., Sherman, C.S., VanderWright, W.J., Lawson, J.M., Walls, R.H.L., Carlson, J.K., Charvet, P., Bineesh, K.K., Fernando, D., Ralph, G.M., Matsushiba, J.H., Hilton-Taylor, C., Fordham, S.V., Simpfendorfer, C.A., 2021. Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. Curr. Biol. 1–15. https://doi.org/10.1016/j.cub.2021.08.062

Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. Fish Fish. 4, 25–64. https://doi.org/10.1046/j.1467-2979.2003.00105.x

Dureuil, M., Boerder, K., Burnett, K.A., Froese, R., Worm, B., 2018. Elevated trawling inside protected areas undermines conservation outcomes in a global fishing hot spot. Science 1403, 1403–1407.

Ebert, D.A., Fowler, S., Compagno, L. 2013. *Sharks of the World.* Wild Nature Press, Plymouth.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506, 216–220. https://doi.org/10.1038/nature13022

Edwards, M., Beaugrand, G., Kléparski, L., Hélaouët, P., Reid, P.C., 2022. Climate variability and multi-decadal diatom abundance in the Northeast Atlantic. Commun. Earth Environ. 3, 1–8. https://doi.org/10.1038/s43247-022-00492-9

Ellis, J.R., Dulvy, N.K., Jennings, S., Parker-Humphreys, M., Rogers, S.I., 2005. Assessing the status of demersal elasmobranchs in UK waters: A review. J. Mar. Biol. Assoc. U. K. 85, 1025–1047. https://doi.org/10.1017/S0025315405012099

Ellis, J., Mancusi, C., Serena, F., Haka, F., Guallart, J., Ungaro, N., Coelho, R., Schembri, T., MacKenzie, K. 2009. Scyliorhinus canicula. The IUCN Red List of Threatened Species 2009: e.T161399A5415204. http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T161399A5415204.en

Ellis, J.R., Silva, J.F., McCully, S.R., Evans, M., Catchpole, T., 2010. UK fisheries for skates (Rajidae): History and development of the fishery, recent management actions and survivorship of discards. Ices Cm 2010/E:10, 38.

Eriksen, E., Bogstad, B., Dolgov, A., Beck, I. M. 2018. Cod diet as an indicator of Ctenophora abundance dynamics in the Barents Sea. Marine Ecology Progress Series, 591, 87–100. https://www.jstor.org/stable/26502938

Espinoza, M., Cappo, M., Heupel, M.R., Tobin, A.J., Simpfendorfer, C.A., 2014. Quantifying shark distribution patterns and species-habitat associations: Implications of Marine Park zoning. PLoS ONE 9, e106885. https://doi.org/10.1371/journal.pone.0106885

Esser, M., Greve, W., Boersma, M., 2004. Effects of temperature and the presence of benthic predators on the vertical distribution of the ctenophore Pleurobrachia pileus. Mar. Biol. 145, 595–601. https://doi.org/10.1007/s00227-004-1348-0

Farrell, E.D., Clarke, M.W., Mariani, S., 2009. A simple genetic identification method for Northeast Atlantic smoothhound sharks (Mustelus spp.). ICES J. Mar. Sci. 66, 561–565. https://doi.org/10.1093/icesjms/fsn218

Ferretti, F., Jacoby, D.M.P., Pfleger, M.O., White, T.D., Dent, F., Micheli, F., Rosenberg, A.A., Crowder, L.B., Block, B.A., 2020. Shark fin trade bans and sustainable shark fisheries. Conserv. Lett. 13, e12708. https://doi.org/10.1111/conl.12708

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K., 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecol. Lett. 13, 1055–1071. https://doi.org/10.1111/j.1461-0248.2010.01489.x

Fogarty, M.J., Murawski, S.A., 1998. Large-Scale Disturbance and the Structure of Marine Systems: Fishery Impacts on Georges Bank. Ecol. Appl. 8, S6–S22. https://doi.org/10.1890/1051-0761(1998)8[S6:LDATSO]2.0.CO;2

Fox, H.E., Holtzman, J.L., Haisfield, K.M., McNally, C.G., Cid, G.A., Mascia, M.B., Parks, J.E., Pomeroy, R.S., 2014. How Are Our MPAs Doing? Challenges in Assessing Global Patterns in Marine

Protected Area Performance. Coast. Manag. 42, 207–226. https://doi.org/10.1080/08920753.2014.904178

Gallagher, A.J., Shipley, O.N., van Zinnicq Bergmann, M.P.M., Brownscombe, J.W., Dahlgren, C.P., Frisk, M.G., Griffin, L.P., Hammerschlag, N., Kattan, S., Papastamatiou, Y.P., Shea, B.D., Kessel, S.T., Duarte, C.M., 2021. Spatial Connectivity and Drivers of Shark Habitat Use Within a Large Marine Protected Area in the Caribbean, The Bahamas Shark Sanctuary. Front. Mar. Sci. 7, 1–15. https://doi.org/10.3389/fmars.2020.608848

Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., Gjerde, K., Bustamante, R., Possingham, H. P., & Richardson, A. J. (2009). Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecology and Evolution, 24(7), 360–369. https://doi.org/10.1016/j.tree.2009.01.011

Gargan, L. M., Morato, T., Pham, C. K., Finarelli, J. A., Carlsson, J. E. L., & Carlsson, J. 2017. Development of a sensitive detection method to survey pelagic biodiversity using eDNA and quantitative PCR: a case study of devil ray at seamounts. Marine Biology, 164, 1–9. https://doi.org/10.1007/s00227-017-3141-x

Gell, F.R., Roberts, C.M., 2003. The fishery effects of marine reserves and fishery closures. Rev. Lit. Arts Am. 18, 90.

Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. A., Hawkins, S. J., 2004. Regional climatic warming drives long-term community changes of British marine fish. Proceedings of the Royal Society B: Biological Sciences, 271, 655–661. https://doi.org/10.1098/rspb.2003.2651

Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., Mchugh, M., Rendle, P., Southall, E. J., Wearmouth, V. J., Hawkins, S. J. 2009. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. Global Change Biology, 16, 517–527. https://doi.org/10.1111/j.1365-2486.2009.02027.x

Gilman, E., Chaloupka, M., Fitchett, M., Cantrell, D.L., Merrifield, M., 2020. Ecological responses to blue water MPAs. PLoS ONE 15, 1–27. https://doi.org/10.1371/journal.pone.0235129

Gluchowska, M., Trudnowska, E., Goszczko, I., Kubiszyn, A.M., Blachowiak-Samolyk, K., Walczowski, W., Kwasniewski, S., 2017. Variations in the structural and functional diversity of zooplankton over vertical and horizontal environmental gradients en route to the Arctic Ocean through the Fram Strait. PLoS ONE 12, 1–26. https://doi.org/10.1371/journal.pone.0171715

Goetze, J.S., Langlois, T.J., McCarter, J., Simpfendorfer, C.A., Hughes, A., Leve, J.T., Jupiter, S.D., 2018. Drivers of reef shark abundance and biomass in the Solomon Islands. PLoS ONE 13. https://doi.org/10.1371/journal.pone.0200960

Goodwin, M., Halvorsen, K.T., Jiao, L., Knausgård, K.M., Martin, A.H., Moyano, M., Oomen, R.A., Rasmussen, J.H., Sørdalen, T.K., Thorbjørnsen, S.H., 2022. Unlocking the potential of deep learning for marine ecology: overview, applications, and outlook. ICES J. Mar. Sci. 79, 319–336. https://doi.org/10.1093/icesjms/fsab255

Graham, W.M., Pagès, F., Hamner, W.M., 2001. A physical context for gelatinous zooplankton aggregations: A review. Hydrobiologia 451, 199–212. https://doi.org/10.1023/A:1011876004427

Gray, C.A., Miskiewicz, A.G., 2000. Larval fish assemblages in south-east Australian coastal waters: Seasonal and spatial structure. Estuar. Coast. Shelf Sci. 50, 549–570. https://doi.org/10.1006/ecss.1999.0595

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J., White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol. Rev. 90, 1215–1247. https://doi.org/10.1111/brv.12155

Greve, W. 1975. Ctenophora. Fiches d'Identification du Zooplancton 146. Conseil International pour l'Exploration de la Mer, Kopenhagen.

Griffin, R.A., Robinson, G.J., West, A., Gloyne-Phillips, I.T., Unsworth, R.K.F., 2016. Assessing fish and motile fauna around offshore windfarms using stereo baited video. PLoS ONE 11, 1–14. https://doi.org/10.1371/journal.pone.0149701

Griffiths, A.M., Miller, D.D., Egan, A., Fox, J., Greenfield, A., Mariani, S., 2013. DNA barcoding unveils skate (Chondrichthyes: Rajidae) species diversity in ‘ray’ products sold across Ireland and the UK. PeerJ 1, e129. https://doi.org/10.7717/peerj.129

Haddock, S.H.D., 2004. A golden age of gelata: Past and future research on planktonic ctenophores and cnidarians. Hydrobiologia 530–531, 549–556. https://doi.org/10.1007/s10750-004-2653-9

Hammerschlag, N., Sulikowski, J., 2011. Killing for conservation: The need for alternatives to lethal sampling of apex predatory sharks. Endanger. Species Res. 14, 135–140. https://doi.org/10.3354/esr00354

Hammerschlag, N., Gallagher, A. J., Lazarre, D. M. 2011. A review of shark satellite tagging studies. Journal of Experimental Marine Biology and Ecology, 398(1–2), 1–8. https://doi.org/10.1016/j.jembe.2010.12.012

Hammond, T.R., Ellis, J.R., 2004. Bayesian Assessment of Northeast Atlantic Spurdog Using a Stock Production Model, with Prior for Intrinsic Population Growth Rate Set by Demographic Methods. J. Northwest Atl. Fish. Sci. 35, 299–308. https://doi.org/10.2960/J.v35.m486

Hardinge, J., Harvey, E.S., Saunders, B.J., Newman, S.J., 2013. A little bait goes a long way: The influence of bait quantity on a temperate fish assemblage sampled using stereo-BRUVs. J. Exp. Mar. Biol. Ecol. 449, 250–260. https://doi.org/10.1016/j.jembe.2013.09.018

Harith, M.N., O’ Donnell, C., Johnston, G., Power, A.M., 2021. A snapshot on composition and distribution of fish larvae across the north atlantic ocean. Biodiversitas 22, 4496–4504. https://doi.org/10.13057/biodiv/d221043

Harris, S. A., Cyrus, D. P., Beckley, L. E. 2001. Horizontal trends in larval fish diversity and abundance along an ocean-estuarine gradient on the northern KwaZulu-Natal coast, South Africa. Estuarine, Coastal and Shelf Science, 53, 221–235. https://doi.org/10.1006/ecss.2001.0803

Harvey, E.S., Santana-garcon, J., Goetze, J., Saunders, B.J., Cappo, M., 2018. The use of stationary underwater video for sampling sharks. In: Carrier, J.C., Heithaus, M.R., Simpendorfer, C. (Eds.), *Shark Research: Emerging Technologies and Applications for the Field and Laboratory*. CRC Press, p 111–132.

Hayes, C., Jiao, Y., Cortés, E., 2009. Stock Assessment of Scalloped Hammerheads in the Western North Atlantic Ocean and Gulf of Mexico. North Am. J. Fish. Manag. 29, 1406–1417. https://doi.org/10.1577/M08-026.1

Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. Trends Ecol. Evol., SPECIAL ISSUE: BUMPER BOOK REVIEW 20, 337–344. https://doi.org/10.1016/j.tree.2005.03.004

Heagney, E.C., Lynch, T.P., Babcock, R.C., Suthers, I.M., 2007. Pelagic fish assemblages assessed using mid-water baited video: Standardising fish counts using bait plume size. Mar. Ecol. Prog. Ser. 350, 255–266. https://doi.org/10.3354/meps07193

Hearn, A., Ketchum, J., Klimley, A.P., Espinoza, E., Peñaherrera, C., 2010. Hotspots within hotspots? Hammerhead shark movements around Wolf Island, Galapagos Marine Reserve. Mar. Biol. 157, 1899–1915. https://doi.org/10.1007/s00227-010-1460-2

Heithaus, M. R., Marshall, G. J., Buhleier, B. M., Dill, L. M., 2001. Employing Crittercam to study habitat use and behavior of large sharks. Marine Ecology Progress Series, 209, 307–310. https://doi.org/10.3354/meps209307

Heithaus, M., 2007. Nursery areas as essential shark habitats: A theoretical perspective Nursery Areas as Essential Shark Habitats. Am. Fish. Soc. Symp. 50, 3–13.

Heithaus, Michael.R., Wirsing, A.J., Dill, L.M., 2012. The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. Mar. Freshw. Res. 63, 1039. https://doi.org/10.1071/MF12024

Heupel, M.R., Carlson, J.K., Simpfendorfer, C.A., 2007. Shark nursery areas: Concepts, definition, characterization and assumptions. Mar. Ecol. Prog. Ser. 337, 287–297. https://doi.org/10.3354/meps337287

Heupel, M.R., Kanno, S., Martins, A.P.B., Simpfendorfer, C.A., 2018. Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. Mar. Freshw. Res. 70, 897–907. https://doi.org/10.1071/MF18081

Heupel, M.R., Knip, D.M., Simpfendorfer, C.A., Dulvy, N.K., 2014. Sizing up the ecological role of sharks as predators. Mar. Ecol. Prog. Ser. 495, 291–298. https://doi.org/10.3354/meps10597

Heupel, M.R., Simpfendorfer, C.A., 2010. Science or Slaughter: Need for Lethal Sampling of Sharks. Conserv. Biol. 24, 1212–1218. https://doi.org/10.1111/j.1523-1739.2010.01491.x

Hiddink, J.G., Shepperson, J., Bater, R., Goonesekera, D., Dulvy, N.K., 2019. Near disappearance of the Angelshark Squatina squatina over half a century of observations. Conserv. Sci. Pract. 1, 1–9. https://doi.org/10.1111/csp2.97

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Mills Flemming, J.E., Whoriskey, F.G., 2015. Aquatic animal telemetry: A panoramic window into the underwater world. Science 348, 1255642. https://doi.org/10.1126/science.1255642

Hyde, C.A., Notarbartolo, G., Sorrentino, L., Boyd, C., Finucci, B., Fowler, S.L., Kyne, P.M., Leurs, G., Simpfendorfer, C.A., Tetley, M.J., 2022. Putting sharks on the map : A global standard for improving shark area-based conservation. Front. Mar. Sci. 1–16. https://doi.org/10.3389/fmars.2022.968853

ICES. 2018. Report of the Working Group on Elasmobranch Fishes (WGEF), 19–28 June 2018, Lisbon, Portugal. ICES CM 2018/ACOM:16. 1306 pp

IUCN Standards and Petitions Committee., 2022. Guidelines for Using the IUCN Red List Categories and Criteria. Version 15.1. Prepared by the Standards and Petitions Committee. Downloadable from https://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Jabado, R.W., Hameli, S.M.A., Grandcourt, E.M., Dhaheri, S.S.A., 2018. Low abundance of sharks and rays in baited remote underwater video surveys in the Arabian Gulf. Sci. Rep. 1–11. https://doi.org/10.1038/s41598-018-33611-8

Jablonski, D., 1991. Extinctions: A Paleontological Perspective. Science 253, 754–757. https://doi.org/10.1126/science.253.5021.754

Jenrette, J., Liu, Z.Y.-C., Chimote, P., Hastie, T., Fox, E., Ferretti, F., 2022. Shark detection and classification with machine learning. Ecol. Inform. 69, 101673. https://doi.org/10.1016/j.ecoinf.2022.101673

Jones, P.J.S., 2002. Marine protected area strategies: Issues, divergences and the search for middle ground. Rev. Fish Biol. Fish. 11, 197–216. https://doi.org/10.1023/A:1020327007975

Jones, R.E., Griffin, R.A., Rees, S.C., Unsworth, R.K.F., 2019. Improving visual biodiversity assessments of motile fauna in turbid aquatic environments. Limnol. Oceanogr. Methods 17, 544–554. https://doi.org/10.1002/lom3.10331

Jorgensen, S., Micheli, F., White, T., Van Houtan, K., Alfaro-Shigueto, J., Andrzejaczek, S., Arnoldi, N., Baum, J., Block, B., Britten, G., Butner, C., Caballero, S., Cardeñosa, D., Chapple, T., Clarke, S., Cortés, E., Dulvy, N., Fowler, S., Gallagher, A., Gilman, E., Godley, B., Graham, R., Hammerschlag, N., Harry, A., Heithaus, M., Hutchinson, M., Huveneers, C., Lowe, C., Lucifora, L., MacKeracher, T., Mangel, J., Barbosa Martins, A., McCauley, D., McClenachan, L., Mull, C., Natanson, L., Pauly, D., Pazmiño, D., Pistevos, J., Queiroz, N., Roff, G., Shea, B., Simpfendorfer, C., Sims, D., Ward-Paige, C., Worm, B., Ferretti, F., 2022. Emergent research and priorities for shark and ray conservation. Endanger. Species Res. 47, 171–203. https://doi.org/10.3354/esr01169

Juan-Jordá, M.J., Murua, H., Arrizabalaga, H., Merino, G., Pacoureau, N., Dulvy, N.K., 2022. Seventy years of tunas, billfishes, and sharks as sentinels of global ocean health. Science. https://doi.org/10.1126/science.abj0211

Kelaher, B.P., Page, A., Dasey, M., Maguire, D., Read, A., Jordan, A., Coleman, M.A., 2015. Strengthened enforcement enhances marine sanctuary performance. Glob. Ecol. Conserv. 3, 503–510. https://doi.org/10.1016/j.gecco.2015.02.002

Kelly, M.L., Collin, S.P., Hemmi, J.M., Lesku, J.A., 2020. Evidence for Sleep in Sharks and Rays: Behavioural, Physiological, and Evolutionary Considerations. Brain. Behav. Evol. 94, 37–50. https://doi.org/10.1159/000504123

Kelly, R. P., Port, J. A., Yamahara, K. M., Martone, R. G., Lowell, N., Thomsen, P. F., Mach, M. E., Bennett, M., Prahler, E., Caldwell, M. R., & Crowder, L. B. 2014a. Harnessing DNA to improve environmental management. Science, 344(6191), 1455–1456. https://doi.org/10.1126/science.1251156

Kelly, R.P., Port, J.A., Yamahara, K.M., Crowder, L.B., 2014b. Using environmental DNA to census marine fishes in a large mesocosm. PLoS ONE 9, 1–11. https://doi.org/10.1371/journal.pone.0086175

Kinney, M.J., Simpfendorfer, C.A., 2009. Reassessing the value of nursery areas to shark conservation and management. Conserv. Lett. 2, 53–60. https://doi.org/10.1111/j.1755-263X.2008.00046.x

Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E., Llewellyn, F., Louzao, M., Ridoux, V., Tetley, M.J., 2014. Migratory marine species: their status, threats and conservation management needs. Aquat. Conserv. Mar. Freshw. Ecosyst. 24, 111–127. https://doi.org/10.1002/aqc.2512

Lenth, R., 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.1. https://CRAN.R-project.org/package=emmeans

Le Port, A., Lavery, S., Montgomery, J.C., 2012. Conservation of coastal stingrays: seasonal abundance and population structure of the short-tailed stingray Dasyatis brevicaudata at a Marine Protected Area. ICES J. Mar. Sci. 2012 8, 1427–1435. https://doi.org/10.1038/278097a0

Lester, S., Halpern, B., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B., Gaines, S., Airame, S., Warner, R., 2009. Biological Effects Within No-Take Marine Reserves: A Global Synthesis. Mar. Ecol.-Prog. Ser. - MAR ECOL-PROGR SER 384, 33–46. https://doi.org/10.3354/meps08029

Letessier, T. B., Meeuwig, J. J., Gollock, M., Groves, L., Bouchet, P. J., Chapuis, L., Vianna, G. M. S., Kemp, K., Koldewey, H. J. 2013. Assessing pelagic fish populations: The application of demersal video techniques to the mid-water environment. Methods in Oceanography, 8, 41–55. https://doi.org/10.1016/j.mio.2013.11.003

Letessier, T.B., Bouchet, P.J., Meeuwig, J.J., 2017. Sampling mobile oceanic fishes and sharks: Implications for fisheries and conservation planning. Biol. Rev. 92, 627–646. https://doi.org/10.1111/brv.12246

Leurs, G., van der Reijden, K.J., Cheikhna Lemrabott, S.Y., Barry, I., Nonque, D.M., Olff, H., Ledo Pontes, S., Regalla, A., Govers, L.L., 2021. Industrial Fishing Near West African Marine Protected Areas and Its Potential Effects on Mobile Marine Predators. Front. Mar. Sci. 8, 1–13. https://doi.org/10.3389/fmars.2021.602917

Leverington, F., Costa, K.L., Pavese, H., Lisle, A., Hockings, M., 2010. A Global Analysis of Protected Area Management Effectiveness. Environ. Manage. 46, 685–698. https://doi.org/10.1007/s00267-010-9564-5

Link, J.S., Almeida, F., Valentine, P., Auster, P., Reid, R., Vitaliano, J., 2005. The Effects of Area Closures on Georges Bank. Am. Fish. Soc. Symp. 41, 345–368.

Liu, Z., Collins, R. A., Baillie, C., Rainbird, S., Brittain, R., Griffiths, A. M., Sims, D. W., Mariani, S., Genner, M. J. 2022. Environmental DNA captures elasmobranch diversity in a temperate marine ecosystem. Environmental DNA, 4, 1024– 1038. https://doi.org/10.1002/edn3.294

Long, J.A. 1995. *The Rise of Fishes: 500 Hundred Million Years of Evolution*. Baltimore: Johns Hopkins University Press. p 22

Lucifora, L.O., García, V.B., Worm, B., 2011. Global Diversity Hotspots and Conservation Priorities for Sharks. PLOS ONE 6, e19356. https://doi.org/10.1371/journal.pone.0019356

Lyle, J.M. 1983. Food and feeding habits of the lesser spotted dogfish, Scyliorhinus canicula (L.), in Isle of Man waters. Journal of Fish Biology. 23, 725-737. https://doi.org/10.1111/j.1095-8649.1983.tb02950.x

MacKeracher, T., Diedrich, A., Simpfendorfer, C.A., 2019. Sharks, rays and marine protected areas: A critical evaluation of current perspectives. Fish Fish. 20, 255–267. https://doi.org/10.1111/faf.12337

Mangi, S.C., Rodwell, L.D., Hattam, C., 2011. Assessing the impacts of establishing MPAs on fishermen and fish merchants: The case of Lyme Bay, UK. Ambio 40, 457–468. https://doi.org/10.1007/s13280-011-0154-4

Marine Scotland., 2021. The Red Rocks and Longay Nature Conservation Marine Protected Area (No. 2) Order 2021. Scottish Ministerial Order. 1–6.

McClenachan, L., 2009. Documenting loss of large trophy fish from the florida keys with historical photographs. Conserv. Biol. 23, 636–643. https://doi.org/10.1111/j.1523-1739.2008.01152.x

McHugh, M., Sims, D.W., Partridge, J.C., Genner, M.J., 2011. A century later: Long-term change of an inshore temperate marine fish assemblage. J. Sea Res. 65, 187–194. https://doi.org/10.1016/j.seares.2010.09.006

Meeuwig, J.J., Thompson, C.D.H., Forrest, J.A., Christ, H.J., Letessier, T.B., Meeuwig, D.J., 2021. Pulling Back the Blue Curtain: A Pelagic Monitoring Program for the Blue Belt. Front. Mar. Sci. 8, 1–7. https://doi.org/10.3389/fmars.2021.649123

Molina, J.M., Cooke, S.J., 2012. Trends in shark bycatch research: Current status and research needs. Rev. Fish Biol. Fish. 22, 719–737. https://doi.org/10.1007/s11160-012-9269-3

Moll, R.J., Millspaugh, J.J., Beringer, J., Sartwell, J., He, Z., 2007. A new 'view' of ecology and conservation through animal-borne video systems. Trends Ecol. Evol. 22, 660–668. https://doi.org/10.1016/j.tree.2007.09.007

Momigliano, P., Harcourt, R., 2014. Sharks: Conservation, governance and management. Sharks Conserv. Gov. Manag. 1–331. https://doi.org/10.4324/9780203750292

Moore, A.B.M., Hiddink, J.G., 2022. Identifying critical habitat with archives: 275-year-old naturalist's notes provide high-resolution spatial evidence of long-term core habitat for a critically endangered shark. Biol. Conserv. 272, 109621. https://doi.org/10.1016/j.biocon.2022.109621

Morel, G.M., Shrives, J., Bossy, S.F., Meyer, C.G., 2013. Residency and behavioural rhythmicity of ballan wrasse (Labrus bergylta) and rays (Raja spp.) captured in Portelet Bay, Jersey: Implications for Marine Protected Area design. J. Mar. Biol. Assoc. U. K. 93, 1407–1414. https://doi.org/10.1017/S0025315412001725

MPAtlas, 2016. Marine Conservation Institute; www.mpatlas.org

Mucientes, G., Vedor, M., Sims, D.W., Queiroz, N., 2022., Unreported discards of internationally protected pelagic sharks in a global fishing hotspot are potentially large. Biological Conservation, 269. https://doi.org/10.1016/j.biocon.2022.109534

Mucientes, G.R., Queiroz, N., Sousa, L.L., Tarroso, P., Sims, D.W., 2009. Sexual segregation of pelagic sharks and the potential threat from fisheries. Biol. Lett. 5, 156–159. https://doi.org/10.1098/rsbl.2008.0761

Muhling, B.A., Beckley, L.E., Koslow, J.A., Pearce, A.F., 2008. Larval fish assemblages and water mass structure off the oligotrophic south-western Australian coast. Fish. Oceanogr. 17, 16–31. https://doi.org/10.1111/j.1365-2419.2007.00452.x

Murawski, S.A., Brown, R., Lai, H.L., Rago, P.J., Hendrickson, L., 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. Bull. Mar. Sci. 66, 775–798.

Murphy, H. M., Jenkins, G. P. 2010. Observational methods used in marine spatial monitoring of fishes and associated habitats: A review. Marine and Freshwater Research, 61, 236–252. https://doi.org/10.1071/MF09068

Myers, R., Worm, B., 2003. Rapid Worldwide Depletion of Predatory Fish Communities. Nature 423, 280–3. https://doi.org/10.1038/nature01610

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H., 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315, 1846–1850. https://doi.org/10.1126/science.1138657

Nakamura, I., Meyer, C.G., Sato, K., 2015. Unexpected Positive Buoyancy in Deep Sea Sharks, *Hexanchus griseus*, and a Echinorhinus cookei. PLoS One. 10. doi: 10.1371/journal.pone.0127667. PMID: 26061525; PMCID: PMC4489517.

Neal, K.J. 2005. *Pleurobrachia pileu*s. Sea gooseberry. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme [on-line]. Plymouth: Marine biological Association of United Kingdom [cited09/12/2022]. http://www.marlin.au.uk/species/Pleurobranchiapileus.htm[accessed09/01/06].

Nelson, J.S. 2006. *Fishes of the World.* 4th ed. New York: John Wiley & Sons. p 6

Oh, B.Z.L., Thums, M., Babcock, R.C., Meeuwig, J.J., Pillans, R.D., Speed, C., Meekan, M.G., 2017. Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery. Mar. Freshw. Res. 68, 1501–1517. https://doi.org/10.1071/MF16131

Ovegård, Mikael, Högvall, J., Ovegård, Maria, Wikström, A., Wennhage, H., 2022. Previously undocumented relationship between spiny dogfish Squalus acanthias and juvenile Atlantic horse mackerel Trachurus trachurus revealed by stereo-BRUV. Environ. Biol. Fishes 105, 453–458. https://doi.org/10.1007/s10641-022-01239-3

Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K.M., Marshall, A.D., Pollom, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J.S., Kindsvater, H.K., Dulvy, N.K., 2021. Half a century of global decline in oceanic sharks and rays. Nature 589, 567–571. https://doi.org/10.1038/s41586-020-03173-9

Pade, N.G., Queiroz, N., Humphries, N.E., Witt, M.J., Jones, C.S., Noble, L.R., Sims, D.W., 2009. First results from satellite-linked archival tagging of porbeagle shark, Lamna nasus: Area fidelity, wider-scale movements and plasticity in diel depth changes. J. Exp. Mar. Biol. Ecol. 370, 64–74. https://doi.org/10.1016/j.jembe.2008.12.002

Padgham, M., 2021. geodist: Fast, Dependency-Free Geodesic Distance Calculations. R package version 0.0.7, https://github.com/hypertidy/geodist

Pala, C., 2013. Giant Marine Reserves Pose Vast Challenges. Science 339, 640–641.

Papastamatiou, Y. P., Watanabe, Y. Y., Bradley, D., Dee, L. E., Weng, K., Lowe, C. G., Caselle, J. E., 2015. Drivers of daily routines in an ectothermic marine predator: Hunt warm, rest warmer? PLoS ONE, 10, 1–16. https://doi.org/10.1371/journal.pone.0127807

Papastamatiou, Y.P., Iosilevskii, G., Leos-Barajas, V., Brooks, E.J., Howey, L.A., Chapman, D.D., Watanabe, Y.Y., 2018. Optimal swimming strategies and behavioral plasticity of oceanic whitetip sharks. Sci. Rep. 8, 551. https://doi.org/10.1038/s41598-017-18608-z

Parry, M., Tierney, M., Wood, L., Stanwell-Smith, D., Northen, K., Abdulla, A., Corrigan, C., Gassner, P., Fletcher, L., n.d. Review of international Marine Protected Area seabed monitoring and assessment of “good practice” to inform application within UK waters 152.

Phillips, N.D., Garbett, A., Wise, D., Loca, S.L., Daly, O., Eagling, L.E., Houghton, J.D.R., Verhoog, P., Thorburn, J., Collins, P.C., 2021. Evidence of egg-laying grounds for critically endangered flapper skate (Dipturus intermedius) off Orkney, UK. J. Fish Biol. 99, 1492–1496. https://doi.org/10.1111/jfb.14817

Pikitch, E.K., 2018. A tool for finding rare marine species. Sci. Mag. 360, 1180–1182. https://doi.org/10.1126/science.aao3787

Pingree, R., Mardell, G., Maddock, L. 1983. A marginal front in Lyme Bay. Journal of the Marine Biological Association of the United Kingdom, 63, 9-15. doi:10.1017/S0025315400049754

Pollnac, R., Christie, P., Cinner, J.E., Dalton, T., Daw, T.M., Forrester, G.E., Graham, N.A.J., McClanahan, T.R., 2010. Marine reserves as linked social–ecological systems. Proc. Natl. Acad. Sci. 107, 18262–18265. https://doi.org/10.1073/pnas.0908266107

Pondella, D.J., Allen, L.G., 2008. The decline and recovery of four predatory fishes from the Southern California Bight. Mar. Biol. 154, 307–313. https://doi.org/10.1007/s00227-008-0924-0

Port, J.A., O’Donnell, J.L., Romero-Maraccini, O.C., Leary, P.R., Litvin, S.Y., Nickols, K.J., Yamahara, K.M., Kelly, R.P., 2016. Assessing vertebrate biodiversity in a kelp forest ecosystem using environmental DNA. Mol. Ecol. 25, 527–541. https://doi.org/10.1111/mec.13481

Poulakis, G., Grubbs, R., 2019. Biology and ecology of sawfishes: global status of research and future outlook. Endanger. Species Res. 39, 77–90. https://doi.org/10.3354/esr00955

Queiroz, N., Humphries, N.E., Noble, L.R., Santos, A.M., Sims, D.W., 2012. Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. PLoS ONE 7. https://doi.org/10.1371/journal.pone.0032374

Queiroz, N., Humphries, N.E., Noble, L.R., Santos, A.M., Sims, D.W., 2010. Short-term movements and diving behaviour of satellite-tracked blue sharks Prionace glauca in the northeastern Atlantic Ocean. Mar. Ecol. Prog. Ser. 406, 265–279. https://doi.org/10.3354/meps08500

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rees, S.E., Ashley, M., Evans, L., Mangi, S., Rodwell, L., Attrill, M., Langmead, O., Sheehan, E., Rees, A.E., 2016. An evaluation framework to determine the impact of the Lyme Bay Fisheries and Conservation Reserve and the activities of the Lyme Bay Consultative Committee on ecosystem services and human wellbeing. 1–146.

Rees, S.E., Mangi, S.C., Hattam, C., Gall, S.C., Rodwell, L.D., Peckett, F.J., Attrill, M.J., 2015. The socio-economic effects of a Marine Protected Area on the ecosystem service of leisure and recreation. Mar. Policy 62, 144–152. https://doi.org/10.1016/j.marpol.2015.09.011

Rees, S.E., Sheehan, E.V., Stewart, B.D., Clark, R., Appleby, T., Attrill, M.J., Jones, P.J.S., Johnson, D., Bradshaw, N., Pittman, S., Oates, J., Solandt, J.L., 2020. Emerging themes to support ambitious UK marine biodiversity conservation. Mar. Policy 117. https://doi.org/10.1016/j.marpol.2020.103864

Rees, S. E., Ashley, M., Evans, L., Mangi, S., Sheehan, E. V., Mullier, T., Rees, A., Attrill, M. J. 2021. An evaluation of the social and economic impact of a Marine Protected Area on commercial fisheries. Fisheries Research, 235. https://doi.org/10.1016/j.fishres.2020.105819

Revill, A.S., Dulvy, N.K., Holst, R., 2005. The survival of discarded lesser-spotted dogfish (Scyliorhinus canicula) in the Western English Channel beam trawl fishery. Fish. Res. 71, 121–124. https://doi.org/10.1016/j.fishres.2004.07.006

Rigby, C., Barreto, R., Fernando, D., Francis, M., 2019. Prionace glauca. The IUCN Red List of Threatened Species2019. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39381A2915850.en

Rigby et al., 2019. Isurus oxyrinchus. The IUCN Red List of Threatened Species2019. https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39341A2903170.en

Roberts, C.M., 2000. Selecting marine reserve locations: optimality versus opportunism. Bull. Mar. Sci. 66, 12.

Rodríguez-Cabello, C., Sánchez, F., Serrano, A., Olaso, I., 2008. Effects of closed trawl fishery areas on some elasmobranch species in the Cantabrian Sea. J. Mar. Syst. 72, 418–428. https://doi.org/10.1016/j.jmarsys.2007.09.010

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y.M., Krueck, N.C., Aurellado, E., Priest, M., Birrell, C., Mumby, P.J., 2016. The Ecological Role of Sharks on Coral Reefs. Trends Ecol. Evol. 31, 395–407. https://doi.org/10.1016/j.tree.2016.02.014

Rogers, S.I., Ellis, J.R., 2000. Changes in the demersal fish assemblages of British coastal waters during the 20th century. ICES J. Mar. Sci. 57, 866–881. https://doi.org/10.1006/jmsc.2000.0574

Rogers, S.I., Maxwell, D., Rijnsdorp, A.D., Damm, U., Vanhee, W., 1999. Fishing effects in northeast Atlantic shelf seas: Patterns in fishing effort, diversity and community structure. IV. Can comparisons of species diversity be used to assess human impacts on demersal fish faunas? Fish. Res. 40, 135–152. https://doi.org/10.1016/S0165-7836(98)00209-4

Rouphael Tony, A.B., 2020. Adaptive management in context of MPAs: Challenges and opportunities for implementation. J. Nat. Conserv. 56, 125864. https://doi.org/10.1016/j.jnc.2020.125864

Rudd, J.L., Bartolomeu, T., Dolton, H.R., Exeter, O.M., Kerry, C., Hawkes, L.A., Henderson, S.M., Shirley, M., Witt, M.J., 2021. Basking shark sub-surface behaviour revealed by animal-towed cameras. PLOS ONE 16, e0253388. https://doi.org/10.1371/journal.pone.0253388

Rudd, M.A., 2015. Pathways from marine protected area design and management to ecological success. PeerJ 3, e1424. https://doi.org/10.7717/peerj.1424

Ruppert, J.L.W., Travers, M.J., Smith, L.L., Fortin, M.J., Meekan, M.G., 2013. Caught in the Middle: Combined Impacts of Shark Removal and Coral Loss on the Fish Communities of Coral Reefs. PLoS ONE 8, 1–9. https://doi.org/10.1371/journal.pone.0074648

Ryan, L.A., Andrzejaczek, S., Gleiss, A.C., Meekan, M.G., Chapple, T.K., Hart, N.S., 2022. Prey interactions in tiger sharks: Accounting for visual perception in animal-borne cameras. J. Exp. Mar. Biol. Ecol. 553, 151764. https://doi.org/10.1016/j.jembe.2022.151764

Santana-Garcon, J., Newman, S.J., Harvey, E.S., 2014a. Development and validation of a mid-water baited stereo-video technique for investigating pelagic fish assemblages. J. Exp. Mar. Biol. Ecol. 452, 82–90. https://doi.org/10.1016/j.jembe.2013.12.009

Santana-Garcon, J., Newman, S.J., Langlois, T.J., Harvey, E.S., 2014b. Effects of a spatial closure on highly mobile fish species: An assessment using pelagic stereo-BRUVs. J. Exp. Mar. Biol. Ecol. 460, 153–161. https://doi.org/10.1016/j.jembe.2014.07.003

Saunders, R.A., Royer, F., Clarke, M.W., 2011. Winter migration and diving behaviour of porbeagle shark, Lamna nasus, in the Northeast Atlantic. ICES J. Mar. Sci. 68, 166–174. https://doi.org/10.1093/icesjms/fsq145

Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W., Votier, S.C., 2014. On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. J. Appl. Ecol. 51, 1575–1583. https://doi.org/10.1111/1365-2664.12330

Schlaff, A.M., Heupel, M.R., Simpfendorfer, C.A., 2014. Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev. Fish Biol. Fish. 24, 1089–1103. https://doi.org/10.1007/s11160-014-9364-8

Sciberras, M., Jenkins, S.R., Kaiser, M.J., Hawkins, S.J., Pullin, A.S., 2013. Evaluating the biological effectiveness of fully and partially protected marine areas. Environ. Evid. 2, 4. https://doi.org/10.1186/2047-2382-2-4

Sheehan, E.V., Stevens, T.F., Gall, S.C., Cousens, S.L., Attrill, M.J., 2013. Recovery of a temperate reef assemblage in a marine protected area following the exclusion of towed demersal fishing. PLoS ONE 8. https://doi.org/10.1371/journal.pone.0083883

Shiffman, D.S., Hammerschlag, N., 2016. Shark conservation and management policy: a review and primer for non-specialists. Anim. Conserv. 19, 401–412. https://doi.org/10.1111/acv.12265

Shipp, R.L., 2003. A perspective on Marine Reserves as a Fishery Management Tool. Fish. Manag. 28, 10–21.

Simpfendorfer, C.A., Dulvy, N.K., 2017. Bright spots of sustainable shark fishing. Curr. Biol. 27, R97–R98. https://doi.org/10.1016/j.cub.2016.12.017

Simpfendorfer, C.A., Kyne, P.M., Noble, T.H., Goldsbury, J., Basiita, R.K., Lindsay, R., Shields, A., Perry, C., Jerry, D.R., 2016. Environmental DNA detects Critically Endangered largetooth sawfish in the wild. Endanger. Species Res. 30, 109–116. https://doi.org/10.3354/esr00731

Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P. J., Sims, D. W., Genner, M. J., 2011. Continental shelf-wide response of a fish assemblage to rapid warming of the sea. Current Biology, 21(18), 1565–1570. https://doi.org/10.1016/j.cub.2011.08.016

Simpson, S.J., Humphries, N.E., Sims, D.W., 2020. The spatial ecology of Rajidae from mark-recapture tagging and its implications for assessing fishery interactions and efficacy of Marine Protected Areas. Fish. Res. 228, 105569. https://doi.org/10.1016/j.fishres.2020.105569

Sims, D.W., Berrow, S.D., O'Sullivan, K.M., Pfeiffer, N.J., Collins, R., Smith, K.L., Pfeiffer, B.M., Connery, P., Wasik, S., Flounders, L., Queiroz, N., Humphries, N.E., Womersley, F.C., Southall, E.J., 2022. Circles in the sea: annual courtship "torus" behaviour of basking sharks Cetorhinus maximus identified in the eastern North Atlantic Ocean. J. Fish Biol. 1160–1181. https://doi.org/10.1111/jfb.15187

Sims, D.W., Witt, M.J., Richardson, A.J., Southall, E.J., Metcalfe, J.D., 2006. Encounter success of free-ranging marine predator movements across a dynamic prey landscape. Proc. Biol. Sci. 273, 1195–1201. https://doi.org/10.1098/rspb.2005.3444

Small, J. 2021a. Undulate Ray (*Raja undulata)* Species Profile. Southern IFCA, Version 1.2., 12/03/2021, 1–8.

Small, J. 2021b. Blonde Ray (*Raja brachyura)* Species Profile. Southern IFCA, Version 1.2., 12/03/2021, 1–9.

Small, J. 2021c. Thornback Ray (*Raja clavata)* Species Profile. Southern IFCA, Version 1.2., 12/03/2021, 1–9.

Smith, C., Uzal, A., Warren, M., 2020. Statistics in R for Biodiversity Conservation. Independently published.

South, A., 2011. rworldmap: A New R package for Mapping Global Data. The R Journal Vol. 3/1 : 35-43.

South, A., 2022. rnaturalearthhires: High Resolution World Vector Map Data from Natural Earth used in rnaturalearth. https://docs.ropensci.org/rnaturalearthhires, https://github.com/ropensci/rnaturalearthhires.

Speed, C.W., Cappo, M., Meekan, M.G., 2018. Evidence for rapid recovery of shark populations within a coral reef marine protected area. Biol. Conserv. 220, 308–319. https://doi.org/10.1016/j.biocon.2018.01.010

Stat, M., John, J., DiBattista, J.D., Newman, S.J., Bunce, M., Harvey, E.S., 2018. Combined use of eDNA metabarcoding and video surveillance for the assessment of fish biodiversity. Conserv. Biol. 33, 196–205. https://doi.org/10.1111/cobi.13183

Stehfest, K., Patterson, T., Barnett, A., Semmens, J., 2014. Intraspecific differences in movement, dive behavior and vertical habitat preferences of a key marine apex predator. Mar. Ecol. Prog. Ser. 495, 249–262. https://doi.org/10.3354/meps10563

Stein, R.W., Mull, C.G., Kuhn, T.S., Aschliman, N.C., Davidson, L.N.K., Joy, J.B., Smith, G.J., Dulvy, N.K., Mooers, A.O., 2018. Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. Nat. Ecol. Evol. 2, 288–298. https://doi.org/10.1038/s41559-017-0448-4

Steinberg, D.K., Landry, M.R., 2017. Zooplankton and the Ocean Carbon Cycle. Annu. Rev. Mar. Sci. 9, 413–444. https://doi.org/10.1146/annurev-marine-010814-015924

Stevens, J.D. 1976. First results of shark tagging in the north- east Atlantic, 1972-1975. J Mar Biol Assoc UK. 56, 929–937.

Stevens, J.D. 1990. Further results from a tagging study of pelagic sharks in the north-east Atlantic. J Mar Biol Assoc UK. 70, 707–720.

Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P.A., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J. Mar. Sci. 57, 476–494. https://doi.org/10.1006/jmsc.2000.0724

Stevens, T.F., Sheehan, E.V., Gall, S.C., Fowell, S.C., Attrill, M.J., 2014. Monitoring benthic biodiversity restoration in Lyme Bay marine protected area: Design, sampling and analysis. Mar. Policy 45, 310–317. https://doi.org/10.1016/j.marpol.2013.09.006

Stobart, B., García-Charton, J.A., Espejo, C., Rochel, E., Goñi, R., Reñones, O., Herrero, A., Crec'hriou, R., Polti, S., Marcos, C., Planes, S., Pérez-Ruzafa, A., 2007. A baited underwater video technique to assess shallow-water Mediterranean fish assemblages: Methodological evaluation. J. Exp. Mar. Biol. Ecol. 345, 158–174. https://doi.org/10.1016/j.jembe.2007.02.009

Stobutzki, I., Miller, M.J., Heales, D.S., Brewer, D.T., 2000. Sustainability of elasmobranchs caught as bycatch in a prawn (shrimp) trawl fishery. Fish. Bull. 100, 800–821.

Stoeckle, M.Y., Soboleva, L., Charlop-Powers, Z., 2017. Aquatic environmental DNA detects seasonal fish abundance and habitat preference in an urban estuary. PLoS ONE 12, 1–15. https://doi.org/10.1371/journal.pone.0175186

Sward, D., Monk, J., Barrett, N., 2019. A Systematic Review of Remotely Operated Vehicle Surveys for Visually Assessing Fish Assemblages. Front. Mar. Sci. 6.

Talwar, B.S., Stein, J.A., Connett, S.M.H., Liss, S.A., Brooks, E.J., 2020. Results of a fishery-independent longline survey targeting coastal sharks in the eastern Bahamas between 1979 and 2013. Fish. Res. 230, 105683. https://doi.org/10.1016/j.fishres.2020.105683

Tang, Y., Wu, Y., Liu, K., Li, J., Li, H., Wang, Q., Yu, J., Xu, P., 2019. Investigating the distribution of the Yangtze finless porpoise in the Yangtze River using environmental DNA. Plos One 14, 1–9. https://doi.org/10.1371/journal.pone.0221120

Taylor, B.L., Martinez, M., Gerrodette, T., Barlow, J., Hrovat, Y.N., 2007. Lessons from monitoring trends in abundance of marine mammals. Mar. Mammal Sci. 23, 157–175. https://doi.org/10.1111/j.1748-7692.2006.00092.x

Torres, L.G., Heithaus, M.R., Delius, B., 2006. Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA. Hydrobiologia. 569, 449–455.

Thomsen, P.F., Møller, P.R., Sigsgaard, E.E., Knudsen, S.W., Jørgensen, O.A., Willerslev, E., 2016. Environmental DNA from seawater samples correlate with trawl catches of subarctic, deepwater fishes. PLoS ONE 11, 1–22. https://doi.org/10.1371/journal.pone.0165252

Thorburn, J., Neat, F., Bailey, D.M., Noble, L.R., Jones, C.S., 2015. Winter residency and site association in the Critically Endangered North East Atlantic spurdog Squalus acanthias. Mar. Ecol. Prog. Ser. 526, 113–124. https://doi.org/10.3354/meps11210

Thorburn, J., Neat, F., Burrett, I., Henry, L.A., Bailey, D.M., Jones, C.S., Noble, L.R., 2019. Ontogenetic variation in movements and depth use, and evidence of partial migration in a benthopelagic elasmobranch. Front. Ecol. Evol. 7, 1–14. https://doi.org/10.3389/fevo.2019.00353

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V., Worm, B., 2010. Global patterns and predictors of marine biodiversity across taxa. Nature 466, 1098–1101. https://doi.org/10.1038/nature09329

Tolotti, M.T., Filmalter, J.D., Bach, P., Travassos, P., Seret, B., Dagorn, L., 2015. Banning is not enough: The complexities of oceanic shark management by tuna regional fisheries management organizations. Glob. Ecol. Conserv. 4, 1–7. https://doi.org/10.1016/j.gecco.2015.05.003

Unsworth, R.K.F., Peters, J.R., McCloskey, R.M., Hinder, S.L., 2014. Optimising stereo baited underwater video for sampling fish and invertebrates in temperate coastal habitats. Estuar. Coast. Shelf Sci. 150, 281–287. https://doi.org/10.1016/j.ecss.2014.03.020

Venables, W. N., Ripley, B. D., 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Vianna, G.M.S., Meekan, M.G., Ruppert, J.L.W., Bornovski, T.H., Meeuwig, J.J., 2016. Indicators of fishing mortality on reef-shark populations in the world's first shark sanctuary: the need for surveillance and enforcement. Coral Reefs 35, 973–977. https://doi.org/10.1007/s00338-016-1437-9

Vince, M.R., 1991. Stock identity in spurdog (Squalus acanthias L.) around the British Isles. Fish. Res. 12, 341–354. https://doi.org/10.1016/0165-7836(91)90017-A

Walker, P.A., Heesen, H.J.L., 1996. Long-term changes in the North Sea ecosystem. ICES J. Mar. Sci. 53, 1085–1093. https://doi.org/10.1139/a01-005

Walker, T., 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. Mar. Freshw. Res. - MAR Freshw. RES 49. https://doi.org/10.1071/MF98017

Walls, R.H.L., Dulvy, N.K., 2021. Tracking the rising extinction risk of sharks and rays in the Northeast Atlantic Ocean and Mediterranean Sea. Sci. Rep. 11, 1–15. https://doi.org/10.1038/s41598-021-94632-4

Ward-Paige, C.A., 2017. A global overview of shark sanctuary regulations and their impact on shark fisheries. Mar. Policy 82, 87–97. https://doi.org/10.1016/j.marpol.2017.05.004

Ward-Paige, C.A., Mora, C., Lotze, H.K., Pattengill-Semmens, C., McClenachan, L., Arias-Castro, E., Myers, R.A., 2010. Large-Scale Absence of Sharks on Reefs in the Greater-Caribbean: A Footprint of Human Pressures. PLOS ONE 5, e11968. https://doi.org/10.1371/journal.pone.0011968

Wearmouth, V.J., Southall, E.J., Morritt, D., Sims, D.W., 2013. Identifying reproductive events using archival tags: egg-laying behaviour of the small spotted catshark Scyliorhinus canicula. J. Fish Biol. 82, 96–110. https://doi.org/10.1111/j.1095-8649.2012.03473.x

Weltz, K., Lyle, J.M., Ovenden, J., Morgan, J.A.T., Moreno, D.A., Semmens, J.M., 2017. Application of environmental DNA to detect an endangered marine skate species in the wild. PLoS ONE 12, 1–16. https://doi.org/10.1371/journal.pone.0178124

White, E.R., Myers, M.C., Flemming, J.M., Baum, J.K., 2015. Shifting elasmobranch community assemblage at Cocos Island-an isolated marine protected area. Conserv. Biol. 29, 1186–1197. https://doi.org/10.1111/cobi.12478

White, J., Simpfendorfer, C.A., Tobin, A.J., Heupel, M.R., 2013. Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. J. Exp. Mar. Biol. Ecol. 448, 281–288. https://doi.org/10.1016/j.jembe.2013.08.004

White, T.D., Carlisle, A.B., Kroodsma, D.A., Block, B.A., Casagrandi, R., De Leo, G.A., Gatto, M., Micheli, F., McCauley, D.J., 2017. Assessing the effectiveness of a large marine protected area for reef shark conservation. Biol. Conserv. 207, 64–71. https://doi.org/10.1016/j.biocon.2017.01.009

Whitmarsh, S.K., Fairweather, P.G., Huveneers, C., 2017. What is Big BRUVver up to? Methods and uses of baited underwater video. Rev. Fish Biol. Fish. 27, 53–73. https://doi.org/10.1007/s11160-016-9450-1

Wiegand, J., Hunter, E., Dulvy, N.K., 2011. Are spatial closures better than size limits for halting the decline of the North Sea thornback ray, Raja clavata? Mar. Freshw. Res. 62, 722–733. https://doi.org/10.1071/MF10141

Woodhouse, E., Homewood, K.M., Beauchamp, E., Clements, T., McCabe, J.T., Wilkie, D., Milner-Gulland, E.J., 2015. Guiding principles for evaluating the impacts of conservation interventions on human well-being. Philos. Trans. R. Soc. B Biol. Sci. 370, 20150103. https://doi.org/10.1098/rstb.2015.0103

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T., Gruber, S.H., 2013. Global catches, exploitation rates, and rebuilding options for sharks. Mar. Policy 40, 194–204. https://doi.org/10.1016/j.marpol.2012.12.034

Wraith, J., Lynch, T., Minchinton, T.E., Broad, A., Davis, A.R., 2013. Bait type affects fish assemblages and feeding guilds observed at baited remote underwater video stations. Mar. Ecol. Prog. Ser. 477, 189–199. https://doi.org/10.3354/meps10137

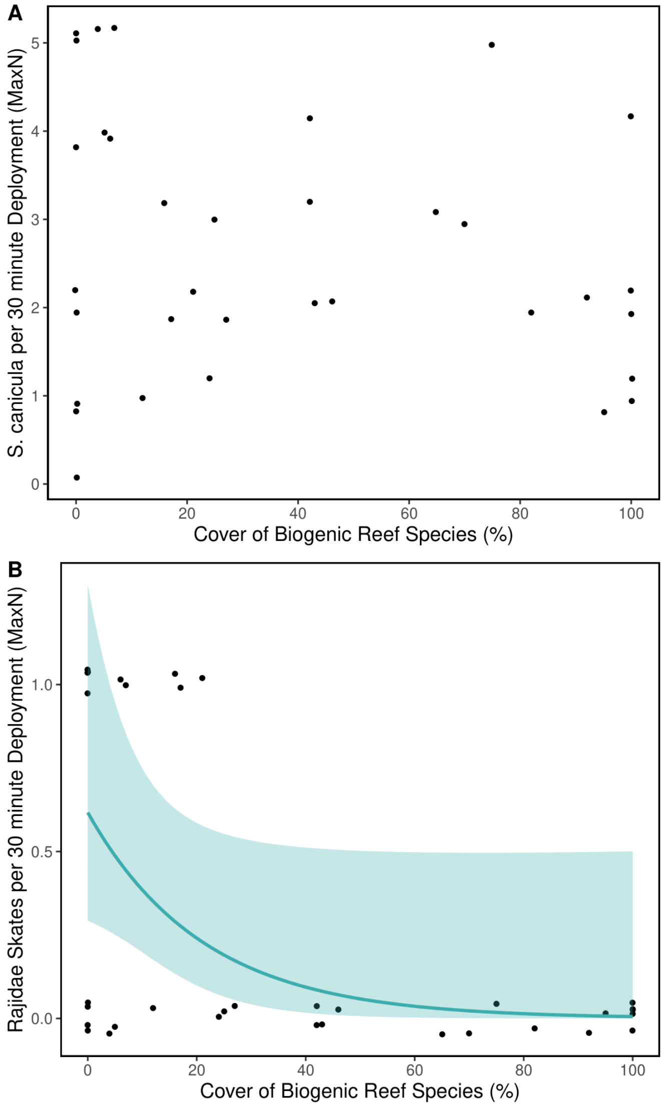
Yamamoto, S., Masuda, R., Sato, Y., Sado, T., Araki, H., Kondoh, M., Minamoto, T., Miya, M., 2017. Environmental DNA metabarcoding reveals local fish communities in a species-rich coastal sea. Sci. Rep. 7, 1–12. https://doi.org/10.1038/srep40368

Youngbluth, M., Sørnes, T., Hosia, A., Stemmann, L., 2008. Vertical distribution and relative abundance of gelatinous zooplankton, in situ observations near the Mid-Atlantic Ridge. Deep-Sea Res. Part II Top. Stud. Oceanogr. 55, 119–125. https://doi.org/10.1016/j.dsr2.2007.10.002

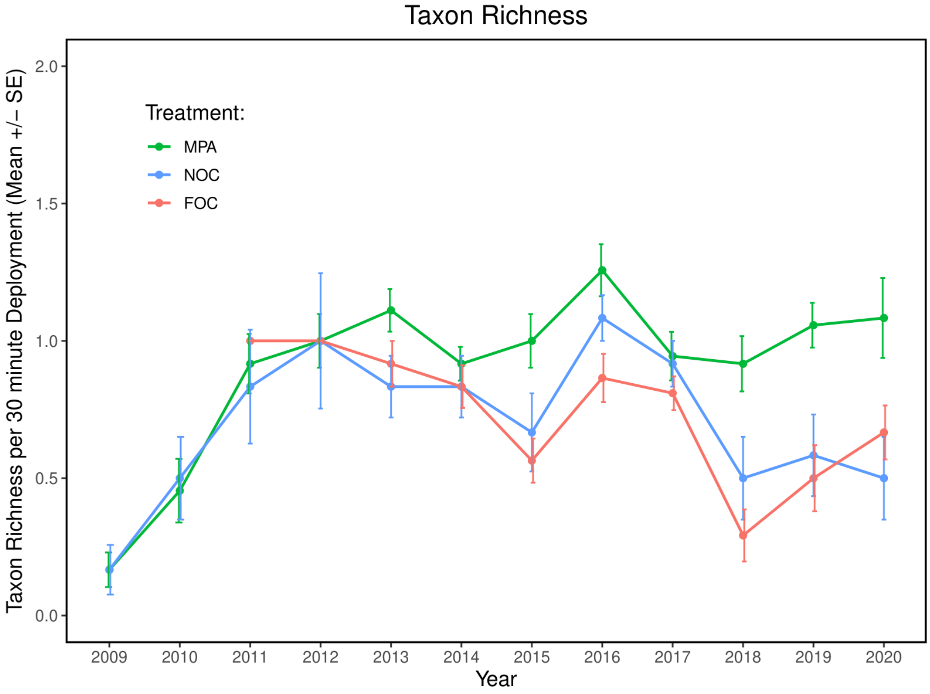
Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Appendices

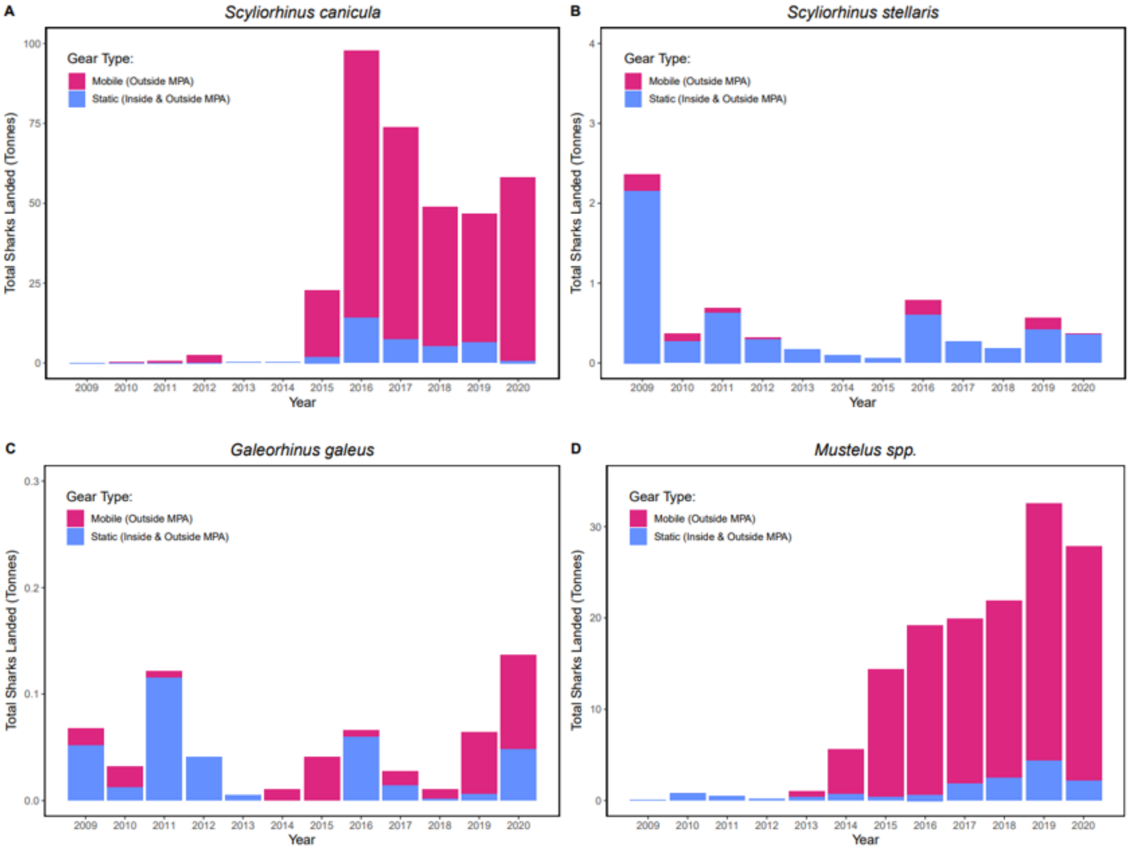
Appendix 1: The relationship between biogenic reef species percentage cover and A) *S.canicula* abundance and b) Rajidae skate abundance in 2016.



Appendix 2: Mean elasmobranch taxon richness documented by BRUVs in Lyme Bay across the experimental treatments: MPA (2009 – 2020), NOC, (2009- 2020) and FOC (2009 – 2020).



Appendix 3: Publicly available species-specific shark landings data (https://www.gov.uk/government/organisations/marine-management-organisation, accessed: 15/02/2022) representing a proxy for the total weight (T) of landed sharks in the wider Lyme Bay region (ICES rectangles: 30E6 & 30E7). Landings are apportioned to those landed by mobile (prohibited inside the MPA) and static gears and represent the sum of all reported landings per year.



Appendix 4: All elasmobranch species reported in publicly available fishery landings data (https://www.gov.uk/government/organisations/marine-management-organisation, accessed: 15/02/2022), in the wider Lyme Bay region (ICES rectangles: 30E6 & 30E7) from 2009 – 2020.

Name in Landings	**Latin Name**
Arctic Skate	*Amblyraja hyperborea*
Basking Shark	*Cetorhinus maximus*
Black Dogfish	*Centroscyllium fabricii*
Blonde Ray	*Raja brachyura*
Blue Shark	*Prionace glauca*
Common Skate	*Dipturus batis*
Cuckoo Ray	*Leucoraja naevus*
Small-spotted catshark	*Scyliorhinus canicula*
Mako Shark	*Isurus sp.*
Nursehound	*Scyliorhinus stellaris*
Sandy Ray	*Leucoraja circularis*
Shagreen Ray	*Leucoraja fullonica*
Small-eyed Ray	*Raja microocellata*
Smoothound	*Mustelus spp.*
Spotted Ray	*Raja montagui*
Spurdog	*Squalus acanthias*
Thornback Ray	*Raja clavata*
Thresher Shark	*Alopias vulpinus*
Tope	*Galeorhinus galeus*
Undulate Ray	*Raja undulata*

Appendix 5: Publicly available species-specific skate landings data (https://www.gov.uk/government/organisations/marine-management-organisation, accessed: 15/02/2022) representing a proxy for the total weight (T) of landed skates in the wider Lyme Bay region (ICES rectangles: 30E6 & 30E7). Landings are apportioned to those landed by mobile (prohibited inside the MPA) and static gears and represent the sum of all reported landings per year.