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**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E
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**DINÂMICA DO ESTÁGIOS INICIAIS DE VIDA DE PEIXES RECIFAIS
NO BANCO DE ABROLHOS, BRASIL.**

ILHÉUS – BAHIA

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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.

Área de concentração: Ecologia e Conservação da Biodiversidade

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Ilhéus, 14 de Abril de 2023.

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DINÂMICA DO ESTÁGIOS INICIAIS DE VIDA DE PEIXES RECIFAIS NO BANCO DE ABROLHOS, BRASIL.

RESUMO

O assentamento de peixes recifais, ou seja, a transição de um ambiente pelágico para bentônico, precedido por metamorfose larval é considerado um precursor necessário para o recrutamento em uma população. Já o termo recrutamento significa a inserção de novos indivíduos em uma população adulta para reabastecer a população. O assentamento e recrutamento bem-sucedidos são influenciados por processos e variáveis que operam espacial e temporalmente (de dias a anos) e em diferentes escalas, e requer a sobrevivência em vários estágios e em diferentes ambientes para espécies com ciclo de vida complexo. Dessa forma, a capacidade de prever assentamento, recrutamento e dinâmica populacional depende da compreensão de como os processos biológicos interagem com o ambiente físico dinâmico e como essa interação reflete na estruturação da população adulta. Assim, considerando que o banco dos Abrolhos é reconhecido como um dos locais de maior biodiversidade do Atlântico Sul mas vêm sofrendo com diversas ameaças principalmente relacionada a exploração de recursos naturais, a seguinte tese teve como objetivo, avaliar os padrões de assentamento e recrutamento de peixes recifais no Banco de Abrolhos e além de descrever quais fatores influenciam nesses processos. Para isso, no primeiro capítulo realizou-se uma revisão bibliográfica buscando identificar quais fatores influenciam no ciclo de vida de peixes recifais, desde o período reprodutivo até o recrutamento além de evidenciar o qual o papel das áreas marinhas protegidas nesses processos. No segundo capítulo, o objetivo foi analisar a distribuição das assembleias de pós-larvas de peixes recifais no Banco dos Abrolhos, considerando a variação espaço-temporal e o papel das áreas marinhas protegidas nesses padrões, além de identificar as variáveis ambientais que possam atuar nessa distribuição. No terceiro capítulo, buscou-se analisar a influência do habitat e da paisagem nos padrões de diversidade das assembleias de pós-larvas e juvenis de peixes recifais, e suas implicações para a conservação dessas espécies. Os resultados mostraram que a importância dos processos pré e pós-assentamento nas populações futuras varia entre as espécies, é fortemente influenciada por variáveis ambientais e está relacionada às características específicas do local. Esses processos atuam em conjunto modificando e regulando a estrutura das populações de peixes recifais. O principal benefício comprovado das áreas marinhas protegidas no assentamento e recrutamento de peixes recifais é que são capazes de exportar maiores quantidades de ovos e larvas para regiões adjacentes e fornecer habitats de maior qualidade e complexidade, favorecendo o assentamento e o recrutamento nessas áreas. Além disso, demonstraram também a importância das variações espaço temporais e do tipo de habitat na distribuição das assembleias de peixes recifais em estágios iniciais de vida no Banco dos Abrolhos. Por fim, considerando que a distribuição dos estágios iniciais de vida dos peixes recifais nas zonas costeiras é o primeiro passo de uma cadeia de eventos sucessivos que culminam na estruturação da população adulta, os resultados gerados nessa tese corroboram com informações necessárias para fomentar estratégias voltadas para a conservação das espécies de peixes recifais no Banco de Abrolhos.

Palavras-chave: Assentamento, Recrutamento, Peixes Recifais, Recifes de Coral

DYNAMICS OF THE EARLY LIFE STAGES OF REEF FISHES IN THE BANK OF ABROLHOS, BRAZIL.

ABSTRACT

Reef fish settlement, namely, the transition from a pelagic to benthic environment, preceded by larval metamorphosis, is considered a necessary precursor for recruitment into a population. The term recruitment means inserting new individuals into an adult population to replenish the population. Successful settlement and recruitment are influenced by processes and variables that operate spatially and temporally (from days to years) and at different scales, and require survival at various stages and in different environments for species with complex life cycles. Thus, the ability to predict settlement, recruitment, and population dynamics depends on understanding how biological processes interact with the dynamic physical environment and how this interaction reflects on the structure of the adult population. Thus, considering that the Abrolhos bank is recognized as one of the places with the greatest biodiversity in the South Atlantic but has been suffering from several threats mainly related to the exploitation of natural resources, the following thesis aims to evaluate the patterns of settlement and recruitment of fish reefs in the Abrolhos Bank and in addition to describing which factors influence these processes. For this, in the first chapter, a bibliographic review was carried out to identify which factors influence the life cycle of reef fish, from the reproductive period to recruitment, in addition to highlighting the role of marine protected areas in these processes. In the second chapter, the objective was to analyze the distribution of reef fish postlarvae assemblages in the Abrolhos Bank, considering the space-time variation and the role of marine protected areas in these patterns, in addition to identifying the environmental variables that may act in this distribution. In the third chapter, we sought to analyze the influence of habitat and landscape on the diversity patterns of postlarvae and juvenile reef fish assemblages, and their implications for the conservation of these species. The results showed that the importance of pre and postsettlement processes in future populations varies among species, is strongly influenced by environmental variables, and is related to specific site characteristics. These processes act together modifying and regulating the structure of reef fish populations. The main proven benefit of marine protected areas in the settlement and recruitment of reef fish is that they are able to export greater quantities of eggs and larvae to adjacent regions and provide habitats of greater quality and complexity, favoring settlement and recruitment in these areas. In addition, they also demonstrated the importance of space-time variations and the type of habitat in the distribution of reef fish assemblages in the early stages of life on the Abrolhos Bank. Finally, considering that the distribution of the initial stages of life of reef fish in coastal zones is the first step in a chain of successive events that culminate in the structuring of the adult population, the results generated in this thesis corroborate with the necessary information to encourage strategies aimed at the conservation of reef fish species on the Abrolhos Bank.

Keywords: Settlement, Recruitment, Reef Fishes, Coral Reefs

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1 INTRODUÇÃO

Os ambientes recifais são reconhecidos como umas das áreas de maior biodiversidade do planeta (MORA 2015) e seus serviços ecossistêmicos são de suma importância para a subsistência e bem estar de milhões de pessoas (SHEPPARD ET AL. 2017). Entretanto, mesmo com toda sua relevância ecológica (WOODHEAD ET AL. 2019; MOBERG AND FOLKE 1999), os ambientes recifais estão entre os ecossistemas mais ameaçados, devido a uma longa história de degradação e exploração antrópica (GRAHAM ET. AL 2007, JACKSON ET. AL 2001). Esses impactos antropogênicos trazem várias consequências negativas e vão desde a perda de habitat (ALVAREZ-FILIP ET. AL 2011, PRATCHETT ET. AL 2014), mudanças na composição bentônica (CHONG-SENG ET. AL 2012) além do declínio na complexidade topográfica (MCCLANAHAN ET. AL 2014), levando a uma diminuição da abundância de muitos organismos associados a essas áreas, principalmente os peixes recifais (PRATCHETT ET. AL 2014). Com isso, entender os padrões e processos que estruturam a população dos peixes recifais é determinante para que estratégias que visem a conservação desses estoques sejam elaboradas e efetivamente implantadas.

A grande maioria dos peixes recifais possuem ciclos de vida complexos, e transitam pelos ambientes planctônico e bentônico de acordo com o seu estágio de vida. A estratégia reprodutiva mais comum utilizada pelos peixes recifais envolve a liberação de propágulos (ovos ou larvas) no oceano, onde os propágulos buscam recursos e proteção durante seu desenvolvimento (DOHERTY E FOWLER 1994; SALE 2002; MILLER E KENDALL-JR 2009). No oceano dinâmico, muitas larvas são dispersadas por correntes para novos locais, alguns dos quais são mais favoráveis do que outros para sua sobrevivência (DOHERTY E FOWLER 1994; SPONAUGLE ET AL. 2012; SHULZITSKI ET AL. 2016; VAZ ET AL. 2016; GOLDSTEIN E SPONAUGLE 2020).

No estágio planctônico, as larvas permanecem em um ambiente espacial e temporalmente diverso e altamente dinâmico, sujeito a diferentes fatores bióticos e abióticos, os quais podem determinar sobrevivência, crescimento e dispersão (COWEN E SPONAUGLE 1997; SPONAUGLE ET AL. 2006; JONSSON E JONSSON 2014; VAGNER ET AL. 2019). Fatores como vento, corrente, maré, temperatura, precipitação, descarga do rio e massas de água são algumas variáveis, dentre outras, que podem

ser responsáveis pela distribuição larval em habitats costeiros (COWEN E SPONAUGLE 1997; SHIMA E FINDLAY 2002; BERGENIUS ET AL. 2005; ALEMANY E 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). Posteriormente, durante os estágios de assentamento e recrutamento, a maioria dos peixes recifais passa por uma mudança ontogenética crítica, de ambientes pelágicos para habitats de recifes bentônicos, o que resulta em alta mortalidade (SOGARD 1997). O assentamento de peixes recifais (transição de um ambiente pelágico para bentônico, precedido por metamorfose larval) é considerado um precursor necessário para o recrutamento em uma população (MYRBERG E FUIMAN 2002; GREENFIELD 2003). O termo “recrutamento” significa a inserção de novos indivíduos em uma população adulta para reabastecer a população (ROBERTSON ET AL. 1988; ROBERTSON 1990).

No período de assentamento, os peixes recifais são influenciados por processos dinâmicos e que variam espacialmente, como produtividade e disponibilidade de alimentos, que afetam o crescimento e a condição das pós-larvas (LEVIN ET AL. 1997; BOOTH E HIXON 1999; LEAHY ET AL. 2015). O tipo de habitat também desempenha um papel fundamental no processo de assentamento (TOLIMIERI 1995; COSTA ET AL. 2020; DOWNIE ET AL. 2021). Habitats, como recifes de corais, rodolitos e leitos de algas marinhas, podem fornecer estruturas tridimensionais que servem como berçários, áreas de assentamento, forrageamento e de refúgio (BERKSTRÖM ET AL. 2012; DÍAZ ET AL. 2015; AMADO-FILHO ET AL. 2016; EGGERTSEN ET AL. 2017; COSTA ET AL. 2020). A interação dos processos biológicos e do ambiente, como estratégias de história de vida, temperatura, comportamento, correntes, marés e configurações da paisagem marinha, entre outros, moldam o assentamento larval (SPONAUGLE ET AL. 2012; FÉLIX-HACKRADT ET AL. 2013b; BROWN ET AL. 2016; GRANDE ET AL. 2019; GOLDSTEIN E SPONAUGLE 2020). Esses processos são críticos para várias espécies de peixes recifais, onde as larvas permanecem no plâncton por dias a anos antes de se estabelecerem no ambiente bentônico (COWEN E SPONAUGLE 1997). A capacidade de prever assentamento, recrutamento e dinâmica populacional depende da compreensão de como os processos biológicos interagem com o ambiente físico dinâmico (WONG-ALA ET AL. 2018; GRANDE ET AL. 2019; LIMA ET AL. 2023).

Os estágios pós-assentamento são ainda mais afetados por eventos como predação, competição, taxas de crescimento e mudanças ontogenéticas na dieta (SHIMA E OSENBURG 2003; DOHERTY ET AL. 2004; HIXON E JONES 2005; ALMANY E WEBSTER 2006; GOLDSTEIN E SPONAUGLE 2020, WEN ET AL. 2012), que consequentemente moldam a estrutura das populações de peixes recifais (D'ALESSANDRO ET AL. 2007; GOLDSTEIN E SPONAUGLE 2020). Além disso, o tipo e a qualidade do habitat também são importantes no processo de recrutamento (JOHNSON 2007; FÉLIX-HACKRADT ET AL. 2013b, SHULZITSKI ET AL. 2016; GOLDSTEIN E SPONAUGLE 2020). As variações espaciais no recrutamento na escala local podem ser explicadas pelas características do habitat (ou seja, extensão espacial, rugosidade, posição geográfica na paisagem marinha, tipos de substrato, complexidade, sons e outros) (COSTA ET AL. 2020; SHIMA E OSENBURG 2003; LEVIN 1991; LEVIN 1993; TUPPER E BOUTILIER 1997, ALMANY 2004, SIMPSON ET AL. 2005, FÉLIX-HACKRADT ET AL. 2013b). Estas características aumentam a capacidade de um habitat abrigar um maior número de recrutas, dependendo da qualidade do habitat (SHIMA E OSENBURG 2003) e do microhabitat (TOLIMIERI 1995; FÉLIX-HACKRADT ET AL. 2014) ou do número de abrigos (JOHNSON 2007) e ainda, algumas espécies têm fortes preferências por tipos de habitat específicos com características diferentes (FÉLIX-HACKRADT ET AL. 2014).

Além dos variados fatores que atuam no ciclo de vida dos peixes recifais, desde o período reprodutivo até o momento do recrutamento de indivíduos nas populações adultas, estudos têm buscado entender o papel das áreas marinhas protegidas (AMPs) nesses processos (LIMA ET AL. 2023). As AMPs são reconhecidas como uma ferramenta poderosa para a gestão, recuperação e conservação dos recursos marinhos e os efeitos positivos das AMPs nas populações adultas de peixes recifais são bem conhecidos (HALPERN E WARNER 2002; HARRISON ET AL. 2012; GARCIA-CHARTON ET AL. 2008; CARTER ET AL. 2017; FELIX-HACKRADT ET AL. 2018; ROLIM ET AL. 2022). Embora evidências crescentes apoiem os benefícios das AMPs, como um aumento na biomassa ou abundância (RUSS E ALCALA 2004; CLAUDET ET AL. 2010; ROLIM ET AL. 2022), restauração da estrutura populacional (GUIDETTI 2006), transbordamento (spillover) (HACKRADT ET AL. 2014 ; ASHWORTH E ORMOND 2005; WATSON ET AL. 2009), diversidade genética (FÉLIX-HACKRADT ET AL. 2013c; BEZERRA ET AL. 2018), e outros, pouco se sabe sobre o efeito das AMPs

no assentamento e o subsequente recrutamento de indivíduos para as populações adultas (PLANES ET AL. 2000; SALE ET AL. 2005; FÉLIX-HACKRADT ET AL. 2018). Estudos recentes mostraram que variações entre AMPs e áreas desprotegidas podem levar a diferentes taxas de assentamento e recrutamento além da sobrevivência dos recrutas (GRORUD-COLVERT E SPONAUGLE 2009; HARRISON ET AL. 2012; LIMA ET AL. 2023) principalmente porque proteger um determinado habitat ou paisagem marinha, as AMPs podem garantir a disponibilidade de áreas de assentamento de maior qualidade para os recrutas (GREEN ET AL. 2015; CARR ET AL. 2017; LIMA ET AL. 2023).

Assim, considerando que a distribuição dos estágios iniciais de vida dos peixes recifais nas zonas costeiras é o primeiro passo de uma cadeia de eventos sucessivos que culminam na estruturação da população adulta, portanto, a compreensão da história inicial dos peixes recifais é um determinante da dinâmica populacional (FÉLIX-HACKRADT 2013a). No entanto, o assentamento e o recrutamento bem-sucedidos são influenciados por processos e variáveis que operam em escalas espaço-temporais distintas (LOZANO E ZAPATA 2003; FÉLIX-HACKRADT ET AL. 2013a; GRANDE ET AL. 2019), além de exigir sobrevivência em vários estágios e em ambientes diferentes no caso da maioria dos peixes recifais (GOLDSTEIN E SPONAUGLE 2020). Dessa forma, tendo em vista que o Banco dos Abrolhos é a área marinha de maior biodiversidade do Atlântico Sul (LEÃO ET AL. 2003) e habitats importantes são encontrados na região (LEÃO ET AL. 2003; AMADO-FILHO ET AL. 2012; MOURA ET AL. 2013) se faz necessário entender o assentamento e recrutamento de peixes recifais e quais fatores influenciam esses processos.

Por fim, esta tese é composta por três capítulos cujo o objetivo geral é avaliar os padrões de assentamento e recrutamento de peixes recifais no Banco de Abrolhos e além de descrever quais fatores influenciam nesses processos. No primeiro capítulo, realizamos uma revisão bibliográfica para investigar quais fatores influenciam nos padrões e processos no ciclo de vida de peixes recifais, desde o período reprodutivo até o recrutamento além de evidenciar o qual o papel das Áreas Marinhas Protegidas nesses processos. No capítulo 2, buscamos analisar a distribuição das assembleias de pós-larvas de peixes recifais no Banco dos Abrolhos, considerando a variação espaço temporal e o papel das áreas marinhas protegidas nesses padrões, além de identificar

as variáveis ambientais que possam influenciar nessa distribuição. No capítulo 3, visamos examinar a influência do habitat e da paisagem nos padrões de diversidade das assembleias de pós-larvas e juvenis de peixes recifais, e suas implicações para a conservação dessas espécies.

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3. CAPÍTULO 1: THE INFLUENCE OF MARINE PROTECTED AREAS ON THE PATTERNS AND PROCESSES IN THE LIFE CYCLE OF REEF FISHES

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THE INFLUENCE OF MARINE PROTECTED AREAS ON THE PATTERNS AND PROCESSES IN THE LIFE CYCLE OF REEF FISHES

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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

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; Sponaugle et al. 2012; Leis et al. 2015; Shulzitski et al. 2015; Shima and Swearer 2019; Shima et al. 2020; Shima et al. 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 2006; 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; Hackradt et al. 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 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 substantially increase the abundance of target species, as in the case of *Epinephelus polyphkadion* 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 (Felix-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).

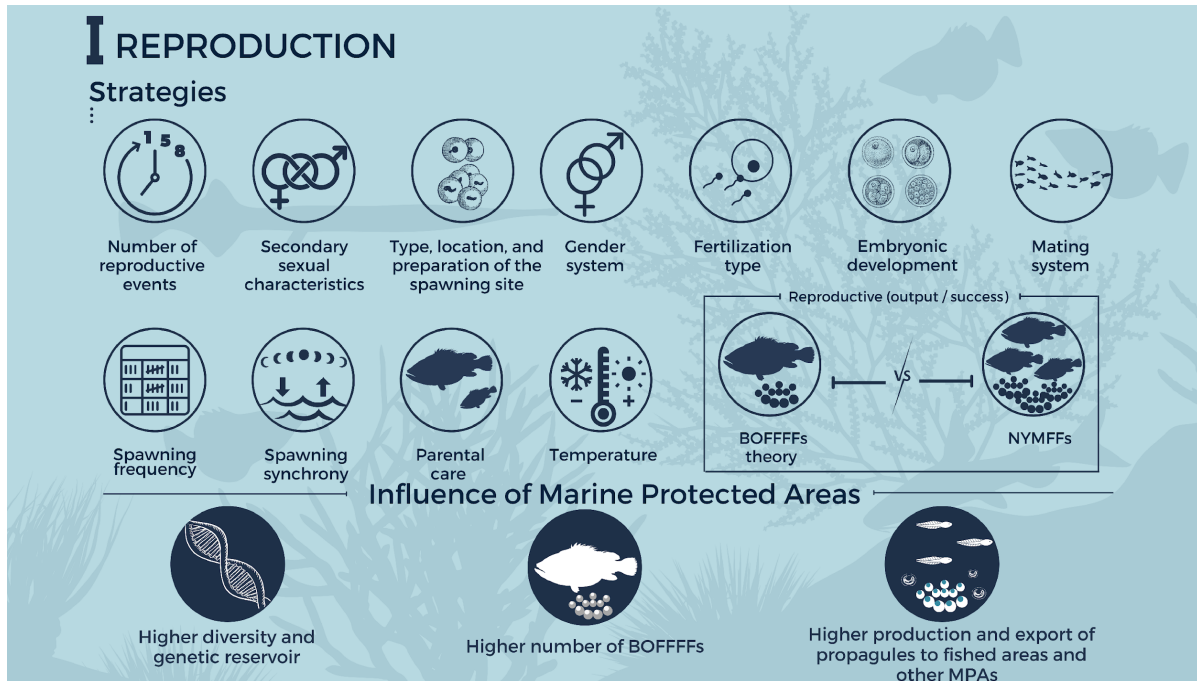


Fig 1 Biotic and abiotic influences in the reproduction stage of reef fish and the influence of MPAs on these processes.

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 one–two 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 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 (Felix-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 above mentioned factors related to larval transport influence the settlement process, larvae are capable of swimming and actively select habitats for settlement (Fisher et al. 2000; Leis et al. 2015; Nanninga and Manica 2018; Downie et al. 2021b; Fisher et al. 2022). This factor is important for the dispersal of reef fish (Leis et al. 2009; Fisher and Leis 2010; Leis et al. 2011; 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 Section 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).

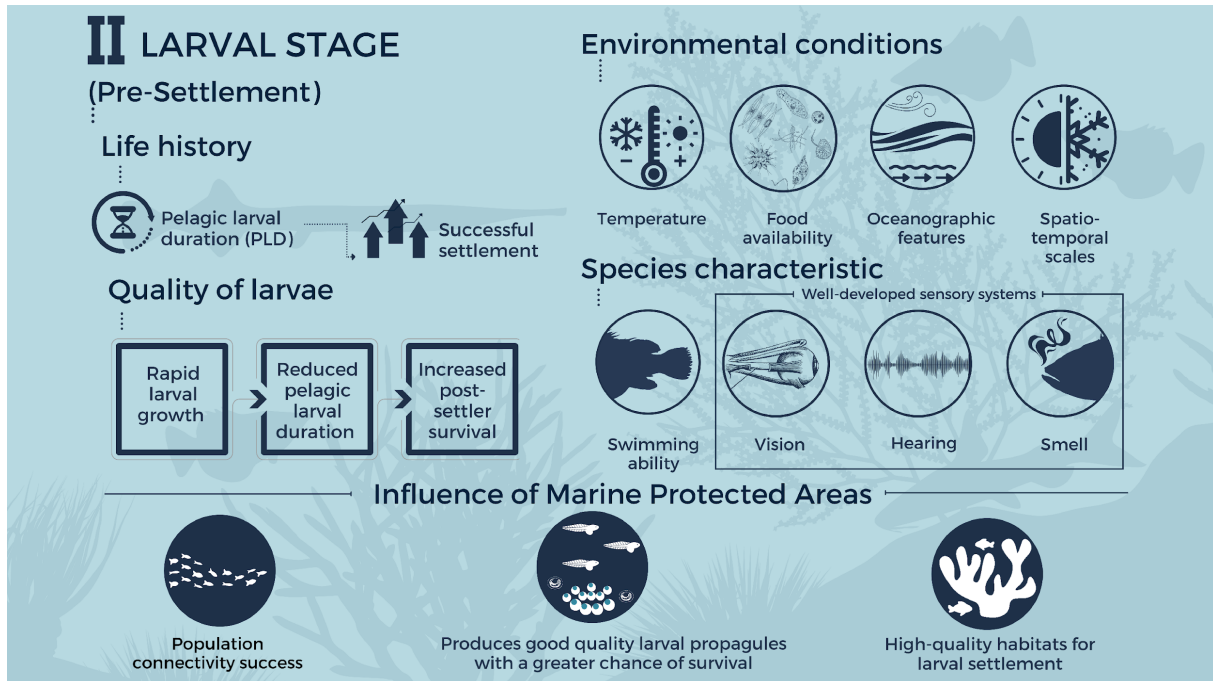


Fig 2 Biotic and abiotic influences in the presettlement stage of reef fish and the influence of MPAs on these processes.

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) 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).

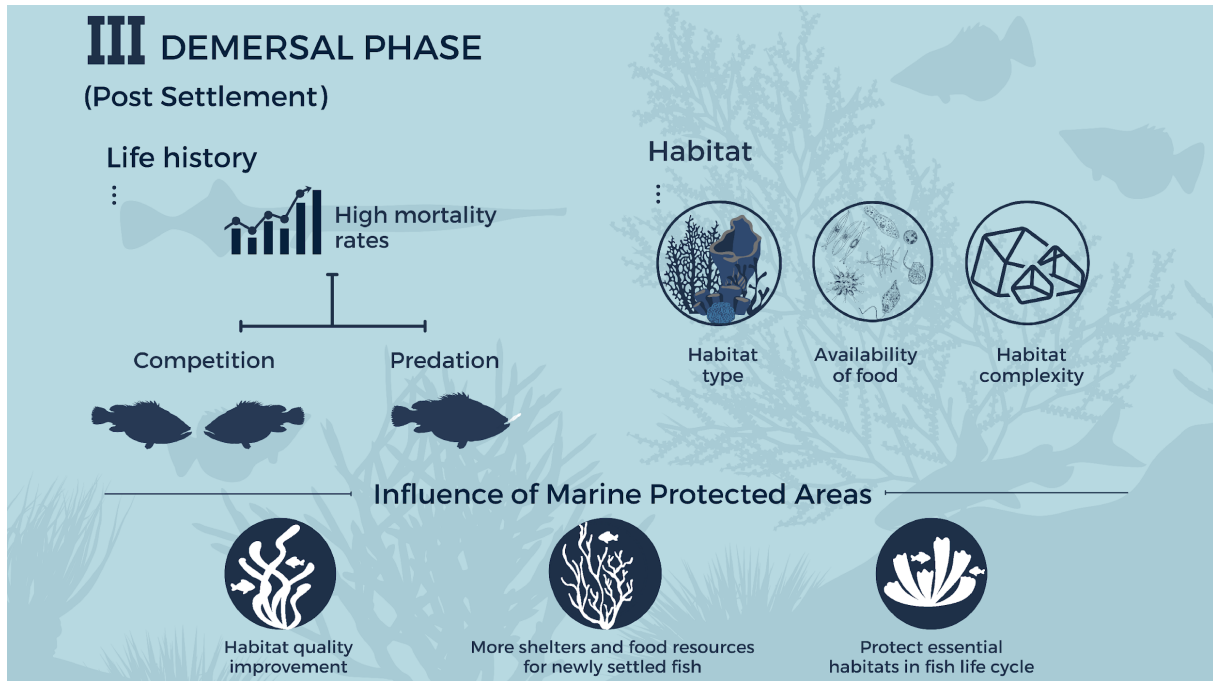


Fig 3 Biotic and abiotic influences in the postsettlement stage of reef fish and the influence of MPAs in these processes.

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; Felix-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; Fisher and Leis 2010; Leis et al. 2011; 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. 2012; 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. 2009; 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 (Felix-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. (2021) 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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4. CAPÍTULO 2: MULTIPLE EVENTS DETERMINE THE DISTRIBUTION OF FISHES' EARLY LIFE STAGES IN THE ABROLHOS BANK, SOUTHEASTERN ATLANTIC.

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MULTIPLE EVENTS DETERMINE THE DISTRIBUTION OF FISHES' EARLY LIFE STAGES IN THE ABROLHOS BANK, SOUTHEASTERN ATLANTIC.

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ABSTRACT

Successful settlement and recruitment can be influenced by processes and variables that operate spatially and temporally on different scales 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. Fluctuations in settlement and recruitment can majorly affect local population dynamics and therefore be determinants of adult population size. Although growing evidence supports the benefits of MPAs such as an increase in biomass or abundance, population structure restoration, spillover, genetic diversity, and others, little is known about the effect of MPAs on settlement and the subsequent recruitment of individuals to adult populations. In this way, this study is the premier evaluation using light traps for understanding the spatial-temporal influences, the environmental determinants, and the possible role of the MPAs on the distribution of early stages reef fishes in the Abrolhos Bank. Our findings demonstrated the importance of spatiotemporal variations and the possible influence of MPAs on these patterns and processes. The environmental factors explained only a small portion of the postlarvae distribution, indicating that other underlying mechanisms may account for substantial variance in some species. Meanwhile, the data corroborate with different studies suggesting that one of the main benefits of MPAs in the early life history of reef fish is the high production of propagules concerning the greater abundance and diversity of species found in protected areas the detriment of areas open to fishing.

Keywords: Reef Fish; Marine Protected Areas; Recruitment; Settlement; Light trap.

INTRODUCTION

Successful settlement and recruitment can be influenced by processes and variables that operate spatially and temporally at different scales (from days to years) (Lozano and Zapata 2003; Félix-Hackradt et al. 2013a; Grande et al. 2019) and requires survival at various developmental stages and in different environments for species with complex life cycles, as is the case for most reef fish (Goldstein and Sponaugle 2020). Fluctuations in settlement and recruitment can majorly affect local population dynamics (Ammann 2004) and can therefore determine adult population size (Macpherson et al. 1997). Additionally, many studies have evaluated the influence of environmental variables on larvae distribution (Vidal-Peñas et al., 2001; Catalán et al., 2006; Sabatés et al., 2007; López-Sanz et al., 2011, Felix-Hackradt et al. 2013a) and have emphasized their importance in driving larval fish dispersal during the pelagic phase. Physical factors such as wind, current, and temperature, among others, have all been considered possible variables accounting for larval fish distribution (Sponaugle and Cowen, 1996; Harris et al., 1999; Wilson, 2003; Alemany et al., 2006; Alvarez et al., 2012; Félix-Hackradt 2013a). In turn, identifying the principal environmental mechanisms that directly influence postlarvae fish distribution is the initial stage for constructing predictive models.

Larval distribution is the first step in a chain of successive events that culminate in the structuring of an adult population and therefore, the early life history of reef fish is a determinant of population dynamics (Félix-Hackradt et al. 2013b; Grorud-Colvert and Sponaugle 2009). As such, light traps are useful tools for sampling presettlement fish larvae that establish themselves in coral reefs (Mwaluma et al. 2009; Carassou et al. 2009; Doherty 1994) and are effective for understanding the taxonomy, early life history, assemblage structure, and spatial distribution of postlarvae reef fishes (Jones 2006; Grande et al. 2019). Additionally, the extended working period of a light trap provides a better characterization of postlarvae availability in a given place and they can be used to assess patterns of larvae distribution in coastal areas, including small-scale patterns, by targeting postlarvae which avoid most sampling devices used in plankton surveys (e.g., bongo nets, fixed stations, crest nets, etc.) (Calò et al. 2013). However, this is a selective sampling device as not all species and families display phototactic responses (Carassou et al. 2009).

Marine Protected Areas (MPAs) are recognized as powerful tools for the management, recovery, and conservation of marine resources and the positive effects of MPAs on reef fish populations are well-known (Halpern and Warner 2002; Harrison et al. 2012; Garcia-Charton et al. 2008; Carter et al. 2017; Felix-Hackradt et al. 2018; Rolim et al. 2022). Although growing evidence supports the benefits of MPAs, such as an increase in biomass or abundance (Russ and Alcala 2004; Claudet et al. 2010; Rolim et al. 2022), 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), among others, little is known about the effect of MPAs on settlement (changing from the pelagic to the benthic environment, preceded by larval metamorphosis) and the subsequent recruitment of individuals to adult populations (Planes et al. 2000; Sale et al. 2005; Félix-Hackradt et al. 2018). Recent studies have shown that variations between MPAs and unprotected areas could lead to differing settlement and recruitment rates beyond the survival of recruits (Grorud-Colvert and Sponaugle 2009; Harrison et al. 2012; Lima et al. 2023). Therefore, by protecting a certain habitat or seascape, MPAs can ensure the availability of higher-quality settlement grounds for recruits (Green et al. 2015; Carr et al. 2017; Lima et al. 2023).

The Abrolhos Bank is recognized for being the most biodiverse marine area in the South Atlantic (Leão et al. 2003). Important habitats are found in the region, such as the Abrolhos Bank reef complex (Leão et al. 2003; Menezes et al. 2021), with high levels of endemism (Leão and Kikuchi, 2005) and commercial species of reef fishes (Freitas et al. 2011), rhodolith beds (Amado-Filho et al. 2012; Moura et al. 2013), seagrass and algae beds (Creed and Amado-Filho, 1999), mangroves, estuarine areas and mesophotic reefs (Moura et al., 2013). Despite the ecological and economic relevance of the Abrolhos Bank, little is known about the settlement and recruitment of reef fish and the factors that influence these processes. Therefore, the main purposes of this study were: (1) to compare the distinctiveness of fish assemblages among different sampled areas and to highlight the influence of MPAs in the postlarvae assemblages of reef fishes in the Abrolhos Bank and (2) to identify the environmental variables that have the most influence on the spatial-temporal patterns of fish assemblages. Given the spatial variation of the study area, the importance of temporal patterns, and the presence of MPAs, we expected variations in early reef fish assemblage stages between the areas

and the sampling years (hypothesis i). Likewise, we also expected that the environmental variables would have a significant influence on the distribution patterns of postlarvae reef fish assemblages (hypothesis ii).

MATERIALS AND METHODS

Study Area

Our sampling zone is characterized by an extension of the Abrolhos Bank continental shelf, which extends up to 200 km offshore (Leão & Kikuchi, 2001). The average depth is very shallow, ~30 m, reaching 70 m near the shelf edge. The Abrolhos Bank is the largest and richest coral reef in the eastern region of Brazil and is considered to have the highest biodiversity in the South Atlantic (Leão 1999; Leão et al. 2003). These reefs form two arcs - one coastal and one offshore arc. The offshore arc is formed by fringing reefs located in the Abrolhos Archipelago (at east; Fig. 1A) and isolated pinnacle reefs forming the Abrolhos Parcel (at east; Fig. 1B), surrounded by water with depths of over 20 m. The coastal margin reefs form a complex of large reef banks of different shapes and sizes, including isolated pinnacle reefs, that extend in a north-south direction forming the Cassurubá reefs (at the south, Fig 1C) and Paredes Parcel (at north; Fig. 1D) (Leão et al. 2003). The coastal reef arc (~10 km offshore) is subject to high fishing pressure and terrigenous turbidity, while the offshore arc (~60 km off the coast) falls within the Abrolhos Marine National Park (ANMP) and is less exposed to fishing and terrestrial stressors (Moura et al. 2021).

Fish sampling

Sampling was carried out yearly during four consecutive summers (January 2019, March 2020, January 2021, and January/February 2022) in coral reef areas. Sample design involved the installation of nine light traps at four locations in a coral reef area (Abrolhos Archipelago = ABR, Parcel de Abrolhos = PAB, Parcel das Paredes = PP, and Cassurubá Reefs = CA) (Fig. 1), where each site was located at a different distance from the coast and experienced different levels of protection from fishing. The sample design considered two locations in an MPA (ABR and PAB) and two locations in unprotected areas (CA and PP) (Fig 1.)

Postlarval fishes were sampled using CARE model light traps (ECOCEAN). The light traps were installed for two consecutive nights for a total of eighteen (18) samples (per location/year), totaling 249 samples. Twenty-one (21) samples were discarded due to anchoring problems and because of the Covid-19 pandemic, it was not possible to collect data in the CA during the March 2020 period. After approximately 12 h of fishing, samples from the light traps were removed and conserved in 70% alcohol. At the laboratory, the postlarval fish catch was selected, measured (using a digital caliper), weighed (in g, using an analytical balance), and identified using the available bibliographies (Richards 2005; Bonecker et al. 2014).

Concurrently to postlarval fishing, environmental and meteo-oceanographic variables such as wave height, atmospheric pressure, precipitation, wind intensity, tide amplitude, and moonlight intensity were extracted from the CPTEC portal (www.cptec.inpe.br). Depth was obtained from boat sonar and current speed was measured using a Fluxometer. Additionally, turbidity, chlorophyll, and temperature data were estimated by satellite images obtained from remote sensing using a MODIS-Aqua sensor (Level-3, 8-day period, available at <https://oceancolor.gsfc.nasa.gov/l3/order/>) and extracted using SeaDAS software. Data from diffuse attenuation coefficient at 490 nm (K_d490 nm) was used as a proxy for water turbidity, data from chlorophyll-a concentration was used for the near-surface concentration of chlorophyll-a (`chlor_a`) in mg/m^3 , and data from sea surface temperature (sst) was used as an estimate for water temperature.

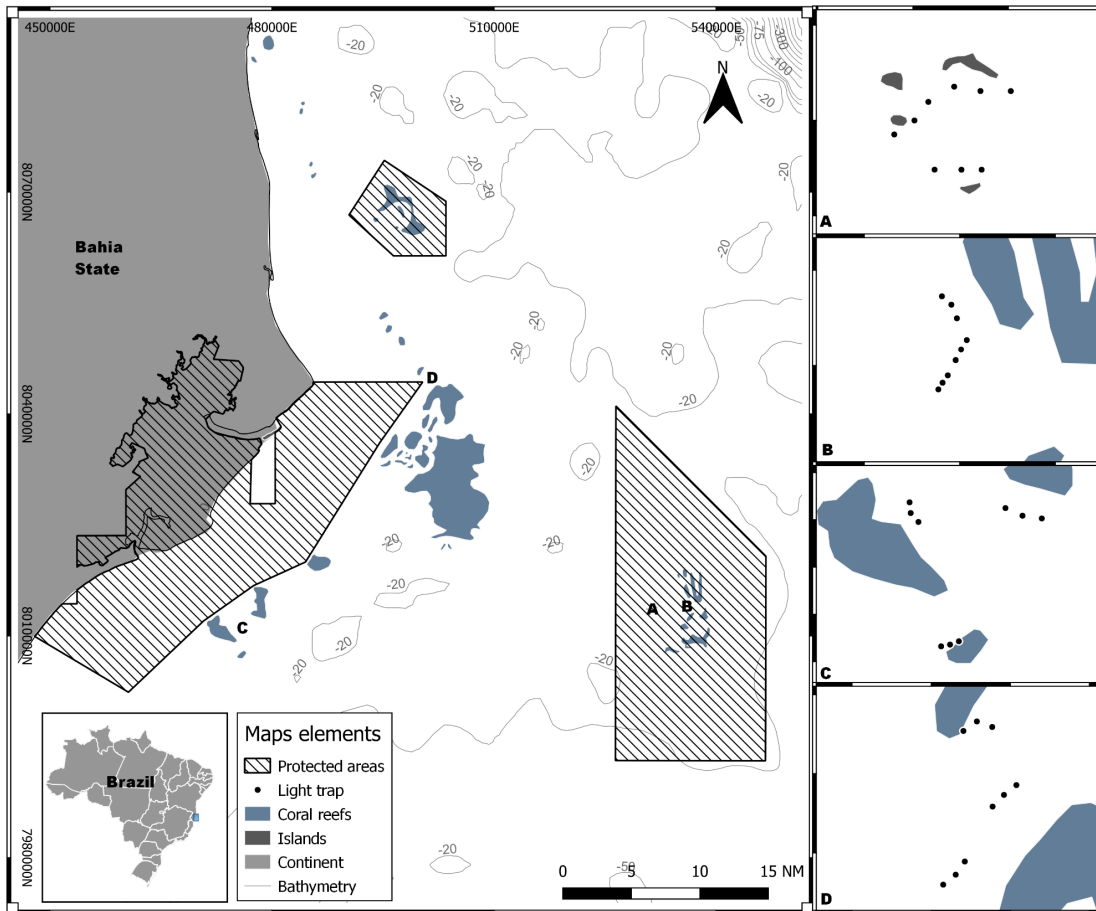


Figure 1- Sampling locations. A= Abrolhos Archipelago (ABR), B= Abrolhos Parcel (PAB), C= Cassurubá (CA) and D= Paredes Parcel (PP)

Data analyses

To assess environmental patterns of variation across sampling locations a Principal Component Analysis (PCA) was performed with variables scaled to have unit variance using the 'FactoMineR' package (Lê et al. 2008) from the R program (R Core Team 2022). Three of the collected environmental variables (wave height, moonlight intensity, and atmospheric pressure) were eliminated due to their correlation with the tide, which was evaluated using the 'stats' package from the R program (R Core Team 2022). Biplots were plotted to identify the environmental variables driving the two components that would best explain variability among locations.

Non-metric Multidimensional Scaling (nMDS) based on the Bray-Curtis similarity matrix of post-larvae species abundance data (i.e., composition) was used to visualize the ordination of multidimensional data within a two-dimensional space (Clarke 1993).

Normal data ellipses (level = 0.95) were computed and drawn around the group centroid (Wickham, 2016). To understand how fish species contribute to spatiotemporal patterns depicted by nMDS, we fit their relevance to ordination axes scaled by their correlation (R^2). The significance of fitted vectors was assessed using the permutation of species abundance (Oksanen et al. 2020). To assess environmental correlation with community structure, the function 'envfit' of package 'vegan' (Oksanen et al. 2020) from the R program (R Core Team 2022) was used in conjunction with the two-dimensional nMDS ordination. The 'envfit' function wraps the function 'vectorfit', which determines directions in ordination space, where vectors of environmental variables change the most and are more strongly correlated with the ordination structure, and 'factorfit', which calculates mean ordination scores for each categorical factor level. The significance of environmental vectors and factors was evaluated using squared correlation coefficients as a goodness-of-fit statistic following 1000 permutations of the environmental data.

Diversity indexes were investigated using "true diversity indices" (*sensu* Jost, 2006), considering the effective number of species equal to Hill numbers (qD) (Hill, 1973). This approach quantifies diversity based on the weight of species abundance by order of diversity q ; when $q=0$ (0D) species abundance is disregarded favoring rare species; $q=1$ (1D) is equivalent to Shannon's entropy and represents the number of common species in a community, and when $q=2$ (2D) dominant species are favored, as more weight is attributed to abundance (Jost, 2007). Diversity indices were calculated using the 'entropart' package (Marcon and Hérault 2015) from the R program (R Core Team 2022).

The responses of the total abundance of species caught per unit of effort (CPUE (N/LT); log-transformed), average total length, true diversity indices (0D , 1D e 2D), and fish assemblage composition were tested according to the evaluated factors through a permutational analysis of variance (PERMANOVA). This analysis was performed using a Bray–Curtis similarity matrix and was achieved using 9999 permutations, using Primer software v6.1.13 (Anderson et al. 2008). Before performing the analyses, postlarvae abundance from 2 consecutive nights was averaged to minimize daily fluctuations in light trap samples (Felix-Hackradt 2014). To determine temporal and spatial patterns of postlarval fish assemblages and the effect of MPA, the analytical design consisted of three factors: Protection (P), fixed with 2 levels; 'Year' (Y), fixed with 4 levels and

'Location' (L), random with 4 levels and nested in the 'Year and Protection' orthogonal interaction. To avoid a possible confounding effect of protection factor and geographical position when the MPA is located offshore, we chose to insert "coast distance" as a covariable in the PERMANOVA analysis.

Generalized linear models (GLMs) were applied to model the relationships between abundance (N), true diversity indices (q^0 , q^1 , and q^2), and environmental variables using the 'stats' package from the R program (R Core Team 2022). The models were selected according to maximum likelihood, using the Akaike information criterion (AICc), where the AICc weight described the relationship for all possible combinations between the predictive variables (Depth, Chlorophyll-a, Diffuse attenuation coefficient at 490 nm, Tide amplitude, and Wind speed). The predictive variables were selected based on the significance found in the nMDS analysis (see above). The best-adjusted model was that which obtained the lowest AICc value and the highest weight (Burnham and Anderson, 2004).

RESULTS

Oceanographic conditions

The first two dimensions of the Principal Components Analysis (PCA) explained 22% and 18.6% of the environmental data variance during the study years and presented a clear distinction between years and locations (Fig 2). Variable contributions (%) indicated that environmental patterns were mainly driven (contribution > 10%) by current speed, depth, wind speed, chlorophyll-a, sea surface temperature, coast distance, and kd490.

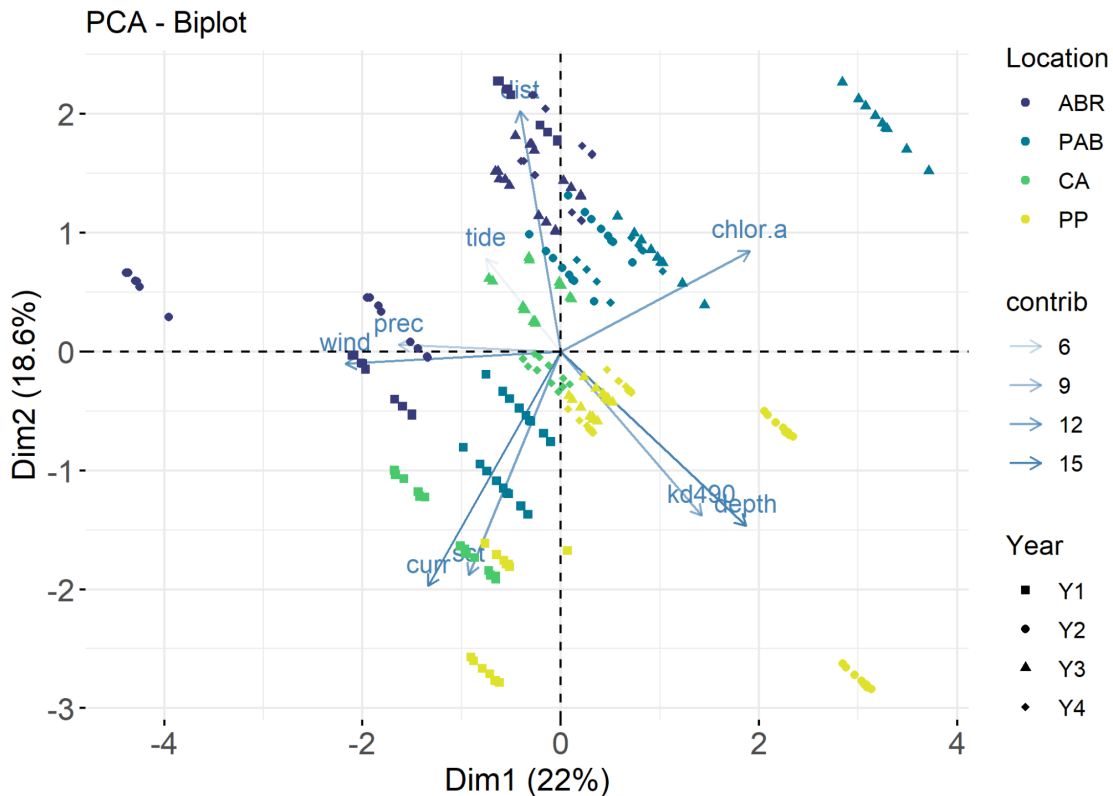


Figure 2- Principal Components Analysis (PCA). Environmental: chlor.a= chlorophyll-a, depth=depth, Kd490=diffuse attenuation coefficient at 490 nm, tide = tide amplitude, wind=wind speed, dist = coast distance, curr = current speed, sst= sea surface temperature and prec = precipitation.

Fish assemblage

Overall, 103 fish *taxa* were identified, accounting for 3,397 individuals (Table 1 and Table 4 - Supplementary material). The postlarvae identified beyond the family level were represented by 36 *taxa* (Figure 6), including 72 at the species level and 20 at the genus level. Among the most represented families, Carangidae presented the highest diversity, with 10 *taxa*, followed by Synodontidae and Lutjanidae, with 8 and 7 *taxa*, respectively. The total species (*taxa*) richness for ABR, PAB, CA, and PP was 72, 57, 40, and 38, respectively (Table 1).

The overall mean \pm SE of postlarvae fish captured per light trap unit (CPUE-N/LT) across locations was 13.71 ± 3.62 ind. LT⁻¹, ranging from 0 to 121 ind. (Table 1). On average, protected areas (ABR and PAB) harbored approximately 4 times more postlarvae than unprotected localities (CA and PP). Additionally, CPUE was approximately 1.3 times higher during the first year compared to the CPUE of all other periods (Table 1).

The most abundant site was ABR, followed by PAB, CA, and PP. However, CA had the lowest richness (38) while ABR had the highest number of species/*taxa* (72). Lutjanidae was the most abundant family with 750 individuals; of which almost 95% were collected in ABR and PAB, followed by Gerreidae with 589 individuals, of which over 50% were captured in ABR (311 individuals). (Fig. 6, Table 4- Supplementary material). The most abundant species was *Stegastes variabilis*, with 374 individuals of which approximately 85% were captured in ABR. During the first year of sampling, the highest total abundance was observed (1,979 individuals), but the greatest species richness (62) was found during the third year of sampling (Table 4 - Supplementary material).

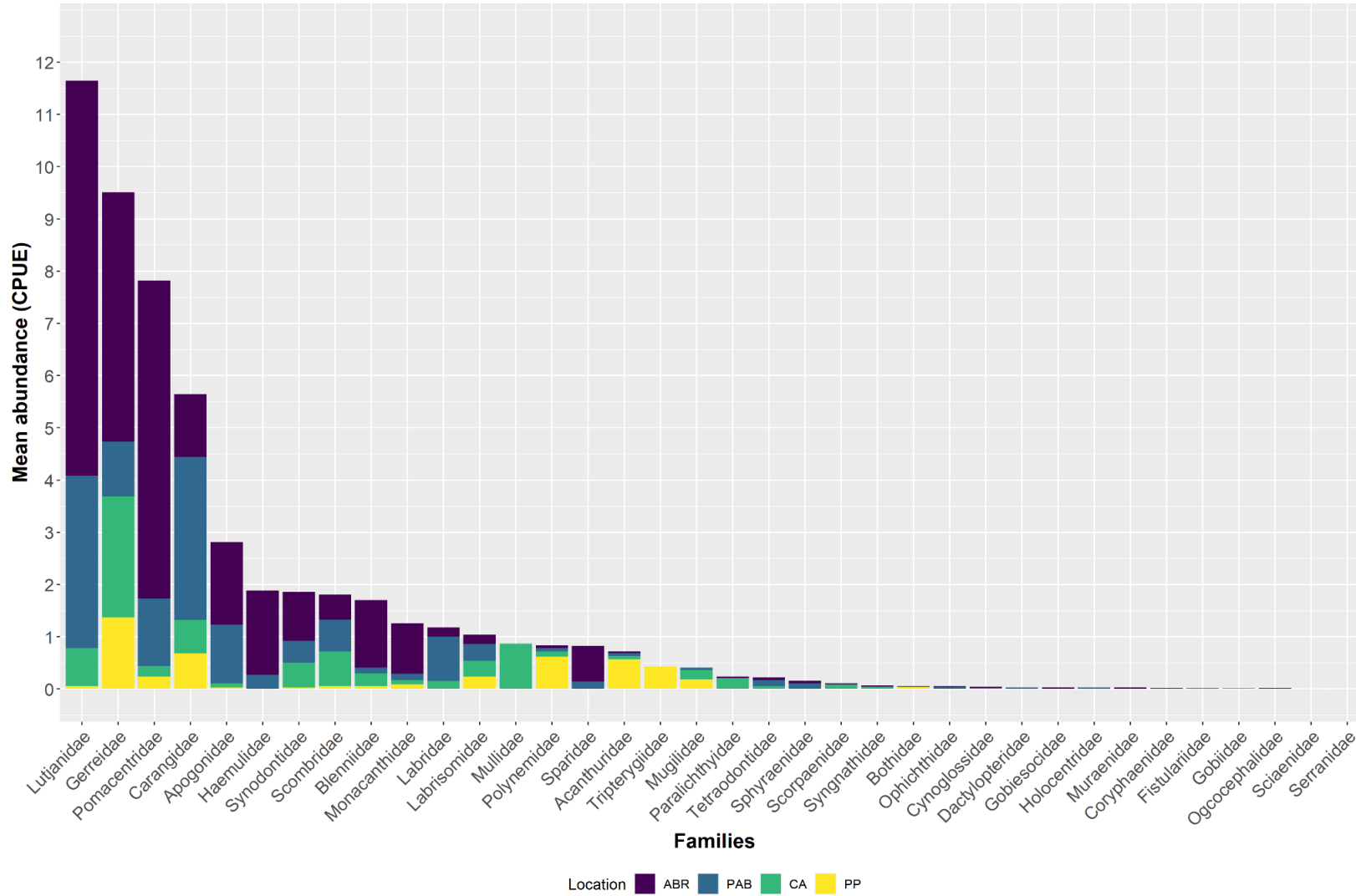


Figure 3- Mean abundance (catch-per-unit-effort (CPUE- N/LT)) by families of reef fish postlarvae caught with a light trap in the sample areas (ABR= Abrolhos Archipelago, PAB= Abrolhos Parcel, CA= Cassurubá e PP= Paredes Parcel)

Tabel 1- Mean of catch-per-unit-effort - CPUE (N/LT) (\pm standard error) by species/*taxa* of fish postlarvae caught with a light trap in the sample areas (ABR= Abrolhos Archipelago, PAB= Abrolhos Parcel, CA= Cassurubá e PP= Paredes Parcel) and sample periods (Y1= January-2019, Y2= March-2020, Y3=January-2021, and Y4= January/February-2022). NI= Not identified

Family	Taxa	Location				Year			
		ABR	PAB	CA	PP	Y1	Y2	Y3	Y4
Acanthuridae	<i>Acanthurus bahianus</i>	0.03 \pm 0.03	0.02 \pm 0.02	0.06 \pm 0.06	0.56 \pm 0.22	0.61 \pm 0.21			
	<i>Acanthurus coeruleus</i>		0.05 \pm 0.03		0.01 \pm 0.01		0.06 \pm 0.05	0.01 \pm 0.01	
Apogonidae	<i>Apogon spp</i>				0.01 \pm 0.01			0.01 \pm 0.01	
	Apogonidae				0.01 \pm 0.01			0.01 \pm 0.01	
	<i>Astrapogon puncticulatus</i>	1.57 \pm 0.31	1.12 \pm 0.38	0.08 \pm 0.05		1.39 \pm 0.37	0.02 \pm 0.02	0.89 \pm 0.26	0.27 \pm 0.11
	<i>Astrapogon stellatus</i>	0.02 \pm 0.02						0.01 \pm 0.01	
Blenniidae	Blenniidae	0.25 \pm 0.11	0.08 \pm 0.05		0.01 \pm 0.01			0.17 \pm 0.08	0.18 \pm 0.10
	<i>Hyleurochilus spp</i>				0.01 \pm 0.01			0.01 \pm 0.01	
	<i>Omobranchus punctatus</i>	0.02 \pm 0.02					0.02 \pm 0.02		
	<i>Parablennius marmoreus</i>	0.38 \pm 0.13	0.03 \pm 0.02	0.14 \pm 0.07	0.03 \pm 0.02	0.25 \pm 0.12	0.04 \pm 0.03	0.21 \pm 0.07	0.02 \pm 0.02
	<i>Scartella cristata</i>	0.65 \pm 0.26		0.04 \pm 0.03		0.24 \pm 0.20	0.04 \pm 0.03	0.10 \pm 0.04	0.32 \pm 0.17
Bothidae	<i>Bothus ocellatus</i>	0.02 \pm 0.02			0.03 \pm 0.02			0.04 \pm 0.02	
	<i>Bothus spp</i>				0.01 \pm 0.01			0.01 \pm 0.01	
Carangidae	<i>Carangoides bartholomaei</i>	0.09 \pm 0.04	0.42 \pm 0.18	0.40 \pm 0.17	0.28 \pm 0.12	0.53 \pm 0.16	0.51 \pm 0.23	0.12 \pm 0.07	0.02 \pm 0.02
	<i>Caranx crysos</i>	0.15 \pm 0.12	0.36 \pm 0.11	0.10 \pm 0.05	0.19 \pm 0.06	0.28 \pm 0.07	0.51 \pm 0.21	0.08 \pm 0.03	0.02 \pm 0.02
	<i>Caranx latus</i>	0.20 \pm 0.16		0.02 \pm 0.02	0.04 \pm 0.03	0.21 \pm 0.14		0.03 \pm 0.02	

	<i>Caranx ruber</i>	0.03±0.03	0.02±0.02			0.01±0.01		0.03±0.03	
	<i>Caranx spp</i>	0.02±0.02						0.02±0.02	
	<i>Chloroscombrus chrysurus</i>	0.03±0.02	0.02±0.02	0.10±0.04	0.09±0.04	0.03±0.02	0.12±0.06	0.06±0.03	0.04±0.03
	<i>Decapterus macarellus</i>	0.35±0.23	1.73±0.48		0.07±0.03	1.50±0.44	0.59±0.33	0.07±0.03	
	<i>Decapterus punctatus</i>	0.26±0.17	0.58±0.20			0.76±0.23			
	<i>Elagatis bipinnulata</i>			0.02±0.02				0.01±0.01	
	<i>Trachurus lathami</i>	0.05±0.03				0.04±0.03			
Coryphaenidae	<i>Coryphaena hippurus</i>	0.02±0.02				0.01±0.01			
Cynoglossidae	<i>Symphurus plagusia</i>	0.02±0.02		0.02±0.02				0.03±0.02	
Dactylopteridae	<i>Dactylopterus volitans</i>		0.03±0.02			0.01±0.01			0.02±0.02
Fistulariidae	<i>Fistularia tabacaria</i>		0.02±0.02						0.02±0.02
Gerreidae	Gerreidae	4.78±0.88	1.05±0.25	2.32±0.53	1.37±0.37	4.71±0.79	0.47±0.16	2.15±0.44	1.29±0.42
Gobiesocidae	<i>Tomicodon australis</i>	0.03±0.02					0.04±0.03		
Gobiidae	<i>Microgobius meeki</i>			0.02±0.02		0.01±0.01			
Haemulidae	<i>Anisotremus virginicus</i>	0.02±0.02	0.02±0.02			0.03±0.02			
	Haemulidae	0.12±0.06					0.02±0.02	0.10±0.05	
	<i>Haemulon aurolineatum</i>	0.08±0.05						0.07±0.05	
	<i>Haemulon parra</i>	0.06±0.04	0.05±0.03				0.02±0.02	0.08±0.04	
	<i>Haemulon plumieri</i>		0.06±0.04					0.06±0.03	
	<i>Haemulon spp</i>	1.34±0.48	0.15±0.07			0.33±0.10		1.00±0.44	0.02±0.02

Holocentridae	<i>Holocentrus adscensionis</i>		0.03±0.03			0.03±0.03			
Labridae	<i>Halichoeres poeyi</i>	0.15±0.07	0.85±0.35	0.14±0.06		0.01±0.01		1.00±0.32	
	<i>Halichoeres spp</i>	0.03±0.03						0.03±0.03	
Labrisomidae	<i>Gobioclinus guppyi</i>	0.03±0.03				0.03±0.03			
	<i>Gobioclinus kalisherae</i>	0.02±0.02	0.03±0.02	0.02±0.02	0.07±0.05			0.12±0.06	
	Labrisomidae	0.02±0.02	0.03±0.02	0.04±0.03					0.09±0.04
	<i>Labrisomus nuchipinnis</i>	0.06±0.04	0.05±0.03	0.14±0.05	0.13±0.09	0.08±0.04		0.21±0.09	0.04±0.03
	<i>Labrisomus spp</i>		0.03±0.03						0.04±0.04
	<i>Malacoctenus spp</i>	0.02±0.02				0.01±0.01			
	<i>Malacoctenus zaluari</i>	0.05±0.03	0.18±0.06	0.16±0.08	0.04±0.03	0.22±0.06	0.02±0.02	0.12±0.05	
Lutjanidae	<i>Lutjanus alexandrei</i>	0.03±0.02	0.39±0.11			0.04±0.02	0.51±0.15		
	<i>Lutjanus analis</i>	1.48±0.40	0.14±0.05	0.04±0.03		1.36±0.36		0.12±0.05	
	<i>Lutjanus cyanopterus</i>	1.68±0.45	0.86±0.28	0.02±0.02	0.04±0.03	2.35±0.45			0.02±0.02
	<i>Lutjanus jocu</i>	2.66±0.73	1.09±0.30	0.16±0.11		3.22±0.68		0.29±0.10	
	<i>Lutjanus spp</i>	0.03±0.02	0.30±0.14			0.28±0.13		0.03±0.02	
	<i>Lutjanus synagris</i>	0.77±0.48	0.12±0.06			0.78±0.43		0.03±0.03	
	<i>Ocyurus chrysurus</i>	0.92±0.25	0.39±0.14	0.50±0.21	0.01±0.01	1.03±0.24	0.22±0.12	0.38±0.15	
Monacanthidae	<i>Aluterus monoceros</i>				0.01±0.01	0.01±0.01			
	<i>Stephanolepis hispidus</i>	0.97±0.46	0.12±0.04	0.08±0.05	0.07±0.03	0.17±0.05	0.10±0.04	0.81±0.42	0.09±0.04
Mugilidae	<i>Mugil curema</i>		0.02±0.02				0.02±0.02		

	<i>Mugil spp</i>		0.03±0.02	0.18±0.08	0.18±0.07	0.11±0.06		0.06±0.03	0.20±0.09
Mullidae	<i>Mulloidichthys martinicus</i>			0.40±0.17		0.28±0.12			
	<i>Pseudupeneus maculatus</i>			0.34±0.19	0.01±0.01	0.24±0.13		0.01±0.01	
	<i>Upeneus parvus</i>			0.12±0.06		0.08±0.04			
Muraenidae	<i>Gymnothorax spp</i>	0.03±0.02						0.03±0.02	
Ogcocephalidae	<i>Ogcocephalus vespertilio</i>	0.02±0.02					0.02±0.02		
Ophichthidae	<i>Ahlia egmontis</i>	0.03±0.02	0.03±0.02		0.01±0.01		0.06±0.03	0.03±0.02	
Paralichthyidae	<i>Citharichthys spp</i>	0.03±0.02		0.06±0.06					0.09±0.06
	<i>Etropus crossotus</i>				0.01±0.01			0.01±0.01	
	Paralichthyidae			0.14±0.09					0.12±0.08
Polynemidae	<i>Polydactylus virginicus</i>	0.06±0.03	0.06±0.03	0.10±0.04	0.62±0.18	0.01±0.01	0.71±0.24	0.06±0.03	0.27±0.06
Pomacentridae	<i>Abudefduf saxatilis</i>	0.08±0.05	0.09±0.05	0.12±0.07	0.13±0.05	0.01±0.01	0.33±0.10	0.10±0.05	0.04±0.04
	Pomacentridae	0.02±0.02						0.01±0.01	
	<i>Stegastes fuscus</i>	0.20±0.08	0.32±0.16			0.39±0.16		0.08±0.05	
	<i>Stegastes pictus</i>	0.68±0.24	0.09±0.05			0.44±0.20		0.24±0.10	0.02±0.02
	<i>Stegastes spp</i>	0.22±0.11	0.11±0.07		0.01±0.01			0.31±0.12	
	<i>Stegastes variabilis</i>	4.91±0.88	0.68±0.20	0.08±0.06	0.09±0.07	2.57±0.57		2.58±0.68	0.05±0.03
Sciaenidae	Sciaenidae				0.01±0.01				0.02±0.02
Scombridae	<i>Euthynnus alletteratus</i>		0.17±0.07			0.15±0.06			
	<i>Scomberomorus brasiliensis</i>	0.45±0.32	0.41±0.13	0.58±0.21		1.18±0.33			

	<i>Scomberomorus cavalla</i>	0.03±0.03	0.02±0.02	0.08±0.05	0.06±0.03	0.11±0.05		0.04±0.02
	<i>Scomberomorus regalis</i>		0.02±0.02			0.01±0.01		
Scorpaenidae	<i>Scorpaena plumieri</i>			0.02±0.02				0.02±0.02
	<i>Scorpaena spp</i>	0.02±0.02		0.04±0.03	0.01±0.01	0.03±0.02		0.01±0.01 0.02±0.02
	Scorpaenidae			0.02±0.02				0.02±0.02
Serranidae	<i>Rypticus spp</i>				0.01±0.01			0.02±0.02
Sparidae	<i>Archosargus probatocephalus</i>	0.17±0.13	0.03±0.03					0.18±0.12
	<i>Calamus penna</i>	0.22±0.08	0.09±0.04			0.28±0.08		
	<i>Calamus spp</i>	0.02±0.02	0.02±0.02					0.04±0.03
	Sparidae	0.29±0.14						0.26±0.13
Sphyraenidae	<i>Sphyraena barracuda</i>	0.05±0.03	0.06±0.03			0.04±0.02	0.02±0.02	0.04±0.02
	<i>Sphyraena guachancho</i>		0.05±0.03			0.04±0.03		
Syngnathidae	<i>Anarchopterus criniger</i>	0.02±0.02						0.01±0.01
	<i>Hippocampus reidi</i>			0.04±0.03		0.01±0.01		0.01±0.01
	<i>Micrognathus crinitus</i>				0.01±0.01	0.01±0.01		
Synodontidae	<i>Saurida spp</i>	0.03±0.03						0.03±0.03
	Synodontidae	0.12±0.11		0.02±0.02				0.12±0.10
	<i>Synodus foetens</i>	0.65±0.16	0.18±0.07	0.46±0.15		0.60±0.15	0.08±0.04	0.42±0.11
	<i>Synodus intermedius</i>	0.02±0.02	0.08±0.05			0.03±0.02	0.08±0.06	
	<i>Synodus poeyi</i>	0.02±0.02						0.01±0.01

Spatial and Environmental variations and the relationship between fish assemblage

The non-metric multidimensional scaling (NMDS) ordination showed a separation of postlarval assemblages during the sample seasons (Y1- ■; Y2 - ●; Y3-▲ and Y4 - ◆) and Location (ABR, PAB, CA, PP). Vector overlays (Envfit, $p < 0.01$) indicated that one group separation was driven by *Astrapogon puncticulatus*, *Calamus pennatula*, *Decapterus punctatus*, *Euthynnus alletteratus*, *Haemulon sp.*, *Halichoeres poyei*, *Malacoptenus zaluari*, *Lutjanus jocu*, *Lutjanus cyanopterus*, *Lutjanus analis*, *Lutjanus synagris*, *Lutjanus sp.*, *Ocyurus chrysurus*, *Parablennius marmoreus*, *Synodus foetens*, Sparidae, *Scomberomorus brasiliensis*, *Stegastes variabilis*, *Stegastes pictus*, *Stegastes sp.*, *Sphyraena barracuda*, Wind, and Coast Distance and was mainly associated with ABR and PAB samples from year 1. Another group separation was driven mainly by *Mugil sp.*, *Polydactilus virginicus*, depth, kd490, and tide and was associated with CA and PP.

When considering years (Fig. 4), vector overlays (Envfit, $p < 0.01$) indicated that one group separation in the first year was driven by *Astrapogon puncticulatus*, *Calamus pennatula*, *Haemulon sp.*, *Lutjanus jocu*, *Lutjanus cyanopterus*, *Lutjanus analis*, *Lutjanus synagris*, *Lutjanus sp.*, *Ocyurus chrysurus*, *Stegastes variabilis*, and Coast Distance and was mainly associated with ABR and PAB. Another group separation was mainly driven by *Acanthurus bahianus*, *Caranx crysos*, *Mulloidichthys martinicus*, *Upeneus parvus*, chlorophyll-a, depth, sea surface temperature, tide, and precipitation and was associated with CA and PP. The second year indicated one group separation of *Carangoides bartholomaei*, *Lutjanus alexandrei*, Gerreidae, Coast Distance, Precipitation, Tide, and Wind and was mainly associated with ABR and PAB. *Polydactilus virginicus*, *Stephanolepis hispidus*, chlorophyll-a, and diffuse attenuation coefficient at 490 nm formed another group that was mainly associated with CA and PP.

In the third year of sampling, Vector overlays (Envfit, $p < 0.01$) indicated that group separation was driven mainly by Gerreidae, *Enneanectes altivelis*, depth, current speed, and wind associated with CA and PP. Another group was driven by *Halichoeres poyei*, chlorophyll-a, coast distance, and diffuse attenuation coefficient at 490 nm and was mainly associated with PAB. Another group was mainly driven by *Astrapogon puncticulatus*, *Haemulon sp.*, *Lutjanus jocu*, *Stegastes variabilis*, *Stegastes pictus*,

Stephanolepis hispidus, tide, and sea surface temperature and was associated with ABR. In the fourth year, it was not possible to observe a clear separation of groups. (Fig. 4).

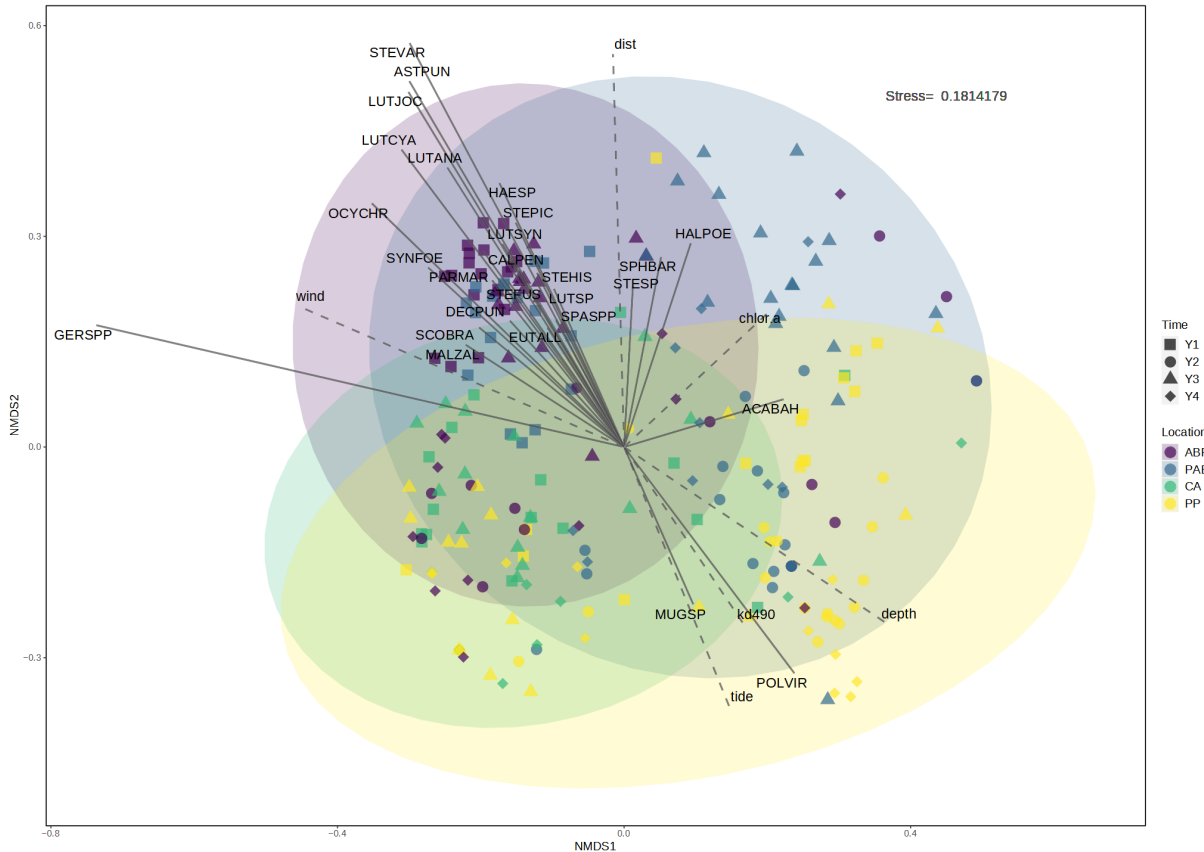


Figure 4-

Non-metric multidimensional scaling (nMDS) ordering of fish postlarvae species composition based on the Bray-Curtis similarity matrix (abundance (Log (x+1))), with significant (R^2) correlations (envfit, $p < 0.01$) of the environmental variables (dotted line) and species (solid line) with the ordination axes, for January/2019 (Y1), March/2020 (Y2) and January/21(Y3) and January/22 (Y4). The ellipse represents the 95% confidence interval of the distribution (t) of the data for each of the sampling locations (ABR= Abrolhos Archipelago, PAB= Abrolhos Parcel, CA= Cassurubá and PP= Paredes Parcel). Environmental: chlor.a= chlorophyll-a, depth=depth, Kd490=diffuse attenuation coefficient at 490 nm, tide = tide amplitude, wind=wind speed, dist = coast distance. Species codes: ACABAH=*Acanthurus bahianus*, ASTPUN=*Astrapogon puncticulatus*, CALPEN= *Calamus penna*, CARCRY= *Caranx crysos*, DECPUN = *Decapterus punctatus*, EUTALL= *Euthynnus alletteratus*, GERSPP= Gerreidae, HAESP= *Haemulon sp.*, HALPOE = *Halichoeres poyei*, LUTANA= *Lutjanus analis*, LUTCYA= *Lutjanus cyanopterus*, LUTJOC= *Lutjanus jocu*, LUTSYN= *Lutjanus synagris*, LUTSP= *Lutjanus sp.*, OCYCHR= *Ocyurus chrysurus*, PARMAR= *Parablennius marmoratus*, MALZAL = *Malacoctenus zaluari*, MUGSP = *Mugil sp.*, POLVIR= *Polydactilus virginicus*, SCOBRA = *Scomberomorus brasiliensis*, SPASPP= Sparidae, SPHBAR= *Sphyrna barracuda*, STEVAR= *Stegates variabilis*, STEFUS = *Stegastes fuscus*, STESP = *Stegastes sp.*, STEPIC= *Stegastes pictus*, STEHIS = *Stephanolepis Hispidus*, TRAMYO = *Trachinocephalus myops*

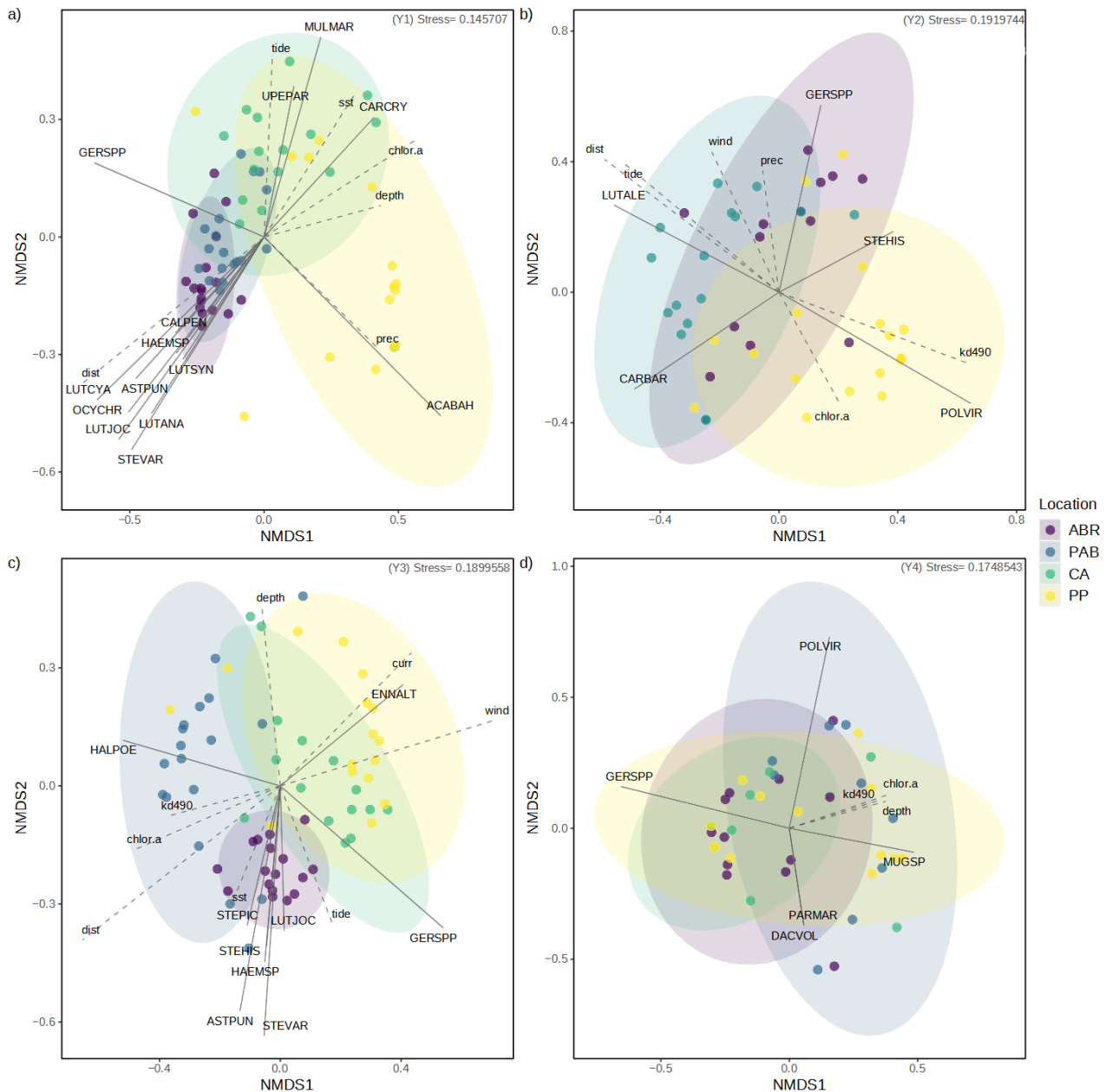


Figure 5- Non-metric multidimensional scaling (nMDS) ordering of fish postlarvae species composition based on the Bray-Curtis similarity matrix (abundance $\log(x+1)$), with significant (R^2) correlations (envfit, $p < 0.01$) of the environmental variables (dotted line) and species (solid line) with the ordination axes, for January/2019 (A), March/2020 (B) and January/21(C) and January/22 (D). The ellipse represents the 95% confidence interval of the distribution (t) of the data for each of the sampling locations (ABR= Abrolhos Archipelago, PAB= Abrolhos Parcel, CA= Cassurubá and PP= Paredes Parcel). Environmental: chlor.a= chlorophyll-a, depth=depth, Kd490=diffuse attenuation coefficient at 490 nm, tide = tide amplitude, wind=wind speed, dist = coast distance. Species codes: ACABAH=*Acanthurus bahianus*, ASTPUN=*Astrapogon puncticulatus*, CARBAR= *Carangoides bartholomaei*, CALPEN= *Calamus penna*, DECPUN = *Decapterus punctatus*, ENNALT= *Enneanectes altivelis*, EUTALL= *Euthynnus alletteratus*, GERSPP= Gerreidae, HAESP= *Haemulon sp.*, HALPOE = *Halichoeres poyei*, LUTALE= *Lutjanus alexandrei*, LUTANA= *Lutjanus analis*, LUTCYA= *Lutjanus cyanopterus*, LUTJOC= *Lutjanus jocu*, LUTSYN= *Lutjanus synagris*, LUTSP= *Lutjanus sp.*, OCYCHR= *Ocyurus chrysurus*, PARMAR= *Parablennius marmoratus*, MALZAL = *Malacoctenus zaluari*, MUGSP = *Mugil sp.*, MULMAR = *Mulloidichthys martinicus*, POLVIR= *Polydactylus virginicus*, SCOBRA = *Scomberomorus brasiliensis*, SPASPP= Sparidae, SPHBAR= *Sphyræna barracuda*, STEVAR= *Stegastes variabilis*, STEFUS = *Stegastes fuscus*, STESP = *Stegastes sp.*, STEPIC= *Stegastes pictus*, STEHIS = *Stephanolepis hispidus*, TRAMYO = *Trachinocephalus myops*, UPEPAR=*Upeneus parvus*

Fish assemblage analyses

In the first, third, and fourth years of sampling, ABR obtained the highest biomass while in the second year, the highest biomass was recorded in PAB (Figure 6). The postlarvae biomass demonstrated significant variations in spatial scale interactions with protection and years [L(PxY)] (Table 2). The same pattern was observed for the abundance of species and the postlarvae abundance demonstrated significant variations in protection interactions with years (PxY), and spatial scale interactions with protection and years [L(PxY)]. (Figures 6, Table 2). On the other hand, the frequency distribution of the average postlarvae size increased towards the coastal reefs, where the smallest averages were found for ABR and PAB and the highest in CA and PP (Figure 6). The average postlarvae size demonstrated significant variations in spatial scale interactions for protection and years [L(PxY)] (Table 2).

Statistics regarding Hill numbers showed similar patterns and variations in the true diversity indices (q^0 , q^1 , and q^2). In the first and second sampling years, ABR and PAB had the highest values of diversity orders and this only varied in the third year where PAB presented the lowest values of q^1 and q^2 compared to the other locations (Figure 6). All ecological indicators (Abundance, Biomass, Average Length, and True diversity indices) were significant in the [Location (Protection x Year)] interaction (Table 2, Figure 6), indicating a strong influence of spatial-temporal and protection effects on the monitored indicators. However, the results showed that the detection of protection effects in the diversity indices mainly depended on the year and varied at the local scale.

The relationships of total abundance and Hill diversity indices (q^0 , q^1 , and q^2) with environmental variables are shown in Table 3. According to the selected models, a higher number of species and abundance were found at low-productivity wind-driven offshore sites for dominant, common, and rare species. Shallow depths were also determinants for total abundance and rare species occurrence.

Figure 6- Total abundance-CPUE (Log) (a), Biomass-CPUE(Log) (b), Total length (mm) and Alpha diversity values (q) of fish post-larvae by location (ABR= Abrolhos Archipelago, PAB= Abrolhos Parcel, CA= Cassurubá and PP= Paredes Parcel) and sampling period (years) (Y1 - January/2019, Y2- March 2020 and Y3- January/2021, Y4 - January/2022), where q represents the order of diversity (d) q^0 – disregarded abundances, greater representation of rare species; (e) q^1 – True diversity values; (f) q^2 – Higher weight for dominant species

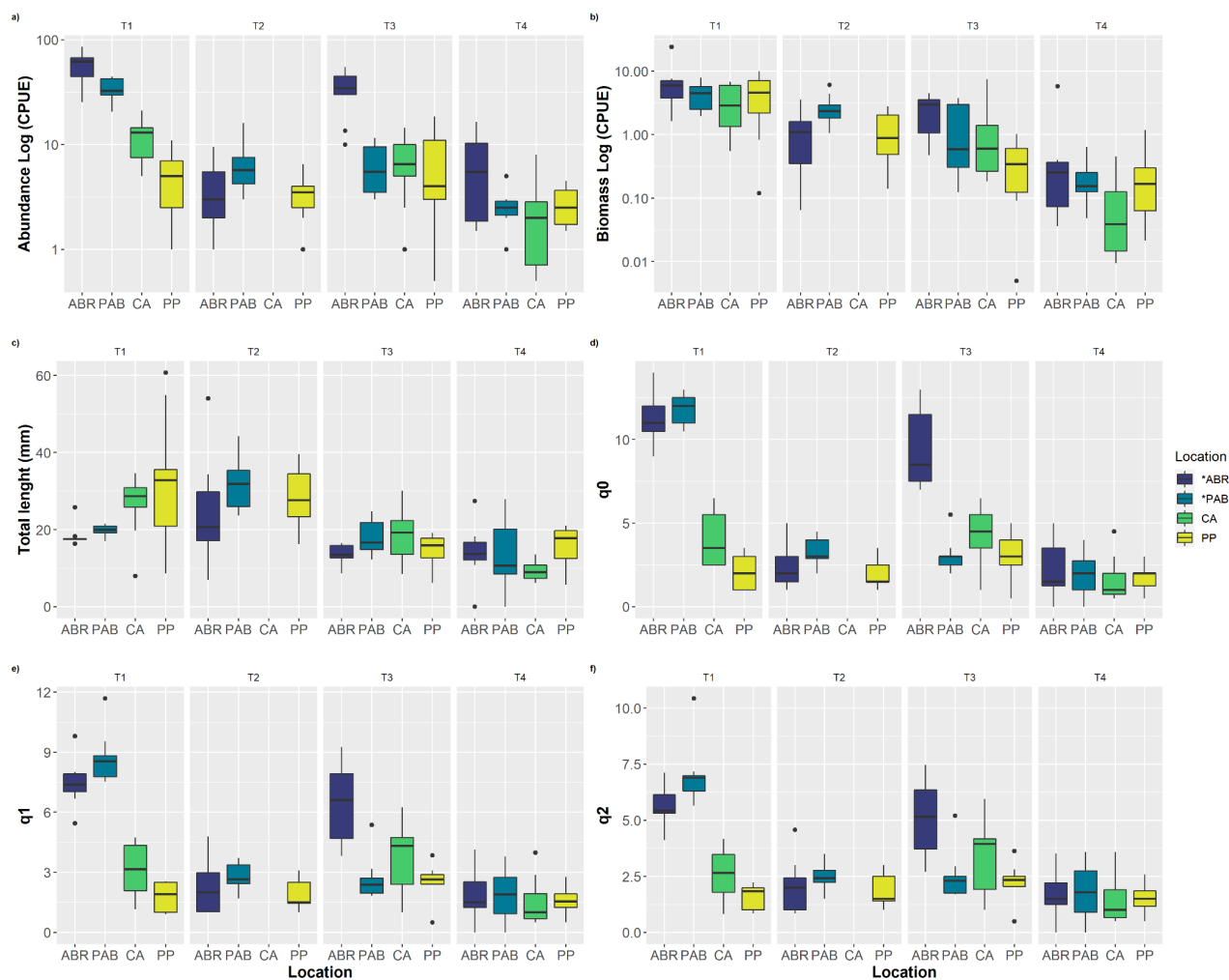


Table 2. A three-factor PERMANOVA testing the effect of Protection ("P", 2 levels, fixed), Year ("Y", 4 levels, fixed), and location ("L", 4 levels, random), on the total abundance, biomass, mean total length and diversity indices (q^0, q^1, q^2) of postlarval fish assemblages at the Abrolhos Bank with coast distance (D) as covariable. F – Pseudo-F, $P(\text{perm})$ – Permanova F statistics. Significance: * $p < 0.05$; ** $0.05 > p > 0.01$; *** $p < 0.01$.

Variables	P		Y		PxY		L (PxY)	
	F	$P(\text{perm})$	F	$P(\text{perm})$	F	$P(\text{perm})$	F	$P(\text{perm})$
Total Abundance	2.789	0.004	2.509	0.001	1.785	0.026	4.020	0.001
Biomass	0.452	0.649	7.744	0.001	0.564	0.712	3.292	0.001
Total Length	2.086	0.156	6.123	0.008	2.548	0.111	4.329	0.001
q^0	2.673	0.116	4.682	0.019	1.792	0.228	7.210	0.001
q^1	2.287	0.153	4.128	0.044	1.746	0.206	6.997	0.001
q^2	1.968	0.198	3,772	0.063	1.783	0.206	6.188	0.001

Table 3 - Results of the multiple regression model selection by maximum likelihood, using the Akaike information criterion (AIC) applied for environmental variables (Depth, Chlorophyll-a (Chlor.a), Diffuse attenuation coefficient at 490 nm (Kd490) Tide amplitude and Wind speed that best explain fish abundance and diversity Hill indices (q0,q1, and q2).

Variable	Best model	df	AIC	Weight	Intercept	β coefficient
Abundance	chlor.a + depth + dist + tide + wind	7	1868.0	0.471	28.090	-5.0430 -1.0470 +0.4254 -16.250 +1.1390
q ⁰	chlor.a + depth + dist + tide + wind	7	1108.8	0.467	4.636	-1.0080 -0.095400 +0.10190 -3.389 +0.33890
q ¹	chlor.a + dist + tide + wind	6	972.6	0.420	2.230	-0.60700 +0.06934 -2.135 +0.26060
q ²	chlor.a + dist + tide + wind	6	891.3	0.413	2.057	-0.3782000 +0.05065 -1.574 +0.19420
Biomass	chlor.a + dist + tide	5	1264.0	0.198	4.134	-0.9107 +0.03309 -2.148

DISCUSSION

This study is the first investigation, using light traps, of the spatial-temporal distribution of early reef fish stages and the environmental determinants in the Abrolhos Bank, in addition to the possible role of MPAs in these processes. We found that wind, coast distance, chlorophyll-a, depth, and tide were significant in predicting larvae occurrence in the study locations, which supported hypothesis ii. Tide, depth, and coast distance were mainly associated with species from the Mugilidae and Polynemidae families that presented higher postlarvae abundance in coastal areas (CA and PP). The wind was mainly associated with the Gerreidae family, which was abundant in all sampling areas, and the Lutjanidae family, which presented higher postlarvae abundance in the ABR and PAB and was associated with coast distance. The interaction between biological processes and the environment (such as life-history strategies, temperature, behavior, currents, tides, and seascape configurations) is greatly important in determining larval settlement (Sponaugle et al. 2012; Félix-Hackradt et al. 2013b; Brown et al. 2016; Grande et al. 2019; Goldstein and Sponaugle 2020). Factors such as wind, current, tide, temperature, precipitation, river discharge, chlorophyll-a, and water mass have been considered the 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 and Ponton; Lemberget et al. 2009; Gamoyo et al. 2011; Álvarez et al. 2012; Sim-smith et al. 2013; Félix-Hackradt et al. 2013a; Beldade et al. 2016, Goldstein and Sponaugle 2020), as well as other oceanographic events, such as topographic characteristics (Mullineaux and Mills 1997; Vaz et al. 2016; Ospina-Alvarez et al. 2018) and seascape configurations (Brown et al. 2016), which are also important for larval dispersal patterns.

An important aspect of this study is the supply of postlarvae marine fish which varied temporally among the sampling areas. For example, almost 60% of the total number of individuals was collected in the first year of sampling, while the second and fourth years combined did not reach 13% of the total catch. However, the greatest species richness was found during the third year of sampling. Temporal differences in larval supply have important

consequences for the structure and dynamics of adult reef fish assemblages, as well as for the management and conservation of fish stocks in these reefs (D'Alessandro et al. 2007). As such, many studies on early life history stages have been dedicated to understanding the variability of settlement/recruitment considering temporal scales (Meekan et al., 1993; D'Alessandro et al., 2007; Sponaugle et al., 2012; Félix-Hackradt et al., 2013b). For example, Sponaugle and Cowen (1996) indicated that for some species (*Stegastes partitus*), spatial variation in larval supply is largely responsible for juvenile recruitment patterns. D'Alessandro et al. (2007) found that temporal variability in larval fish supply was comprised of 3 main components: (1) an interannual seasonal pattern, (2) a within-season cyclic pattern, and (3) stochastic within-season variability. Félix-Hackradt et al. (2013b) evaluated the inter-annual, multi-species variability in the recruitment of temperate Mediterranean rocky reef fish species and found a strong pattern of settlement periods, namely in summer and winter months, where the first period was the most important in terms of species richness. Harrison et al. (2020), in a study in the Great Barrier Reef, found that effective reserve networks take advantage of a “connectivity portfolio effect” that mitigates temporal volatility in larval supply to ensure the stability of recruitment dynamics, with potential long-term sustainability benefits for exploited fish stocks. In our study, sampling was performed annually and was concentrated during the summer when most species reproduce and settle. However, evaluations at finer temporal scales would be necessary to describe the richness of species present and to better evaluate their temporal dynamics

Another relevant observation is that some species present in the study area belonging to the Carangidae, Gerreidae, Haemulidae, Lutjanidae, Mugilidae, Sparidae, Scombridae, and Sphyraenidae families, constitute important fishery resources, whether by subsistence, artisanal or industrial fishing. Spatial-temporal variations and the possible effect of MPAs on abundance and distribution were also observed in these families. All species from the Lutjanidae family, except for *L. alexandrei*, were more abundant in the samplings carried out in the first year, which may indicate a previously successful reproductive season. The same pattern was observed concerning the sampling site. ABR had the highest abundance of Lutjanidae in total, except

for *L. alexandrei* which was more abundant in PAB. Only *L. cyanopterus* and *O. chrysurus* were collected at all sampling sites. Fish from the family Lutjanidae (snappers) are important fishery resources and act as top predators in reef ecosystems (Claro et al. 2003; Freitas 2011, Previero and Gasalla 2018). With a high commercial value, and reproductive characteristics, such as late sexual maturation and spawning aggregations (Bezerra et al. 2021; Previero and Gasalla 2018; Frédou et al. 2009), most snapper fisheries are declining or collapsing (Freitas 2011; Coleman et al. 2009). All these factors, combined with the absence of studies seeking to identify breeding areas, contribute to the increased risk of these species disappearing and suffering irreversible consequences to their reproductive dynamics due to overfishing (Bezerra et al. 2021).

For the species found in this study area, *L. cyanopterus*, *L. analis*, *L. jocu*, *L. synagris*, and *O. chrysurus* experience some level of threat according to the Brazilian Extinction Red List and the International Union for Conservation of Nature's Red List of Threatened Species (IUCN 2022). Of these species, *L. cyanopterus* is the most threatened and is categorized as vulnerable (VU) while the others are classified as near threatened (NT). Recently, Previero and Gasalla (2020) found that *L. jocu* stocks were the most threatened in the Abrolhos region, due, in particular, to their life history traits which are incompatible with the current intense fishing levels. Stocks of *L. synagris* and *O. chrysurus* face a moderate risk of overexploitation, mainly because catches occur across most of the stocks' distribution areas, imposing major threats that result in population size reduction and changes in stock age and size structures (Previero and Gasalla 2020). Regarding *L. jocu*, some studies performed on the Brazilian coast have previously suggested cross-shelf ontogenetic migration (e.g., Moura et al., 2011; Aschenbrenner et al., 2016a; Reis-Filho et al., 2019), indicating estuarine dependency in early life stages and migration to reef systems in adulthood. However, through otolith microchemistry assessments, Menezes et al. (2021) inferred two patterns for *L. jocu* across the Abrolhos Bank shelf: marine migrants and marine residents. Marine residents (56% of sampled fish) comprised fish that spent their entire lifetime in inner-shelf marine waters and did not display any estuarine dependency as once believed. In addition,

Silva (2022) described Lutjanidae postlarval growth through otolith measurement and verified that all the *L. jocu* individuals caught in the ABR and PAB older than 25 days showed settlement marks, indicating that they are using the Abrolhos Bank as a nursery area. This information corroborates our results concerning the abundance of *L. jocu* postlarvae in offshore reefs (ABR and PAB) and confirms the importance of these reef areas in the Abrolhos Bank for the conservation of the species.

Our major finding was that the communities of presettlement coral reef fishes across the sample areas differ for all diversity indices. According to the true diversity indices (sensu Jost, 2006), ABR and PAB (no-take MPAs) had the highest rates of rare (q^0), common (q^1), and dominant (q^2) species compared to CA and PP (fished areas), considering the distance from the coast as a covariable. This pattern may be related to the influence of different factors, as well as the role of MPAs that act on the early stages of the spatial distribution of reef fish (Lima et al. 2023).

The influence of MPAs on the life cycle of reef fish has been the focus of many studies by different authors (Planes et al. 2000; Kough et al. 2009; Di Franco et al. 2012; Harrison et al. 2012; Andrello et al. 2013; Pujolar et al. 2013; Félix-Hackradt et al. 2018; Harrison et al. 2020). Robust evidence shows that variations in composition, structure, and function at various levels of hierarchical organization, ranging from species to landscapes between MPAs and unprotected areas, can lead to differing settlement and recruitment rates (Grorud-Colvert and Sponaugle 2009; Lima et al. 2023). An MPA's influence can act positively from the reproductive stage until the postsettlement phase and may increase recruitment rates in these local and adjacent areas (Lima et al. 2023). Several studies have shown that MPAs lead to the production of a greater number of propagules (Planes et al. 2009; Christie et al. 2010; Crec'Hriou et al. 2010; Di Franco et al. 2012; Harrison et al. 2012; Carter et al. 2017) and the export of eggs and larvae from MPAs to adjacent areas is one of the main proven benefits of protected areas (Planes et al. 2000; Planes 2009; Di Franco et al. 2012; Lima et al. 2022). This may be related to MPAs harboring a high density of mature and large individuals (BOFFFF) that have a greater potential for egg and larvae production (Di Franco et al. 2012; Harrison et al.

2012; Carter et al. 2017), as well as a greater probability of survival (Shima and Findlay 2002; Raventos and Macpherson 2005; Searcy and Sponaugle 2001). Results from studies in the Abrolhos region have shown a higher density of larger adults of target species, such as for the families Lutjanidae, Haemulidae, Labridae, Epinephelidae, and Carangidae, within protected areas compared to open-fishing areas (Ferreira and Gonçalves, 1999; Ferreira, 2005; Rolim et al. 2022). Thus, considering the BOFFFF theory, the high density of large adults of these species found in the protected areas of the Abrolhos region corroborates our findings.

MPAs can also provide high-quality habitats for larval settlement (Almany 2004; Almany and Webster 2006; Johnson 2007) and, consequently, assist in larval navigation by producing acoustic fingerprints that increment the distance of reef detection by fish larvae (Piercy et al. 2014) and result in higher colonization rates (Jaquiéry et al. 2008). Additionally, some authors have suggested that large MPAs (e.g., 10–20 km) are subjected to more local retention than smaller ones (0.5–1 km) (Green et al. 2015; Carr et al. 2017). As such, sample areas located within an MPA (ABR and PAB) may be influenced by protection effects (Lima et al. 2023) and therefore, explain the greater diversity, richness, and abundance of species in these areas. The PERMANOVA analysis also detected the influence of protection on the abundance and hill diversity indices, considering that the result was significant for total abundance with the factor P (protection), despite confounding geographic location effects. All parameters (total abundance, biomass, total length, q^0 , q^1 , and q^2) were significant, presenting interactions between protection and years, nested by location - L(PxY) which supported hypothesis i. However, the effectiveness of protecting nursery habitats differs according to the characteristics of each species in terms of their habitat particularities, specific food needs, ideal growing conditions, and the environmental variations to which they will be subjected (Planes et al. 2000; Lima et al. 2022).

CONCLUSION

This study provides the first assessment regarding postlarval assemblage distribution in the Abrolhos Bank. Our findings demonstrated the

importance of spatial-temporal variations in the distribution of early-life reef fish assemblages in the Abrolhos Bank, in addition to the possible influence of MPAs on these patterns and processes. The postlarvae occurrence was mainly influenced by local winds and coast distance, and our data corroborate the results of different studies which suggest that one of the main benefits of MPAs in the early life history of reef fish is the high production of propagules. This is due to the greater abundance and diversity of species found in protected areas, to the detriment of areas open to fishing. However, several factors may be related to these patterns, among which habitat type, quality, complexity, seascape configuration, and the location of the protected area, can be highlighted. Although areas open to fishing have lower abundances and diversities, some species found in these places are ecologically and commercially important, thereby indicating the need for further studies that seek the potential of these areas as a nursery and for the conservation of fish stocks in the region. Therefore, we strongly recommend that new studies should be carried out in the Abrolhos Bank, considering the different factors that influence the initial stages of reef fish and that may encompass both finer spatial-temporal scales, as well as species-specific characteristics. Finally, we suggest in order to achieve the conservation objectives of marine reserves, early life history patterns should be taken into consideration during the design and selection of spatial management units for the establishment of marine protected areas.

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SUPPLEMENTARY MATERIAL

Tabel 4- Total Abundance by species/taxa of fish postlarvae caught with a light trap in the sample areas (ABR= Abrolhos Archipelago, PAB= Abrolhos Parcel, CA= Cassurubá and PP= Paredes Parcel) and sample periods (Y1= January-2019, Y2= March-2020, Y3=January-2021, and Y4 =January/February- 2022.). NI= Not identified

Family	Species / Taxa	Locations				Total Abundance	Years				Total Abundance
		ABR	PAB	CA	PP		Y1	Y2	Y3	Y4	
Acanthuridae	<i>Acanthurus bahianus</i>	2	1	3	38	44	44				44
	<i>Acanthurus coeruleus</i>		3		1	4		3	1		4
	<i>Apogon spp</i>				1	1			1		1
Apogonidae	Apogonidae				1	1			1		1
	<i>Astrapogon puncticulatus</i>	102	74	4		180	100	1	64	15	180
	<i>Astrapogon stellatus</i>	1				1			1		1
Blenniidae	Blenniidae	16	5		1	22			12	10	22
	<i>Hypoleurochilus spp</i>				1	1			1		1
	<i>Omobranchus punctatus</i>	1				1		1			1
	<i>Parablennius marmoreus</i>	25	2	7	2	36	18	2	15	1	36

	<i>Scartella cristata</i>	42		2		44	17	2	7	18	44
Bothidae	<i>Bothus ocellatus</i>	1			2	3			3		3
	<i>Bothus spp</i>				1	1			1		1
	<i>Carangoides bartholomaei</i>	6	28	20	19	73	38	25	9	1	73
	<i>Caranx crysos</i>	10	24	5	13	52	20	25	6	1	52
	<i>Caranx latus</i>	13		1	3	17	15		2		17
	<i>Caranx ruber</i>	2	1			3	1		2		3
	<i>Caranx spp</i>	1				1		1			1
Carangidae	<i>Chloroscombrus chrysurus</i>	2	1	5	6	14	2	6	4	2	14
	<i>Decapterus macarellus</i>	23	114		5	142	108	29	5		142
	<i>Decapterus punctatus</i>	17	38			55	55				55
	<i>Elagatis bipinnulata</i>				1	1			1		1
	<i>Trachurus lathami</i>	3				3	3				3
Coryphaenidae	<i>Coryphaena hippurus</i>	1				1	1				1
Cynoglossidae	<i>Symphurus plagusia</i>	1			1	2			2		2
Dactylopteridae	<i>Dactylopterus volitans</i>		2			2	1			1	2

Fistularidae	<i>Fistularia tabacaria</i>		1			1			1	1	
Gerreidae	Gerreidae	311	69	116	93	589	339	23	155	72	589
Gobiesocidae	<i>Tomicodon australis</i>	2				2		2			2
Gobiidae	<i>Microgobius meeki</i>			1		1	1				1
	<i>Anisotremus virginicus</i>	1	1			2	2				2
	Haemulidae	8				8		1	7		8
Haemulidae	<i>Haemulon aurolineatum</i>	5				5			5		5
	<i>Haemulon parra</i>	4	3			7		1	6		7
	<i>Haemulon plumieri</i>		4			4			4		4
	<i>Haemulon spp</i>	87	10			97	24		72	1	97
Holocentridae	<i>Holocentrus adscensionis</i>		2			2	2				2
Labridae	<i>Halichoeres poeyi</i>	10	56	7		73	1		72		73
	<i>Halichoeres spp</i>	2				2			2		2
	<i>Gobioclinus guppyi</i>	2				2	2				2
Labrisomidae	<i>Gobioclinus kalisherae</i>	1	2	1	5	9			9		9

	Labrisomidae	1	2	2		5			5	5	
	<i>Labrisomus nuchipinnis</i>	4	3	7	9	23	6		15	2	23
	<i>Labrisomus spp</i>		2			2				2	2
	<i>Malacoctenus spp</i>	1				1	1				1
	<i>Malacoctenus zaluari</i>	3	12	8	3	26	16	1	9		26
	<i>Lutjanus alexandrei</i>	2	26			28	3	25			28
	<i>Lutjanus analis</i>	96	9	2		107	98		9		107
	<i>Lutjanus cyanopterus</i>	109	57	1	3	170	169			1	170
Lutjanidae	<i>Lutjanus jocu</i>	173	72	8		253	232		21		253
	<i>Lutjanus spp</i>	2	20			22	20		2		22
	<i>Lutjanus synagris</i>	50	8			58	56		2		58
	<i>Ocyurus chrysurus</i>	60	26	25	1	112	74	11	27		112
	<i>Aluterus monoceros</i>				1	1	1				1
Monacanthidae	<i>Stephanolepis hispidus</i>	63	8	4	5	80	12	5	58	5	80
	<i>Mugil curema</i>		1			1		1			1
Mugilidae	<i>Mugil spp</i>		2	9	12	23	8		4	11	23

	<i>Mulloidichthys martinicus</i>			20		20		20			20
Mullidae	<i>Pseudupeneus maculatus</i>			17	1	18		17		1	18
	<i>Upeneus parvus</i>			6		6		6			6
Muraenidae	<i>Gymnothorax spp</i>	2				2				2	2
Ogcocephalidae	<i>Ogcocephalus vespertilio</i>	1				1			1		1
Ophichthidae	<i>Ahlia egmontis</i>	2	2		1	5		3	2		5
	<i>Citharichthys spp</i>	2		3		5				5	5
Paralichthyidae	<i>Etropus crossotus</i>				1	1			1		1
	Paralichthyidae			7		7				7	7
Polynemidae	<i>Polydactylus virginicus</i>	4	4	5	42	55	1	35	4	15	55
	<i>Abudefduf saxatilis</i>	5	6	6	9	26	1	16	7	2	26
	Pomacentridae	1				1			1		1
Pomacentridae	<i>Stegastes fuscus</i>	13	21			34	28		6		34
	<i>Stegastes pictus</i>	44	6			50	32		17	1	50
	<i>Stegastes spp</i>	14	7		1	22			22		22

	<i>Stegastes variabilis</i>	319	45	4	6	374	185	186	3	374
Sciaenidae	Sciaenidae				1	1			1	1
	<i>Euthynnus alletteratus</i>		11			11	11			11
	<i>Scomberomorus brasiliensis</i>	29	27	29		85	85			85
Scombridae	<i>Scomberomorus cavalla</i>	2	1	4	4	11	8	3		11
	<i>Scomberomorus regalis</i>		1			1	1			1
	<i>Scorpaena spp</i>	1		2	1	4	2	1	1	4
Scorpaenidae	<i>Scorpaena plumieri</i>			1		1			1	1
	Scorpaenidae			1		1			1	1
Serranidae	<i>Rypticus spp</i>				1	1			1	1
	<i>Archosargus probatocephalus</i>	11	2			13		13		13
Sparidae	<i>Calamus penna</i>	14	6			20	20			20
	<i>Calamus spp</i>	1	1			2			2	2
	Sparidae	19				19		19		19
Sphyraenidae	<i>Sphyraena barracuda</i>	3	4			7	3	1	3	7

	<i>Sphyraena guachancho</i>		3			3		3			3
	<i>Anarchopterus criniger</i>	1				1			1		1
Syngnathidae	<i>Hippocampus reidi</i>			2		2	1		1		2
	<i>Micrognathus crinitus</i>				1	1	1				1
	<i>Saurida spp</i>	2				2			2		2
	Synodontidae	8		1		9			9		9
	<i>Synodus foetens</i>	42	12	23		77	43	4	30		77
	<i>Synodus intermedius</i>	1	5			6	2	4			6
Synodontidae	<i>Synodus poeyi</i>	1				1			1		1
	<i>Synodus spp</i>	2	3			5	5				5
	<i>Synodus synodus</i>	2				2	2				2
	<i>Trachinocephalus myops</i>	3	7		2	12	10		2		12
	<i>Sphoeroides spengleri</i>	2	6	3		11	2	8	1		11
Tetraodontidae	<i>Sphoeroides spp</i>	1	1			2				2	2
	<i>Enneanectes altivelis</i>				28	28			28		28
Tripterygiidae	<i>Enneanectes spp</i>				1	1		1			1

NI	2	1	2	4	9			8	1	9
Total Abundance	1820	871	376	330	3397	1979	238	988	192	3397
Richness	72	57	40	38	103	58	28	62	30	103

5. CAPÍTULO 3: SEASCAPE AND HABITAT STRUCTURE AS DRIVES OF SETTLEMENT AND RECRUITMENT PATTERNS OF REEF FISHES IN THE ABROLHOS BANK, SOUTHEASTERN ATLANTIC

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SEASCAPE AND HABITAT STRUCTURE AS DRIVES OF SETTLEMENT AND RECRUITMENT PATTERNS OF REEF FISHES IN THE ABROLHOS BANK, SOUTHEASTERN ATLANTIC

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ABSTRACT

Despite all the ecosystem services provide by coral reefs and associated habitat like mangroves, seagrass, and rhodolith beds, they are the most marine threatened areas leading to a decline in the abundance of many reef-associated organisms, especially coral reef fish. Thus, understanding the dynamic of settlement and recruitment of reef fish and their relationship with the habitat is essential for the conservation of these species. In order to achieve the objectives of conservation of ecosystems and, consequently, of species, it is necessary to define priorities and strategies, considering mainly the choice of areas with greater richness and/or diversity of species, combined with the richness and density of species threatened by exploitation at the local level and regional. To accurately measure species losses and understand the processes that maintain species diversity, the additive partition of biodiversity can be an alternative to statistically evaluate spatial patterns and generate data that strengthen conservation and management. Our study generated pioneering information about the patterns of alpha and beta diversity of postlarvae and juvenile coral reef fish species along the Abrolhos bank. The results showed there was a spatial variation between postlarvae and juvenile assemblages considering these diversity indices and the study sites. Our analysis indicates that coastal reefs (Cassurubá Reefs and Parcel das Paredes), as well as the rhodolith beds, are essential habitats for the maintenance of fish stocks in the region and indicate that these areas should be considered a priority for conservation and efforts that seek connectivity between these locations considering the larval input and recruitment of reef fish are encouraged in the Abrolhos bank.

Keywords: Recruitment; Settlement; Rhodolith beds; Spatial Turnover; Nestedness.

INTRODUCTION

Coral reefs are iconic tropical ocean ecosystems and the diversity of species in these areas exceeds that of any other habitat on Earth. Furthermore, coral reefs host the most diverse communities of marine fish (Mora 2015), and are very productive ecosystems, supplying resources for many millions of people (Sheppard et al. 2017). Within tropical seascapes, reefs are connected to other habitats such as mangroves, seagrass, and rhodolith beds, enhancing the biomass and diversity of reef fish assemblages (Moura et al. 2021). Despite all the ecosystem services these habitats provide (Woodhead et al. 2019; Moberg and Folke 1999), they are the most threatened marine areas, owing to a long history of anthropogenic degradation and exploitation (Graham et al. 2007, Jackson et al. 2001). These anthropogenic factors can have several impacts on these ecosystems such as habitat loss (Alvarez-Filip et al. 2011, Pratchett et al. 2014), changes in benthic composition (Chong-Seng et al. 2012) and declines in topographic complexity (McClanahan et al. 2014), leading to a decline in the abundance and diversity of many reef-associated organisms, especially coral reef fish (Pratchett et al. 2014).

However, the management and protection of critical habitats can improve the conservation of reef fish species and promote the restoration of fish stocks (Murray et al. 1999; Green et al. 2015; Carr et al. 2017). Several studies have demonstrated that marine protected areas (MPAs) positively affect 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, Lima et al. 2023). The benefits of MPAs include 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), genetic diversity (Félix-Hackradt et al. 2013c; Bezerra et al. 2018) and propagule exportation (Felix-Hackradt et al. 2018; Lima et al. 2023). In addition to MPAs, other management actions such as fishery regulations, Ecosystem-Based Fisheries Management (EBFM), and Marine Spatial Planning (MSP) can improve the conservation of fish stocks (Moura et al. 2013; Weijerman et al. 2016; Previero and Gasalla 2020)

The early life stages distribution is the first step in a chain of successive events that culminate in the structuring of an adult population and therefore, fluctuations in settlement and recruitment can be determinants of population dynamics (Félix-Hackradt et al. 2013b; Grorud-Colvert and Sponaugle 2009). Therefore, it is necessary to identify priority areas for these processes (settlement and recruitment) to achieve conservation objectives (Lima et al 2023). For example, areas acting as “sources” of larval fish exportation can help stabilize and restore fisheries in connected “sinks” (Harrison et al 2012; Fontoura et. al 2022). Therefore, determining whether these areas act as larval sources or sinks for a given population is essential (Bode et al. 2006). As a “source”, MAPs can boost larval export capacity and, consequently, connectivity to nearby reefs or MPAs in a network (Harrison et al. 2012; Le Port et al. 2017), and as a sink, MPAs can provide quality habitat for recruits, thereby increasing survival (Felix-Hackradt et al. 2014; Cheminée et al. 2016).

Thus, understanding the dynamics of reef fish settlement and recruitment and their relationship with habitat is essential for the conservation of these species. Additionally, the management and protection of nursery areas (Lima et al. 2023) and dispersal corridors, which are functionally important for maintaining larval connectivity, are likely to benefit biodiversity conservation (Fontoura et al. 2022; Lima et al. 2023). However, due to knowledge gaps on the distribution and abundance of early-life stage and adult reef fishes (Felix-Hackradt et. al 2018; Lima et al 2023), management and conservation measures are often based on poorly substantiated assumptions about species' nestedness and turnover patterns or other diversity indices of the species (Socolar et. al 2016; Araújo et. al 2020; Moura et al. 2021)

To design robust protected area networks, accurately measure species loss, or understand the processes that maintain species diversity, conservation science must consider the organization of biodiversity in space (Socolar et. al 2016). Thus, the additive partition of biodiversity can be an alternative method to statistically evaluate spatial patterns and generate data that strengthen conservation and management strategies (Rodríguez-Zaragoza et. al 2011). Additive partitioning estimates the relative contributions of alpha-diversity (within-habitat) and beta-diversity (between habitats) to gamma-diversity (landscape). Central to this is beta-diversity i.e., the component of regional diversity that accumulates from compositional differences between local species assemblages (Socolar et. al 2016). Assigning different beta-diversity patterns to

respective biological phenomena is essential for analyzing the causality of the processes underlying biodiversity. Therefore, the differentiation of spatial turnover and nestedness components of beta diversity is crucial to our understanding of central biogeographic, ecological, and conservation issues (Baselga 2010).

Finally, considering that the Abrolhos Bank is recognized as the region with the greatest biodiversity in the South Atlantic, and the high degree of threat to which the reef areas and their associated organisms are exposed, the present study aims to analyze the habitat and seascape influences on the diversity patterns of reef fish early stages and the conservation implications for these species.

MATERIALS AND METHODS

Study Area

Our sampling zone is characterized by an extension of the Abrolhos Bank continental shelf, which extends up to 200 km offshore (Leão & Kikuchi, 2005). The average depth is very shallow, ~30 m, reaching 70 m near the shelf edge (Moura et al. 2013). The Abrolhos Bank is the largest and richest coral reef in the eastern region of Brazil and is considered to have the highest biodiversity in the South Atlantic (Leão 1999; Leão et al. 2003). These reefs form two arcs – one coastal and one offshore arc. The offshore arc is formed by fringing reefs located in the Abrolhos Archipelago (Figure 1- A) and isolated pinnacle reefs form the Abrolhos Parcel (Figure 1- B), surrounded by water with depths greater than 20 m. The coastal margin reefs form a complex of large reef banks of different shapes and sizes, including isolated pinnacle reefs, that extend in a north-south direction forming Paredes Parcel (at the north – Figure 1 -D) and Cassurubá reefs (at the south-Figure 1- C) (Leão et al. 2003). The coastal reef arc (~10 km offshore) is subject to high fishing pressure and turbidity of terrigenous origin, while the offshore arc (~60 km off the coast) is within the Abrolhos National Marine Park (ANMP) and is less exposed to fishing and terrestrial stressors (Moura et al. 2021). The Rhodolith beds in the Abrolhos bank (Figure 1 – E) are regarded as the largest in the world (Moura et. al 2013; Brasileiro et al. 2016; Moura et al. 2021; Anderson et. al 2022) and they harbor a diverse biota, comparable (considering the richness of vertebrates, invertebrates, and macroalgae) to that of rocky and coral reefs (Moura et al. 2021).

Fish sampling

Sampling was carried out in January/2021 in coral reef areas. The sampling design included five locations (Abrolhos Archipelago = ABR, Abrolhos Parcel = PAB, Rhodolith beds= ROD, Paredes Parcel = PPA, and Cassurubá Reefs = CAS) (Figure 1) where nine light traps were installed and underwater visual censuses (UVC) were performed. (Fig 1.)

Postlarval fishes were sampled using CARE model light traps (ECOCEAN). The light traps were installed for two consecutive nights for a total of 18 samples (per location), totaling 90 samples. After approximately 12 h of fishing, samples from light traps were removed and conserved in alcohol 70%. At the laboratory, the postlarval fish catch was selected, measured (using a digital caliper), weighed (in g, using an analytical balance), and identified using the available bibliography (Richards 2005; Bonecker et al. 2014). Parallel to postlarval fishing, UVC and diurnal underwater visual censuses of juvenile reef fish were carried out in 135 strip transects, where three 10 × 2 m replicate transects were set out haphazardly for each light trap installed at each location. Juveniles of all species were identified to the lowest possible taxonomic level and their sizes were estimated in size classes of 1 cm. Fish abundance was recorded in abundance classes following a geometric scale (cf. Harmelin 1987; García-Charton & Pérez-Ruzafa 2001; Hackradt et al. 2011). Additionally, environmental data were collected as habitat heterogeneity (percentage cover of the consolidated reef, sand, gravel, and frondose algae/grassland), rugosity (scale 1 to 5), slope (categorized as 0°-30°, 30°-60°, 60°-90°) (cf. Félix-Hackradt et al. 2014), depth and temperature.

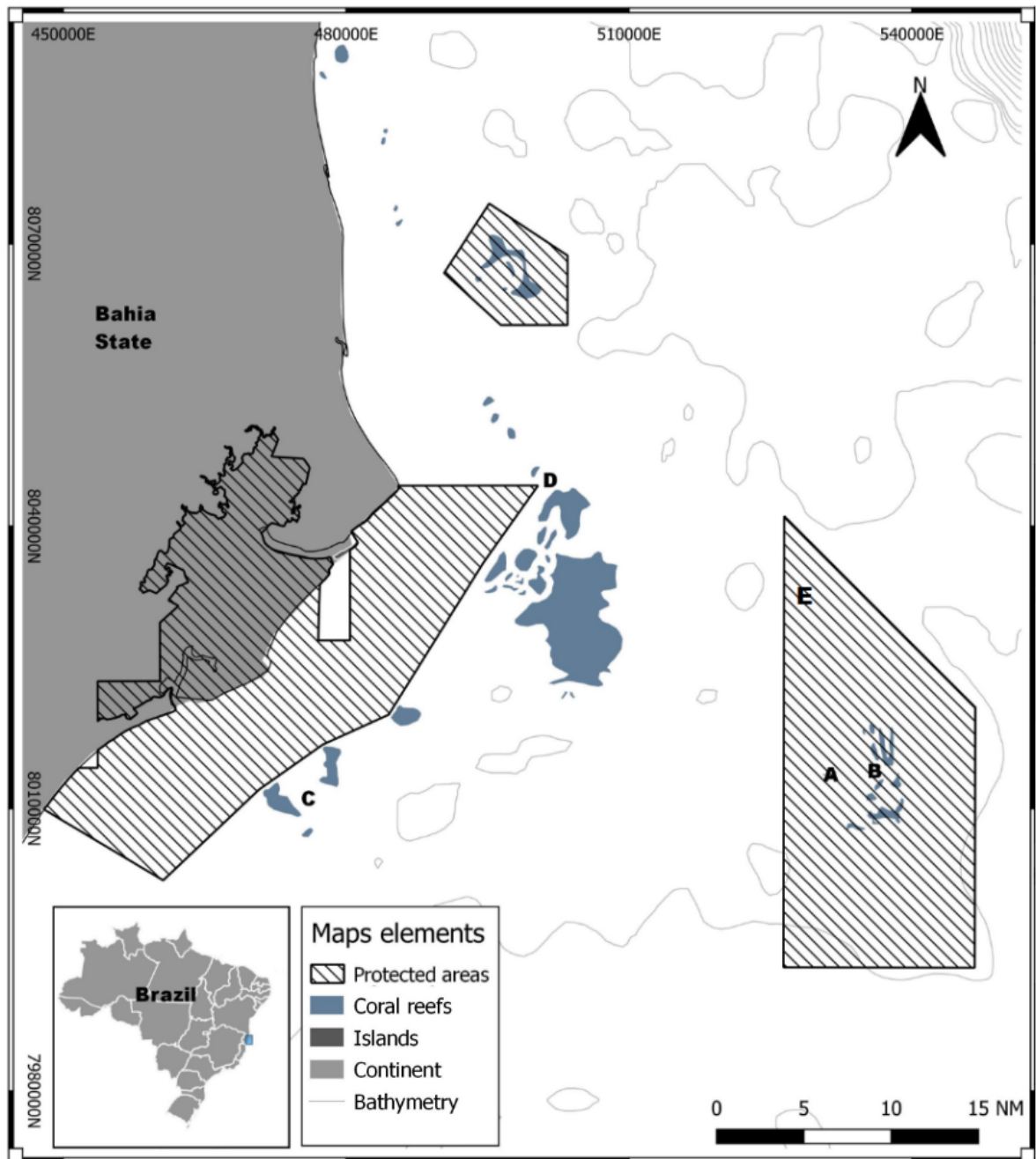


Figure 1- Sampling locations. A= Abrolhos Archipelago (ABR), B= Abrolhos Parcel (PAB), C= Cassurubá (CAS), D= Paredes Parcel (PPA) and E = Rodoliths (ROD).

Data analyses

Diversity indexes were investigated using “true diversity indices” (*sensu* Jost, 2006), considering the effective number of species equal to Hill numbers (qD) (Hill, 1973). This approach quantifies diversity based on the weight of species abundance by order of diversity q ; when $q=0$ (0D) species abundance is disregarded, favoring rare species; $q=1$ (1D) is equivalent to Shannon's entropy and represents the number of

common species in a community, and when $q=2$ (2D) dominant species are favored, as more weight is given to abundance (Jost, 2007). Diversity indices were calculated using the 'entropart' package (Marcon and Hérault 2015).

Total beta diversity was calculated with the Sørensen dissimilarity index and decomposed into the Simpson index, which is related to the spatial turnover of species, and the nestedness component. Calculations were conducted using the betapart package (Baselga and Orme 2012) and both turnover and nestedness were calculated between all site pairs. The package adespatial (Dray et al. 2022) was used to calculate species contribution to beta diversity.

The heatmap was built using relative abundances (rows), by the sampled area (columns). Absences are colored white, whereas increasing relative abundances are colored from dark blue (0.02) to light green (0.98). Unique occurrences are shown in light yellow. Column orders were arranged by transforming a matrix of Bray–Curtis dissimilarities between sample areas into distances (UPGMA) (Moura et al. 2021), using the package gplots (Warnes et al. 2015).

A Redundancy analysis (RDA) was used as a direct gradient approach to determine how much variation in fish assemblages could be explained by environmental variables. Fish abundance (postlarvae and juveniles) data were Hellinger transformed using the function 'decostand' in the package vegan (Oksanen et. al 2020), to reduce the weight of abundant species while preserving Euclidean distances between samples in the multidimensional space (Legendre and Gallagher 2001). For this analysis with postlarvae, we chose to only use the species that were shared with juvenile reef fish assemblages, since these species probably had a greater influence on the habitat and on their compositions. A preliminary detrended correspondence analysis (DCA), performed on the transformed species data, revealed a gradient length <4 Standard deviation units (SD) along the first axis, suggesting that the redundancy analysis (RDA) was appropriate (ter Braak and Šmilauer 2015). RDA was performed using the function 'rda' and significance was tested using the function 'anova'. All Statistical analyses were carried out with the R program (R Core Team 2022)

RESULTS

Overall, 79 postlarval fish *taxa* were identified, accounting for 1187 individuals (Table 1). Postlarvae identified beyond the family level was represented by 35 *taxa*, including 55 at the species level and 15 at the genera level. Of the most represented families, Carangidae presented the highest diversity with 10 *taxa*, followed by Pomacentridae and Lutjanidae/Synodontidae, with 6 and 5 *taxa*, respectively. The total species (*taxa*) richness for ABR, PAB, CAS, PPA, and ROD was 43, 24, 22, 25, and 41, respectively (Table 1). The most representative specie was *Stegastes variabilis* with 190 identified individuals and the most representative family was Pomacentridae with 250 individuals. The most abundant site was ABR with 612 individuals, followed by ROD, PPA, CAS, and PAB with 199, 135, 127, and 114 individuals, respectively (Table 1; Figure 2).

Regarding the juvenile reef fish, 54 *taxa* were identified, accounting for 4010 individuals (Table 1). Juvenile reef fish identified beyond the family level was represented by 19 *taxa* (Figure 2), including 51 at the species level and 3 at the genera level. Among the most represented families, Labridae presented the highest diversity with 11 *taxa*, followed by Haemulidae and Pomacentridae, with 6 and 5 *taxa*, respectively. The total species (*taxa*) richness for ABR, PAB, CAS, PPA, and ROD was 31, 29, 23, 35, and 18, respectively (Table 1). The most representative specie was *Haemulon aurolineatum* with 1811 identified individuals and the most representative family was Haemulidae with 2100 individuals. The most abundant site was ABR with 1284 individuals followed by CAS, ROD, PPA, and PAB with 1134, 700, 487, 405, and individuals, respectively (Table 1, Figure 2).

ABR presented the highest postlarval biomass followed by CAS (Figure 3). The same pattern was observed for species abundance (Table 1, Figure 2). On the other hand, for the frequency distribution of average postlarval assemblage size, the smallest average was observed in ABR and PPA, and the largest in CAS and PAB (Figure 3). Regarding juvenile assemblages, the highest biomass was observed in CAS, followed by PPA, while the lowest value was observed in ROD (Figure 3). In the frequency distribution of the average juvenile assemblage size, CAS, and PAB had the highest average while ABR and ROD have the smallest average (Figure 3).

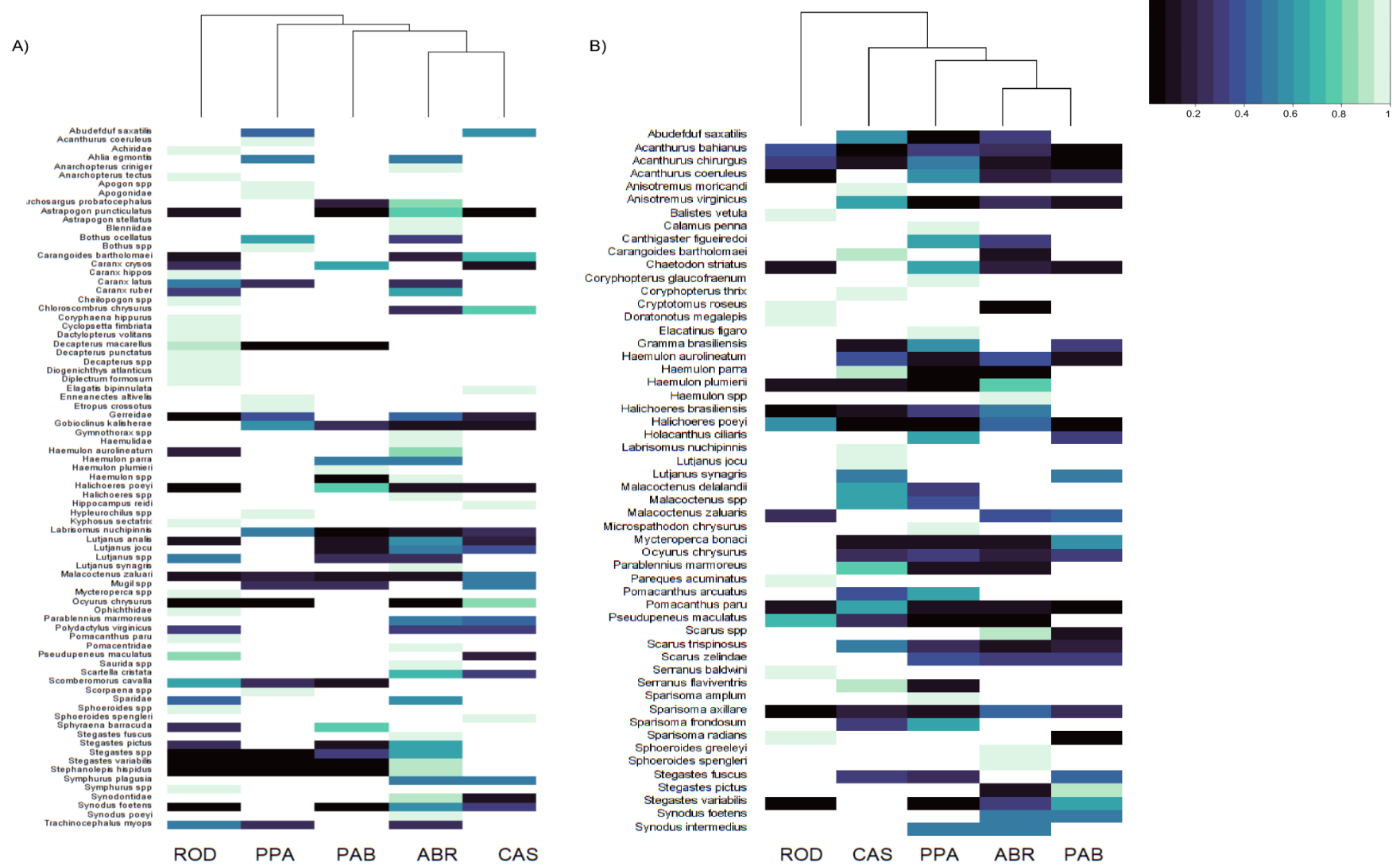


Figure 2- Reef fish Postlarvae (A) and Juvenile (B) relative abundance in the Abrolhos Bank.

Table 1 - Total Abundance by species/taxa of fish postlarvae (LARV) and juveniles (JUV) caught with a light trap in the sample areas (ABR= Abrolhos Archipelago, PAB= Abrolhos Parcel, CAS= Cassurubá, PPA= Paredes Parcel and ROD = Rodoliths). NI= Not identified.

Family	Specie/Taxa	Location											
		ABR		CAS		PAB		PPA		ROD		Total	
		LARV	JUV	LARV	JUV	LARV	JUV	LARV	JUV	LARV	JUV	LARV	JUV
Acanthuridae	<i>Acanthurus bahianus</i>		67		9		5		94		119		294
	<i>Acanthurus chirurgus</i>		13		14		4		77		49		157
	<i>Acanthurus coeruleus</i>		10				14	1	36		1	1	61
Achiridae	<i>Achiridae</i>									1			1
Apogonidae	<i>Apogon sp.</i>							1					1
	<i>Apogonidae</i>							1					1
	<i>Astrapogon puncticulatus</i>	56		4		4				6			70
	<i>Astrapogon stellatus</i>	1											1
Balistidae	<i>Balistes vetula</i>										1		1
Blenniidae	<i>Blenniidae</i>	12											12
	<i>Hypleurochilus sp.</i>							1					1
	<i>Parablennius marmoratus</i>	8	1	7	6				1				15
	<i>Scartella cristata</i>	5		2									7
Bothidae	<i>Bothus ocellatus</i>	1						2					3
	<i>Bothus sp.</i>							1					1
Carangidae	<i>Carangoides bartholomaei</i>	2	1	7	9					1			10
	<i>Caranx crysos</i>			1		5				2			8
	<i>Caranx hippos</i>									1			1
	<i>Caranx latus</i>	1						1		2			4
	<i>Caranx ruber</i>	2								1			3
	<i>Chloroscombrus chrysurus</i>	1		3									4
	<i>Decapterus macarellus</i>					2		3		37			42
	<i>Decapterus punctatus</i>									59			59
	<i>Decapterus sp.</i>								1				1
	<i>Elagatis bipinnulata</i>			1									1
Chaetodontidae	<i>Chaetodon striatus</i>		2				1		8		1		12
Coryphaenidae	<i>Coryphaena hippurus</i>									1			1
Cynoglossidae	<i>Symphurus plagusia</i>	1		1									2
	<i>Symphurus sp.</i>									2			2

Dactylopteridae	<i>Dactylopterus volitans</i>								1		1		
Exocoetidae	<i>Cheilopogon sp.</i>								2		2		
	<i>Coryphopterus glaucofraenum</i>							3				3	
Gobiidae	<i>Coryphopterus thrix</i>			1								1	
	<i>Elacatinus figaro</i>							4				4	
Gerreidae	<i>Gerreidae</i>	67	26				62		2		157		
Grammatidae	<i>Gramma brasiliensis</i>			1		2		4				7	
	<i>Anisotremus moricandi</i>			1								1	
Haemulidae	<i>Anisotremus virginicus</i>		9	27		4		1				41	
	<i>Haemulidae</i>	7									7		
	<i>Haemulon aurolineatum</i>	5	690	713		256		152	1		6	1811	
	<i>Haemulon parra</i>	3	10	142	3			3			6	155	
	<i>Haemulon plumieri</i>		36	6	4			2		4	4	48	
	<i>Haemulon sp.</i>	68	86		4						72	86	
Kyphosidae	<i>Kyphosus sectatrix</i>								2		2		
	<i>Cryptotomus roseus</i>		3							127		130	
	<i>Doratonotus megalepis</i>									1		1	
	<i>Halichoeres brasiliensis</i>		9	2				6		1		18	
	<i>Halichoeres poeyi</i>	10	206	7	12	55	8	6	1	269	73	501	
	<i>Halichoeres sp.</i>	2									2		
	<i>Scarus sp</i>		8				1					9	
Labridae	<i>Scarus trispinosus</i>		3	16		5		8				32	
	<i>Scarus zelindae</i>		4			4		5				13	
	<i>Sparisoma amplum</i>							3				3	
	<i>Sparisoma axillare</i>		61	22		27		18		1		129	
	<i>Sparisoma frondosum</i>			1				2				3	
	<i>Sparisoma radians</i>					3				88		91	
	<i>Gobioclinus kalisherae</i>	1		1		2		5			9		
	<i>Labrisomus nuchipinnis</i>	2		4	1	1		8			15	1	
Labrisomidae	<i>Malacoctenus delalandii</i>			2						1		3	
	<i>Malacoctenus sp</i>			5				3				8	
	<i>Malacoctenus zaluari</i>	1	7	5		1	8	2		1	4	10	19
Lutjanidae	<i>Lutjanus analis</i>	6		2		1				1		10	
	<i>Lutjanus jocu</i>	11		8	3	2						21	3
	<i>Lutjanus sp.</i>	1				1				2		4	

	<i>Anarchopterus tectus</i>									1		1	
	<i>Hippocampus reidi</i>			1								1	
Synodontidae	<i>Saurida sp.</i>	2										2	
	<i>Synodontidae</i>	8		1								9	
	<i>Synodus foetens</i>	18	1	10		2	1			1		31	2
	<i>Synodus intermedius</i>		1						1			1	2
	<i>Synodus poeyi</i>	1										1	
	<i>Trachinocephalus myops</i>	1						1		2		4	
Tetraodontidae	<i>Canthigaster figueiredoi</i>		1						2				3
	<i>Sphoeroides greeleyi</i>		3										3
	<i>Sphoeroides sp.</i>									16		16	
	<i>Sphoeroides spengleri</i>		2	1								1	2
Tripterygiidae	<i>Enneanectes altivelis</i>							28				28	
NI	NI	1		2		1		4				8	
Total		612	1284	127	1134	114	405	135	487	199	700	1187	4010
Richness		43	31	24	29	22	23	25	35	41	18	79	54

Related statistics to Hill numbers showed similar patterns and variations in the true diversity indices (q^0 , q^1 , and q^2) for postlarval assemblages. ABR showed the highest value, considering rare (q^0), common (q^1), and dominant (q^2) species. ROD and CAS showed intermediate values compared to other sites, while PAB and PPA had the lowest values of diversity orders (Figure 3). This pattern was not observed in juvenile assemblages. ABR showed the highest value of rare juvenile reef fish species, followed by CAS, while the lowest values were observed in PPA, ROD, and PAB, respectively. The highest value of common species (q^1) was observed in PPA, followed by CAS and ABR. The lowest values were observed in ROD and PAB. The highest value of dominant species (q^2) was observed in PPA followed by ROD. The other locations (PAB, ABR, and CAS) showed the lowest and most similar values (Figure 3).

For the beta diversity indices, the overall compositional variation of postlarval reef fish, considering all sites, was relatively small (multi-site beta diversity = 0.42 - Turnover = 0.25, and Nestedness = 0.16), as was the compositional variation of juvenile reef fish (multi-site beta diversity = 0.32 - Turnover = 0.18, and Nestedness = 0.14). However, the beta diversity indices varied between locations and showed relatively high values in some places, considering the postlarvae and juvenile assemblages (Figure 4). For example, the highest beta diversity value found was between CAS and PPA for postlarvae assemblages (0.70), while the lowest value was found between CAS and ABR (0.49). On the other hand, regarding juvenile assemblages, the highest beta diversity value was found between CAS and ROD (0.65), and the lowest value was found between CAS and PPA (0.28). Another important consideration is that these beta diversity values were mainly related to turnover. Turnover was proportionally highest than nestedness between all sites, and these values varied from 100% of beta diversity composed by turnover (CAS-PPA postlarvae) to 54% of beta diversity composed by turnover (ABR-PAB postlarvae) (Figure 4). Postlarval species' contribution to beta diversity was mainly driven by *Halichoeres poeyi*, Gerreidae, *Decapterus punctatus*, *Stegastes variabilis*, and *Enneanectes altivelis*, while juvenile species' contribution to beta diversity was mainly driven by *Haemulon aurolineatum*, *Halichoeres poeyi*, *Cryptotomus roseus*, *Acanthurus bahianus*, and *Sparisoma radians* (Fig 5).

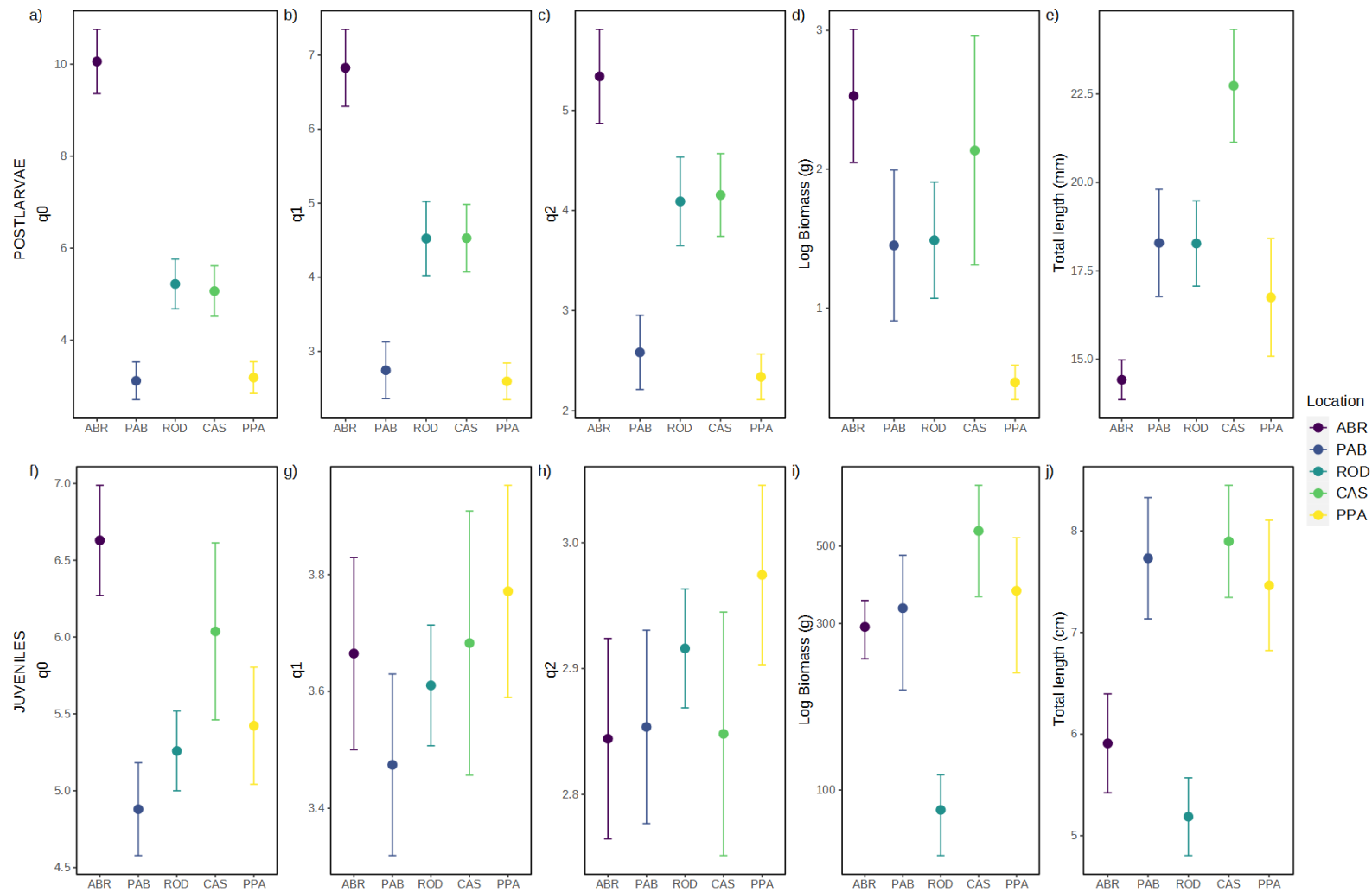


Figure 3 - Alpha diversity values ($q\alpha$), Biomass (Log), and Total length of fish postlarvae and juveniles by location (ABR= Abrolhos Archipelago, PAB= Abrolhos Parcel, CAS= Cassurubá, PPA= Paredes Parcel and ROD= Rodolith) where q represents the order of diversity (a) (f) q^0 – disregarded abundances, greater representation of rare species; (b) (g) q^1 – True diversity values; (c) (h) q^2 – Higher weight for dominant species

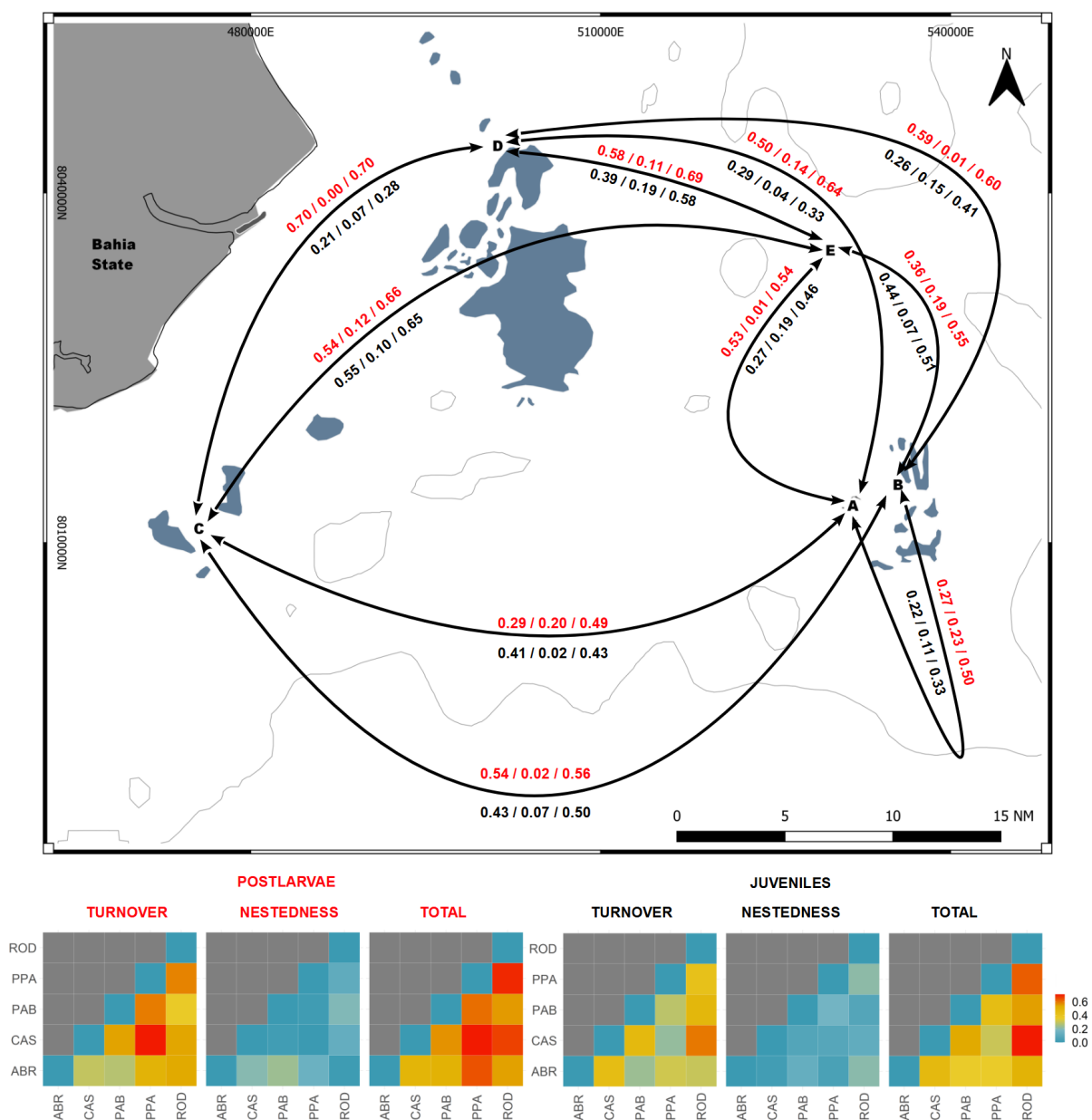


Figure 4 - Turnover, Nestedness, and Total Beta diversity values between locals (ABR= Abrolhos Archipelago (A), PAB= Abrolhos Parcel (B), CAS= Cassurubá (C), PPA= Paredes Parcel (D) and ROD= Rodolith (E)). Values are represented by turnover, followed by nesting, and finally, total beta diversity, in red for post larvae and in black for juveniles

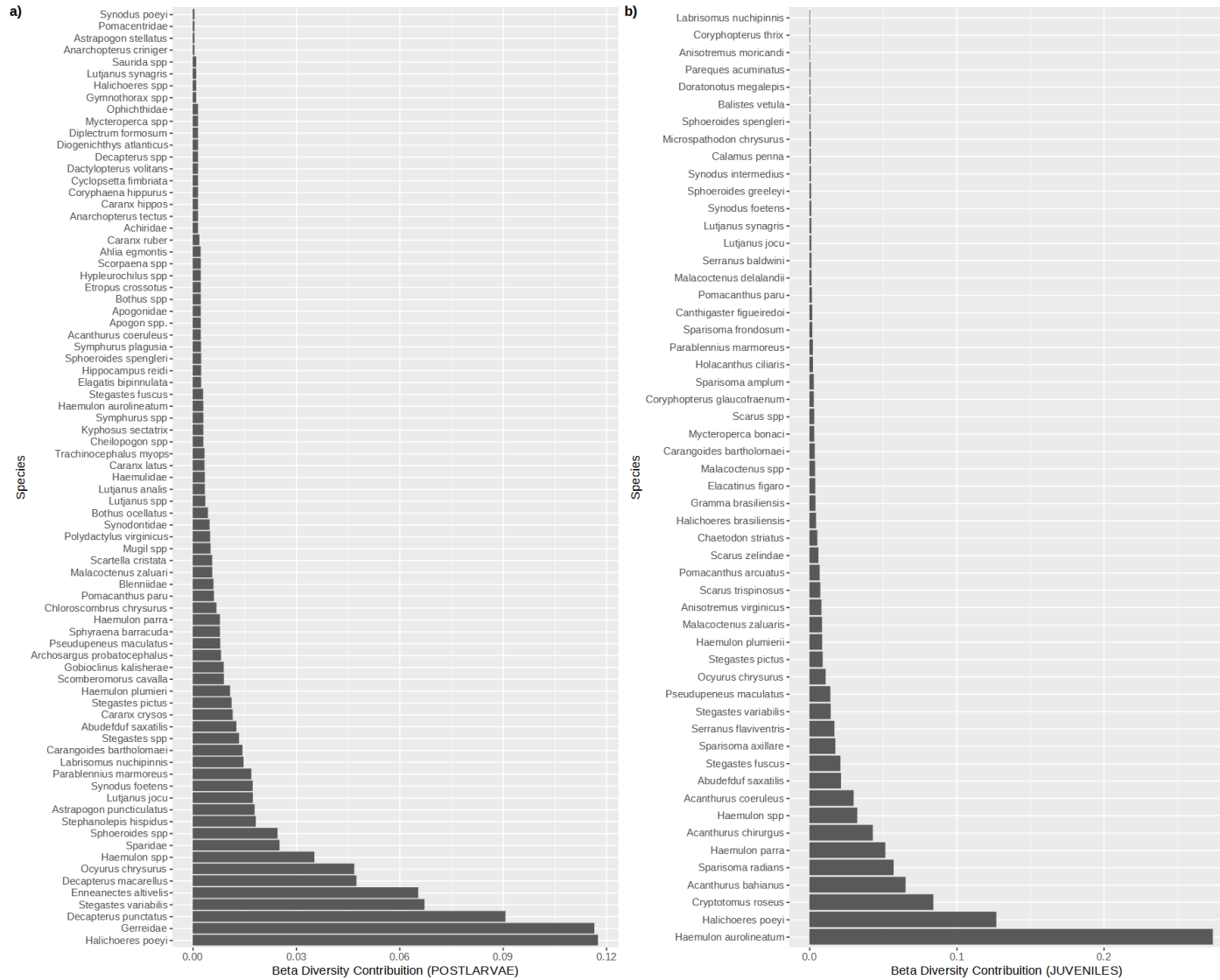


Figure 5- Species contribution for beta diversity

For the postlarvae at RDA (Figure 6), the first two main axes explained 60% of the relationship between fish assemblage and environmental variables. The first axis accounted for 36.87% of the variation and was mainly related to Coast distance, *Stegastes variabilis*, and *Ocyurus chrysurus*. The second axis accounted for 23.23% of the variation and was mainly related to Temperature, Rugosity, Reef, *Halichoeres poeyi*, and *Stegastes pictus*. Our data showed that the first three dimensions represented a significant variation in species composition ($P = 0.001$). The important predictors of species composition were Coast Distance, Depth, Temperature, Rugosity, Frondosa algae, and Reef, but coast distance stood out with the highest F value. Furthermore, the adjusted R^2 value of 0.2056 did not indicate a substantial contribution of these predictive variables, and other factors (including randomness) affecting the variability of the explained variable. Regarding the RDA juveniles (Fig. 7), the first two main axes explained 69.17% of the relationship between fish assemblage and environmental variables. The first axis accounted for 54.29% of the variation and was mainly related to Frondosa algae, Reef, Temperature, *Halichoeres poeyi*, *Cryptotomus roseus*, and *Sparisoma radians*. The second axis accounted for 14.88% of the variation and was mainly related to Coast distance, Rugosity, *Serranus flaviventris*, and *Stegastes variabilis*. Our data showed that the first three dimensions represent a significant variation in species composition ($P = 0.001$). The important predictors of species composition were Coast Distance, Depth, Temperature, Rugosity, and Reef, but coast distance stood out with the highest F value. Furthermore, the adjusted R^2 value of 0.1852 did not indicate a substantial contribution of these predictive variables, and other factors (including randomness) affecting the variability of the explained variable.

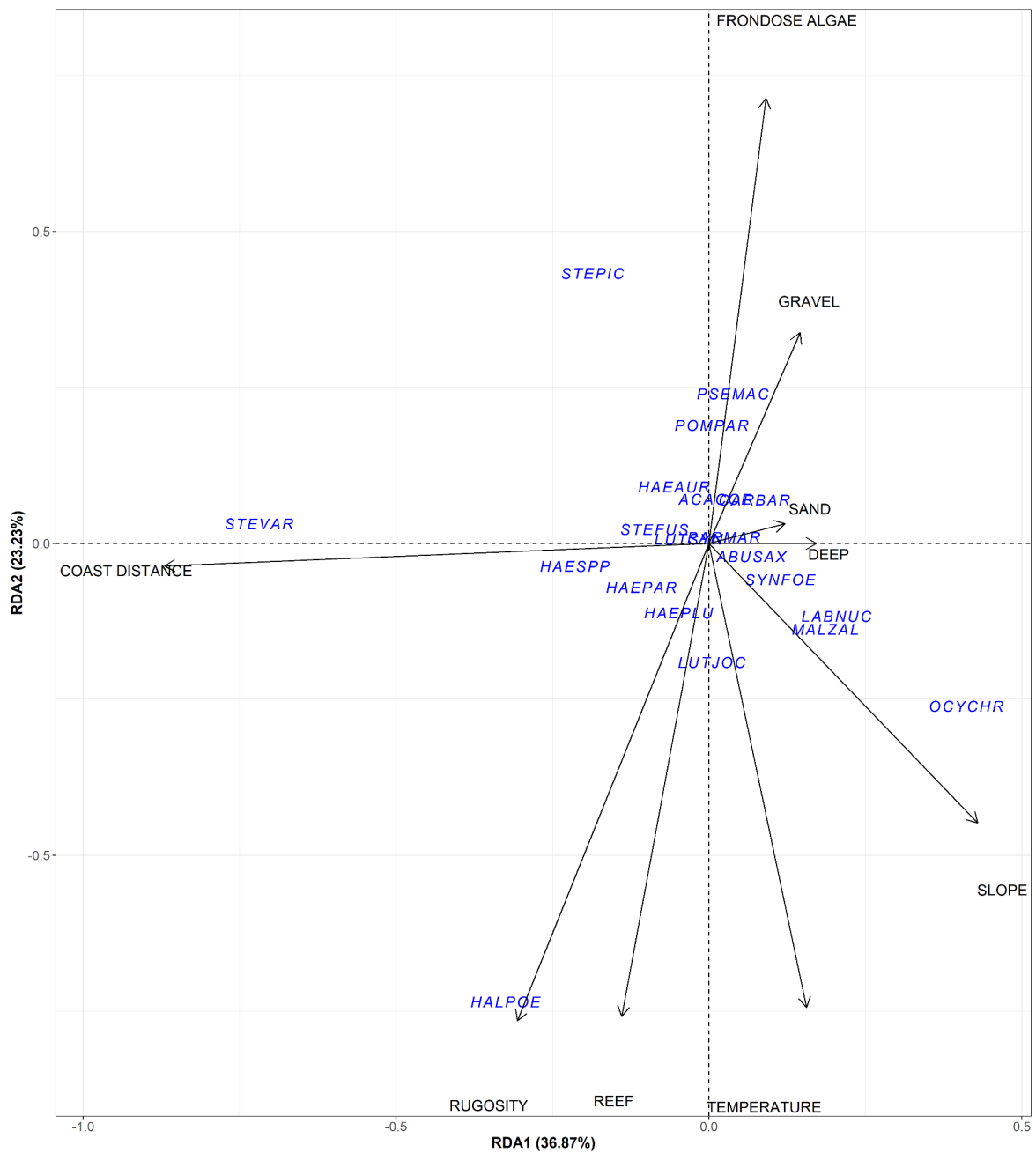


Figure 6 - Redundance analysis (RDA) between postlarvae of coral reef fishes and environmental variables. Proportion explained = 0.3687 (RDA 1) and 0.2323 (RDA 2). (DCA eigenvalues <4, Legendre & Gallagher (2001). $R^2=0.3009$. R^2 adjusted= 0.2056

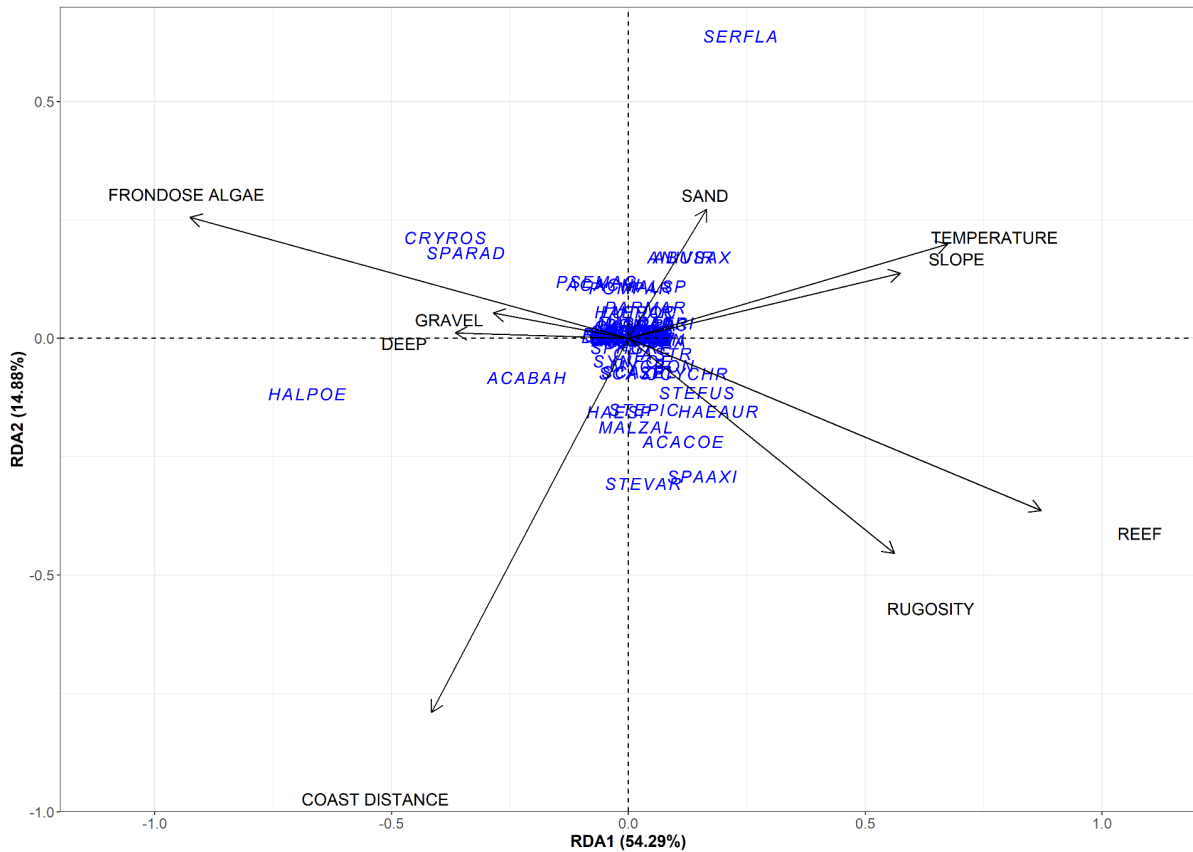


Figure 7 - Redundance analysis (RDA) between juvenile coral reef fishes and environmental variables. Proportion explained = 54.29% (RDA 1) and 14.88% (RDA 2). (DCA eigenvalues <4, Legendre & Gallagher (2001). $R^2=0.2429$. R^2 adjusted= 0.1852

DISCUSSION

Our study provides pioneering information about the alpha and beta diversity patterns of postlarvae and juvenile coral reef fish species along the Abrolhos bank. The results showed that there was spatial variation between postlarvae and juvenile assemblages considering these diversity indices. Beta diversity can reflect two different phenomena: Nestedness and spatial turnover (Baselga et al. 2007; Baselga 2010). The Nestedness of a species assemblage reflects a non-random distribution process of species loss (Gaston and Blackburn 2000; McAbendroth et al. 2005) and occurs when biotas from sites with fewer species are subsets of biotas from richer sites (Wright and Reeves, 1992; Ulrich & Gotelli 2007). Whereas turnover implies the replacement of some species by others, as a result of environmental order or spatial and historical constraints (Qian et al., 2005). Our results showed that beta diversity is mainly driven by turnover between sample areas. However, the additive partitioning of species diversity is effective for identifying and understanding spatial scales,

where species turnover is the main contributor to overall biodiversity (Gering et al. 2003; Rodríguez-Zaragoza et al. 2010). As such, in order to better understand species diversity patterns and therefore, infer conservation strategies, it is also necessary to consider alpha diversity (Araújo et al. 2020) because evaluating both components together helps to match diversity drivers with scale-appropriate conservation action (Karkarey et al. 2022).

Postlarval assemblages showed the highest beta diversity values between sample areas compared to juvenile assemblages. Even among the reef areas, species composition was highly diverse, and the same pattern was also observed in the rhodolith beds. Despite the beta diversity values, as well as the strong relationship between juvenile assemblages and turnover, these patterns demonstrate that different factors likely influence the distribution and composition of juvenile and larval reef fish assemblages. For example, many variables can influence the distribution and composition of postlarvae assemblages (Lima et al. 2023) and MPAs may also play an important role in these processes. 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. 2012), in addition to providing quality larvae with the highest chance of survival (Shima and Findlay 2002; Raventos and Macpherson 2005; Searcy and Sponaugle 2001) and provide high-quality habitats for larval settlement (Almany 2004; Almany and Webster 2006; Johnson 2007). These observations can explain the most diverse (ABR and ROD) and abundant (ABR) postlarvae assemblages found in ABR and ROD because these sites are located in a No-Take reserve, however, this pattern was not observed in PAB (also located in a No-take reserve). Though another possible hypothesis for this pattern is that offshore locations can be closer to spawning areas of some species (Bezerra et al. 2021), therefore, can be used by a higher number of species as settlement areas compared to coastal ones. On their way to preferred coastal habitats, mid and shallow-water reefs can act as filters for larval species that do not rely on coastal nursery habitats to develop. This variation also may be related to habitat type, considering that PPA and PAB, both of which are located in pinnacle reefs, also presented lower diversities and abundances compared to the other sampled areas. Habitat type plays a key role in the settlement process (Tolimieri 1995; Costa et al. 2020; Downie et al. 2021). Habitats, such as coral reefs, seagrass, rhodoliths, and

seaweed beds, can provide three-dimensional structures that serve as nurseries, settlements, foraging, 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 a habitat, the more shelter it provides, especially for larvae in the early stages of development (Costa et al. 2020; Felix-Hackradt et al. 2014). However, environmental factors such as wind, current, tide, temperature, precipitation, river discharge, and water mass may also 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).

Regarding juvenile reef fish assemblages, ROD showed the highest values of beta diversity among the sampled sites and demonstrated that rhodolith beds have more dissimilar species compositions among the study areas. Recently, several studies demonstrated the importance of rhodolith beds, indicating these mega-habitats as a diversity hotspot, due to the large number of fish species that inhabit this ecosystem (Anderson et al. 2022; Pinheiro et al. 2018; Moura et al. 2021; Carvalho et al. 2020a; Amado-Filho et al. 2016). The high turnover recorded at the marine landscape level indicates that reefs and rhodolith beds have distinct functional properties in juvenile assemblages, and of the five species that most contributed to the composition of beta diversity, only two were highly abundant in this habitat (*C. roseus* and *S. radians*). Moura et al. (2021) found similar results for adult assemblages and associated this fact with the dominance of turf in reefs (~50% cover), since turf algae are the main trophic connections with herbivorous fish, which normally avoid macroalgae (Nicholson and Clements 2020). Despite the lower richness of juvenile species found in the rhodolith beds in this study compared to the other locations, this mega-habitat was recognized as an important nursery area, mainly through the provision of substrates and structural complexity that favor the spawning and development of reef fish species (Costa et al. 2020, Moura et al. 2021; Anderson et al. 2022). 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, consequently, 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) and this relationship between habitat type, quality, and complexity has been described as a relevant factor for reef fish recruitment (Lima et al 2023, Eggertsen et al 2017; Fontoura et. al 2022), reinforcing the importance of rhodolith beds for the population structure of reef fishes.

However, we found that coastal reefs (CAS and PPA) were also essential habitats for juvenile reef fish assemblages, corroborating the results of previous studies (Sartor 2015; Previero and Gasala 2018). Despite the lowest observed beta diversity between these coral reefs and the other sampled reefs (PAB and ABR), indicating more similar species compositions, PPA had the highest richness of juvenile reef fishes and a greater incidence of common and dominant species, considering the Hill series. Additionally, CAS had a high abundance and incidence of rare species, second only to ABR. Considering that PPA and CAS are open-access areas and ABR, PAB, and ROD are inserted in a No-Take Reserve, this information can improve the conservation status of these locations. To contextualize this, the period following 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) and these density-dependent factors, such as 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 greater abundance of predators (Planes et al. 2000) but 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). However, juvenile distribution patterns are also associated with habitat characteristics (i.e., spatial extension, roughness, geographical position in seascape, substrate types, complexity, sounds, etc.) (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). Thus, considering our results, it seems that juvenile distribution patterns are influenced by these different variables.

Conservation implications of biodiversity patterns

To achieve the objectives of the ecosystem and consequently, species conservation, it is necessary to define priorities and strategies. This is mainly achieved through the consideration of areas with greater richness and/or species diversity, combined with the richness and density of species threatened by exploitation at a local and regional level (Carvalho and Felfili 2011). The Abrolhos bank is recognized as the most biodiverse area in the southern Atlantic and encompasses a complex benthic habitat mosaic composed of the world's largest rhodolith bed which extends ~20,900 km² and coralline reefs covering ~8,800 km² (Moura et al. 2013), in addition to unique mushroom-shaped coralline pinnacles (Leão and Kikuchi, 2005), seagrass and algae bottom (Creed & Amado-Filho, 1999) and mangroves (Moura et al., 2011). However, these habitats are threatened, and the Abrolhos Bank is not yet adequately protected by fishery regulations (Freitas et al. 2011; Freitas et al. 2014; Previero and Gasalla 2018; Previero and Gasalla 2020), marine protected areas (MPAs) (Freitas et al. 2011; Moura et al. 2013; Freitas et al. 2014; Amado-Filho et. al 2016; Moura et al. 2021), or marine spatial planning (Moura et. al 2013, Moura et al. 2021). These threats include highly destructive mine waste from the southern coast (Magris et al, 2019; Previero and Gasalla 2020), dredging (Previero and Gasalla 2020), overfishing and destructive fishing methods (Freitas et al. 2014; Previero and Gasalla 2018; Anderson et. al 2022), oil and gas exploitation (Moura et al. 2013, dos Santos et al. 2023), carbonate mining (Moura et al. 2021; dos Santos et al. 2023), in addition to other anthropogenic impacts (Anderson et. al 2022)

Thus, our study demonstrates the importance of rhodolith beds and coastal reefs (Paredes Parcel and Cassurubá Reefs) for the settlement and recruitment of reef fish species in the Abrolhos Bank considering the alpha and beta diversity indices of postlarval and juvenile assemblages. Some studies also identified these areas as conservation priorities and indicated management measures for the conservation of these habitats (Freitas et al. 2011, Moura et al. 2013; Previero and Gasalla 2018; Previero and Gasalla 2020; Moura et al. 2021; Bezerra et. al 2021;

Magris et al. 2019). Among the various management proposals, we can highlight: the establishment of buffer zones around MPAs as a suitable framework for managing reef fisheries; alternative methods for protecting spawning aggregation areas (temporal and/or spatial bans); adopting Ecosystem-Based Fishery Management (EBFM), and Marine Spatial Planning (MSP) for the Abrolhos Bank, considering the data generated by different studies carried out in this region; definition of management actions for overexploited fish stock groups and implementation of some fishing restrictions; routine monitoring of key ecosystems networks such as rhodolith beds, coral reefs, and seagrasses across the whole Abrolhos Bank; improvement of regional governance and fishery self-governance and an increase in MPA networks (No-Take and Multiple Use) including rhodoliths beds, as these habitats are threatened by activities such as oil and gas exploration and carbonate mining and less than 1% of the area is under some type of legal protection in the Abrolhos bank. As such, we conclude that the Abrolhos bank is greatly important for the conservation of reef fish species and several actions have already been proposed based on extremely relevant studies that can effectively improve and protect the ecosystems found in this region, thereby, promoting the conservation of biodiversity. Finally, we emphasize the importance of coastal reefs and the rhodolith beds for the maintenance of fish stocks in the region and indicate that these areas should be considered conservation priorities and that efforts that seek to protect and maintain these ecosystems, as well as their connectivity with other habitats, and those that consider the larval contribution and the recruitment of reef fish, should be encouraged in the Abrolhos Bank.

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6 CONSIDERAÇÕES FINAIS

Considerando que a distribuição dos primeiros estágios de vida dos peixes recifais nas zonas costeiras é o primeiro passo de uma cadeia de eventos sucessivos que culminam na estrutura da população adulta, portanto, a compreensão da história inicial dos peixes recifais é um determinante da dinâmica populacional. Com isso, essa tese buscou identificar em seu primeiro capítulo, quais fatores influenciam os padrões e processos do ciclo de vida dos peixes recifais, desde o período de assentamento até o recrutamento as populações adultas, evidenciando o papel das áreas marinhas protegidas nestes processos. A revisão bibliográfica mostrou que permanecem lacunas no conhecimento sobre a distribuição e estrutura da assembléia de peixes antes do assentamento. Além disso, ainda não existem informações suficientes para determinar se a estrutura e a variabilidade espacial das populações são definidas principalmente durante os processos de assentamento ou em fases posteriores. Em teoria, a importância relativa dos processos pré e pós-assentamento nas populações futuras varia entre as espécies, é fortemente influenciada por variáveis ambientais e está relacionada às características específicas do local. Esses processos atuam em conjunto modificando e regulando a estrutura das populações de peixes recifais.

Com relação as AMPs, o principal benefício comprovado é que essas áreas são capazes de exportar ovos e larvas para regiões adjacentes. No entanto, em AMPs maiores, a proporção relativa de larvas que permanecem na área imediata pode ser maior do que a de larvas dispersas e exportadas para fora de seus limites. As AMPs podem fornecer habitats de maior qualidade e complexidade, o que pode favorecer o assentamento e o recrutamento nessas áreas. Além disso, as redes MPA podem minimizar os efeitos negativos das mudanças climáticas. No entanto, apenas alguns estudos determinaram a importância relativa das AMPs na oferta de juvenis e pouca informação está disponível sobre o assentamento e recrutamento em AMPs e áreas de pesca para grandes espécies de peixes exploradas

comercialmente. Estas são lacunas críticas de conhecimento que limitam nossa compreensão dos benefícios mais amplos das AMPs para a conservação, considerando os estágios iniciais de vida dos peixes recifais.

O segundo capítulo desta tese forneceu a primeira avaliação sobre a distribuição da assembleia de pós-larvas de peixes no Banco de Abrolhos. Os resultados demonstraram a importância das variações espaço-temporais na distribuição das assembleias de pós-larvas no Banco dos Abrolhos, além da influência dos fatores ambientais e das AMPs nesses padrões e processos. A ocorrência de pós-larvas foi influenciada principalmente pelos ventos locais e distância da costa, além disso, os dados corroboram com estudos que sugerem que um dos principais benefícios das AMPs no início da história de vida dos peixes recifais é a alta produção de propágulos em relação à maior abundância e diversidade de espécies encontradas em áreas protegidas em detrimento das áreas abertas à pesca. No entanto, vários fatores podem estar relacionados a esses padrões, entre os quais podemos citar o tipo, qualidade e complexidade do habitat, configuração da paisagem marinha, localização da área protegida, entre outros. Embora as áreas abertas à pesca sejam menos abundantes e diversificadas, algumas espécies encontradas nesses locais são ecologicamente e comercialmente importantes, indicando a necessidade de novos estudos que busquem o potencial dessas áreas como berçário e para a conservação dos estoques pesqueiros da região.

O terceiro capítulo gerou informações pioneiras sobre os padrões de diversidade alfa e beta de pós-larvas e juvenis de peixes recifais ao longo do banco dos Abrolhos além de demonstrar a influência do habitat para a estruturação da assembleia. Os resultados obtidos reiteram a importância dos recifes costeiros e do banco de rodólitos nos processos de assentamento e recrutamento corroborando com outros estudos realizados na região que demonstraram a importância dessas áreas para a conservação e manutenção dos estoques de peixes recifais no Banco de Abrolhos. Por fim, considerando a relevância ecológica da região para a conservação da biodiversidade e o grau de ameaça relacionada a ações antrópicas que variam desde a sobreexploração de recursos pesqueiros até a exploração de óleo e gás e mineração de carbonatos, indicamos que essas áreas devem ser

consideradas prioritárias para a conservação e que esforços que busquem proteger e manter a conectividade desses locais com outros habitats considerando a contribuição larval e o recrutamento de peixes recifais devem ser incentivados.