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The influence of marine protected areas on the patterns and processes in the life cycle of reef fishes

André L. R. Lima · Linda M. Eggertsen ·
Jessyca L. S. Teixeira · Alexandre Schiavetti ·
Fabiana C. Félix-Hackradt · Carlos W. Hackradt

Abstract Successful settlement and recruitment of reef fish are influenced by spatial and temporal processes and variables on distinct scales. Moreover, they require survival at various stages in different environments for species with a complex life cycle, as in the case of most reef fish. The variability in those processes can be explained by biotic and abiotic factors that affect pre and postsettlement stages. Despite the many benefits of marine protected areas (MPAs) for fish and fisheries, the positive effects of protected areas on the reproduction, settlement, and recruitment of reef fish are still unclear. The present study reviewed the biotic and abiotic factors that influence the settlement and recruitment of reef fish, especially regarding the role of MPAs in these processes. This bibliographic review shows that the larval settlement is shaped by the interaction of biological traits (e.g., life history) and environmental factors (e.g., temperature, currents), which are determinants of the life cycle and population structure of reef fish. The main contribution of MPAs to these processes is the export of eggs and larvae to adjacent regions. However, further research is needed on the issues of settlement and recruitment in the specific context of MPAs. The absence of studies on this topic, particularly how protection affects, directly and indirectly, recruitment variability and how this is reflected in the adult population, hinders MPAs objectives and seems to be a serious shortcoming in attempts to support future populations at ecologically adequate levels.

Keywords Recruitment · Settlement · Marine protected areas · Reef fish

A. L. R. Lima (✉) · J. L. S. Teixeira ·
F. C. Félix-Hackradt · C. W. Hackradt
Marine Ecology Conservation Lab. Centre
for Environmental Science, Universidade Federal do Sul
da Bahia, Campus Sosígenes Costa, Rod BR 367 Km 10,
Porto Seguro, Bahia 45810-000, Brazil
e-mail: alrlima@uesc.br

A. L. R. Lima
Programa de Pós-Graduação em Ecologia E Conservação
da Biodiversidade, Universidade Estadual de Santa Cruz,
Rod Jorge Amado Km 16, Bairro Salobrinho, Ilhéus,
Bahia 45662-900, Brazil

L. M. Eggertsen
Marine Macroecology and Conservation Lab,
Departamento de Ecologia E Evolução, Universidade
Federal de Santa Maria, Avenida Roraima, 1000,
Prédio 17, Sala 1140I, Bairro Camobi, Santa Maria,
Rio Grande Do Sul, Brazil

A. Schiavetti
Ethnoconservation and Protected Areas Lab.
Departamento de Ciências Agrárias E Ambientais
(DCAA), Universidade Estadual de Santa Cruz, Ilhéus,
BA, Brazil

A. Schiavetti
CESIMAR, CENPAT, Puerto Madryn, Chubut, Argentina

Introduction

Reef fish settlement (transition from a pelagic to a benthic environment, preceded by larval metamorphosis) is considered a necessary precursor for recruitment into a population (Myrberg and Fuiman 2002; Greenfield 2003). The term "recruitment" means the insertion of new individuals into an adult population to replenish the population (Robertson et al. 1988; Robertson 1990). Successful settlement and recruitment are influenced by processes and variables that spatially and temporally (from days to years) operate on different scales (Lozano and Zapata 2003; Félix-Hackradt et al. 2013a; Grande et al. 2019), and require survival at various stages and in different environments for species with a complex life cycle, as in the case of most reef fish (Goldstein and Sponaugle 2020).

The variability in these processes can be explained by biotic and abiotic factors that affect the presettlement stages, such as adult reproduction (Robertson et al. 1988; Meekan et al. 1993; Cowen and Sponaugle 1997; Jonsson and Jonsson 2014; Vagner et al. 2019). This variability can also affect the pelagic larval stage, where hydrodynamic features, oceanographic processes, the lunar cycle, larval sensory systems, and swimming behavior and ability influence the growth, survival, condition, and transport of larvae before settlement (Shima and Osenberg 2003; Sponaugle et al. 2006; D'Alessandro et al. 2007; Leis et al. 2011, 2015; Sponaugle et al. 2012; Shulzitski et al. 2015; Shima and Swearer 2019; Shima et al. 2020, 2021).

The most common reproductive strategy used by reef fish involves the release of propagules (eggs or larvae) into the ocean, where the propagules seek resources and protection during their development (Doherty and Fowler 1994; Sale 2002; Miller and Kendall-Jr 2009). In the dynamic ocean, many larvae are dispersed by currents to new locations, some of which are more favorable than others for their survival (Doherty and Fowler 1994; Sponaugle et al. 2012; Shulzitski et al. 2016; Vaz et al. 2016; Goldstein and Sponaugle 2020). This reproductive strategy is characterized by high risk and almost total mortality of propagules compared with other approaches, especially parental care strategies (Sale 2002; Miller and Kendall-Jr 2009; Green and McCormick 2005).

Many species compensate for this extreme mortality rate by producing a large number of zygotes. This combination of high fertility and variable rates of larval mortality may result in large variations in replenishment strength (Roughgarden 1988; Meekan et al. 1993; Russ et al. 1996; Goldstein and Sponaugle 2020). Moreover, these factors can substantially impact the dynamics, demographics, population structure, and community composition (D'Alessandro et al. 2007; Grorud-Colvert and Sponaugle 2009). Thus, the spatial and temporal variability in the presettlement stage can be considered a key factor for the replenishment of adult populations (Robertson et al. 1988, Tolimieri et al. 1998; Goldstein and Sponaugle 2020). Therefore, understanding the factors that influence these variations in the presettlement stages and their ecological implications for recruitment is essential for the conservation of reef fish species (Sponaugle and Grorud-Colvert 2006a, b; Félix-Hackradt et al. 2013b), mainly because variations in larval supply can lead to recruitment failure and affect fish stocks (Russ et. al 1996; Harrison et al. 2020).

During the settlement and recruitment stages, most fish undergo a critical ontogenetic shift from pelagic environments to benthic reef habitats, which results in high mortality (Sogard 1997). Moreover, settling fishes are influenced by dynamic and spatially variable processes, such as productivity and food availability, which affect the growth and condition of the postlarval fish (Levin et al. 1997; Booth and Hixon 1999; Leahy et al. 2015). Postsettlement stages are further affected by events such as predation, competition, growth rates, and ontogenetic shifts in diet (Shima and Osenberg 2003; Doherty et al. 2004; Hixon and Jones 2005; Almany and Webster 2006; Goldstein and Sponaugle 2020; Wen et al. 2012), which consequently shape the structure of reef fish populations (D'Alessandro et al. 2007; Goldstein and Sponaugle 2020).

The marine protected area (MPA) designation has been recognized as a powerful tool for the conservation, recovery, and management of marine resources (Fenberg et al. 2012; Lima et al. 2021), including restoring population structure, increasing the abundance and diversity of fish, increasing the biomass and average size of individuals, and remediating degraded marine habitats (García-Charton et al. 2008; Félix-Hackradt et al. 2018). Thus, these variations in composition, structure,

and function at various levels of hierarchical organization from species to landscapes (i.e., ecological integrity) between MPAs and unprotected areas can lead to differing settlement and recruitment rates in addition to differing recruit survival rates (Grorud-Colvert and Sponaugle 2009). Specifically, by protecting a certain habitat or seascape, MPAs can ensure the availability of settlement grounds for recruits (Green et al. 2015; Carr et al. 2017).

Understanding larval settlement and recruitment is essential for the implementation and management of MPAs, whereas the geographical position and design of an MPA at the local scale may determine whether nursery habitats are included, which favors species settlement (Grorud-Colvert and Sponaugle 2009; Félix-Hackradt et al. 2018) and the sustainability of future populations (Halpern 2003). At regional and global scales, the location of MPAs may help maintain dispersal corridors, which favor the connectivity and flow of larvae and propagules between reefs (Fontoura et al. 2022; Krueck et al. 2017). In this study, we aimed to review the factors that influence the settlement and recruitment of reef fish; identify the variables that affect the reproduction, presettlement, postsettlement, and subsequent recruitment of adult populations; and highlight the role of MPAs in these processes.

Processes that influence larval settlement, recruitment, and population dynamics

The interaction of biological processes and the environment, such as life-history strategies, temperature, behavior, currents, tides, and seascape configurations, shapes larval settlement (Sponaugle et al. 2012; Félix-Hackradt et al. 2013b; Brown et al. 2016; Grande et al. 2019; Goldstein and Sponaugle 2020). These processes are critical for several species of reef fish, where the larvae remain in plankton for days to years before settling in the benthic environment (Cowen and Sponaugle 1997). The ability to predict settlement, recruitment, and population dynamics depends on understanding how biological processes interact with the dynamic physical environment (Wong-ala et al. 2018; Grande et al. 2019).

Reproductive factors

The reproductive period is the first stage of the life cycle and is characterized by several strategies that are used to minimize larval mortality and ensure recruitment success in adult populations (Meekan and Fortier 1996; Jonsson and Jonsson 2014; Vagner et al. 2019). Some of these strategies include the number of reproductive events (iteroparous or semelparous), spawning type (total vs. patch), mating system (reproductive aggregations, monogamy, or polygamy), sex system (gonochoristic or hermaphrodite), secondary sexual characteristics (with or without sexual dimorphism), preparation of spawning sites, spawning sites, fertilization type (internal or external), embryonic development (oviparous and viviparous), and degree of parental care (Cowen and Sponaugle 1997; Murua et al. 2003; Lowerre-Barbieri et al. 2016). These strategies are related to the supply of eggs and can affect the quality and quantity of larvae during development (Kerrigan 1997) and the survival of propagules (McCormick and Hoey 2004). Moreover, these strategies were selected over evolutionary timescales to ensure population persistence within a given spatial context (Roy et al. 1992; Lowerre-Barbieri et al. 2016). Thus, reproductive success is achieved through trade-offs between the rate of reproductive output and the survivorship rate associated with that output. At the species level, if egg, larval, and juvenile mortality is high, fecundity must also be high to offset losses due to mortality. However, if offspring mortality is reduced through parental investment, reproductive success can be achieved with much lower fecundity (Lowerre-Barbieri et al. 2016). Specifically, parental care is related to the large size and growth of eggs and larvae of some species (Jonsson and Jonsson 2014). Green and McCormick (2005) observed that the larval size of clownfish species at metamorphosis is mainly affected by parental care. In this specific case, males play an extensive role in nest-tending and parental care during the relatively long embryonic period of the larvae. This trait enhances growth and development and influences survival before and after settlement.

Maternal contributions are generally considered more important because of the nutrition supplied to the embryo (Bernardo 1996). Embryonic and larval characteristics, such as egg size, rate of development,

metabolism, growth, and viability, are affected by the body condition and genotype of the mother (Kerrigan 1997; Marteinsdottir and Steinarsson 1998). This factor is related to the big old fat fecund female fish (BOFFFF) theory, where larger and older females produce larger quantities of eggs and larvae of bigger size and with larger fat reserves (Hixon and Conover 2007; Carter et al. 2017), resulting in increased growth and survival rates (Jonsson and Jonsson 2014; Palumbi 2004; Barneche et al. 2018; Lavin et al. 2021). Despite high fecundity, the scarcity of larger individuals suggests that their overall contribution to population replenishment may be low because the higher abundance of numerous young mature female fish (NYMFF) may account for a substantial proportion of the larval production that drives population replenishment (Lavin et al. 2021).

Many species exhibit lunar spawning periodicity with tidal cycles (spring tides and/or neap tides) (Robertson et al. 1988; Robertson 1990; D'Alessandro et al. 2007). Spawning during the new or full moon (i.e., spring tides) can facilitate the transport of eggs away from shallow waters and rapidly increase the distance between eggs and potential predators, thus increasing the chances of survival (Robertson 1990). Additionally, spawning during a new moon may be related to an attempt to minimize the predation risk from visual predators (Robertson et al. 1988). Spawning during neap tides reduces larval dispersion and maintains larvae near settlement habitats (Jones et al. 2005). Variations in environmental conditions during the reproductive stage are also related to the development and survival of fish larvae and eggs (Jonsson and Jonsson 2014). Water temperature is a key factor in early life history and influences reproduction through the development and maturation of gametes as well as spawning, hatching, and later development of larvae (Jonsson and Jonsson 2014; Vagner et al. 2019). Suitable temperatures during egg development can increase growth rates and give organisms an advantage over those developed under less favorable conditions (Jonsson and Jonsson 2014). Maintaining eggs in warmer water may lead to faster larval and juvenile growth, consequently decreasing the time spent at each developmental stage (Sponaugle et al. 2006; Grorud-Colvert and Sponaugle 2011). Because individuals are exposed to a high risk of predation during the larval stage, shortening this stage may

reduce this pressure and lead to higher survival rates (Vagner et al. 2019).

Despite the many variables that act in reproductive processes, MPAs can also influence this crucial part of the life cycle of reef fish (Fig. 1). In MPAs, the number of fish and the biomass within their boundaries are increased (Anderson et al. 2014; Hackradt et al. 2014, 2020). They also potentially improve fishing in adjacent areas because of the spillover of adult individuals (Hackradt et al. 2014; Silva et al. 2015; Grüss et al. 2011). Additionally, MPAs lead to the production of more propagules (Planes et al. 2009a; Christie et al. 2010; Crec'Hriou et al. 2010; Di Franco et al. 2012b; Harrison et al. 2012; Carter et al. 2017). The export of eggs and larvae from MPAs to adjacent areas is one of the main benefits of protection (Planes et al. 2000; Planes et al. 2009a; Di Franco et al. 2012b). MPAs with a high density of mature and large individuals (BOFFFF) create a higher potential for egg and larval production compared with fished areas (Di Franco et al. 2012b; Harrison et al. 2012), especially for sedentary fish species (Carter et al. 2017). Larger females have disproportionately higher fecundity and produce offspring of larger size, lipid content, and possibly higher quality (Palumbi 2004; Hixon and Conover 2007; Carter et al. 2017; Barneche et al. 2018), leading to an increased probability of survival (Shima and Findlay 2002; Raventos and Macpherson 2005; Searcy and Sponaugle 2001). The fact that larger female fish may participate in as many reproductive events in each reproductive season as smaller female fish may explain why larger fish are so important for the replenishment of marine fish populations (Barneche et al. 2018). According to Marshall et al. (2019), the MPA contribution to fish offspring is underestimated: in MPAs, fish produce an estimated 224 times as many eggs as those in fished areas of equal size, as shown for *Dicentrarchus labrax*. This is possible because in approximately 95% of fish, an increase in body size leads to a hyperallometric increase in reproductive output (Barneche et al. 2018). Therefore, MPA protection can have a more notable effect on the production of eggs and larvae than previously thought (Marshall et al. 2019).

Several reef fish species spawn in large groups, known as fish spawning aggregation (FSA) events, which can be favored by protection measures, as shown by Hamilton et al. (2011). The establishment of community-based MPAs at FSA sites can
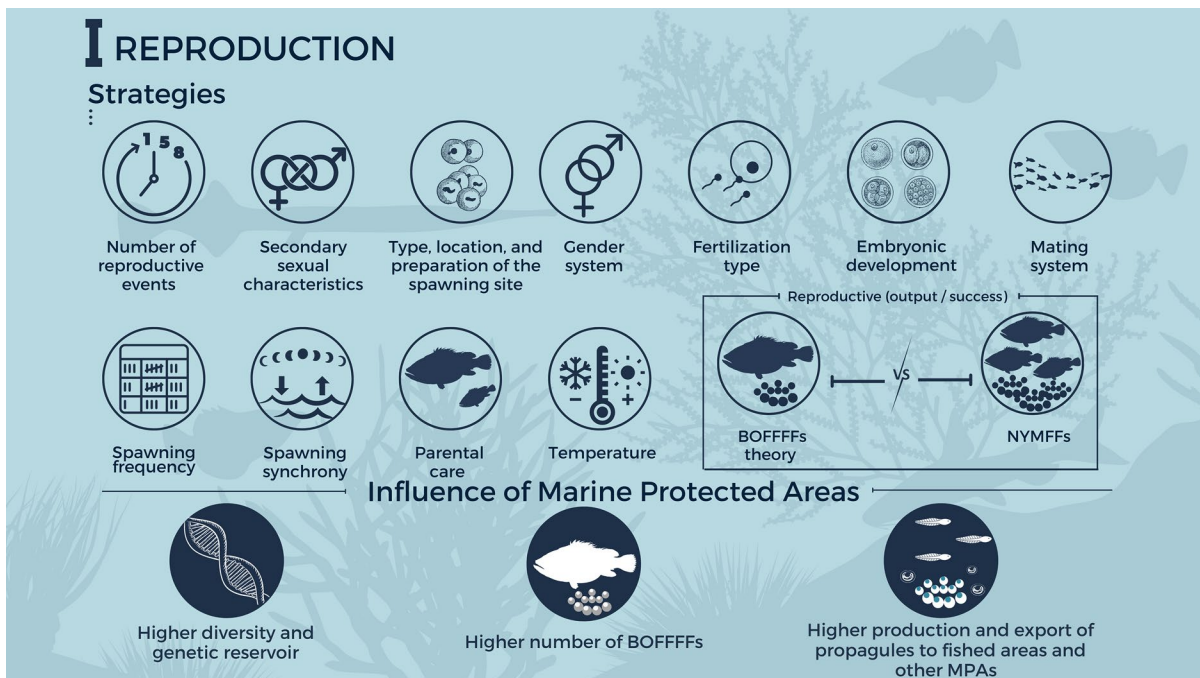
I REPRODUCTION

Strategies

Number of reproductive events

Secondary sexual characteristics

Type, location, and preparation of the spawning site

Gender system

Fertilization type

Embryonic development

Mating system

Spawning frequency

Spawning synchrony

Parental care

Temperature

Reproductive (output / success)

BOFFFFs theory

vs

NYMFFs

Influence of Marine Protected Areas

Higher diversity and genetic reservoir

Higher number of BOFFFFs

Higher production and export of propagules to fished areas and other MPAs

Fig. 1 Biotic and abiotic influences in the reproduction stage of reef fish and the influence of MPAs on these processes

substantially increase the abundance of target species, as in the case of *Epinephelus polyphekadion* populations, which increased tenfold after the establishment of an MPA and contributed to the sustainability of local fisheries. In addition to contributing to increasing spawning-stock biomass, MPAs at FSA sites can normalize the sex ratio in protogynous fish populations (Grüss et al. 2014), which increases egg fertilization and influences reproductive success. However, these effects can be depressed when the fishing pressure remains high outside the MPAs. Furthermore, MPAs can play an important role in preserving the genotypic diversity, along with age structure, of the exploited fish population (Field et al. 2006). A recognized fishing effect is the artificial selection of small, fast-growing fish with early maturation (Law 2007; Pinsky and Palumbi 2014). MPAs can act as a genetic reservoir for allelic richness (Pérez-Ruzafa et al. 2006; Bezerra et al. 2018) and heterozygosity (Félix-Hackradt et al. 2013c), thus contributing to the restoration of the genetic potential of exploited species through gene flow.

Eggs and larvae can be retained and/or exported beyond their limits, with potential effects on population recovery and replenishment in other MPAs and surrounding fished areas (Carr et al. 2017). MPA networks can act as an important source of propagules for local populations and areas open to fishing on a regional scale. According to Harrison et al. (2012), in a study of two families of reef fish (Lutjanidae and Serranidae) in the Great Barrier Reef, Australia, MPAs exported a high proportion of offspring to the adjacent fished areas. Additionally, these authors reported substantial larval retention and connectivity between the neighboring MPAs. Additionally, the proportion of dispersion trajectories observed below 30 km was consistent with the findings of recent studies, according to which coral reef fish larvae may disperse over relatively short distances (Jones et al. 2005), despite spending several weeks in a pelagic environment. Christie et al. (2010) found no notable larval retention patterns; in contrast, they found high rates of ecologically important population connectivity between MPAs around an island in Hawaii, as well as direct evidence of larval contribution to unprotected areas, thus leading to the replenishment of exploited populations. In large MPAs (e.g., 10–20 km), the relative proportion of larvae that remain in the immediate area is larger than the proportion that disperses and is exported outside

the limits (Green et al. 2015). In contrast, smaller MPAs (0.5–1 km) export proportionately more larvae to adjacent areas, including other MPAs (Green et al. 2015; Carr et al. 2017). Although smaller MPAs increase the proportion of larvae that replenish adjacent populations, they must be large enough to support a persistent and productive adult population (Green et al. 2015; Cabral et al. 2016). Therefore, MPAs must provide high-quality productive adult habitats and well-enforced protection (Jones et al. 2009; Carr et al. 2017).

Presettlement factors

In the planktonic stage, larvae remain in a spatially and temporally diverse environment that is highly dynamic and subjected to biotic and abiotic factors, all of which may determine survival, growth, and dispersion (Cowen and Sponaugle 1997; Sponaugle et al. 2006; Jonsson and Jonsson 2014; Vagner et al. 2019) (Fig. 2). Early life history traits are considered extremely important for success in the presettlement stage (Vigliola and Meekan 2002; Raventos and Macpherson 2005; Searcy and Sponaugle 2001). In this regard, Bergenius et al. (2002)

observed a positive relationship between larval growth 1–2 weeks after hatching, during the pelagic larval duration (PLD), and successful settlement and recruitment for the surgeonfish *Acanthurus chirurgus*. Similarly, for the pomacentrid *Stegastes partitus*, fast larval growth rates are related to higher larval survival rates (Wilson and Meekan 2002). The findings of several other studies have corroborated the theory that fast growth rates in larvae and postsettlers lead to a higher rate of survival and, consequently, contribute to the success of recruitment (Meekan and Fortier 1996; Shima and Findlay 2002; Vigliola and Meekan 2002; Jenkins and King 2006; Hoey and McCormick 2004).

Shima and Findlay (2002) showed that larval quality is related to the success of reef fish settlement and recruitment, with rapid larval growth correlated with reduced PLD and increased postsettler survival. Fast larval development may indicate high fitness of parents (maternal condition and genetics) and/or favorable pelagic conditions (e.g., temperature, food availability, and oceanographic features) (Shima and Findlay 2002). The environmental conditions in a settlement location may further influence survival after settlement. Large larvae at hatching (Meekan and
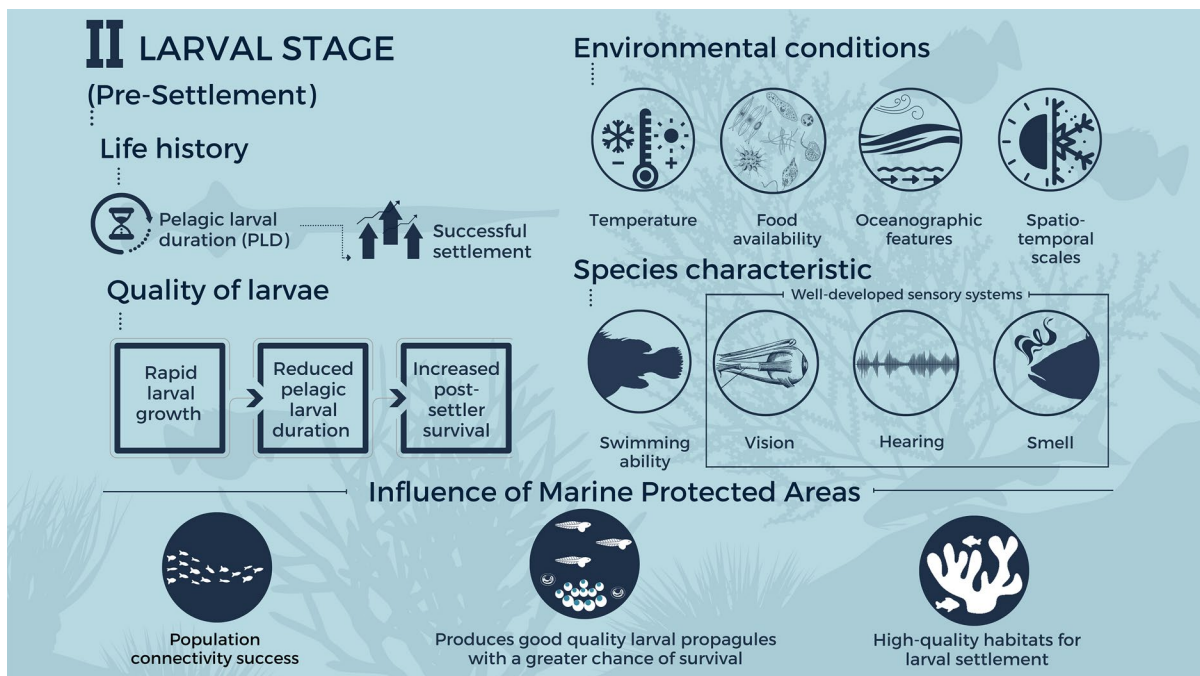

Fig. 2 Biotic and abiotic influences in the pre-settlement stage of reef fish and the influence of MPAs on these processes

Fortier 1996; Palumbi 2004; Raventos and Macpherson 2005) are more developed (McCormick and Hoey 2004) and in better condition during the metamorphosis period (Searcy and Sponaugle 2001); consequently, the survival rate of settlers is higher (Shima and Findlay 2002), thus supporting the growth–mortality theory (Anderson 1988).

The "growth-mortality" theory suggests that the survival of individuals during the planktonic stage is selective due to a range of events related to the size of larvae in predator–prey interactions. Mortality rates in planktonic larvae decline with growth, as fewer predators can consume larger larvae (Anderson 1988). For this reason, development during the first stages of larval life is more important in determining survival than later periods during PLD, as they directly influence mortality rates and recruitment success. However, despite the advantages of larger body size, high growth rates may not always be beneficial (Sogard 1997). Behavioral selection of habitats or social conditions that improve the chance of survival can result in lower growth rates, as behavioral responses to potential predators and competitors may lead to energy losses and thus reduced growth. Under these conditions, the advantages of large size are outweighed by the advantages of better protection against predation and balanced physiological functions, such as the costs related to growth (Sogard and Olla 2002).

Factors such as wind, current, tide, temperature, precipitation, river discharge, and water mass are variables that may be responsible for larval distribution in coastal habitats (Cowen and Sponaugle 1997; Shima and Findlay 2002; Bergenius et al. 2005; Alemany and Deudero 2006; Hamilton et al. 2008; Carassou et al. 2009; Lemberget et al. 2009; Gamoyo et al. 2019; Álvarez et al. 2012; Sim-Smith et al. 2013; Félix-Hackradt et al. 2013a; Beldade et al. 2016). Other oceanographic events, such as fronts (Sabatés and Masó 1990; Shulzitski et al. 2016), whirlpools (Shulzitski et al. 2016; Vaz et al. 2016), eddies (Shulzitski et al. 2016), topographic characteristics (Mullineaux and Mills 1997; Vaz et al. 2016; Ospina-Alvarez et al. 2018), seasonal configurations (Brown et al. 2016), and surface slicks (Whitney et al. 2021) are also considered important in shaping larval dispersal patterns.

The positive relationship between water temperature and the growth rate of larval fish and reduced PLD is well described in the literature (e.g., Benoît et al. 2000; Sim-smith et al. 2013). Higher temperatures usually increase metabolic rates and food consumption in fish, leading to an increase in growth rates and a reduction in PLD (Benoît et al. 2000; Sim-smith et al. 2013). A higher abundance of species in the summer in coastal waters of the Mediterranean was correlated with the configuration of the thermocline together with increased temperature (Álvarez et al. 2012). These factors produce a food-rich environment in the water column (i.e., phytoplankton bloom), thus influencing the spawning processes of some fish species and, consequently, the mortality of larvae due to reduced starvation-associated processes.

Onshore transport mechanisms may be particularly important for populations of snapper *Chrysophrys auratus* (Sparidae) on the western coast of New Zealand, which are subject to very strong winds and tidal currents (Sim-Smith et al. 2013). In this case, the temperature, tidal range, and wind may be important factors in the survival and transport of the larvae of *C. auratus* to settlement habitats (Sim-Smith et al. 2013). In the Mediterranean, currents and cross- and alongshore winds are important for predicting larval occurrence in coastal zones (Félix-Hackradt et al. 2013a).

Fronts and eddies can create patchiness in pelagic habitats and produce variability in the physical parameters and predator and prey densities that larvae may encounter (McGillicuddy et al. 1998; Galarza et al. 2009; Shulzitski et al. 2016). Mesoscale eddies have long been hypothesized to serve as important larval habitats because they potentially enhance and concentrate productivity (Bakun 2006). Larvae that encounter high-productivity eddies are larger and faster (Shulzitski et al. 2015). Eddies have also been hypothesized to function as both a larval retention mechanism (Beldade et al. 2016) and an onshore transport mechanism (Sponaugle et al. 2005; D'Alessandro et al. 2007). Surface slicks structure the surface of the ocean, thus strongly influencing the distribution and ecology of larvae by providing critical early life habitats for fish development from eggs to larvae to juveniles. Moreover, they concentrate food and shelter for developing larvae, which potentially increases their survival rates and bolsters the recruitment of young fish (Whitney et al. 2021).

Although the abovementioned factors related to larval transport influence the settlement process,

larvae are capable of swimming and actively select habitats for settlement (Fisher et al. 2000, 2022; Leis et al. 2015; Nanninga and Manica 2018; Downie et al. 2021b). This factor is important for the dispersal of reef fish (Leis et al. 2009, 2011; Fisher and Leis 2010; Downie et al. 2021b; Fisher et al. 2022) and for self-recruitment processes (Jones et al. 2005). The swimming abilities of reef fish during early life-history stages determine the degree to which individuals may influence their dispersal, which is essential for the feeding and predation factors of their basic ecology (Fisher and Leis 2010; Downie et al. 2020; Fisher et al. 2022). Thus, the hypothesis that reef fish larvae inefficiently swim in a hydrodynamic environment seems unjustified for most of their pelagic stages (Leis et al. 2009; Fisher and Leis 2010). Leis et al. (2009) measured the swimming speeds and orientation ability of the larvae of three families (Ephippidae, Lutjanidae, and Serranidae) and found that these larvae could directly influence dispersal outcomes through horizontal swimming because their average swimming speeds were higher than those of average currents in many coastal areas. However, larvae do not swim faster than ambient currents, which influences their dispersal outcomes. By controlling their vertical distribution, larvae can potentially indirectly influence their dispersal, where the current velocity differs with depth, as occurs in many coastal environments, and change their horizontal swimming direction (Leis et al. 2009). In addition, Downie et al. (2021b) highlighted the role of habitat in swimming performance because reef fish larvae show impressive swimming capabilities compared with their pelagic and demersal counterparts. According to these authors, reef fish larvae need to grow larger to swim against oceanic and reef currents and select new or natal reef habitats in which to settle.

In addition to their swimming capability, fish larvae possess well-developed sensory systems (Majoris et al. 2021) to locate suitable habitats and orient themselves by following and/or detecting magnetic fields, smells, sounds, and visual cues (Leis et al. 2011; Huijbers et al. 2012; Lecchini et al. 2013). However, their perception varies according to spatial scale and type of stimuli, in which magnetic (10–1000 km) and olfactory cues are perceived at longer distances (0–50 km) than acoustic (0–10 km) and visual (0–100 m) cues (Leis et al. 1996; Staaterman et al. 2012). Thus, the relative importance of

active behavior in the settlement of larvae of some reef fish species may be similar in magnitude to that of oceanic processes, or the combination of these factors can be decisive to their success in finding and recruiting suitable settlement habitats (Downie et al. 2021b; Fisher et al. 2022). The ability of larvae to "choose" their settlement habitat was related to higher levels of self-recruiting populations than expected (Leis and Carson-Ewart 2003).

The habitat type plays a key role in the settlement process (Tolimieri 1995; Costa et al. 2020; Downie et al. 2021b). Habitats, such as coral reefs, seagrass, rhodoliths, and seaweed beds, can provide three-dimensional structures that serve as nurseries, settlements, forage, and refuge areas (Berkström et al. 2012; Díaz et al. 2015; Amado-Filho et al. 2016; Eggertsen et al. 2017; Costa et al. 2020). Some species can even delay settlement until they find the perfect site for metamorphosis and settlement (McCormick 1999). The more structurally complex the habitat, the more shelter it provides, especially for larvae in the early stages of development (Costa et al. 2020; Felix-Hackradt et al. 2014), indicating that habitat quality (i.e., healthy or degraded) is also related to settlement patterns (McCormick et al. 2010; Gordon et al. 2018). For example, Gordon et al. (2018) found evidence of a relationship between reef degradation and two processes that are fundamental to fish recruitment: larval preferences and juvenile settlement behavior. Their findings demonstrated that pristine soundscapes are more attractive than degraded soundscapes to some reef fishes. Similarly, Downie et al. (2021a) found that oxygen consumption was reduced in new recruits found in degraded habitats, which impacted growth, survival, and, ultimately, recruitment.

The presence of other species or other members of the same species can also influence settlement (Risk 1998; Benkwitt 2017). Adult fish can increase the settlement of conspecifics while decreasing the settlement of other species (Booth 1992; Risk 1998; Benkwitt 2017). Moreover, when adults of the same species are present, the survival rate of juvenile fish may be higher, although growth may be lower (Tolimieri 1995). According to Risk (1998), the presence of conspecifics increased settlement for the two studied species, which could be explained in part by the relative value of adults to settlers as indicators of suitable settlement sites. A strong positive relationship between adult density and settler density would

be expected if adults, adult habitat, or both confer fitness advantages to settlers. For example, the presence of damselfish adults significantly reduces the settlement of heterospecific larvae (Sweatman 1985). Risk (1998) also observed that ocean surgeonfish larvae avoided areas with resident damselfish settlement sites. The observed avoidance may be caused either by an aggressive response by damselfishes to ocean surgeonfish larvae, which prevents the larvae from settling, or by a behavioral decision of the larvae against settling.

Several studies of early life history stages have focused on understanding the variability in settlement considering spatial and temporal scales (Robertson et al. 1988; Meekan et al. 1993; Sponaugle and Cowen 1996, Carassou and Ponton 2007; D'Alessandro et al. 2007; Kaunda-Arara et al. 2009; Hogan et al. 2012; Sponaugle et al. 2012; Félix- Hackradt et al. 2013b; Pusack et al. 2014; Huyghe and Kochzius 2015; Harrison et al. 2020). Robertson et al. (1988) studied the settlement variability of *Stegastes partitus* in the Caribbean and stressed the importance of considering larval production patterns on a variety of temporal scales and the factors that contribute to this temporal variability. Sponaugle and Cowen (1996) indicated that for some species (*Stegastes partitus*), spatial variation in larval supply is largely responsible for the patterns of juvenile recruitment, whereas for others (*Acanthurus tractus*), presettlement patterns of abundance may be substantially modified by postsettlement processes. Félix-Hackradt et al. (2013b) evaluated the interannual, multispecies variability in the recruitment of Mediterranean temperate rocky reef fish species and found a strong pattern of settlement periods, namely in the summer and winter months, with the first period being the most important in terms of species richness. Abundances and timing of settlement were consistent between the years for most species in this study, but settlement success could not be predicted from postlarval abundances. According to Harrison et al. (2020), in a study at the Great Barrier Reef, effective reserve networks take advantage of a "connectivity portfolio effect," which mitigates the temporal volatility in larval supply to ensure the stability of recruitment dynamics, with potential long-term sustainability benefits for exploited fish stocks.

In addition to contributing to temporal stability in larval supply (Harrison et al. 2020), MPA networks can influence several processes in the presettlement stage of reef fish. These processes include enhanced population connectivity success owing to high adult abundance. Therefore, increased offspring output (Christie et al. 2010) can either settle inside the MPA boundaries (self-recruitment) or be exported to fished zones, thus replenishing exploited populations (see Sect. 2.1. Reproductive factors) and providing quality larvae with the highest chance of survival due to healthy fish stocks and large female individuals (Shima and Findlay 2002; Raventos and Macpherson 2005; Searcy and Sponaugle 2001). MPAs can provide high-quality habitats for larval settlement (Almany 2004; Almany and Webster 2006; Johnson 2007) and, consequently, assist in larval navigation by producing substantially louder and richer acoustic fingerprints that increase the distance of reef detection by fish larvae (Piercy et al. 2014) and ultimately result in higher colonization rates (Jaquiéry et al. 2008). However, in a study conducted on an MPA network on the southwest coast of Spain, Félix-Hackradt et al. (2018) found more abundant postlarvae of commercially important species (pelagic and demersal) outside the reserves. To explain their findings, the authors proposed the active selection of habitats for settlement (a mosaic of shallow rocky reefs, boulders, and seagrass meadows), which was better represented outside no-take reserves, as well as the retention of larvae favored by the geomorphological configuration of the coast. Another factor to be considered in this study was that the high abundance of postlarvae in unprotected areas may reflect the production of eggs and larvae in adjacent MPAs by adults, which were remarkably more abundant inside the evaluated MPAs. Therefore, the geographic location of an MPA must consider critical habitats for the fish life cycle, especially nursery habitats, their replication, and their representation (McLeod et al. 2009), thus favoring the settlement process. Additionally, the effectiveness of protecting nursery habitats differs according to the characteristics of each species in terms of their particularities, specific food needs, ideal growing conditions, and the environmental variations to which they are subjected (Planes et al. 2000). In this regard, MPAs that host a large diversity of habitats can be more effective in promoting juvenile fish production because they provide more suitable conditions for settlers to survive, especially for species with a complex life cycle (e.g., multihabitat/ontogenetic habitat

shifts) (Lindholm et al. 2001; Carr et al. 2017). In contrast, in MPAs, larval mortality may be increased by elevated predation, thereby hindering the above-mentioned effects (Planes et al. 2000). MPAs can also improve ecosystem resilience and protect important habitats for reef fish life cycles from climate change (Fox et al. 2016; Carr et al. 2017) (Fig. 2).

Postsettlement factors

The period after settlement is characterized by high mortality rates (Félix-Hackradt et al. 2013b), which are usually caused by predation, mainly within the first days of settlement (Doherty et al. 2004; White 2007; Planes et al. 2009b). Studies have reported the presence of predators (adults or juveniles) with the subsequent recruitment of the analyzed species (Almany 2004; Doherty et al. 2004; Almany and Webster 2006; Arceo et al. 2012). Predators can substantially affect prey survival; therefore, the ability of prey to recognize and defensively respond to predator cues is beneficial to their survival (e.g., avoidance) (Benkwitt 2017) (Fig. 3).

Predation is a key process that influences coral reef fish communities immediately following settlement (Hixon 2015). In an experiment, Benkwitt (2017) found lower recruitment of *Lutjanus mahogani* in reefs with caged native piscivores than in reefs with caged invasive predators. This process appears to be density-dependent because the density of conspecific recruits modifies the effects of predator presence on recruitment, suggesting that extremely high densities may lead to intraspecific competition among recruits. This also influences the distribution of settlers on reefs. In contrast, recruitment of the bicolor damselfish *Stegastes partitus* was unaffected by predator presence or recruitment density, highlighting the importance of species-specific variability in the processes that influence settlement (Benkwitt 2017).

Other density-dependent factors such as competition can also influence recruitment (Fig. 3). Competition for resources (e.g., space, shelter, and food) can lead to a lower status for individuals and therefore result in higher mortality due to predation (Hixon and Jones 2005; White 2007; Planes et al. 2009b). Thus, density-dependent processes (predation and competition) are considered relevant biotic factors in the structuring of adult populations, either directly by predation of recruits or indirectly by competition for resources. Goldstein and Sponaugle (2020)
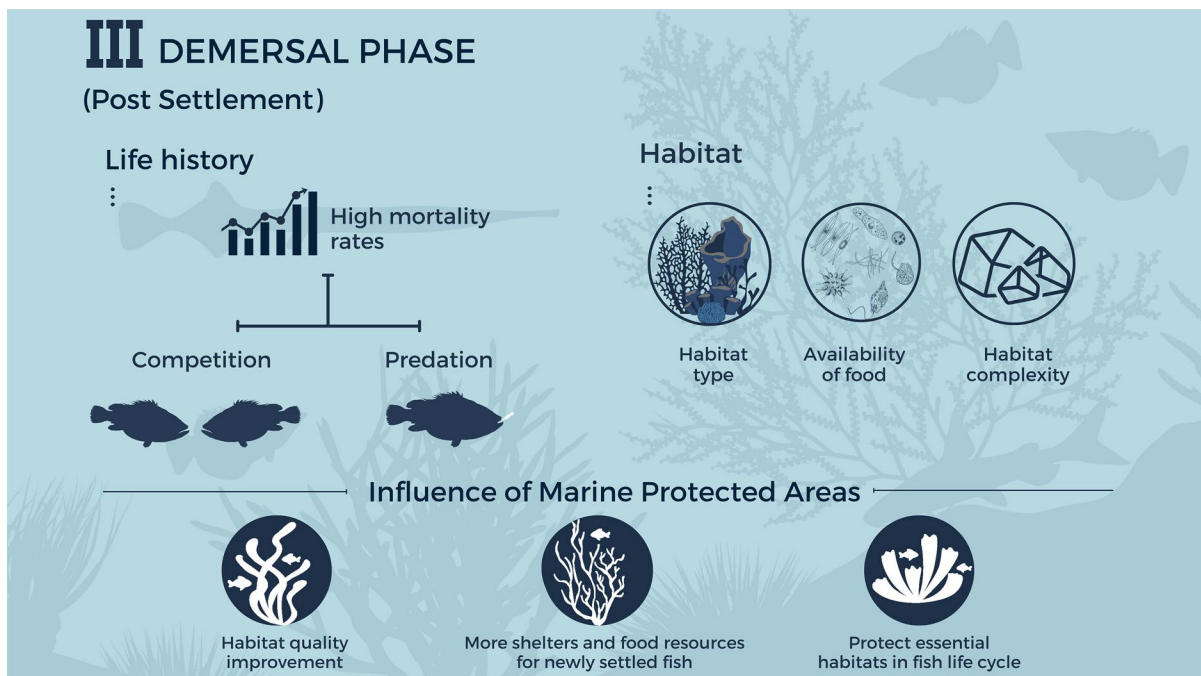

Fig. 3 Biotic and abiotic influences in the post-settlement stage of reef fish and the influence of MPAs in these processes

suggested that a high availability of food might mitigate the effects of juvenile densities and competition for resources. The authors demonstrated that spatial environmental variations, such as productivity (chlorophyll-a production) and habitat heterogeneity (e.g., back reef areas, seagrass meadows, and mangroves) can locally enhance reef fish recruitment rates (Sponaugle et al. 2012; Shulzitski et al. 2016; Goldstein and Sponaugle 2020) and postsettlement growth rates. Consequently, these locations may support large populations despite naturally high mortality rates (Goldstein and Sponaugle 2020).

Habitat type and quality are also important in the recruitment process (Johnson 2007; Félix-Hackradt et al. 2013b; Shulzitski et al. 2016; Goldstein and Sponaugle 2020) (Fig. 3). The spatial variations in settlement and settlement survival at the local scale can be explained by habitat characteristics (i.e., spatial extension, rugosity, geographical position in seascape, substrate types, complexity, sounds, and others) (Costa et al. 2020; Shima and Osenberg 2003; Levin 1991; Levin 1993; Tupper and Boutilier 1997, Almany 2004, Simpson et al. 2005, Félix-Hackradt et al. 2013b). These characteristics increase the capacity of a habitat to shelter a larger number of recruits, depending on the quality of the habitat (Shima and Osenberg 2003) and microhabitat (Tolimieri 1995; Félix-Hackradt et al. 2014) or the number of shelters (Johnson 2007). The presence of organisms, such as macroalgae, seagrass, rhodoliths, and corals, can modify an environment or create microhabitats that provide shelter and food (Tolimieri 1998; Pereira and Munday 2016; Costa et al. 2020), which influence recruitment processes and, therefore, the structure of reef fish communities (Tolimieri 1995; Steele 1999; Shima and Osenberg 2003). Notably, some species have strong preferences for specific habitat types with different characteristics (Félix-Hackradt et al. 2014). Mangroves and seagrass beds, for example, contain a high diversity and abundance of juvenile coral reef fish in the Caribbean (Verweij et al. 2008; Pollux et al. 2007). Pollux et al. (2007) found that *Acanthurus tractus* preferentially settled on shallow reef flats and in adjacent seagrass beds, *Lutjanus apodus* exclusively settled in mangroves, and *Ocyurus chrysurus* settled in both mangrove and seagrass beds. The settlement patterns of these three species reflect their habitat use through later juvenile stages, and suggest that higher juvenile densities in mangroves and seagrass beds are determined by habitat selection during settlement rather than by postsettlement processes (Pollux et al. 2007). In temperate rocky reefs, important ontogenetic movements were observed for several species between the young-of-the-year and later juvenile stages, in which they migrated from shallow steeper rocky habitats to deeper complex rocky bottoms with a high total benthic cover (Félix-Hackradt et al. 2014).

Concerning the influence of MPAs on postsettlement processes, the main benefits are related to providing quality habitat, shelter, and food, which are essential in this part of the life cycle of reef fish (Syms and Carr 2001; Rodwell et al. 2003; Shima and Osenberg 2003; Green et al. 2015; Carr et al. 2017) (Fig. 3). In the postsettlement period, density-dependent factors, such as predation and competition, are important for structuring adult populations (Doherty et al. 2004; White 2008; Planes et al. 2009b; Pineda et al. 2010). In theory, the mortality of new settlers should be higher within MPAs because of the larger abundance of predators (Planes et al. 2000). Arceo et al. (2012) found that the recruitment of *Diplodus sargus* was lower within reserve boundaries than in areas open to fishing and that this pattern could be attributed to predation. However, compensatory effects, such as increased survival associated with high-quality habitat provided by MPAs, can compensate for these differences (Syms and Carr 2001; Shima and Osenberg 2003; Grorud-Colvert and Sponaugle 2009; Green et al. 2015; Carr et al. 2017).

Lessons on role of MPAs on early fish life stages

MPAs have positive effects on reef fish populations (Halpern and Warner 2002; Harrison et al. 2012; Garcia-Charton et al. 2008; Carter et al. 2017; Felix-Hackradt et al. 2018). Although growing evidence supports the benefits of MPAs, such as an increase in biomass or abundance (Russ and Alcala 2004; Claudet et al. 2010), population structure restoration (Guidetti 2006), spillover (Hackradt et al. 2014; Ashworth and Ormond 2005; Watson et al. 2009), and genetic diversity (Félix-Hackradt et al. 2013c; Bezerra et al. 2018), and others, little is known about the effects of MPAs on the settlement and subsequent recruitment of individuals to adult populations (Planes et al. 2000; Sale et al. 2005; Félix-Hackradt et al. 2018). The lack

of knowledge of marine reserves affecting the early life history stages (ELHSs) of fish was first recognized by Planes et al. (2000), which hindered MPA objectives from being met. Three main processes were outlined as being fundamental: (1) the relationship between the ecology of pelagic stages and the designated location and oceanographic regime of the MPA; (2) the effects of the protection of nursery habitats on settlement success; and (3) the effects of protection on the survival of settlers and juveniles (density-dependent factors). Next, we address the advances and existing caveats in ELHS knowledge that hinder the proper use of MPAs in marine population management and conservation.

Two decades after that review (Planes et al. 2000), many studies have been conducted to solve the ELHS puzzle and contribute to MPA science. Most marine fish species have dispersive pelagic stages that can travel large distances by passive transport with the aid of ocean currents and winds (Sim-Smith et al. 2013; Félix-Hackradt et al. 2013a). The results of both biophysical modeling (Cowen and Sponaugle 2009; Sponaugle et al. 2012) and genetic studies (Schunter et al. 2011; Bezerra et al. 2018) have revealed that the homogeneity of fish populations over large spatial scales is mainly attributed to larval connectivity. However, larval fish may not act as passive particles, but rather show substantial vertical movements (Leis et al. 2009, 2011; Fisher and Leis 2010; Downie et al. 2021b; Fisher et al. 2022). Coupled with mesoscale oceanographic events (such as eddies and fronts), these movements can retain larval fish close to their native habitat (Cowen et al. 2000), thus resulting in population substructuring (Saenz-Agudelo et al. 2012a; Truelove et al. 2017). In effect, the accumulated evidence indicates that larval retention is as frequent as larval export and may reach 60% of propagule production for some reef-associated species, especially in remote islands (Almany et al. 2007). However, in most cases, one-third of propagule production is retained and not exported (Jones et al. 2005). Furthermore, larval retention is not related to fish life-history features or geographic location (Swearer et al. 2002).

The results of many modeling studies have demonstrated the beneficial effects of MPAs as a potential source of eggs and larvae using modeling (Kough et al. 2019; Di Franco et al. 2012b;

Andrello et al. 2013; Pujolar et al. 2013) or genetic tools (Christie et al. 2010; Harrison et al. 2012; Le Port et al. 2017). Determining whether these areas act as larval sources or sinks for a given population is essential (Bode et al. 2006). As a source, MPAs can boost larval export capacity and, therefore, connectivity to nearby reefs or MPAs in a network (Harrison et al. 2012; Le Port et al. 2017) when they can maintain a reproductive adult population within their boundaries (Hackradt et al. 2014). As a sink, MPAs can provide quality habitat for recruits, thereby increasing survival (Felix-Hackradt et al. 2014; Cheminée et al. 2016). However, high predation pressure can outweigh the positive effects of MPAs on recruitment (Arceo et al. 2012).

ELHS studies have failed to indicate any significant relationship between the level of recruitment and protection by MPAs (Macpherson et al. 1997; Di Franco et al. 2013; Cheminée et al. 2017; Félix-Hackradt et al. 2018). This is probably due to the decoupling effects caused by early mortality (Félix-Hackradt et al. 2013b) or dispersal movements (Di Franco et al. 2013) during the transition between the larval and adult stages. Seascape attributes are critical for recruitment patterns (Cuadros et al. 2017; Cheminée et al. 2021) because habitat quality and complexity appear to support early survival (Cheminée et al. 2016). Consequently, the strength of protection benefits for recruits is indirect and manifested through the proportion of nursery habitats secured within MPA borders (Cheminée et al. 2021).

In addition to the larval and adult export from protected areas, juveniles can potentially perform this function (i.e., spillover). Although postsettlers can move beyond MPA limits to distances of 30 km (Di Franco et al. 2012a), the relative importance of this movement for the replenishment of fishery-target species remains undefined.

In this section, we demonstrated that many of the questions raised by Planes et al. (2000) have been extensively addressed in the past 20 years, and that new information from these studies can now be used in the implementation and management of MPAs. However, the direct and indirect effects of protection on recruitment variability and how this is reflected in the adult population remain an important gap that needs further attention.

Including early life history stages in MPA management

MPAs have been idealized as ecosystem-based fishery management, the aim of which is to mitigate the effects of fisheries on marine fish stocks (Halpern et al. 2010; Fenberg et al. 2012; Di Franco et al. 2016) and prevent them from collapsing (Kerwath et al. 2013). From this perspective, some marine reserves were created mainly to benefit fishing through the spillover effect (exportation of juvenile and adult fish biomass) and by exporting eggs and larvae to surrounding areas and, consequently, helping replenish targeted fish populations (Fenberg et al. 2012).

The dilemma of "one large vs. multiple small areas" regarding the establishment of protection measures for the conservation of marine fish species has been intensely debated (Halpern 2003). Ecological theory suggests that larger areas are always better because they house more populations of more species than smaller areas (Claudet et al. 2008). However, recent evidence suggests that local retention is increased in large MPAs (e.g., 10–20 km) compared with smaller ones (0.5–1 km). Small MPAs export proportionately more larvae to adjacent areas, including other MPAs (Green et al. 2015; Carr et al. 2017), but only if they can support a persistent and productive adult population (Green et al. 2015; Cabral et al. 2016). Although large, enforced, and well-designed MPAs have proven to be effective, the results of small MPAs widely vary (Turnbull et al. 2018). In large MPAs, several ecosystems and habitats interact without the connectivity problems often found in networks of small MPAs, which can be largely affected by human activities (Willhelm et al. 2014). Therefore, large MPAs (approximately 10–20 km in diameter) can more easily protect the full range of available habitat types and ecological niches (McLeod et al. 2009), which, in turn, protects fish species and ecological functions.

The representation of critical habitats, such as nursery grounds, spawning aggregations, and areas of high species diversity (Green et al. 2007) is most effectively achieved with larger MPAs, which must be considered during MPA design to achieve conservation goals in ELHSs. At least 20–30% of each local habitat should be represented within protected areas, as well as at least three entities of each habitat type, to ensure that disturbance events do not simultaneously affect all habitats (McLeod et al. 2009). Moreover, as several species undergo ontogenetic movement after settlement (Nagelkerken et al. 2000; Félix-Hackradt et al. 2014; Aschenbrenner et al. 2016), protected areas that aim to secure essential habitats for fish at distinct life stages should guarantee habitat representation, replication, and connectivity among various habitats (McLeod et al. 2009).

Another important consideration, especially for future networks of MPAs, is whether no-take areas are located in sink or source areas to favor the exchange of propagules. McLeod et al. (2009) attested that MPAs separated by distances of at least 15–20 km guarantee population connectivity by promoting dispersal corridors (Fontoura et al. 2022) and ensuring high levels of mutual replenishment.

The location of the protected area is also relevant for larval survival. Researchers evaluated the protective effect on different life stages (e.g., adult, juvenile, and larval stages) and found that the protective effect on larval fish may have been confounded by the geomorphological features of the no-take area (Félix-Hackradt et al. 2018). The evaluated no-take zones harbored steeper rocky areas and were located in promontory zones that were exposed to prevailing winds and currents. These features may have favored the concentration of larvae in adjacent unprotected areas characterized by shallow rocky bays mixed with seagrass meadows. Thus, both the geological characteristics and bottom cover and substrate can directly impact the ELHS distribution and must be considered when evaluating location eligibility for MPA placement and establishment.

Finally, the timing of establishing a marine reserve is important for the success of recruitment. Hopf et al. (2022) showed that establishing a marine reserve during a recruitment peak can hide the sustainability of long-term metapopulation patterns, as protection during a recruitment peak or trough is directly related to enhanced or delayed post-reserve population increases, respectively. Therefore, knowledge of the temporal and spatial variability in recruitment can boost MPA efficiency.

We are aware that in many MPAs worldwide, information regarding the ELHSs of fish is not always available and cannot be included in the MPA design and establishment. However, we strongly recommend that when such data are accessible, managers consider MPA planning to achieve the best possible results

in terms of sustaining fished populations outside the MPAs, protecting the evolutionary potential of populations, and enhancing resilience to a changing future.

Conclusions

Despite considerable efforts to study the larval and postsettlement stages of reef fishes, gaps in knowledge remain regarding the occurrence and structure of fish assembly before settlement. The extent to which pre- and postsettlement and recruitment processes are responsible for the final population structure has been the subject of debate in the scientific community since the mid-1980s. However, we still do not have sufficient information to determine whether the structure and spatial variability of populations are defined mainly during the settlement processes or in later stages. In theory, the relative importance of pre- and postsettlement processes in future populations varies among species, and is strongly influenced by environmental variables and is related to the specific characteristics of the location. These processes act together by modifying and regulating the structure of reef fish populations.

The main proven benefit of MPAs in reef fish settlement and recruitment is that these areas are capable of exporting eggs and larvae to adjacent regions. However, in larger MPAs, the relative proportion of larvae that remain in the immediate area may be larger than that of larvae dispersed and exported outside their limits. MPAs may provide higher quality and complexity of habitat, which can favor settlement and recruitment in these areas. Moreover, MPA networks can minimize the negative effects of climate change. However, only a few studies have determined the relative importance of MPAs in juvenile supply. Little information is available on the settlement and recruitment in MPAs and fished areas for large commercially exploited fish species. These are critical knowledge gaps that limit our understanding of the broader benefits of MPAs for the conservation and management of fisheries. Studies that seek to determine the connectivity between spawning sites and areas of settlement and recruitment by considering the importance of MPA networks in these processes, and using techniques such as dispersal models and genetics, can generate important knowledge to answer these questions.

Finally, further research is needed on the most basic issues of settlement and recruitment in the specific context of MPAs. The absence of studies on this topic, particularly on how protection directly and indirectly affects recruitment variability and how this is reflected in the adult population, hinders the achievement of MPA objectives and is a serious shortcoming in the attempts to support future populations at ecologically adequate levels.

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