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HENRIQUE GRANDE

DIVERSIDADE LARVAL DE PEIXES RECIFAIS E OS EFEITOS DOS PROCESSOS
PRÉ E PÓS-ASSENTAMENTO: um estudo no Atlântico Tropical

Recife
2018

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Tese apresentada ao Programa de Pós-Graduação em Oceanografia (PPGO) da Universidade Federal de Pernambuco (UFPE), como parte dos requisitos para obtenção do título de Doutor em Oceanografia.

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Dedico este trabalho a minha esposa
Nayara e aos meus pais H lio e Genilda.

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RESUMO

O conhecimento sobre a história de vida inicial dos peixes é de grande importância para os estudos ecológicos, uma vez que os processos que ocorrem durante os estágios iniciais são responsáveis por impactos significativos na população subsequente. O presente trabalho teve como objetivo fornecer informações sobre a composição das assembleias de peixes pré-assentantes capturados por armadilhas de luz no complexo recifal de Tamandaré-PE, e investigar o papel relativo dos processos pré e pós-assentamento na estrutura das populações da espécie *Ophioblennius trinitatis*. Larvas pré-assentantes foram coletadas mensalmente por três dias consecutivos durante a lua nova de dezembro de 2010 a abril 2016, utilizando armadilhas de luz do modelo CARE®. Os registros possibilitaram a publicação da primeira lista de peixe recifais pré-assentantes capturadas por armadilhas de luz no Atlântico Sudoeste Tropical, composta por registros fotográficos e informações taxonômicas de 76 espécies. Embora algumas espécies não tenham sido capturadas devido à seletividade de armadilhas, a composição e a diversidade taxonômica desta coleção sugerem que as armadilhas luminosas são úteis no estudo da história de vida inicial de uma ampla gama de peixes recifais. Na investigação dos processos que ocorrem durante a fase pré-assentante, os resultados indicaram uma variação interanual no suprimento larval e uma evidente periodicidade sazonal-lunar na desova e assentamento da espécie modelo *O. trinitatis*. Os traços da história de vida inicial desempenharam um papel importante nos padrões de assentamento/recrutamento. Além disso, parte da variabilidade no suprimento larval pode estar relacionada às diferenças na temperatura da água e velocidade do vento. Evidências indicam que as mudanças climáticas, que acarretaram aumento da temperatura nos anos de 2010 e 2015, apresentaram consequências sobre os eventos reprodutivos e subsequente suprimento larval de *O. trinitatis*. Em relação aos processos pós-assentamento, os resultados sugerem que mesmo que o fornecimento de larvas possa determinar o número de recrutas adicionados à população, as diferenças observadas na abundância de adultos entre os locais indicam que a estrutura populacional final pode ter sido determinada por processos que ocorrem após a colonização. Neste caso a seleção de microhabitats, combinada com efeitos de predadores e competidores, foram considerados fatores importantes na estruturação de padrões populacionais em escalas locais. Constatou-se que a presença de ouriços-do-mar *Echinometra lucunter*, disponibilizou abrigos alternativos, sendo um dos principais fatores responsáveis na seleção de microhabitats para o blenídeo *O. trinitatis*. Por outro lado, a reserva marinha aparentemente não teve influência sobre a magnitude de larvas pré-assentantes, uma vez que a densidade de novos

recrutas não diferiu significativamente entre os locais com diferentes níveis de proteção. Contudo, as elevadas densidades de potenciais predadores, sugerem que áreas fechadas podem exercer uma maior pressão predatória sobre as larvas recém-colonizadas. Os resultados desta tese demonstram a importância dos diferentes processos que ocorrem durante o período inicial da história de vida dos peixes e a necessidade de uma abordagem interdisciplinar que combine aspectos da taxonomia, ecologia e oceanografia, para aumentar a compreensão da complexidade e interações subjacentes aos processos de recrutamento dos peixes recifais.

Palavras-chave: Suprimento larval. Assentamento. Recrutamento. Armadilhas de luz. Peixes recifais. Reservas marinhas.

ABSTRACT

Knowledge about reef fish early life history is very important in ecological studies, since the processes that occur during the early stages are responsible for significant impacts on subsequent population dynamics. The present study aimed to determine the composition and structure of the assembly of pre-settlement fish caught by light traps in the Tamandaré-PE reef complex, and to investigate the relative role of pre and post-settlement processes on population structure of the *Ophioblennius trinitatis*. Pre-settlement larvae were collected monthly for three consecutive days during the new moon between December 2010 and April 2016, using light traps of the CARE® model. The records enabled the publication of the first list of pre-settlement reef fish larvae sampled by light traps in the south-west Tropical Atlantic, composed by photographic records and taxonomic information of 76 species. Although some common species have not been captured due to the light traps selectivity, the composition and taxonomic diversity of this collection suggest that the light traps are useful for studies of the initial life history of a wide range of reef fishes. The investigation of the role of processes that occur during the pre-settlement phase, the results indicated an interannual variation in larval supply and an evident seasonal-lunar periodicity in the spawning and settlement of the model specie *Ophioblennius trinitatis*. The early life history traits played an important role in settlement /recruitment patterns. In addition, part of the variability in supply and larval growth rates may be related to differences in water temperature and wind speed. Evidence indicates that climatic changes leading to an increase in temperature in the years 2010 and 2015 have had an impact on the reproductive events and subsequent larval supply of *O. trinitatis*. Regarding the post-settlement processes, the results suggest that even though larval supply probably determined the number of recruits added to the population, the observed differences in adult abundance between sites, implying that the final population structure of *O. trinitatis* may have been determined by processes that occur after colonization. In this case the selection of microhabitats, combined with the effects of predators and competitors, were considered important factors in structuring population patterns at local scales. It was verified that the presence of sea urchins *Echinometra lucunter* provided alternative shelters, being one of the main factors responsible in the selection of microhabitats for the blennid *O. trinitatis*. On the other hand, the marine reserve apparently had no influence on magnitude on the *O. trinitatis* pre-settlement larvae supply, since the density of new recruits did not differ significantly between sites with different protection levels. However, the high densities of potential predators, suggest that the establishment of the enclosed area

may exert a greater pressure on predation newly settled larvae. The results of this thesis demonstrate the importance of the different processes that occur during early life history of fishes and the need for an interdisciplinary approach combining aspects of taxonomy, ecology and oceanography to increase understanding of the complexity and reef fish recruitment processes.

Keywords: Larval supply. Settlement. Recruitment. Light traps. Reef fish. Marine reserves.

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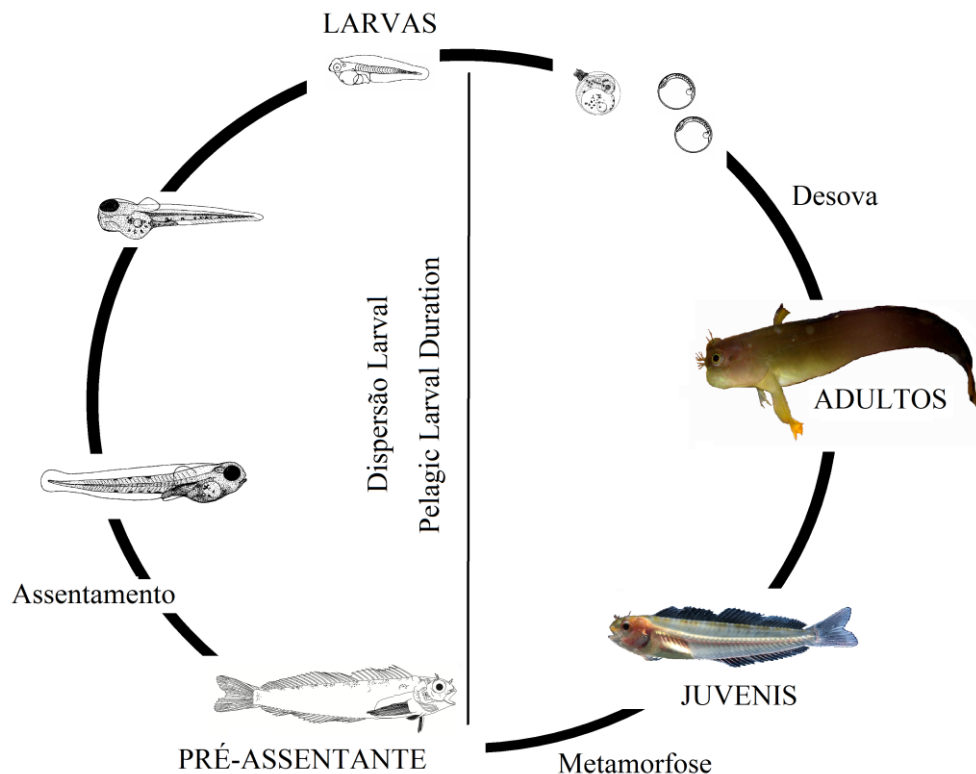
1 INTRODUÇÃO

O conhecimento da história de vida inicial de muitos organismos marinhos é um dos principais focos no estudo da ecologia marinha. Na verdade, respostas a questões vitais sobre a ecologia residem na compreensão do estágio pelágico (Doherty & Williams, 1988), uma vez que muitos dos processos que ocorrem durante os estágios iniciais da vida têm sido responsável por impactos significantes na dinâmica populacional subsequente (Doherty, 1983; Hellriegel, 2000; De Roos *et al.*, 2003).

1.1 Ciclo de vida dos peixes recifais

A maioria dos peixes recifais apresentam distintas fases ao longo de sua história de vida, com uma fase pelágica dispersiva e uma fase bentônica com indivíduos adultos e relativamente sedentários (Sale, 1980; Leis, 1981). O complexo ciclo de vida destas espécies, começa com a liberação de ovos diretamente na coluna d'água (ovos pelágicos) ou ligados a substratos (ovos demersais). Após a eclosão, as larvas de peixes recifais (em sua grande maioria) passam por um estágio pelágico dispersivo e que corresponde a uma parte substancial de sua vida, resultando após o processo de metamorfose, no estágio juvenil e competente para se recrutar a população adulta (Fig. 1).

Figura 1- Desenho esquemático representando o ciclo de vida do peixe recifal *Ophioblennius trinitatis*.



Fonte: O Autor (2018).

Segundo Sale (1991), pelágico é um termo ecológico que se refere a “águas abertas” e não apresenta nenhuma referência ao tamanho do organismo. Cientificamente conhecida como fase larval pelágica esta fase tem uma duração (Pelagic Larval Duration - PLD), a PLD, que pode variar bastante entre as espécies, se estendendo desde dias até meses (Victor, 1986; Beldade *et al.*, 2007). Esta fase é considerada dispersiva, pois o transporte por correntes marinhas permite deslocamentos por distâncias de ordem de 10 a 100 km (Roberts, 1997). Este fase é considerado o principal mecanismo de dispersão e conectividade populacional para a maioria dos peixes marinhos bentônicos (Cowen *et al.*, 2007, Cowen & Sponaugle 2009), sendo essencial para a colonização de novos habitats e manutenção das populações (Sale, 1978; Doherty *et al.*, 1985; Leis & McCormick, 2002). No entanto, alguns trabalhos sugerem que proporções significativas de larvas podem ser retidas nas proximidades ou até mesmo voltarem aos recifes de origem (Jones *et al.*, 1999; Jones *et al.*, 2005).

O início do estágio larval planctônico caracteriza-se por altas abundâncias de ovos e larvas, somado a elevadas taxas de mortalidade devido à predação, inanição, parasitismo e doenças (Keough & Swearer, 2007). Ao final do estágio pelágico ocorre o processo conhecido como assentamento larval, definido aqui como a transição do ambiente pelágico para associar-se ao habitat juvenil bentônico. Para a maioria dos peixes de recife, o período pelágico que antecede o assentamento é equivalente ao pré-assentamento (Kingsford, 1988), contudo o termo pré-assentamento pode ser inapropriado para larvas de peixes semipelágicos associados a recifes como os carangídeos (Sale, 1991).

O processo de assentamento é acompanhado pela metamorfose larval, responsável pela transição ao estágio juvenil/adulto e considerado um precursor necessário para o recrutamento da população (Myrberg & Fuiman, 2002; Leis & McCormick, 2002). O termo recrutamento geralmente descreve a adição de novos indivíduos e o responsável pelo reabastecimento de populações de peixes de recife de coral e que pode ser altamente variável no espaço e no tempo (Sale *et al.*, 1984, Robertson *et al.*, 1988).

1.2 Recrutamento e dinâmica populacional

Descobrir a importância relativa dos processos pré e pós-recrutamento e como estes são determinantes na estrutura final das populações tem sido tema de amplo debate desde a década de 1980 (Hixon, 2011). Desde então, várias hipóteses tentam explicar a variabilidade do recrutamento e sua importância sobre a estrutura populacional.

Em contraste com a “Hipótese da Loteria” (Sale, 1978), que postulava que as espécies competem em uma loteria por espaço no ambiente recifal, onde os primeiros a chegar tem

maior probabilidade de encontrar um espaço livre e concluírem seu ciclo de vida, a “Hipótese do Recrutamento Limitado” (Doherty, 1981) afirma que a alta taxa de mortalidade no período larval resulta em taxas de recrutamento muito baixas, no qual as populações juvenis e adultas nunca atingem tamanhos próximos a capacidade de carga do habitat, nos quais a competição e outros processos denso-dependentes possam ser relevantes na regulação na dinâmica das populações.

Por outro lado, em situações de elevadas taxas de suprimento larval, os fatores pós-assentamento tornam-se determinantes sobre a dinâmica populacional (Jones, 1990). Foi a partir da década de 1990, que o debate sobre a “Hipótese da Dependência da Densidade” (Doherty, 1981; Caley, 1998) ganhou novamente atenção no processo de recrutamento. Neste caso os fatores dependentes da densidade como interações entre espécies (competição e predação) e a disponibilidade de habitat, foram identificadas como potenciais modificadores da correlação entre a oferta e o assentamento larval (Pineda *et al.*, 2010) e os principais reguladores na ecologia populacional.

Contudo, não se sabe ao certo em que momento, se durante o assentamento ou após este, que a estrutura populacional e a variabilidade espacial da mesma são definidas. Provavelmente, a importância relativa dos processos pré e pós-assentamento em populações futuras é espécie-específica (Sponaugle & Cowen, 1996a) e pode depender das diferenças específicas do local (Warner & Hughes, 1988; Caley *et al.*, 1996; Tupper & Boutilier 1997), ou ainda ambos os processos podem atuar em conjunto como preditores na regulação e estruturação das populações de peixes recifais.

1.3 Processos que influenciam o assentamento/recrutamento larval

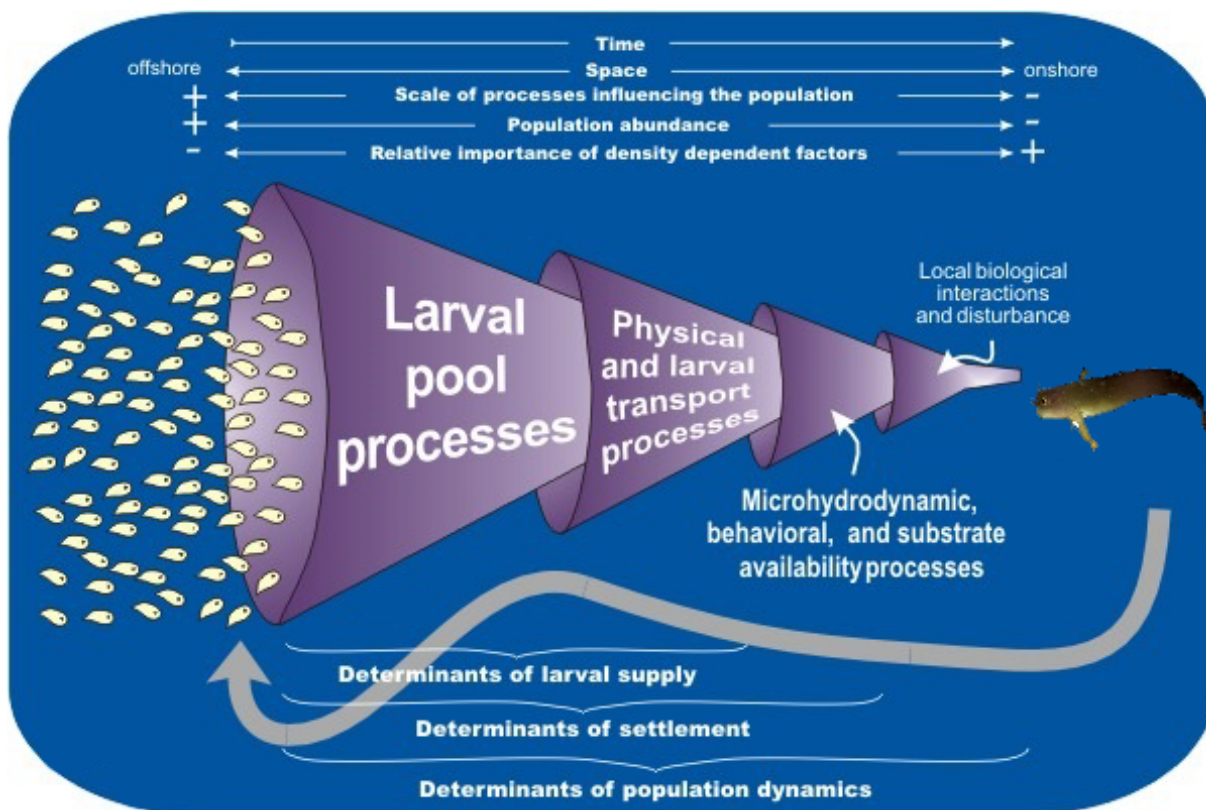
O recrutamento de peixes recifais é influenciado por diferentes processos e variáveis que podem operar espacial e temporal em escalas de dias a anos (Robertson *et al.*, 1999; Lozano & Zapata, 2003; Fontes *et al.*, 2009). Parte dessa variabilidade temporal pode ser explicada por processos bióticos e abióticos, que afetam tanto a fase que antecede o assentamento larval quanto à etapa pós-assentamento.

Os eventos que antecedem o assentamento larval em peixes recifais (processos pré-assentamento), como a reprodução dos adultos (Robertson *et al.*, 1988; Meekan *et al.*, 1993), os eventos pelágicos (Shenker *et al.*, 1993; Thorrold *et al.*, 1994; Paris & Cowen 2004; Sponaugle & Pinkard, 2004; Sponaugle *et al.*, 2005; D'Alessandro *et al.*, 2007; Shima & Swearer, 2009), assim como os processos que ocorrem pós-assentamento (Sweatman, 1985;

Shima & Osenberg, 2003) são essenciais para a conclusão do ciclo de vida de muitos peixes recifais e determina em grande parte sua estrutura populacional.

Durante a fase pelágica, os fenômenos que influenciam a magnitude no suprimento larval são na maioria das vezes influenciados por processos estocásticos que ocorrem em grandes escalas. Já na fase pós-assentamento, os processos denso-dependentes são os principais estruturadores na dinâmica populacional ocorrendo em pequenas escalas (Pineda, 2000; Pineda *et al.*, 2010) (Fig. 2).

Figura 2. Representação dos processos e escalas que influenciam a taxa de assentamento e a densidade populacional.



Fonte: Adaptado de Pineda (2000).

1.3.1 Influências durante a fase reprodutiva

O período reprodutivo dos peixes pode ser considerado a primeira etapa do seu ciclo de vida, onde as espécies apresentam diversas adaptações selecionadas ao longo do tempo (adaptações evolutivas) com o intuito de maximizar o recrutamento das larvas e lidar com a variação previsível e imprevisível na mortalidade larval. Sabe-se que a condição corporal e fisiológica parental pode influenciar diretamente no fornecimento de ovos e, consequentemente, a qualidade e quantidade das larvas, podendo impactar o desenvolvimento (Kerrigan, 1997; Meidel & Scheibling 1999) e sobrevivência das larvas (McCormick, 1999;

Riveiro *et al.*, 2000). Em um estudo de Green & McCormick (2005) sobre um peixe-palhaço tropical revelou que a taxa de crescimento e o tamanho das larvas estavam relacionado às influências paternas e maternas. Raventos & Planes (2008) também constataram que o labrideo *Symphodus roissali* (Risso, 1810), as fêmeas maiores produziam ovos e larvas maiores.

Variações nas condições ambientais que ocorre durante a fase reprodutiva também pode afetar diretamente o desenvolvimento e sobrevivência de ovos e larvas de peixes. Sabe-se que a temperatura é fundamental na vida dos peixes, afetando principalmente os processos reprodutivos desde o desenvolvimento e maturação dos gametas, desova, e eclosão (Pauly & Pullin, 1988; Jobling, 1997; Pankhurst & Munday, 2011). Por exemplo, o aumento das temperaturas pode contribuindo para o desenvolvimento reprodutivo em espécies que desovam na primavera e verão (Stacey, 1984, Scott & Pankhurst, 1992; Pankhurst & Munday, 2011), mas temperaturas elevadas também podem retardando o início da maturação e ovulação em espécies que desovam no outono (Pankhurst & King 2010).

1.3.2 Influencias pré-assentamento

Na fase pelágica, as larvas estão sujeitas a um ambiente dinâmico e irregular no espaço e tempo, sofrendo influências de diversos fatores físicos-químicos e biológicos, que podem afetar sua sobrevivência, crescimento e dispersão (Cushing, 1990; Rutherford & Houde 1995; Meekan *et al.*, 2003; Bergenius *et al.*, 2005; Sponaugle *et al.*, 2006). Tais processos estocásticos e fatores físicos cíclicos podem afetar a entrega de larvas para o habitat de assentamento e introduzindo variações adicionais na magnitude dos eventos de recrutamento (Robertson *et al.*, 1988; Sponaugle & Cowen 1996; Kingsford & Finn, 1997).

Condições ambientais como processos oceanográficos e características do habitat, podem influenciar o recrutamento dos peixes recifais, afetando o crescimento, sobrevivência e a dispersão larval. Neste caso, fatores ambientais como temperatura e disponibilidade de alimentos, podem influenciar o crescimento durante o início da vida dos peixes (Houde, 1989; Pepin, 1991; Houde & Zastrow, 1993), a condição para assentamento (McCormick & Molony, 1995) e até mesmo a duração da vida pelágica (Gillooly *et al.*, 2002). Outros fatores, como radiação solar, ventos, precipitação pluviométrica (Bergenius *et al.*, 2005) e massas de água (Shima & Findlay, 2002; Hamilton *et al.*, 2008) também têm afetado as características larvais e padrões subsequentes de recrutamento.

O vento (direção e intensidade) pode influenciar diretamente no transporte de larvas (Lemberget *et al.*, 2009; Sim-Smith *et al.*, 2013) ou no caso relacionado à turbulência

induzida pelo vento, pode influenciar as condições de alimentação e a sobrevivência das larvas (Lemberget *et al.*, 2009). Embora os processos relacionados ao transporte demonstrem influenciar diretamente o recrutamento (Milicich & Doherty, 1994; Sponaugle *et al.*, 2005; D'Alessandro *et al.*, 2007), as larvas dos peixes de recife não são simples partículas passivas (Fisher *et al.*, 2000), e mesmo no início da ontogenia podem apresentar comportamentos que afetam sua dispersão geral (por exemplo, Cowen *et al.*, 2000; Cowen 2002; Paris & Cowen, 2004), como migração vertical (Leis, 1991; Paris & Cowen 2004) ou natação horizontal (Leis *et al.*, 1996).

Alem disso, alguns traços da história de vida inicial dos peixes marinhos (Early Life History Traits - ELHT), também podem influenciar o sucesso no recrutamento e a sobrevivência juvenil subsequente (Searcy & Sponaugle 2001; Shima & Findlay, 2002; Vigliola & Meekan, 2002; McCormick & Hoey 2004; Raventos & Macpherson 2005). Diversos estudos revelaram que um maior tamanho da larva na eclosão (Meekan & Fortier, 1996; Vigliola & Meekan, 2002; Raventos & Macpherson, 2005), taxa de crescimento larval mais rápida (Meekan & Fortier, 1996; Searcy & Sponaugle, 2001; Shima & Findlay, 2002; Raventos & Macpherson 2005a), menor duração das larvas pelágicas (Meekan & Fortier, 1996; Shima & Findlay, 2002), maior tamanho no momento de assentamento (McCormick & Hoey, 2004), melhor condição na metamorfose e crescimento juvenil mais rápido (Searcy & Sponaugle, 2001; Sponaugle & Grorud-Colvert, 2006), geralmente aumentam a sobrevivência dos peixes após o assentamento.

Os processos relacionados ao crescimento larval podem influenciar diretamente as taxas de mortalidade e consequentemente os pulsos de recrutamento, uma vez que taxas de crescimento mais rápido podem resultar em indivíduos maiores em uma determinada idade e serem menos vulneráveis à predação (Hipótese "bigger is better", Miller *et al.*, 1988; Leggett & Deblois, 1994). Além disso, os indivíduos podem avançar mais rapidamente para o próximo estágio de vida, onde as pressões de predação e de fome deverão diminuir (mecanismo da "stage duration" Houde, 1987). Por outro lado, contrariando a hipótese "growth-mortality" (Anderson, 1988), em algumas espécies de peixes marinhos o menor tamanho também pode favorecer a sobrevivência juvenil, pois apesar de serem mais vulneráveis à predação, peixes menores podem achar abrigos com maior facilidade que indivíduos maiores (Sogard, 1997).

Da mesma forma, eventos de desova e/ou assentamento larval geralmente são sincronizados com o ciclo lunar ou marés (Robertson *et al.*, 1988; Robertson, 1990; Sponaugle & Cowen, 1996, Kingsford & Finn, 1997; D'Alessandro *et al.*, 2007), o que pode

ter implicações para a sobrevivência. Sponaugle & Pinkard (2004) verificaram desovas ocorrendo em marés de amplitude mínima, com o objetivo de reduzir a dispersão das larvas e aumentar a retenção próxima ao habitat de assentamento onde os nutrientes são mais elevados. Além disso, alguns estudos registraram desovas e assentamentos larvais ocorrendo durante períodos escuros, particularmente em noites de lua nova, com o intuito de reduzir o risco de predação por predadores visuais (Johannes, 1978; Victor, 1986; Robertson *et al.*, 1988).

1.3.3 Influências pós-assentamento

Enquanto a fase pelágica está sujeita a variações estocásticas, o período pós-assentamento é influenciado por processos densos-dependentes como a predação e competição, considerados importantes fatores responsáveis pela estrutura de uma população adulta (McCormick & Meekan, 2007; Samhuri *et al.*, 2009; Pineda *et al.*, 2010). Jones (1990) foi um dos primeiros a mostrar que em situações de baixas taxas de assentamento larval, se manifestam os processos relacionados à limitação de recrutamento, enquanto em taxas mais altas os processos predadores sobre a dinâmica populacional é dependente da densidade.

Diversos estudos apontam a predação como a principal fonte de mortalidade precoce pós-assentamento e o responsável pela organização comunitária (Connell, 1996; Beets, 1997; Hixon & Carr, 1997; Caselle 1999). Outros demonstraram a importância da estrutura do recife no processo de recrutamento e estrutura subsequente das comunidades de peixes de recife (por exemplo, Shulman *et al.*, 1983; Kaufman & Ebersole, 1984). A variação espacial no assentamento e sobrevivência de assentantes pode ser explicada por características de habitat, como a capacidade de abrigar uma maior abundância de recrutas em função da qualidade do habitat (Shima & Osenberg, 2003) e microhabitat (Tolimieri, 1995; Caselle & Warner, 1996; Félix-Hackradt *et al.*, 2014), ou por oferecer uma maior quantidade de refúgios contra predadores (Hixon & Beets, 1993; Caley & St. John 1996; Almany, 2004) e conspecíficos (Forrester & Steele, 2004), bem como pela pressão competitiva por abrigos (Robertson, 1996; Schmitt & Holbrook, 1999).

Em muitos casos, a presença de organismos como macroalgas (Chaves *et al.*, 2013), corais (Munday *et al.*, 1997, Pereira & Munday, 2016), anêmonas (Elliott, 1992), esponjas (Bohlke & Robins, 1969) e organismos móveis como ouriços do mar, pepinos e crinóides (Karplus, 2014), podem atuar como fontes biogênicas capazes de modificar o ambiente ou criar

micro-habitats, aumentando a complexidade do micro-habitat fornecendo refúgio contra predadores e disponibilizando fontes de alimentos (Dahlgren & Eggleston, 2000).

Eventualmente, uma grande quantidade de estudos demonstraram que a dinâmica local dos peixes de recife é de fato dependente da densidade, e que a fonte de regulação da dinâmica populacional é tipicamente predatória, seja diretamente pela predação aos novos recrutas ou indiretamente através de competição por refúgios (Osenberg *et al.*, 2002).

1.4 Dificuldades de amostragem e técnicas empregadas

Apesar de crucial o conhecimento sobre as fases iniciais da vida dos peixes recifais, uma grande dificuldade nesses estudos esta na coleta e/ou observação de peixes recifais em seu estágio pelágico. Isto ocorre devido à irregularidade acentuada em suas distribuições, raridade em comparação com outros zooplânctons, ausência de metodologia de coleta apropriada para todas as idades, padrões espaciais que mudam temporalmente e a natureza tridimensional nas distribuições de larvas de peixes (Sale, 1991).

Como o estágio pelágico dos peixes recifais é uma fase de desenvolvimento e crescimento, geralmente são necessários diferentes métodos de amostragem dependendo da abundância, idade-tamanho, mobilidade e comportamento da larva ou juvenil (Choat *et al.*, 1991). Uma variedade de métodos foi desenvolvida para coletas de larvas e monitorar o recrutamento de peixes marinhos, incluindo redes de arrasto (*towed nets*) (McGowan & Brown, 1966; Methot, 1986), redes de cerco (Kingsford & Choat, 1985), redes de canal (Shenker *et al.*, 1993), redes de crista (Dufour & Galzin, 1993), armadilhas de luz (Doherty, 1987) e censo visuais (Robertson *et al.*, 1988; Ackermann & Bellwood, 2000).

Todos esses métodos diferem em sua eficiência de coleta e apresentam vantagens e desvantagens. Por exemplo, amostragem com redes de plâncton rebocadas, podem subestimar as larvas em estágio avançado antes do recrutamento, devido à capacidade de evitar as redes de arrasto (Choat *et al.*, 2003; Catalán *et al.*, 2014). Já as redes fixas de plâncton, como redes de canal e de crista, precisam de correntes permanentes direcionando as larvas para o interior do dispositivo (Anderson *et al.*, 2002). O censo visual subaquático pode ser essencial para monitorar padrões de recrutamento (Doherty, 1991; Meekan *et al.*, 2003). Entretanto espécies pequenas e crípticas podem ser subestimadas por se camuflar em habitats de difícil visualização (Ackermann & Bellwood, 2000).

Já as armadilhas de luz podem oferecer algumas vantagens adicionais em relação aos métodos mais tradicionais que precisam ser rebocadas, como a possibilidade de amostragem em múltiplos locais simultaneamente (Wolanski *et al.*, 1997; Doherty & Carleton, 1997),

coletas em áreas onde não é prático puxar uma rede (Hernandez & Shaw, 2003; Strydom, 2003), a fácil utilização, o baixo custo e mínimo de manutenção (Floyd *et al.*, 1984, Hernandez & Lindquist 1999), além da alta qualidade na condição dos espécimes coletados pelas armadilhas de luz.

Por outro lado as armadilhas de luz são considerados dispositivos de coletas bastante seletivos capturando um número restrito de táxons em sua fase de assentamento (Gregory & Powles, 1988; Hickford & Schiel, 1999), com tamanhos e idades específicos (Choat *et al.*, 1993; Brogan, 1994; Hernandez & Lindquist, 1999, Marchetti & Moyle, 2000). A eficácia da armadilha de luz depende do comportamento das larvas em relação à luz ou das condições da clareza da água que dependendo do horário ou ciclo lunar podem influenciar a intensidade da luz que potencialmente atraem as larvas de peixes (Gehrke, 1994).

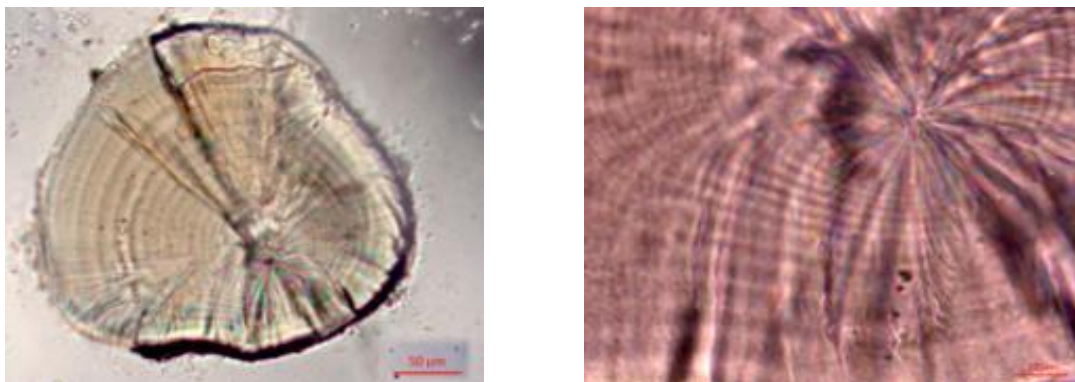
No entanto, as armadilhas de luz tornaram-se um dos principais métodos de coletas em ambientes de recifes tropicais, especialmente para espécimes de larvas tardias (Stobutzki & Bellwood, 1994; Hair & Doherty, 2003). Esta metodologia foi usada pela primeira vez em larvas de peixes de água doce (Faber, 1981) e posteriormente no ambiente marinho para monitorar o abastecimento de larvas de peixes marinhos em recifes de corais (Doherty, 1987).

1.4.1 Uso do otólito no estudo da vida larval dos peixes

A determinação de idade e, portanto do tempo de vida larval é uma etapa crucial nos estudos da ecologia dos peixes recifais. Esta determinação é feita principalmente com o uso de estruturas calcificadas conhecidas como otólitos, presentes na cavidade do ouvido interno dos peixes teleósteos, e que podem ser consideradas perfeitas “caixas pretas” por gravarem diversas informações sobre a história de vida dos peixes. O crescimento do otólito ocorre através da deposição de proteína e cálcio secretados em taxas diferentes pelas células maculares circundantes na superfície do otólito, o que promove a formação de intervalos de incrementos de crescimento.

Os otólitos têm sido usados no manejo de pesca há mais de um século, fornecendo características fundamentais da história de vida dos peixes (Green *et al.*, 2009). A partir das técnicas descritas por Williams & Bedford (1974) e Blacker (1974), o uso de otólitos na determinação da idade (por meio de marcas incrementais de crescimento anuais) se tornou bastante conhecido. Entretanto somente com a descoberta de incrementos diários nos otólitos de peixes teleósteos temperados e tropicais (Panella, 1971, 1974; Campana & Neilson, 1985) é que foi possível um considerável avanço nas análises de crescimento e tamanhos de juvenis de peixes (Fig. 3).

Figura 3. Incrementos diários observados no otólito lapilli sob microscópio óptico (aumento 20x) (A); e aumento próximo ao núcleo do otólito, observados sob microscópio óptico (aumento 100x) (B) de um indivíduo de *Lutjanus synagris* com comprimento total de 19,59 mm.



Fonte: O Autor (2018)

A combinação da idade e comprimento pode ser usada para determinar taxas de crescimento, estimativas de sobrevivência, mortalidade e idade-específica de recrutamento (Campana & Thorrold, 2001; Fowler, 2009). Além disso, registros de crescimento e composição elementar incorporados em otólitos também foram usados para avaliar a mortalidade seletiva por tamanho para dinâmica populacional (Sinclair *et al.*, 2002), determinar a duração larval pelágica (Pastén *et al.*, 2003), identificar espécies (Campana, 2004) e distinguir populações (Secor *et al.*, 2002). As medidas de larguras incrementais dentro de otólitos também podem ser usadas para inferir taxas individuais de crescimento somático, devido à relação proporcional entre o crescimento do otólito e o crescimento dos peixes (Black *et al.*, 2013)

A microestrutura diária dos otólitos nos permitiu identificar processos ecológicos e oceanográficos importantes no reabastecimento populacional e o recrutamento pesqueiro. Tais processos não apenas influenciam a sobrevivência de peixes larvais, mas também têm o potencial de afetar uma variedade de outros organismos, uma vez que a compreensão desses processos geram dados necessários para o manejo adequando em programas de conservação.

1.5 Área de estudo

A área de estudo da presente tese, está localizada na Costa Nordeste do Brasil, e é caracterizada por uma plataforma tipicamente carbonática e pobre em sedimentos, com larguras em torno de 18 milhas náuticas (~ 29 Km), com formações recifais e esparsas (Kempf *et al.*, 1970), apresentando paleocanais bem preservados (Camargo *et al.*, 2015). O talude tem início na isóbata de 70 metros, e apresenta um declive acentuado até o sopé dos

canyons a profundidades de mais de 1000 metros (Almeida *et al.*, 2015). A porção mais externa da plataforma continental, considerada como uma área de relevante interesse ecológico (EBSA - Environmental Biologically and Significant Area) funciona como um corredor ecológico (Olavo *et al.*, 2005) e abriga fenômenos de agregações de peixes recifais.

A região costeira caracteriza-se por deltas e estuários, com formações recifais lineares, formando lagunas na área emersa próxima a costa, típicas das formações recifais do sistema Pirangi-Maceió (Rodriguez-Ramirez *et al.*, 2008). A zona costeira também apresenta grande diversidade de ecossistemas, incluindo mata atlântica, manguezais, restingas, estuários, pradarias de fanerógamas e recifes de corais (Ferreira *et al.*, 2004). Estes ecossistemas formam um mosaico de ambientes interconectados, nos quais suportam diferentes processos ecológicos relacionados com diversas espécies de crustáceos, moluscos, peixes, aves e mamíferos.

Este ambiente costeiro é reconhecido como hotspot de biodiversidade (MMA, 2002) e a presença de unidades de conservação reflete esta característica, tanto pela necessidade de proteção a estes ambientes, que incluem os diversos ecossistemas supracitados, quanto pela ocupação e dependência humana. Para tal, o estabelecimento e sobreposição de unidades de conservação de uso sustentável (APA's de Guadalupe e Costa dos Corais) (Fig. 4) foram fundamentais para o fortalecimento de um mosaico local e do estreitamento das relações entre o poder público municipal, estadual e federal, bem como com a sociedade civil organizada.

Em abril de 1999, através de um acordo celebrado entre a comunidade pesqueira, as autoridades locais, a Universidade Federal de Pernambuco (UFPE) e o Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Nordeste (CEPENE/ICMBio), também foi estabelecida em Tamandaré a primeira zona de recuperação recifal. Informalmente conhecida como 'Área Fechada de Tamandaré', é considerado temporalmente o mais longo e contínuo experimento no Brasil de monitoramento, recuperação e conservação de recifes costeiros.

Como parte da estratégia de mitigação dos impactos causados pelas obras do PRODETUR aos ecossistemas costeiros, em 2003, foi criado uma unidade de Proteção Integral o Parque Natural Municipal do Forte de Tamandaré (PNMFT), com área de 349 ha e contemplando uma área à beira-mar e que engloba "Área Fechada de Tamandaré". Este macro-ecossistema também faz parte de um Programa de Pesquisa Ecológica de Longa Duração (PELD), que é uma rede de sítios de referência para a pesquisa científica. Aqui denominado sítio PELD-Tamandaré (PELD-TAMS), abrange ambientes aquáticos estuarinos

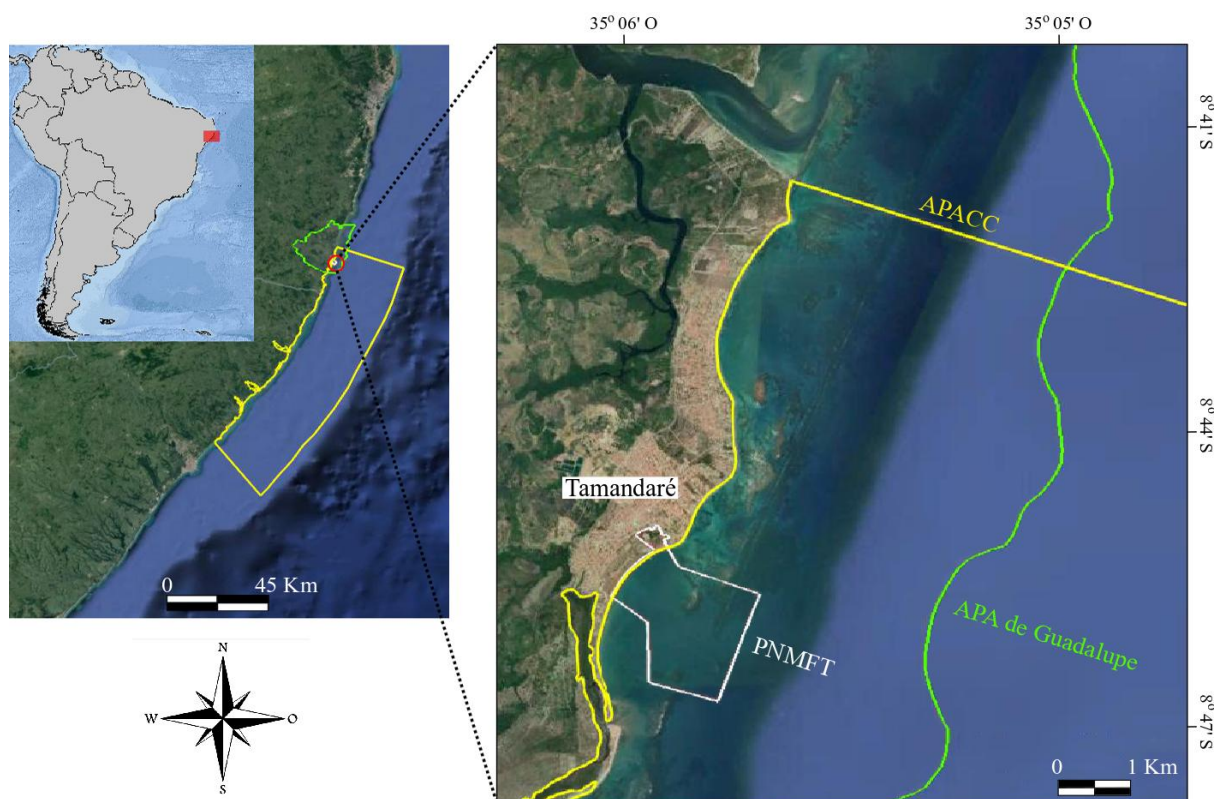
e marinhos de grande biodiversidade e submetidos a uso intenso, numa área reconhecida como prioritária para conservação.

Áreas marinhas protegidas (AMP) são ferramentas de gerenciamento imprescindíveis para a proteção da biodiversidade e conservação de recursos marinhos (Pauly *et al.*, 2002). Diversos estudos apontam os efeitos positivos de áreas marinhas protegidas sobre as comunidades de peixes recifais dentro dos limites da reserva e em áreas adjacentes como o aumento na abundância e diversidade de espécies (i) o aumento na abundância e diversidade de peixes (García-Charton *et al.*, 2000), (ii) maior biomassa e/ou abundância de espécies-alvo (Mora *et al.*, 2006), (iii) presença de indivíduos maiores e/ou mais velhos (Watson *et al.*, 2009) e (iv) o restabelecimento de grandes predadores (Claudet *et al.*, 2011).

Ao abrigar populações reprodutoras mais densas, com indivíduos maiores e de maior biomassa (Halpern, 2003), espera-se uma maior produção de ovos e larvas nas reservas marinhas do que nas áreas adjacentes (Palsson & Pacunski, 1995; Manríquez & Castilla, 2001; Branch & Odendaal, 2003). Portanto, presume-se que o transbordamento de indivíduos de áreas protegidas para fora de seus limites não ocorra somente pelo movimento de adultos (Kellner *et al.*, 2007), mas também pela exportação de larvas produzidas nas áreas protegidas (Gell & Roberts 2003; Halpern & Warner, 2003). Além disso, AMPs podem atuar como importantes receptores de larvas oriundas de outras áreas, uma vez que a alta qualidade de habitat possibilita maior sobrevivência juvenil devido à maior disponibilidade de recursos (Caselle & Wamer, 1996; Holbrook & Schmitt, 2002).

A eficácia de uma reserva marinha depende claramente do conhecimento sobre todas as etapas da vida dos organismos residentes (Carr & Reed, 1993; Polunin & Roberts, 1993; Rowley, 1994; Nowlis & Roberts, 1999). Entretanto pouco se sabe a respeito da composição e suprimento larval, assim como os padrões de recrutamento e dispersão em áreas marinhas protegidas, sobretudo na “Área Fechada de Tamandaré”. A compreensão sobre o fornecimento e recrutamento larval em reservas marinhas e áreas adjacentes é essencial para a implementação e manejo de reservas, uma vez que áreas marinhas adequadamente localizadas podem amortecer a variabilidade de recrutamento em áreas adjacentes (Bohnsack, 1990) e contribuir para a sustentabilidade de populações futuras (Halpern & Warner 2003). Nesse contexto, os resultados do presente estudo representam um primeiro passo rumo a compreensão destes processos, podendo contribuir de forma importante para a compreensão da ecologia populacional dos peixes recifais tanto na área de estudo como em muitas outras áreas do sudoeste do Oceano Atlântico.

Figura 4. Mapa da área de estudo com destaque para a unidade de conservação de uso sustentável APA Costa dos Corais.



Fonte: O Autor (2018).

Legendas: APACC - Área de Proteção Ambiental Costa dos Corais; APA de Guadalupe - Área de Proteção Ambiental de Guadalupe; PNMFT - Parque Natural Municipal do Forte de Tamandaré.

1.6 Objetivos da Tese

O objetivo geral do presente trabalho foi fornecer informações sobre a composição das assembleias de peixes pré-assentantes capturados por armadilhas de luz no complexo recifal de Tamandaré-PE. Além disso, foi investigado o papel relativo dos processos pré-assentamento (provenientes da fase pelágica, como o aporte de larvas ao recife) e dos processos pós-assentamento (interações bióticas e seleção de habitats) na estrutura das populações das espécies do peixe recifal, usando como modelo a espécie *Ophioblennius trinitatis*.

1.6.1 Objetivos específicos

- A) Descrever a primeira lista das espécies de larvas de peixes pré-assentantes capturados por armadilhas de luz no Atlântico, e fornecer informações sobre abundância,

características taxonômicas, ocorrência e capturabilidade por armadilhas de luz (Capítulo 2).

- B) Examinar a variação temporal no suprimento larval e conduzir uma análise comparativa para determinar se determinados traços larvais (Idade larval, PLD, comprimento da vida larval, tamanho na taxa de assentamento, taxa de crescimento) estão correlacionados com padrões temporais do assentamento (Capítulo 3).
- C) Investigar quais variáveis ambientais pode influenciar nos padrões de suprimento larval (Capítulo 3).
- D) Investigar se a variação espacial e temporal da população adulta de *O. trinitatis* é afetada pelo suprimento larval (proveniente da fase pelágica) ou por processos que ocorrem após o assentamento, como predação, presença de coespecíficos e seleção de microhabitats (Capítulo 4).
- E) Verificar os possíveis efeitos de uma área marinha protegida no recrutamento e subsequente população de *Ophioblennius trinitatis* (Capítulo 4).

1.7 Estrutura e disposição da Tese

A presente tese apresenta informações sobre a composição das assembleias de peixes pré-assentantes capturados por armadilhas de luz no complexo recifal de Tamandaré-PE, além disso, descreve o papel relativo dos processos pré e pós-assentamento sobre o recrutamento e estrutura populacional do blenídeo *Ophioblennius trinitatis*. Para esta finalidade iniciamos a tese com uma “Introdução Geral” (Capítulo 1) fazendo uma revisão dos estudos sobre a ecologia dos processos pré e pós-recrutamento, contextualizando o tema e fornecendo ao leitor informações sobre o ambiente pesquisado. Neste capítulo são apresentados informações e bases conceituais dos principais temas presentes nos subsequentes capítulos desta tese. Fazem parte ainda deste capítulo os objetivos (gerais e específicos) e disposição da Tese.

Em sequência, do capítulo 2 ao 4, o desenvolvimento da tese está disposta em formatos artigos científicos. Nesse sentido, com o intuito de investigar o papel relativo dos processos pré e pós-assentamento na estrutura das populações das espécies de peixes recifais, no Capítulo 2 intitulado: “Diversity of settlement-stage reef fish captured by light-trap in a coastal reef system, Tropical South-West Atlantic”, descrevemos a eficácia do uso de

armadilhas de luz, como uma técnica de estudo em peixes no estágio inicial de vida e registramos a primeira lista das espécies de peixes pré-assentantes no Atlântico Sul Tropical. Além de apresentar um checklist comentado, são apresentadas informações sobre abundância, características taxonômicas, ocorrência e capturabilidade por armadilhas de luz.

Confirmando a eficácia do método no estudo da vida inicial dos peixes recifais (capítulo 2) foi escolhido indivíduos de uma das espécies mais abundante, *Ophioblennius trinitatis* Miranda Ribeiro 1919, como espécie modelo no intuito de estudar com mais detalhes a variação temporal-interanual no suprimento larval, os traços de história de vida larval (ELHT) e a influência de variáveis ambientais sobre padrões e magnitude de suprimento larval (Capítulo 3). Para tal, foi testada a hipótese de que existem diferenças na abundância das larvas pré-assentantes de *O. trinitatis* entre anos e estações. A microestrutura dos otólitos também foi analisada para determinar ELHTs como crescimento inicial de peixes, idade e tamanho no assentamento. Além disso, análises multivariadas foram realizadas para verificar quais variáveis ambientais “melhor explicam” o padrão e magnitude do suprimento larval e as taxas de crescimento larval.

No capítulo 4, foi investigada a importância dos processos pós-assentamento sobre o recrutamento e dinâmica populacional. Testamos se a variação espacial e temporal da população adulta foi afetada pelo suprimento larval (proveniente da fase pelágica) ou por processos que ocorrem após o assentamento (predação, presença de coespecíficos, congeneros e seleção de microhabitats). Além disso, também foram verificados os possíveis efeitos de uma área marinha protegida no recrutamento e estrutura populacional de *Ophioblennius trinitatis*.

O Capítulo 5, Discussão Geral, integra e discute os resultados dos capítulos 2 a 4 dentro da visão geral da tese. Além disso, este capítulo inclui implicações para conservação e manejo e sugestões para pesquisas futuras. Ao final apresentamos conclusões relativas ao objetivo geral do trabalho. Deste modo, esta dissertação amplia e aprofunda as informações existentes sobre os peixes recifais do sistema costeiro do Nordeste do Brasil e oferece subsídios para projetos de conservação em ambientes recifais.

2 DIVERSITY OF SETTLEMENT-STAGE REEF FISH CAPTURED BY LIGHT-TRAP IN A TROPICAL SOUTH-WEST ATLANTIC OCEAN COASTAL REEF SYSTEM

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2.1 Abstract

The majority of reef fishes presents life cycles in which pelagic larval phases precede demersal juvenile and adult phases. Settlement-stage larvae of many species are attracted by light and are therefore susceptible to capture by light traps. We present here the results of five years monitoring of reef fish post-larvae using light traps (CARE®) in the Bay of Tamandaré, NE Brazil. An annotated checklist of pre-settlement fishes, their frequency of occurrence, and taxonomic characteristics are provided. In total, 4,422 post-larval fishes belonging to 36

families, 56 genera and 76 species were captured. The most speciose families were Carangidae (7), Lutjanidae (6) and Pomacentridae (4), while the families Gerreidae (30.47%), Holocentridae (16.54%), Blenniidae (12.01%), Labrisomidae (8.36%), Lutjanidae (8.29%) and Acanthuridae (5.95%) were the most abundant. This is the first account of capture of settlement-stage reef fishes in the Tropical Southwest Atlantic. Although a few common species were not captured due to the selectivity of light traps, the composition and taxonomic diversity of this first collection suggests that this technique is a useful tool in studies on the history of early life stages of a wide range of pre-settlement reef fishes.

Key words: coral reefs; post-larvae fish; recruitment; sampling methods.

2.2 Significance Statement

Knowledge about the pelagic larval phase of coral reef fishes is a key to understanding population dynamics. Here we report the results of five years monitoring of reef fish post-larvae using light traps in Northeast Brazil. An annotated checklist of pre-settlement fishes, their frequency of occurrence and taxonomic characteristics is provided. These first data on the composition and taxonomic diversity of pre-settlement fishes in the Tropical South Atlantic suggests that this sampling technique is very useful in early life history studies of a wide range of species and can be considered a baseline to understand the ecology of many adult fishes.

2.3 Introduction

Many tropical reef fishes have life cycles in which pelagic larval phases precede demersal juvenile and adult phases. At the end of the pelagic phase, settlement-stage reef fishes must locate a suitable reef habitat in a vast seascape (Doherty, 2002; Myrberg & Fuiman, 2002; Leis & McCormick, 2002).

Since the dispersive pelagic phase in coastal zones is the first of several events that culminate in adult population structure, understanding processes affecting life history at this early life stage is key for understanding marine fish population dynamics (Grorud-Colvert & Sponaugle, 2009). Several aspects can influence the ability of larvae to locate suitable settlement habitats, such as their sensory ability (Tolimieri *et al.*, 2000; Atema *et al.*, 2002; Leis *et al.*, 2002), swimming performance (Leis & Carson-Ewart, 1997; Stobutzki & Bellwood, 1997) and/or hydrodynamic characteristics (Poulin *et al.*, 2002; Sponaugle *et al.*,

2002). More recently, studies have also reported on the impacts of anthropogenic activities on this capacity and its possible consequences (Simpson *et al.*, 2008).

Due to the need for information about the early life history of fishes, several methods have been used to collect larvae and juveniles, such as plankton nets (Severi *et al.*, 2008; Marcolin *et al.*, 2010), trawl nets (Choat *et al.*, 1993) and plankton pumps (Taggart & Leggett, 1984; Brander & Thompson, 1989). As many larvae are attracted by light, light traps to capture settlement stage larvae have been adapted and employed in the marine environment since the 1980s (Doherty, 1987; Choat *et al.*, 1993; Brogan, 1994; Doherty & Carleton, 1997; Reyns & Sponaugle, 1999; Hendriks *et al.*, 2001). Light traps are considered to be efficient in sampling most coastal fish families (Lecaillon & Lourié, 2007), particularly post-larval reef fishes (Doherty, 1987), because they exploit the positive response of mature larvae to light (phototaxis). Thus light traps are favored over other methods (Choat *et al.*, 1993; Milicich & Doherty, 1994; Wilson, 2001).

Surveys using light traps have already been performed in various types of habitats and regions of the world, such as the Great Barrier Reef (Doherty, 1987; Milicich & Doherty, 1994; Fisher & Bellwood, 2002), Caribbean (Wilson, 2001), New Zealand (Hickford & Schiel, 1999), coast of California (Steele *et al.*, 2002), Mediterranean Sea (Felix-Hackradt *et al.*, 2013) and Africa (Valles *et al.*, 2001). However, in Brazil, most studies on marine fish larvae have used plankton nets and have focused on estuarine habitats (Ekau *et al.*, 1999; Severi *et al.*, 2008; Marcolin *et al.*, 2010; Souza *et al.*, 2010; Dantas *et al.*, 2013; Marques *et al.*, 2015). Thus the composition of settlement stage larval reef fish assemblages remains poorly known.

The aim of the present work is to provide the first checklist of post-larval reef fishes caught by light traps in the Tamandaré Reefs, Northeast Brazil. Information on abundance, taxonomic composition, occurrence and suitability of light traps for different taxa are also provided. This is the first study to use light traps to sample post-larval reef fishes along the Tropical south-west Atlantic coast.

2.4 Material and methods

2.4.1 Study area and sample design

The study was carried in the Bay of Tamandaré, Pernambuco State, Tropical Southwestern Atlantic. Sampling was performed within the boundaries of three Marine Protected Areas (MPAs): the Coral Coast Environmental Protection Area (APA), the Guadalupe State MPA (both multiple use MPAs), and the Tamandaré Fortress Municipal Park

(no-take zone), Northeast Brazil (Fig. 1). The climate in the region is tropical, with air temperatures varying between 25 and 30° C ('As' in the Köppen system). The rainfall is interspersed between rainy (May to September) and dry (October to May) seasons (Maida & Ferreira, 1997), with prevailing SE and NE winds respectively (Lira & Fonseca-Genevois, 1998).

The area is characterized by a mosaic of coastal ecosystems that include estuaries with mangroves, seagrass meadows and a coral reef complex with reef formations arranged parallel to the coast (Maida & Ferreira, 1997; Ferreira & Maida, 2006), with influences from nearby rivers such as the Mamucabas, Formoso and Ilhetas. These rivers deliver suspended solids and reduce salinity, especially in the rainy season (Lira & Fonseca-Genevois, 1998).

The continental shelf is predominantly carbonate, with reef formations distributed along a depth gradient shaped by fluctuating sea levels (Camargo *et al.*, 2015). Several commercially important species are distributed across the shelf, occupying different habitats according to the phases of their life cycle (Frédou & Ferreira, 2005).

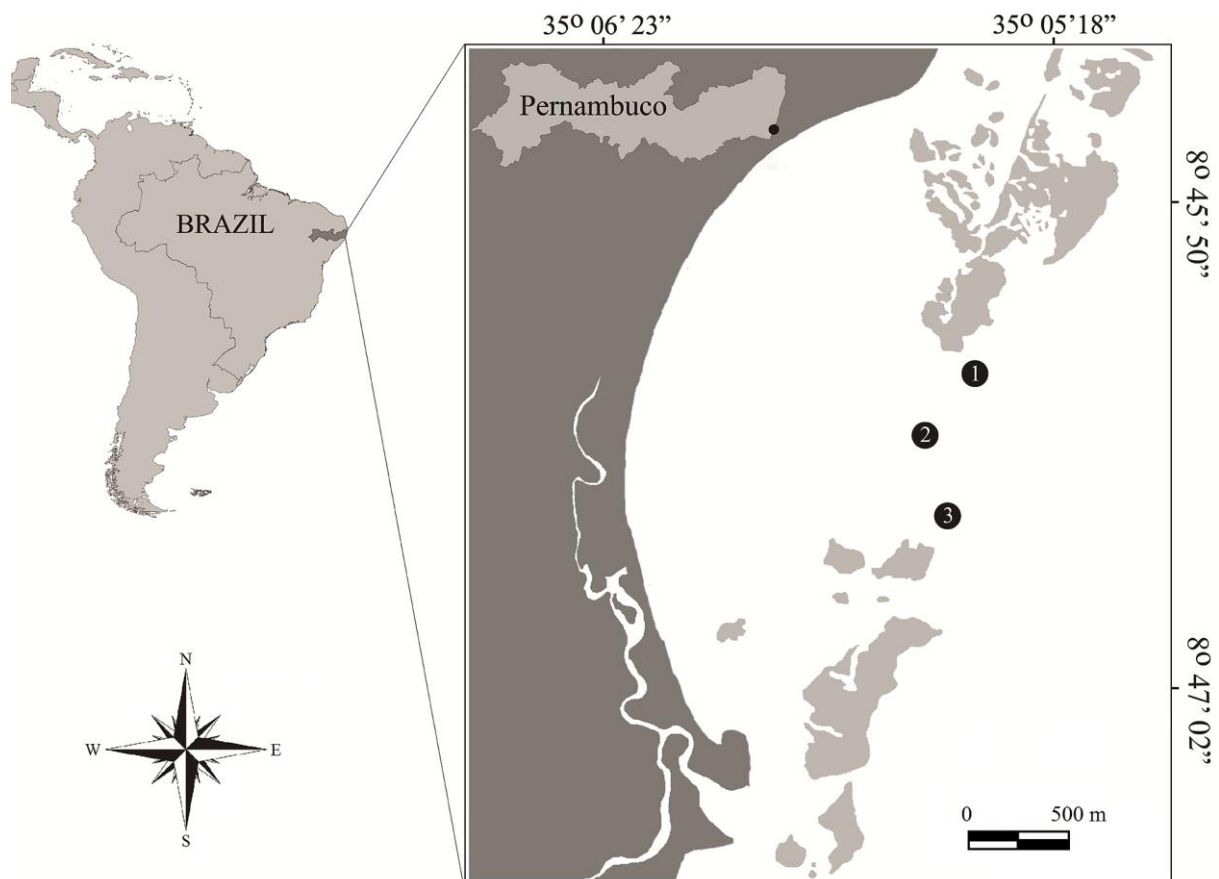


Fig. 1. Map of the study area, showing light trap deployment sites 1, 2 and 3 in Tamandaré Bay, Northeast Brazil.

2.4.2 Collection procedure

Post-larval fishes were collected monthly from January 2011 to April 2016, using CARE® model light traps ("Capture by Artificial Reef Eco-friendly"; ECOCEAN, Montpellier, France). These devices have been previously used to effectively sample several families of reef fishes immediately prior to settlement both in the Mediterranean and Pacific Oceans (Carassou & Ponton, 2007; Félix-Hackradt *et al.*, 2013; Catalán *et al.*, 2014). Each CARE® trap consisted of a buoyant water-tight block containing a 12 V battery and a 55 W 90 LED light, under which a 2 m conical net of 2 mm mesh size with a narrow mesh funnel in the middle was attached vertically (Lecaillon, 2004).

Three light traps were fixed transversely to the navigational access channel of the Tamandaré Bay, in depths ranging from 10 to 12 m. Traps were located outside the last reef barrier at least 200 m away from the reef systems and from each other (Fig. 1). The traps were anchored and maintained vertical using buoys. Each month, traps were installed after dusk for three consecutive days during the new moon period, remaining one meter beneath the surface for approximately 10–12 h each. Sampling was only carried out in the region near the surface, since most post-larval reef fish taxa aggregate on the surface during the nocturnal period to feed (Haney, 1988; Leis, 1991). The new moon period was chosen because moonlight is at its minimum and catch efficiency is higher (Wilson & Meekan, 2001; D'alessandro *et al.*, 2007), with previous studies showing higher catches of post-larvae in days around the new moon (Milicich, 1994; D'Alessandro *et al.*, 2007). During this period, sampling was carried out for a total of 155 days, as some days were cancelled due to bad wind and/or rough seas. This resulted in a total of 465 samples (catch/trap/night), with 40 samples discarded due to mechanical failures (light off, floater or anchoring problems).

Collected post-larvae were transported in aerated buckets, transferred to tanks or aquaria and kept alive for photographic records. In order to solve identification problems, individuals of some taxa were photographed, measured at the time of capture and kept in closed-circulation aquaria with submerged filters until the meristic traits and pigmentation developed with growth, thus allowing them to be identified.

Individuals were subsequently sacrificed by immersing in ice water slush for at least 5 minutes to ensure their death before processing. This procedure is widely used and considered as adequate to minimize the suffering of individuals (McCormick, 2016). After death, the individuals were transferred to vials and preserved in 70% alcohol for further refinement of taxonomic identification. A voucher of each species was selected for deposit at the

ichthyological collection of the Federal University of Pernambuco (UFPE) Oceanographic Museum.

In the laboratory, post-larvae were separated into large taxonomic groups and individuals were measured to the nearest 0.01 cm total length (L_T) and identified at the lowest possible taxonomic level using various published identification keys (Fahay, 1983; Menezes & Figueiredo, 2000; Carpenter & Niem, 2001; Richards, 2005). Identification to the species level was not possible for a total of 78 post-larval and juvenile fish (1.86% of all collected individuals) because they were damaged or lacked characteristics allowing their placement within any of the identified groups.

We examined post-larval reef fish species richness and sampling effort using a species accumulation curve with a non-parametric bootstrap (Smith & van Belle, 1984) to assess whether the post-larval reef fish community was sufficiently sampled. This method assumes that all species occur randomly, without taking into account species abundance. The index and standard deviations of the estimates were obtained through the analytical equation of Colwell *et al.* (2004) using the EstimateS software (Colwell, 2013). Rank-abundance curves were generated using species-specific values for each post-larval reef fish (Whittaker, 1972). A higher slope in a log-transformed rank-production curve indicated that fewer species dominated total assemblage-wide production compared to an assemblage curve with a shallower slope. We also evaluated the number of families and species and the percentage similarity between this collection of post-larvae and previous works in the study area focusing on adult fishes (Ferreira *et al.*, 1995; Ferreira & Cava, 2001; Araújo *et al.*, 2004; Paiva *et al.*, 2009; Pereira *et al.*, 2014).

The definition of reef fish followed Bellwood & Wainwright (2002), where: "reef fish refers to those taxa that are found on, and are characteristic of, coral reefs (*i.e.*, the consensus list *sensu* Bellwood, 1998; plus taxa characteristic of reefs in specific areas)". Clupeidae, Engraulidae and Atherinidae fishes were very abundant in the capture. These families represented, in term of numbers, approximately 81% of the total catch between January 2015 and April 2016 (reference sample year established for calculations), but were removed from analyses due to their lack of direct association with reef habitat.

2.5 Results

2.5.1 Taxonomic composition

In total, 425 light trap catches (trap.night⁻¹) were obtained from January 2011 to April 2016, from which 4,422 post-larval fishes were collected corresponding to 36 families, 56

genera and 76 species (Table I and Supporting Information Figures S1-S72). Of these, Carangidae (7), Lutjanidae (6) and Pomacentridae (4) presented the highest number of species per family (Fig. 2) (Table I and Supporting Information Figures S1-S72).

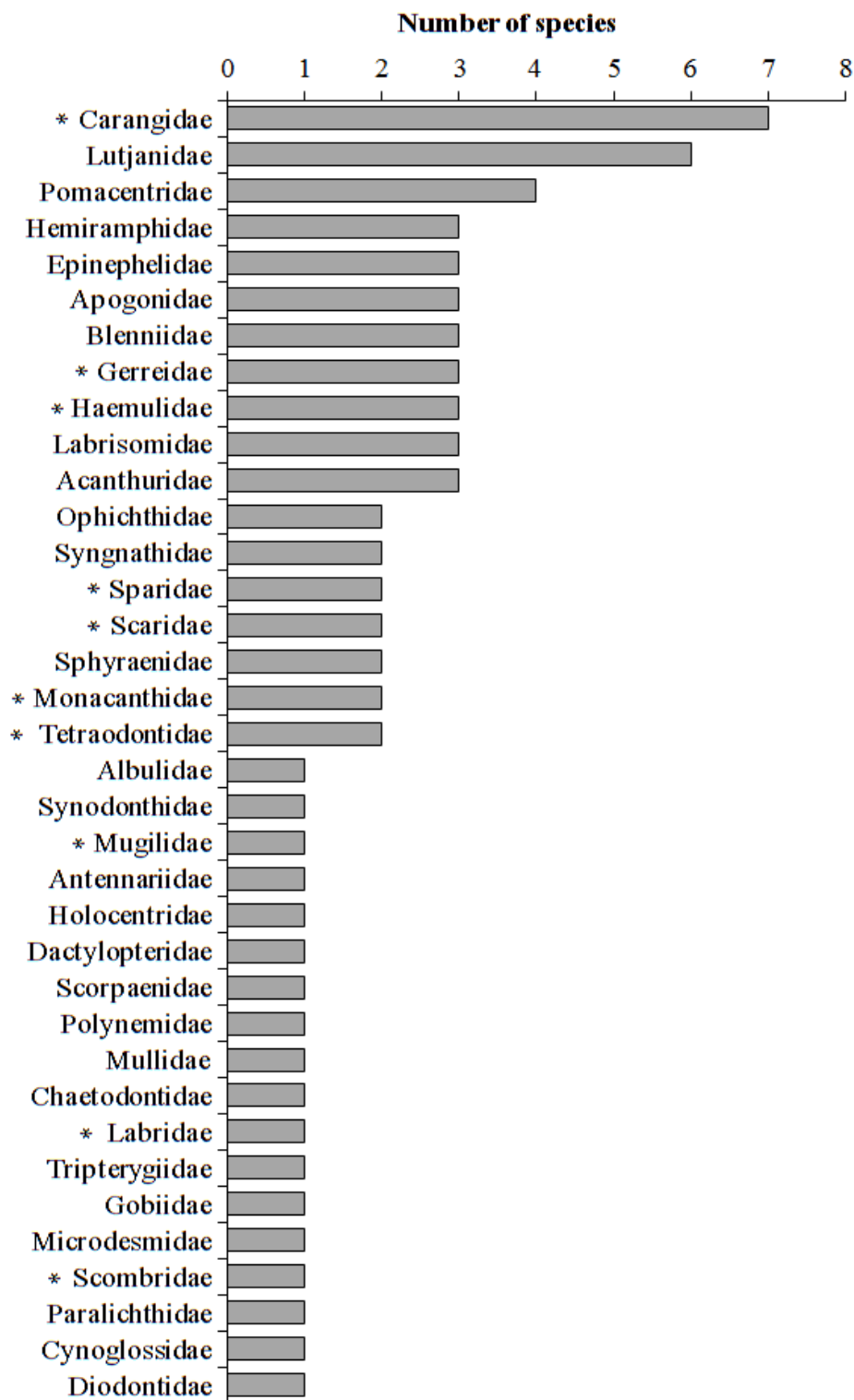


Fig. 2. Number of species per family recorded in light trap collections in Tamandaré Bay, Pernambuco, Brazil. (*) Families with additional unidentified individuals at the species level.

Table I. Composition, month of occurrence, and relative abundance of late-stage reef fish larvae caught by light traps, with comments on species' time of reproduction (months or seasons) in South and North Atlantic Oceans. Abbreviations: Spr = spring, Sum = summer, Aut = autumn, Win = winter, F.O. = frequency of occurrence, R.A. = relative abundance (%).

Family / species	F.O.	R.A.	Capture	Reproduction		Reference
				South Atlantic	North Atlantic	
Albulidae						
<i>Albula vulpes</i>	5.92	0.23	Oct-Mar	Unknown	Nov-Jun (Aut-Spr) ^a	^a (Crabtree <i>et al.</i> , 1997)
Ophichthidae						
<i>Myrichthys ocellatus</i>	1.32	0.05	Jan	Unknown	Unknown	
<i>Myrophis punctatus</i>	0.66	0.02	Sep	Unknown	Unknown	
Synodontidae						
<i>Synodus</i> spp.	2.63	0.09	Mar-Apr	Unknown	<i>S. intermedius</i> April (Spr) ^a	^a (Munro <i>et al.</i> , 1973)
Mugilidae						
<i>Mugil</i> spp.	11.18	0.81	Jan-Oct	-	-	
Antennariidae						
<i>Histrio histrio</i>	0.66	0.02	Mar	Unknown	Unknown	
Hemiramphidae						
<i>Hemiramphus brasiliensis</i>	1.32	0.05	Feb, Mar	Jan-Dec (peak Apr) ^a Jan-Jun (Sum-Aut) ^b	Jan-Dec ^c	^a (Oliveira & Chellappa, 2014) ^b (Oliveira <i>et al.</i> , 2015) ^c (McBride & Thurman, 2003)
<i>Hyporhamphus roberti</i>	1.97	0.08	Feb, Apr, May	Unknown	Unknown	
<i>Hyporhamphus unifasciatus</i>	4.61	0.21	Oct- May	Unknown	Unknown	
Holocentridae						
<i>Holocentrus adscensionis</i>	33.55	16.54	Sep-Apr	Oct-Mar (Spr-Sum) ^a	Unknown	^a (Shinozaki-Mendes <i>et al.</i> , 2007)
Syngnathidae						
<i>Bryx dunckeri</i>	1.32	0.05	Jan, Feb	Unknown	Unknown	
<i>Hippocampus reidi</i>	0.66	0.02	Jun	Jan-Dec ^a	Unknown	^a (Freret-Meurer & Andreatta, 2008)

Family / species	F.O.	R.A.	Capture	Reproduction		Reference
				South Atlantic	North Atlantic	
Dactylopteridae						
<i>Dactylopterus volitans</i>	0.66	0.02	Jun	Unknown	Unknown	
Scorpaenidae						
<i>Scorpaena</i> spp.	0.66	0.02	Mar	-	-	
Epinephelidae						
<i>Alphestes afer</i>	1.97	0.07	Oct, Dec	Aug-Dec (Win-Spr) ^a	Unknown	^a (Marques & Ferreira, 2011)
<i>Epinephelus adscensionis</i>	1.97	0.09	Oct	Jun-Nov (Aut-Spr) ^a	Unknown	^a (Marques, 2011)
<i>Mycteroperca bonaci</i>	1.97	0.07	Sep, Oct	Apr-Sep (Aut-Win) ^a	Unknown	^a (Teixeira <i>et al.</i> , 2004)
Apogonidae						
<i>Apogon americanus</i>	5.26	0.21	Jan-Mar	Unknown	Unknown	
<i>Astrapogon puncticulatus</i>	1.97	0.12	Dec-Mar	Unknown	Unknown	
<i>Phaeoptyx pigmentaria</i>	1.97	0.09	Jan-Feb, Apr	Unknown	Unknown	
Carangidae						
<i>Carangoides bartholomaei</i>	9.87	0.91	Jan-Dec	Sep-Mar (Aut-Sum) ^a	Unknown	^a (Santos, 2012)
<i>Caranx crysos</i>	10.53	1.43	Dec-May	Unknown	Jan, Aug (Win, Sum) ^a	^a (Smith, 1997)
<i>Caranx hippos</i>	1.97	0.19	Jan, Apr May	Unknown	Feb-Oct (Win- Aut) ^a	^a (Smith, 1997)
<i>Caranx latus</i>	1.97	0.12	Jan-Feb	Unknown	Unknown	
<i>Caranx ruber</i>	2.63	0.12	Jan-Mar	Unknown	Unknown	
<i>Chloroscombrus chrysurus</i>	26.97	1.95	Jan-Oct	Unknown	Unknown	
<i>Seriola rivoliana</i>	1.32	0.05	Jan,Mar			
Lutjanidae						
<i>Lutjanus alexandrei</i>	16.45	0.79	Oct-May	Nov-Mar (Spr-Sum) ^a	-	^a (Fernandes <i>et al.</i> , 2012)
<i>Lutjanus analis</i>	23.68	1.66	Sep-May	Nov-Apr (Spr-Aut) ^a	May-Aug (Spr-Sum) ^b	^a (Teixeira <i>et al.</i> , 2010) ^b (Burton <i>et al.</i> , 2005)
<i>Lutjanus cyanopterus</i>	1.32	0.05	Nov, Apr	Dec-Apr (Unp. Data)	Apr-Jun (Spr) ^a May-Aug (Spr-Sum) ^b Jun-Sep (Spr-Sum) ^c	^a (Heyman <i>et al.</i> , 2005) ^b (Claro & Lindeman, 2003) ^c (Lindeman <i>et al.</i> , 2000)

Family / species	F.O.	R.A.	Capture	Reproduction		Reference
				South Atlantic	North Atlantic	
<i>Lutjanus jocu</i>	17.11	1.25	Oct-Jun	Jun-Oct (Win-Spr) ^a	Jul (Sum) ^b Apr-Mai (Spr) ^c Feb-Mar(Win) ^d	^a (Freitas <i>et al.</i> , 2011) ^b (Domeier & Colin, 1997) ^c (Heyman <i>et al.</i> , 2001) ^d (Kadison <i>et al.</i> , 2006)
<i>Lutjanus synagris</i>	26.32	3.73	Oct-May	Sep-Mar (Spr-Sum) ^a Aug-Mar (Spr-Sum) ^b	May-Sep (Spr-Sum) ^c Aug-Nov(Sum-Aut) ^d	^a (Freitas <i>et al.</i> , 2011) ^b (Freitas <i>et al.</i> , 2014) ^c (Luckhurst <i>et al.</i> , 2000) ^d (Gómez <i>et al.</i> , 2001)
<i>Ocyurus chrysurus</i>	11.18	0.81	Dec-May	Aug-Oct (Win-Spr) ^a	Mar-Sep (Win-Sum) ^b	^a (Freitas <i>et al.</i> , 2011) ^b (Domeier <i>et al.</i> , 1996)
Gerreidae						
<i>Eucinostomus</i> spp.	72.37	30.47	Jan-Dec	-	-	
<i>Eucinostomus melanopterus</i>						
<i>Ulaema lefroyi</i>						
<i>Diapterus auratus</i>	0.66	0.02	Mar			
Haemulidae						
<i>Anisotremus surinamensis</i>	1.32	0.05	Mar	Unknown	Unknown	
<i>Haemulon aurolineatum</i>	0.66	0.02	May	Unknown	Unknown	
<i>Haemulon parra</i>	8.55	0.54	Nov-Jun	Unknown	Unknown	
Sparidae						
<i>Archosargus</i> spp.	0.66	0.02	Dec	-	-	
<i>Calamus</i> spp.	0.66	0.02	Nov	-	-	
Polynemidae						
<i>Polydactylus virginicus</i>	18.42	3.24	Jan-Dec	Jan-Dec ^a	Unknown	^a (Motomura, 2004)
Mullidae						
<i>Pseudupeneus maculatus</i>	2.63	0.21	Nov-Mar	Unknown	Unknown	
Chaetodontidae						
<i>Chaetodon striatus</i>	1.97	0.29	Oct-Dec	Unknown	Unknown	
Pomacentridae						
<i>Abudefduf saxatilis</i>	9.87	0.49	Nov-Jun	Nov-Feb (Spr-Sum) ^a	Unknown	^a (Bessa <i>et al.</i> , 2007)

Family / species	F.O.	R.A.	Capture	Reproduction		Reference
				South Atlantic	North Atlantic	
<i>Microspathodon chrysurus</i>	0.66	0.02	Mar	Unknown	Jan-Dec ^a	^a (Robertson, 1990)
<i>Stegastes fuscus</i>	1.97	0.09	Oct-Dec	Jan, Sep-Oct (Sum, Win-Spr) ^a	Unknown	^a (Canan <i>et al.</i> , 2011)
<i>Stegastes variabilis</i>	26.97	2.61	Jan-Dec	Oct-Jan (Spr-Sum) ^a	Unknown	^a (Bessa <i>et al.</i> , 2007)
Labridae						
<i>Halichoeres</i> spp	7.89	0.44	Oct-Jun			
Labridae - Scarinae						
Scaridae spp.	0.66	0.02	Sep			
<i>Sparisoma axillare</i>	0.66	0.02	Feb	Jan-Dec ^a	Unknown	^a (Véras, 2008)
Tripterygiidae						
<i>Enneanectes altivelis</i>	5.26	0.26	Jan-Apr	Unknown	Unknown	
Labrisomidae						
<i>Labrisomus kalisherae</i>	18.42	2.35	Nov-Apr	Unknown	Unknown	
<i>Labrisomus nuchipinnis</i>	30.92	2.56	Jan-Dec	Unknown	Unknown	
<i>Malacoctenus</i> spp.	35.53	3.45	Oct-Jul			
Blenniidae						
<i>Entomacrodus vomerinus</i>	14.47	1.73	Oct-Jun	Unknown	Unknown	
<i>Hypleurochilus pseudoaequipinnis</i>	25.00	2.69	Jan-Dec	Unknown	Unknown	
<i>Ophioblennius trinitatis</i>	26.97	7.59	Oct-Jul	Unknown	Unknown	
Gobiidae						
Gobiidae spp.	0.66	0.02	Mar	-	-	
Microdesmidae						
<i>Microdesmus longipinnis</i>	1.32	0.05	Mar, Jul	Unknown	Unknown	
Acanthuridae						
<i>Acanthurus bahianus</i>	25.66	5.27	Sep-Apr	Unknown	Nov-Apr (Aut-Spr) ^a	^a (Richards, 2005)
<i>Acanthurus chirurgus</i>	1.32	0.05	Nov-Apr	Unknown	Unknown	
<i>Acanthurus coeruleus</i>	12.50	0.63	Oct-Apr	Nov-Feb (Spr-Sum) ^a	Unknown	^a (Sátyro, 2008)
Sphyraenidae						
<i>Sphyraena barracuda</i>	13.16	1.10	Jan-Apr	Unknown	Apr-Nov (Spr-Aut) ^a	^a (Kadison <i>et al.</i> , 2010)
<i>Sphyraena guachancho</i>	0.66	0.02	Jan	Unknown	Unknown	
Scombridae						

Family / species	F.O.	R.A.	Capture	Reproduction		Reference
				South Atlantic	North Atlantic	
<i>Scomberomorus brasiliensis</i>	5.26	0.27	Jan-Jun	Unknown	Unknown	
Paralichthyidae						
<i>Citharichthys</i> spp.	0.66	0.02	Apr	-	-	
Cynoglossidae						
<i>Symphurus</i> spp.	0.66	0.02	Jan, Apr	-	-	
Monacanthidae						
<i>Cantherhines pullus</i>	1.32	0.05	Dec	Unknown	Unknown	
<i>Stephanolepis hispidus</i>	3.29	0.28	Dec-Jan	Unknown	May-Oct (Spr-Aut) ^a	^a (Mancera-Rodríguez & Castro-Hernández, 2015)
Tetraodontidae						
<i>Sphoeroides</i> spp.	2.63	0.16	Jan, Mar	-	-	
<i>Sphoeroides greeleyi</i>	0.66	0.02	Mar	Nov-Jan (Spr-Sum) ^a	Unknown	^a (Schultz <i>et al.</i> , 2002)
<i>Sphoeroides testudineus</i>	1.32	0.05	Jan	Oct-Jan (Spr-Sum) ^a	Unknown	^a (Rocha <i>et al.</i> , 2002)
Diodontidae						
<i>Diodon hystrix</i>	0.66	0.02	Jan	Unknown	Unknown	

The species accumulation curve did not reach an asymptote, due to the regular collection of rare species (Fig. 3). A bootstrap index was calculated indicating that the total number of species in the area would stabilize at about 86 species. Most common taxa present and susceptible to be captured by the gear were represented, indicating that both the light trap method and the sampling period length were sufficient to form a representative collection of post-larval and juvenile reef fishes for the study area.

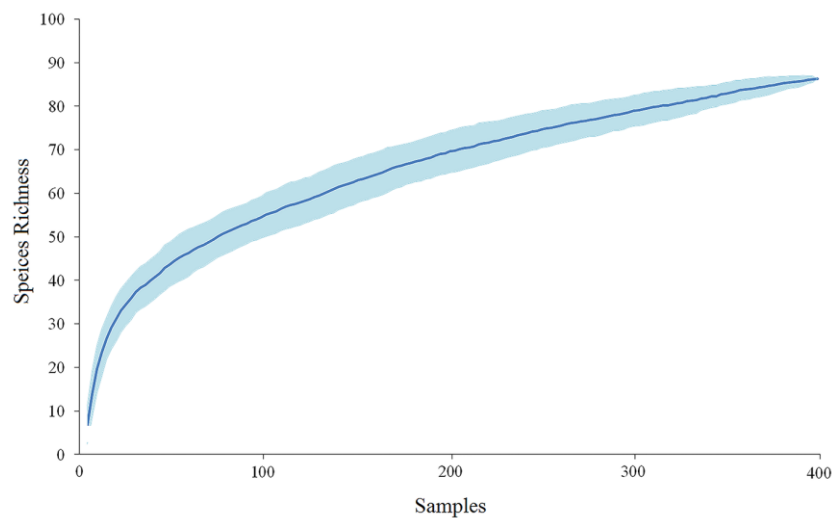


Fig. 3. Species accumulation curve for the study area, generated by non-parametric bootstrap. Mean species value $\pm$ 95% confidence interval.

The families Gerreidae (30.47% of individuals caught), Holocentridae (16.54%), Blenniidae (12.01%), Labrisomidae (8.36%), Lutjanidae (8.29%), Acanthuridae (5.95%), Carangidae (4.77%), Pomacentridae (3.21%), Polynemidae (3.24%) and Sphyraenidae (1.12%) had the highest relative abundances, comprising more than 90% of captured reef fishes (Table I). At the species level, species of the family Gerreidae (30.47%), *Holocentrus adscensionis* (Osbeck 1795) (16.54%), *Ophioblennius trinitatis* Miranda Ribeiro 1919 (7.59%), *Acanthurus bahianus* Castelnau 1855 (5.27%), *Lutjanus synagris* (Linnaeus 1758) (3.73%), *Malacoctenus* spp. (3.45%), *Stegastes variabilis* (Castelnau 1855) (2.61%), *Labrisomus nuchipinnis* (Quoy & Gaimard 1824) (2.56%) and *Polydactylus virginicus* (Linnaeus 1758) (3.24%) represented 75% of the total (Table I). Some species were notable for their high frequency of occurrence, such as gerreids (*Eucinostomus* spp., *Ulaema* spp.), *Malacoctenus* spp., *Labrisomus nuchipinnis*, *Stegastes variabilis* and *Hyppleurochilus pseudoaequipinnis* Bath 1994.

The rank-abundance curve showed a pattern of few species with high abundance and many rare species (Fig. 4). Approximately 80% of post-larval fish species constituted less than 1% of the total number of individuals sampled.

Correspondence of families and species between the present pre-settlement larvae collection and checklists available for the area (underwater visual census observations and fish landings) was higher for reef fishes than for estuarine fishes (Table II). Similarity with reef fish lists was approximately 60% for families and 50% for species, while for estuarine fishes it ranged from 40 to 60% (Table II).

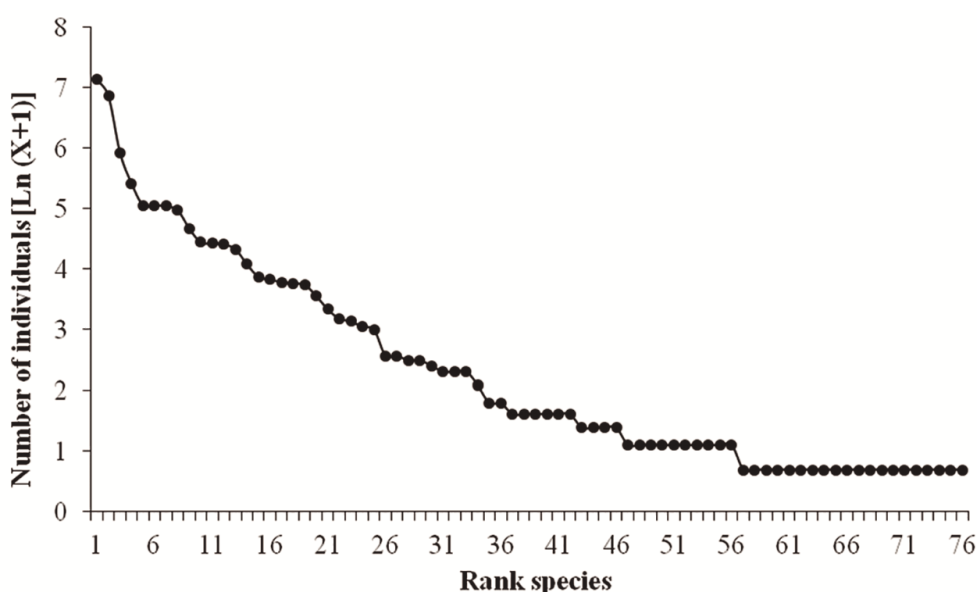


Fig. 4. Rank-abundance curve of each post-larval reef fish taxon between January 2011 and April 2016. The log-transformed abundance is represented on the y-axis, while species are ranked in decreasing abundance order on the x-axis.

Table II. Number of families and species reported in checklists available for the study area and their percentage similarity with taxa collected in the present study.

	Ferreira <i>et al.</i> , 1995	Ferreira and Cava, 2001	Araujo <i>et al.</i> , 2004	Paiva <i>et al.</i> , 2009	Pereira <i>et al.</i> , 2014
Nº of families	40	47	36	39	29
Nº of species	94	149	92	78	59
Percentage similarity					
Family	69.23%	64.15%	63.89%	64.11%	72.42%
Species	51.07%	44.96%	26.03%	43.60%	50.10%

2.5.2 Sizes of pre-settlement fish

The post-larval reef fishes caught by the light trap had an average size of 38.5 ± 24.8 mm total length (L_T), with individuals measuring 10 to 20 mm L_T among the most abundant (approximately 50%). The largest specimen captured was a post-larva of *Myrichthys ocellatus* (Lesueur 1825) (Ophichthidae) measuring 190.2 mm L_T , and the smallest specimen, with 4.7 mm L_T , belonged to the family Tetraodontidae.

Among species belonging to the family Gerreidae, the average size of the post-larvae was 13.68 ± 1.58 mm L_T , while for the pomacentrids it was 14.53 ± 1.45 mm L_T . For both families, most specimens measured between 10 and 15 mm L_T (84% of Gerreidae and 73% of Pomacentridae). Pre-settlers of *Holocentrus adscensionis* – one of the most abundant species – had the highest average size (73.14 ± 5.60 mm L_T), with most individuals measuring between 65 to 80 mm L_T (83%).

Labrisomids and lutjanids measured an average of 18.66 ± 2.78 mm and 21.69 ± 2.20 mm L_T , respectively, with most individuals ranging 15 to 25 mm L_T (96% of Labrisomidae and 95% of Lutjanidae). The average size of blennids was 35.60 ± 14.57 mm L_T , presenting high amplitude due to the difference in size between the species *Ophioblennius trinitatis* and *Hypleurochilus pseudoaequipinnis*: while the specimens of *O. trinitatis* had common sizes of 40 to 50 mm L_T (96%), *H. pseudoaequipinnis* varied in size from 10 to 15 mm L_T (92%). For the Acanthuridae, the mean size was 36.90 ± 3.04 mm L_T , with a predominance of individuals between 30 and 40 mm L_T (86%). The carangids, with a mean size of 32.46 ± 25.42 mm L_T , had the largest size range, recording individuals ranging from 7.78 to 161 mm L_T (Fig. 5).

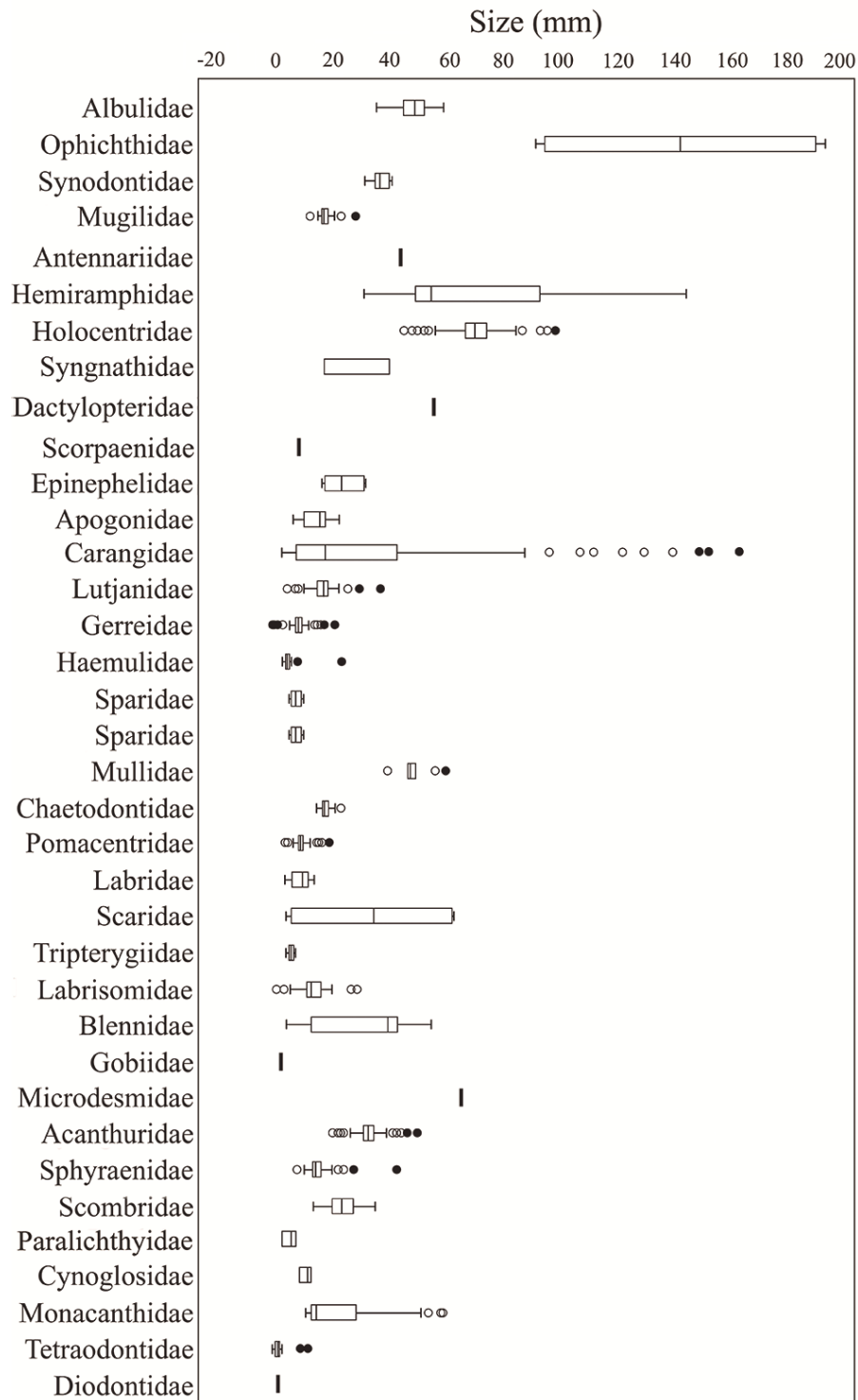


Fig. 5. Ranges of body size (L_T) for each family sampled in this study. Inner line in a box corresponds to the mean value; the lower and upper limits correspond to 25% and 75% percentiles; whiskers represent non-outlier variation; blank circles correspond to outliers (more than 1.5 times the interquartile range) while black circles correspond to far outliers (more than 2 times the outlier variation).

2.6 Discussion

Light traps are considered to be an effective tool in sampling late-stage larvae that are established in coral reefs (Milicich *et al.*, 1992; Valles *et al.*, 2001; Wilson, 2001; D'Alessandro *et al.*, 2007), even though the abundance of early larval stages and the sampling of some species may be underestimated due to their lack of phototaxis (Hickford & Schiel, 1999; Chícharo *et al.*, 2009).

In the present work, the composition of post-larval reef fishes collected by light traps was similar to the reef fish fauna known to be present in the region, even though some species were absent or rare in the collection. In fact, this may also reflect a common pattern among reef fishes, as most communities contain many more rare species than common ones (Jones *et al.*, 2002). In spite of the great diversity, post-larval reef fishes are much less abundant than other components of the zooplankton (Sale, 1991). Some factors are fundamental to explain this low abundance, such as recruitment limitation, geographical restriction and three-dimensional distribution (Sale, 1991; Gaston, 1994, 1998).

The diversity of fishes collected in this study suggest that light traps are quite useful in studies on the early history of most reef fishes, confirming the assumption that light traps are capable of capturing a large number of many different fish species at the pre-settlement stage (Doherty, 1987; Milicich, 1992). Species that exhibit notably cryptic behavior during the juvenile phase, such as the labrisomids *Malacoctenus* spp. and *Labrisomus* spp., and the blennids *O. trinitatis* and *H. pseudoaequipinnis*, had a high frequency of occurrence in the samples. This study's capture of *H. pseudoaequipinnis* post-larvae represented the first record for this species in the region. Its absence in previous works (Ferreira *et al.*, 1995; Ferreira & Cava, 2001) can be attributed to both its small size and to its habits, as this species inhabits oyster-covered mangrove roots during its adult phase (Humann & Deloach, 2002). Pelagic larvae, however, often have a wider range of occurrence, so both its capture as a larva and abundance in the sample indicate dispersal from estuaries to shallow platforms. This also might be the case for the wormfish *Microdesmus longipinnis* (Weymouth, 1910): with only two individuals collected, the species had previously only been observed in estuarine areas (Severi *et al.*, 2008).

Dominance of the family Gerreidae seems to be related to local estuarine influence in the sample area. Gerreidae is composed of marine migrants to estuaries with high tolerance for variable salinity, and is one of the most abundant in coastal ecosystems of Northeast Brazil (Vieira, 1991), including the nearby estuarine complex of the Formoso River (Paiva *et al.*, 2009; Merigot *et al.*, 2016; Silva-Junior *et al.*, 2016). Gerreid dominance in nearby

estuaries has been attributed to their connectivity with other coastal habitats (Mérigot *et al.*, 2016). The continuous occurrence of gerreid larvae throughout the year, with records in all months, is due to the long spawning periods reported for gerreid species (Cyrus & Blaber, 1984; Sarre *et al.*, 1997). As identification at the species level was not possible due to overlapping meristic ranges, it is also possible that the long recruitment period was created by successive recruitment pulses of different species within the family.

Some fish species that are abundant and commonly found in the reef areas of Tamandaré were rare or absent in the samples of the present study. Susceptibility of post-larvae to our sample gear depends on phototaxis which, although common, is not observed in all species (Grorud-Colvert & Sponaugle, 2009). The behavioral response of individuals to light may also change during the ontogeny of the species and consequently vary according to their size (Bulkowski & Meade, 1983; Murphy & Willis, 1996). In addition, other correlated parameters may affect the susceptibility of post-larvae to capture, such as how a species is dispersed throughout the water column and how good they are at swimming (Murphy & Willis, 1996; Leis, 1991). Thus, abundance and frequency of post-larvae are not always representative of the relative abundances and frequency of adults in the natural environment (Leis & Goldman, 1987) due to the biases and selectivity of light traps (Doherty, 1987; Thorrold, 1992; Choat *et al.*, 1993).

Rarity in light traps is a pattern that has previously been demonstrated for several species that are negatively phototactic, substrate associated, or poor swimmers (Sponaugle & Cowen, 1996; Wilson, 2001; Watson & Munro, 2004; Grorud-Colvert & Sponaugle, 2009). One example is the labrid *Halichoeres* spp. Labrid larvae tend to remain close to the substrate (Vitor, 1983; Sponaugle & Cowen, 1996), and to not be phototactic (Grorud-Colvert & Sponaugle, 2009). Haemulidae is another group that is quite common in reefs, but were rare in our collections, a pattern also observed in other studies (Riley & Holt, 1993). This is likely due to their short larval life cycle (Purcell *et al.*, 2009) and short-range larval dispersal.

The low occurrence of the pomacentrid *Stegastes fuscus* (Cuvier 1830) in relation to its abundance in coastal reefs (Ferreira *et al.*, 1995; Ferreira & Cava, 2001; Pereira *et al.*, 2014) was quite surprising, since pomacentrids are known to be susceptible to light traps (Doherty, 1987). Moreover, post-larvae of the congener *Stegastes variabilis* were common in the samples, as well as larvae of other pomacentrid species. One possible explanation is that differences in the distribution patterns of adult populations of the two species may have caused their apparently differing susceptibility: while *S. fuscus* is the dominant species in the inner reef, *S. variabilis* is more abundant in the exposed front reef areas (BPF pers. obs.).

Therefore, it is possible that after hatching of demersal eggs, there is considerable larval retention within the coastal lagoon. Although speculative at the moment, this is corroborated by the observation made by Daros *et al.* (2016), who analyzed the chemical composition of otoliths of *S. fuscus* and established spatial signatures corresponding to fine scale stratification.

Overall, most larvae collected in this study were in the last larval stage that precedes their settlement, with most of them already having their juvenile coloration. In many cases fishes rapidly acquired their juvenile coloration after only a few minutes or hours in captivity. The majority of captured individuals ($n = 2,693$) were 10 to 20 mm L_T . For some families such as Carangidae, the broad size range of captured individuals can be explained by their positive phototaxis and pelagic life history (Catalán *et al.*, 2014), which does not include a clear division between pelagic and demersal phases. Therefore, as carangids are both pelagic and reef-associated as adults, maximum size and capture may be determined more by behavior (sustained attraction by light and catchability) than duration of the pre-settlement phase.

This study reported a high richness and high abundance of post-larvae from several important families of reef fishes, confirming that light traps are an effective tool for understanding the taxonomy, early life-history, assemblage structure and spatial distribution of pre-settlement fishes in the region. This is the first record of post-larval reef-associated fishes in the tropical South Atlantic using light traps, and results of the present work can be considered a baseline to understand the ecology of adult fishes both in the study area and in many other areas of the Southwestern Atlantic (Köster *et al.*, 2001; Zhou *et al.*, 2011).

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2.9 Supporting information

Annotated checklist of settlement-stage reef fish collected by light traps

Below is an annotated checklist of late-stage reef fishes collected by light traps in the Tamandaré reef system, Tropical South-West Atlantic. Families are listed phylogenetically according to Nelson (2006). Genera and species are ordered alphabetically. Annotations for each species refer to:

(1) Relative abundance, R.A. = $(Na * 100/NA)$, where Na is the total number of post-larval fish recorded for each species and NA is the total number of fishes. A species was considered abundant when the percentage catch was higher than the average total catch ($R.A > \mu R.A \text{ total}$); frequency of occurrence, F.O. = $(Ta * 100/TA)$; where Ta is the number of samples where the species occurred and TA the total number of samples, with each species classified as very frequent (> 70%), frequent (40% to 70%), common (10% to 40%), occasional (5% to 10%) and rare (<5%);

(2) Body size range (minimum and maximum L_T);

(3) Collection period;

(4) Geographical distribution: Brazil Province (Br) (according to Briggs & Bowen, 2012 and Pinheiro *et al.*, 2018), Central Atlantic (CA), Circumglobal (CG), Circumtropical (CT), East Atlantic (EA), South Western Atlantic (SW), Transatlantic (TA), Western Atlantic (WA - North Atlantic and South Atlantic), Midwest Atlantic (WC);

(5) Main habitat in the adult phase (following Richards, 2005 and Froese & Pauly, 2015);

(6) Conservation status according to the IUCN Red List and CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora): Data deficient (DD), Least concern (LC), Near threatened (NT), Vulnerable (VU), Endangered (EN) and Critically endangered (CR);

(7) Additional notes refer to the reference collection deposited at the UFPE Oceanographic Museum.

Albulidae

Albula vulpes (Linnaeus 1758)

(1) Rare post-larvae (10 individuals); (2) 42.39 - 58.5 mm L_T ; (3) Captured from October to March (2011 to 2016); (4) EA/WA; (5) Reef-associated and estuarine; (6) NT; (7) MOICT0001051; (Fig. S1).



Fig. S1. *Albula vulpes*

Ophichthidae

Myrichthys ocellatus (Lesueur 1825)

(1) Rare post-larvae (2 individuals); (2) 99.41 - 190.2 mm L_T ; (3) Captured in January of 2014 and 2015; (4) WA; (5) Reef-associated; (6) LC; (7) MOICT0001019; (Fig. S2).



Fig. S2. *Myrichthys ocellatus*

Myrophis punctatus Lütken 1852

(1) Rare post-larvae (1 individual); (2) 42.39 - 58.5 mm L_T ; (3) Captured in September of 2014; (4) WA; (5) Inhabits beds of seaweed, mangroves and offshore reefs; (6) LC; (7) MOICT0001003; (Fig. S3).



Fig. S3. *Myrophis punctatus*

Synodontidae

Synodus spp.

(1) Rare post-larvae (4 individuals); (2) 35.9 - 44.13 mm L_T ; (3) Captured in March of 2013, 2016 and April of 2015, 2016; (4) WA; (5) Inhabits sandbanks or consolidated substrates near reefs; (6) LC; (7) MOICT0001073; (Fig. S4). Note: due to overlapping of meristic characters, the species could be either *Synodus intermedius* (Spix 1829) or *Synodus foetens* (Linnaeus 1766).



Fig. S4. *Synodus* sp.

Mugilidae

Mugil spp.

(1) Occasional post-larvae (34 individuals); (2) 17.7 - 32.7 mm L_T ; (3) Captured from January to October (2012 to 2015), with peaks in June to September (67.7%); (4) WA (*Mugil liza* Valenciennes 1836) and WA/EA/EP (*Mugil curema* Valenciennes 1836); (5) Inhabit coastal marine waters and estuaries; (6) DD (*M.*

liza), LC (*M. curema*); (7) MOICT0001045; (Fig. S5). Note: due to overlapping in the meristic characters, the species could be one of the six species that occurring in the area (see Menezes *et al.*, 2015).



Fig. S5. *Mugil* sp.

Antennariidae

Histrion histrio (Linnaeus 1758)

(1) Rare post-larvae (1 individual); (2) 48.06 mm L_T ; (3) Captured in March 2011; (4) CT; (5) Associated with reefs and usually found under floating objects; (6) LC; (7) MOICT0001008; (Fig. S6).



Fig. S6. *Histrion histrio*

Hemiramphidae

Hemiramphus brasiliensis (Linnaeus 1758)

(1) Rare post-larvae (2 individuals); (2) 52.57 and 57.24 mm L_T ; (3) Captured in February of 2012 and March of 2015; (4) WA/EA; (5) Coastal species, associated to

seagrass; (6) LC; (7) MOICT0001021; (Fig. S7).



Fig. S7. *Hemiramphus brasiliensis*

Hyporhamphus roberti (Valenciennes 1847)

(1) Rare post-larvae (3 individuals); (2) 58.32 - 103.02 mm L_T ; (3) Captured in February and April of 2012 and May of 2015; (4) WA; (5) Coastal surface species, foraging estuaries and adjacent areas; (6) LC; (7) MOICT0001061; (Fig. S8).



Fig. S8. *Hyporhamphus roberti*

Hyporhamphus unifasciatus (Ranzani 1841)

(1) Rare post-larvae (9 individuals); (2) 45.29 - 143.57 mm L_T ; (3) Captured from October to May (2013 to 2015), with peaks in December and March (67.9%); (4) WA; (5) Marine, estuarine and associated to reefs; (6) LC; (7) MOICT0001021; (Fig. S9).



Fig. S9. *Hyporhamphus unifasciatus*

Holocentridae

Holocentrus adscensionis (Osbeck 1765)

(1) Common and abundant post-larvae (959 individuals); (2) 52.08 - 74.53 mm L_T ; (3) Captured from September to April (2011 to 2016), with peaks in December and January (69.17%); (4) TA; (5) Inhabits shallow and deep reefs; (6) LC; (7) MOICT0001009; (Fig. S10).



Fig. S10. *Holocentrus adscensionis*

Syngnathidae

Bryx dunckeri (Metzelaar 1919)

(1) Rare post-larvae (2 individuals); (2) 22.17 and 44.13 mm L_T ; (3) Captured in February 2013 and January 2015; (4) BR; (5) Reef-associated and estuarine; (6) LC; (7) MOICT0001030; (Fig. S11).



Fig. S11. *Bryx dunckeri*

Hippocampus reidi Ginsburg 1933

(1) Rare post-larvae (1 individual); (2) 44.03 mm L_T ; (3) Captured in June of 2013; (4) WA; (5) Reef-associated and estuarine; (6) NT; (7) MOICT0001072; (Fig. S12).



Fig. S12. *Hippocampus reidi*

Dactylopteridae

Dactylopterus volitans (Linnaeus 1758)

(1) Rare post-larvae (1 individual); (2) 59.4 mm L_T ; (3) Captured in June of 2013; (4) WA/EA; (5) Reef-associated and estuarine, found in sandy bottoms; (6) LC; (7) MOICT0001014; (Fig. S13).



Fig. S13. *Dactylopterus volitans*

Scorpaenidae

Scorpaena spp.

(1) Rare post-larvae (1 individual); (2) 13.53 mm L_T ; (3) Captured in March 2011; (4) WA/WC; (5) Inhabits shallow reefs and rocky substrates; (6) LC; (7) MOICT0001070; (Fig. S14).

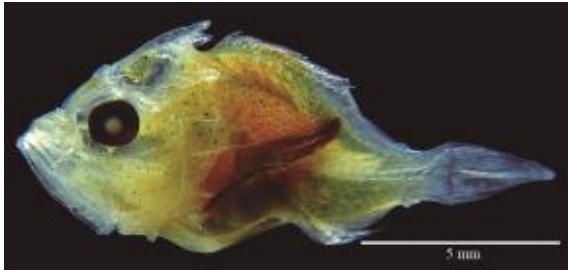


Fig. S14. *Scorpaena* sp.

Epinephelidae

Alphestes afer (Bloch 1793)

(1) Rare post-larvae (3 individuals); (2) 32.84 - 35.9 mm L_T ; (3) Captured in October and December of 2014; (4) WA; (5) Inhabits sea grass, rocky or reefs areas; (6) LC; (7) MOICT0001071; (Fig. S15



Fig. S15. *Alphestes afer*

Epinephelus adscensionis (Osbeck 1765)

(1) Rare post-larvae (4 individuals); (2) 34.43 - 38.22 mm L_T ; (3) Captured in October (2013 to 2015); (4) TA; (5) Reef-associated; (6) LC; (7) MOICT0001054; (Fig. S16).



Fig. S16. *Epinephelus adscensionis*

Mycteroperca bonaci (Poey 1860)

(1) Rare post-larvae (3 individuals); (2) 21.6 - 23.3 mm L_T ; (3) Captured in

September and October (2014 and 2015); (4) WA; (5) Reef-associated; (6) NT; (7) MOICT0001002; (Fig. S17).

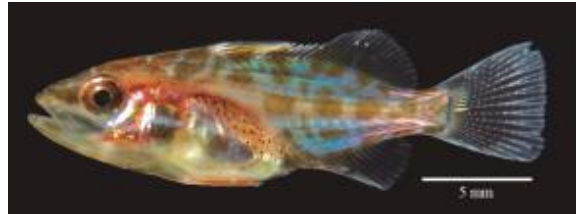


Fig. S17. *Mycteroperca bonaci*

Apogonidae

Apogon americanus Castelnau 1855

(1) Rare post-larvae (9 individuals); (2) 16.56 - 24.98 mm L_T ; (3) Captured from January to March of 2011, 2014 and 2016; (4) BR; (5) Reef and associated to consolidated substrates hiding in cracks and holes during the day; (6) DD; (7) MOICT0001035; (Fig. S18).



Fig. S18. *Apogon americanus*

Astrapogon puncticulatus (Poey 1867)

(1) Rare post-larvae (5 individuals); (2) 11.81 - 23.7 mm L_T ; (3) Captured from December to March 2014 and 2015; (4) WA; (5) Reef-associated; (6) LC; (7) MOICT0001047; (Fig. S19).



Fig. S19. *Apogon puncticulatus*

Phaeoptyx pigmentaria (Poey 1860)

(1) Rare post-larvae (4 individuals); (2) 17.18 - 21.62 mm L_T ; (3) Captured in January and February of 2015 and April of 2016; (4) WA; (5) Reef-associated or gravel bottoms; (6) LC; (7) MOICT0001052; (Fig. S20).



Fig. S20. *Phaeoptyx pigmentaria*

Carangidae

Carangoides bartholomaei (Cuvier 1833)

(1) Occasional post-larvae (22 individuals); (2) 14.06 - 79.1 mm L_T ; (3) Captured from January to December (2011 to 2016); (4) WA/CA; (5) Inhabits marine waters associated to reefs and mangroves; (6) LC; (7) MOICT0001083; (Fig. S21). Note: due to overlap in the meristics characters between *C. bartholomaei* and *C. ruber*, others 15 individuals had difficulty in identification.



Fig. S21. *Carangoides bartholomaei*

Caranx crysos (Mitchill 1815)

(1) Occasional post-larvae (45 individuals); (2) 12.2 - 161.15 mm L_T ; (3) Captured from December to May (2011 to 2016); (4) WA/EA/M; (5) Inhabits marine waters associated to reefs; (6) LC; (7) MOICT0001007; (Fig. S22).



Fig. S22. *Caranx crysos*

Caranx hippos (Linnaeus 1766)

(1) Rare post-larvae (4 individuals); (2) 31.3 - 54.84 mm L_T ; (3) Captured in January, April and May of 2012; (4) WA/EA; (5) Inhabits marine waters associated to reefs and estuaries; (6) LC; (7) MOICT0001017; (Fig. S23). Note: due to overlap in the meristics characters between *C. latus* and *C. hippos*, others 27 individuals had difficulty in identification.

Caranx latus Agassiz 1831

(1) Rare post-larvae (4 individuals); (2) 41.69 - 77.55 mm L_T ; (3) Captured in

January and February of 2011; (4) WA/EA; (5) Adults are associated to reefs with juveniles found in estuaries and sandy beaches; (6) LC; (7) MOICT0001015; (Fig. S23).



Fig. S23. *Caranx latus* or *Caranx hippos*

Caranx ruber (Bloch 1793)

(1) Rare post-larvae (5 individuals); (2) 31.89 - 38.85 mm L_T ; (3) Captured from January to March of 2012; (4) WA; (5) Inhabits marine waters associated to reefs with juveniles found associated to macroalgae; (6) LC; (7) MOICT0001020; (Fig. S24). Note: due to overlap in the meristics characters between *C. bartholomaei* and *C. ruber*, others 15 individuals had difficulty in identification.



Fig. S24. *Caranx ruber*

Chloroscombrus chrysurus (Linnaeus 1766)

(1) Common and abundant post-larvae (75 individuals); (2) 8.35 - 28.22 mm L_T ; (3) Captured from January to October (2011 to

2016), with peaks from January to June (92.107%); (4) WA; (5) Pelagic species, but commonly found near estuaries and reef areas; (6) LC; (7) MOICT0001053; (Fig. S25).

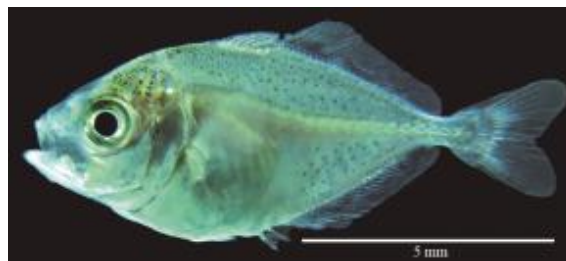


Fig. S25. *Chloroscombrus chrysurus*

Seriola rivoliana Valenciennes 1833

(1) Rare post-larvae (2 individuals); (2) 44.39 - 55.06 mm L_T ; (3) Captured in January and March of 2014; (4) CG; (5) Adults are benthopelagic founded in the outer reefs and deep reefs; (6) LC; (7) MOICT0001016, (Fig. S26).



Fig. S26. *Seriola rivoliana*

Lutjanidae

Lutjanus alexandrei Moura and Lindeman 2007

(1) Common and not abundant post-larvae (41 individuals); (2) 17.02 - 23.55 mm L_T ; (3) Captured from October to May (2011 to 2016), with peaks in March and April (65.78%); (4) BR; (5) Inhabits shallow waters with vegetation and/or sandy

bottoms when juveniles and in deeper areas and reefs when adults; (6) DD; (7) MOICT0001025; (Fig. S27).



Fig. S27. *Lutjanus alexandrei*

Lutjanus analis (Curvier 1828)

(1) Common and abundant post-larvae (84 individuals); (2) 15.03 - 25.66 mm L_T ; (3) Captured from September to May (2011 to 2016), with peaks in March and April (53.57%); (4) WA; (5) Inhabits shallow waters with vegetation and/or sandy bottoms when juveniles and in deeper areas and reefs when adults; (6) VU; (7) MOICT0001026; (Fig. S28).



Fig. S28. *Lutjanus analis*

Lutjanus cyanopterus (Curvier 1828)

(1) Rare post-larvae (2 individuals); (2) 20.22 - 20.8 mm L_T ; (3) Captured in November of 2011 and April of 2015; (4) WA; (5) Adults found close to consolidated substrates at depths of about

40 m; (6) VU; (7) MOICT0001063; (Fig. S29).



Fig. S29. *Lutjanus cyanopterus*

Lutjanus jocu (Bloch and Schneider 1801)

(1) Common and not abundant post-larvae (58 individuals); (2) 17.2 - 25.01 mm L_T ; (3) Captured from October to June (2011 to 2016), with peaks in April (70.58%); (4) TA; (5) Juveniles are found in estuaries and adults are common near reef areas; (6) DD; (7) MOICT0001062; (Fig. S30).

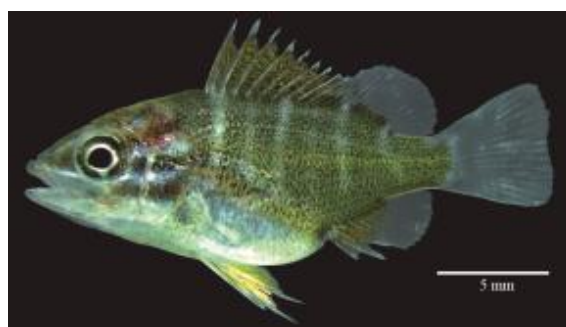


Fig. S30. *Lutjanus jocu*

Lutjanus synagris (Linnaeus 1758)

(1) Common and abundant post-larvae (156 individuals); (2) 12.73 - 25.80 mm L_T ; (3) Captured from October to May (2011 to 2016), with peaks from January to April (91.66%); (4) WA; (5) associated to reefs and sandy bottoms near consolidated substrates; (6) NT; (7) MOICT0001024; (Fig. S31).



Fig. S31. *Lutjanus synagris*

Ocyurus chrysurus (Bloch 1791)

(1) Common and not abundant post-larvae (43 individuals); (2) 15.16 - 24.03 mm L_T ; (3) Captured from December to May (2012 to 2016), with peaks in March and April (79.54%); (4) WA; (5) Adults inhabit coastal waters near the reef areas; (6) DD; (7) MOICT0001064; (Fig. S32).



Fig. S32. *Ocyurus chrysurus*

Gerreidae

(1) Frequent and abundant post-larvae (1271 individuals); (2) 9.5-23.84 mm L_T ; (3) Captured throughout all period, with peaks in March to July (83.05%); (4) TA; (5) Most of gerreids are coastal marine-estuarine species; (6) LC; (7) MOICT0001055 and MOICT0001027; (Fig. S33). Note: due to overlap in the meristic characters, individuals were not identified at the specific level, except for some individuals of the species of *Eucinostomus melanopterus* (Bleeker

1863), and *Ulaema lefroyi* (Goode 1874) which already had characteristic pigmentation.



Fig. S33. *Eucinostomus melanopterus*

Diapterus auratus Ranzini 1842

(1) Rare post-larvae (1 individual); (2) 15.4 mm L_T ; (3) Captured in March of 2014; (4) WA; (5) Inhabits shallow coastal waters; (6) LC; (7) MOICT0001056; (Fig. S34).

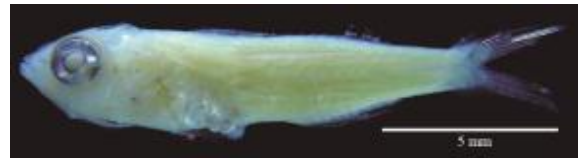


Fig. S34. *Diapterus auratus*

Haemulidae

Anisotremus surinamensis (Bloch 1791)

(1) Rare post-larvae (2 individuals); (2) 10.77 - 13.51 mm L_T ; (3) Captured in March of 2014; (4) WA; (5) Inhabits patches reefs and consolidated bottoms; (6) DD; (7) MOICT0001058; (Fig. S35).



Fig. S35. *Anisotremus surinamensis*

Haemulon aurolineatum Curvier 1830

(1) Rare post-larvae (1 individual); (2) 28.22 mm L_T ; (3) Captured in May of 2012; (4) WA; (5) Marine species

associated to reefs, seagrass and sandy bottoms; (6) LC; (7) MOICT0001059; (Fig. S36).

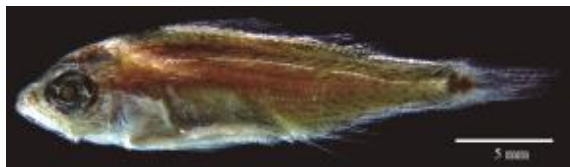


Fig. S36. *Haemulon aurolineatum*

Haemulon parra (Desmarest 1823)

(1) Occasional post-larvae (23 individuals); (2) 8.44 - 10.65 mm L_T ; (3) Captured from November to June (2012 to 2015); (4) WA; (5) Inhabits shallow reef areas, with juveniles found in seagrass and adults in open areas; (6) LC; (7) MOICT0001012; (Fig. S37).



Fig. S37. *Haemulon parra*

Sparidae

Archosargus spp.

(1) Rare post-larvae (1 individual); (2) 11.91 mm L_T ; (3) Captured in December of 2011; (4) WA; (5) Estuarine species, occasionally observed in reefs; (6) LC; (7) MOICT0001079; (Fig. S38).

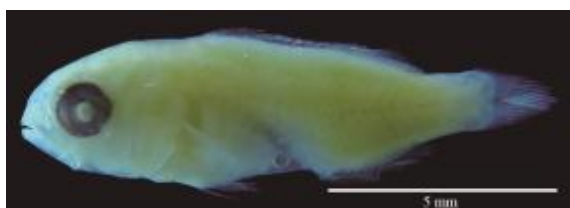


Fig. S38. *Archosargus* sp.

Calamus spp.

(1) Rare post-larvae (1 individual); (2) 14.3 mm L_T ; (3) Captured in November of 2014; (4) WA; (5) Marine species associated to reefs; (6) LC; (7) Collection - (MOICT0001076); (Fig. S39).



Fig. S39. *Calamus* sp.

Polynemidae

Polydactylus virginicus (Linnaeus 1758)

(1) Common and abundant post-larvae (156 individuals); (2) 18.02 - 51.58 mm L_T ; (3) Captured from January to December (2011 to 2016), with peaks in October to April (93.52%); (4) WA; (5) Inhabits estuaries, mangroves and sandy bottoms, with aggregate juveniles near the mouths of the rivers; (6) LC; (7) MOICT0001039; (Fig. S40).



Fig. S40. *Polydactylus virginicus*

Mullidae

Pseudupeneus maculatus (Bloch 1793)

(1) Rare post-larvae (9 individuals); (2) 43.18 - 62.74 mm L_T ; (3) Captured in November to March (2011 to 2015); (4)

WA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001067; (Fig. S41).



Fig. S41. *Pseudupeneus maculatus*

Chaetodontidae

Chaetodon striatus Linnaeus 1758

(1) Rare post-larvae (11 individuals); (2) 19.54 - 26.89 mm L_T ; (3) Captured in October to December of 2011, 2013 and 2015; (4) WA; (6) LC; (7) MOICT0001004; (Fig. S42).



Fig. S42. *Chaetodon striatus*

Pomacentridae

Abudefduf saxatilis (Linnaeus 1758)

(1) Occasional post-larvae (20 individuals); (2) 14.54 - 21.22 mm L_T ; (3) Captured from November to July (2011 to 2016); (4) TA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001029; (Fig. S43).



Fig. S43. *Abudefduf saxatilis*

Microspathodon chrysurus (Cuvier 1830)

(1) Rare post-larvae (1 individual); (2) 10.28 mm L_T ; (3) Captured in March of 2014; (4) WA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001023; (Fig. S44).

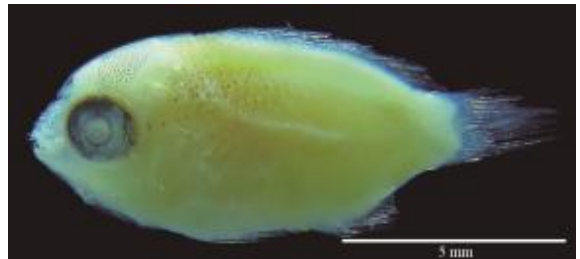


Fig. S44. *Microspathodon chrysurus*

Stegastes fuscus (Cuvier 1830)

(1) Rare post-larvae (4 individuals); (2) 10.51 - 19.51 mm L_T ; (3) Captured in October to December of 2015; (4) BR; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001068; (Fig. S45).



Fig. S45. *Stegastes fuscus*

Stegastes variabilis (Castelnau 1855)

(1) Common and abundant post-larvae (154 individuals); (2) 10.51 - 19.51 mm L_T ; (3) Captured from January to December (2011 to 2016), with peaks in November to February (89.61%); (4) BR; (5) Marine species associated to reefs; (6) DD; (7) MOICT0001069; (Fig. S46).



Fig. S46. *Stegastes variabilis*

Labridae

Halichoeres spp.

(1) Occasional post-larvae (19 individuals); (2) 9.95 - 18.86 mm L_T ; (3) Captured from October to July (2012 to 2016); (5) Marine species associated to reefs; (6) LC; (7) MOICT0001049; (Fig. S47). Note: due to overlapping in the meristic characters, the species may be *Halichoeres poeyi* (Steindachner 1867) or *Halichoeres brasiliensis* (Bloch 1791).



Fig. S47. *Halichoeres* sp.

Labridae - Scarinae

Scarinae spp.

(1) Rare post-larvae (1 individual); (2) 6.54 mm L_T ; (3) Captured in September of 2012; (7) MOICT0001040; (Fig. S48).



Fig. S48. Scarinae sp.

Sparisoma axillare (Steindachner 1878)

(1) Rare juvenile (1 individual); (2) 64.58 mm L_T ; (3) Captured in February of 2013; (4) BR; (5) Marine species associated to reefs; (6) DD; (7) MOICT0001006; (Fig. S49).



Fig. S49. *Sparisoma axillare*

Tripterygiidae

Enneanectes altivelis (Rosenblatt 1960)

(1) Rare post-larvae (11 individuals); (2) 9.63 - 11.8 mm L_T ; (3) Captured in January to April (2014 and 2016); (4) WA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001075; (Fig. S50).



Fig. S50. *Enneanectes altivelis*

Labrisomidae

Labrisomus kalisherae (Jordan 1904)

(1) Common and abundant post-larvae (81 individuals); (2) 16.10 - 24.1 mm L_T ; (3) Captured from November to April (2011 to 2016), with peaks in January and March (79.01%); (4) WA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001031; (Fig. S51).



Fig. S51. *Labrisomus kalisherae*

Labrisomus nuchipinnis (Quoy and Gaimard 1824)

(1) Common and abundant post-larvae (106 individuals); (2) 18.56 - 33.45 mm L_T ; (3) Captured from January to December (2011 to 2016), with peaks in November to April (88.67%); (4) TA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001032; (Fig. S52).



Fig. S52. *Labrisomus nuchipinnis*
Malaccoctenus spp.

(1) Common and abundant post-larvae (144 individuals); (2) 13.57 - 22.24 mm L_T ; (3) Captured from October to July (2011 to 2016), with peaks in November to April (95.83%); (4) WA; (5) Marine species associated to reefs; (6) LC; (7)

MOICT0001042; (Fig. S53). Note: due to overlapping in the meristic characters, the species may be *Malaccoctenus delalandii* (Valenciennes 1836) or *Malaccoctenus triangulatus* Springer 1959.



Fig. S53. *Malaccoctenus* sp.

Blenniidae

Entomacrodus vomerinus (Valenciennes 1836)

(1) Common and not abundant post-larvae (42 individuals); (2) 15.2 - 21.51 mm L_T ; (3) Captured from October to June (2011 to 2016), with peaks in January to June (61.90%); (4) BR (endemic to the Northeast of Brazil and the Island of Fernando de Noronha); (5) Marine species associated to reefs; (6) LC; (7) MOICT0001033; (Fig. S54).



Fig. S54. *Entomacrodus vomerinus*

Hypleurochilus pseudoaequipinnis Bath 1994

(1) Common and abundant post-larvae (83 individuals); (2) 9.95 - 15.45 mm L_T ; (3) Captured from January to December (2011 to 2016), with peaks in January to April (76.19%); (4) WA; (5) The species can be

found in oyster-covered mangrove roots, and shallow rocky outcrops; (6) LC; (7) MOICT0001034; (Fig. S55).



Fig. S55. *Hypleurochilus pseudoaequipinnis*

Ophioblennius trinitatis Miranda Ribeiro 1919

(1) Common and abundant post-larvae (375 individuals); (2) 38.24 - 57.89 mm L_T ; (3) Captured from October to July (2011 to 2016), with peaks in December to March (81.6%); (4) BR; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001044; (Fig. S56).



Fig. S56. *Ophioblennius trinitatis*

Gobiidae

Gobiidae spp.

(1) Rare post-larvae (1 individual); (2) 7.59 mm L_T ; (3) Captured in March of 2014; (7) MOICT0001057; (Fig. S57).

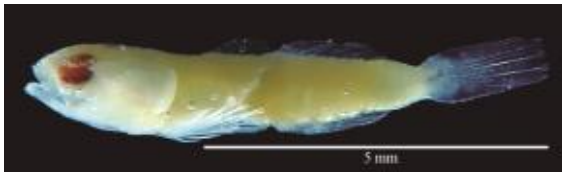


Fig. S57. Gobiidae sp.

Microdesmidae

Microdesmus longipinnis (Weymouth 1910)

(1) Rare post-larvae (2 individuals); (2) 54.96 and 67.88 mm L_T ; (3) Captured in March of 2011 and July of 2015; (4) WA/EA; (5) Demersal marine species; (6) LC; (7) MOICT0001065; (Fig. S58).

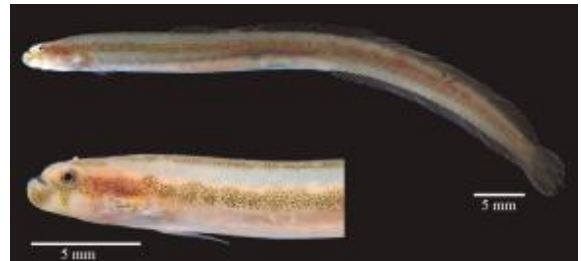


Fig. S58. *Microdesmus longipinnis*

Acanthuridae

Acanthurus bahianus Castelnau 1855

(1) Common and abundant post-larvae (225 individuals); (2) 28.59 - 48.2 mm L_T ; (3) Captured from September to April (2011 to 2016), with peaks in December (70.22%); (4) WC; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001013; (Fig. S59).



Fig. S59. *Acanthurus bahianus*

Acanthurus chirurgus Bloch and Schneider
1801

(1) Rare post-larvae (2 individuals); (2) 31.45 and 36.41 mm L_T ; (3) Captured in November of 2013 and April of 2014; (4) PA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001011; (Fig. S60).



Fig. S60. *Acanthurus chirurgus*

Acanthurus coeruleus (Bloch 1787)

(1) Occasional post-larvae (27 individuals); (2) 33.35 - 43.65 mm L_T ; (3) Captured from October to April (2011 to 2016), with peaks in December to February (81.48%); (4) WC; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001038; (Fig. S61).



Fig. S61. *Acanthurus coeruleus*

Sphyraenidae

Sphyraena barracuda (Edwards 1771)

(1) Common and not abundant post-larvae (47 individuals); (2) 13.20 - 30.24 mm L_T ; (3) Captured in January to April (2011 to 2016), with peaks in March to April (81.82%); (4) CT; (5) Juveniles may occur in mangroves, estuaries and reef areas, when adults inhabit open seas; (6) LC; (7) MOICT0001022; (Fig. S62).



Fig. S62. *Sphyraena barracuda*

Sphyraena guachancho Cuvier 1829

(1) Rare post-larvae (1 individual); (2) 46.28 mm L_T ; (3) Captured in January of 2011; (4) WA; (5) Coastal marine species found in estuaries and brackish waters; (6) LC; (7) MOICT0001078; (Fig. S63).



Fig. S63. *Sphyraena guachancho*

Scombridae

Scomberomorus brasiliensis Collette,
Russo and Zavala-Camin 1978

(1) Rare post-larvae (12 individuals); (2) 30.24 - 39.39 mm L_T ; (3) Captured in January to July (2011 to 2016); (4) WA; (5) Marine species reef-associated and oceanodromous; (6) LC; (7) MOICT0001046; (Fig. S64).



Fig. S64. *Scomberomorus brasiliensis*

Paralichthidae

Citharichthys spp.

(1) Rare post-larvae (1 individual); (2) 11.10 mm L_T ; (3) Captured in April of 2013; (5) Demersal species, mostly found in sand sites and mud sediments; (7) MOICT0001082; (Fig. S65).

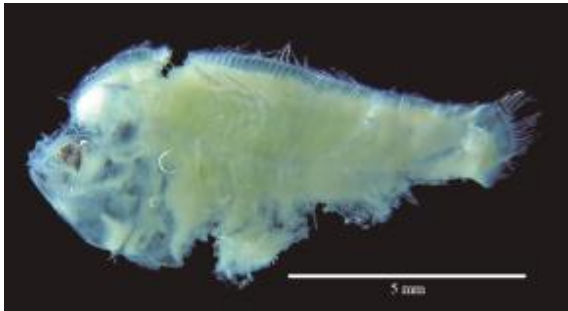


Fig. S65. *Citharichthys* sp.

Cynoglossidae

Symphurus spp.

(1) Rare post-larvae (3 individuals); (2) 13.93 - 17.61 mm L_T ; (3) Captured in January and April (2011 and 2013); (5) Demersal species, mostly found in sand sites and mud sediments; (7) MOICT0001050; (Fig. S66).



Fig. S66. *Symphurus* sp.

Monacanthidae

Cantherhines pullus (Ranzani 1842)

(1) Rare post-larvae (2 individuals); (2) 60.91 and 61.56 mm L_T ; (3) Captured in December (2014 and 2015); (4) TA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001001; (Fig. S67).



Fig. S67. *Cantherhines pullus*

Stephanolepis hispidus (Linnaeus 1766)

(1) Rare post-larvae (12 individuals); (2) 15.79 - 20.58 mm L_T ; (3) Captured in December of 2013 and January of 2014 and 2015; (4) TA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001066; (Fig. S68).

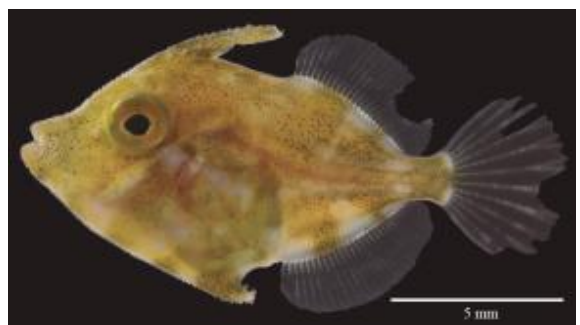


Fig. S68. *Stephanolepis hispidus*

Tetraodontidae

Sphoeroides spp.

(1) Rare post-larvae (7 individuals); (2) 4.7 - 7.85 mm L_T ; (3) Captured in January and March (2014 and 2015); (4) WA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001074; (Fig. S69).



Fig. S69. *Sphoeroides* sp.

Sphoeroides greeleyi Gilbert 1900

(1) Rare post-larvae (1 individual); (2) 16.41 mm L_T ; (3) Captured in March of 2014; (4) WA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001077; (Fig. S70).



Fig. S70. *Sphoeroides greeleyi*
Sphoeroides testudineus (Linnaeus 1758)

(1) Rare post-larvae (2 individuals); (2) 4.88 and 7.28 mm L_T ; (3) Captured in January of 2014; (4) WA; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001036; (Fig. S71).



Fig. S71. *Sphoeroides testudineus*

Diodontidae

Diodon hystrix Linnaeus 1758

(1) Rare post-larvae (2 individuals); (2) 6.21 and 7.21 mm L_T ; (3) Captured in January of 2014; (4) CT; (5) Marine species associated to reefs; (6) LC; (7) MOICT0001048; (Fig. S72).



Fig. S72. *Diodon hystrix*

3 EARLY LIFE HISTORY OF BLENNY *OPHIOBLENNIUS TRINITATIS* (PISCES: BLENNIIDAE) AND ENVIRONMENTAL DETERMINANTS IN LARVAL SUPPLY

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3.1 Abstract

Events prior to larval settlement are essential for the completion of the life cycle and determinants for subsequent population structure. In the present work, the interannual variation and the influence of environmental variables on the larval supply were examined for the reef fish *Ophioblennius trinitatis*. Pre-settlement larvae were collected using light traps, fixed to the navigational access channel of the Tamandaré Bay, Tropical South Atlantic, from December 2010 to April 2016. Subsequent collections of recruits were conducted on the reefs located in the Tamandaré reef complex. The initial life history events and growth records during the pelagic larval phase were obtained from microincrements analyzes in otoliths of the post-larvae and recruits. Temporal patterns were compared with environmental variables (water temperature, chlorophyll concentration, intensity and direction of the wind, rainfall and salinity). The results indicate an interannual variation, and a marked seasonal and lunar periodicity in the spawning and settlement of the reef fish *Ophioblennius trinitatis*. Besides the many traces of early life history (ELHT) played an important role in recruiting, the variability of larval supply may also be related to the surface water temperature and wind speed. This study provides evidence that climate change, which led to increase in temperature associated to ENSOs events of the years 2010 and 2015, had consequences on the reproductive and subsequent larval supply *Ophioblennius trinitatis*. The results presented here, can be translated into valuable information for the study of climate change, especially with regard to the increase of the global temperature.

Key words: Pelagic larval duration, Reef fish, Settlement, Recruitment.

3.2 Introduction

Most marine fish exhibit complex life cycles and may include a dispersive pelagic larval stage with a period ranging from days to months (Laws, 1991). Transport and delivery of pelagic larvae to habitats suitable for settlement is essential for the completion of the life cycle of many coral reef fish, and the pelagic larval period is the main mechanism responsible for population connectivity for most benthic marine fish (Cowen *et al.*, 2007; Cowen & Sponaugle, 2009) in particular reef fish of restricted habitat and reduced body size (Leis, 1991; Victor, 1991).

Processes occurring during the early life stages of fish may be determinant in the subsequent dynamics and ecology (Beckerman *et al.*, 2002), including population abundance and spatial distribution (Caley *et al.*, 1996). Thus, while the mechanisms that lead to temporal and spatial patterns can be influenced by adult reproduction and larval production (Victor 1983; Sale *et al.*, 1984; Robertson *et al.*, 1988), stochastic processes occurring along the pelagic larval life as winds (Raventos & Macpherson, 2005), marine currents, temperature (Rutherford & Houde, 1995; Sponaugle *et al.*, 2006; Rankin & Sponaugle, 2011) and precipitation (Bergenius *et al.*, 2005) control larval survival and population replenishment.

In addition, early life history traits (ELHTs) such as age, size at settlement and growth rate often vary among individuals, and may impact both recruitment and subsequent juvenile survival (Searcy & Sponaugle, 2001; McCormick & Hoey, 2004). For many species the larval growth rate (Searcy & Sponaugle, 2001; Takasuka *et al.*, 2003), the time they remain in the pelagic environment (Meekan & Fortier, 1996), the size at the time of settlement (Searcy & Sponaugle, 2001; McCormick & Hoey, 2004) and overall condition at the time of settlement (Sponaugle & Grorud-Colvert, 2006; Hamilton *et al.*, 2008) are determinant for survival. Thus, small changes in growth, pelagic larval duration and mortality can lead to large fluctuations in the magnitude of recruitment (Houde, 1987).

The blennid *Ophioblennius trinitatis* Miranda-Ribeiro 1919, is a Southwestern Atlantic endemic species commonly found on shallow reef habitats along the northeast coast of Brazil and oceanic islands (Lastrucci *et al.*, 2018). They are considered phylogenetically close to other congeners of the Atlantic Ocean (Lastrucci *et al.*, 2018), and presents two distinct phases in its life cycle, a larval pelagic phase that is potentially dispersive and a demersal juvenile and adult phase that is sedentary and associated with reef environments (Leis, 1991).

In this study we looked into the temporal-interannual variation in the larval supply of

the blenny *Ophioblennius trinitatis* collected monthly over 5 years in the NE Brazilian coast in relation to the climatic conditions of the area. We also investigated if larval traits (larval age, PLD, settlement size) are correlated with temporal recruitment, once settlement and recruitment patterns are associated with several early life history traits. In addition, we have tested how environmental variables can influence larval supply patterns.

3.3 Materials and methods

3.3.1 Study sites and sample design

The study was conducted in the reef complex off Tamandaré, an ILTER (International Long Term Ecological Research Network) site located on the coast of the State of Pernambuco (08°22'S, 35°05'W, Western Tropical Atlantic) (Figure 1). The study area is located inside a multiple use Marine Environmental Protection Area (APA) known as the Coral Coast and Tamandaré Forte Municipal Park. The area harbours a mosaic of coastal ecosystems that include estuaries with mangroves, sea grass and algal beds and a reef complex with coralline formations arranged parallel to the coast (Maida & Ferreira, 1997; Ferreira & Maida, 2006).

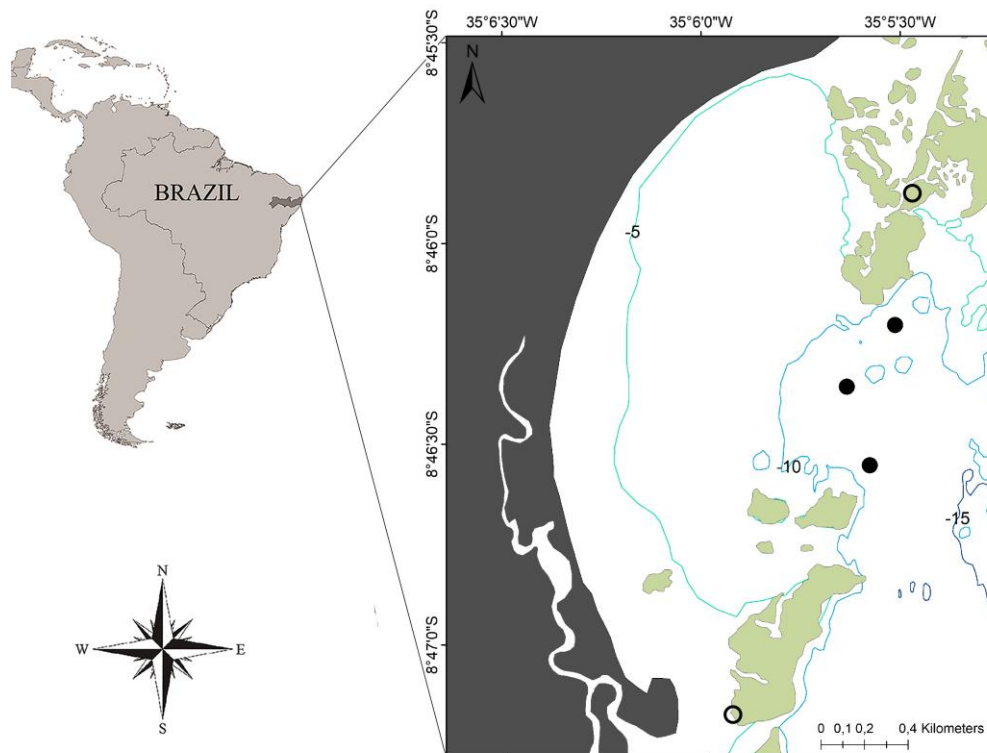


Figure 1. Map of the study area, showing light trap deployment in Tamandaré Bay (●) and sites collection of post-settlement juveniles of *O. trinitatis* (○). Labels: Gray area is land; Green areas are reefs; and blue lines are the bathymetry.

3.3.2 Larval supply

We used light traps of the type CARE® "Capture by Artificial Reef Eco-friendly" (ECOCEAN, Montpellier-France) to capture pre-settlement larval fish. Each light trap is formed of a floating waterproof cylindrical block containing a 12V battery and 55 to 90W LED bulbs, under which a conical network of 2 meters, with a 2 millimeter mesh, and a mesh funnel closely linked vertically (Lecaillon, 2004).

From December 2010 to April 2016 three light traps were deployed for three consecutive days at least once a month, during the new moon, at a channel pass at the reef entrance of the Tamandaré Bay reef system. Traps were installed at 10 to 12 m of depth, anchored at 250m of each other and located at distances from the reef systems of more than 200 meters. Each day traps were installed after dusk and collected before dawn, remaining for approximately 12 hours in subsurface (1 m depth). Collection failed only at periods during winter months when due to poor climatic and oceanographic conditions it was not possible to safely install the traps.

To determine the best time for collection in relation to moon phase, a pilot test was carried out in different lunar cycles between 2011 and 2014. More than 90% of the *O. trinitatis* specimens were captured near the new moon cycle (Fig. 3C), therefore this lunar phase was selected for this study.

Collection of recruits and juveniles of *O. trinitatis* was carried out in the Tamandaré reef complex (Fig. 1) during dives throughout the year of 2015. Two shallow costal reef sites were selected (Camurupim and Pirambu) due to their relative morphological similarity and proximity to light traps. Juveniles found on the reef top of each area were anesthetized using clove oil (250mg L⁻¹) and captured with aquarium nets. The individuals collected were sacrificed by immersing in ice water slush for at least 5 minutes to minimize the suffering of the individuals (McCormick, 2016) and later were preserved in 70% ethanol for laboratory processing.

3.3.3 Laboratory procedure

In the laboratory, a sub-sample of 30 pre-settlement larvae was chosen and matched by a sample of 30 juveniles examined in order to determine larval age and PLD (Pelagic Larval duration). For each individual, the total length (TL) was determined with the aid of a digital caliper (approximation of 0.01 mm).

The otolith pair sagittae was extracted under a stereomicroscope and inserted into a

drop of dip oil on a microscope slide for cleaning for a period of 15 to 30 days. Initially the otoliths were manually sandpapered (800 and 1200 grit) and subsequently mounted on a glass slide using pre-heated CRYSTAL BOND™ 509 resin. The assembled sagittae were again sanded into papers at a right angle until the nucleus was exposed. They were then removed and reassembled face down with the polished face facing the blade and again sanded to obtain a thin cross-section.

The larval age was determined by counting the number of increments using a light microscope at a magnification of 400x under immersion oil. In many cases, not all increments were visible along the same axis and, therefore, the counts were made following the closest possible path (Campana, 1992). Micro-increment measurements was done along the longest axis of the sagittal otolith using the image analysis program ZEN 2 (Blue edition, Carl Zeiss Microscopy GmbH, 2011). We assume that the increment closer to the otolith nucleus was formed on the day of hatching (Campana & Neilson, 1985; Wellington & Victor, 1989), and that these increments were deposited daily as observed in many species of the tropical and temperate blennids (Hernandez-Miranda et al., 2009; Carvalho et al., 2004).

3.3.4 Environmental variables

Physical and biological environmental data were used to describe the oceanographic conditions close to the study area, including sea surface temperature (SST - °C), sea surface salinity (SSS - PSU), chlorophyll-a concentration (mg/m³), rainfall (mm), wind speed (m/s) and wind direction (incident angle) respect to January of 2010 to December of 2015.

Satellite derived data was used for the acquisition of STT data (NOAA ERSSTv4, 2° x 2° grid), SSS (SMOS level-2, 1° x 1° grid) and chlorophyll-a (Aqua MODIS, NPP, L3SMI, 4km). In order to verify the periods of occurrence of the climatic variations, indexes that indicate the anomaly of sea surface temperature in the study area (Latitude -8,7; longitude 325.7) were obtained from sensor AVHRR (Advanced Very High Resolution Radiometer) and data stream GAC (Recorder Global Area Coverage) with 0.1 degrees spatial grid. Data was accessed through the website <https://coastwatch.pfeg.noaa.gov/erddap/index.html>.

The rainfall data (mm/month) was obtained from a weather station distant approximately 20 km from site collection and part of the same catchment area of Tamandaré-PE (Serinhaem-Rio Formoso basin), while data on the direction and speed of the wind (m/s), was obtained from the Recife airport station distant 100 km from the study site (www.weatherunderground.com).

3.3.5 Data analysis

Temporal variability in larval supply (mean number of post-larvae collected by the light traps) was examined using the permutational multivariate analysis of variance and pairwise tests (PERMANOVA; Anderson, 2001), with year and seasons as fixed factors. For operational purpose we the austral seasons as: summer (from January to March), autumn (from April to June), winter (from July to September) and spring (from October to December). PERMANOVA was carried out in Primer 7.0.8 using a resemblance matrix constructed using Euclidean distance.

Otoliths were examined to determine the post-larval age, pelagic larval duration (PLD - number of concentric increments from the primordium to the settlement mark) and larval growth rates (measured by distance between increments). The Kruskal-Wallis tests were used to examine differences in total length and number of increments of post-larval among years, followed by Dunn's multiple comparison tests to determine significant pairwise differences (Zar, 1996). To estimate size-at-settlement (intercept), a linear regression was fitted to length and age data of the recruits and juveniles collected.

The spawning and settlement dates were re-calculated and examined by the Rayleigh test to verify the effects of lunar periodicity (Batschelet, 1981; Zar, 1984). Where the Rayleigh test indicated nonrandom spawning and settlement, the mean about which the data were distributed was calculated (new moon = 1; full moon = 16). In order to determine the settlement date, the number of increments after the settlement mark was subtracted of the total age on the catch date, while to examine the spawning time, the larval age was subtracted from the collection date. Before the retro-calculated analyzes could be examined, the spawning standards had to be lagged for a period of time equivalent to the incubation. In the case of *Ophioblennius trinitatis* a period similar to that observed for the congener *Ophioblennius atlanticus* (Valenciennes, 1836), was assumed, which ranged from 5 days of incubation (Labelle & Nursall, 1985).

To verify if there is a relationship between species growth and otolith growth, a linear regression was fitted between the sagittal otolith radius and total larval length. Otolith growth was used as an estimate of somatic growth thus avoiding the errors introduced by back-calculation of fish size from otoliths (Chambers & Miller 1995). Total length in relation to age of pre-settlement larvae of *Ophioblennius trinitatis* sampling in 2011 and 2015 was modeled using linear regression analysis.

A two-way factorial ANOVA was used to test that exist significant differences in environmental variables between the years (fixed, 6 levels: 2010 to 2015) and season (fixed, 4 levels: summer, autumn, winter and spring). The dependent variables used were: SST ($^{\circ}\text{C}$), SSS (PSU), chlorophyll-a (mg/m^3), rainfall (mm), wind speed (m/s) and wind direction (incident angle). The assumptions of normality and homoscedasticity were tested by Kolmogorov-Smirnov and Levene's Tests and, where necessary, data were square-root transformed. Tukey's studentized range test (HSD) was used to make *a posteriori* comparisons of means.

The influence of anomaly and sea surface temperature on post-larval supply was investigated by plotting seasonal averages (spring-summer) of recruit abundance against indexes of anomaly of sea surface temperature and sea surface temperature of period from autumn to winter. The choice of anomaly and sea surface temperature relating to the autumn and winter occurred due the possibility of these periods to reflect the development and maturation of the gametes, as observed in the congeners and the phylogenetically proximate *Ophioblennius atlanticus* (Labelle & Nursall, 1992). The average abundance of post larvae related to the spring and summer seasons were used due to the main peaks of recruitment of the present study occurred during these seasonal periods (see Fig. 2).

In order to evaluate the influence of the environmental variables on post-larval abundance of *O. trinitatis*, the generalized additive models was used (GAM; Hastie & Tibshirani, 1986). GAMs were used due to the expectancy of non-linear response of species abundance and predictor variables (Dixon, 1999). Models were constructed using a default degrees of freedom using "gam" package in R. Model selection was done using Akaike information criteria (AICc) and the relative importance of each added predictor to the selected model was evaluated by R^2 statistic, as well as the complete model selected.

3.4 Results

A total of 374 post-larvae of *O. trinitatis* were collected by light traps during monthly collections over a period five years. The results of the PERMANOVA indicate that abundance of post-larvae catch per unit effort (number of individuals/trap) showed significant variations between years and seasons (Table I). During the five years sampling period, a seasonal occurrence of post-larval was observed during austral springer/summer months was observed as well as a strong inter-annual fluctuation, with exceptional peaks during the spring-summer 2010/2011 and 2015/2016 (Fig. 2).

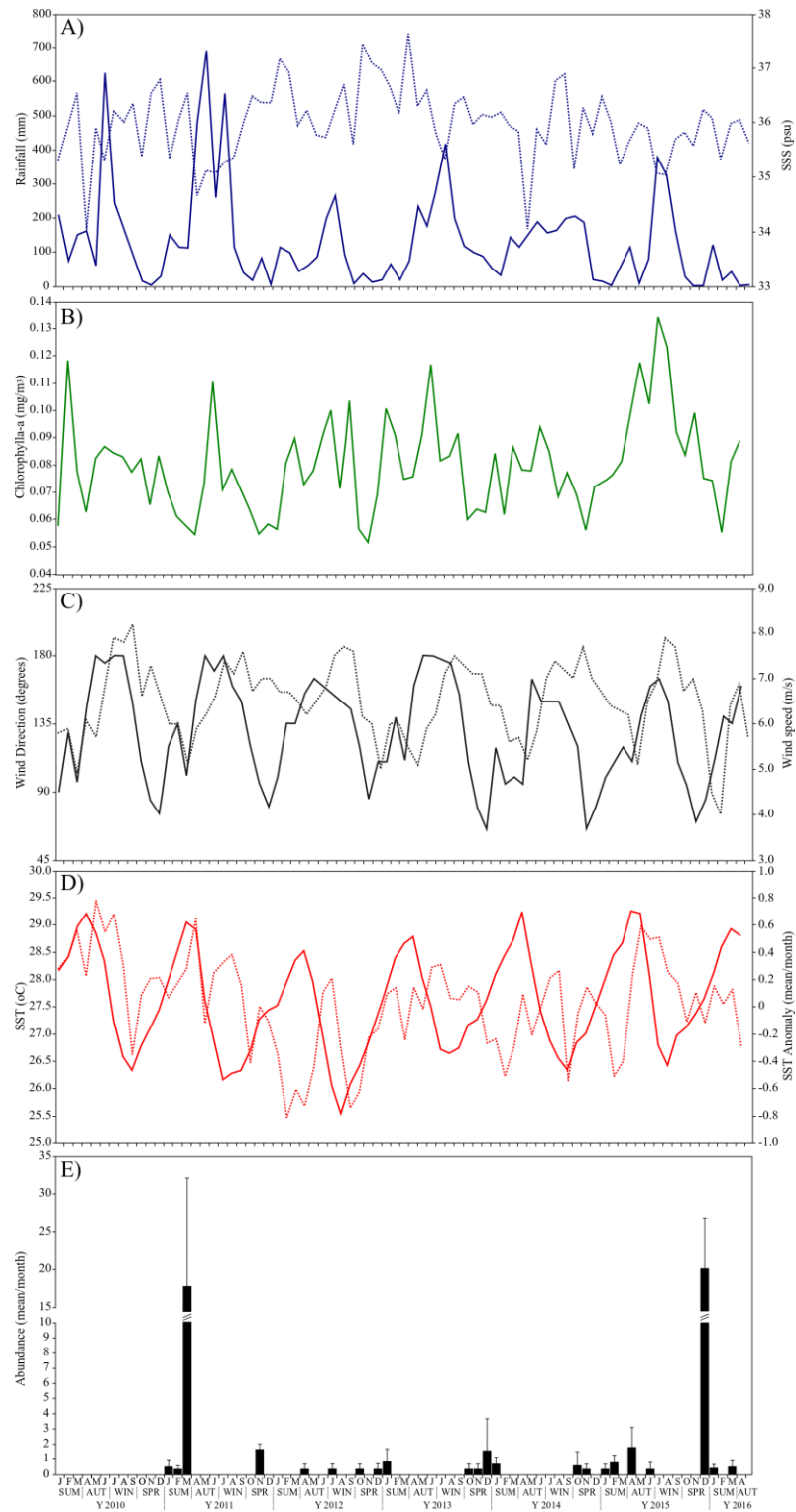


Figure 2. Environmental conditions in study area: (A) Rainfall (blue line) and Salinity (dashed blue line); (B) Chlorophyll-a (green line); (C) Wind direction (gray line) and wind speed (dashed gray line); (D) Sea surface temperature (red line) and anomaly of sea surface temperature (dashed red line); and (E) monthly abundance $\pm$ standard error of the post-larvae of *O. trinitatis* from January 2010 to April 2016.

3.4.1 Periodicity in spawning and larval settlement

The back-calculation revealed spatial peaks and larval settlement rates quite regular and periodic, with the majority of spawning pulses occurring predominantly during the period close to the full moon (Fig 3A), while larval settlement occurred in the periods near the new moon (Fig. 3B). The periods close to the new moon recorded the largest catches of *O. trinitatis* pre-settlement larvae by light traps, according to the pilot study conducted on different lunar days in the period from 2011 to 2014 (Fig. 3C).

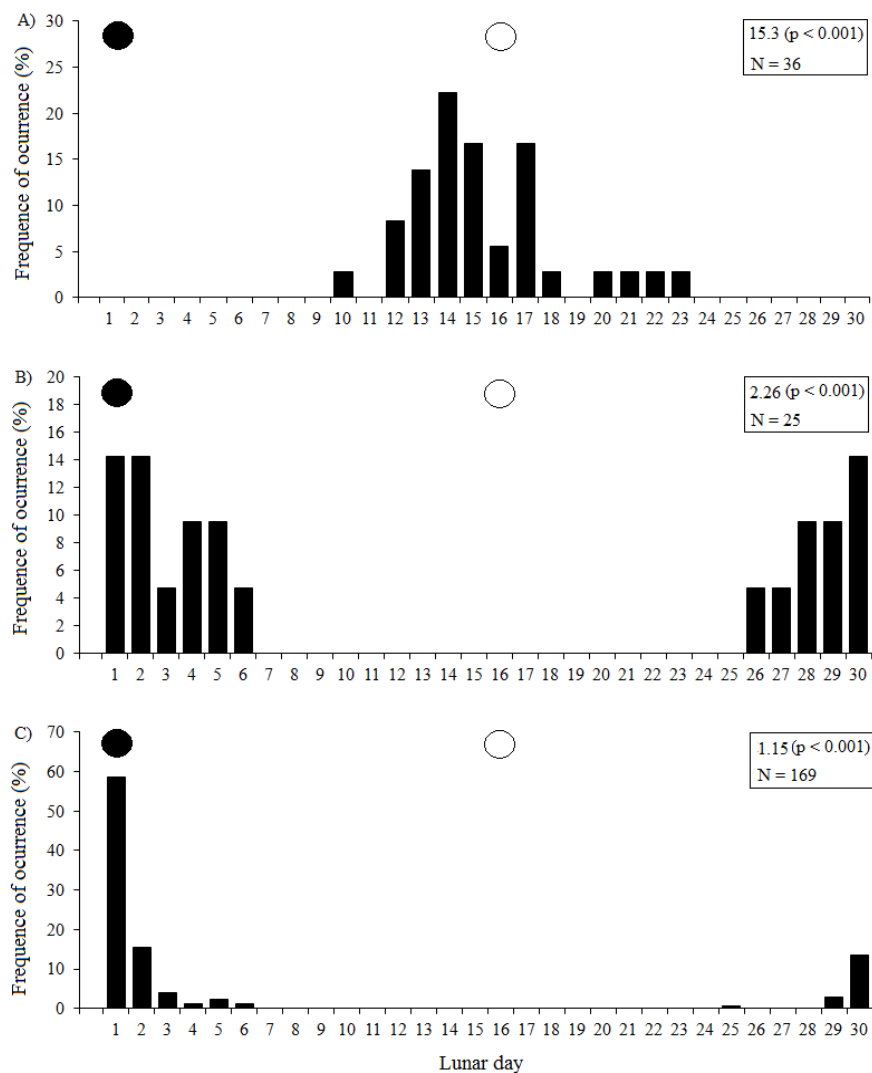


Figure 3. A) Back calculation indicating the frequency of spawning compiled in a single lunar cycle; B) Back calculation indicating the frequency of larval settlement and; C) Frequency of supply of *Ophioblennius trinitatis* larvae collected by light trap during 2011 to 2014, compiled in a single lunar cycle. Labels: 1st Lunar day corresponds to the new moon (●) and 16th lunar day to the full moon (○). The results of the circular test and the lunar day on which the data were distributed were presented.

Table I. The PERMANOVA based on Euclidian distance of the post-larval abundance data among years and seasons.

Source Variation	d.f	SS	MS	Pseudo-F	p	Unique perm
Years	4	19.359	3.8717	4.2262	0.003	998
Seasons	3	38.733	12.911	14.093	0.001	999
Years x Seasons	14	30.553	2.0368	2.2233	0.006	997
Residual	192	175.9	0.9161			
PERMANOVA pairwise tests						
Years	2011 2015 2012 2013 2014					
Season	Summer Spring Autum Winter					

3.4.2 Early life history traits

The individuals captured by light trap ranged from 38.24 to 50.6 mm, with a mean of 45.44 ± 2.61 mm of total length, showing similarity in the catch size between the years of collection, with the exception of individuals captured in 2015 that in average were significantly larger than individuals collected during other periods (Kruskal-Wallis test, $H = 121.14$; $P < 0.001$; Dunnu's test: $2011=2012=2013=2014 \neq 2015$) (Fig. 4).

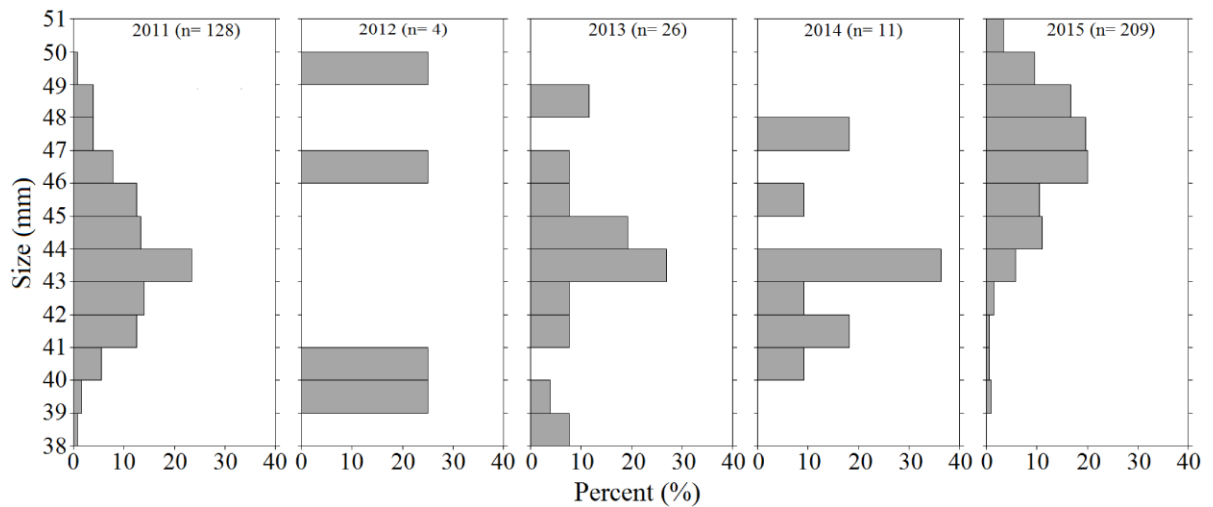


Figure 4. Length-frequency distribution for *Ophioblennius trinitatis* caught by light traps from 2011 to 2015.

The estimated size of settlement of *O. trinitatis* (as inferred from counting of daily rings and settlement mark) was 41 mm of total length, close to the average size of the pre-settlement larvae collected by the light traps ($y = 0.11134x + 40.96$, $R^2 = 0.904$). The age of the post-larvae (Fig. 5A) sampled in 2011 (range of 38 to 48 increments) was significantly lower than 2015 (range of 42 to 51 increments) (Kruskal-wallis, $p = 0.004$). In young recruits

the deposition of incremental rings up to the settlement mark (Fig. 5B) averaged 49 days $\pm$ 1.48 (range: 47 to 52 days), indicating that the duration of the larval period of *Ophioblenius trinitatis* was close to age of the larvae collected in light traps.

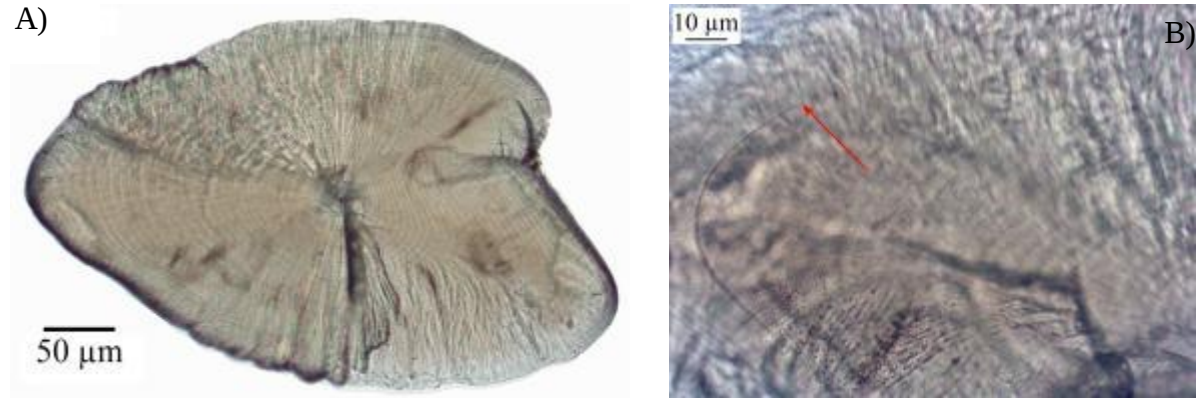


Figure 5. A) Sagittal otolith with a 100x magnification, of an individual of 48.85mm of total length with 48 incremental rings (daily rings); B) Sagittal otolith with a 400x magnification, highlighting the settlement mark (47 incremental rings) of an individual of 41.38mm total length and age of 75 incremental rings (daily rings).

3.4.3 Growth and otoliths growth

The post-larval of *O. trinitatis*, with ranged in size from 39.8 mm to 49.84 mm TL, showed a length-age relationship represented by the linear regression ($y=0.8383x + 7.8124$; $R^2=0.88$, $P< 0.001$) with a slope representing the mean growth rate of all individuals (0.84 mm day^{-1}) during pré-settlement phase (Fig 6A). The total length of the post-larvae and recruits showed a strong linear relation with sagittal radius (linear regression: $R^2 = 0.76$; $p < 0.001$; $n = 25$; intercept (a) = 24.22; regression coefficient (b) = 0.051), supported the assumption that there was a proportional relationship between otolith growth and somatic growth of post-larvae and young *O. trinitatis*. The growth of the daily increment in the otolith was slower in the first 7-8 days of life, accelerating rapidly to a peak of approximately 30-35 days after hatching, slowly declining until settlement, which occurred between 47 and 52 days after hatching (Fig. 6B).

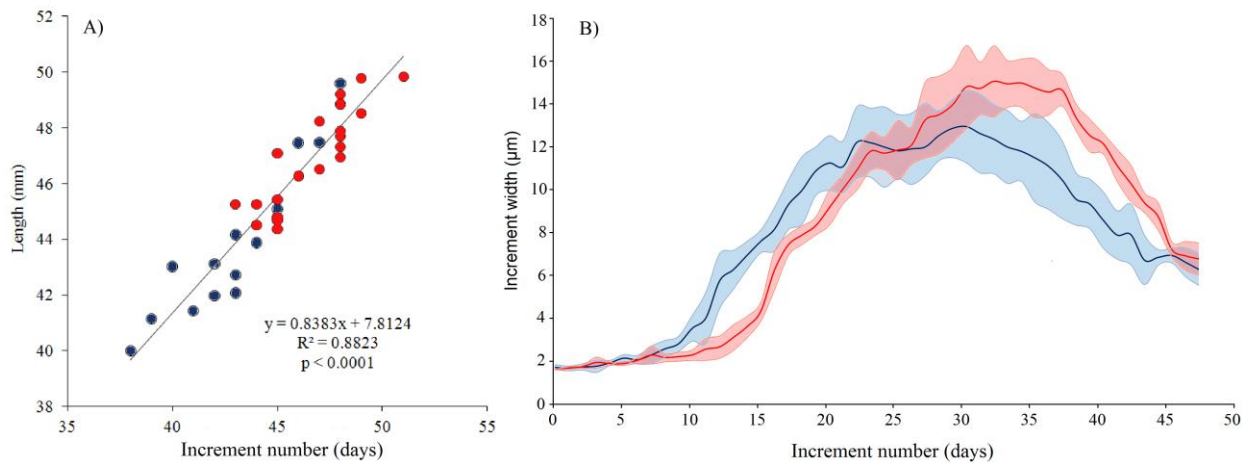


Figure 6. (A) Length-age relationship, and (B) Mean width of the otolith increment ($\mu\text{m} \pm \text{SD}$, area sombreada) of the post-larvae of *O. trinitatis* collected by the light trap in 2011 and 2015, plotted as a function of the number of increments. First increment rings (daily rings) were added after the otolith nucleus represented by zero (0). Labels: red circle and line represent specimens of 2011 and blue circle and line represent specimens of 2015; The shaded area indicates the standard deviation.

3.4.4 Environmental seasonality parameters

The environmental parameters in the study area varied significantly between the years, presenting distinct seasonal patterns for most environmental data (Table II). The sea surface temperature had the highest average in austral summer until the early autumn (January to April), while the lowest averages were recorded at the late autumn and winter (June to September). The SST was significantly higher in the years 2010 and 2015, while the lowest temperature occurred in 2012, also congruent with the lower SST anomalies recorded in the study area (see Fig. 2). The main differences interaction between years and seasons were observed in the autumn season (April to July) of the years 2010 and 2015, which were significantly higher than the one recorded for the same period in the other years.

In relation to the intensity and direction of the wind, there were no significant differences between years, although an evident seasonal pattern can be observed. The highest intensity winds were observed in winter and spring, while conditions of mild wind speeds occurred in summer and autumn. Incident winds from the 90 to 135° quadrant predominated in the summer while in the autumn and winter winds from 135 to 180° prevailed. In the spring the direction of the wind change, predominating winds from the 75 to 125° quadrant (Fig. 2).

The salinity and concentration of Chlorofilla-a were related to the annual and seasonal rainfall patterns. During 2011, La Niña event (Boening *et al.*, 2012), a higher rainfall index was observed, with the same year registering the lowest values of salinity, and for Chlorofilla-a the highest values of concentration occurred in 2011 and 2015. Seasonally weather in the region is divided in wet (autumm and winter) and dry (spring and summer). In a wet periods, the Chlorofilla-a recorded the highest concentration, while salinity presented significantly lower values. In the dry season, the highest values of salinity and the lowest concentration of Chlorofilla-a were recorded.

Table II. Results of two-way factorial ANOVA testing the effects of years and seasons on environmental variables.

Source of variation	d.f.	SS	MS	<i>F</i>	<i>P</i>
SST (°C)					
Years	5	102.6	20.5	51.04	0.000
Seasons	3	1340.5	447	1128.21	0.000
(Years*Seasons)	15	71.7	5.79	12.11	0.000
Residual	48	813	0.00		
Chlorophylla-a (mg/m ³)					
Years	5	0.005262	0.001052	5.32	0.007
Seasons	3	0.004543	0.001514	7.66	0.000
(Years*Seasons)	15	0.003317	0.000221	1.12	0.366
Residual	48	0.01	0.00		
Wind speed (m/s)					
Years	5	0.392	0.078	0.28	0.922
Seasons	3	24.315	8.105	28.85	0.000
(Years*Seasons)	15	9.344	0.623	2.22	0.039
Residual	48	13.48	0.281		
Wind direction (degrees)					
Years	5	4722	944	2.619	0.036
Seasons	3	56768	18923	52.464	0.000
(Years*Seasons)	15	3516	234	0.650	0.818
Residual	48	17313	361		
Rainfall (mm)					
Years	5	128341	25668	1.665	0.041
Seasons	3	419193	139731	9.063	0.000
(Years*Seasons)	15	194315	12954	2.840	0.039
Residual	48	740049	15418		
SSS (PSU)					
Years	5	6.09	1.22	3.5	0.009
Seasons	3	5.68	1.89	5.4	0.002
(Years*Seasons)	15	5.16	0.34	1.0	0.492
Residual	48	16.88	0.35		

3.4.5 Environmental correlates with supply larval

The general additive models (GAM) showed two significant variables, sea surface temperature and wind speed, as predictor for abundance of *O. trinitatis* post-larvae, explaining approximately 34% of the variation (Table III). Total abundance of *O. trinitatis* was positively and significantly related to increased of SST and to intermediate levels of winds speed (between 6.7 and 7 m/s) (Fig. 7).

Table III. Results of GAM fitted model between total post-larval abundance of *O. trinitatis* with environmental variables: chlorophyll-a (Chlo), sea superficie temperature (SST), sea superficie salinity (SSS), rainfall (Rain), wind speed (WSP) and wind direction (WDI). Labels: res.df - Residual Degrees of freedom, ns – non significative.

Variáveis	AICc	Pseudo-F	p	res.df	R ²	Nº Var.
Null	-50.708	0.353	0.561 (ns)	39	0.403	6 (All)
SST	-55.391	14.211	0.001	38	0.267	1
SST + WSP	-57.216	4.0562	0.047	37	0.347	2

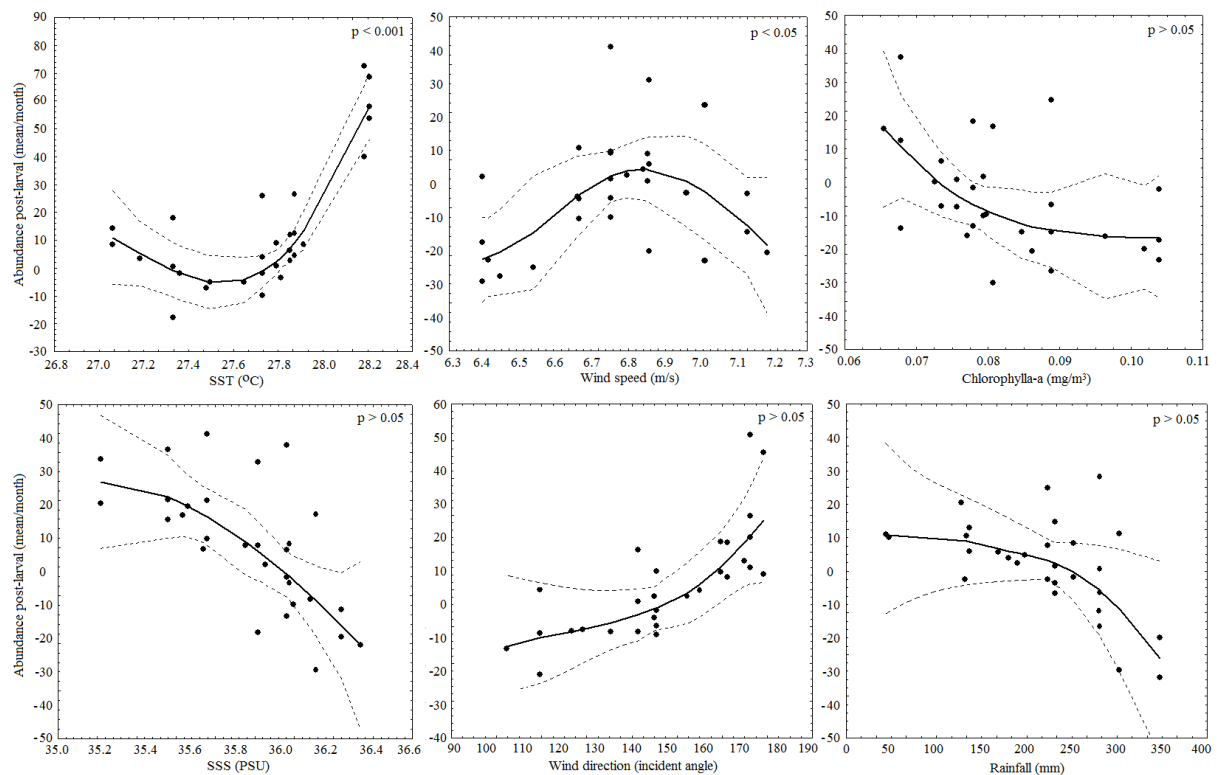


Figure 7. GAM analysis illustrating relationships of pre-settlement larvae of *O. trinitatis* abundance with environmental variables. Lines represent the estimates of the best models, dashed lines are confidence intervals (95%) and symbols represent partial residuals.

The abundance of post-larval of *O. trinitatis* in spring-summer was correlated to anomaly of sea surface temperature and SST in autumn-winter, which accounted for approximately 48% and 90% of the variance respectively (Fig. 8A, B). The periods preceding spawning (autumn-winter) had high anomaly rates and higher average temperatures, showed a large numbers of recruits in spring-summer.

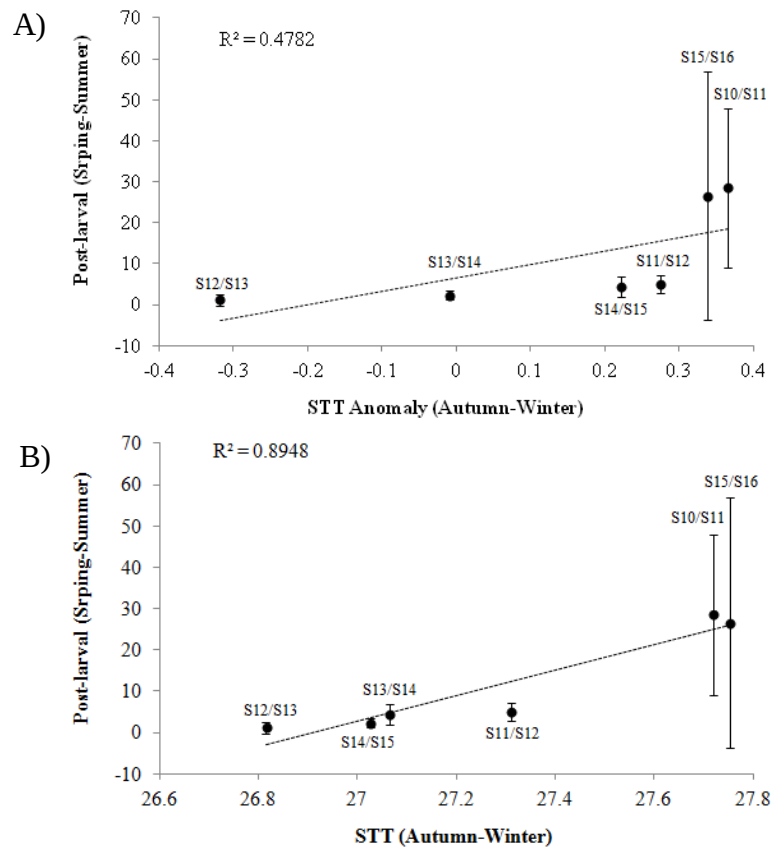


Figure 8. Averages abundance of post-larval of *O. trinitatis* (spring-summer) plotted against the mean of anomaly of sea surface temperature (A) and sea surface temperature (B) in the period of autumn to winter. Labels: S – springer year / S – summer year.

3.5 Discussion

Temporal-interannual fluctuations of recruitment of populations are long known phenomena in fished species (Hjort, 1914), thought to be determined by changes in nutrition and transport resulting from a variety of physical-chemical and biological processes that interact and may vary inter-annually in frequency, intensity and spatial scale (Hjort, 1914; Levin, 1992; Botsford *et al.*, 2014). For reef fishes the phenomena has been reported since the 80's with the first studies using light traps, with the year-to-year variability in recruiting

pulses seen as evidence of the action of physical processes within the plankton (Sale, 1985; Doherty & Williams, 1988). In fact, the post-larvae of *Ophioblennius trinitatis* showed very clear seasonal changes and interannual variation with temperature was the main predictors on larval abundance variation in the present study.

The results of this time series of more than five years indicate a regular seasonal and lunar periodicity in the spawning and settlement of the reef fish *Ophioblennius trinitatis*. Although no reproductive studies were conducted, the occurrence of post-larvae of the species *O. trinitatis* observed during several months of the year, suggest an extended reproductive period. This year-round reproductive pattern with seasonal peaks, was also observed in several reef fish species in the Caribbean (Erdman, 1976) and Jamaica (Munro *et al.*, 1973) as well as for the congener species *Ophioblennius atlanticus* in Barbados (Labelle & Nursall, 1992).

It may be that reproductive propagation throughout the year is a mean of competing for available space in coral reefs, as suggested by Sale (1974), Russel *et al.* (1974) and Sale and Dybdahl (1975). On the other hand, the main peaks of recruitment occurred in late spring and summer, coinciding with periods where the climatic and oceanographic conditions in the region are calmer. As suggested for the redlip blenny *O. atlanticus* (Labelle & Nursall, 1992), it is probably that *Ophioblennius trinitatis* may have been adapted to maximize recruitment in periods with favorable conditions for the survival of new recruits.

The larval settlement was also closely associated with the new moon, occurring at night and in low light. Previous works have observed higher abundance of pre-settlers in the days near to the new moon (Milicich, 1994; D'Alessandro *et al.*, 2007), including for the congener *Ophioblennius atlanticus*, with settlement recorded at night and close to the time of new moon in the region of Barbados (Labelle & Nursall, 1992). The adaptive implications of settling in low-light periods are to avoid visually oriented predators (Johannes, 1978, Victor, 1991). Robertson (1992), reports that the recruitment of some reef species in Panama was also synchronized with the new moon. Patterns in larval supply and recruitment may also be related to favorable transport at specific times in the tide cycle. In these cases the swimming ability is probably linked to the size that precedes the settlement. Relatively large post-larvae species such as *O. trinitatis* may be more successful in swimming against strong currents, so recruiting pulses may increase in heavy flood tides occurring on darker nights near the new moon (Sponaugle & Cowen, 1997). It is also possible that the detection of a suitable settlement site can only occur during specific flow regimes (eg, offshore flow over the reef).

O. trinitatis inhabits shallow lagoon reefs in the study site and thus passing the reef breakers is an important step during recruitment process.

The post-larvae of *Ophioblennius trinitatis* had increasing rates of larval growth up to approximately 35 days and then decreased suggesting rather slow growth rates at settling time. This phase with marked reduction in increments widths of otoliths is the beginning of the competent stage for larval settlement (Bruce, 1989). However, in many reef fish this slow-growing phase can be extended by delaying the competent stage and metamorphosis of the species (Victor, 1986; Cowen, 1991; Sponaugle & Cowen, 1994).

This appears to be the case of *O. trinitatis*, where low otolith growth rates at about 35 days after hatching, suggests that competence is already possible at this age. However the registration of a long larval life ranging from 47 to 52 days indicates that *Ophioblennius trinitatis* has the capacity to prolong its pelagic phase and delay the settlement. The ability to delay metamorphosis and thus extend the larval duration, also allowed the larvae to settle in a relatively large size (estimated size of settlement approximately 41 mm and pre-established larvae approximately 45 mm) when compared to other pre-established reef fish species recorded in the study area (Grande et al, 2019).

The ability to extend larval life and delay metamorphosis may promote advantages for larvae such as the possibility of dispersal to distant sites (Scheltema, 1977; Barlow, 1981), increase the likelihood of finding a suitable settlement location (Jackson & Strathmann, 1981, Cowen, 1991), or allows a larva to choose when to install, waiting to do so during a particular lunar phase (Sponaugle & Cowen, 1996), thus increasing your chances of colonization.

In addition, a longer larval life and the large size reached by larvae of *O. trinitatis* provide disadvantages during the pelagic period and advantages at the time of settlement and territorial adult life. It is widely assumed that larvae experience high mortality rates in planktonic phase, and that the survival rate is lower if the length of time spent in plankton is reduced (hypothesis of stage length, Anderson, 1988; Cushing, 1990). Although rapid larval growth leads to potentially improved survival in the larval stage, early settlement may jeopardize size, so small settlement sizes may lead to reduced survival on the reef. Mortality, in particular that caused by predation, is widely considered as the basis to be size-based (Hixon, 1991; Sogard, 1997), so colonization of smaller fish should suffer greater mortality on the reef. When they remain in the plankton for a longer period, the larvae of *O. trinitatis* can reach a minimum stage of development and condition necessary for settlement and better juvenile survival. Larger colonizers are less vulnerable to predation and can allocate more

energy to their development and defense of territories than smaller settlers (compensatory growth theory, Metcalfe & Monaghan, 2001; Sogard & Olla, 2002; Ali *et al.*, 2003; Alvarez & Metcalfe, 2007).

Throughout their larval pelagic life, species may be influenced by different stochastic events that randomly affect abundance, dispersal, growth and larval survival (ie, lottery effect; Hedgecock, 1994). Although there are a large number of environmental conditions potentially capable of affecting the abundance of post-larvae, here the most parsimonious model to explain larval abundance in relation to environmental variables included temperature and winds speed. The temperature positively influenced the arrival of post-larvae. Not coincidentally, the capture of post-larvae predominated in the hotter periods of each year (late spring and summer) and the exceptional peaks of larval supply occurred in warmer years of the time series studied, coincided with high surface temperature anomalies observed during the 2010 and 2015 and that were correlated and equivalent to El Niño Southern Oscillations (ENSO) events in this periods.

Most often El Niño episodes tend to negatively affect marine food webs, with primary productivity declines (Barber & Chaves, 1983), zooplankton decline in previously productive regions (Miller *et al.*, 1985), declining reproduction and fish populations (Peracy, 1992) and even population collapses of birds and marine mammals (Wooster, 1960; Idyll, 1973). The significant increase in sea surface temperature in autumn season of 2010 and 2015 years, however, may have been the main responsible for the reproductive success and increase of the larval supply of *O. trinitatis* reflected in higher catches in the years of 2011 and 2015.

It is known that temperature is fundamental in fish life and this effect particularly affects the reproductive processes from the development and maturation of gametes, spawning, embryogenesis and hatching to larval and juvenile development and survival (Pauly & Pullin, 1988; Howell *et al.*, 1998; Jobling, 1997; Sponaugle & Cowen, 1996; Pankhurst & Munday, 2011). The effect of temperature may have different consequences depending on the spawning period, with increasing temperatures contributing to reproductive development in spring and summer spawning species (Stacey, 1984, Scott & Pankhurst, 1992; Shimizu, 2003; Pankhurst & Munday, 2011). It seems to be the case of the *O. trinitatis* which presents the main spawning peaks during spring and probable period of development and maturation of the male and female gonads throughout the autumn and winter, as observed in the congener *Ophioblennius atlanticus* (Labelle & Nursall, 1992). This is corroborated by positive correlation between SST anomalies in autumn-winter with abundance of post-larvae

in spring-summer, suggesting that the highest values of the SST anomaly had consequences on the reproductive events and certain traces of the initial life history of the reef fish *Ophioblennius trinitatis*. Most notably, the increase in water temperature in the periods prior to spawning has possibly caused an increase in reproduction and consequent exceptional larval supply peaks in spring/summer of 2011 and 2015.

Wind speed has been shown to be an important structuring factor of larval fish assemblages (Milicich 1994, Munk *et al.*, 2004). The optimum wind speed that favor larval delivery of *O. trinitatis*, between 6.7 and 7 m/s, may produce favorable conditions (transport and feeding) to post-larvae actively migrate to suitable habitats. Wind velocity may directly influence larval transport (Sim-Smith *et al.*, 2013) or in the case related to wind-induced turbulence, may influence feeding conditions and larval survival (Lemberget *et al.*, 2009). It is probable that under conditions of lower wind speeds, the induced turbulence at small scale influences negatively the contact and catch rates of prey (Gallego *et al.*, 1996; Dower *et al.*, 1997; Utne-Palm & Stiansen, 2002). In higher winds, surface currents can damage the transport mechanisms, making it difficult for larvae to protrude on reefs, as well as requiring a high energy expenditure to settle in suitable habitats (Kingsford & Choat, 1986; Kingsford, 1990).

In the present work, the variation and intensity of larval supply and consequent success in recruitment may have resulted from the interaction between biological/behavioral processes (Kerrigan, 1997; McCormick, 1999) and physical-environmental processes (McCormick & Molony, 1992, 1995) that occur during planktonic phase. Aspects of the life of the larvae, reflected in several early life history traits (ELHTs), played an important role in recruitment patterns (Bergenius *et al.*, 2002, Wilson & Meekan, 2002; Bergenius *et al.*, 2005).

In addition, part of the variability in larval supply was related to differences in water temperature and wind speed. This study provides evidence that climate change, which led to increase in temperature associated to El Niño Southern Oscillations events of the years 2010 and 2015, had consequences on the reproductive and subsequent larval supply *Ophioblennius trinitatis* events. The larval stage of fishes is usually more sensitive than adults to environmental fluctuations and may be especially vulnerable to climate change (Pankhurst & Munday, 2011). In this context, the results presented here about early life history of the redlip blenny *O. trinitatis*, can be translated into valuable information for the study of climate change, especially with regard to the increase of the global temperature.

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4 EFFECTS OF POST-SETTLEMENT PROCESSES AND MARINE PROTECTED AREA ON RECRUITMENT OF BLENNY *OPHIOBLENNIUS TRINITATIS* (PISCES: BLENNIIDAE)

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4.1 Abstract

The processes and patterns that occur during settlement and post-settlement processes are extremely important in ecology and population dynamics. However, many species it is unclear at what point, whether during or after settlement, that the population structure is defined. In this context, the present study investigated the importance of post-settlement processes on recruitment and population dynamics of *Ophioblennius trinitatis*, examining whether the spatial and temporal variation of the adult population is affected by larval supply (from the pelagic phase) or by processes that occur after settlement (predation, competition and selection of microhabitats). The possible effects of a protected marine area on the recruitment and population structure of *O. trinitatis* were also verified. Even though the larval supply recorded by light traps has determined the number of recruits added to the population, results obtained from visual censuses indicated that larvae arrival was not responsible for differences observed in adult abundance between sites, implying that the final population structure of *O. trinitatis* at local scale, may have been determined by post-settlement processes, such as microhabitat selection, combined with predator and conspecific pressure. The high abundance and availability of food in the area assumes that this was not a limiting resource for this species. On the other hand, the availability of shelter, provided by sea urchins probably was the main limiting factor in the selection of microhabitats for the blennid *O. trinitatis*. The marine reserve apparently had no influence on the supply of pre-settlement larvae, since the density of new recruits did not differ significantly between sites with different levels of protection. However, the high densities of potential predators (carnivorous fish) found in the protected area suggest that the establishment of the enclosed area may present different responses in recruitment patterns according to the species, such as greater pressure on predation or due to a possible higher quality of habitat quality.

Key Words: Larval supply, reef fish, conspecifics, predators, micro-habitat selection.

4.2 Introduction

Reef fishes have a complex life cycle that often includes a dispersive larval phase in the early stages of life. For many coral reef fishes, at the end of the pelagic larval phase it happens the transition from the pelagic environment to the suitable reef habitat (settlement), in order to proceed to the next stage of the life cycle, a necessary precursor to recruitment of the population (Doherty, 2002; Myrberg & Fuiman, 2002; Leis & McCormick, 2002).

The replenishment of coral reef fish populations can be highly variable in space and time (Victor, 1983, Sale *et al.*, 1984, Robertson *et al.*, 1988) wherein the processes and patterns that occur during settlement and post-settlement processes have been shown to be extremely important in ecology and population dynamics (Victor, 1983; Doherty & Fowler, 1994; Caley *et al.*, 1996; Caselle, 1999; Beckerman *et al.*, 2002). In situations where the adult population does not follow the same pattern of recruitment, it can be assumed that the post-settlement processes predominate over the population structure (Schmitt & Holbrook, 1996), as predation (Caley, 1993; Carr & Hixon, 1995), competition (Tupper & Hunte, 1994, Almany, 2003) and habitat and micro-habitat selection (Tolimieri, 1995; Shima & Osenberg, 2003; Holbrook & Schmitt, 2003).

The relative importance of pre and post-settlement processes in defining population structure and the temporal and spatial variability has stimulated debates and research since the 1990s (Hixon, 2011) with recent evidence on the role of settlement patterns and post-settlement modification rather than simply focusing on one factor (Caley *et al.*, 1996; Steele, 1997; Schmitt & Holbrook, 1999). However, it is unclear at which point, whether during or after settlement, that the population structure and spatial variability of is defined.

Probably the relative importance of pre and post-settlement processes on future populations is species-specific (Sponaugle & Cowen, 1996) and may depend on the site-specific differences (Warner & Hughes, 1988; Caley *et al.*, 1996; Tupper & Boutilier, 1997). It is quite clear that protected marine areas promote increased in the abundance and species diversity in addition to increase in biomass and in the average size of individuals (Charton *et al.*, 2000; Micheli *et al.*, 2004; Claudet *et al.*, 2008; Guidetti *et al.*, 2008). Differences in the ecological integrity of protected and unprotected marine areas can also result in differences in settlement/recruitment rates and survival of recruits (Gronrud-Covert & Sponaugle, 2009). Understand the settlement/recruitment rates of larvae in marine reserves is essential to implementation and management of reserves, once properly located marine areas can buffer recruitment variability in adjacent areas (Bohnsack, 1990) and contribute to the sustainability of future populations (Halpern & Warner, 2003).

The present study focus on the role of pre and post-recruitment processes in the population structure of the redlip blenny *Ophioblennius trinitatis* Miranda-Ribeiro 1919, an endemic reef fish found along the Northeast coast of Brazil and associated oceanic islands (Lastrucci *et al.*, 2018). This highly sedentary species presents two distinct phases in its life cycle, a potentially dispersive phase with pelagic larval duration of approximately 50 days (Grande & Ferreira, chapter 3) and a juvenile and adult phase restricted to the reef environment (Leis, 1991).

Specifically, we examined how the spatial and temporal variation of the adult population is affected by fluctuations the larval supply (coming from the pelagic phase) and by post-settlement processes such as predation, competition, through presence of conspecifics and microhabitat selection. In addition, we verified the possible effects of a protected marine area on the recruitment and subsequent population of *Ophioblennius trinitatis*.

4.3 Materials and Methods

4.3.1 Study area and sample design

The present study was conducted in the Tamandare reef complex of Pernambuco State, Brazil. The coral reef formations in Tamandare resemble fringing reefs, with formations arranged along three lines parallel to the coast, that act as a breakwater barrier, forming shallow lagoons between the coastal line and the back reef (Maida & Ferreira 1997; Rodriguez -Ramirez *et al.*, 2008). The study area is located at the northern limit of the Costa dos Corais marine protected area (i.e. APA Costa dos Corais), which extends 135 km along the north-eastern coast of Brazil and located within a Integral Protection Conservation, the Forte of Tamandaré Municipal Park.

Eigth shallow costal reefs were selected within this area: one reef site, *Ilha da Barra* (IBa), informally known as the 'Tamandaré Closed Area', is the first reef recovery zone with exclusion of fishing and tourism since 1999. Located inside the Tamandaré reefs complex, the "closed area" is considered the longest and continuous experiment in Brazil for monitoring, recovery and conservation of coastal reefs (Fig. 1). Seven sites were located in areas open to fishing and /or tourism: *Camurupim* (Cam), *Pirambú* (Pir), *Váu das Campas* (Vau), *Cordão do Mero* (CMe), *Ilha do Norte* (INo), *Caieiras* (Cai) and *Culumin* (Cul) (Fig. 1).

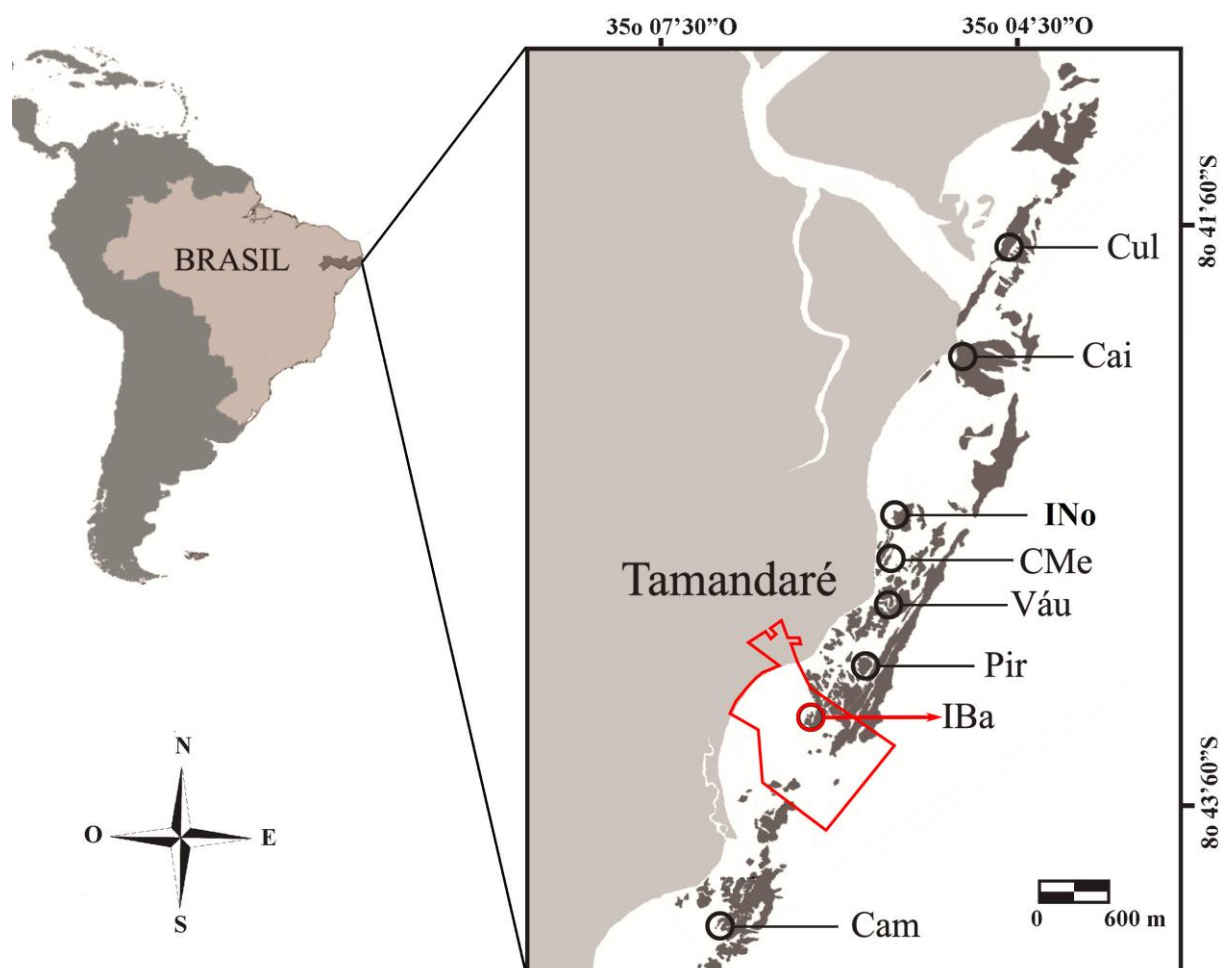


Figure 1. Map indicating the location of study areas on the southern coast of the state of Pernambuco. Label: Camurupim (Cam), Ilha da Barra (IBa), Pirambú (Pir), Váu das Campas (Vau), Cordão do Mero (CMe), Ilha do Norte (INo), Caieiras (Cai) and Culumin (Cul). Red line is the reef recovery zone with exclusion of fishing and tourism.

4.3.2 Pre-settlement sampling

In order to verify the magnitude of larval supply of *O. trinitatis* in the study area, the abundance of post-larvae was surveyed using data from March 2015 to March 2016, referring to the broader work of collecting of pré-settlement stage reef fish (Grande *et al.*, 2019), captured by light trap model CARE® ("Capture by Artificial Reef Eco-friendly" ECOCEAN, France) (complete description see Carassou *et al.*, 2009).

Light traps (n=3) were deployed transversely to the navigational access channel of the Tamandaré Bay using a buoys and anchored at 10-12 m depth. Traps were located outside the last reef barrier at least 200 m away from the reef systems and maintaining a minimum distance of 300 m apart from each other to ensure independence (Fig. 1). Light traps were

installed every month after dusk for three consecutive days, remaining one meter beneath the surface for approximately 10–12 h each. In this study, we used the data collected around the new moon period. According to Grande *et al.* (2019), in the pilot test carried out in different lunar phases, more than 90% of the post-larvae of *O. trinitatis* were capture near the new moon cycle.

Samples were recovered each morning and transported in aerated buckets for photographic records. Individuals were subsequently sacrificed by immersing in ice water slush for at least 5 minutes to ensure their death and minimize the suffering (McCormick, 2016). After death, the individuals had their total length measured and then transferred to vials, labelled and preserved in 70% alcohol.

4.3.3 Recruitment sampling

To assess temporal and spatial patterns of recruitment, monthly underwater observations were conducted by free diving techniques between March 2015 and March 2016, same period of post-larvae collection and period with records of the highest peaks of recruitment from 2011 to 2016 (see chapter 3). Sampling was conducted during daylight hours during low tides ranging from 0.0 to 0.4 m. The visual census were made when the horizontal visibility of water was greater than 4 m - estimated using the acrylic plate method of Dominici-Arosemena *et al.*(2005). Over the period June to August 2015, no visual census was performed due to the low visibility of the water.

In each site a previous quick survey was conducted in different reef zones in order to determine the preferred habitats of blenny *Ophioblennius trinitatis*. The reef flat was chosen, as individuals were not recorded in sand bottoms or in caves and rarely in reef crest. To quantify fish size and abundance, belt transects of 10 x 2 m (20 m²), with at least 3 replicates were arranged haphazardly in the reef top of the sampled area. All fishes, included potential predators and intra/inter-specific competitors of *O. trinitatis*, were counted along belt transects while a diver swimming slowly and near the substrate. The total length of juveniles and adults reef fishes were estimated in 1 cm TL size classes. Larger individuals were accounted in 10 cm TL size class. To insure accurate length assessment of fishes underwater eliminating inter-observer bias, the same diver repeatedly estimated the sizes on fish models of various lengths before the survey (Rooker & Recksiek, 1992).

The potential predators of *O. trinitatis* included species of the family Muranidae, Synodontidae, Scorpaenidae, Epinephelidae, Serranidae, Carangidae and Lutjanidae, belonging to the trophic guild of carnivorous and piscivorous (Ferreira *et al.*, 2004). The

interspecific competitor is mainly composed by *Stegastes fuscus* Cuvier, 1830, a Brazilian endemic damselfish which has aggressive behavior over competitor species that invade their territories (Medeiros *et al.*, 2010; Leal *et al.*, 2013) and one of the most abundant fish species in the shallow waters of the Tamandare reef complex, northeast Brazil (Ferreira *et al.*, 1996).

For each species life stage categories were based on size at first maturity (L_{50}) obtained from FishBase World Wide Web (Froese & Pauly, 2018) and information found in the bibliography. Juveniles were defined as individuals smaller than half the maturation size, to be able to distinguish them from larger subadults and adults. The life stage of *Ophioblennius trinitatis* were categorized according to estimated size of settlement (41mm) and sizes range of pré-settlement fishes captured by light traps prior to recruitment (38.24 to 50.6 mm)(see chapter 3): (i) specimens smaller than 50 mm were considered new recruits; (ii) established juveniles were individuals smaller than 65 mm, and (iii) adults were specimens larger than 65 mm, stage life estimated based on the congener *Ophioblennius atlanticus* (Valenciennes, 1836) (Hunte & Côté, 1989).

4.3.4 Benthic composition effects

Benthic cover was determined using the photo-quadrat method (Preskitt *et al.*, 2004). We used a quadrat of 0.12 m² disposed regularly every 2m along the 20 m transect. The percentage of benthic cover were recorded using the classification of 50 random points in each quadrat according to the software Coral Point Count with extensions Excel (CPCE v4.0) (Kohler e Gill, 2006). Quantitative analyzes were performed considering the following benthic categories: (1) unconsolidated substrate (US), including sand and gravel; (2) turf algae (TA), consisting mainly of filamentous, leaf-shaped and geniculate coralline macroalgae; (3) macroalgae (MA), including mainly *Sargassum* spp. (4) Halimeda sp. (HA); (5) soft coral (SC) and (6) hard coral (HC).

In each quadrat we also counted abundance of the sea urchins *Echinometra lucunter* (Linnaeus, 1758). Key species in coral reef structure (Johansson *et al.*, 2010) with wide distribution in the Brazilian coast (Xavier, 2010) and considered indicators of reef degradation (McManus & Polsenberg, 2004).

4.3.5 Data analysis

Temporal variation in the mean number of post-larvae of *O. trinitatis* captured by light trap was examined by non-parametric Kruskal-wallis test. Two-way ANOVA was used to compare density of juvenile, density of adult residents and potential predators of *O. trinitatis*

between sites and periods. The assumptions of normality and homoscedasticity were tested by Kolmogorov-Smirnov and Levene's Tests and, when necessary, data were square-root transformed. Tukey's tests were performed when ANOVA results were significant.

The relationship between larval supply and recruitment of *O. trinitatis* was examined by linear regression the mean density of newly settled juveniles against the mean of post-larva captured by light-trap. The density of conspecifics was regressed against density of newly settled juveniles (class of 40 mm) and juveniles (class of 50 mm) to determine if recruitment is influenced to densities of conspecifics. To verify the influence of interspecific competitors, the density of juveniles (size class < 7 mm) and adults (size class >7 mm) of *Stegastes fuscus* was regressed against density of recruits/juveniles and adults of *Ophioblennius trinitatis*.

The density of predators was also regressed against juveniles of *O. trinitatis* to verify if abundance of predators was related to presence of recruits. In order to test the effect of the closed area on the recruitment of reef fish, comparisons of density of most abundant species of potential predators of *O. trinitatis* (*Epinephelus adscensionis*, *Lutjanus alexandrei* and *Cephalopholis fulva*) among sites were performed using one-way analysis of variance.

Mortality estimates were determined over a short time interval after peak of recruitment (December to February of 2016) at each reef site. Estimates of the instantaneous rate of total mortality (Z) were obtained using the age-based catch curve method of Ricker (1975). The number of fish in each age class was regressed against the corresponding age, and the descending slope provided an estimate of Z.

The influence of substratum composition and sea urchins on abundance of recruits, juveniles and adults of *O. trinitatis* was performed a distance-based linear model (DistLM; Anderson, 2000). This technique analyzes the relationship between a multivariate data cloud, as described by a resemblance matrix and predictor variables. Resemblance matrices were calculated using Euclidean distance. A redundancy ordination analysis (RDA; Leps & Smilauer 2007), was used for spatial representation of influence of substratum composition and sea urchins on abundance of recruits, juveniles and adults of *O. trinitatis*. We obtained the ordination diagram, the marginal effect (i.e. the total amount of variability in the data that would be explained by that environmental variable alone) and conditional effects (the effect that the environmental variable brings in addition to other variables already in the model) of each environmental variable studied. These effects were expressed by the λ value, which provides an estimate of relative variation (%) of the abundance of recruits, juveniles and adults of *O. trinitatis* that could be explained by each factor (Leps & Smilauer 2007).

To assess relationship between sea urchin abundance and density of adult residents of *O. trinitatis*, we used polynomial regressions with a parabolic shaped relation, since the relationships were not described by a simple linear relationship. Anova one-way was used to verify differences of abundance of sea urchins between sites.

4.4 Results

4.4.1 Temporal patterns of larval supply, juveniles and adults of *O. trinitatis*

The post-larval of *Ophioblennius trinitatis* varied between the sampled months, being significantly more abundant in December 2015 (Kruskal-wallis, d.f = 9, $p = 0.03$). The highest densities of new recruits occurred in April and May of 2015 and December and January of 2015 (ANOVA $p < 0.05$, Table I), coinciding with the periods in which the main larval supply events suggested by light traps collections. The arrival of new recruits seems to have an effect on the increases abundance of juveniles in the periods subsequent to the peaks of recruitment, registering higher densities in April-March 2015 and January-February 2016. In relation to adults, the highest densities were recorded in May 2015 and February 2016 (Fig. 2).

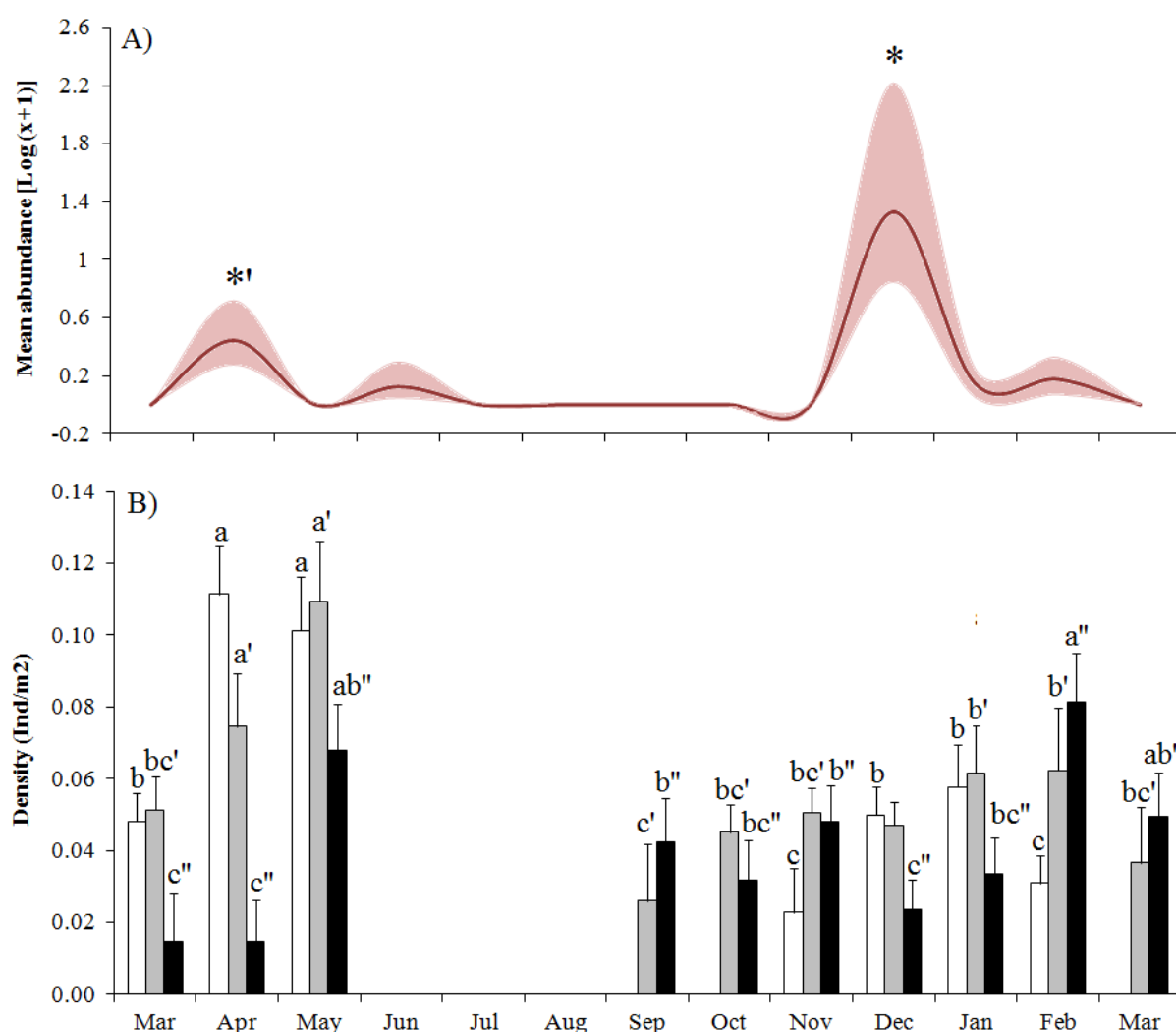


Figure 2. Post-larval abundance (mean $\pm$ standard error) collected by light traps (A), and density (mean $\pm$ standard error) of juveniles (□) and adults (■) of *O. trinitatis* by month. Labels: Red line represent post-larval abundance and the shaded area indicates the standard deviation; Different letters and * represents significant differences between months ($p < 0.05$).

4.4.2 Spatial variation

There are no significant differences in density of new recruits of *Ophioblennius trinitatis* between sites (ANOVA, $P > 0.05$; Table I) (Fig. 3). However the density of juveniles and adults varied significantly among the sites sampled, showing the highest densities in Camurupim, Pirambu and Caieiras, while the lowest densities were recorded in Ilha da Barra, Vau das Campas, Cordão do Mero and Ilha do Norte (Fig. 3).

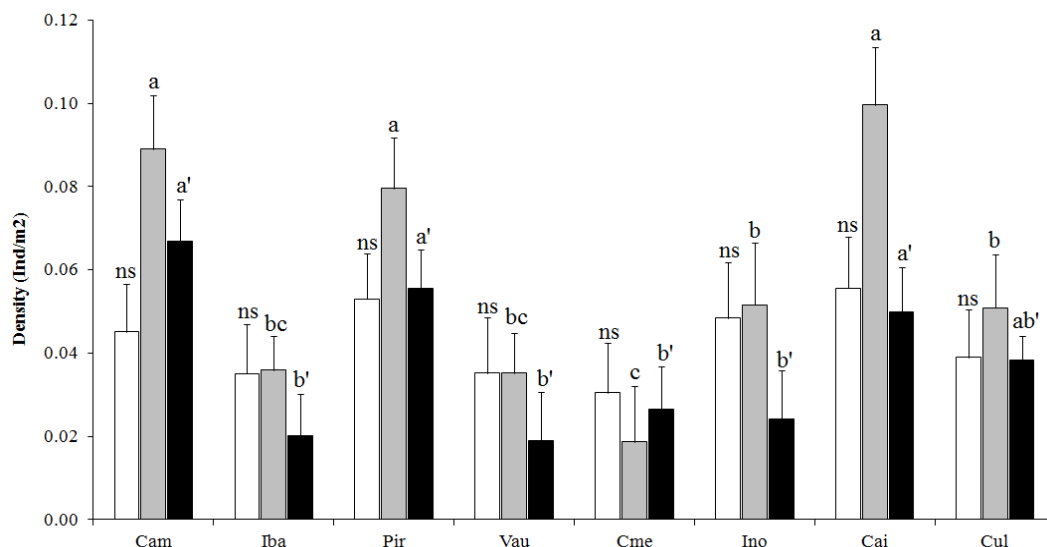


Figure 3. Density (mean $\pm$ confidence interval 95%) of juveniles ($\square$) and adults ($\blacksquare$) of *O. trinitatis* at the eight sites of the Tamandaré reef complex. Different letters designate a significant difference between sites ($p < 0.05$); ns = non significative.

Table I. Results of factorial ANOVA testing the effects of periods and sites on density of recruits, adults and potential predators of *O. trinitatis*.

Source of variation	d.f.	SS	MS	F	P
Density of recruits					
Site	7	0.0316	0.0045	1.0140	0.0654
Periods	9	0.5953	0.0661	32.834	0.0000
Site x Perids	63	0.0245	0.0015	3.3243	0.0451
Residual	474	0.9549	0.0021		
Density of juveniles					
Site	7	0.1745	0.0193	7.6971	0.0000
Periods	9	0.3129	0.0447	17.7430	0.0000
Site x Perids	63	0.5544	0.0088	3.4930	0.0000
Residual	474	1.1942	0.0025		
Density of adults					
Site	7	0.1326	0.0147	9.8140	0.0000
Periods	9	0.1257	0.0179	11.9602	0.0000
Site x Perids	63	0.1751	0.0027	1.1841	0.0482
Residual	474	0.7120	0.0015		
Density of predators					
Site	7	0.114654	0.016379	28.512	0.0000
Periods	9	0.035138	0.003904	6.796	0.0000
Site x Perids	63	0.135697	0.002154	3.749	0.0000
Residual	474	0.272292	0.000574		

4.4.3 Influence of larval supply on recruitment

When we examined the monthly recruiting pulses, there was a significant correlation between the number of post-larvae of *O. trinitatis* collected by light traps and the number of recruits recorded by the visual census, with approximately 66% of the variance of recruitment explained by abundance of post-larval ($R^2 = 0.664$; $p < 0.001$; $y = 0.036x + 0.232$).

4.4.4 Influences of competitors

The new recruits of *O. trinitatis* did not present any relation to the density of conspecifics ($R^2 = 0.16$; $p > 0.05$; $y=0.099x - 0.003$). However, the density of established juveniles was negatively correlated with the density of conspecific, but with a low explicability value of the model ($R^2 = 0.09$, $p = 0.04$, $y=-0.109x + 0.042$).

The interactions between recruits and juveniles of *O. trinitatis* did not present any relation to the density of juveniles and adults of *Stegastes fuscus* ($R^2_{\text{juveniles } S. fuscus} = 0.0011$; $p > 0.05$; $y=0.8634x - 0.2029$; $R^2_{\text{adults } S. fuscus} = 0.001$; $p > 0.05$; $y = -0.242x + 0.0115$). The density of adults of *O. trinitatis* was positive but non significant with the density of juveniles of *S. fuscus* ($R^2 = 0.011$; $p > 0.05$; $y=0.4661x + 0.1967$), and was negatively and significative correlated with density of adults of *S. fuscus* ($R^2 = 0.015$, $p = 0.004$, $y=-1.443x + 0.7439$).

4.4.5 Influence of predators

In all sites, the density of potential predators (carnivorous and piscivorous guild) was significantly and positively correlated with the density of recruits-juveniles of *Ophioblennius trinitatis* ($R^2 = 0.214$; $p < 0.05$; $y=0.403x + 0.013$). Not coincidentally that predators densities were significantly higher in April, May of 2015 and January of 2015 (ANOVA, $p < 0.05$; Table I), which coincides with the periods of higher density of new recruits and juveniles of *O. trinitatis* (Fig. 4).

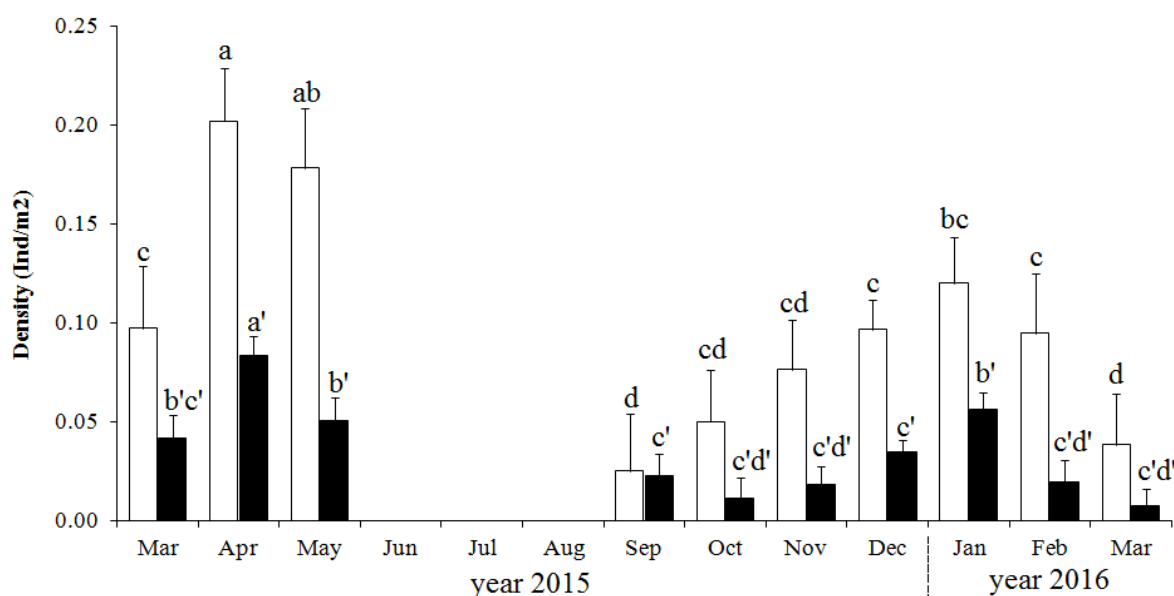


Figure 4. Density (mean $\pm$ confidence interval 95%) of recruits and juveniles of *O. trinitatis* (□) and predators (■) by month. Different letters designate a significant difference between months ($p < 0.05$).

The influence of predators on the recruitment of *Ophioblennius trinitatis* may have been more evident on the no-take area of Ilha da Barra, since this site had a significantly higher density of large predators in relation to the unprotected areas (ANOVA $p < 0.001$; Fig. 5A), mainly in target species such as *Lutjanus alexandrei* and *Cephalopholis fulva* (Figs. 5C e 5D).

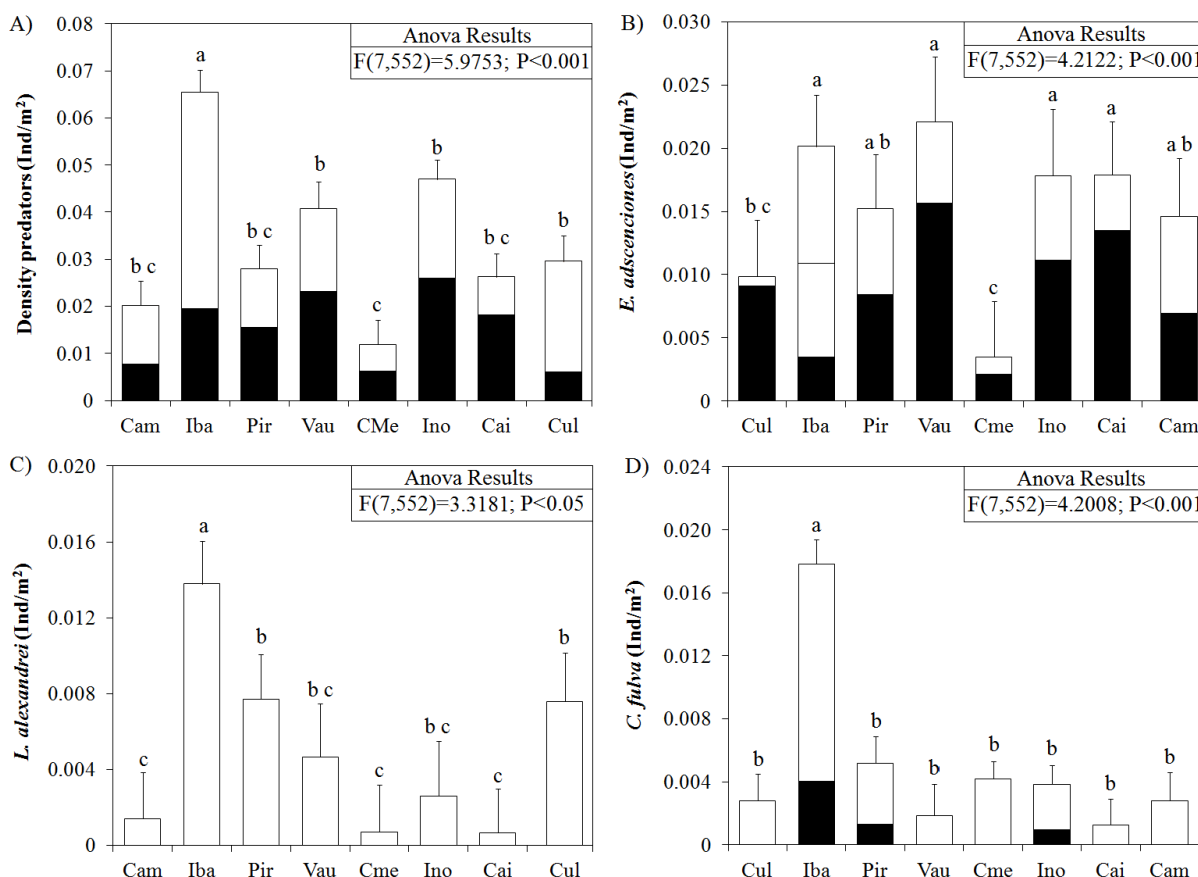


Figure 5. Mean density of potential predators of *O. trinitatis* (A), and the most abundant species of these potential predators: *Epinephelus adscensionis* (B), *Lutjanus alexandrei* (C) and *Cephalopholis fulva* (D) recorded at the eight sites of the Tamandaré reef complex. Labes: Black and white histograms represent fish of classe size smaller and greater than 10 cm respectively. Different letters designate a significant difference ($p < 0.05$).

4.4.6 Mortality

The period after peak recruitment (December 2015 to February 2016) recorded the highest mortality rates in the “closed area” Ilha da Barra, while the lowest rates of mortality were recorded at sites with the highest adult densities of *O. trinitatis* (Camarupim, Culumin, Caieiras, e Pirambu) (Fig. 6).

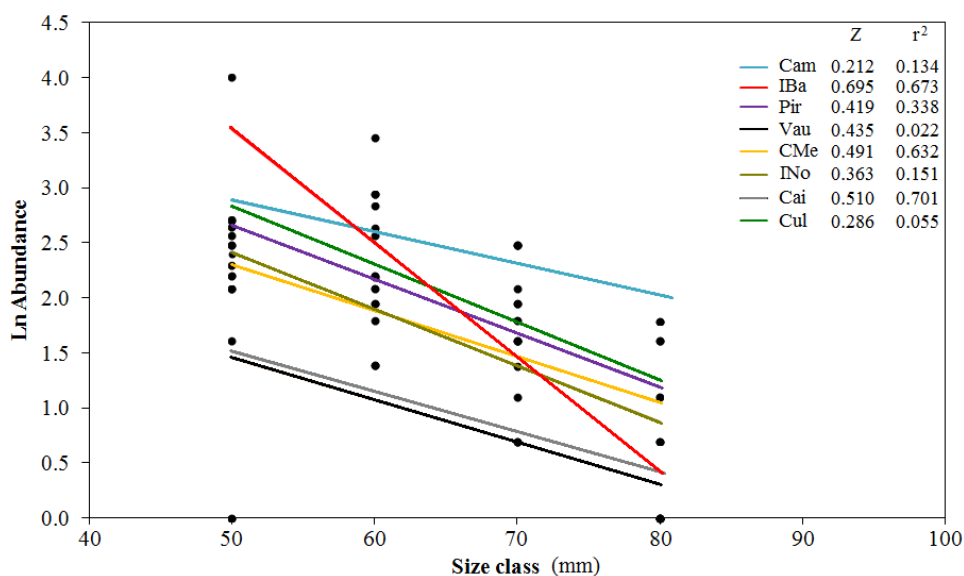


Figure 6. Estimates of total mortality Z for *O. trinitatis* in each reef site a short time interval after peak of recruitment registered by censo visual (December 2015 to February 2016). Labels: Cam - Camurupim, IBa - Ilha da barra, Pir - Pirambú, Vau - Váu das Campas, CMe - Cordão do Mero, INo - Ilha do Norte, Cai - Caieiras and Cul - Culumin.

4.4.7 Microhabitat selection

For *O. trinitatis* recruits, the best model explained approximately 8 % of the variance, with turf algae, *Halimeda* sp., macroalgae and sea-urchins included in the best model (Table III). The best model to predict the distribution of *O. trinitatis* juveniles had six variables (turf algae, *Halimeda* sp. macroalgae, hard coral, soft coral and sea-urchins), and combined, these variables explained 22 % of the variance in the data (Table II). For adults, turf algae, *Halimeda* sp., hard coral and sea-urchins descriptors were the best overall predictors of *O. trinitatis* abundance, and combined, these variables explained 19 % of the variance in the data (Table II).

The microhabitat preferences of recruits, juveniles and adults of *Ophioblennius trinitatis*, suggested by the redundancy analysis (RDA), indicated that abundance of recruits was associated to areas with greater cover of *Halimeda* sp. and turf algae cover, while turf algae, hard coral coverage and abundance of sea urchin were the variables most correlated with juveniles and adult abundances (Fig. 6, Table III). Among the sites, the reef area of Ilha da Barra (closed area) was the most distinguishable among the other reef areas (open areas), however turf algae, *Halimeda* and *Dictyota* algae were the most abundant benthic coverage among reef areas (Fig. 7).

Table II. Distance-based linear model (DistLM) comparing the abundance of juveniles and adults of *O. trinitatis* with environmental. Label: TA (turf algae); SU (sea urchins); HA (Halimeda); HC (Hard coral); SC (Soft coral); MA (Macroalgae); R (Rubble); Prop (proportion of variability explained); res.df (residuals degrees of freedom).

RECRUITS - Marginal tests						
Variables	SS	Pseudo-F	p	Prop	Person's Correlation	
					r	p
HÁ	1.764	25.914	0.001	0.042	0.0851	0.039
TA	0.538	7.680	0.002	0.013	0.0472	0.033
SU	0.355	5.042	0.019	0.008	0.0426	0.041
R	0.183	2.594	0.107	0.004	-0.0059	0.886
HC	0.126	1.783	0.198	0.003	-0.0257	0.533
SC	0.126	1.782	0.194	0.003	-0.0156	0.704
MA	0.014	0.191	0.649	0.001	-0.0915	0.027
Sequential tests						
Variables	AIC	R ²	SS	Pseudo-F	p	res.df
HA	-1594.1	0.0419	1.7642	25.914	0.001	592
HÁ + SU	-1603.1	0.0595	0.73752	11.016	0.002	591
TA + HÁ + SU	-1606.1	0.0673	0.32924	4.9507	0.032	590
TA + HÁ + MA + SU	-1612.2	0.0830	0.40149	6.1201	0.018	589
JUVENILES - Marginal tests						
Variables	SS	Pseudo-F	p	Prop	Person's Correlation	
					r	p
TA	3.740	58.517	0.001	0.090	0.1857	0.001
HÁ	1.632	24.191	0.001	0.039	0.0527	0.201
SU	1.414	20.832	0.001	0.034	0.1439	0.001
SC	1.169	17.134	0.001	0.028	0.0943	0.023
HC	0.098	1.392	0.243	0.002	-0.1207	0.003
R	0.139	1.990	0.158	0.034	-0.0667	0.106
MA	0.042	0.610	0.411	0.001	-0.1693	0.001
Sequential tests						
Variables	AIC	R ²	SS	Pseudo-F	p	res.df
TA	-1631.6	0.090	3.740	58.517	0.001	592
TA + SU	-1662.1	0.138	2.015	33.251	0.001	591
TA + HC + SU	-1679.0	0.165	1.122	19.081	0.001	590
TA + HA + HC + SU	-1704.7	0.203	1.581	28.117	0.001	589
TA + HÁ + HC + SC + SU	-1714.3	0.219	0.641	11.589	0.002	588
TA + HÁ + MA + HC + SC + SU	-1716.5	0.224	0.231	4.213	0.036	587
ADULTS - Marginal tests						
Variables	SS	Pseudo-F	p	Prop	Person's Correlation	
					r	p
TA	3.099	50.413	0.001	0.078	0.1820	0.001
SU	2.896	46.838	0.001	0.073	0.3361	0.001
HÁ	0.774	11.840	0.004	0.019	0.0815	0.048
R	0.709	10.825	0.001	0.018	0.0368	0.372
MA	0.661	10.070	0.002	0.017	-0.2324	0.001
SC	0.452	6.845	0.011	0.011	0.0959	0.021
HC	0.086	1.300	0.265	0.002	-0.0447	0.278
Sequential tests						
Variables	AIC	R ²	SS	Pseudo-F	p	res.df
TA	-1654.6	0.078	3.099	50.413	0.001	592
TA + SU	-1715.7	0.171	3.671	66.285	0.001	591
TA + HC + SU	-1719.7	0.180	0.328	5.979	0.011	590
TA + HA + HC + SU	-1724.7	0.189	0.375	6.911	0.007	589

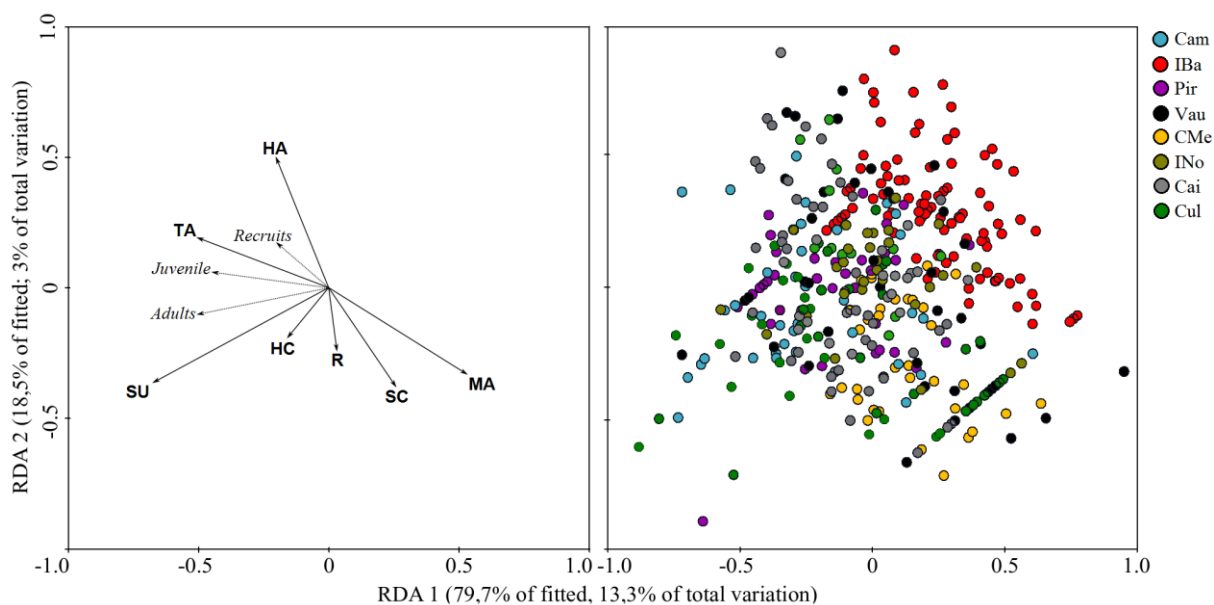


Figure 7. Redundancy analyses (RDA) diagram for the relationship between benthic composition with density of recruits, juveniles and adults of *Ophioblennius trinitatis* at the eighth sites in the Tamandare reef complex. Labels: Benthic composition (SU - sea urchins, TA - turf algae, HA - *Halimeda*, MA - macroalgae, HC - hard coral, SC - soft coral, R - rubble); Reef sites : (Cam - *Camurupim*, IBa - *Ilha da barra*, Pir - *Pirambú*, Vau - *Váu das Campas*, CMe - *Cordão do Mero*, INo - *Ilha do Norte*, Cai - *Caieiras* and Cul - *Culumin*).

Table III. Marginal and conditional effects of benthic composition on density of new recruits, juveniles and adults of *Ophioblennius trinitatis*.

Marginal effects		Conditional effects			
Variable	λ	Variable	λ	A	P
Sea urchins	0.04	Sea urchins	0.04	0.002	26.16
Macroalgae	0.04	Turf	0.05	0.002	32.51
Turf	0.03	Halimeda	0.02	0.002	14.67
Hard coral	0.01	Hard coral	0.02	0.002	15.26
Halimeda	0.01	Macroalgae	0.03	0.004	2.35
Soft coral	0.01	Rock	0.01	0.084	1.77
Rock	0.00	Soft coral	0.00	0.164	

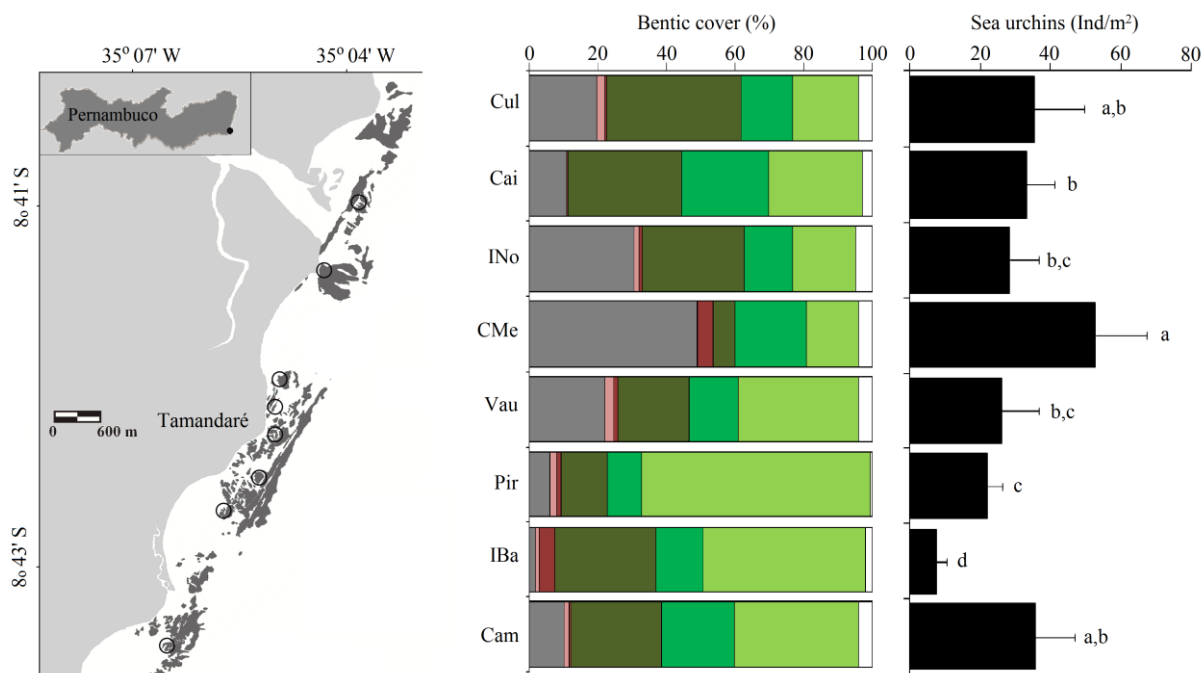


Figure 8. Relative percent cover of benthic groups by localities (A); Sea urchins abundance (Ind/m² ± SD) between the eighth sites sampled (B). Different letters designate a significant difference ($p < 0.05$).

It can be seen that the relationship between the abundance of adults of *Ophioblennius trinitatis* and sea urchins, showed an optimal range of functioning (Fig. 9). The results suggest a possible interspecific interaction with the best performance occurring in a certain abundance of sea urchin. Under these conditions, the greatest number of adults of *O. trinitatis* occurred in conditions of intermediate abundance of sea urchin, whereas in situations of low or high sea urchin abundances, a decrease in interaction performance occurs, registering low densities of adults of *Ophioblennius trinitatis*.

This condition can be easily visualized when comparing the density of adults of *O. trinitatis* and the density of sea urchins between sites (Fig. 7). In this case, areas with low density of sea urchins, such as those recorded in the MPA Ilha da Barra, or areas with high densities of sea urchins, such as the site Cordão do Mero, presented the lowest densities of adult compared to other areas reefs.

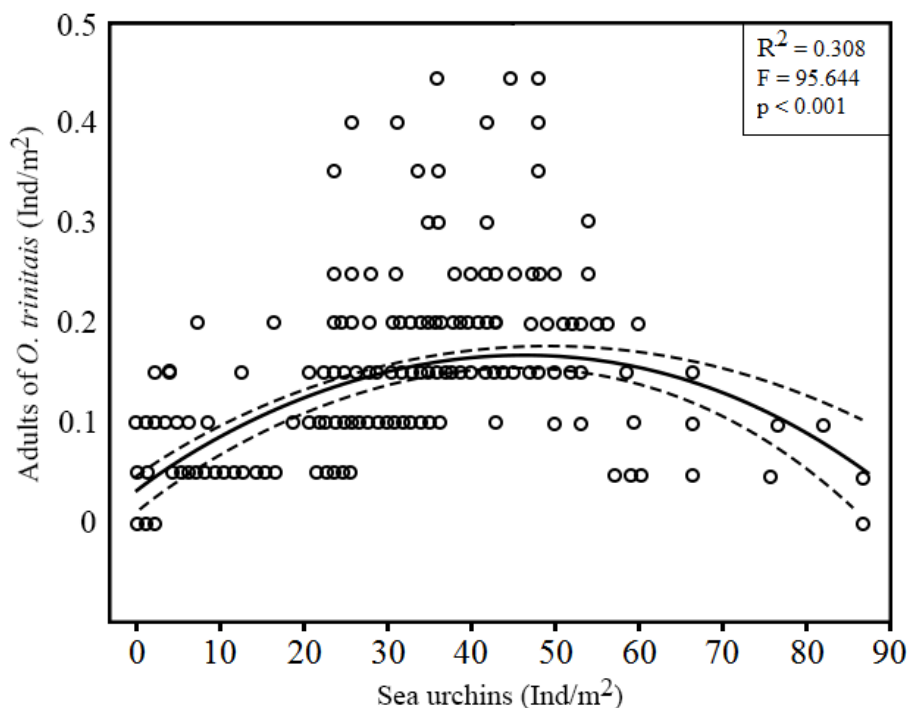


Figure 9. Relationship between density of adults residents of *O. trinitatis* and density of sea urchins; the polynomial regression curve of the data is shown.

4.5 Discussion

In this study, we simultaneously examined the importance of larval supply, settlement and post-settlement processes in the control of recruitment and subsequent population of *Ophioblennius trinitatis*. The contribution of post-settlement processes, such as the selection of microhabitats, combined with predator and competitor intra/interspecifics effects were considered important factors in structuring population patterns.

4.5.1 Larval supply

Overall, the presence of recruits was consistent with the magnitude of larval supply recorded by the light traps, suggesting that in the initial stages of recruitment, larval supply probably determines the number of recruits added to population of *Ophioblennius trinitatis*. However, despite the relationship between larval supply and settlement densities, the arrival of larvae was not responsible for the differences observed in adult abundance among sites, implying that the final population structure of *O. trinitatis* may have been determined by processes that occur post-settlement.

Several studies have reported the absence of a relationship between larval supply and recruitment (Robertson *et al.*, 1993), while others have found recruitment patterns correlated

with larval supply (Milicich *et al.*, 1992; Meekan *et al.*, 1993). Therefore, the degree to which recruitment patterns are influenced by availability of post-larvae is species-specific. As example, Sponaugle & Cowen (1996) suggest that for the damselfish *Stegastes partitus* (Poey, 1868) spatial patterns of recruitment were controlled by variation in larval supply, while the surgeonfish *Acanthurus bahianus* Castelnau, 1855 the initial selection of habitat may have nullified the patterns of larval supply.

Two other factors may have masked the effect of the larval supply on the final abundance of adult population: 1) The samplings of the present study may not have been long enough to reveal the dependence of the adult population to magnitude of larval supply. Maybe in situations of inadequate larval supply the structural patterns of the adult population could be directly affected, varying according to the rate of colonization rather than post-settlement processes (Recruitment-Limited Hypothesis; Doherty 1981). Jones (1990) showed that the dynamics of adult populations of damselfish *Pomacentrus amboinensis* is a reflection of recruitment in situations of low settlement rates, whereas in good recruitment periods adult densities may have been limited by post-settlement processes. 2) The impact and effect of the larval supply may also have been masked by the spatial scale adopted. Probably in studies of larger spatial scales, the effects of limited recruitment are more evident than those observed in small scales as in the present work. According to Steele & Forrester (2002), small-scale settlement patterns may be obscured by pos-settlement processes, so the relationship between recruitment and larval supply may be more evident as spatial scale increases.

4.5.2 Predators and competitors effects

Several studies suggest that recruitment patterns may be influenced by post-recruitment phase (Macpherson *et al.*, 1997; Schmitt & Holbrook, 1999; Shima, 2001), with density-dependent mortality being the main regulator of adult density (Density-dependent Hypothesis). Here, the presence of predators was directly related to the abundance of recruits and juveniles of *O. trinitatis*, with indications that the establishment of larvae may be regulated by predation. It is no coincidence that one of the strategies of post-larvae in order to avoid visually oriented predators is settlement during dark nights close to the new moon period (see chapter 3). We suggest that predation was an important predictor in density and structure of adult populations, and it is possible to be one of the factors responsible for demographic differences between sites.

The presence of conspecifics may favor settlement rate (Lecchini *et al.*, 2007), inhibit it (Almany, 2003) or may not have any effect on the larval settlement (Doherty, 1983; Jones,

1984). In the present work, the presence of conspecific had different effects according to the size of the recruits, suggesting that the impact of adults on settlement rate and juvenile survival varied according to the ontogeny of the species.

Although not significant, the relationship between the density of newly settled recruits and mature adults tends to a positive, suggesting that the presence of conspecifics may have initially served as an indication to suitable and high-quality habitat for settlement (Levin, 1993). In addition, newly settled recruits may not represent effective competitors for mature adults. According to Labelle & Nursal (1985), the species of *Ophioblennius atlanticus* does not appear to feed until the end of the metamorphosis that occurs after settlement, assuming that fat deposits in the liver are the main source of energy in that period. The same can occur with the specie *O. trinitatis* due to ecological and phylogenetic similarity (Lastrucci *et al.*, 2018), which probably causes a reduction of ecological niche overlap, attenuating competition in the early stages of recruitment and accommodating more individuals in the territory size of adults. It is important to emphasize that food is not the only limiting resource in the reef system, especially for small species susceptible to predation such as blennid *Ophioblennius trinitatis*. In this case, the number of holes, crevices and structures that serve as refuges can become an important limiting resource, so that even if there is no competition for food, high density of recruits may result in competition for shelters and refuges on the reef.

The negative and significant relationship between juveniles and mature adults shows an intraspecific interaction involving negative effects. In this size class individuals have already through metamorphosis and already share the same food and space as resident adults, making them potential competitors. This type of interaction was already expected due to the aggressive nature and territoriality of *Ophioblennius trinitatis* adults in the defense of resources present within their resident area (Medeiros *et al.*, 2014).

The identity of the species and different sizes between individuals of the same trophic guild, appear to have an important influence on the interspecific aggressive interactions. Among species with similar morphology and behavior, dominance hierarchies seem to be largely based on size (Webster, 2000). This seems to be the case between the damselfish *Stegastes fuscus* and the blennid *O. trinitatis*. However, the negative and significant relationship shows negative effects only among adults of these species.

As post-recruitment mortality is density dependent, the competitive intensity proceeds to increase as the carrying capacity approaches its limit. Here two situations can occur: 1) in areas with low complexity, inter and intraspecific competition intensifies due to limitation number of shelters; 2) The second situation occurs when individuals grow, their territorial size

also increases, reaching twice the size of the recruits, in the case of females of the genus *Ophioblennius* (Hunte & Cotê, 1989). The apparent absence of interspecific competition between smaller individuals of *S. fuscus* and *O. trinitatis* can be explained by their small territories, which at this stage of life still do not overlap. However, as they grow in size, individuals need a larger foraging and breeding territories, increasing the chances of territorial overlap and intensifying competition as adults.

4.5.3 Microhabitat selection

Although the density of recruits was very similar between reef areas suggesting a similar larval supply between sites, the final distribution of the adult population differed between reefs, contrasting with juvenile recruitment patterns. Therefore, in addition to predation and competition effects, we suggest that variations in habitat characteristics is the one of main principal responsible for modeling patterns of distribution and abundance of the adult population in the present work.

Microhabitat characteristics can affect the distribution and abundance of fish during colonization or improve their survival. Sale *et al.* (1984) suggest that variation in recruitment of coral reefs fishes at small-scale may occur due to microhabitat characteristics. It appears to be the case in the present study, where recruits and juveniles occupied areas with greater coverage of alga turf and *Halimeda*, while adults showed higher densities in places with alga turf and sea urchins. These findings corroborate the results of Randall (1996) and Medeiros *et al.* (2014), which report that algae turf and associated filamentous algae are the benthic items preferred inhabited by *Ophioblennius trinitatis*. However, the high abundance of algae turf in the study area presupposes that food availability is unlikely to be a limiting resource for this specie.

The relation of adult of *Ophioblennius trinitatis* to presence of sea urchins *Echinometra lucunter* seems to be related to the use of the sea urchins and the cavities in which they are housed as alternative shelter and protection to blennids. When they provide shelter and protection, sea urchins can reduce predation rates, becoming a determining factor in the abundance of reef fish on the local scale. In fact, blennids of the genus *Ophioblennius* are associated with substrates with sufficient structural complexity to provide shelter. Several studies report that individuals alter fast foraging with periods of rest within crevices and cavities as a means of reducing the risk of predation (Nursall, 1981; Mendes, 2006). However, we observe that the capacity of sea urchins to act as a refuge for *O. trinitatis* presents an

optimal range of performance. The results suggest an increased fitness of *O. trinitatis* occurs at intermediate levels of aggregation of sea urchins.

It is likely that at low densities of sea urchins there are not enough individuals to provide protection and shelters against predators when compared to situations of higher sea urchin densities. On the other hand, at high densities, sea urchins can drastically reduce the algae cover and can transform large expanses of substrate into simplified sterile grounds (Lawrence, 1975; Vadas & Elner, 1992). Thus, in places with high density of sea urchin, food can become a rather scarce resource for the blenny *O. trinitatis*, so the availability of shelters and protection provided by sea urchins may not compensate for food shortages.

4.5.4 Influence of Marine Reserves

The density of young recruits of *O. trinitatis* did not differ between the protected and unprotected areas, implying that larval supply did not vary between sites. However, the subsequent population in the closed area had one of the lowest densities of resident adults among sites. This suggested that the level of protection had no influence on the settlement rate, but on the other hand, can have great effects on post-settlement processes recruitment patterns of *Ophioblennius trinitatis*.

Protected marine areas due to high habitat quality are expected to increase juvenile survival due to greater availability of food resources and shelter for new recruits (Caselle & Warner, 1996; Tupper & Boutilier, 1997; Holbrook & Schmitt, 2002). However the opposite pattern found for the population of *O. trinitatis* in the protected area can be explained by the availability of shelters and predation pressure.

The high percentage of benthic cover of algal turf and *Halimeda*, confirms that the availability of food resources was not considered a limiting resource for the species which helps to explain the low densities of adults found on the site. Furthermore, as shelter availability is probably one of the major limiting features in the present study, the success of larval recruitment becomes strictly dependent on this resource. Because sea urchins at intermediate levels of abundance appear to be being used as an alternative refuge for blennids, sites with low densities or super-populated areas of sea urchins may result in poor recruitment success of *O. trinitatis*.

One of the possible effects of the exclusion of fishing and tourism in the reef area of Ilha da Barra is the reduction of the density of sea urchin *Equinometra lucunter* through the re-establishment of predators. Several studies report the effect of re-establishment of predators that control the abundance of sea urchins in marine protected areas (Brown-

Saracino *et al.*, 2007; Harborne *et al.*, 2009). The low density of sea urchins in the enclosed area probably reduced on-site shelter availability, which would limit the presence of recruits by increasing competition for on-site refuge and causing an increase in predation rates. Another possibility is due to the high density of potential predators of this blennid in the protected area, including species exploited by fishing (*Epinephelus adscensionis*, *Cephalopholis fulva* and Lutjanids), and that may have exerted a greater pressure on the *O. trinitatis* recruits, reducing the success of the recruitment in the area.

In fact, the effect of protected area is most expected (among other objectives) on protection of a critical spawning stock biomass to ensure recruitment and the maintenance / enhancement of yields to areas adjacent to reserves by post-settlement movements (eg Alcala & Russ, 1990; Bohnsack, 1990; Plunking & Roberts, 1993; Dugan & Davis, 1993), than in the success in the settlement/recruitment rates within their delimitations (Gorud-Colvert & Sponaugle, 2009).

4.5.5 Conclusions

In conclusion, a clear link between larval supply and recruit abundance was observed, indicating the potential of pre-settlement processes as regulators of population structure. However, pos-settlement processes were as the main factors controlling post recruitment survival and consequently abundance. It appears probable that recruitment and early survival of *Ophioblennius trinitatis* are influenced by three interacting factors: (1) the microhabitat type and availability of appropriate shelter sites, (2) predation pressure and (3) intra and interspecific aggression among fishes using and defending territories.

The choice of microhabitat in the settlement processes was one of the main factors responsible for the survival of the individuals. In the case of *O. trinitatis*, the individuals were correlated to sites with sea urchins, since these organisms provide shelter against predators. The strong influence of microhabitat on the survival of the blennid *O. trinitatis* and species associated with reefs, demonstrates that the loss and degradation of reef habitats can have a considerable impact on the population structure of coral reef fishes.

Although the protected marine area does not present benefits in the recruitment of blennid *O. trinitatis*, conducting further research is still required to assess the effects of marine reserves on recruitment levels at broad spatial scales (Carr & Reed, 1993; Man *et al.*, 1995). If such recruitment benefits do occur, they will tend to apply at the larger spatial scale of the stock since larvae may disperse great distances.

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5 DISCUSSÃO GERAL

Os peixes de recife de coral possuem em sua grande maioria um ciclo de vida bipartido apresentando um estágio larval dispersivo e pelágico (Leis, 1991; Victor, 1991), precedendo estágios juvenis e adultos relativamente sedentários e associados a determinados tipos de substratos (Sale, 1980; Victor, 1991).

Como a fase pelágica potencialmente dispersiva é considerado o primeiro passo de uma cadeia de eventos sucessivos que culminam na estrutura da população adulta, compreender o início da história de vida de peixes marinhos é determinante na dinâmica populacional (Grorud-Colvert & Sponaugle, 2009). Contudo, o estudo sobre a fase inicial da vida dos peixes é um campo de pesquisa difícil e intrigante, em especial no seu estágio planctônico final ou pré-assentante, sendo que um dos primeiros desafios nesta empreitada é a escolha de técnicas e métodos de amostragens adequados e capazes de fornecer informações básicas e necessárias sobre as espécies.

5.1 Considerações gerais

O presente estudo teve o registro de uma grande diversidade de espécies, apresentando uma composição taxonômica muito semelhante a levantamentos anteriores de peixes marinhos realizados na região (Ferreira *et al.*, 1995; Ferreira & Cava 2001; Araujo *et al.*, 2004; Paiva *et al.*, 2009; Pereira *et al.*, 2014). Trabalhos de Dorety (1987) e Milicich (1992) já mostravam que a armadilha da luz é capaz de coletar grandes quantidades de peixes de estágio de assentamento de uma ampla gama de taxa.

O uso de armadilhas de luz no presente estudo permitiu realizar a primeira investigação e registro de peixes recifais pós-larvares associados no Atlântico Sul (Capítulo 2) podendo ser considerado uma linha de base para entender a ecologia de peixes adultos tanto na área de estudo quanto em outras áreas do Atlântico Sudoeste.

Por outro lado, espécies relatadas como comuns na área, como por exemplo, o Pomacentrideo *Stegastes fuscus* (Ferreira *et al.*, 1995; Ferreira & Cava, 2001; Pereira *et al.*, 2014), foram raras ou não registradas em nossa amostragem. A ausência de algumas espécies na coleção do presente trabalho pode ser explicada pela própria natureza das armadilhas de luz, no qual produzem estimativas tendenciosas da comunidade planctônica, devido a sua seletividade (Thorrold 1992, 1993; Choat *et al.*, 1993). Não são todas as larvas de peixes que são atraídas pela luz das armadilhas (Hickford & Schiel, 1999; Chícharo *et al.*, 2009; Grorud-Colvert & Sponaugle, 2009), além disso, a resposta positiva das larvas à luz, pode mudar

durante a ontogenia das espécies (Bulkowski & Meade, 1983; Murphy & Willis, 1996). Já algumas espécies de peixes recifais apresentam um período de dispersão larval extremamente curto, indicando uma retenção larval a poucos metros dos locais de eclosão (Jones *et al.*, 2005), o que afetaria diretamente a probabilidade de serem capturadas por armadilhas de luz. Como a eficácia das armadilhas de luz também dependem das condições oceanográficas locais, fatores físicos como a clareza da água e a velocidade da corrente, podem afetar a capacidade das larvas de ver a luz emitida pela armadilha e de sua capacidade de nadar e entrar em um recinto iluminado (Doherty, 1987; Milicich *et al.*, 1992; Thorrold, 1992).

Apesar de poucas espécies comuns na área de estudo não terem sido capturadas pelas armadilhas luminosas, sugerimos que o uso de armadilhas de luz Ecocean é uma ferramenta útil no estudo da taxonomia, história de vida precoce, estrutura de assembléias e distribuição espacial de uma ampla gama de pré-assentamentos peixes na região, confirmando que armadilha de luz são consideradas uma ferramenta eficaz na amostragem de larvas em estágio avançado que são estabelecidas em recifes de corais (Milicich *et al.*, 1992; Valles *et al.*, 2001; D'Alessandro *et al.*, 2007) e particularmente valioso para estudos de conectividade em áreas litorais, já que a presença de pré-colonos indica o desfecho de ambos os processos de transporte e comportamentais ocorridos antes da mudança para um estilo de vida demersal.

A eficácia do método de armadilha luz pode ser observada em muitas espécies coletadas regularmente neste estudo. Este é o caso do blenídeo *Ophioblennius trinitatis* Miranda-Ribeiro 1919, considerado uma espécie endêmica frequentemente encontrada no sistema recifal e amplamente distribuído ao longo da costa Nordeste do Brasil e ilhas oceânicas associadas (Lastrucci *et al.*, 2018).

Por ser uma parte integrante da dinâmica trófica da comunidade (Randall, 1967; Emery, 1968) e um importante elo energético entre produtores primários e carnívoros (Labelle & Nursall, 1992), o blenídeo *O. trinitatis* foi a espécie modelo selecionada para o estudo da variação sazonal e interanual no suprimento larval, do efeito dos traços iniciais da história de vida sobre o assentamento /recrutamento e na influencia de variáveis ambientais na magnitude larval (Capítulo 3). Além disso, também foi examinado o papel dos processos pós-assentamento sobre os padrões de recrutamento e subsequente população adulta e verificado o efeito da área marinha protegida sobre a população do blenídeo *Ophioblennius trinitatis* (Capítulo 4).

Os resultados revelaram padrões interanuais, sazonais e padrões lunares no assentamento do blenídeo *Ophioblennius trinitatis* (Capítulo 3). A oferta de larvas variou

interanualmente, apresentando picos excepcionais na oferta de larvas nos anos de 2011 e 2015. Os resultados da presente tese revelaram que a magnitude do recrutamento foi significativamente correlacionada com a temperatura da água e velocidade do vento, indicando que o assentamento / recrutamento é afetado por vários fatores ambientais (Caselle *et al.*, 2010).

O recrutamento mensal consistentemente atingiu o pico durante o final da primavera e verão (dezembro a março). A variação sazonal do recrutamento é provavelmente impulsionada em grande parte pelos padrões de produção (Robertson *et al.*, 1988) ou por condições oceanográficas favoráveis (Labelle & Nursall, 1992). Já a chegada de larvas pré-assentantes foi diretamente relacionado com o ciclo lunar, como também descrito para outras espécies de peixes de recifais (Robertson, 1992; Lozano & Zapata, 2003; Ben-David & Kritzer, 2005). O período de assentamento retro-calculado atingiu picos próximos a lua nova. Uma explicação frequentemente assumida para esse padrão é a de evitar o risco de predação relacionado às condições noturnas de luz (Robertson *et al.*, 1988, Sponaugle & Cowen, 1994). Outro comportamento adaptativo é a possível capacidade das larvas de *O. trinitatis* de protelar o assentamento larval, estendendo a etapa dispersiva, e assim aumentando as chances de encontrar habitats adequados e de assentarem em tamanhos maiores (Barlow, 1981; Cowen, 1991), favorecendo as chances de colonização.

O estudo relacionado a fase pelágica de *O. trinitatis* demonstrou que a variação e intensidade do suprimento larval, e o consequente sucesso no recrutamento podem ser resultado da interação entre processos biológicos/comportamentais (Kerrigan, 1997; McCormick, 1999) e de eventos estocásticos como os processos oceanográficos físico-ambientais (McCormick & Molony, 1995). A fase larval dos peixes é geralmente mais sensível que os adultos às flutuações ambientais e podem ser especialmente vulneráveis às mudanças climáticas (Pankhurst & Munday, 2011). Neste contexto, os resultados aqui apresentados em relação ao estágio inicial da vida e os padrões de recrutamento do blenídeo *O. trinitatis*, podem ser traduzidos em informações valiosas para verificar os possíveis efeitos da mudança climática, principalmente no que se refere ao aumento da temperatura global.

Na fase pós-assentamento do *O. trinitatis*, foi analisando os padrões de recrutamento em uma escala fina de março de 2015 a março de 2016. Os resultados sugerem que a demografia juvenil e adulta foi afetada principalmente por processo que ocorrem pós-assentamento (Capítulo 4). De fato, a mortalidade durante a fase de assentamento e pós-assentamento é considerada muito alta (Caselle, 1999; Almany, 2004; Doherty *et al.*, 2004;

Planes *et al.*, 2009) e, portanto, o efeito do recrutamento na população adulta pode ser dependente da densidade.

Nesta tese, verificamos que a magnitude no suprimento larval refletiu em parte a abundância de novos colonos adicionados à população, indicando que a abundância de peixes em estágio de assentamento foi um bom preditor na abundância de novos recrutas. Isso sugere que eventos de desova e/ou processos planctônicos podem determinar, pelo menos em parte, no padrão observado nos estágios iniciais do recrutamento. Contudo, a influência do suprimento larval sobre os padrões de recrutamento e subsequente população pode ter diferentes respostas de acordo com a espécie (Milicich *et al.*, 1992; Meekan *et al.*, 1993, Robertson *et al.*, 1993).

Embora a densidade de recrutas não tenha variado significativamente entre as áreas amostradas, a distribuição final da população adulta diferiu entre os recifes não seguindo o mesmo padrão demográfico dos juvenis, sugerindo que a variação observada na abundância de adultos pode ter sido determinada por processos que ocorrem após o assentamento. A contribuição dos processos de pós-assentamento como a seleção de microhabitats, combinado com os efeitos de predadores e coespecíficos, foram considerados importantes fatores para estruturar os padrões populacionais de *O. trinitatis*.

Com base em levantamentos de *O. trinitatis* realizados em 2015 e 2016, as densidades de novos recrutas não apresentou correlação significativa com a densidade de conspecíficos adultos, enquanto a densidade de juvenis foi negativamente correlacionada com a densidade de coespecíficos, sugerindo que a presença de adultos de *O. trinitatis*, pode atuar como um indicativo para o assentamento em um habitat adequado e de alta qualidade (Levin, 1993), contudo, a medida que os novos recrutas vão crescendo, passam a competir com os adultos pelos recursos presente área. Embora significativo, a baixa explicabilidade do modelo sugere que a competição intraespecífica não foi o principal preditor na estrutura populacional.

Já a presença de predadores foi diretamente relacionada a abundância de recrutas e juvenis de *O. trinitatis*, sendo considerado um dos fatores preditores na densidade e estabilidade da população adulta, e provavelmente um dos principais fatores responsáveis pelas diferenças demográficas observadas entre as áreas recifais.

A intensa pressão predatória torna a presença de refúgios um importante recurso limitante para populações de presas. Parece ser o caso do *O. trinitatis*, onde a interação com o ouriço do mar *Echinometra lucunter*, provavelmente está relacionado ao uso indireto dos ouriços e as cavidades em que se abrigam como um refúgio alternativo para o bennídeo. A

seleção de microhabitats provalmente é diretamente influenciada de acordo com as interações pós-assentamento como a predação (Holbrook e Schmitt 2002) e competição (Jones e McCormick, 2002). Além disso, diversos trabalhos afirmam que os indivíduos do gênero *Ophioblennius* alteram o rápido forrageamento com períodos de repouso dentro de fendas e cavidades como meio de reduzir o risco de predação (Mendes, 2006; Nursall, 1981).

Ao verificar os possíveis efeitos de uma área marinha protegida no recrutamento e subsequente população adulta de *Ophioblennius trinitatis*, observamos que a densidade de jovens recrutas não diferiu entre as áreas protegidas e desprotegidas, implicando que o fornecimento de larvas não variou entre os locais. Já a população adulta subsequente na “área fechada” da Ilha da Barra foi significativamente uma das menores entre os locais. Presume-se, portanto, que o nível de proteção não teve influência sobre a taxa de assentamento, mas que, por outro lado, pode ter efeitos sobre os padrões de recrutamento do *Ophioblennius trinitatis*. Um possível efeito resultante da implementação da área fechada, é o aumento da pressão de predação sobre os recrutas de *O. trinitatis* devido ao aumento dos potenciais predadores do blenídeo, incluindo espécies exploradas pela pesca.

De fato a instalações de áreas marinhas protegidas são voltadas muito mais na manutenção das populações em níveis ecologicamente sustentáveis, com benefícios que incluem o aumento da abundância e biomassa de grandes peixes (por exemplo, McClanahan *et al.*, 1999; Halpern, 2003; Russ & Alcala, 2003). Entretanto, compreender a importância da contribuição das áreas marinhas protegidas para o fornecimento e recrutamento de larvas, tanto na reserva como nos recifes adjacentes, é fundamental para a gestão e justificação das reservas. Reservas corretamente localizada podem amortecer a alta variabilidade de recrutamento em áreas deplecionadas (Bohnsack, 1990) e contribuir para uma recuperação mais rápida dos efeitos causado pela sobrepesca nessas áreas (Bohnsack & Ault, 1996).

5.2 Implicações na conservação e manejo

Nesta tese os dados a respeito do assentamento e recrutamento exibiram padrões temporais claros, contribuindo para os padrões gerais da estrutura populacional do blenídeo *O. trinitatis*. Os resultados aqui apresentados fornecem novos conhecimentos sobre o estágio inicial da vida e os padrões de recrutamento de uma espécie modelo de peixe recifal, e que podem ser traduzidos em informações valiosas para o manejo e conservação de áreas recifais costeiras.

Devido à influência do recrutamento na dinâmica e persistência das populações, a compreensão dos processos e padrões de recrutamento tem sido um objetivo de longa data na ecologia marinha. Estudar a relação entre os padrões de recrutamento e os processos oceanográficos é essencial para estimar os efeitos das mudanças ambientais e climáticas, o que possibilitaria uma gestão e manejo da conservação mais sustentável. Além disso, a conservação e gestão da biodiversidade de importantes recursos pesqueiros e dos diferentes habitats visam saber como a persistência das populações pode ser mantida e, neste sentido, a investigação de padrões e processos do assentamento/recrutamento assume grande importância, em particular para a concepção e gestão de áreas marinhas protegidas.

Os padrões interanuais e sazonais do assentamento/recrutamento encontrados nesta tese demonstram que as condições oceanográficas de diferentes escalas espaço-temporais afetam a dinâmica e a estrutura das populações de peixes e precisam ser considerados no manejo de conservação. Assim, os resultados fornecidos por este estudo podem fornecer informações úteis para a gestão da APA Costa dos Corais.

5.3 Pesquisas futuras

Idealmente, um monitoramento permanente (continuado) dos padrões de assentamento e recrutamento deve ser estabelecido, a fim de compreender melhor os padrões espaço-temporais das estruturas populacionais. Em particular, análises feitas para testar relações com processos oceanográficos ganham precisão com séries temporais de dados mais longas, cobrindo uma gama maior de condições oceanográficas e permitindo compreender com mais profundidade o efeito das mudanças ambientais e climáticas.

De grande interesse, também seria estudos combinando diferentes métodos de amostragem, como armadilhas luminosas, redes de arrasto, censos visuais, entre outros, a fim de coletar vários estágios ontogenéticos de uma gama de diferentes taxons. Além disso, para uma melhor compreensão dos padrões de assentamento/recrutamento em pequena escala e sua relação com processos oceanográficos, recomenda-se um esquema de amostragem ainda mais fino para analisar o efeito de padrões ambientais, como o ciclo lunar e processos relacionados a amplitudes de maré (Findlay & Allen, 2002).

No que se refere ao blenídeo *O. trinitatis*, um monitoramento do recrutamento durante vários anos poderá confirmar a importância da espécie como um indicador de distúrbios ambientais. A fim de compreender a influência da condição larval no sucesso do recrutamento em relação a fatores ambientais, seria necessário estimar a perda de novos

recrutas devido a processos pós-assentamento, como por exemplo, investigando a predação com experimentos em gaiolas (Steele & Forrester, 2002).

Apesar do conhecimento sobre conectividade populacional ser essencial para a proteção das populações de peixes, muito pouco se sabe sobre a dispersão larval e conectividade populacional das espécies de peixes da costa Nordeste do Brasil. Portanto, é importante abordar esses tópicos de pesquisa em estudos futuros, que poderiam visar várias espécies ecologicamente e economicamente importantes na região. Neste caso, abordagens diretas e indiretas, como por exemplo, a análise da estrutura populacional genética e/ou modelo de dispersão biofísico, revelaria mais informações críticas para a gestão da pesca e conservação, uma vez que para o estabelecimento de áreas marinhas protegidas é fundamental informações prévias sobre conectividade populacional, o movimento e a dispersão de larvas, juvenis e peixes adultos (Christie *et al.*, 2010; Grorud-Colvert *et al.*, 2014, Green *et al.*, 2015).

Além dos processos oceanográficos, a investigação comportamental da larva pode fornecer informações relevantes para a compreensão dos padrões de recrutamento e da dispersão e/ou retenção de larvas perto dos recifes. A integração de dados comportamentos em modelos biofísicos será de grande importância para se obter estimativas mais realistas de dispersão (Leis, 2007).

6 CONCLUSÃO GERAL

Este primeiro estudo de peixes recifais pré-assentantes utilizando armadilhas luminosas no Oceano Atlântico tropical sudoeste, adiciona a um crescente banco de dados global, conhecimento sobre a estrutura da assembleia de larvas de peixes recifais em fase de assentamento.

Os resultados indicam que apesar dos diferentes desafios enfrentados no estudo das fases iniciais da vida dos peixes, incluindo métodos de amostragem tendenciosos e a dificuldade de identificação taxonômica, o registro de um grande número de espécies, com uma elevada diversidade de cores e formas corporais, contrapõem a ideia de que as larvas de peixes são notoriamente opacas.

No geral, o uso de armadilhas de luz Ecocean se mostrou bastante efetivo na coleta de larvas de peixes recifais pré-assentantes em Tamandaré, sendo considerada uma ferramenta útil no estudo da taxonomia, história de vida, ecologia e dispersão dos peixes recifais,

mesmo que a ausência de poucas espécies comuns na área de estudo revele o viés e seletividade das armadilhas luminosas.

Esta tese também enfatiza a importância dos processos pré e pós-assentamento na dinâmica populacional do blenídeo *Ophioblennius trinitatis*. Os resultados de cinco anos de coletas revelaram variações sazonais no recrutamento, com picos registrados na primavera-verão e em períodos próximos a lua nova, provavelmente como uma estratégia de sobrevivência, seja por assentarem em períodos com condições oceanográficas favoráveis ou para evitarem predadores orientados visualmente.

A magnitude do recrutamento de larvas pré-assentantes de *Ophioblennius trinitatis* também foi significativamente correlacionada com a temperatura superficial da água e velocidade do vento, apresentando picos excepcionais na oferta de larvas nos anos de 2011 e 2015, períodos em que registrou-se elevadas temperaturas da superfície do mar associados aos eventos de El Niño. Esses resultados apontam o blenídeo *Ophioblennius trinitatis* como uma espécie chave no estudo dos possíveis efeitos da mudança climática, principalmente no que se refere ao aumento da temperatura global.

Na fase pós-assentamento, apesar da magnitude no suprimento larval refletir na abundância de novos colonos adicionados à população, os resultados apontam que o padrão demográfico de juvenis e adultos foi afetado por processos que ocorrem pós-assentamento, de modo que a seleção de micro-habitats (disponibilidade de refúgios e abrigo), combinado com efeitos de predadores e competidores, foi considerada importantes fatores na estruturação dos padrões populacionais de *O. trinitatis*.

Sabe-se que a importância relativa dos processos pós-assentamento é espécie-específico e pode depender das diferenças encontradas em cada local. No caso do blenídeo *O. trinitatis*, a área marinha protegida da Ilha da Barra aparentemente não teve influência sobre a taxa de recrutamento, por outro lado, a presença significativa de predadores pode ter resultado em um aumento da pressão predatória sobre recrutas e juvenis.

Os resultados obtidos nesta tese mostram a importância de estudar a fase inicial da vida dos peixes recifais, aumentando o entendimento não apenas sobre o blenídeo *O. trinitatis*, mas também fornece uma base para estudos de recrutamento, dos efeitos das mudanças climáticas globais e no manejo de espécies ecologicamente e economicamente importantes.

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