Patellid Limpets: An Overview of the Biology and Conservation of Keystone Species of the Rocky Shores

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Abstract

This work reviews a broad spectrum of subjects associated to Patellid limpets' biology such as growth, reproduction, and recruitment, also the consequences of commercial exploitation on the stocks and the effects of marine protected areas (MPAs) in the biology and populational dynamics of these intertidal grazers. Knowledge of limpets' biological traits plays an important role in providing proper background for their effective management. This chapter focuses on determining the effect of biotic and abiotic factors that influence these biological characteristics and associated geographical patterns. Human exploitation of limpets is one of the main causes of disturbance in the intertidal ecosystem and has occurred since prehistorical times resulting in direct and indirect alterations in the abundance and size structure of the target populations. The implementation of MPAs has been shown to result in greater biomass, abundance, and size of limpets and to counter other negative anthropogenic effects. However, inefficient planning and lack of surveillance hinder the accomplishment of the conservation purpose of MPAs. Inclusive conservation approaches involving all the stakeholders could guarantee future success of conservation strategies and sustainable exploitation. This review also aims to establish how beneficial MPAs are in enhancing recruitment and yield of adjacent exploited populations.

Keywords: Patellidae, limpets, fisheries, MPAs, conservation

1. Introduction

The Patellidae are one of the most successful families of gastropods that inhabit the rocky shores from the supratidal to the subtidal, a marine habitat subject to some of the most

variable and unpredictable environmental conditions. Therefore, many of their peculiar morphological and biological characteristics can be understood as adaptations to this environment. The biological traits of limpets vary inter- and intraspecifically as a result of genetic differences and environmental influences [1]. Parameters such as growth, reproduction, and mortality are dependent on a complex array of selective forces and are important in understanding the distribution and abundance of a species [2, 3]. Differences in limpet populations from distinct geographic areas are most probably explained by specific environmental and anthropogenic conditions, essentially oligotrophy, sea water temperature, and fishing pressure. Thus, for some of the biological traits, it is expected to find patterns, like temperature which changes somewhat consistently with latitude and has a profound effect on the growth of limpet species, with species inhabiting higher latitudes growing more slowly and achieving larger maximum sizes, therefore having a longer lifespan than limpets from lower latitudes.

Patellid limpets are also subjected to anthropogenic impacts on the coastal ecosystems such as, pollution, habitat removal, and harvest which in some cases has led to the reduction of abundance or even the disappearance of limpets from large areas. The decline of these species, which may have been further accelerated by the progressive deterioration of the coastline, continues at an alarming rate and many of their stocks are on the verge of disappearance. To avert this situation, regulators have established several measures including the implementation of closed seasons and areas where limpet harvest is interdicted, minimum size of capture, and catch limits. Limpet populations seem to respond, in general, in a positive way to these measures; however, the response is closely linked to the ability of the regulators to enforce said measures.

Another popular strategy adopted in the protection of the rocky shores and limpets is the implementation of marine protected areas (MPAs). The effectiveness of MPAs in protecting exploited populations of limpets and underlying their overall success in increasing density and abundance as well as promoting healthy size composition with impact on the reproductive output of these species is well known. Nonetheless, several limitations are recognized that can negatively affect the protective role of MPAs such as, naturally occurring variations of the species biology and ecology as well as limitations regarding the management of MPAs, for instance, the lack of surveillance and enforcement of protection regulations.

The aim of this work is to review a broad spectrum of subjects associated to Patellid limpets' biology such as growth and reproduction, also the consequences of commercial exploitation on the stocks of these species and the effects of marine protected areas in the biology and populational dynamics of these intertidal grazers. The focus is on determining the effect of identified biotic and abiotic factors that influence these biological characteristics and geographical patterns recognized to be closely connected to growth and reproduction, such as latitude. Regarding conservation of Patellidae, the authors aim to elucidate how beneficial MPAs are in their role of protection of exploited populations and in enhancing recruitment and yield of adjacent exploited populations.

2. Biology and ecology of Patellid limpets

2.1. Taxonomy and distribution

Patellid limpets are marine gastropod grazers belonging to the family Patellidae Rafinesque, 1815 that comprises the genera *Patella* Linnaeus, 1758, *Cymbula*, H. Adams & A. Adams, 1854, *Helcion* Montfort, 1810, and *Scutellastra* H. Adams & A. Adams, 1854. The worldwide distribution of Patellidae species is anti-tropical with half of the known species restricted to southern Africa and the North-Eastern Atlantic where a high diversity of species is found, while relatively few species are present in the Indian and Pacific Oceans [4, 5]. The Patellidae family is currently represented by, at least, 49 recognized species [6]. The genus *Patella* is comprised of 14 recognized species with a geographical distribution restricted to the North-Eastern Atlantic and the Mediterranean Sea; the genus *Cymbula* includes 10 species found in Southern Africa, South-Eastern Atlantic, and Mediterranean; the genus *Helcion* is represented by four species restricted to Southern Africa, while *Scutellastra* encompasses 21 species with a wide distribution ranging from Southern Africa to the Indo-West and Eastern Pacific [4, 7–10]. Limpets are subject to an array of environmental stresses as a result of their extended vertical distribution, which ranges from the upper to the lower shore levels. Thus, limpets can exhibit varying degrees of structural adaptations since their position relative to the shore influences their exposure to desiccation, hydrodynamic action of the waves, temperature variation, and tidal width [11–14]. This impressive pheno-typic plasticity allied to the relatively simple shell geometry, convergent shell shape, and sculpturing results in an unclear Patellid limpet's taxonomy, in such a way that the initial generic names, with broad geographical range, had to be re-evaluated based on superficial similarities [15].

2.2. Feeding habits and ecological importance

Limpets are grazing herbivores that feed, by scraping the rocky substrate with the radula, on microbial biofilms which are primarily composed of cyanobacteria and microalgae, including diatoms, spores, and other propagules of macroalgae and invertebrates [16, 17]. Limpets' feeding habits are essential in structuring intertidal communities [16–19] since limpet grazing is a key process in rocky shores involved in determining macroalgal abundance and in modifying eco-system stability, indirectly enhancing or inhibiting the establishment of other organisms [17]. The decline of population density of limpets might result in an abnormal development of algae diversity as reported by Boaventura et al. [20] or in the occupation of their ecological niche by competing organisms such as barnacles or sea urchins [21–23]. However, the effect of these grazers is not limited to the removal of algae, and very often they can affect other animal species through competitive interactions [24] and by providing secondary habitats for other invertebrates that settle either on top of, or beneath, their shells [19, 25, 26]. Grazers may also affect the rate of succession [27] or cause different assemblages to develop [28]. Thus, limpets are rightfully considered to be keystone species in intertidal communities [29].

2.3. Movement and homing

Patellid limpets are considered to some extent semi-sessile organisms; nonetheless, they perform small movements in the area surrounding their usual fixation site. This behavior is designated as homing and can often be observed through the scar that remains in the rocky substrate where the limpet settles. Limpet movement patterns and homing behavior have been extensively studied for *Patella vulgata* Linnaeus, 1758 [30], *Patella depressa* Pennant, 1777 [31], *Patella rustica* Linnaeus, 1758 [32], *Patella ferruginea* Gmelin, 1791 [33], *Scutellastra flexuosa* (Quoy & Gaimard, 1834), and *Scutellastra argenvillei* (Krauss, 1848) [34]. This homing behavior has different functions in different species such as avoiding desiccation [35, 36], reducing predation and intraspecific competition [37–40], responding to wave action [41, 42] and defending territory or asserting dominance [43, 44]. The mechanism that is most widely accepted as being responsible for the homing behavior reports limpets following chemical trails, laid down on the outward trip, on their way back to the fixation site [31, 45, 46].

2.4. Growth

Biological parameters such as growth rate, asymptotic length, and age structure reflect the overall state of health of a population and are commonly used as stock assessment tools of exploited marine organisms. Growth, reproductive strategy, and mortality are dependent on a complex array of selective forces [2] and are important in understanding the distribution and abundance of a species [3]. To determine these parameters, most studies usually resort to the capture-recapture method [22, 47–50] or length-frequency distribution analysis [51–53]. Over the past decades, intensive research has focused on the biology of limpets, due to their diversity and ecological significance; however, there remain gaps in the knowledge concerning these species' age structure and growth patterns.

Patellid limpets, like many marine gastropods, exhibit both intra- and interspecific seasonal variation in growth rates [54]. Although some intraspecific variation may be genetically controlled [55], external factors such as changes in food availability [56, 57], wave action [58–60], and vertical distribution on the shore [61] are thought to influence growth rates. Other factors such as population density, available grazing area, predation, and competition are indicated as influencing growth rates of mollusks supporting the idea that the strategy of diverting energy to reproduction and vice versa, according to the organisms' needs, influences growth rates [24, 49, 62, 63]. It has been suggested that limpets with greater growth rates have smaller lifespan while limpets with slow growth are generally long-lived [46]. As such, rapidly growing limpets are usually associated with early maturation, high mortality, and a short lifespan [46, 64].

Clarke et al. [49] observed a latitudinal cline in annual shell growth of the polar limpet *Nacella concinna* (Strebel, 1908). This latitudinal pattern could nevertheless be masked by inter-annual variability. The authors suggest that the observed variation could be the result of a simultaneous change in both growth rate and the duration of the growth period. This change would result from the shorter duration of the seasonal blooming of epiphytic microalgal and microbial biomass at higher latitudes. Another factor influencing growth rates in *N. concinna* is seawater temperature, with warmer temperatures that last longer producing higher growth rates.

Scutellastra and *Cymbula* species that occur at similar latitudes present variations in terms of growth, namely in maximum size and growth rates. When compared to tropical limpets belonging to the genus *Cellana* H. Adams, 1869, limpets from temperate regions are generally larger, with wider lifespan and slower growth rates. Additionally, limpets inhabiting the artic regions such as *N. conccina* achieve larger sizes, even wider lifespans, and slower growth rates. This latitudinal pattern has been usually associated with the latitudinal variation of temperature, photoperiod, and insolation [49]. Even though it is consensual that species from lower latitudes grow more rapidly than species from higher latitudes [49, 52], it is not yet clarified whether physiological constraints, a reduced or prolonged growing season, or combination of both might be the cause of dissimilar growth rates at differing latitudes [49].

Nevertheless, due to Patellids' anti-tropical distribution, growth patterns are difficult to observe, particularly when considering latitude. Within this family, variations in growth are mostly derived from prevalent local environmental factors. Nonetheless, when comparing to other Patellogastropoda, a latitudinal pattern becomes apparent, in which at lower latitudes limpets grow at faster rates and achieve smaller sizes, while at higher latitudes, they grow at slower rates and achieve larger sizes. For instance, for the polar limpet *N. concinna* reported growth rates range between 0.059 and 0.323 year^{-1}, while the highest growth rate is exceptionally high for a limpet inhabiting the polar regions, probably due to specific characteristics of the habitat in Signy Island [49]. The overall growth rates are inferior to those reported for limpets of the genus *Cellana* that inhabit lower latitudes in temperate and tropical regions with growth rates ranging from 0.400 to 1.661 year^{-1}. Patellid limpets exhibit intermediate growth rates ranging from 0.117 year^{-1} in *Scutellastra choclear* (Born, 1778) and 1.020 year^{-1} in *Cymbula oculus* (Born, 1778) reflecting their anti-tropical distribution.

However, the nonlinearity of growth of marine organisms renders the direct comparison of growth parameters impossible [65]. As such, determination and comparison of the overall growth performance of different marine species is achieved using the growth performance index (GPI) of Pauly and Munro [66], which relates the asymptotic length and growth rate [66]. Nonetheless, the growth performance index in Patellogastropod limpets exhibits the same pattern as growth rates with decreasing GPI as latitude increases and ranging from 1.942 in *N. concinna* to 3.653 in *Cymbula granatina* (Linnaeus, 1758), suggesting that growth performance of limpets varies with latitude. Within the Patellidae family the variation of GPI is reduced with values ranging from 2.42 for *S. cochlear* to 3.65 for *C. granatina* from South Africa [62], which is in agreement with Sparre et al. [67] who claim that the growth performance index remains relatively constant at similar rates between related taxa. The variability results therefore due to abiotic and biotic factors that different species are subject to, such as greater or lesser extent of hydrodynamics, desiccation, predation, competition, and temperature.

2.5. Reproduction

Patellid limpets have a simple reproductive system, consisting of a simple gonad inserted in the visceral mass and a reduced gonoduct leading to the right nephridium [68, 69]. These species are not externally sexually dimorphic, and sex determination is only possible through macroscopic observation of the gonads. Spawning results in the release of oocytes and sperm

directly in the ocean where fecundation occurs. According to Orton et al. [68], spawning is stimulated by environmental triggers, such as high wind speed and wave action. An increase in phytoplankton concentration may also stimulate spawning as suggested by Underwood [24] who observed that gastropod species with planktotrophic larvae spawn when phytoplankton concentration is high.

Most limpet species have a reproductive cycle with a gonadal development stage culminating in a spawning period followed by a resting phase. The spawning period varies inter- and intraspecifically; it may also vary from year to year and is supposed to be triggered by temperature variations, increased wave action, and onshore winds [70]. In regions with higher temperatures, spawning occurs in a short period contrary to what happens in regions with colder waters, where the development of the gonads requires a longer time period [71]. *P. vulgata* is believed to be a winter breeder, with spawning occurring from October to March; however, in colder localities, sexual maturation occurs earlier [68]. On the other hand, in south-west England, *P. depressa* is considered a summer breeder [72] with spawning occurring between late July and early September and without a resting phase unlike *P. vulgata*. The same authors suggested that an increase in temperature associated with wave action stimulates spawning in this species. *Patella ulyssiponensis* Gmelin, 1791 has a spawning period that lasts from October to December, being also considered a winter breeder in south-west England [59, 68, 73]. Orton et al. [68] and Orton and Southward [72] suggested that although the development of the gonad in *P. vulgata* and *P. depressa*, respectively, is well related with temperature, the act of spawning is triggered by violent onshore storms. Thompson [59] also found *P. ulyssiponensis* spawning during the autumn storms. Hence, it seems likely that spawning cannot take place until a population is sufficiently mature, but after that stage is reached, the first strong windstorm will trigger spawning [59]. Another factor that potentially affects the timing of spawning in limpets is food availability; Underwood [24] reported that species with planktotrophic larval stage time spawning with periods when phytoplankton concentrations are high. One such case is that of the closely related species of *P. ulyssiponensis* from the Portuguese mainland and *Patella aspera* Röding, 1798 from Madeira Island. *P. ulyssiponensis* is reported to be a summer breeder while *P. aspera* was reported to be a winter breeder with spawning occurring when the phytoplankton concentration is higher (P. Henriques, pers. comm.). Similarly, it has been reported that in limpets with restricted geographic distribution, the reproductive cycle is influenced by geographic locality, namely in the timing of gametogenesis and spawning [62, 74]. For limpets with broader geographic distribution, it is possible that the reproductive cycle is adjusted to regional environmental conditions [74].

Limpets, like many sessile or sedentary marine invertebrates, have life cycles that include a prolonged pelagic larval phase that can last up to 2 weeks as reported by Hawkins et al. [75] for *Patella* species. Veliger larvae remain in the water column as plankton until eventually fixating in the rocky substrate on the inferior level of the coast. As the juveniles grow, they begin a slow vertical migration, colonizing different levels of the rocky shores [76], leading to variability in patterns of recruitment [77]. Moreover, larvae in the water column are subject to processes of physical transport that can disperse them from the site of reproduction [78]. Thus, the number of recruits on a specific location may be independent of the local larvae production [16, 79] and influenced by current regimes. Nonetheless, limpet populations cannot be

considered fully open or fully closed, since some local larval retention is likely to occur despite larval dispersal [80, 81].

Orton [82] suggested the existence of the phenomenon of protandrous hermaphroditism in limpets of the genus *Patella* based on sexual dimorphism in size-frequency of *P. vulgata*; subsequently Thompson [59], Branch [46], and Le Quesne [83] observed that some individuals reach maturity as males and become females in the more advanced stages of their life cycle. This phenomenon of sequential hermaphroditism is also suggested to occur in species of the genera *Cymbula* [46], *Helcion* [74], and *Scutellastra* [62, 84, 85]. Not all male limpets change sex, since a considerable proportion of males can be found in the larger size-groups, these individuals might eventually change sex or remain as males if the signals that lead to sex change are not present [86]. Also, some limpet species are sequential hermaphrodites in which the sex change can be reverted as reported for *P. ferruginea* by Guallart et al. [87].

Sex change in limpet species is thought to be genetically controlled. However, high variability in the timing or on the limpet size at which the change occurs suggests that environmental factors may influence the process. Species such as *C. oculus* have a relatively fixed timing of sex change [88], while in other species, the sex change occurs at sizes that are highly variable. These differences in size and age at which the sex change occurs are often mediated by environmental factors [46, 89–92]. For instance, sex change in mollusks can be delayed in populations where large females are present [89, 90]. Additionally, in populations subjected to higher mortality rates or slower growth rates, sex change seems to occur earlier [93]. Also, it has been reported that social control of sex change occurs in Patellogastropod limpets [91, 92]. In this case, several possible cues for sex change have been suggested such as, contact frequency between individuals, available movement area, food availability, growth rate, pheromonal information, and communication by mucus traces left by individuals during foraging excursions [91].

Hermaphroditism is an evolutionarily advantageous strategy for species with low population densities or low motility such as limpets, since under such conditions, hermaphroditism is supposed to increase the likelihood of successful fertilization [87]. Reproductive success in broadcast spawners, such as limpets, is correlated to the quantity of gametes released into the water column. It is believed that larger limpets produce more gametes than smaller individuals. Additionally, sex change in protandrous hermaphrodite species results in an increase of female individuals in the larger size classes. Thus, the sex distribution through sizes in protandrous hermaphrodite limpets makes these species extremely vulnerable to harvest [33], since the depletion of larger and more fecund individuals and females in a higher percentage may potentially alter the sex ratio and reduce the reproductive output of populations [86].

3. Anthropogenic impact on Patellid limpets

Patellid limpets are common gastropods of intertidal rocky shores; however, some species are in serious decline mainly as a consequence of overexploitation [94]. These intertidal and shallow-water grazers are highly vulnerable because of their restricted habitat and its accessibility to human activity [26]. Worldwide, shellfish exploitation has often been shown

to lead to decreased biomass and species richness and cause shifts in community composition [95–98]. These effects are driven by the increase of human population density along the coast, the replacement of subsistence by commercial exploitation, and technological advances in methods of collection, processing, storage, and transport [99, 100]. As a result, the effects of human exploitation add to those of natural processes that influence population size of exploited limpets and are a concern in conservation biology [101]. Limpets have been exploited by human populations since the Palaeolithic period [102] at a subsistence level and used as food and bait in several parts of the world, including Mexico, the United States of America [101], Hawaii [103], Australia [104], South Africa [105], Chile [106], and Macaronesia [53, 107, 108]. More recently, this subsistence activity has been replaced, in many parts of the world, by heavy and highly profitable commercial exploitation, increasing the pressure on these species' stocks. Limpet harvest results in reductions in density and shifts toward smaller individuals and can decrease reproductive output since individual fecundity is greater in larger individuals [44, 109, 110]. Thus, harvesting has both direct and indirect effects on these species. There are also effects on the overall community composition as removal of grazing limpets facilitates the growth of algae [20, 111, 112], leading to further changes within the rocky shore communities [16, 17].

The direct effects of limpet exploitation are the decline of the exploited species' abundance and a shift in size composition of their populations that results from the size-selective nature of limpet harvest [100]. This is a result of larger individuals being more visible, thus more prone to be caught, and due to their greater commercial value [22, 113, 114]. The loss of older and larger individuals results in cascading effects on the biology of these species and the affected populations, including changes in life-history parameters, demographics, reproductive success, and ecological interactions [98].

For instance, the decline of larger individuals in an exploited population of limpets might lead to the complete disappearance of the population's viable size as a consequence of a seriously diminished reproductive success, affecting different species in a differentiated manner, as observed by Martins et al. [115] in the Azores. Protandrous hermaphrodite species are particularly susceptible to changes in their population size composition that promote a decline of frequency of larger individuals, since it directly affects the sex ratio of the population resulting in a decrease in female specimens that in natural conditions occur with higher frequency in the larger size classes. Also, larger individuals represent a greater contribution to the reproductive effort in limpets [104], thus the harvest of larger individuals contributes to a decrease in the reproductive success of marine invertebrates such as reported for *P. ferruginea* [33] and may eventually result in the collapse of exploited populations [86, 116, 117].

Reduction of sizes and abundance of larger individuals in exploited populations of limpets have been reported for *Patella candei* d'Orbigny, 1840 [116] and *Patella candei crenata* [114] in the Canaries, *P. candei* e *P. aspera* in the Azores [115], *Helcion concolor* (Krauss, 1848) [44], and *P. ferruginea* in Algeria [118] and Spain [86], as well as for the species *C. oculus* in Southern Africa [88]. The overexploitation of limpets has prompted the implementation of management strategies in order to protect the exploited populations and mitigate human impacts in several parts of the world [26, 53]. The establishment of species-specific total allowable catch,

minimum size of capture, closed seasons, and closed areas has been the most common measures ensued with this objective. These strategies are thought to maintain sex ratios, preserve age structure, prevent sperm limitation, enhance yield, and restrict evolutionary changes in response to fishing, such as shifts to early maturation [119–122]. When considering limpets, due to the phenomenon of protandrous hermaphroditism, in addition to minimum size limits used to prevent recruitment overfishing, management policies should also consider minimum and maximum size limits [122].

For instance, in Madeira archipelago the harvest of *Patella candei* sensu lato and *P. aspera* is regulated since 2006, enforcing the maximum allowable commercial catch of 15 kg/person/day or 200 kg/boat/day and a minimum capture size of 40 mm. Additionally, the competent authorities became responsible for issuing harvest licenses, limiting the number of active fishermen involved in limpet harvest. A closed season was also implemented between November and February in order to prevent limpet harvest during the reproductive season. More recently, the closed season was modified in order to more effectively provide protection to these heavily exploited species, now lasting from December to March. In the Azores, the over-exploitation of limpets resulted in a drastic decline in population density and abundance of limpet populations, and in order to prevent a complete collapse of the stocks, regulation was implemented through the establishment of limpet protected zones that comprise stretches of coast of a few kilometers where the collection of limpets is strictly prohibited throughout the year, seasonal fishing closures, and minimum legal catch sizes [123].

Martins et al. [123] studied the effect of regulation on the recovery of the exploited populations of limpets in the Azores and concluded that the legislation and current levels of enforcement were insufficient to protect the exploited populations and greater levels of enforcement, such as the establishment of physical barriers and other protective strategies should be considered to protect limpet populations. The authors further elaborate that in the absence of adequate enforcement, a complementary approach that has had positive results is co-management [124], due to increasing awareness of the need to increase ownership of conservation areas and to involve all interested parties in the development of management schemes [125, 126].

4. Marine protected areas and their protective role in exploited limpet populations

Marine protected areas are frequently considered as a key tool in the conservation of marine biodiversity in coastal regions [127, 128] due to its ecosystem-level approach for exploited species. Reserves are supposed to restore and protect exploited marine organisms within their boundaries and have been shown to harbor denser populations, larger individuals, and higher biomass of exploited species [129].

MPAs potentially offer a way to conserve marine biodiversity by prohibiting harvest and at the same time sustaining fisheries by re-establishing natural conditions for reproduction [129–131]. Thus, protected populations would have higher densities and larger individuals

leading to greater production of larvae that would eventually settle outside of the protected area [88, 132–134]. However, increase in recruitment outside reserves can be difficult to verify in the field [135, 136], and there is debate about whether marine reserves can benefit fisheries, as well as act as a conservation tool [137–139].

Human harvesting of limpets is usually size-selective with a strong preference for larger individuals [98] that may potentially alter the sex ratio and reduce the reproductive output of populations in successive hermaphrodite species [75, 140]. A reduction in the abundance of large limpet species, induced by high harvesting pressure, has been observed worldwide with several documented cases of drastic declines such as in the case of the endemic limpet *P. candei* in the Macaronesian Archipelagos [115, 141, 142], *P. ferruginea* considered one of the most endangered marine invertebrates on western Mediterranean rocky shores [118, 143] and *C. oculus* in South Africa [88]. In a more extreme case, the overexploitation as a food source and adornments [144], since pre-Columbian times [145] of *Scutellastra mexicana* (Broderip & G. B. Sowerby I, 1829), resulted in this species being thought extinct [146]. However, some populations of this species were reported to have survived and now the species is considered endangered [147, 148].

MPAs are zones where the harvest of marine organisms is interdicted and are considered a popular alternative to traditional marine resource management measures [149]. Exploited marine organisms in general achieve higher abundance, biomass, and size in MPAs [104, 150]. Halpern [129] reported that abundance and species diversity of marine invertebrates were significantly higher in MPAs regardless of their size.

Halpern and Warner [149] reported that establishing MPAs results in significant increases in the average level of density and biomass in a period of 3 years and that these values are persistent over time. Even though it is considerably difficult to predict the amount of time needed for a community to respond to MPA protection, evidence collected by some authors suggests that the response occurs within 2 years [151, 152]. The speed of response to MPA protection depends on the degree of exploitation to which the species is subjected. If exploitation levels are high, the species are more probable to respond rapidly to the MPA protection, when recruitment occurs at the required levels, as a consequence of the removal of the fishing activity that limits population size, demographics of the species [153–155], and the trophic level occupied by the species, since recruitment is associated to the species' life-history parameters.

In general, for marine invertebrates with a long lifespan and slow growth, it is assumed that the response to protection from MPAs occurs at a slower rate [149]. Some limpet species such as *P. candei* sensu lato and *P. aspera* are considered to have slow growth and relatively long lifespan, thus they are extremely vulnerable to size-selective harvest and would have a slower response to MPA protection [53] (P. Henriques, pers. comm.).

Another possible effect of MPAs is the enhancement of recruitment on adjacent exploited populations, since the higher densities and larger individuals in reserves are expected to lead to greater production of larvae than in nearby exploited areas [88]. Therefore, MPAs are expected to enhance adjacent fisheries through the export of larvae [132, 133]. However, it is still unclear how and to what extent reserves influence exploited populations regarding the renewal of recruitment on these populations, due to the export of larvae originated in MPAs

[137, 138, 156]. For instance, Hockey and Branch [157] found that limpet populations closer to protected areas benefit from an increase in juvenile individuals, suggesting a spillover of recruitment from MPAs. Nevertheless, the correlation between larvae production in MPAs and recruitment on exploited populations is difficult to predict, due to the difficulties in determining patterns of physical transport, especially at small scales [78, 79, 158].

According to Halpern [129], the average values of several biological variables are 20 to 30% higher in populations of MPAs when compared to exploited populations, independent of MPA size, indicating that small MPAs can also produce high values. Several studies have reported a pattern of better preserved populations of limpets in MPAs regarding abundance and biometric structure, for example *P. candei* in Fuerteventura [116], *P. candei crenata, P. aspera* and *P. rustica* in the Canaries archipelago [114], *P. ferruginea* in the Mediterranean [159], *C. oculus* in South Africa [88] as well as *H. concolor, Scutellastra longicosta* (Lamarck, 1819) and *Scutellastra granularis* (Linnaeus, 1758) in South Africa [26].

Núñez et al. [116] studied the abundance and size composition of eight populations of the heavily exploited *P. candei* in the island of Fuerteventura, two of which were included in two protected areas, and reported that these two populations were the best preserved in terms of abundance and size composition, while the areas closer to human settlement, thus more accessible, exhibited less abundance and smaller size individuals. Another study in the Canaries archipelago by Ramírez et al. [114] showed that the populations of limpets exposed to anthropogenic effects return lower levels of abundance and smaller size composition compared to more isolated populations; even when the populations are encompassed in an MPA, the non-enforcement of the imposed regulations and lack of surveillance may compromise their effectiveness. Coppa et al. [159] also reported that the impact of MPAs in the protection of the endangered limpet *P. ferruginea* in terms of population density, spatial distribution, and morphometric characteristics is inversely correlated to accessibility.

The effect of MPAs in population density, size structure, and biomass of the exploited limpet *C. oculus* in South Africa was assessed by Branch and Odendaal [88], resulting in important increases of the studied parameters in MPAs when compared to exploited populations. Also, survivability, sex ratio, and reproductive output were significantly higher in MPAs. Other examined parameters such as growth rate and age at maturity were apparently unaffected by the protection of MPAs. Conversely, recruitment was higher in exploited populations than in protected areas. These results clearly show the necessity for MPAs among the tools used for coastal management.

Nakin and McQuaid [26] reported the effect of MPAs in the populations of heavily exploited limpets *S. longicosta* and *H. concolor* and the less exploited *S. granularis*. The authors evidenced a subtle enhancement of population density and size structure, more evident in heavily exploited species. However, the effects of spatial and temporal variation allied to the existence of poaching activities appear to dilute the effect of marine reserves.

Even though these studies put in evidence the overall benefits of establishing MPAs in protecting the intertidal habitat and the species that inhabit it, they also raise important questions regarding their effectiveness. If on one side, MPAs allow exploited limpet populations to recover in regard

to certain biological parameters, on the other hand their effectiveness is in some cases hindered by the lack of surveillance and poor enforcement of protection regulations. In fact, these two factors seem the most important in determining the effectiveness of MPAs. Nonetheless, the implementation of MPAs even when unable to fully stop illegal harvest of limpet species, results in direct improvements for the protected populations in terms of abundance, size structure, and population density and indirect effects regarding reproductive output of these broadcast spawners. For this reason, the implementation of MPAs has become one of the most widely advocated tools for the management and conservation of coastal marine ecosystems in the recent decades [160, 161].

Several factors affect the response of protected populations, thus comparison between different MPAs is somewhat difficult. In fact, the recovery indicators reported for protected populations may be a consequence not only of MPA protection but also of changes in environmental conditions, biological characteristics of the species and, level of exploitation to which they are subjected [162–164]. The degree of exposure to wave action, as well as the vertical distribution of the species is thought to play an important role in the recovery of limpet populations; limpets more exposed to wave action as well as species exposed for longer periods to desiccation have a less pronounced response to the protection given by MPAs as shown by Branch and Odendaal [88] for *C. oculus* in South Africa.

Unsatisfactory results generally occur in those MPAs that are affected by inappropriate planning, ineffective surveillance, poor acceptance by local communities, and the lack of political will to reinforce the importance of environmental protection [140, 165–167]. For instance, Coppa et al. [159] concluded that although the designation of MPAs as a tool to preserve the remaining populations of the heavily exploited *P. ferruginea* is of extreme importance, for these MPAs to fulfil their goal, additional measures must be considered. In 2015, Coppa et al. [163] suggested that without a joint effort toward the protection of intertidal habitats by enforcement bodies, regulators, researchers, and sea users, the MPAs will not be able to achieve their conservation objectives.

The effectiveness of MPAs' conservation of limpet populations could be enhanced through the implementation of several additional measures that encompass a broader view of these exploited populations and the biological and ecological factors that influence their capacity to recover. For instance, it is necessary to determine which actions are required to ensure the reproductive success of individuals, essential to maintain the genetic biodiversity of overexploited species, particularly in species with absent gene flow between populations, since inbreeding increases the extinction probability of wild populations [168]. Also, the reintroduction or reinforcement of recruitment of depleted populations with allochthonous specimens produced by artificial fertilization procedures could be considered as a strategy to further fulfil the MPAs' conservation objective [169].

The establishment of MPAs as a conservation tool of marine coastal habitats and species has returned valuable contributions over the years, particularly in terms of density, abundance, and size structure of exploited species. However, to overcome limitations a possible route to improve the success of conservation strategies could be the establishment of networks of MPAs

based on solid scientific information that identifies the type of measures that need to be imple-
mented. Planning should consider the number and size of MPAs, which should be large enough
to ensure the recovery of protected populations but sufficiently spaced in order to allow the
spillover of recruits and adults to the exploited populations. MPA planning should ultimately
target the ecosystem and not a specific exploited species, since the success of a reserve depends
not only on the recovery of a single species but on the recovery of the ecosystem to which the
species belongs. Additionally, due to geographic specificities, the prevalent abiotic factors and
how they influence the target ecosystem should be considered when planning MPAs. Also,
continuous monitoring of the effects of MPAs on the exploited populations would allow for a
more adequate management of MPAs, allowing for the adjustment of the protective measures
as needed.

Besides adequate planning of MPAs, new conservation strategies are required to imple-
ment measures that raise public awareness and the political will of decision makers that
would allow for innovative approaches involving not only decision makers but also the
end users of these marine resources in the conservation effort of exploited species, par-
ticularly to avoid illegal poaching, which is one if not the greatest factors hindering MPA
success.

Acknowledgements

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