**Marine Protected Areas – A review of their potential effects on lobster ecology and management**

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**Abstract**

Marine Protected Areas (MPAs) are proven to protect sessile organisms and territorial commercial fish successfully. These areas may also protect populations of commercial lobster species, many of which are nomadic and resident. Several MPAs for lobsters have been studied for potential effects on lobster ecology and management. These MPAs were established for specific lobster species or include lobsters in their protected zones, including commercial clawed, spiny, and slipper lobsters. Studies have shown the positive effects on lobsters within MPAs, such as increased abundance, density, biomass, catch-per-unit-effort (CPUE), and size. These outcomes may benefit lobster fisheries because the MPAs can supply propagules, juveniles, and adults via the “spillover” process to unprotected areas. Some MPAs have even demonstrated that reduced fishing areas from MPA designation significantly increase total catch after several years of protection. Such MPAs can also benefit other industries, such as marine tourism and commercial fisheries of different species. Some reserves fail to show positive effects, perhaps due to factors such as MPAs that are small relative to the home ranges of lobster species, location, size, shape, protection of lobster predators, ineffective policing of illegal fisheries, and “edge effects”. Factors for successful MPAs include being a “no-take” zone, adequate enforcement, size, shape, and age of the reserves. Additional factors are proper MPA location for larval recruitment, suitable habitats, absence of anthropogenic disturbance, and full participation of the affected community, including the fisheries industry. Controlled before-and-after studies that explore the biological and fishery impacts of MPAs on surrounding fisheries are scarce but needed to assess the value of MPAs in fishery management. In view of dwindling lobster populations and possible conflicts between conservation scientists and fishermen, long-range studies of lobster populations inside and outside of MPAs and engaging all stakeholders are imperative.

**Keywords:** Conservation, Fishery, No-take zone, Spillover, Spill-in, Edge effect

*Abbreviations*: CIMR, Columbretes Islands Marine Reserve; CL, Carapace length; CMR, Capture-mark-recapture; CPUE, Catch-per-unit-effort; CPUA, Catch per unit area; FAO, Food and Agriculture Organization of the United Nations; GAM, generalized additive model; ITQ, Individual transferable quotas; IUCN, International union for conservation of nature; MEY, Maximum economic yield; MPA, Marine protected area; ROV, remotely operated underwater vehicle; TL, Total length.

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1. **Introduction**

A nature reserve, also known as a wildlife refuge, wildlife sanctuary, biosphere reserve or bioreserve, natural or nature preserve, or nature conservation area park is a [protected area](https://en.wikipedia.org/wiki/Protected_area" \o "Protected area) of importance for [flora](https://en.wikipedia.org/wiki/Flora" \o "Flora), [fauna](https://en.wikipedia.org/wiki/Fauna" \o "Fauna), [geological](https://en.wikipedia.org/wiki/Geological" \o "Geological) features, or other special interest. These areas are reserved and managed for [conservation](https://en.wikipedia.org/wiki/Conservation_(ethic)" \o "Conservation (ethic)) and special opportunities for study or [research](https://en.wikipedia.org/wiki/Research" \o "Research) (Lausche, 2011). Nature reserves may be designated by [government](https://en.wikipedia.org/wiki/Government" \o "Government) institutions in some countries or by private landowners, such as charities and research [institutions](https://en.wikipedia.org/wiki/Institution" \o "Institution). Reserves fall into different International Union for Conservation of Nature ([IUCN) categories](https://en.wikipedia.org/wiki/IUCN_protected_area_categories" \o "IUCN protected area categories) depending on the level of protection afforded by local laws. Normally, nature reserves are more strictly protected than [nature parks](https://en.wikipedia.org/wiki/Nature_park" \o "Nature park). Various jurisdictions may use other terminology, such as ecological or private protected areas, in legislation and official titles of the reserves (Lausche, 2011).

Early reservations were often based on religious background, such as the "evil forest" areas of West Africa that were forbidden to humans, who were threatened with spiritual attack upon entry (Njoku et al., 2017). Cultural practices resembling the establishment and maintenance of modern animal reserves date back to antiquity. Sacred areas that are taboo to human entry for hunting and fishing are known in numerous ancient cultures. According to the Sri Lanka Wildlife Conservation Society, King [Tissa](https://en.wikipedia.org/wiki/Devanampiya_Tissa_of_Anuradhapura" \o "Devanampiya Tissa of Anuradhapura) of [Ceylon](https://en.wikipedia.org/wiki/Ceylon" \o "Ceylon) established one of the world's earliest [wildlife sanctuaries](https://en.wikipedia.org/wiki/Wildlife_sanctuary" \o "Wildlife sanctuary) in the 3rd century BC. Modern terrestrial reserves originated in medieval times when landowners established game preserves to protect the animals they hunted. The awareness of protecting animals solely to prevent their death arose in the 19th century when the naturalist and explorer Charles Waterton established the world's first modern nature reserve in 1821. He constructed a high wall around his UK estate to protect his park from [poachers](https://en.wikipedia.org/wiki/Poacher" \o "Poacher) and encouraged bird life by planting trees and hollowing out trunks for owl nesting (Humphreys and Clark, 2020).

The establishment of [marine](https://www.sciencedirect.com/topics/earth-and-planetary-sciences/marine-protected-area" \o "Learn more about marine protected area from ScienceDirect's AI-generated Topic Pages) protected areas (MPAs) lagged that of terrestrial reserves probably due to the relatively hostile marine environment, its three-dimensional nature, the vast area of oceans, and the complex life cycles of many marine organisms. The need to manage and protect marine environments and resources became apparent during the 1950s and early 1960s (Kelleher and Kenchington, 1992). The first MPAs were declared early in the 20th century, and 430 MPAs were created by 1985, but most covered relatively small coastal areas ([Silva et al., 1986)](javascript:%20MM_openBrWindow('../bibliography.htm" \l "bib08','biblio','scrollbars=yes,width=568,height=550')). Although forms of MPAs have existed for most of the 20th century, the beginning of a modern global movement was the first World Congress on National Parks in 1962. A global MPA area target of 10% was established after the 1992 Rio Earth Summit. Failure to achieve the target by the 2010 deadline was followed by its replacement with Aichi Target 11, requiring 10% coverage by 2020 (Humphreys and Clark, 2020). Proposals to increase the area target to 30% by 2030, known as Protect 30 X 30 (Lawton, 2022), are also questionable due to a conflict of interests among marine stakeholders, including the fisheries section. In 2023, close to 17,000 zones meet the IUCN definition of fully or highly protected MPAs (Gonçalves, 2023), according to the Marine Conservation Institute, the Marine Protection Atlas <http://mpatlas.org>). This source also reports that as of 21 April 2023, only 2.9% of the ocean is fully or highly protected from fishing impacts.

MPAs are powerful conservation and management tools that often include zones varying in the levels of fishing restrictions, including fully protected no-take zones, partially protected limited fishing zones, and less protected open fishing zones (Hall et al., 2023). MPAs are also effective tools for restoring ocean biodiversity and ecosystem services (Sala and Giakoumi, 2018; Sala et al., 2021; Worm et al., 2006). Positive effects of MPAs include increased abundance, biodiversity, density, biomass, and target species size. Larger males and females of a given species often correlate with higher reproductive potential.

MPAs are considered successful for sessile organisms such as kelp (Peleg et al., 2023), seaweed, sponges (Padiglia et al., 2015), and corals (Edgar et al., 2014). They are also effective for territorial fish, like groupers (Anderson et al.,2014; Desiderà et al., 2022; Nemeth et al., 2023). Frid et al. (2022) found clear benefits of fully protected MPAs on Israel's Mediterranean coast, as evident by greater numbers of large groupers within protected areas. The group also showed a clear increase in grouper number over time, within and outside MPAs. The Rosh-Hanikra-Achziv is the largest (10 km2) and oldest (>30 years of enforcement) marine reserve. Frid et al. (2022) also found greater total and commercial fish biomass within the MPA compared to a controlled fished area. The MPA contained groupers larger than first maturity, mega-spawners with higher reproductive potential, and most mature individuals. There were positive effects of no-take MPAs on exploited fish and invertebrate populations within their boundaries in the last decade (Edgar et al., 2014; Costello and Ballantine, 2015; Giakoumi et al., 2017; Sala and Giakoumi, 2018). These studies also clearly demonstrate advantageous ecological functions and resource preservation of no-take reserves compared to partially protected areas. Factors responsible for the success of an MPA include a no-take policy, enforcement effort, reserve size, reserve age, and detachment from anthropogenic disturbance (Edgar et al., 2014). The enforcement effort is a key factor in the efficacy of MPAs, even for small reserves of up to 30 km2 (Giakoumi et al. 2017). However, Costello and Ballantine (2015) indicate that 94% of world MPAs allow fishing, and most MPAs are focused on fishery management, not conservation. Also, less than 1% of the ocean is in no-take MPAs, while less than 25% of coastal countries have no-take MPAs.

There are three main families of lobsters: Nephropidae (clawed lobsters), Palinuridae (spiny lobsters), and Scyllaridae (slipper lobsters). Several species are highly prized as seafood. According to the Food and Agriculture Organization of the United Nations (FAO) and the Fisheries and Resources Monitoring System, these species are economically important as they are among the most profitable commodities in the coastal areas they populate. In fact, lobsters are important resources throughout the world’s oceans, offering food security, employment, and trade (Spanier et al., 2015). However, in recent years, specific populations of commercial lobster species have shown disturbing signs of yield reduction from overfishing. Several heavily fished lobster stocks have declined, including the clawed lobster *Homarus gammarus* (Pettersen et al., 2009; Kleiven et al., 2012; Sørdalen et al., 2022), the spiny lobsters *Palinurus elephas* (Pollock,1993; Yeap et al., 2022; FAO, 2021), *Panulirus homarus* (Ajdari and Mirzaei, 2022), *P. argus* (Butler et al., 2011; FAO, 2019), *P. marginatus* (Schultz et al., 2011), and the slipper lobsters (Spanier and Lavalli*,* 2007; 2013a) *Thenus orientalis* (Radhakrishnan et al., 2007), *Scyllarides squammosus* (Schultz et al., 2011), and *S. latus* (Spanier and Lavalli, 1998; Miller et al., 2023).

Some MPAs are designed for populations of commercial lobster species, many of which are nomadic and resident, whereas others include lobsters within their protected zones. A major challenge is whether MPAs can effectively recover overfished populations while still managing the lobster fishery. We will discuss this challenge and potential solutions in this article, based on peer-reviewed literature dealing with MPAs, lobsters, and related management tools published in scientific sources within the last 40 years.

1. **Early Conservation Efforts**

Early efforts to protect lobsters primarily involved regulating fishing seasons and limiting lobster size, traps, and harvesting quotas to ensure sustainable fishing practices. However, the regulations were not always effective or obeyed (Nunes et al., 2023; Alzugaray et al., 2018; Saputra, 2020) due to the vast marine inspection areas compared to the relatively small numbers of inspectors/rangers.

Canada began regulating American clawed lobster fisheries on its Atlantic coast in the 1870s. A closed season was introduced in the Bay of Fundy in 1887 to protect lobsters during their spawning period (Cook, 2005). Acheson (1987) pointed to local rules limiting trap numbers that might fish for *H. americanus* or the length of the fishing season in Maine. The US lobster industry, especially in Maine, has more than 120 years of historically effective regulations in which the fishing industry played a key role. These regulations have included a minimum size law, an oversized measure, a V-notch program, and the trap escape vent (Herrick, 1898; Acheson et al., 2000).

Norwegian lobster fisheries of *H. Gammarus* are regulated by closed season, minimum legal total length (TL) of greater than 250 mm, and since 2008, a ban on harvesting egg-bearing females (Sørdalen et al., 2018). Management of the species in several European countries also includes a minimum landing size and protection of ovigerous females. For the smaller *Nephrops norvegicus,* some European countries imposed minimum mesh size regulations reinforced by minimum landing size (Bennett et al., 1980).

Atherley et al. (2021 and references therein) summarize fishery regulations in all areas where *P. argus* was harvested. The regulations include minimum landing sizes and closed seasons, which typically coincide with reproductive maturity and reproductive periods. Other management options include restrictions on capturing or holding molting soft-bodied lobsters or those carrying eggs. Several countries prohibit landing females with intact spermatophores. Certain states also prohibit the landing of ovigerous females and lobsters with less than 95 mm carapace length (CL) but do not enforce a closed season. Some Caribbean countries employ other management tools for *P. argus,* including no-take MPAs. Cochrane and Chakalall (2001) suggested, back in 2001, that the minimum sizes and closed seasons for this species were frequently insufficient and that both spawner biomass and potential yield would benefit from increases in the minimum size. Exploitation rates in the South African *Jasus lalandii* fishery were controlled using commercial quotas and catch limits in individual fishing grounds (Pollock, 1986). Similar harvest controls (season, size, no egg-bearing females, efforts, quotas) were implemented for other spiny lobster species in different areas but were not always sufficient due to increasing market demand and related growing fishing pressure (Fonteles-Filho, 2000; Punt and Kennedy, 1997; Fielder, 1964; Caputi et al., 2015; Cockcroft and Payne, 1999; Breen and Kendrick, 1997; Bowen, 1980, Díaz et al., 2011; Kizhakudan and Radhakrishnan, 2019; Nonaka et al., 2000).

Most slipper lobster fisheries were and are characterized by insufficient regulations or absent or inadequate enforcement of existing regulations. In response to spiny lobster overfishing, fishermen in countries including Australia, India, the Galápagos Islands, and the US state of Hawaii quickly shifted to slipper lobsters, which further threatened slipper lobsters (Spanier and Lavalli, 2007). Regulations to protect slipper lobster populations may produce unexpected negative effects. The prohibition against landing ovigerous females of *Scyllarus arctus* in Northeast Spain has biased the fishery toward males. This bias ultimately affects natural sex ratios, mating opportunities for females, and population structure (Alborés et al., 2019).

Nonetheless, a few places have established proper regulations and effective enforcement. Some regulations are implemented in response to population changes or mortality associated with fisheries activities. Occasionally, such regulations are too little, too late for the dwindling populations to recover sufficiently, as witnessed for *S. latus* in the Azores (Spanier and Lavalli, 2007) and Italy (Bianchini et al., 2001; Bianchini and Ragonese, 2007; Butler et al., 2013) and for *T. orientalis* in India (Radhakrishnan et al., 2007).

Catch quotas were adopted to manage slipper lobsters in the Northwestern Hawaiian Islands (NWHI) in 1992 (DiNardo and Moffitt, 2007). In the Galápagos Marine Reserve, a preliminary, but not yet enforced, zonation scheme for *S. astori* prohibits extraction in 18% of the coastal waters (Hearn et al., 2007). Yet weaknesses in governance, inefficient planning, and poor monitoring of existing management measures have caused fishery unsustainability in the Galápagos Islands, leading to little protection of critical species and a failure to ensure the socioeconomic well-being of the population (Riofrío-Lazo et al., 2023). In Australia, regulations ban the retention of egg-bearing females of all *Ibacus* species, and a minimum legal size carapace width is established for respective species in different regions (Haddy et al., 2007). In several countries, there are specific regulations for different areas or provinces within the same nation, and regulations often are not strictly enforced, such as the fishing of *T. orientalis* in India (Radhakrishnan et al., 2007). The complete closure of an area to slipper or other lobster species fishing is usually a final tool to prevent complete population extermination (DiNardo & Moffitt, 2007). Slipper lobsters are frequently a by-catch of fisheries targeting other species, such as the combined trap-fishery for *S. elisabethae* and *P. delagoae* off the east coast of South Africa (Groeneveld et al. 1995). Thus, there is a need to consider both lobster species in any management strategy.

In the late 20th century, lobster specific MPAs emerged in response to declining lobster populations in some regions. One example is the establishment of the V-notching program in the US. An identifying mark is made by cutting a small triangular piece from one uropod. Lobsters are V-notched before being returned at sea and designated illegal for commercial sale until the V-notch is reduced to 50% of the initial size. This program serves as aform of MPAfor female lobsters, allowing them to contribute to future population growth. This widely used management procedure delays the mortality of egg-bearing females in fisheries of clawed lobsters of the genus Homarus ([Tully, 2001](javascript:;); [DeAngelis et al., 2010](javascript:;)), but the procedure has been tried in spiny lobsters (Mallol et al., 2014).

As scientific understanding of spillover effects increases (Lizaso et al., 2000 and references therein), the concept of MPAs has expanded to include the conservation and management of lobsters.

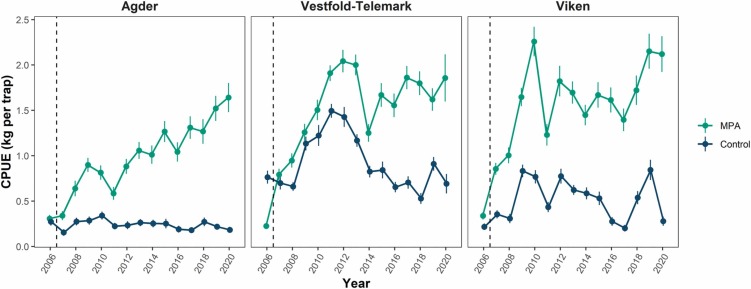
1. **Effect of MPAs on lobster populations**

Lester et al. (2009) compared 124 declared no-take MPAs in 29 countries to fished area controls outside the reserves. They revealed that the protection afforded by the MPAs led to a significant improvement in all four criteria examined: biomass, density, size of individuals, and species richness. According to these and additional, criteria, there are three main methods to estimate the success/failure of an MPA for lobsters. The first is experimental lobster fishing within the MPAs and control areas using pots/traps/nets to reveal catch-per-unit-effort (CPUE). Second, are estimations of lobster numbers, sizes, sex, and reproductive stage by diving transects for a visual census. Third is acoustic and manual T-bar tagging of individual lobsters, namely capture-mark-recapture (CMR). In addition, ROVs are useful as non-invasive tools for deep-sea MPA monitoring of lobsters (Vigo et al., 2023).

* 1. *Clawed lobsters*

Collins (2010) reported that a small Eastport MPA in Bonavista Bay, Newfoundland, promoted the sustainability of *H. americanus* through increased density, mean size, and reproductive potential. Analyzing 15 years of CMR data and egg samples from the same Canadian MPA, Howse (2021) reported increased lobster egg production but no significant trend in fecundity or size along a distance gradient from the MPA boundary. In the same region, Rowe (2001) studied tagged *H. americanus* within and outside two no-take MPAs. He found the frequency of lobster emigration from MPAs was relatively low, whereas harvesting pressure outside reserves was intense, indicating that the MPAs offered increased survival to lobsters. In the same study, lobster density, female and male sizes, and the proportion of ovigerous females were greater within one MPA at Round Island compared to an adjacent fished area. At another MPA at the Duck Islands, females and males were larger within the reserve. However, no difference in density or the proportion of ovigerous females was found in the reserve compared to an adjacent harvested area (Rowe, 2002).

Considerable research has been conducted on MPAs for European lobster *H. gammarus* in Norway. Moland et al. (2011) studied this species in a small MPA of 1 km2 on the Norwegian coast for about one year. During this period, 95% of their tagged lobsters remained within or near the reserve boundaries. They estimated the lobsters’ home range and concluded that small coastal MPAs could confer complete or partial protection by designing their boundaries to engulf or intersect patches of habitat preferred by *H. gammarus*. Similarly, limited movement out of the MPA was reported by Øresland and Ulmestrand (2013). Moland et al. (2013a) further reported a 13-year study of the non-migratory behavior of *H. gammarus* in MPAs. They found strong evidence for a long-term decrease in sex-specific natural mortality throughout and positive trends in mean body size and CPUE, indicating an increase in abundance. Moland et al. (2013b) reported that CPUE had increased by 245 % in MPAs, compared to only 87 % in the control, and the mean size increased by 13 % in MPAs with a negligible increase in control areas. Moland et al. (2021) reviewed studies in MPAs in Southeast Norway aimed at protecting *H. gammarus* by banning fixed gear and reported the effect of increasing population density, survival, body size, and catch per trap. CMR of lobster populations from three experimental MPAs in Southern Norway shows that lobsters respond rapidly by a substantial increase in CPUE after implementation (Fig. 1). After four years of protection, the MPAs displayed more than a two-fold average increase in CPUE, whereas the average change in CPUE in three control areas was modest (Knusten et al., 2022). Similar results were reported by Fernández‐Chacón et al. (2020)



**Fig. 1.** CPUE in kg per trap per day of *Homarus gammarus* lobsters in three experimental MPAs (green) and control areas (blue) in Southern Norway from 2006 to 2020 (from Knusten et al., 2022).

Annual population survival rates and abundances of *H. gammarus* were greater in the MPAs than in unprotected sites. The authors also highlighted demographic differences between sexes and [geographic areas](https://www.sciencedirect.com/topics/earth-and-planetary-sciences/geographic-areas" \o "Learn more about geographic areas from ScienceDirect's AI-generated Topic Pages).

In an eight-year CMR study of *H. gammarus* in MPAs and control areas, protection shifted the demography, with an increase in mean TL of 15% in all MPAs, as opposed to the effects of a size-selective fishery (Thorbjørnsen et al., 2018). Sørdalen et al. (2018, 2020) demonstrated that males tend to be larger in the MPA, and females mated with males larger than their own body size. The relative size difference was significantly larger in the MPA than in the control area. Sexual selection acted positively on body and claw size in males in the MPA, whereas it was nonsignificant in fished areas. Sørdalen et al. (2022) demonstrated that females molt more frequently and grew more during each molt in the MPAs. In another study, the population of Norway lobster, Nephrops norvegicus, displayed greater abundance and biomass and slightly larger body sizes within a deep water, no-take MPA than in a control area without fishing prohibition (Vigo et al., 2023).

* 1. *Spiny lobsters*

Extensive research exists on the palinurid family of spiny lobsters and MPAs. Direct field evidence of changes in lobster populations following MPA creation generally detects an increase in lobster abundance and mean size (Cole et al., 1990; MacDiarmid and Breen, 1993; Goñi et al., 2001; Follesa et al., 2008) and fishing effort and catch per unit area (CPUE) (Follesa et al., 2011).

Reviewing the effects of MPAs on spiny lobster populations, Childress (1997) concluded there was convincing proof that lobster abundance, mean size, and spawning stock biomass were usually greater within MPAs than in adjacent fished areas. The scale of the difference was a function of the MPA dimensions, sets of habitats within the MPA, and lobster movement patterns. These factors have reappeared in recent studies, which continue to generate confirmations that population abundance, size, and egg production of palinurids typically increase in no-take MPAs.

Several studies reveal that MPAs result in increased density of the rock lobster, *J. edwardsii* (Kelly et al., 2000; Shears et al., 2006; Barrett et al., 2009a; Freeman and MacDiarmid, 2009). Using linear models, Kelly et al.(2000) estimated temporal pattern changes in populations of *J. edwardsii* in MPAs of different ages in New Zealand (NZ). The lobsters showed rapid changes, with density increasing by ~4% per year in shallow areas (<10 m) and ~10% in deeper parts of the MPAs. The lobster size in MPAs also increased by an average of 1.14 mm CL per year. By coupling patterns of size and abundance, the authors estimate that lobster biomass increased by ~5% per year in shallow areas and ~11% per year in deeper parts of the MPAs. Egg production also increased with increasing biomass. Similar patterns were reported for the same species in the same region (Cole et al., 1990; MacDiarmid and Breen, 1993) and another NZ MPA (Davidson et al*.,*2002). In contrast, MacDiarmid and Breen (1993) reported that in the first five years after the creation of an MPA, the spiny lobster population increased 4.5-fold, but in the subsequent nine years, the abundance of large males declined. *J. edwardsii* males moved to deeper waters beyond the MPA boundary in the summer and were caught by commercial fishers specifically targeting the migrants. Babcock et al. (1999) studied this species in Northern NZ MPAs and found similar trends, with lobsters approximately 1.6 to 3.7 times more abundant inside the reserves than outside. Lobsters within MPAs had a mean CL of 109.9 mm, compared to 93.5 mm outside the MPAs. Freeman et al. (2009) found that *J. edwardsii* densities on a fully protected reef were 8-fold greater than densities on the less protected part of a reef. In a Tasmanian MPA, Barrett et al. (2009a) found that limited movement of J. edwardsii within the MPA resulted in a substantial increase in biomass and large mature individuals relative to adjacent fished locations. A four-fold increase in female fecundity in the MPA potentially enhanced larval export. Shears et al. (2006) compared the density of this species in a fully protected MPA, a partially protected MPA allowing recreational but not commercial fishing, and an unprotected area. Lobster densities before the establishment of the reserves were similar in both areas. Twenty-eight years later, lobster density and biomass in the no-take MPA increased 11 and 25 times, respectively. However, lobster densities within the partially protected MPA were similar to the adjacent fully fished area. A 2017 survey of a *J. edwardsii* population in a South Australia MPA, three years after implementation, estimated that the relative abundance of legal size lobsters was 4.4 times greater inside the MPA than outside (,. Since 2014, when fishing was last permitted within the same MPA, the relative abundance of lobsters increased by 75%. The mean size of legal size female and male lobsters has also increased by 4.1% and 12.5%, respectively. These recorded population responses are consistent with those for southern rock lobster stocks in MPAs in other jurisdictions. For a different species, the South African rock lobster J. lalandii, some AMPs were successful regarding greater lobster abundance and size compared to adjacent fished areas (.

In Western Australia, surveys of *P. cygnus* populations in shallow waters surrounding the Rottnest Island MPA revealed much greater density, biomass, and egg production than in fished areas (Babcock et al. 2007). The density of lobsters was approximately 34 times greater in the sanctuary, and the density above the minimum legal size was approximately 50 times greater than in other areas around the island that allowed recreational fishing. The mean CL, total biomass, and egg production of lobsters in the MPA were significantly greater than in adjacent fished areas. Large individuals (≥100 mm CL), especially large males, were found almost exclusively within the MPA. Recently, Lindstedt et al. (2022) studied the impact of recreational fishing on the wariness of *P. cygnus* by comparing fished sites and no-take reserves of Rottnest Island. The density of legal-sized lobsters in the MPAs was twice that in fished sites, and lobsters spent less time with bait in fished sites than in the MPAs (Fig. 2). This study provides evidence that lobster behavior is sensitive to noninjury-related disturbance associated with recreational fishing, with higher wariness in fished areas.

Significant research has been conducted on *P. elephas*, the European spiny lobster in the central and Western Mediterranean. In fact, this speciesis recognized as an important indicator for measuring MPA successes in the Mediterranean (Mouillot et al., 2002). In ten years of monitoring the 20-year-old 55 km2 no-take Columbretes Islands Marine Reserve (CIMR) off eastern Spain, lobster abundance declined slightly with a gradual increase in biomass (Goñi et al., 2006, 2008, 2010). The average abundance and biomass of lobsters in this MPA were eight and 14 times greater than in an adjacent fished area. The mean and maximal size of lobsters in this MPA

A comparison of a number of lobsters

Description automatically generated

**Fig. 2.** (a) The density of legal-sized lobsters per 2 m section of reef sampled during the observational surveys, and (b) the aggregate time spent at the bait per lobster within the sampled dens (from Lindstedt et al., 2022).

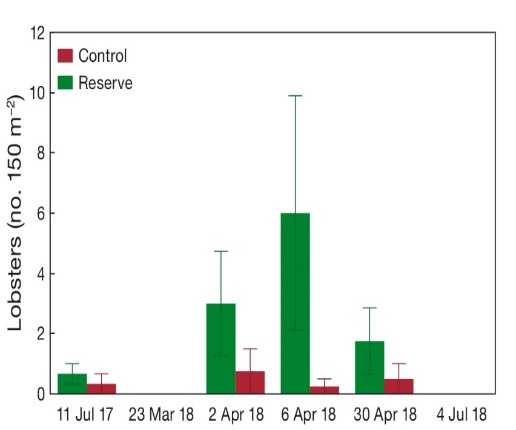
continued to increase over 20 years of protection (Groeneveld et al., 2013). In a long-term study of a small 3.4 km2 no-take MPA in Sardinia, Follesa et al. (2007, 2008, 2009, 2011, 2014) and Bevacqua et al. (2010) discovered an increased abundance of *P. elephas* over time in the reserve using the CMR method. The total mean abundance within the MPA (CPUE = 0.23 ± 0.10 kg/50 m/boat) was 7.5 times greater than that of the fished neighboring zone (CPUE = 0.03 ± 0.07 kg/50 m/boat). Lobsters also moved to adjacent fishing grounds, where they became susceptible to capture. The inter-annual analysis of lobster size inside the area indicated a progressive increase in the mean CL of adults and juveniles over eight years (Follesa et al., 2008). Several MPAs protect *P. elephas in the Atlantic*, including Ireland and Brittany (Groeneveld et al., 2013 and references therein).

MPAs were established to protect the Caribbean spiny lobster*, P. argus,* and its habitats because the species contributes the largest global portion of spiny lobsters (Phillips et al., 2013). However, *P. argus* yields have declined in the Caribbean (Ehrhardt et al., 2010). Apart from a handful of well-enforced MPAs, size-selective fishing has nearly eliminated the largest individuals (Bertelsen and Matthews, 2001). These largest lobsters disproportionately produce higher-quality offspring (MacDiarmid and Butler, 1999; Gnanalingam and Butler, 2018). Density and mean size increased significantly over time in two relatively large MPAs (30 and 500 km2) along the Florida Keys that include the entire suite of habitats used by *P. argus*. However, 12 smaller MPAs (0.34 - 5.15 km2) contained only adult habitats (Davis, 1977; Cox and Hunt, 2005). Similar increases in lobster density and sizes in MPAs were reported by Bertelsen and Cox (2000) and Bertelsen and Mathews (2001). Acosta (2002) used a simple logistic rate model and empirical data to study *P. argus* (and queen conch) from an isolated MPA in Belize. The model predicted the lobster population within the MPA would increase 2.5-fold within five years of MPA establishment. This prediction was close to the observed data. Some MPAs for the South African rock lobster, *J. lalandii,* were unsuccessfulbecause of periodic harmful algal blooms and large areas of unsuitable substrate (Mayfield et al., 2005).

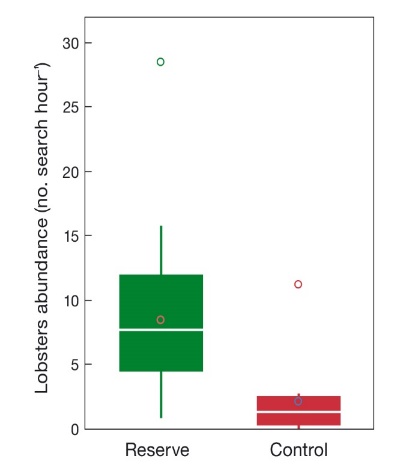
The oceanic currents regime associated with the dispersal of planktonic larvae and post-larvae supply are also important for MPA success. The geographical location and connectivity characteristics of sites selected as MPAs can alter spiny lobster larval dispersal patterns and settlement (Butler et al., 2006; Kough et al., 2013).

* 1. *Slipper lobsters*

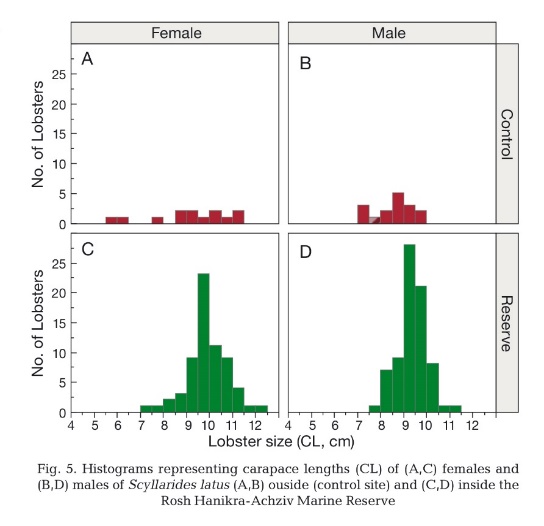
Slipper lobster fisheries are negligible compared to those of clawed and spiny lobsters, so there is less research on MPAs scyllarid species within the genus *Scyllarides*. Spanier and Lavalli (2007 and references therein) found that although attempts were made to create MPAs for slipper lobsters in Hawaii, the Galápagos and Azores Islands, and the Mediterranean, their long-term effect was unclear. Scyllarids that dwell and reside in rocky habitats for at least part of the year may be preferred for protection by no-take MPAs. Miller et al. (2023) studied *S. latus* adults over two years in a well-protected (>30 years of enforcement) 10 km2 no-take MPA on the north coast of Israel and in a nearby unprotected control site with similar geomorphologic and depth characteristics. Using transects for diving visual census and CMR with T-bar of individual lobsters, they found a significant increase in the abundance, density, and size of male and female lobsters in the MPA compared to the control (Fig. 3). Thirty percent of the marked lobsters were



b)



a)



c)

**Fig. 3.** (a) Number of *Scyllarides latus* detected per search hour inside the MPA and control site. (b) Mean densities (number of lobsters per 150 m2) detected in transects inside the MPA and control site and (c) CL of female (A, C) and male (B, D) lobsters in the MPA and control sites (from Miller et al., 2023).

subsequently recaptured inside the MPA but none in the control area. Recaptures during the same season and between seasons indicated individual fidelity for specific dens. The findings indicate that a well-protected reserve can enhance the conservation of adult *S. latus*. Lobster size is positively correlated with reproductive potential in both sexes. Thus, MPAs can serve as refuges that supply propagules to unprotected areas. After the completion of their study and the success regarding lobsters and fish (Frid et al., 2022), this same MPA in Northern Israel was expanded to 100 km2 (Miller et al., 2023). However, this was not the case for Galápagos slipper lobsters, *S. astori,* and the red and green spiny lobsters, *P. penicillatus* and *P. gracilis*, within the Galápagos Marine Reserve where their populations dwindled probably due to weak enforcement and illegal fishing (Hearn, 2008; Buglass et al., 2018).

Similarly, the population of the scaly slipper lobster, *S. squammosus,* and theHawaiian spiny lobster, *P. marginatus,* in fully protected MPAs in the NWHI did not recover despite a fishery closure in 1993. The lack of recovery of this and other taxa may result from reduced fitness in small populations due to Allee effects, inter-specific competition, and time lags. In addition, largescale climate processes may have altered the carrying capacity of the entire system (Schultz et al., 2011).

1. **Spillover and spill-in effects**

Spillover can be defined as the net export of individuals from a protected area to an adjacent area open to fishing (Goñi et al., 2006). It can develop as an effect of density-independent factors, such as movement within a home range, nomadism, adult migration, and ontogenetic migrations, and density-dependent factors, including competition for resources in the MPA, such as shelter and food (Grüss et al., 2011).

Butler et al. (2006) found that despite the documented advances within MPAs, there were uncertainties about measurable impacts on spiny lobster populations outside the reserves. In fact, they argued that the importance of adult spillover into adjacent fisheries was questionable. However, a more recent review of MPAs for *P. argus* argued that increased lobster density within the MPA may eventually rest on the spillover of lobsters to adjacent fished areas (Briones‐Fourzán and Lozano‐Álvarez, 2013 and references therein).

Six studies found spillover from MPAs for clawed lobsters (Moland et al., 2013b), spiny lobsters (Bevacqua et al., 2010; Follesa et al., 2011; Goñi et al., 2006, 2010; Lenihan et al., 2021, 2022; Ley-Cooper et al., 2014). Three other studies found no or limited evidence of spillover of legal-sized individuals of clawed lobsters (Hoskin et al., 2011; Rowe, 2002) or spiny lobsters (Barrett et al., 2009a). Another study did not find the exclusive spillover of *H. gammarus* lobsters much larger than most lobsters caught beyond the MPA borders (Thorbjørnsen et al., 2018).

A two-year study of artisanal fisheries using a generalized additive model around two Spanish MPAs revealed increased *P. elephas* CPUA near the MPA boundaries, indicating spillover benefits (Goñi et al., 2008). Follesa et al. (2007, 2008, 2009, 2011) also found *P. elephas* spillover from a no-take Sardinian MPA to a neighboring fishing ground in the 12 years since its establishment. Similarly, spillover *of J. edwardsii* from an NZ MPA was limited to within one km of the sanctuary boundary (Edgar and Barrett 1999). Using CMR data from a small MPA, Kelly and MacDiarmid (2003) found that adult *J. edwardsii* moved back and forth across the reserve boundary seasonally, thus spilling over to a fishing area. Butler et al. (2006) indicated that rates of movement, MPA area, habitat structure, and fishing intensity along the MPA boundary were critical factors governing spillover from MPAs and the equilibrium density of spiny lobsters within MPAs. These spillover findings may also apply to other commercial lobster taxa.

The MPA residency and home range of lobsters and spillover from the reserve depend on their movements. Movements may depend on the lobster species, density-dependent factors, ontogenetic stage, seasonality, climate regime, habitat, food availability, natural predatory pressure, and behavioral traits, such as nomadism and migration. Some species move only hundreds of m and remain mainly inside even small MPAs (Barrett et al., 2009a; Huserbråten et al., 2013; Øresland and Ulmestrand, 2013; Withy-Allen and Hovel, 2013). Other species move for tens to hundreds of km (Moore and MacFarlane, 1984; Prescott et al., 1986; Booth, 1997; Groeneveld and Branch, 2002; Linnane et al., 2005). Butler et al. (2006 and references therein) present migratory distances for three species of spiny lobsters. Meanwhile, *P. argus* migrates approximately 20 to 30 km, *P. cygnus* migrates 40 to 50 km, and *P. ornatus* can migrate hundreds of km. In contrast, species such as *Jasus edwardsii* tend to be limited to preferred rocky reef habitats in NZ (Freeman et al., 2009).

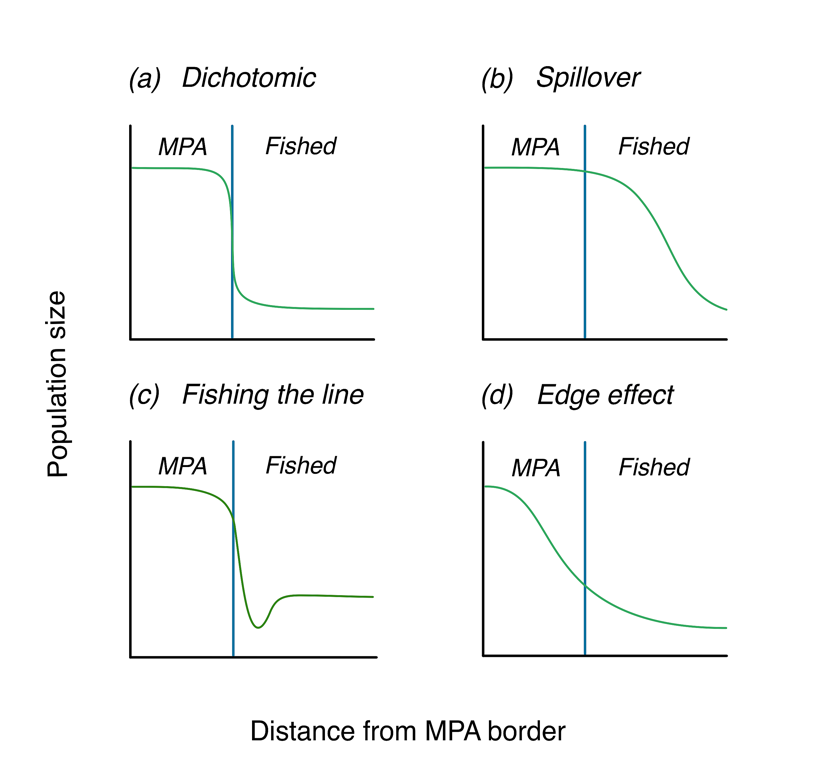
Just as animals can move out of a protected area, they can move into an MPA if they sense more favorable conditions inside than outside. Spillover is well studied and is an important argument in promoting the benefits of marine MPAs for public support. Few studies, however, examine the behavioral mechanisms of colonization or migration into MPAs, termed “spill-in” (Eggleston and Parsons, 2008), found in highly mobile gregarious species. The authors provide evidence for spill-in in the Caribbean spiny *P. argus* by comparing the change in lobster density inside and outside the MPAs in the Florida Keys following an intensive, three-day window of recreational spear-fishing. As expected, lobster density outside the MPAs declined. However, lobster density inside the MPAs increased, indicating net lobster movement from the fishing grounds to the MPAs. The presumed increase was because lobsters moved more in the fishing grounds and less in the MPAs due to differences in fishing-induced disturbance. The sport-diving fisheryelevated the *P. argus* abundance in nearby MPAs, particularly those with relatively high densities of non-disturbed lobsters. Presumably, these areas increased their densities through conspecific attraction where lobsters follow chemical cues to undisturbed sites in MPAs. It is unclear how long such spill-in effects last, but even temporary protection of lobsters in reserves could enhance population fecundity. Although spill-in to reserves may facilitate a rapid refuge from fishing pressure, density-dependent spill-in could also exacerbate the spread of diseases, parasites, and exotic species. For example, density-dependent spill-in for *P. argus* could worsen the spread of a lethal virus identified in this species (Behringer et al., 2011). Grüss et al. (2011) also present a review of spill-in for fish.

In an eight-year CMR study of *H. gammarus* in MPAs and control areas in Norway, protection shifted the demography, increasing the mean total length by 15% in all MPAs **(**Thorbjørnsen et al., 2018). No difference was found in spillover or spill-in rates between MPAs and control areas. None of the MPAs generated more spillover in lobster numbers compared to fished grounds in adjacent control areas. Nevertheless, spillover lobsters from MPAs caught in fished areas were significantly largerthan lobsters spilling over from control areas, which may mean greater fishery profits. In comparison, there was more emigration than the immigration of American clawed lobsters, *H. americanus,* from an MPA located in Bona Vista Bay, Newfoundland, Canada, resulting in a net spillover from the MPA (Rowe 2001). Also, harvests originating from the MPA were generally much larger than lobsters caught beyond MPA borders.

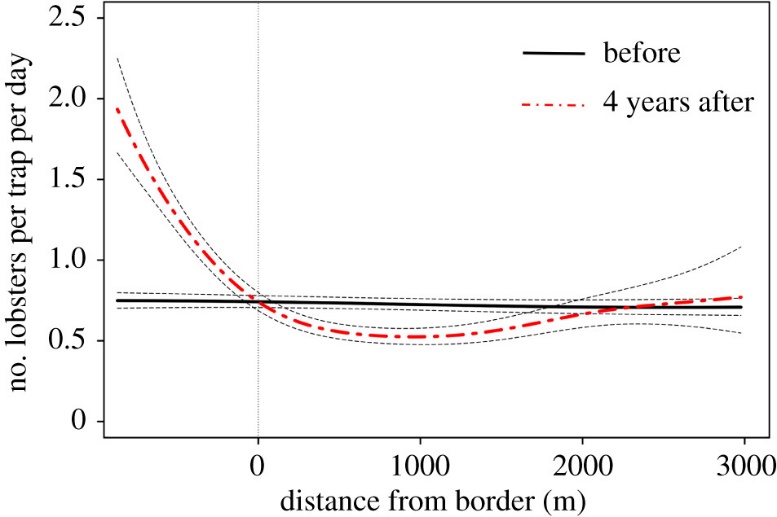
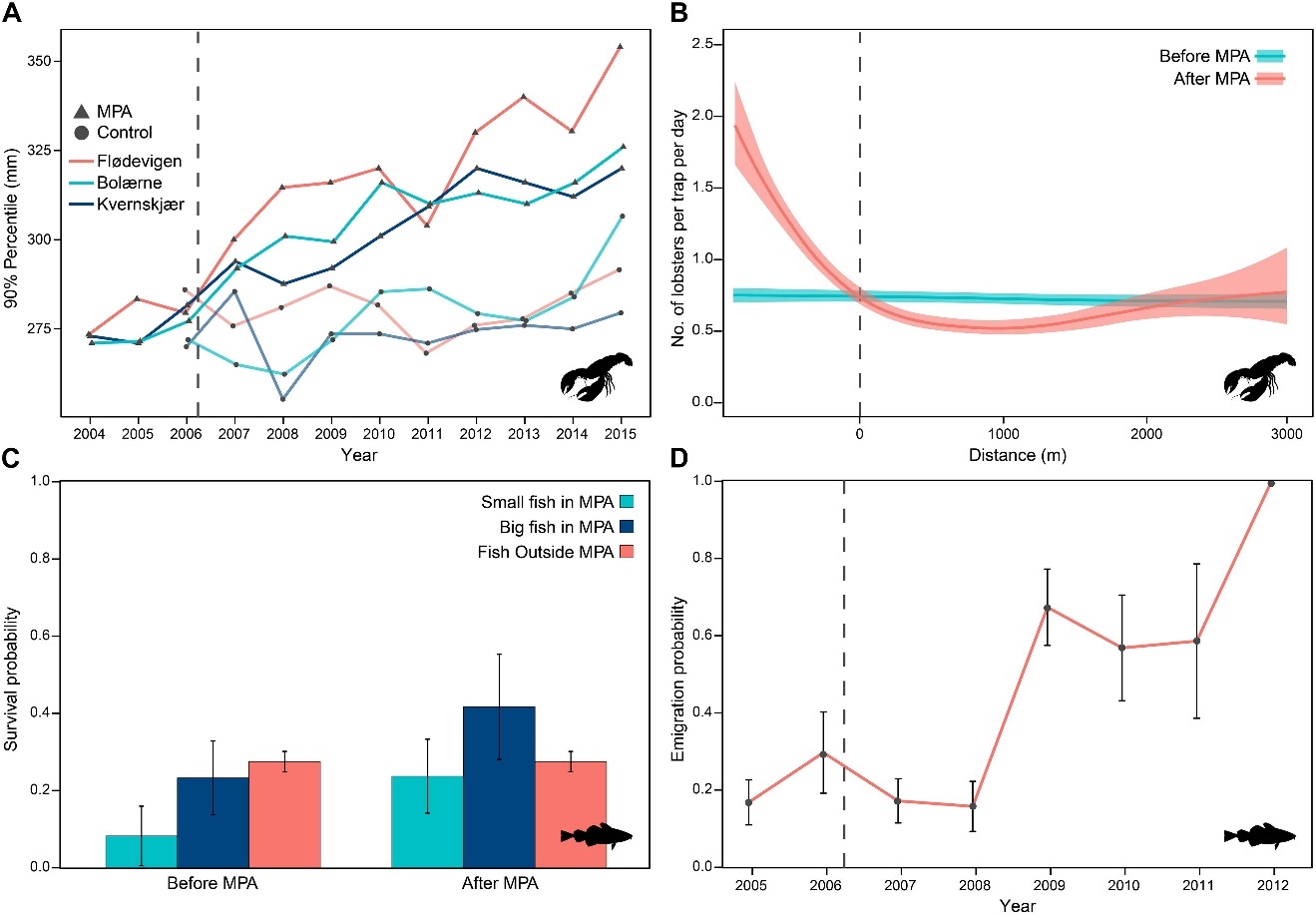
1. **Fishing-the-line, edge effect, and predation impact**

The degradation of the effective size of protected areas by human-related stressors in the surrounding regions is known as the ‘edge effect’ (Ohayon et al., 2021 and references therein). In a recent meta-analysis of the spatial patterns of 72 taxa of fish and invertebrates, including lobsters, across the borders of 27 no-take MPAs around the world, four main potential spatial patterns were hypothesized across MPA borders (Fig. 4). The patterns included 1) Dichotomic - a clear transition with steep density changes across the MPA border (Fig. 4a), (2) Spillover - a gradual decrease in population size from the MPA border towards fished areas indicating a net export of organisms from within the MPA to its surroundings (Fig. b), (3) Fishing the line - a concentration of fishers at the MPA border aiming to benefit from protection outcomes, resulting in a depression of population densities in proximity to the MPA border (Fig. 4c), and (4) Edge effect - a reduction in density beginning within the MPA (Fig. 4d). The analysis showed a prominent and consistent edge effect that extended approximately 1 km into the MPA, where population sizes on the border were 60% smaller than those in the MPA core area.

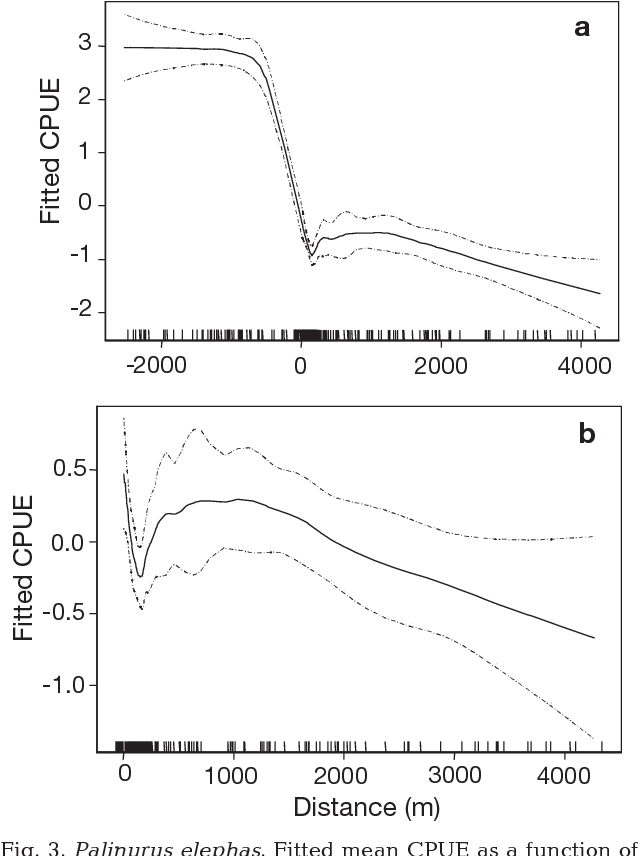
In a fine-scale spatial gradient study conducted before and after the implementation of a 5 km2 lobster MPA in Southern Norway, Nillos Kleiven et al. (2019) determined that after four years, *H. gammarus* CPUE values inside the MPA had increased by a magnitude of 2.6 compared to pre-protection values. The CPUE indicated a significant nonlinear decline from the center of the MPA, with a depression immediately outside the border and a plateau in fished areas (Fig. 5). Fishing pressure at the MPA perimeter caused depletion further inside the MPA, resulting in an edge effect (Fig. 4d), owing to movement from the MPA to outside fished areas.



**Fig. 4.** Hypotheses for spatial patterns of marine populations across MPA borders. The blue line depicts the MPA border, and the green line represents population size. (a) Dichotomic -population size is high inside the MPA and transitions to low just outside the border. (b) Spillover-density-dependent processes inside the MPA create a net flux of organisms from the MPA to fished areas, observed as a gradual decline in population size moving away from the MPA borders. (c) Fishing the line - concentrated fishing effort on MPA borders causes a sharp decrease in population size along the border with a moderate increase further away. (d) Edge effect - fishing pressure and other environmental stressors around MPA borders degrade population size within the MPA and reduce its effective size. (from Ohayon et al., 2021).



**Fig. 5.** Model-predicted lobster CPUE at an optimal depth of 20 m before (black line) and after four years of protection (red dashed line). The vertical dotted line at zero indicates the MPA border. Black dashed lines are 95% confidence intervals around the prediction line (modified from Nillos Kleiven et al., 2019).

**Fig. 6.** For *Palinurus elephas*, a fitted mean CPUE as a function of distance from fishing set to the MPA boundary derived from a Generalized Additive Model (GAM). (a) Commercial and experimental data combined, (b) commercial data only. Models incorporate a logarithmic link, gamma variance function, smooth variable distance, linear predictor depth, and factor side (in b only). Each plot is the contribution of the tested variable to the additive predictor. Units in the y-axis are scaled, so zero corresponds to the mean in the link scale. Marks in the x-axis indicate individual observations. Dashed lines indicate two standard errors (from Goñi et al., 2006).

Goñi et al. (2006) investigated the effects of a no-take MPA (CIMR, Western Mediterranean) on the adjacent *P. elephas* fishery. After 9 to 12 years of protection, a gradient of lobster density was found from the interior up to about four km from the MPA boundary. CPUE demonstrated a significant non-linear decline with distance from the MPA center, with a depression at the boundary followed by a plateau (Fig. 6). The depression was associated with concentrated fishing at the MPA boundary, indicating a fishing-the-line scenario (Fig. 4c), causing an edge effect. In contrast, the plateau indicates that spillover from the reserve is sufficient to maintain stable catch rates up to 1500 m from the boundary. Analysis of recaptures of lobsters tagged and released inside the MPA indicated that the density gradient was caused by spillover from the MPA. Similarly, densities and average sizes of fished *P. cygnus* were higher in the MPA center than at the edges (Babcock et al., 2007). The abundance of *J. edwardsii* across the boundaries of two Northeastern NZ marine reserves was quantified using catch survey data collected over two years by Hanns and Shears (2023). However, they found little evidence of edge effects and spillover within and adjacent to the surveyed MPAs, which might reflect the low populations within these reserves.

No-take MPAs frequently protect not just lobsters but their predators as well.

Studies of coastal rocky areas show that fish and invertebrate predators of lobsters became more abundant inside MPAs following cessation of fishing (Díaz et al., 2005 and references therein). Although fisheries-related mortality and MPAs are well studied, the effect of natural predators on lobster survival in MPAs is rare. Díaz et al. (2005) monitored temporal patterns in abundance of early benthic stages of *P. elephas* using tethering experiments. The relative mortality of recently settled juveniles inside the MPA was much greater than in adjacent non-protected control sites. Predation on recently settled juvenile spiny lobsters was moderated by the availability of suitable shelter. The decline or absence of fish predators in the fished area may be why juvenile lobsters outside the MPA experienced lower predation than within the MPA. The effect of differential predation may constitute one of the mechanisms for the observed decline of lobsters (>50%) in transect counts in the Medes Islands MPA over ten years (Marí et al., 2002). However, Díaz et al. (2005) suggested other factors might contribute to this effect. Although *P. elephas* typically had low mobility, individuals might forage beyond the MPA boundaries and become vulnerable to fishers. Miller et al. (2023) did not report any predation of *S. latus* adults in a well-protected no-take MPA in Israel.

The typical predator of adult *P. elephas* slipper lobsters in the southeastern Mediterranean is the Mediterranean triggerfish, *Balistes carolinensis* (Lavalli et al., 2019). This large predator was rare in transect surveys performed by Frid et al. (2022) in this same MPA (Maximum mean abundance and biomass: 0.068/300 m2 and 2.9 g/300 m2 respectively) compared to the dusky grouper, *Epinephelus marginatus,* (Maximum mean abundance and biomass: 1352/300 m2 and 2094 g/300 m2 respectively). Groupers can prey on juvenile *S. latus* (Lavalli et al., 2019), yet juvenile stages are extremely rare (Spanier and Lavalli, 2013b) and are not reported in any MPA. Lobsters themselves are predators of other invertebrates, such as mollusks and sea urchins. The greater densities of lobsters inside MPAs, especially of large specimens, can lead to density reductions of their prey items in MPAs compared to unprotected areas (Langlois et al., 2005, 2006; Barrett et al., 2009b).

1. **Economic benefits of MPAs**

Estimating the economic benefits of MPAs is complicated due to variables associated with this management and conservation tool. Some MPAs result in lower catch and loss of economic profit, whereas others benefit fisheries through increased egg and larval production or the spillover of mobile juveniles and adults (Gardner et al., 2013). The economic benefits may also involve the combined fisheries of lobsters and other commercial species, such as fish (Moland et al., 2013b). Gardner et al. (2013) pointed out that MPAs might have a range of purposes, including enhanced recreational diving and research sites for monitoring unfished populations. These non-extractive activities, associated with the greater density and sizes of lobsters in the protected zone, also have economic value. There can be financial loss for fisheries due to greater travel distances to fishing grounds that remain open for lobster fisheries (Daw, 2008). If the management costs of surveillance and enforcement can be reduced, MPAs may contribute to their own economic benefit. In fact, (Armstrong and Reithe, 2001) found that MPAs of certain sizes can be more advantageous management tools than traditional quotas.

Frequency-dependent distribution models predict that animals prefer to move toward areas of low density relative to available resources if beneficial to fitness (Treganza and Thompson, 1998). Therefore, increases in the density of exploited species within no-take MPAs could result in enhanced yields in neighboring fisheries through emigration or seasonal or random movements (Goñi et al., 2006 and references therein).

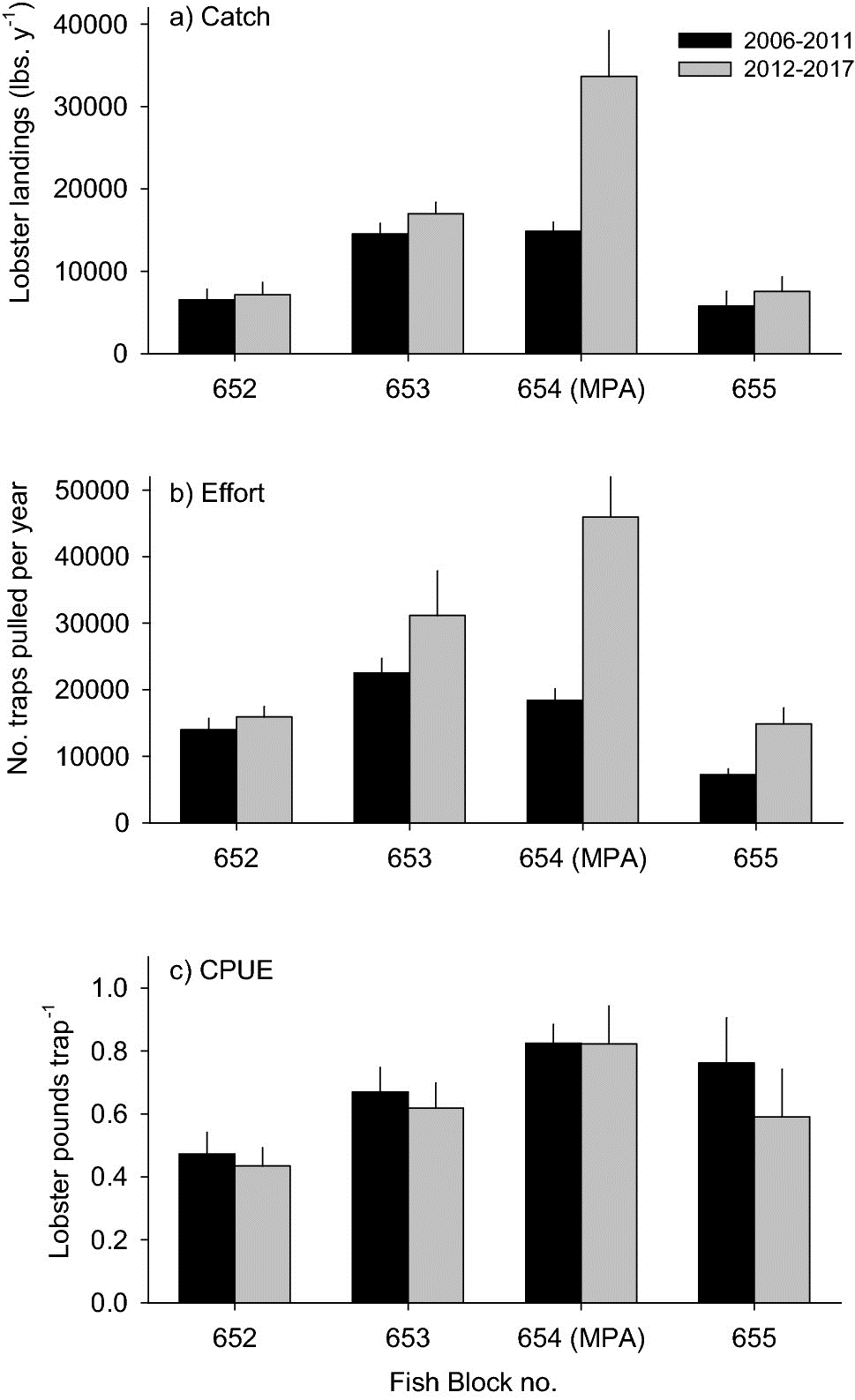
There are, however, only a limited number of empirical studies demonstrating the economic benefit of such spillovers in lobsters. Goñi et al. (2010) used a decade of CMR data for the *P. elephas* slipper lobster from the CIMR in the Western Mediterranean. They estimated annual emigration probabilities of 3.7% for females and 6.7% for males and quantified the resulting spillover to adjacent fished areas. During an 8 to 17-year protection period, harvested spillover offset the yield loss from reduced fishing grounds set aside for the MPA. The spillover produced a mean annual net benefit of 10% of the catch weight. Although lobster numbers spilling over from the MPA annually almost compensated for fishing ground losses, the mean size and weight of emigrating lobsters was greater inside than outside the MPA.

One of the best examples of MPA benefits for fisheries was recently demonstrated for the sustainable California spiny lobster, *P. interruptus*, fishery.Lenihan et al. (2021, 2022**)** tested whether an increase in the lobster population inside two newly established MPAs influenced local catch, fishing effort, and CPUE within the lobster fishery. There was a greater build-up of lobsters within MPAs relative to unprotected areas. There were also greater increases in fishing effort and total lobster catch, but not CPUE, in fishing zone blocks containing MPAs than blocks without MPAs. Remarkably, a 35% reduction in fishing area from MPA designation was compensated by a 225% increase in total catch after six years (Fig. 7). This increase indicates that the trade-off of fishing grounds for no-fishing zones benefits the fishery, at least at the local scale.

A CMR study estimated that 15 - 20% of all adult *P. argus* dwelling in an offshore unfished MPA in the Mexican Caribbean moved into the inshore fishery and were exploited (Ley‐Cooper et al., 2014). It was suggested that the offshore unfished MPA protected most stock within its area while adding to and maintaining fishing yields within the inshore commercial fishery.

What produces greater benefits for exploited populations of lobsters, spillover of adults from MPAs, or increased recruitment from eggs and larvae exported from MPAs? Assessment of egg production of the spiny lobster, *P. elephas,* in an MPA in the Western Mediterranean (Díaz et al., 2011) revealed that after nearly two decades of protection, regional egg production was six times greaterthan predicted without the MPA. Compared to the net benefit of +11% of annual catch biomass from spillover to the regional lobster fishery**,** such an increase in egg production indicates that propagule exports may have far greater potential to benefit exploited populations than spillover. Thus, MPAs can benefit fisheries despite restricted home ranges and limited spillover of adult lobsters. It is assumed, however, that spillover and egg production may complement each other in contributing to fisheries.

Exploring the effects of spatial closures on a *P. cygnus* fishery in Western Australia, Lozano-Montes et al. (2012) analyzed combinations of no-fish zones and fishery reductions*.* They found that lobster biomass increased by approximately 20% when no-fish zones covered 25% of the MPA. The largest predicted increases in biomass for *P. cygnus* were from 25% no-fish zones combinedwith a 50% reduction in fishing pressure. Simulations also predicted that current management zones with 4% sanctuaries produced a modest benefit of approximately 5% in rock lobster biomass after 20 years. This analysis revealed the positive effect of protection provided by sanctuary no-fish zones.



**Fig. 7.** California Department of Fish and Wildlife fishing block data for (a) catch, (b) effort, and (c) CPUE of spiny lobster, *P. interruptus*, off the mainland coast of Santa Barbara. Values are means ± SE for six years before and after establishing MPAs in block 654 (from Lenihan et al., 2021).

Finally, MPAs are assumed to contribute to conservation, such as increasing and restoring marine biodiversity and ecosystem services (Sala and Giakoumi, 2018; Sala et al., 2021; Worm et al., 2006). However, the economic value of these facets is very complicated, and the estimations may be incorrect or incomplete (Martino and Kenter, 2023).

1. **Collaboration and international cooperation**

Collaboration and international cooperation should play a significant role in MPA establishment for lobsters because of the migratory nature of some species and the interconnectedness of marine ecosystems where essential habitats cross international borders. Lobster stocks are often shared across jurisdictions, including between nations (Gardner et al., 2013). Such cooperation may lead to resource-sharing agreements such as the Torres Strait Treaty between Australia and Papua New Guinea regarding the *P. ornatus* fishery during annual migrations (Ye and Denis, 2009). Such cross-jurisdictional issues may have implications for MPAs near or on the borders of two or more nations. Gardner et al. (2013) noted that this problem was most common through larval source and sink dynamics, implying the need for collaborative approaches to manage egg production, including MPA management tools. Dividing catches between nations is complicated for many lobster fisheries, such as the European fisheries for *P. Elephas* (Bonaviri et al., 2005) and the west-central Atlantic *P. argus* fisheries, where source-sink dynamics and harvesting occur across more than 30 countries in Central America (Steneck et al., 2009; Kough et al., 2013; Gnanalingam et al., 2020).

Genetic homogeneity was found across *S. latus* at 15 locations from the Northeast Atlantic and Western Mediterranean across a huge distance greater than 3000 km (Faria et al., 2013). This panmixia of the Mediterranean slipper lobster across its distribution range indicates that future conservation strategies may jointly manage all *S. latus* populations as a single stock. The stock would include MPAs in proper habitats where *S. latus* stocks have been decimated, so these populations may not recover in Italy, for example (Butler et al., 2013). Complete closures of preferred *S. latus* habitats in these areas may aid population recovery via larval recruitment from healthier stocks, such as in Southeastern Spain. Similarly, using genetic techniques, Truelove et al. (2015) found strong connectivity among *P. argus* populations residing in MPAs in Central America. They suggested these results were evidence of the importance of international cooperation in managing Caribbean lobster fisheries.

In discussing slipper lobster fisheries, Spanier and Lavalli (2007) emphasized the need for international cooperation regarding exchanging knowledge, information, and joint biological and fisheries-associated research and management. Collaboration is required because of the extensive geographical distribution of species, such as *H. americanus, H. gammarus*, *P. argus, P. elephas,* and *T. orientalis*,with overlapping populations or metapopulation fragments that span the territorial waters of many countries.

Kough et al. (2013) predicted and empirically verified spatiotemporal patterns of larval supply and described the Caribbean-wide pattern of larval connectivity for *P.* *argus.* The results provided important information for international cooperation in managing marine resources by identifying lobster larval connectivity and dispersal pathways throughout the Caribbean. Some identified nations were sources for the export of lobster larvae to the Caribbean, whereas others were sinks, importing lobster larvae. Thus, the relevancy of connectivity in designing Caribbean-wide networks of MPAs was emphasized.

1. **Discussion**

No-take MPAs are widely recognized as effective conservation tools for protecting marine resources, including lobsters, within their boundaries. Establishing and enforcing MPAs often leads to increased size, density, and spawning biomass of harvested lobster species (Lenihan et al., 2021 and references therein). MPAs can additionally enhance reproductive activities and improve lobster growth inhabiting them through increased molting frequency and enhanced growth during each molt (Sørdalen et al., 2018, 2020, 2022). MPAs can also facilitate the recovery of overfished lobster populations (Kelly et al., 2000; Hobday et al., 2005; Lipcius et al., 2006; Freeman et al., 2012).

However, not every MPA results in a thriving lobster population. MPA failure for lobsters can be due to ineffective enforcement, illegal fisheries (Lipcius et al., 2001; Hearn, 2008; Schultz et al., 2011; Brill and Raemaekers, 2013; Buglass et al., 2018), young MPA age resulting in a shorter reinforcement period, Allee effects of small populations, and interspecific competition. Additional factors responsible for lobster MPA ineffectiveness can be climate processes altering the carrying capacity of the entire system (Schultz et al., 2011), natural predation (Díaz et al., 2005), periodic harmful algal blooms, and unsuitable substrate (Mayfield et al., 2005). An MPA may be incorrectly placed regarding ocean currents and recruitment activity without understanding the spatial processes, such as source-sink dynamics, the role of larval connectivity (Lipcius et al., 2001; Steneck et al. 2009; Kough et al., 2013; Gnanalingam et al., 2020), and the influx levels of post-larvae (Briones‐Fourzán and Lozano‐Álvarez, 2013 and references therein). Unsuccessful MPAs may also result from being too small in relation to the home range of their lobster species (Díaz et al., 2005) and, to an extent, edge effects (Ohayon et al., 2021). In discussing the management of coral reef ecosystems, including lobsters, Steneck et al. (2009) indicated they often established no-take reserves that, in practice, were too small or scattered or had low stakeholder compliance.

Placement of MPAs and their coverage area are basic questions when designing MPAs. McLeod et al. (2009) outlined rules of thumb for general MPA design principles. TThe considerations include:

1. Bigger is better, and protected areas should be at least 10 to 20 km in diameter.

2. Simple shapes such as squares and rectangles will minimize edge effects.

3. MPA units should be no more than 15 to 20 km apart.

4. Protect at least three examples of each habitat for representation, replication, spread, and catastrophe minimization as a best practice.

5. Select a variety of temperature regimes to minimize future climate warming impacts.

6. Protect nursery areas, spawning aggregations, and areas of high uniqueness and diversity.

7. Maintain functional groups of predators, herbivores, and detrivores.

Based on the theory of island biogeography, larger reserves are likely to protect more species and individuals, whereas smaller reserves positively influence populations (Young et al., 2016). Giakoumi et al. (2017) indicated that in the Mediterranean Sea, even small MPAs (<30 km2) can be effective for some species when MPAs are fully protected and well-enforced for sufficient time to allow recovery of local populations. They hypothesized that three mechanisms resulted in recovery: (1) small MPAs are more likely enforced because surveillance requires relatively fewer resources and small MPAs are more readily accepted by local communities, (2) the effects of spill-in into MPAs of commercially targeted species are more apparent, and (3) MPAs are often sufficiently large to protect the home ranges (<10 km2) of primary commercial targets displaying relatively low adult mobility. It should be noted that the analyzed species had relatively small home ranges, approximately the size of very small, fully protected areas in the Mediterranean. Di Franco et al. (2018) compiled peer-reviewed literature specific to home ranges of finfishes and invertebrates of ecological and commercial importance in the Mediterranean Sea. The home ranges were then related to the size of 184 fully protected Mediterranean MPAs. The European [spiny lobster](https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/spiny-lobster" \o "Learn more about spiny lobster from ScienceDirect's AI-generated Topic Pages), P. *[elephas](https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/elephas" \o "Learn more about elephas from ScienceDirect's AI-generated Topic Pages),* had the smallest home range (0.0039 ± 0.0014 km2; mean ± 1 SE). Approximately 25% of fully protected Mediterranean MPAs are more than twice the size of the largest home range recorded, demonstrating a direct link between the effectiveness of fully protected MPAs and home range. The link indicates that MPAs of at least 3.6 km2 may increase the local population densities of this coastal marine species. Strong site fidelity and small home ranges were also reported for *P. interruptus* (Withy-Allen and Hovel, 2013) and *J. edwardsii* (Barrett et al., 2009a).

These limited home ranges may not be characteristic of all lobster species. Ohayon et al. (2021) recommended a no-take MPA of at least 10 km2 and as circular as possible to limit the proportion of total MPA area degraded by edge effects. They also noted that MPAs with buffer zones displayed no edge effects. Hence, extending no-take areas beyond target habitats and managing fishing activities around MPA borders is critical to boosting MPA performance. In a different study, changes in modeled MPA areas led to predictable alterations in lobster population size. However, changes in fishing intensity along the border resulted in equally dramatic alterations in lobster density in the MPA because of nomadic foraging by adult *P. argus* outside the reserve (Acosta 2002).

Follesa et al. (2011) studied a small ( approximately 4 km2)no-take MPA in the Western Mediterranean for 12 years using experimental CPUE and reported significant increases in the abundance and biomass of *P. elephas.* The small size of their study area made recording a significant biological response after the first year of protection easy. However, for long-lived species such as *P. elephas*, a 12-year horizon could provide only partial evidence of benefits that may also apply to other long-lived species of lobsters. Eggleston and Dahlgren (2001) reported that a two-day recreational fishing season reduced the density of P. argus by an average of 80% across several habitats, including three small MPAs, and reduced CL by more than 7 cm. Thus, relatively small MPAs (0.3 - 1.5 km2) might be too small to protect the population of mobile P. argus. In addition, lobster density depended on proper habitats, which was related to the density and volume of large sponges. Thus, large MPAs may include all the habitats required for different life stages of lobsters. The importance of a complete set of habitats essential for spiny lobsters in relatively large MPAs was emphasized in a review by Childress (1997) and in other studies (Davis, 1977; Bertelsen and Cox, 2000; Bertelsen and Mathews, 2001; Cox and Hunt, 2005; Butler et al. 2006). The conclusion that a single large MPA is preferable to several small ones is supported by a heuristic model for a hypothetical overexploited population of *P. argus* (Stockhausen and Lipcius (2001). The conclusion resulted in a proposal that large single regional MPAs would function most effectively within a broad scale (1000s of km) of MPA networks, barring local catastrophes.

Many MPAs are established with assurances to local fisheries that MPA capacity to increase fish stocks and yield will outweigh the costs of losing fishing grounds. However, whether positive conservation outcomes also benefit fisheries is less certain. Several recent studies highlight clear benefits to the lobster fisheries industry of no-take, well-protected, and properly designed MPAs (Lenihan et al., 2021, 2022 and references therein). MPAs are assumed to enhance adjacent fisheries mainly in two ways: through increased egg export and larvae that will eventually enhance target lobster populations and increased lobster biomass near MPA borders as spillover catch in fished areas. Numerous studies report evidence for spillover of large mobile lobsters from MPAs into adjacent fished areas (see Lenihan et al., 2021, 2022 for details).

Some MPAs result in lower catches outside of MPAs and, consequently, loss of economic profits. Gardner et al. (2013 and references therein) claim that, in general, catch displaced from MPAs results in lower catch (reduced revenue) and lower catch rate (higher cost), implying a loss of economic yield. This outcome did not occur when the lobster stock was severely overfished. The economic loss from MPAs could also occur despite constant catch revenue if there was extra cost for greater travel distances to remaining open fishing grounds or a loss of revenue through reduced quotas. However, the overall economic benefits of MPAs to the community should be considered, including reduced enforcement expenses and fishing of other commercial taxa, such as fish. Additional considerations include recreational fisheries, non-extractive diving tourism, and perhaps the economic contribution of maintaining biodiversity and ecosystem services. MPAs are widely used research sites due to the cost-effectiveness of sampling where a high density of lobsters, including large individuals rarely encountered in fished areas, are accessible (Jeffs et al., 2013).

Management tools in addition to MPAs include harvest slot maximum and minimum size limits, limited or closed seasons, banned fishing of berried females, limited entry, restricted license numbers to lobster fishers, and quotas. Caputi et al. (2015) found that, for over 30 years, the Australian western rock lobster fishery had catch predictions based on post-larval settling recorded three to four years earlier. Preventive management action was taken with an approximately 70% effort reduction to protect the breeding stock better. The fishery was also moved to the maximum economic yield (MEY) level of effort for the projected recruitment. The fishery was managed using input controls to restrict fishing efforts but became a catch quota-controlled fishery with individual transferable quotas (ITQ). Reducing fishing efforts to a level associated with MEY increased egg production well above threshold levels.

It is possible to use one or more of these non-MPA management tools. However, another possibility is to combine MPA with management tools. A good example of such an approach was the study of Gnanalingam et al. (2020) concerning the most fecund large *P. argus* that contributed disproportionately to Caribbean population replenishment. When combined, no-take MPAs and harvest slot limits rebuilt and maintained the population of large mature individuals even under significant harvest pressure. The most conservative model, using a 30% MPA and harvest slot limit of 75–105 mm, increased spawner abundance considerably compared with the fishing status quo at the end of 30 years. The study considered that regulatory mechanisms restricting harvests were likely contentious, but the long-term benefits of protecting mature spawning individuals were undeniable. The authors concluded that decisions on the most suitable management strategy for a fishery require balancing ecological desirability with economic and social feasibility. Despite possible difficulties, the effective application and maintenance of MPAs and other management tools can occur only with the full participation of affected communities, including the fisheries industry. As noted by Caputi et al. (2015), whereas many fishers strongly resisted the MEY assessment and the move to ITQ, the MEY target was formally accepted by industry and management after the changes were implemented for sustainability.

While commercial fishing is undeniably the primary cause of differences in lobster population attributes between MPAs and unprotected areas, substantial recreational fisheries also contribute (. SCUBA diving is popular with the rise in living standards in many countries, so these leisure activities are widespread, requiring more research on the interrelationships between this sport and MPAs. Also, traps used by recreational fishers affect lobster populations in MPAs. Nillos Kleiven et al., (2019) discovered more traps closer to MPA borders seven years after the designation of an MPA, and this fishing-the-line trend was more strongly driven by recreational than commercial fishers. Therefore, future MPA studies should focus more on this growing branch of lobster fisheries.

Most past research has centered on adult lobsters and MPAs. Although adult lobsters are the reproductive part of the population, it is imperative to study juvenile stages and the recruitment process in more taxa because juveniles are the basis for future lobster populations. Furthermore, most studies of lobsters and MPAs refer to fishing that is “man-made predation” and largely ignore natural lobster predation within MPAs and fished areas. It is essential to study this facet to understand the true scope of lobster mortality. MPA design should be based on the behavioral ecology of the target lobster species. Insufficient knowledge of the ecology of different lobster species and life stages, including habitat preference, anti-predator adaptation, movement, reproductive activity, seasonality, and inter- and intraspecific interactions, may impair the success of MPAs as conservation and management tools.

Anthropogenic climate change is driving the warming of marine environments and is expected to affect fisheries productivity (Hunt et al., 2023 and references therein). For MPA networks to be climate smart, Arafeh-Dalmau et al. (2023) suggest that their design address the vulnerability of biodiversity to current and future climate change impacts. To buffer climate change impacts, they recommend expanding MPA coverage by focusing on protecting critical network nodes and climate refugia, where impacts may be less severe. This approach should be considered when designing future MPAS for lobsters.

Largescale fishery management could explicitly recognize metapopulation structure by considering larval transport dynamics and pelagic larval sanctuaries (. Certain regions contribute disproportionately to the broader Caribbean larval pool, so maintaining healthy spawning stocks in those countries should be an international priority. Cooperative management among countries should ignore geopolitical borders, as lobster larvae do, and nations absorbing disproportionally more larvae from the international larval pool bear an ethical responsibility and financial incentive to assist in spawning stock preservation in other areas best suited for larval export. In addition, Kough et al. (2013) also proposed a strategy, like carbon credit trading, that would assign each nation larval credits based on regional larval export production. Similarly, Arafeh-Dalmau et al. (2023) refer to guidelines for designing MPA networks and their application in the Southern California Bight, a 692-kilometer stretch of coastline on the [west coast](https://en.wikipedia.org/wiki/West_Coast_of_the_United_States" \o "West Coast of the United States) of the [US](https://en.wikipedia.org/wiki/United_States) and [Mexico](https://en.wikipedia.org/wiki/Mexico" \o "Mexico). Large self-sustained MPAs for isolated areas to support larval self-replenishment, incorporating transboundary connectivity, are also discussed. Additionally, species with long dispersal distances, such as *P. interruptus,* require transboundary international coordination for the entire region. Such an approach to international cooperation should be considered for every metapopulation of lobsters distributed between nations.

Lengthy multiyear research and monitoring of lobsters in MPAs and fished areas, using up-to-date knowledge and technology, is essential for MPA success, considering lobster longevity, complex life cycle, and anthropogenic factors that may affect these large commercial decapod crustaceans. For example, future studies could use improved acoustic tagging of lobsters. Insufficient service life and the resulting need for battery replacements is a great challenge for implantable electronic devices. This issue is particularly true for animal tracking applications because recapturing animals is unlikely once released into the wild. To address this problem, a biomechanical energy [harvester](https://www.sciencedirect.com/topics/engineering/harvester" \o "Learn more about harvester from ScienceDirect's AI-generated Topic Pages) has been developed (Li et al., 2022) and may upgrade the tagging and tracking of lobsters in MPAs and adjacent fished areas.

1. **Conclusions**

1. MPAs for lobsters are proven to conserve lobster populations while significantly boosting some lobster fisheries. Such MPAs can benefit other industries, including marine tourism and fisheries of other commercial species.

2. If MPAs are well designed, including location, size, and shape, according to the behavioral ecology of the target lobster species and implemented according to international standards, they provide multiple environmental and socioeconomic benefits.

3. Combinations of management tools, such as closed seasons, maximum and minimum size limits, and harvest and effort quotas, should be considered with no-take MPAs. However, decisions about which management strategy best suits a fishery require balancing ecological desirability with economic and social feasibility.

4. Successful implementation of MPAs and their ongoing maintenance will only occur with the full participation of affected communities, including the fisheries industry.

5. Sustained perennial research and monitoring of lobsters in MPAs and fished areas, using up-to-date knowledge and technology, are essential for the success of MPAs, considering their longevity, complex life cycles, and anthropogenic factors that may affect lobsters.

**Funding**

This research received no specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

**Declaration of Competing Interest**

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Data Availability**

Data is available from published research or open-source internet pages.

**Acknowledgments**

The author is thankful to many colleagues who have studied the interrelationships of MPAs and lobsters for supplying valuable information, especially to Prof. Mark Butler and Dr. Tim Langlois. Prof. Roee Diamant from the Hatter Department of Marine Technologies, the Leon H. Charney School for Marine Sciences, University of Haifa, is acknowledged for his advice on the acoustic tagging of marine animals. Thanks are also due to the support services of the Younes and Soraya Nazarian Library, University of Haifa, for their help in the literature survey.

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