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**Diversidade e vetores de invasão de espécies introduzidas  
marinhas em Angola**

**Diversity and vectors of invasion of marine introduced  
species in Angola**

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Diversidade e vectores de invasão de espécies introduzidas marinhas em  
Angola

Diversity and vectors of invasion of marine introduced species in Angola

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Co-Orientador: Gustavo Muniz Dias

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*A minha filha Lwini, minha companheira de Doutorado*

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## INTRODUÇÃO GERAL

### Bioinvasões marinhas e vetores de introdução

A diversidade nas comunidades locais é o resultado de processos históricos, regionais e locais que afetam a extinção, especiação e dispersão de espécies que, por sua vez, determinarão as biotas e os domínios biogeográficos regionais (Rickefs, 1987; Mittelbach & Schemske, 2017). No entanto, desde o início das grandes rotas interoceânicas, a humanidade muda significativamente a distribuição de espécies e os padrões biogeográficos, introduzindo organismos além de sua distribuição nativa. Portanto, mapas clássicos da demografia histórica humana são bons preditores das rotas de introdução de muitas espécies de animais e plantas (Carlton, 2003). Espécies introduzidas<sup>1</sup> são aquelas que foram transportadas, intencionalmente ou não, através de meios mediados por humanos, para regiões onde elas não existiam anteriormente (Hewitt *et al.*, 2010). Espécies que não tenham um história biogeográfica conhecida, não podem ser identificadas de forma confiável como sendo introduzidas ou nativas, sendo denominadas por espécies criptogênicas. A maioria das espécies que agora são categorizadas como criptogênicas foram previamente tratadas como nativas; por sua vez, muitas espécies que deveriam ser reconhecidas como criptogênicas ainda são consideradas nativas, o padrão categórico em biogeografia e biologia evolutiva (Carlton, 1996). Pelas definições adotadas pela Convenção Internacional sobre Diversidade Biológica (COP-6, Decisão VI/23, 2002), se a espécie introduzida consegue reproduzir-se e gerar descendentes férteis, com alta probabilidade de sobreviver no novo habitat, ela é considerada estabelecida. Caso a espécie estabelecida expanda a sua distribuição no novo habitat, ameaçando a diversidade biológica nativa, ela passa a ser considerada uma espécie introduzida invasora (UNEP, 2002).

Embora as espécies introduzidas tenham sido amplamente documentadas e estudadas em ambientes terrestres e de água doce (por exemplo, Simberloff & von Holle, 1999; D'Antonio & Kark, 2002; Cadotte & Colautti, 2005), o estudo de espécies introduzidas costeiras e marinhas é um campo relativamente novo. Em ambientes costeiros, a taxa observada de invasões aquáticas aumentou rapidamente ao longo do século XX, e continua a aumentar a cada década que passa (Cohen & Carlton, 1998; Ruiz *et al.*, 2000, 2011).

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<sup>1</sup> Outros termos: adventícia, alienígena, exótica, não-indígena, não-nativa.

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O processo no qual um organismo introduzido chega a um novo local diretamente a partir de sua região nativa é chamado de introdução primária, enquanto a sua disseminação subsequente do local de fundação é considerada uma introdução secundária. Essa disseminação pode ocorrer por meio de uma combinação de mecanismos naturais de dispersão e de transporte associados ao homem. À medida que uma espécie introduzida expande sua ocupação, outras oportunidades de propagação por vetores adicionais podem se apresentar (ex. Carlton, 1999; Sakai *et al.*, 2001; Minchin e Gollasch, 2002; Occhipinti-Ambrogi & Galil, 2004).

Eventualmente, a chegada de um invasor pode ser resultante de diferentes vetores, que podem atuar em alternância para disseminar a mesma espécie (Minchin, 2007), tais como: aquicultura, comércio de aquários, construção de canais ligando mares desconectados, atividades de pesquisa, mas principalmente transporte marítimo, que é uma atividade responsável por quase 80% do comércio mundial, e também pela maioria das introduções documentadas de espécies estuarinas e marinhas (por exemplo, Carlton 1985, 1996, 2001; Cohen & Carlton 1998; Cranfield *et al.*, 1998; Ruiz *et al.*, 2000; Gollasch, 2002; Fofonoff *et al.*, 2003; Hewitt *et al.*, 2004). As embarcações podem transportar organismos sésseis ligados aos seus cascos, hélice, leme, superfícies expostas de tubulações de água e túneis propulsores (denominadas então “fouling”), bem como em lastro úmido ou seco (Carlton, 1985, 1996; Ruiz *et al.*, 2000) na forma de propágulos reprodutivos ou potenciais estágios reprodutivos que podem estabelecer novas populações introduzidas.

### **Impacto das espécies marinhas introduzidas**

Uma vez no novo habitat, as espécies introduzidas podem se dispersar para substratos naturais e artificiais, causar impactos ecológicos e socioeconômicos, dentre os quais se destacam os prejuízos em biodiversidade (ex. redução na riqueza de espécies), habitats (ex. perda de habitat), interações bióticas (ex. competição por recursos ou espaço), genéticos (ex. alteração na pool de genes por hibridização), turismo (ex. redução de atividades turísticas), pesca (ex. redução da abundância de espécies comerciais), aquicultura (ex. redução na qualidade dos produtos) e embarcações-amarrações (ex. aumento do custo de manutenção como resultado da presença de organismos incrustantes) (Ruiz *et al.*, 2000; Hewitt *et al.*, 2006; Çinar *et al.*, 2014). Os impactos ecológicos também podem ser observados em diferentes níveis biológicos de organização, como genéticos, individuais, populacionais,

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comunitários, ecossistêmicos, regionais e globais, tendo em mente que o que afeta um nível de organização frequentemente afeta outros níveis (Lockwood *et al.*, 2007). Os efeitos negativos causados pelas espécies invasoras podem ser motivo de especial preocupação em regiões do mundo onde o estado de conhecimento da biota marinha é relativamente pobre, pois podem promover a perda da biota nativa antes mesmo antes de ser conhecida pela ciência (Nuñez & Pauchard , 2010).

### **Baías e marinas como “hotspots” para invasões**

A maioria das invasões marinhas é mais conhecida em águas protegidas de baías e estuários que em costas mais expostas (Preisler *et al.*, 2009). A maior parte do comércio mundial ocorre por transporte marítimo entre portos, concentrados em baías e estuários, criando oportunidades para transferências de espécies associadas a cascos de navios e materiais de lastro (Carlton, 1985). Além disso, as baías são focos para muitas outras atividades conhecidas por transferir organismos, como aquicultura, pesca e recreação ao ar livre (Fofonoff *et al.*, 2009). De fato, marinas são alguns dos equipamentos marinhos mais invadidos no mundo (Lambert & Lambert, 1998), como resultado do aumento da pressão de propágulos e condições ambientais alteradas. As condições hidrológicas e ambientais locais modificadas permitem fornecer proteção aos barcos, mas também criam condições favoráveis para a chegada de espécies introduzidas (Floerl, 2003). Desta forma, as marinas são pontos ideais para a detecção precoce dessas espécies, o que pode ser um aspecto essencial para uma potencial erradicação e um manejo efetivo (Williams *et al.*, 2013), além de fornecerem um excelente ambiente para experimentos que visem testar teorias sobre mecanismos subjacentes ao processo de invasão, especialmente durante as fases de assentamento e estabelecimento (Gestoso *et al.*, 2018).

### **Fatores bióticos que influenciam a distribuição e a abundância de espécies introduzidas em uma comunidade**

Distúrbios biológicos e físicos influenciam a estrutura das comunidades marinhas e terrestres (Dayton, 1971; Grime, 1977). Uma grande variedade de fatores bióticos (ex. competição, predação e parasitismo) e abióticos (ex. hidrodinamismo, temperatura e salinidade) podem determinar o desenvolvimento e dinâmica das comunidades incrustantes (Nydam & Stachowicz, 2007). Os competidores dominantes podem traçar a estrutura da comunidade ao monopolizar os recursos-

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chave, através de atributos específicos de suas histórias de vida, como altas taxas de crescimento e/ou capacidade de recobrir os concorrentes (Nandakumar *et al.*, 1993; Claar *et al.*, 2011; Lord & Whitlatch, 2015). A predação, por outro lado, pode impactar a estrutura da comunidade influenciando na sobrevivência dos recrutas (Osman & Whitlatch, 2004; Nydam & Stachowicz, 2007), ou por meio do consumo preferencial que pode modular a monopolização de recursos por espécies competitivamente superiores (Osman *et al.*, 1992; Nydam & Stachowicz, 2007).

Para as comunidades em que o espaço para assentamento é o recurso limitante, como aquelas formadas por animais sésseis marinhos, características de história de vida e exclusão competitiva podem desempenhar um papel importante na diversidade de espécies (Dayton, 1971; Connell, 1978; Sousa, 1984), fazendo dessas comunidades bons modelos para testar os processos que influenciam o desenvolvimento da comunidade (Cifuentes *et al.*, 2007; Nydam & Stachowicz, 2007), incluindo o impacto de espécies não-nativas nos padrões das comunidades (Gittenberger & Moons, 2011).

A predação, por exemplo, pode ter um efeito intenso no desenvolvimento da comunidade quando grandes predadores, mas também micropredadores, estão presentes (Osman *et al.*, 1992; Osman & Whitlatch, 1995, 2004; Nydam & Stachowicz, 2007). Enquanto que os micropredadores podem influenciar a estrutura da comunidade durante o período inicial de pós-assentamento (Oricchio *et al.*, 2016), predadores maiores podem afetar até mesmo comunidades estabelecidas (Lavender *et al.*, 2014; Osman & Whitlatch, 2004). Em várias comunidades marinhas, predadores altamente seletivos poderiam teoricamente ser muito eficazes na redução da abundância de espécies não nativas (Byers, 2002; Harding, 2003; Dudas *et al.*, 2005).

De acordo com Freestone *et al.* (2013), a pressão da predação em uma região tropical é forte o suficiente para eliminar espécies não nativas em pequenas escalas espaciais experimentais, sugerindo que tais interações fortes têm o potencial de reduzir a abundância e distribuição de espécies não nativas através de escalas espaciais maiores e, possivelmente reduzindo seus impactos.

### **Angola como local de estudo**

Angola está localizada no sudoeste da África, na fronteira com o Oceano Atlântico Sudeste. A costa angolana tem cerca de 1.600 km de comprimento, desde c. 5° S até c. 17° S (Bianchi, 1992). A plataforma continental é de cerca de 51.000 km<sup>2</sup>

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(utilizando o contorno de 200 m de profundidade), com uma largura média de cerca de 20 milhas náuticas. A região mais meridional, de Cunene até Tombwa, tem uma plataforma relativamente larga e pouco profunda, mas com uma encosta íngreme, exceto na parte sul extrema. De Tombwa a Benguela, a plataforma é muito estreita e a inclinação é muito íngreme. De Benguela para norte a plataforma é geralmente larga até Cabinda, mas com uma parte estreita de Luanda e um desfiladeiro subaquático íngreme adjacente ao Rio Congo. O litoral angolano é fortemente afetado por dois sistemas atuais. As águas costeiras do norte do país são principalmente influenciadas pela corrente angolana saturada de oxigênio, mas pobre em nutrientes, que flui para o sul. Esta corrente corre paralela à costa, tem origem equatorial e é quente. Geralmente a água é altamente salina (Lass *et al.*, 2000). Ao sul, a Corrente de Benguela, impulsionada por ventos regionais a sudeste, transmite, na direção noroeste, água fria, submersa, menos salina, rica em nutrientes e pobre em oxigênio da Namíbia (Lass *et al.*, 2000; Lin & Chen, 2002). Mais informações sobre os locais estudados são mencionadas nos capítulos subsequentes.

### **Justificativas, objetivos e estrutura da tese**

Estudos sobre espécies marinhas não nativas e seus impactos sobre os ecossistemas do hemisfério sul são escassos quando comparados à Europa e América do Norte, e concentrados em algumas áreas, como Nova Zelândia e Austrália. Estudos do Atlântico Sul que descrevem táxons introduzidos e/ou criptogênicos estão, na sua maioria, restritos às costas argentina, brasileira e sul-africana. Dentre os estudos mais importantes, foram relatadas mais de 75 espécies não-nativas na região ao largo do Uruguai e da Argentina (Orensanz *et al.*, 2002); 42 introduzidas e 187 espécies de invertebrados bentônicos criptogênicos associadas a incrustações em cascos de embarcações na costa brasileira (Rocha *et al.*, 2013); e 36 táxons introduzidos e 53 táxons invasores para a África do Sul (Robinson *et al.*, 2016).

Considerando o grande número de espécies não-nativas reportadas para a região do Atlântico Sul e o intenso tráfico de escravos que ligaram os continentes americano e africano desde o século XVI, é esperado que a pouco conhecida costa ocidental de África esteja exposta à intensa introdução de espécies exóticas. No entanto, as mesmas são desconhecidas ou relatadas, na sua maioria, em revistas locais ou na literatura cinza (Orensanz *et al.*, 2002; Mead *et al.*, 2011).

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Angola possui vários portos internacionais e marinas, com uma história de navegação de mais de 500 anos, iniciada pela chegada dos primeiros colonos europeus e intensificada por um forte tráfico de escravos (Fleisch, 2004). No entanto, o conhecimento sobre a fauna nativa e introduzida da costa angolana é escasso, impedindo uma melhor compreensão da distribuição das espécies para o Atlântico Sudeste. A falta de avaliação ecológica e estudos das espécies introduzidas marinhas em Angola criou uma lacuna em relação à sua distribuição atual e impacto nas comunidades nativas. Os principais objetivos deste estudo são revelar e avaliar o estado atual das espécies costeiras marinhas bentônicas introduzidas registadas em duas baías angolanas e compreender alguns dos fatores que podem afetar a sua abundância e distribuição.

A tese está organizada de maneira direta em três capítulos:

**Capítulo 1:** O primeiro objetivo desta tese de doutoramento é o levantamento da literatura para fornecer uma lista abrangente de invertebrados marinhos sésseis colonizando substratos duros ao longo da costa angolana, usando estes dados para inferir o estado de introdução dos invertebrados sésseis angolanos de acordo com a sua distribuição biogeográfica e história natural. Este trabalho cria uma ‘baseline’ para comparação, rara para o continente africano – de fato, a segunda a ser publicada. Este trabalho foi publicado em Outubro de 2017, no Jurnal Marine Pollution Bulletin.

**Capítulo 2:** Com base em experimentos e nas descobertas do levantamento de campo, o objetivo deste capítulo foi descrever a diversidade espacial e temporal de espécies bentônicas costeiras introduzidas de Hydrozoa, Polychaeta, Cirripedia, Bryozoa e Asciadiacea em duas baías angolanas, avaliando a prevalência de espécies introduzidas e criptogênicas ao longo de duas temporadas. O manuscrito referente a esta parte está submetido para a publicação.

**Capítulo 3:** Com base nos mesmos experimentos e resultados da pesquisa de campo do Capítulo 2, o objetivo deste capítulo foi determinar os fatores bióticos, como a predação e a competição, que podem afetar a abundância e a distribuição das espécies introduzidas. Não há estudos publicados que abordem este tema para todo o continente africano, demonstrando a importância e ineditismo do mesmo.

Os resultados obtidos nessa tese contribuem para o estudo e gestão de invasões marinhas em um contexto africano em geral, e em um angolano, em particular. A pesquisa apresentada nesta tese (Capítulos 1-3) foi preparada como manuscritos independentes para publicação. Como tal, pode haver alguma

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redundância entre os capítulos. Um dos capítulos já foi publicado e outro foi submetido para publicação.

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## A CENTURY OF INTRODUCTIONS BY COASTAL SESSILE MARINE INVERTEBRATES IN ANGOLA, SOUTH EAST ATLANTIC OCEAN

O capítulo corresponde ao artigo científico de autoria de Lueji Barros Pestana, Gustavo Muniz Dias e Antonio Carlos Marques, publicado pelo periódico Marine Pollution Bulletin, 125: 426-437.

### Abstract

South Atlantic studies referring to non-native taxa are mostly restricted to Argentinean, Brazilian, and South African coasts. In this study we examined the literature to provide a list of sessile marine invertebrates along the Angolan coast, to infer its introduction status according to their biogeographical distribution and natural history. We reported 29 non-native and 7 cryptogenic species, a small number when compared to other South Atlantic regions of similar extension. Half of the non-native species were reported for Luanda. The majority of the introduced species had a northern hemisphere origin, a consequence of the main introduction route being from the North Atlantic/Mediterranean Sea during the Portuguese colonization. This is the first comprehensive assessment of this kind for the Angolan coast and the diversity of introduced species is certainly underestimated. Regular and rigorous assessments and monitoring of introduced marine species will help to understand the vectors, routes and time of introductions.

*Keywords:* non-native species, marine sessile invertebrates, South Atlantic Ocean, Africa.

### Resumo

Estudos do Atlântico Sul referentes a taxa não nativos estão restritos principalmente às costas Argentinas, Brasileiras e Sul-africanas. Neste estudo examinámos a literatura para fornecer uma lista de invertebrados marinhos sésseis ao longo da costa Angolana, para inferir o seu estado de introdução de acordo com a sua distribuição biogeográfica e história natural. Foram reportadas 29 espécies não-nativas e 7 espécies criptogênicas, um número pequeno quando comparado a outras regiões do Atlântico Sul de extensão similar. Metade das espécies não nativas foram reportadas para Luanda. A maioria das espécies introduzidas tinha origem no hemisfério norte, uma consequência da principal rota de introdução do Atlântico Norte / Mar Mediterrâneo durante a colonização portuguesa. Esta é a primeira avaliação abrangente deste tipo para a costa Angolana e a diversidade de espécies introduzidas é certamente subestimada. Avaliações regulares e rigorosas e monitoramento de espécies marinhas introduzidas ajudarão a entender os vetores, rotas e tempo de introdução.

*Palavras-chave:* espécies não-nativas, invertebrados marinhos sésseis, Atlântico Sul, África.

## Introduction

The diversity in local communities is the result of historical, regional and local processes that affect extinction, speciation and species dispersal, which, in turn, will determine the regional biotas and biogeographical domains (Mittelbach *et al.*, 2007). However, since the start of the great interoceanic and transoceanic navigations, humankind is significantly changing species distribution and biogeographical patterns, introducing organisms beyond their native range. Therefore classical maps of human historical demography are good predictors of the introduction routes of many species of animals and plants (Carlton, 2003).

The transport of coastal species beyond their original distribution occurs by a variety of vectors such as aquaculture, aquarium trade, construction of canals linking disconnected seas, research activities, but mainly by shipping, an activity responsible for almost 80% of the world trade and also for most of the documented introductions of estuarine and marine species (e.g. Carlton 1985, 1996, 2001; Cohen & Carlton 1998; Cranfield *et al.*, 1998; Hewitt *et al.*, 2004; Ruiz *et al.*, 2000; Gollasch 2002; Fofonoff *et al.*, 2003). Vessels can transport sessile organisms attached to their hulls, propeller, rudder, exposed surfaces of water piping, and thruster tunnels, as well as in wet or dry ballast (Carlton 1985, 1996; Ruiz *et al.*, 2000), either in the form of reproductive propagules or potential reproductive stages that can establish new introduced populations.

Once in the new habitat, introduced species can spread to natural and artificial substrata, changing the structure of native communities and ecosystem functioning and sometimes causing economical issues, such as the increase of the costs associated to industrial and commercial activities (Ruiz *et al.*, 2000; Çinar *et al.*, 2014). The harmful effects caused by invasive species may be of special concern in regions of the world where the state of knowledge of the marine biota is relatively poor, because they can promote the loss of native biota even before it was known to science (Nuñez & Pauchard, 2010).

Studies on non-native species and their impacts on ecosystems from the southern hemisphere are scarce when comparing to Europe and North America (Ruiz *et al.*, 2000), and mostly concentrated to a few areas, such as New Zealand and Australia. South Atlantic studies referring to introduced and/or cryptogenic taxa are mostly restricted to Argentinean, Brazilian, and South African coasts (Orensanz *et al.*, 2002; Rocha *et al.*, 2013; Robinson *et al.*, 2016). For instance, more than 75 non-native species have been reported for the region off Uruguay and Argentina (Orensanz *et al.*, 2002), 42 introduced and 187 cryptogenic benthic invertebrate species were associated with hull fouling on the Brazilian coast (Rocha *et al.*,

2013), and 36 introduced and 53 invasive taxa were reported for South Africa (Robinson *et al.* 2016).

Considering these large numbers of non-native species reported for the South Atlantic region, and the intense traffic of slaves that connected American and African continents since the XVI century, it is expected that the poorly known Western Coast of Africa would be exposed to intense introduction of exotic species. Still, introduced species on the tropical coast of the African continent are either unknown, or reported in local journals or in grey literature (Orensanz *et al.*, 2002; Mead *et al.*, 2011).

In this study we assess the status of the exotic species from the Angolan coastline, extending from 5°-17°S (ca. 1,600 km long) (Bianchi, 1992). Angolan coastline is strongly affected by two current systems. The northern coastal waters of the country are mainly influenced by the oxygen-saturated, but nutrient-poor, southward-flowing Angola Current. This current runs parallel to the coast, has an equatorial origin and is warm. Generally the water is highly saline (Lass *et al.*, 2000). To the south, the Benguela Current, driven by regional southeasterly winds, conveys in a northwesterly direction cold, upwelled, less saline, nutrient-rich and oxygen-depleted water from Namibia (Lass *et al.* 2000; Lin & Chen, 2002). Angola has several international harbors and marinas, with a navigation history of over 500 years, initiated by the arrival of the first European settlers and intensified by a strong slave trade (Fleisch, 2004). However, knowledge on native and introduced fauna from Angolan coast is scarce, preventing from a better understanding of species distribution for the southeastern Atlantic. In this context, the aim of this review is to survey the literature to provide a comprehensive list of sessile marine invertebrates colonizing hard substrata along the Angolan coast, using these data to infer the introduction status of Angolan sessile invertebrates according to their biogeographical distribution and natural history.

## Material and Methods

This literature review presents a list of non-native sessile species of Porifera, Cnidaria, Annelida, Mollusca, Crustacea, Bryozoa, and Tunicata (Asciidiacea) based on records from scientific literature survey of the Web of Science (<https://www.webofknowledge.com>) but also including grey literature, museum collections, unpublished Angolan surveys, from both natural and artificial substrata of the marine biodiversity in Angolan waters from 1912 to 2016 up to 100 m deep. Search in the Web of Science combined region names, including Angola, Luanda and other regions, with taxonomic and popular names of the main sessile invertebrate groups. Original entries were checked for synonymies and nomenclatural

changes using recent taxonomic articles and the World Register of Marine Species (WoRMS) (<http://www.marinespecies.org>). The resulted list is a current assessment of non-native taxon in Angolan coast.

Species were categorized as introduced or cryptogenic based on previously proposed criteria (Chapman, 1988; Chapman & Carlton, 1991; Carlton, 1996), viz. (1) introduced species have native and introduced ranges well established in the literature and native range do not include the South West Atlantic Ocean; and (2) cryptogenic species have no definitive evidence of presenting either native or introduced status.

As the date of introduction is rarely known, we refer to the date of the first record in the country (date of collection - DOC). Whenever these dates were not reported, we assumed the date of the documents or publications (DOP) as a minimum estimate of the first record, but we recognize that DOPs may be many years after the date a species was first collected, sighted or introduced. The also plausible vectors (or mechanisms) for each introduction based upon peer-reviewed literature imparting knowledge life history, habitat utilization, and ecological attributes of the species, such as shipping boring (SB), shipping fouling (SF), ballast water (BW) and solid ballast (SB) were evaluated.

The original distribution of species was indicated to classify their distribution status. This included type of locality and the geographical distribution recorded in several published articles. Note that the total number of species records in the results per original distribution is higher than the actual total species, because the species were counted for each different native region, and several of them are present in more than one region. Distribution in Angola was based upon primary literature records, museum and field records. The potential source areas were inferred by searching information on the current range of distribution of each species (including both native and introduced ranges) in the literature, as well as reports of introductions or first records of each species in Angola.

## Results

We reported 29 introduced and 7 cryptogenic species for the Angolan Coast (Table 1). Introduced species included 2 Porifera, 2 Cnidaria, 1 Annelida (sedentary Polychaeta), 5 Mollusca, 2 Crustacea (Cirripedia), 11 Bryozoa, and 6 Tunicata (Asciidiacea). Cryptogenic species are represented by 2 Cnidaria, 1 Annelida, 1 Bryozoa, and 3 Asciidiacea. The highest number of introductions (20 species) is reported for Luanda region, contrasting to more extensive sites from the northern region (9 species) and southern region (11 species) (Figure 1).

Most of marine introduced species recorded in Angola are native from the Mediterranean Sea and North Atlantic Ocean, with 19.5% and 13% of the species, respectively (Figure 2). Additionally, shipping (hull fouling and ballast water) is likely the commonest vector of species introduction for the Angolan coast (see Table 1).

Since the first report of sessile marine invertebrates for the Angolan coast in 1912, the number of introduced species increased, especially between 1940-1960 and 2000-2016 (21 and 11 species, respectively) (Figure 3).

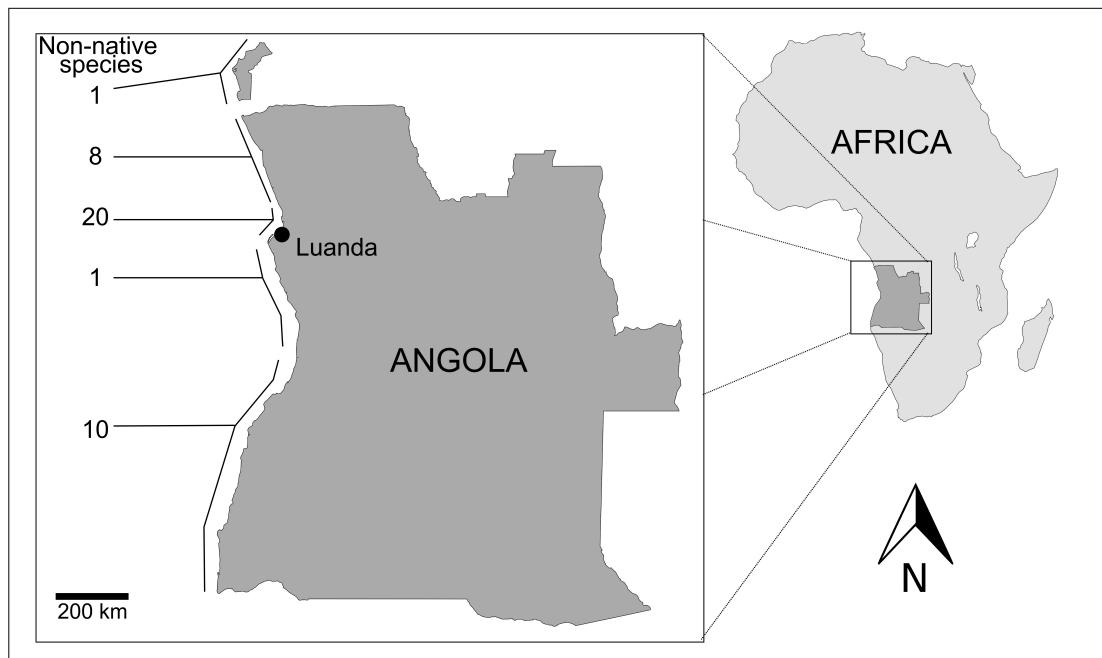


Figure 1. Distribution of non-native species along the Angolan coast. From North to South, the regions are: Cabinda, Center-North, Luanda; Central; Benguela/Namibe.

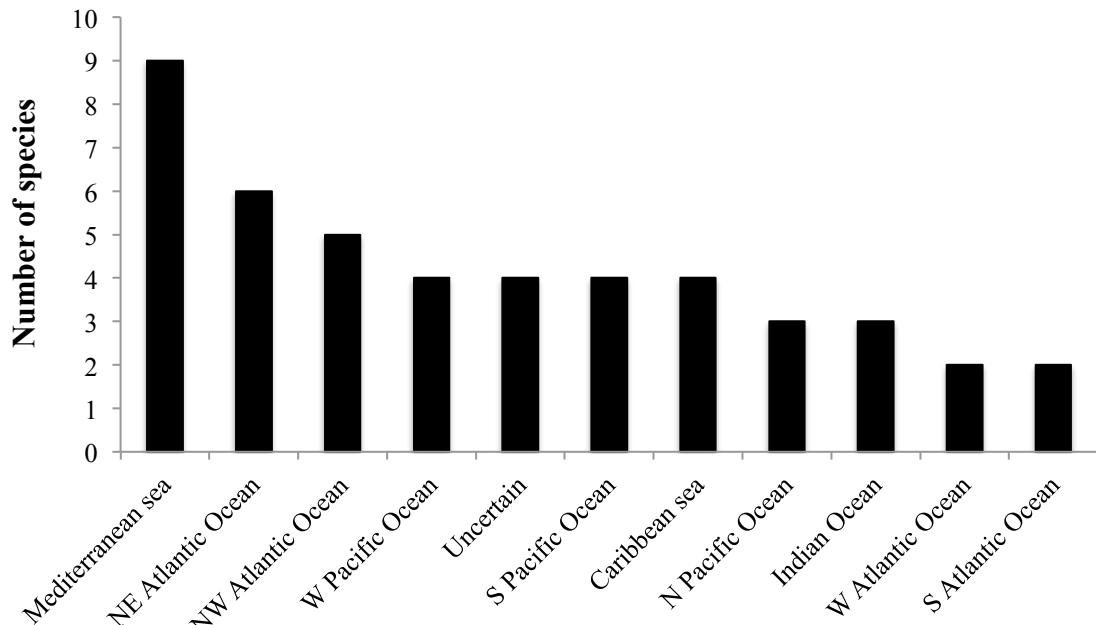


Figure 2. Native distribution of the non-native species recorded in Angola.

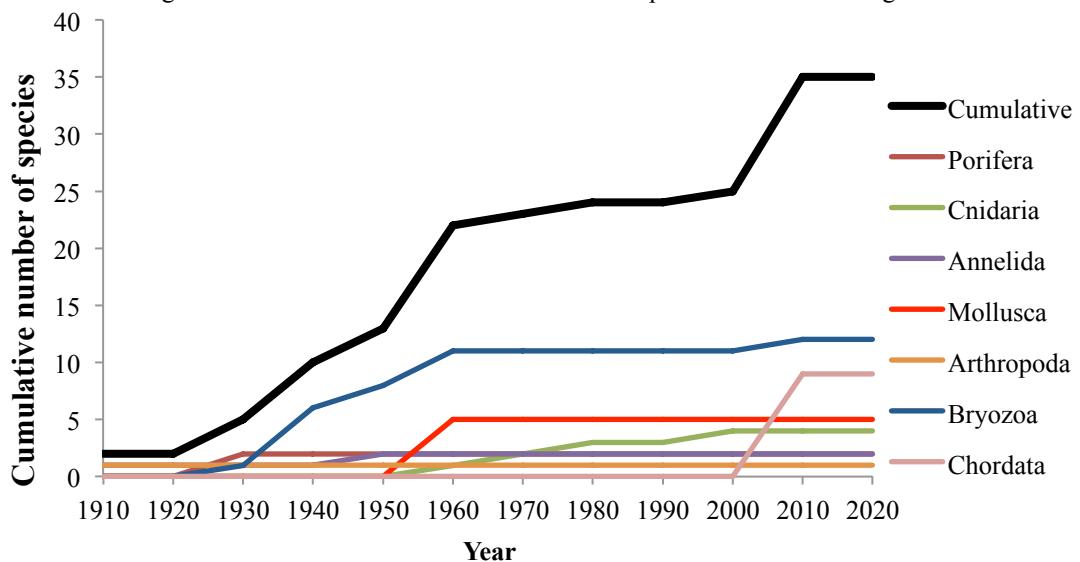


Figure 3. Estimated moment of introduction of marine species in Angola.

## Discussion

Thirty-six (29 introduced and 7 cryptogenic) non-native species are reported for the Angolan Coast. This number is small when compared to other South Atlantic regions of similar extension (see Orensanz *et al.*, 2002; Mead *et al.*, 2011; Robinson *et al.*, 2016). This low numbers may happen because of (1) the few taxonomic and faunal studies dealing with Angolan marine biodiversity in general; (2) most of the available reports are restricted to soft bottom substrates up to 100 m deep; (3) very few studies dealt specifically with artificial

substrates (e.g., harbors, marinas, wharfs, quays, etc.) (see Cook, 1968; Andrade, 2011). Therefore, this baseline of non-native species of sessile taxa is conservative, and the number of introduced species in Angola is expected to be much higher than described here.

A detailed analysis of the records reveals that both bryozoans and ascidians were focus taxa sampled in those few studies on artificial substrates (see Cook, 1968; Andrade, 2011). As a result, these two groups present the highest numbers of non-native species in this report (11 bryozoans, 6 ascidians), therefore corroborating the underestimation of non-native species in general.

The regional knowledge on introductions is diverse. At least half of the non-native species were reported for the capital Luanda. This is certainly related to the more extensive sampling effort, the large number of researchers based or visiting Luanda, the better infrastructure of the city and, evidently, to the presence of the most important Angolan harbor. The southern region shares with Namibia and South Africa an ecosystem influenced by the cold and rich Benguela Current (von Bodungen *et al.*, 2008); the region has several poorly studied rocky beaches, and includes the third most important harbor of the country, which contributes to relatively high number of species recorded. The knowledge concerning the Center-North region is partly a by-product of the Luanda studies and also due to the Atlantide Expedition (1945-1946), especially relating to bryozoans, where we considered 7 non-native species besides those of Luanda (see Cook, 1968). Other regions, viz. Cabinda and Central Angola, are poorly studied, and have only 1 non-native species reported so far. Cabinda Province is an important region in Angola and it is influenced by the Guinea Current, and plays an important role in oil production and encompasses an important harbor. Thus, more studies are needed in the region to assess the actual state of bioinvasions.

International marine shipping traffic connecting Angola (mainly Luanda) to the European and American continents has been important for the last 500 years (Fleisch, 2004), what can explain the large number of introduced species with native distribution in the Mediterranean and North Atlantic. This long navigation trading history however is not accompanied by the scientific knowledge of its consequences. The first expedition along the Angolan coast apparently was the “Deutschen Tiefsee-Expedition” by the end of the XIX Century (1898-1899) (see Schott, 1902). The oldest report of a potentially non-native species for the Angolan coast dates from 1909, and it is certainly an effect of occasional, infrequent and sporadic nature of marine biodiversity studies in the past in Angola. Many of the present non-native species may have been introduced decades or even centuries earlier than they were documented, a pattern similar to other less intensively studied regions of the world (Carlton,

2009). Presently, Angola is an important oil producer, and the contribution of introduced fouling species on oil platforms are not only in direct competition with native species for substrate space (Atchison *et al.*, 2008; Sammarco *et al.*, 2010), but the relocation of decommissioned platforms may act as a distribution vector (Yeo *et al.*, 2010).

Indeed, faunal knowledge for the Angolan waters was accumulated in sparse pulses related to specific studies of a given taxon: Porifera in the 1920s, Annelida from 1920-1950, Bryozoa from 1920-1960, Mollusca in the 1950s, Cnidaria from 1950-2000, Ascidiacea in the 2000s. Summarizing, three taxa (Mollusca, Bryozoa and Ascidiacea) in four studies (Cook, 1968; Kensley, 1973, 1980; Andrade, 2011) are the major contributors for present knowledge. The higher number of reports in the last decades is a consequence of the increase in the sampling efforts and more focused taxonomical studies instead of broader and generalist surveys. For example, ascidians are among the most diverse group of sessile organisms growing on artificial substrata in harbor areas (López-Legentil *et al.*, 2015; Oricchio *et al.*, 2016), and although data is available since the beginning of the XX century, the first study exclusively focusing ascidians colonizing artificial substrate was published in 2011 (Andrade, 2011).

The affinities and vector of introduction of non-native Angolan fauna corroborate its trading history. Most of the introduced species has a northern hemisphere origin, a consequence of the main introduction route probably being from the North Atlantic Ocean during the Portuguese colonization. Although it is the first assessment for Angola and more work is needed to assess Angola's marine bioinvasions status, this study allowed for the preliminary comparison with other regions such as South Africa, where bioinvasions also appear to originate from historical shipping mainly from Europe (Mead *et al.*, 2011). The Mediterranean Sea may also have contributed to the introduction of species, probably because there was important european ports, which used the the African coast to cross to the Indian ocean (Ringrose, 1996).

Detecting the vector of introduction is challenging since many species use several vectors. Most ascidians and bryozoans were probably introduced as adult forms on ships' fouling, because some of their larvae could not survive to long voyages in ballast water (Carlton, 1985). Cnidaria, Mollusca, Polychaeta, and Cirripedia could have been introduced both through ballast water as planktonic forms, and through ship fouling as benthos (Galil, 2000 for cnidarians and mollusks; Carlton *et al.*, 2011 for barnacles; Çinar, 2013 for polychaetes). Porifera possible have been introduced by ship fouling, since they have short-life and poor dispersive larvae (Uriz *et al.*, 1998).

Several synanthropic species, known for causing ecological and economic losses in coastal habitats around the world were recorded for the region, viz., the polychaete *Hydroides elegans*, the barnacle *Amphibalanus amphitrite*, the bryozoan *Bugula neritina*, and the ascidians *Ciona intestinalis* and *Styella plicata* (Carballo & Naranjo, 2002; Daigle & Herbinger, 2009; Schwan *et al.*, 2016). These species may represent highly eurytopic and tolerant taxa frequently considered to be harmful for the local economy and native fauna (Bax *et al.*, 2003). Among these taxa, *H. elegans* is abundant in many warm-water harbors, and polluted marinas, where it competes with native fouling organisms and may cause economical damage for naval industry (Glasby *et al.*, 2001; Kocak & Kucuksezgin, 2000; Schwan *et al.*, 2016). *Amphibalanus amphitrite* also causes costly impacts for shipping lines and navies and competes directly with native barnacles in some parts of the world (Zvyagintsev & Korn, 2003), while *Bugula neritina*, *Styella plicata* and *Ciona intestinalis* are known to foul aquaculture nets and cages, slowing down the growth of cultured bivalves and increasing mortality rates (Ryland 1971; Hodson *et al.*, 1997; Sá *et al.*, 2007; Ramsay *et al.*, 2009; Daigle & Herbinger, 2009; Rocha *et al.*, 2009). Other species may also be introduced, like the Mediterranean mussel *Mytilus galloprovincialis*, a well known invasive species along the Southern African coast (from central Namibia in the west African coast to East London on the east coast), competing with native species and altering trophic structure and physical appearance in the invaded area (Robinson *et al.*, 2005). The presence of these species in Angolan waters represents a threat to the poorly known and described native fauna and economy. This is especially important once Angolan economy is centralized on the importation of consumer goods transported mainly by the sea (UCAN, 2015). Thus, the investment in strategies for managing and monitoring non-native species is mandatory for the Angolan Coast.

## Conclusions

This is the first comprehensive assessment of coastal sessile marine invertebrates introduced to the Angolan coast. It is noted that the west coast of Africa is among the least known regions in the world and information on species distribution and biodiversity of both native and non-native species is wanting.

This survey represents only the second study of this type for the countries of the African Atlantic Ocean. The number of introduced species is most probably underestimated, and regular assessments, especially in relation to other taxa not included in this study, is essential. The monitoring of introduced marine species will help to better understand the

vectors, routes and time of introductions as well the role of harbors and marinas as sources of marine invasions along this coast.

Several synanthropic species, that cause ecological and economic losses in coastal habitats around the world are known for the region. Thus, the development of a national strategy for monitoring and managements of non-native species in Angolan waters should be mandatory.

Taxonomic assessments are essential to improve the data related to marine organisms in Angolan waters. This fundamental science is vital and a critical resource tool in developing countries with an emerging scientific environment.

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Table 1 – Marine cryptogenic and introduced species along the Angolan coast. Status: C- cryptogenic; I- introduced. Date: DOC - date of collection; DOP - date of publication; NDD - no date determined. Likely vectors: SB – shipping boring; SF – shipping fouling; BW – ballast water; SB – solid ballast.

Táxon	Status	Source	Date	Locality	Presumed native range	Information about native distribution and/or introduction	Probably vectors
<b>PORIFERA</b>							
<i>Haliclona</i> <i>(Halichociona) fulva</i>	I	1	1938 (DOC)	Luanda	NW Atlantic, Mediterranean Sea	Evcen <i>et al.</i> , 2016	SF
<i>Lissodendoryx</i> <i>(Lissodendoryx)</i> <i>isodictyalis</i>	I	1, 2	1938 (DOC)	Luanda	Caribbean Sea	Rützler <i>et al.</i> , 2007	SF
<b>CNIDARIA</b>							
<i>Sertularella</i> <i>mediterranea</i>	C	3	1969 (DOC)	Namibe	Mediterranean	Ramil <i>et al.</i> , 1992	SF/BW
<i>Ectopleura crocea</i>	I	4	2006 (DOP)	Namibe	NW Atlantic	Fofonoff <i>et al.</i> , 2003	SF/BW
<i>Obelia dichotoma</i>	C	3	1973 (DOP)	Namibe	Cosmopolitan	Galea <i>et al.</i> , 2007	SF/BW
<i>Caryophyllia</i>	I	5	1984 (DOC)	Luanda	N and SW Atlantic and	Ryland &	SF/BW

*(Caryophyllia) smithii*

Mediterranean Sea

Hayward, 1995

**POLYCHAETA**

<i>Branchiomma nigromaculatum</i>	C	2, 7	1915 (DOC)	Luanda	Probably SW Atlantic and Caribbean Sea	Jones, 1962; Keppel, 2015	SF/BW
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<i>Hydroides elegans</i>	I	6	1955 (DOC)	Ambriz	Probably Australasia and Indian Ocean	Cinar, 2013	SF/BW
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**MOLLUSCA**

<i>Gibbula divaricata</i>	I	3	1969 (DOC)	Namibe	Mediterranean	Coll <i>et al.</i> , 2010	SF/SB
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<i>Leiosolenus aristatus</i>	I	3, 9, 10	1969 (DOC)	Namibe	Caribbean	Ignacio <i>et al.</i> , 2010	SF/SB
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<i>Saccostrea cucullata</i>	I	2, 3	1969 (DOC)	Luanda; Namibe	Western Indo Pacific	Coles <i>et al.</i> , 1999	SF/SB
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<i>Semimytilus algosus</i>	I	3, 11, 12	1969 (DOC)	Namibe; Luanda	S Pacific	Tokeshi and Romero, 1995	SF/SB
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<i>Trimusculus afer</i>	I	3	1969 (DOC)	Namibe	S Pacific	Gofas <i>et al.</i> , 2001	SF/SB
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**ARTHROPODA**

<i>Amphibalanus amphitrite</i>	I	3, 4, 13, 14, 18, 19	NDD	Ambrizete, Moita Seca, Off	Western Indo Pacific	Carlton <i>et al.</i> , 2011	SF
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<i>Balanus trigonus</i>	I	13, 14, 15, 18, 19	1909 (DOC)	Kwanza river Luanda, Lobito, Namibe	Pacific	Zullo, 1992	SF/SB
<b>BRYOZOA</b>							
<i>Bugula neritina</i>	C	16	1950 (DOC)	Luanda	Unknown, maybe Mediterranean	Gordon & Mawatari, 1992	SF
<i>Bugulina fulva</i>	I	16	1950 (DOC)	Luanda	Probably NW Atlantic	Ryland <i>et al.</i> , 2011	SF
<i>Cleidochasma affinis</i>	I	5	2014 (DOP)	Malembe	W Atlantic, Caribbean	Trott, 2004	SF
<i>Crisia denticulata</i>	I	16	1967 (DOP)	Quisembo	NE Atlantic, Mediterranean	Ryland, 2005	SF
<i>Electra pilosa</i>	I	5	1934 (DOC)	Cabinda	NE Atlantic (including the North Sea and the western Baltic Sea)	Nikulina <i>et al.</i> , 2007	SF
<i>Electra verticillata</i>	I	12, 16	1967 (DOP)	Luanda, Namibe, Malembe	NE Atlantic, Mediterranean	Nikulina <i>et al.</i> , 2012	SF
<i>Hagiosynodos latus</i>	I	16	1967 (DOP)	Ambrizete	NW Europe, Mediterranean	Hayward, 2001	SF

<i>Microporella ciliata</i>	I	16	1946 (DOC)	N'zeto	Probably Mediterranean	Kuklinski & Taylor, 2008	SF
<i>Rhynchozoon bispinosum</i>	I	16	1946 (DOC)	N'Zeto	Europe	Gordon & Hayward, 2005	SF
<i>Schizomavella</i> ( <i>Schizomavella</i> ) <i>auriculata</i>	I	16	1946 (DOC)	N'Zeto	Europe	Cook, 1985	SF
<i>Schizoporella errata</i>	I	16	1946 (DOC)	Luanda	Mediterranean	Hayward & Mckinney, 2002	SF
<i>Watersipora cucullata</i>	I	16	1946 (DOC)	Luanda	Mediterranean	Vieira <i>et al.</i> , 2014	SF

**CHORDATA**

<i>Ascidia curvata</i>	I	17	2010 (DOC)	Luanda	Probably Tropical W Atlantic	Rocha & Kremer, 2005	SF
<i>Ascidia aspersa</i>	I	8	2012 (DOC)	Luanda	NE Atlantic and Mediterranean	Kott 1998	SF
<i>Botrylloides giganteum</i>	C	17	2010 (DOC)	Luanda	Uncertain	Rocha <i>et al.</i> ,	IC

						2009		
						Rocha <i>et al.</i> , 2009		IC
<i>Botrylloides nigrum</i>	C	17	2010 (DOC)	Luanda	Probably W Atlantic	Dybern, 1965		IC
<i>Ciona intestinalis</i>	I	8, 17	2010 (DOC)	Luanda	N Atlantic	Mead <i>et al.</i> , 2011		IC
<i>Diplosoma listerianum</i>	I	17	2010 (DOC)	Luanda	NE Atlantic	Turon & Pereira, 1988		IC
<i>Polyandrocarpa zorritensis</i>	I	17	2010 (DOC)	Luanda	S Pacific	Rocha <i>et al.</i> , 2009		IC
<i>Polyclinum constellatum</i>	C	17	2010 (DOC)	Luanda	Uncertain	Mead <i>et al.</i> , 2011		IC
<i>Styela plicata</i>	I	8, 17	2010 (DOC)	Luanda	WN Pacific			IC

Sources: NHM (2014) – 1 (<http://data.nhm.ac.uk/object/b63ca3f9-dbeb-4d38-8082-40e390656a41>); Santos (2007) – 2; Kensley (1973) – 3; Nsiangango (2006) – 4; NHM (2014) – 5 (<http://data.nhm.ac.uk/object/b63ca3f9-dbeb-4d38-8082-40e390656a41>); Jeldes (1959) – 6; Augener (1918) – 7; Cassoma (2012) – 8; Gofas (1985) – 9; Ardovini (2004) – 10; Inácio (2015) – 11; Kensley (1980) – 12; Stubbings (1961) – 13; Stubbings (1963) – 14; Gruvel (1912) – 15; Cook (1968) – 16; Andrade (2010) – 17; Stubbings (1964) – 18; Nilson-Cantell (1938) – 19.

**SPATIAL AND TEMPORAL DIVERSITY OF NON-NATIVE BENTHIC SPECIES ASSOCIATED WITH MARINAS IN TWO ANGOLAN BAYS**

O capítulo corresponde ao artigo científico de autoria de Lueji Barros Pestana, Gustavo Muniz Dias e Antonio Carlos Marques, submetido ao periódico Biofouling em 2019.

**Abstract**

Artificial coastal and offshore structures provide hard substrates enabling the spread of marine non-native species that use these structures as “stepping stones”. The goal of this study is to describe spatial and temporal diversity of non-native coastal benthic species in two Angolan bays, assessing the prevalence of introduced and cryptogenic species along different seasons. We deployed three oyster cultivation systems in each site and season, with settlement plates. We identified 12 introduced species in Luanda and 14 in Lobito in 2016; and 10 introduced species in Luanda and 13 introduced in 2017. Composition of introduced species varied between seasons and sites and thirteen taxa (introduced or cryptogenic) were recorded for the first time for Angolan waters. Twenty-one out of the 35 sampled taxa were introduced species, and only 2 were native to the Angolan Coast, corroborating the prominent role of marinas and ports as main pathways for introductions, as well as demonstrating the vulnerability of Luanda and Lobito bays to biological invasions and corroborating the lack of studies for the country and the African continent in general. Characterization of both native and introduced species within marinas with different environmental and physical features is a mandatory policy for further studies for the African continent in general, once new introductions shall continue. Species interactions, like competition and predation, must be also considered as they may influence the richness and diversity of non-native species, leading to differences between the two sites.

*Keywords:* non-native species, benthic invertebrates, marinas, Atlantic Ocean.

**Resumo**

Estruturas artificiais costeiras e offshore fornecem substratos duros que permitem a disseminação de espécies marinhas não nativas que usam essas estruturas como “pedras de piso”. O objetivo deste estudo é descrever a diversidade espacial e temporal de espécies bentônicas costeiras não nativas em duas baías Angolanas, avaliando a prevalência de espécies introduzidas e criptogênicas ao longo de diferentes estações do ano. Nós implantamos três sistemas de cultivo de ostras em cada local e época, com placas de assentamento. Identificámos 12 espécies introduzidas em Luanda e 14 no Lobito em 2016; e

10 espécies introduzidas em Luanda e 13 introduzidas em 2017. A composição das espécies introduzidas variou entre estações e locais e treze táxons (introduzidos ou criptogénicos) foram registados pela primeira vez para as águas angolanas. Vinte e um dos 35 taxa amostrados foram introduzidos espécies, e apenas 2 eram nativos da Costa Angolana, corroborando o papel proeminente das marinas e portos como principais vias de introdução, bem como demonstrando a vulnerabilidade das baías de Luanda e Lobito às invasões e corroborando a falta de estudos para o país e o continente africano em geral. A caracterização das espécies nativas e introduzidas dentro de marinas com diferentes características ambientais e físicas é uma política obrigatória para futuros estudos para o continente africano em geral, uma vez que novas introduções devem continuar. Interações entre espécies, como competição e predação, também devem ser consideradas, pois podem influenciar a riqueza e a diversidade de espécies não-nativas, levando a diferenças entre os dois locais.

**Palavras-chave:** espécies não-nativas, invertebrados bentônicos, marinas, Oceano Atlântico.

## Introduction

Human activity has altered biodiversity and impacted terrestrial, freshwater, and marine communities for centuries, by causing addition and extinction of species and/or changes in population dynamics (Carlton, 2009). One of these phenomena, bioinvasions may lead to declines or even extinctions of native species, disrupt ecosystem functions, enhance transmission of viruses and pathogens, and cause substantial damage to natural resources and ecosystem services (Simberloff *et al.*, 2013). Bioinvasions cause significant global economic and social impacts, estimated to \$120 billion annually (Pimentel *et al.*, 2005)

Artificial coastal (e.g., harbors, pontoons in leisure craft marinas, groins, armored coastlines erosion protections) and offshore structures (e.g., oil and gas platforms, energy farms, floating buoys, traps, aquaculture facilities) provide hard substrates enabling the spread of marine non-native species that use these structures as “stepping stones” (Lehtiniemi *et al.*, 2015), by connecting marinas and harbors through maritime transportation. Marinas and ports are then ideal focal points for early detection of these species, which may be critical for potential eradication and effective management (Williams *et al.*, 2013).

A large proportion of marine introduced species are benthic organisms (Minchin *et al.*, 2013). These include sessile organisms that grow on hard substrata and vagile clinging organisms that live within or on sessile communities (Murray *et al.*, 2012). Records of marine introduced species in Angola are scarce, totaling 29 non-native and 7 cryptogenic coastal benthic (Pestana *et al.*, 2017). However, transportation of species between European,

American and African continents has occurred during the last 500 years, and therefore the richness of introduced species might be underestimated, being more an artifact of the lack of studies instead of actual low introduction history (Pestana *et al.*, 2017). Historical records of synanthropic species in the Angolan Coast, such as the polychaete *Hydroides elegans*, the barnacle *Amphibalanus amphitrite*, the bryozoan *Bugula neritina*, and the ascidians *Ciona intestinalis* and *Styela plicata*, suggest that current communities are dominated by non-native species, known by causing ecological and economical losses in coastal habitats around the world (Carballo & Naranjo, 2002; Daigle & Herbinger, 2009; Schwan *et al.*, 2016).

Although a diagnostic of non-native and cryptogenic species has been provided (Pestana *et al.*, 2017), the current composition and diversity of sessile communities in the Angolan Coast are still unknown. Thus, the goal of this study is to describe spatial and temporal diversity of non-native coastal benthic species of Hydrozoa, Polychaeta, Cirripedia, Bryozoa, and Asciadiacea in two Angolan bays, assessing the prevalence of introduced and cryptogenic species along different seasons.

## **Material & methods**

### *Study areas*

The study was carried out at two marinas in Luanda and Lobito bays, Angola. The “Clube Naval de Luanda” (hereafter CNL) at 08°47’S; 13°13’E, supports 104 boats of different sizes, most of them recreational boats from several regions of Angola. It is located in the western part of the Luanda Bay, a bay with weak currents (<0.15 m/s) that occupy approximately 19 km<sup>2</sup> (Holisticos, 2010). Luanda Bay is under strong anthropic pressure, including the influx of domestic and industrial sewage, unmanaged tourism and by the presence of the Port of Luanda (Nicolau, 2016), built in 1945, considered to be the most important of Angola since 1975, when Angola became independent (Fair, 1988). The “Clube Náutico do Lobito” (hereafter CNO), at 12°19’S; 13°34’E is a small recreational marina supporting only 20 boats. It is located at Lobito Bay, a semi-closed system ca. 4 km long and 2 km wide nearby urban areas (Lobito city), touristic zones (“Restinga”), industrial zones, and the harbor of Lobito, built in 1928, being the most important harbor for Angolan economy until its independence (Fair, 1988; Meuchi, 2016). Currents within the bay are generally slow, with maximum intensities at the mouth zone, reaching up to 5 cm/s due to the small tide range and small dimensions of the bay (Evaristo, 2017) (Figure 1).

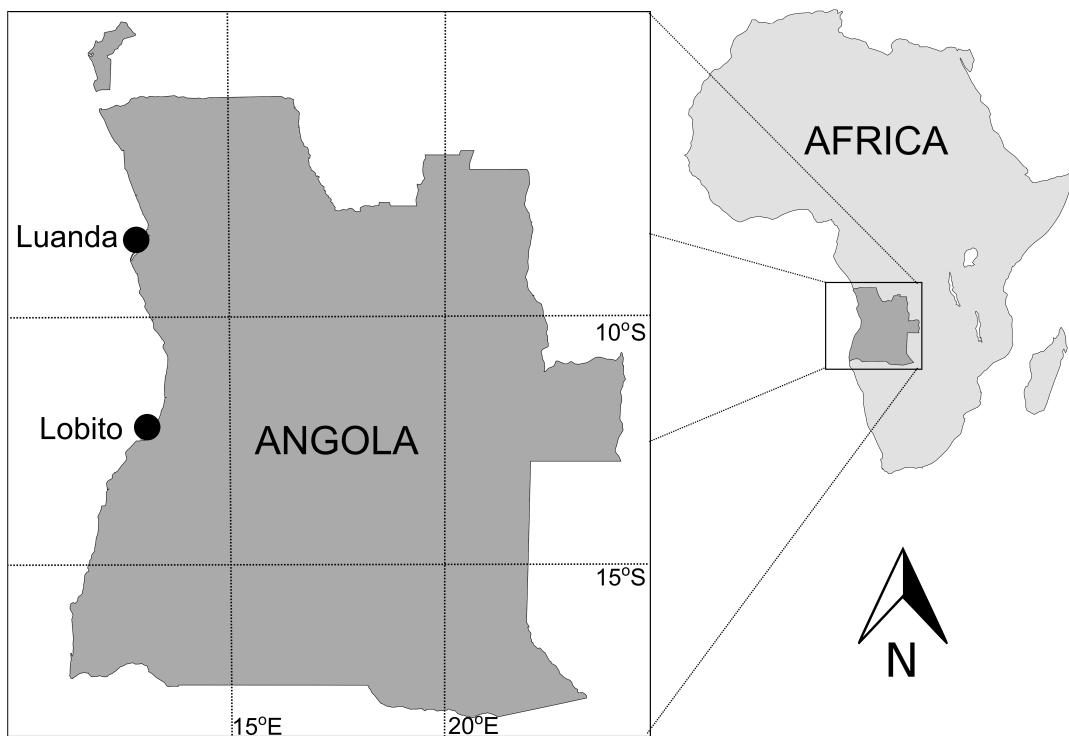


Figure 1 – The two sampling sites located in Luanda and Lobito bays, Angola.

### ***Experimental design***

To assess the diversity of non-native species in the Angolan Bays, three oyster cultivation systems were deployed (OCS) in each site and season (dry and wet seasons). OCSs had circular, perforated, plastic trays (40 cm diameter, trays separated from each other by 20 cm), were about 1 m tall and covered by a nylon screen with 5 mm mesh (Kremer and Rocha, 2016). In each of the 3 OCS, four plates were suspended attached to the underside of each tray and two attached on the outside, and hung the OCS between columns in the marinas. OCSs were deployed in April 2016 and retrieved in July 2016 (dry season), and in October 2016 and retrieved in January 2017 (wet season). While frequencies of occurrence were estimated by plates, for data analysis, it was combined the data from all six plates belonging to the same OCS and used those as a replicate because the study focused on the identity of species and their invasive status, instead on a quantitative analysis.

### ***Data processing and statistical analysis***

It was registered the benthic invertebrates growing in each plate at the end of each sampling period, and classified all species regarding their invasive status in native (N),

introduced (I) or cryptogenic (C) (cf. Chapman & Carlton, 1991). Frequencies of occurrence of the species were calculated to be compared.

It was used permutational multivariate analysis of variance (PERMANOVA) (Anderson et al., 2008) to estimate how spatial (sites) and temporal (seasons) scales affect the communities' structure. The similarity of the benthic community composition at each site and at the two different seasons was assessed using non-metric multi-dimensional scaling (nMDS) based on a Jaccard similarity matrix. Analyses were performed both for the total community and only for non-native species. Similarity percentage procedure (SIMPER) was used to determine which species were the primary contributors to the differences in the benthic community at each sampling site during the sampling periods. Analyses were carried out in PRIMER 6.1.10 (Clarke & Gorley, 2006).

## Results

35 taxa were catalogued: 21 introduced, 2 cryptogenic, 2 native, and 10 unidentified species (Table 1). Thirteen taxa (introduced or cryptogenic) are recorded for the first time for Angolan waters, viz. *Clytia* cf. *gracilis*, *Calycella gracilis* (Hydrozoa), *Branchiomma luctuosum*, *Spirobranchus tetraceros* (Polychaeta), *Amphibalanus eburneus* (Cirripedia), *Bugulina stolonifera*, *Amathia verticillata*, *Biflustra perambulata*, *Buskia socialis*, *Watersipora subtorquata* (Bryozoa), *Ascidia* cf. *multotentaculata*, *Styela canopus*, and *Symplegma* cf. *brakenhielmi* (Asciidae).

15 morphospecies were identified (12 introduced) in Luanda and 27 (14 introduced) in Lobito in 2016; and 15 morphospecies (10 introduced) in Luanda and 18 (13 introduced) in 2017. Composition of introduced species varied between seasons and sites. Eight introduced species were present in both Luanda and Lobito, viz. *Obelia* cf. *dichotoma*, *Spirobranchus tetraceros*, *Hydroides elegans*, *Balanus trigonus*, *Amphibalanus eburneus*, *Bugula neritina*, *Amathia verticillata*, and *Schizoporella errata*, with frequencies between 33 and 100% (Table 1).

Both analyses, considering the whole community and based only on the introduced species, resulted in site/season interactions (Figure 2, Table 2). Sessile communities from Lobito and Luanda are composed by distinct species, regardless of the sampling period, however in Luanda sessile communities showed more temporal variation than those from Lobito, resulting in the site/season interactions. SIMPER analysis revealed an average dissimilarity of 47.6% between the two marinas, and 4 introduced species (*Watersipora subtorquata*, *Ciona intestinalis*, *Styela plicata*, and *Symplegma* cf. *brakenhielmi*) are among

the 7 species that contributed the most to differentiate the sites (Table 3). For instance, *Ciona intestinalis* and *Styela plicata* were more frequent in Lobito in the two seasons, contrarily to Luanda, where they were only found in 2016.

Table 1 – Frequency of occurrence (%) of the benthic invertebrate species in both marinas and seasons. Status: Native (N), Introduced (I) and Cryptogenic (C); ‘Clube Naval de Luanda’ (Luanda) and ‘Clube Náutico do Lobito’ (Lobito); August/2016 (Aug16) and January/2017 (Jan17). Species marked with an asterisk (\*) are new records for Angola.

Species	Status	Luanda		Lobito	
		Aug16	Jan17	Aug16	Jan17
<b><u>Cnidaria</u></b>					
<i>Obelia cf. dichotoma</i>	I	100	100	67	100
<i>Clytia cf. gracilis</i> *	I			11	
<i>Calycella gracilis</i> *	I			6	
<i>Coryne</i> sp.			6	6	
<i>Turritopsis nutricula</i>	I			6	
<i>Eudendrium</i> sp.		6			
<i>Lovenella chiquita</i>	N		33		
<b><u>Annelida</u></b>					
<i>Branchiomma luctuosum</i> *	I	11	56	78	
<i>Branchiomma nigromaculatum</i>	I	33			
<i>Spirobranchus tetraceros</i> *	I	33	100	83	72
<i>Hydroides elegans</i>	I	100	67	100	67
<i>Parasabella</i> sp.		33	6	6	
<i>Branchiomma</i> sp.			17		
<b><u>Cirripedia</u></b>					
<i>Balanus trigonus</i>	I	33	28	78	39
<i>Amphibalanus eburneus</i> *	I	78	94	72	11
<b><u>Bryozoa</u></b>					
<i>Bugula neritina</i>	I	17	11	100	67
<i>Bugulina stolonifera</i> *	I	39		72	56
<i>Amathia verticillata</i> *	I	33	33	56	39
<i>Biflustra perambulata</i> *	C			28	
<i>Schizoporella errata</i>	I	61	100	100	67
<i>Watersipora subtorquata</i> *	I		33	33	
<i>Buskia socialis</i> *	I	33			
<i>Amathia</i> sp.				6	
<b><u>Asciidiacea</u></b>					
<i>Ascidia</i> sp. 1				17	17
<i>Ascidia cf. multotentaculata</i> *	C				11
<i>Ascidia</i> sp. 2				6	11
<i>Styela plicata</i>	I	11		22	33

<i>Styela canopus</i> *	I		17	
<i>Styela</i> sp. 1			50	44
<i>Styela</i> sp. 2			11	
<i>Polyclinum constelatum</i>	I		17	
<i>Phallusia nigra</i>	N		28	33
<i>Ciona intestinalis</i>	I	6	33	28
<i>Didemnum</i> sp. 1			44	
<i>Symplegma cf brakenhielmi</i> *	I		89	22

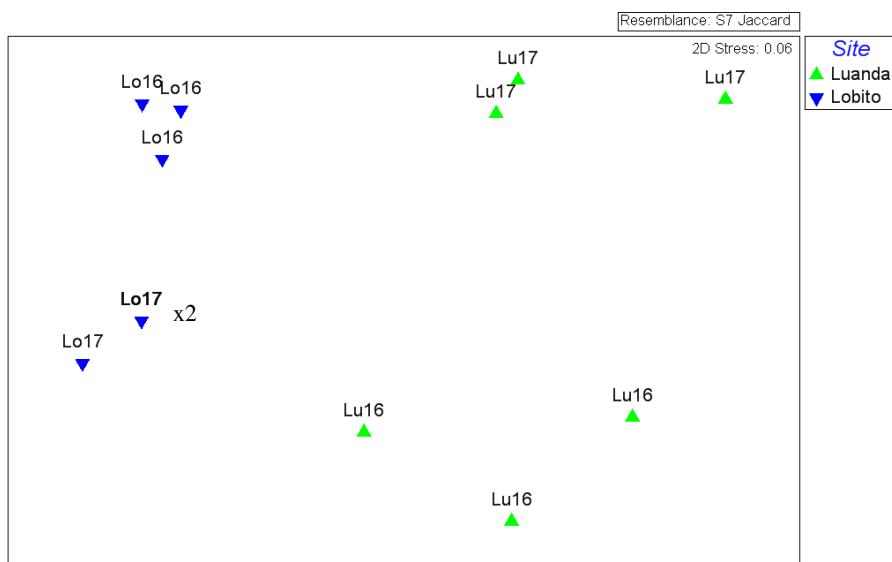
Table 2 – PERMANOVA analyses of the effects of sampling sites and season on all species and only non-native species from benthic communities; *p*-values were obtained using 999 permutations. \* *p* < 0.05

	All species			Non-native species		
	d f	MS	F	df	MS	F
Site	1 f	6823.4	14.36*	1	3979.5	15.29*
Season	1	2048.8	4.31	1	958.86	3.68*
Site x Season	1	3761.7	7.916*	1	2640.6	10.15*
Error	8	3801.8		8	2081.7	

Table 3 - SIMPER analysis showing the contribution of species to the dissimilarities (47.6%) between the two sampling sites (Clube Naval de Luanda – Luanda; Clube Náutico do Lobito – Lobito) across the two seasons. Introduced species are marked with an asterisk (\*).

Species	Contrib. %	Cum. %
<i>Watersipora subtorquata</i> *	6.85	6.85
<i>Ascidia</i> sp. 1	6.85	13.69
<i>Styela</i> sp. 1	6.85	20.54
<i>Phallusia nigra</i>	6.85	27.39
<i>Ciona intestinalis</i> *	5.87	33.26
<i>Styela plicata</i> *	4.87	38.14
<i>Symplegma</i> <i>brakenhielmi</i> *	cf. 4.77	42.90

A



B

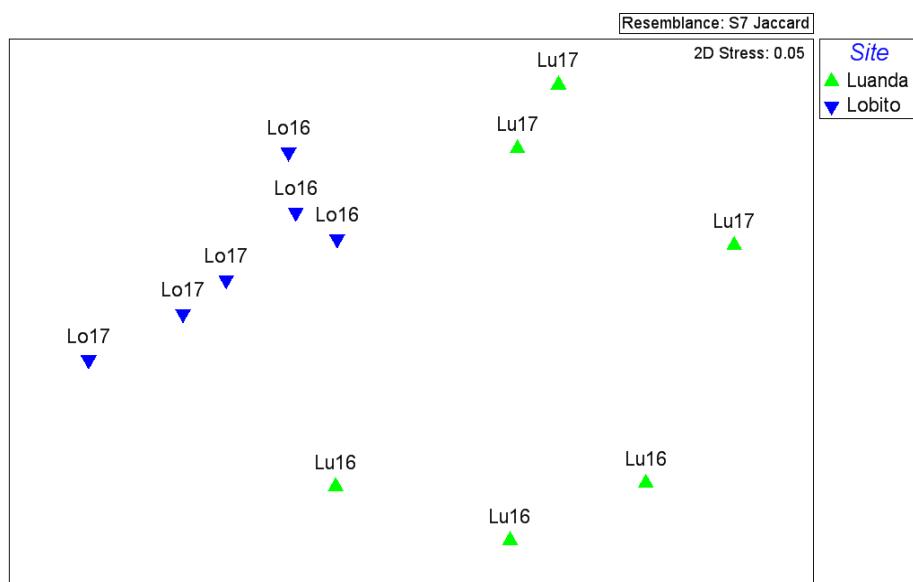


Figure 2 – Two-dimensional, non-metric multidimensional scaling (nMDS) plot showing ordination of assemblages of benthic coastal species found in the two sampled marinas, based on Jaccard similarities. A: all species; B: introduced species only. Lu16: Clube Naval de Luanda in August 2016; Lu17: Clube Naval de Luanda in January 2017; Lo16: Clube Náutico do Lobito in August 2016; Lo17: Clube Náutico do Lobito in January 2017.

## Discussion

Bioinvasion is widely recognized as the second main cause of biodiversity loss (IUCN, 2000). However, while non-native species are well-known in temperate regions of the northern hemisphere, a baseline for sessile organisms from most of the southern hemisphere, mainly for the African continent, is still lacking. In the current study, 21 out of the 35

sampled taxa are introduced species, and only 2 are considered to be native to the Angolan Coast, corroborating the prominent role of marinas and ports as main pathways for introductions, as well as demonstrating the vulnerability of Luanda and Lobito bays to biological invasions. Some of the species recorded in this study are invasive in harbors and marinas worldwide, suggesting that transportation by recreational boats and vessels may have contributed to the introduction of these species in the Angola. There are also 12 unidentified taxa and 3 cryptogenic species, highlighting the need for biodiversity surveys in the Angolan Coast and also ultimately reflecting an underestimated number of introduced species and their impacts.

This study adds 13 new records of introduced or cryptogenic species for Angolan waters in comparison to a previous literature review (Pestana *et al.*, 2017), corroborating the lack of studies for the country and Africa in general. The new records are 2 Hydrozoa, 2 Polychaeta, 1 Cirripedia, 5 Bryozoa, and 3 Ascidiacea, with origin from different regions of the world. *Spirobranchus tetraceros* and *Styela canopus* are native from the Indo-Pacific (Sun *et al.*, 2017; Kott, 1985); *Amphibalanus eburneus* from the Western Atlantic (Henry & McLaughlin 1975; Young, 1994); *Amathia verticillata* is suggested to be native from the Caribbean Sea (Galil & Gevili 2014). Finally, *Bugulina stolonifera*, considered to probably be native to the Northwest Atlantic, introduced in the South and East Atlantic (Fofonoff *et al.*, 2018) with records for Ghana in the west coast of Africa (Cook, 1968), could be either a new introduction into Angolan waters or, more likely, an artifact of the lack of information concerning Angolan marine biota and former introductions.

The port of Lobito has the highest number of introduced species in this study, what may be related to its history, as it was the most important port of Angola for decades. This may also indicate that introductions in Lobito may be older than those in Luanda, a pattern overlooked by the lack of studies and similar to what is observed in other less intensively studied regions of the world (Carlton, 2009). However, some other introductions may be more recent, like for *Spirobranchus tetraceros* and *Styela canopus*, both being possible native of the Indo-West Pacific (Kott, 1985; Carlton, 2000), that may be a consequence of the increase in commercial trade between Angola and countries, like China, for the last decades (Khan, 2015).

Lobito is ca. 400 km away from Luanda, and their communities have consistent differences through time. Using the only set of introduced species, there are distinct species' composition between the sites for both seasons. However, there is a Site vs. Season interaction, probably because of the variation in the magnitude of the difference between

sampling moments. Sessile communities from Luanda were more variable along time than those from Lobito. The plates from Luanda supported less species than those from Lobito, and were heavily colonized by polychaetes with calcareous tubes, forming tridimensional structures that occupied most of the surface of the plates. The differences in species diversity among sites can be a consequence of predation, once most of the species present only in Luanda are hidrozoans and ascidians, organisms with no structural defense and then prone to be removed by fish (Dias *et al.*, *in preparation*).

Difference among sites can be also the result of the anthropic effects on water quality. Over decades, a significant part of Luanda's wastewater, including domestic effluents, industrial, agricultural, rainwater, and street washing dumps is disposed in Luanda Bay without previous treatment, resulting in waters with high microbial activity and low oxygen concentration (Nicolau, 2016). In contrast to Luanda Bay, waters from Lobito Bay are constantly renewed, and discharges from ditches nearby do not jeopardize the quality of the water in the same way of Luanda Bay (Evaristo, 2017). Also, the suspended fine sediments found in Luanda Bay can increase mortality of suspensivorous, like juvenile ascidians (Young & Chia, 1984), by clogging ascidian siphons (Bakus, 1968), consequently altering epifaunal community development (Maughan, 2001). The combination of both natural and anthropic restriction may explain why communities from Luanda only held three ascidian species, all non-native, constrating with the 11 species of ascidians reported to Lobito. Marinas remain relatively different from each other and environmental filtering might be selecting species at each marina, despite the fact they are not far from each other, they do have intense traffic between them, and that port and marina faunas have long been observed to be similar even across different geographic regions (Ignacio *et al.*, 2010).

The general composition of the communities from Luanda presents mainly polychaetes and bryozoans, while in Lobito, besides these groups, ascidians are also frequent. Another interesting fact is that, comparing with Pestana *et al.* (2017), there are differences concerning the identity of the species among the taxa sampled. Bryozoans and ascidians are the most represented taxa and new species' records were detected for both groups. In the current study, bryozoans are represented by species frequently associated to artificial substrates around the world, like *Bugula neritina*, *Bugulina stolonifera*, *Amathia verticillata*, *Watersipora subtoquarta*, and *Schizoporella errata*. Concerning ascidians and comparing to a previous revision (Pestana *et al.*, 2017), we record the new findings *Styela canopus*, *Ascidia cf. multotentaculata* and *Symplegma cf. brakenhielmi*.

Comparatively, the species with the highest contributions to distinguish the communities from the two sites were introduced species, two of them new records for Angola and both frequent only in Lobito (*Watersipora subtorquata* and *Symplegma* cf. *brakenhielmi*). This means that the most frequent non-native species observed in the investigated localities were not only ancient introductions, such as *Hydroides elegans* or *Bugula neritina* (cf. Pestana *et al.*, 2017), but also non-native species never reported before. Considering that *W. subtorquata* and *Symplegma* cf. *brakenhielmi* are both conspicuous species, their detection suggests that they were introduced recently or were not detected (or identified) earlier, due to its taxonomic complexity. To confirm this, additional investigation should be done on the fouling communities colonizing the hulls of recreational boats, also taking into account the travel history of these boats. Besides, studies on the rocky shore near the two marinas could highlight the spread of non-native species to natural substrates.

## Conclusions

This study provides primary occurrence data of marine introduced species to the central-south Angola. The presence of 13 new records of introduced or cryptogenic species indicates gaps of knowledge concerning bioinvasions in Angola, demonstrating that broad faunal studies including natural and artificial substrates are mandatory. Characterization of both native and introduced species within marinas with different environmental and physical features is an important next step for further studies for the African continent in general, since we predict that there will be continued new introductions. In addition to the abiotic factors, species interactions, like competition and predation, must be also considered as they can also influence the richness and diversity of non-native species, leading to differences between the two sites. The study of the African component of bioinvasions is incipient but decisive to have a global picture of the situation and select actions towards conservation of marine habitats.

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## IS PREDATION IMPORTANT TO DETERMINE THE DIVERSITY OF SESSILE ORGANISMS IN THE PALEOTROPICS?

### Abstract

Studies that evaluate the effect of predation and competition in marine communities are concentrated in specific regions of the world, mainly in North America and Europe, and evidences of that are lacking for the African continent. This study intends to investigate how predation affects the success of settlement of non-native species and, consequently, determines the composition of species in two bays of Angola. The studies dealing with biotic factors are fragmentary in relation to the magnitude of the existing marine environments, and consequently there is a lack of knowledge about biotic factors and its influence on fouling communities with non-native species, especially in Africa. Considering only communities exposed to predators, temporal variation was more intense in Luanda, a site under strong anthropogenic pressure. Luanda was dominated by *Hydroides elegans* and *Amphibalanus erbuneus*, while Lobito by *Schizoporella errata* and *Spirobranchus tetraceros*. Although *Amphibalanus erbuneus* occurred in both sites, its coverage percentage was higher in Luanda. At the end of the experiment, the observed patterns of dominance (barnacles in the predated plates and ascidians in the caged plates) indicate that predation has redirected the successional process, leading to the formation of differentiated communities. Predation influenced the species composition in both sites by reducing the number of dominant competitors susceptible to predation, like *Ciona intestinalis* and *Branchiomma luctuosum*, and allowing the increase of less competitive species with more efficient defense against predators, like the armored species of bryozoans (*Schizoporella errata*) and barnacles (*Amphibalanus erbuneus*). We highlight some mechanisms beneath biotic interactions that affect and promote invasions in fouling communities, and the demand for upcoming studies to obtain responses about biotic interactions and physical disturbance as important drivers involved in marine bioinvasions in the tropics.

**Keywords:** biotic factors, incrusting communities, non-natives species, tropics.

### Resumo

Estudos que avaliam o efeito da predação e da competição em comunidades marinhas estão concentrados em regiões específicas do mundo, principalmente na América do Norte e na Europa, e suas evidências são escassas para o continente africano. Este estudo pretende investigar como a predação afeta o sucesso de

povoamento de espécies não-nativas e, consequentemente, determina a composição de espécies em duas baías de Angola. Os estudos que tratam de fatores bióticos são fragmentários em relação à magnitude dos ambientes marinhos existentes e, consequentemente, há uma falta de conhecimento sobre fatores bióticos e sua influência em comunidades incrustantes com espécies não-nativas, especialmente na África. Considerando apenas as comunidades expostas aos predadores, a variação temporal foi mais intensa em Luanda, local sob forte pressão antrópica. Luanda foi dominada por *Hydroides elegans* e *Amphibalanus erbuneus*, enquanto Lobito por *Schizoporella errata* e *Spirobranchus tetraceros*. Embora *Amphibalanus erbuneus* tenha ocorrido em ambos os locais, a sua percentagem de cobertura foi maior em Luanda. Ao final do experimento, os padrões observados de dominância (cracas nas placas predadas e ascídias nas placas protegidas) indicam que a predação redirecionou o processo sucessional, levando à formação de comunidades diferenciadas. A predação influenciou a composição de espécies nos dois locais, reduzindo o número de competidores dominantes suscetíveis à predação, como *Ciona intestinalis* e *Branchiomma luctuosum*, permitindo o aumento de espécies menos competitivas com defesa mais eficiente contra predadores, como as espécies blindadas de briozoários (*Schizoporella errata*) e cracas (*Amphibalanus erbuneus*). Destacamos alguns mecanismos de interações bióticas que afetam e promovem invasões em comunidades incrustantes, e a necessidade por estudos futuros para obter respostas sobre interações bióticas e distúrbios físicos, como fatores importantes envolvidos nas bioinvasões marinhas nos trópicos.

Palavras-chave: fatores bióticos, comunidades incrustantes, espécies não-nativas, trópicos.

## Introduction

Biological and physical disturbances influence the structure of marine and terrestrial communities (Dayton, 1971; Grime, 1977). A wide variety of biotic (e.g., competition, predation, parasitism) and abiotic (e.g., ocean proximity, hydrodynamics, temperature, salinity) factors contribute to the development and dynamics of the fouling communities (Nydam & Stachowicz, 2007). Dominant competitors can shape the community structure by monopolizing key resources, through key biological traits such as high growth rates and/or ability to overgrowth competitors (Nandakumar *et al.*, 1993; Claar *et al.*, 2011; Lord & Whitlatch, 2015).

Predation, on the other hand, can impact the community structure by influencing on the survival of the recruits (Osman and Whitlatch, 2004); Nydam & Stachowicz, 2007), or through preferential consumption that can modulate resource monopolization by competitively superior species (Osman *et al.* 1992; Nydam & Stachowicz, 2007).

For communities in which space for settlement is the limiting resource, as those composed by marine sessile animals, life-history characteristics and competitive exclusion may play an important role in shaping the species diversity (Dayton, 1971; Connell, 1978; Sousa, 1984), ultimately making these communities good models to test the processes behind community development (Cifuentes *et al.*, 2007); Nydam & Stachowicz, 2007), including the impact of non-native species on patterns of community assemblage (Gittenberger & Moons, 2011).

According to Freestone *et al.* (2013), predation pressure in a tropical region is strong enough to eliminate non-native species at small experimental spatial scales, suggesting that such strong interactions have the potential to reduce the abundance and distribution of non-native species across larger spatial scales possibly reducing their impacts and nonnative tunicates were excluded at small spatial scales. A study in Australia demonstrated that latitudinal gradients in consumer effects were apparent for individual functional groups (Lavender *et al.*, 2017). Solitary ascidians displayed the pattern consistent with predictions of greater direct effects of predators at low than high latitude. As consumers reduced the biomass of this and other competitive dominants, groups less prone to predation (e.g., hydroids, various groups of bryozoans) were able to take advantage of freed space in the presence of consumers and show increased abundances there (Lavender *et al.*, 2017). An experimental study comparing three distinct regions (tropical, subtropical, and temperate) observed that predation in tropical sites reduces both alpha and beta diversity, determining the identity of dominant species and reducing the number of non-native species (Dias *et al.*, *in prep.*). This contrasts with subtropical and temperate regions, in which predation only determined the relative abundance of species but not alpha/beta diversity.

Predation can have an intense effect on fouling community development when large predators but also micropredators are present (Osman *et al.* 1992; Osman & Whitlatch 1995, 2004; Nydam & Stachowicz, 2007). Micropredators can influence community structure during the early post-settlement period and megapredators would affect

established communities (Lavender *et al.*, 2014); Osman & Whitlatch 2004). In several marine communities, highly selective predators could theoretically be very effective in reducing large non-native species communities (Byers, 2002; Dudas *et al.*, 2005; Harding, 2003). Studying the role of invertebrate predators and micropredators on non-native species is a necessary step to better understand the potential role of predation as a viable control management tool (Kremer & Rocha, 2016) and, therefore, there is a need in more studies to evidence such role because the different studies showed differences on the results.

Non-native species are relevant to the dynamics of certain communities, making recreational marinas or harbors excellent environments for experiments to test theories regarding mechanisms underlying the invasion process, especially during the phases of settlement and establishment (Gestoso *et al.*, 2018). Although we have a general idea of how certain biotic factors may work controlling bioinvasion, the information available is constrained to the geographical regions in which the experiments were performed, and it is of utmost importance to extend this coverage. Studies that evaluate the effect of predation and competition in marine communities are concentrated in specific regions of the world, mainly in North and South America and Europe, and evidences of that are lacking in the African continent. Also, Africa is one of the places where we probably have the longest history of colonization and, consequently, a greater chance of introduced species affecting the local diversity. For that reason, this study aims to investigate how predation affects the success of settlement of non-native species and, consequently, determine the composition of species in two bays of Angola. Herein we present (1) the spatial and temporal patterns of the most dominant non-native species recorded, (2) species turnover within the two sites and (3) comparisons with other sites with similar dominance of species.

## Material and Methods

### *Study sites*

This study was carried out at two marinas in different bays from Angola, Luanda Bay and Lobito Bay, both with high risk of bioinvasion (Pestana *et al.*, submitted). The Clube Naval de Luanda (CNLU) is located at 08°47'S, 13°13'E, and the Clube Náutico do Lobito (CNLO) is located at 12°19'S; 13°34'E (Figure 1). The sites are described in Pestana *et al.* (submitted).

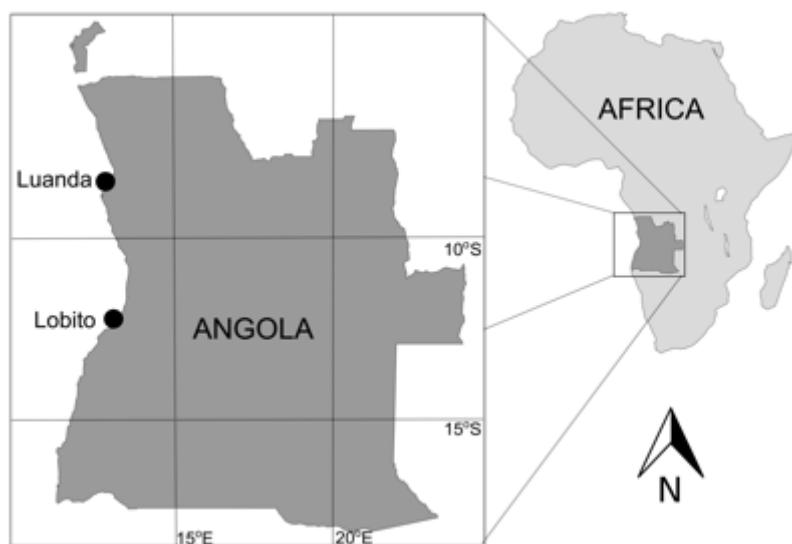


Figure 1 – Map of Angola with the two sampling sites, Luanda and Lobito (adapted from Pestana *et al.*, submitted).

To support how evidences from experimental studies testing the effect of predation on the organization of sessile communities are biased to the northern hemisphere, we used the database Web of Science to conduct an exhaustive literature review considering the following terms and all combinations among them from papers published between 1977 and 2019: predation, diversity, sessile, encrusting, experiment. From the obtained results we produced a map showing the global distribution of experiments that aimed to test the effect of predation on the diversity of sessile organisms.

### ***Experimental sampling***

We used square 36 22.5cm x 22.5cm x 0.63cm white PVC plates as hard substrate for settlement and development of the sessile communities. Plates were placed in oyster cultivation systems with five circular, perforated, plastic trays (40 cm diameter, trays separated from each other by 20 cm). Oyster cultivation systems were about 1 m tall, covered by a thick nylon screen with 5 mm mesh. Each plate was attached to the underside of each tray and all system was hung between columns in the two marinas (cf. Kremer & Rocha, 2016). The plates were assigned to three distinct treatments: “Caged” treatment was protected against all large predators; “Fenced” treatment had a rectangular aperture (about 20 cm wide) to allow some predators, and “Open” treatment were those plates hanged outside the oyster

cultivation system, allowing full access to the predators. Six oyster cultivation systems, consisting of two replicates for each treatment, were used in each of the two marinas. All plates remained submerged in the field for 90 days, but in distinct seasons. Half of the plates were set up in April 2016 at the end of the rainy season and retrieved in July 2016 during the dry season, and the other half were set up in October 2016 in the middle of the dry season and retrieved in January 2017 during the early rainy season. Unfortunately, we were unable to obtain the results from Luanda in 2017 for the caged treatment because of technical failures.

### ***Data processing and statistical procedures***

At the end of every phase of the experiment, the identity of the species and its status (i.e., native, cryptogenic, and non-native) were recorded. Fouling communities collected on settling plates were then analyzed by measuring the cover percentage of sessile species, including hydrozoans, polychaetes, ascidians, bryozoans, and crustaceans, using the image analysis software Coral Point Count with Excel extensions (CPCE) (Kohler & Gill, 2006). For the statistical analysis we used only data from non-native species with >9% of cover percentage area in at least one of the treatments.

The collected data was organized in resemblance matrices using Bray–Curtis distances on square-root transformed data. Analyses of the community similarity, using average percentage cover in the different treatments, we represented the similarity among samples and treatments using a non-metric Multi-Dimensional Scaling (nMDS). This procedure was followed by an analysis of the taxa most contributing to the observed differences, using Species Contribution to Similarity (SIMPER). The effects of site, treatment and sampling moment on the community structure were assessed using a PERMANOVA analysis on Bray-Curtis similarity matrix based on data coverage. Significant effects ( $P < 0.05$ ) were further investigated through pairwise comparisons between factors. The homogeneity of multivariate dispersion was tested using PERMDISP. Due to the technical failures mentioned above, only data from 2016 was considered to test the effect of the biotic factors. Data from both sites and seasons were used to compare temporal variation between predated treatments (Open and Fenced). All statistical analyses were performed using PRIMER software (Clarke & Gorley, 2001; Clarke & Warwick, 2001).

## Results

Fouling communities in Angola were characterized by the presence of 21 non-native, 2 cryptogenic, 2 native, and 10 unidentified species (Supplemental material for complete list). The polychaetes *Branchiomma luctuosum*, *Hydroides elegans*, *Spirobranchus tetraceros*, the barnacle *Amphibalanus erbuneus*, the bryozoans *Bugula neritina* and *Schizoporella errata*, and the ascidian *Ciona intestinalis* were the most abundant species (>9%) in at least one of the treatments/sites (Figure 2).

### ***Global distribution of predation effects on sessile diversity***

The 31 studies (totaling 42 sampling sites) represent a range of taxa and incrusting communities diversity, from a broad geographical area, including both hemispheres and five continents (Figure 3). The majority of them (>50%) were implemented in North and South America (Osman, 1977; Bertness *et al.*, 1981; Ortega, 1986; Rico *et al.*, 2015; Osman *et al.*, 1992; Osman & Whitlatch, 1995; Osman & Whitlatch, 1998; Reusch, 1998; Osman & Whitlatch, 2004; Nydam & Stachowicz, 2007; Vieira *et al.*, 2012, 2016; Freestone *et al.*, 2013; Kremer & Rocha, 2016; Oricchio *et al.*, 2016; Rogers *et al.*, 2016; Jurgens *et al.*, 2017; Theuerkauf *et al.*, 2017; Dias *et al.*, *in prep*), mainly on the Atlantic Ocean of these continents. Australia and Europe have only 10 sampling sites together (Leclerc *et al.*, 2017; Gestoso *et al.*, 2018; Dias *et al.*, *in prep*), Africa only 4 sampling sites, 2 in Angola (Diaz *et al.*, *in prep*) and 2 in South Africa (Barkai & Branch, 1998) and, so far, no experiment on this subject was carried out in Asia.

### ***Temporal turnover in predicated sessile communities***

Temporal turnover of species was distinct between the studied sites (site x season interaction) (Figure 4 and table 1). Both sites have community structures affected by the sampling season (Luanda *p*: 0.006 with 50.2% of similarity between seasons; Lobito *p*: 0.004 with 68.4% of similarity between seasons). In 2016, *H. elegans* (57.9%) and *A. erbuneus* (36.8%) contributed for temporal variation in Luanda. On the other hand, *S. errata* (34.9%), *H. elegans* (34.2%) and *S. tetraceros* (23.1%) were the species that contributed in Lobito. *Schizoporella errata* (47.5%) and *S. tetraceros* (19.0%) contributed for temporal variation in Luanda in season 2017, and for the same season, *S. tetraceros* (55.2%), *S. errata* (27.2%) and *H. elegans* (17.5%) contributed in Lobito.

*Schizoporella errata*, *Amphibalanus erbuneus*, *Spirobranchus tetraceros*, and *Bugula neritina* contributed to the dissimilarities between sites within the sampled season (Table 2). The two first were more abundant in Luanda2016 and Luanda2017, respectively, while *S. tetraceros* and *B. neritina* were more abundant in Lobito2016 (Figure 2). Sessile communities from both sites were susceptible to temporal variation, and differences among wet and dry season communities were more evident in Luanda than in Lobito (PERMDISP  $F = 4.38$ ,  $p = 0.2$ ). Luanda2016 had high cover percentage of *Amphibalanus erbuneus*. On the other hand, Lobito2017 was formed by the presence of high cover percentage of *Spirobranchus tetraceros* and *Schizoporella errata*. Finally, the group Luanda2017+Lobito2016 had *Hydroides elegans* with similar cover percentage in both sites, and *Spirobranchus tetraceros* and *Schizoporella errata* without similar coverage (Figures 2 and 4).

#### ***The effect of predation on the sessile communities***

The effect of predation on the structure of sessile communities was variable among sites (treatment x site interaction) (Figure 2, Table 3). Overall, the area occupied by sessile organisms was bigger in treatments exposed to predators (open and fenced plates) (25% of bare space) than in the protected to predators (54%). *Hydroides elegans* with similar cover percentage in both sites, and the encrusting bryozoan *Schizoporella errata* in Lobito, occupied most of the substrate in open and fenced treatments. In Luanda, predation affected positively *Amphibalanus erbuneus*, being this species abundant in treatments exposed to predators (open and fenced) (Figure 5, Table 3).

Caged communities were distinct in the two sampled sites, with a dominance of *Ciona intestinalis* in Lobito and *Hydroides elegans* in Luanda. In Lobito, *Ciona intestinalis* tended to decrease in abundance when exposed to predators (open and fenced plates), as occurred in Luanda for *Hydroides elegans*, reinforcing a treatment x site interaction (Figure 5, Table 4). However, pairwise tests showed no significant differences in the community structure between treatments tested in each site (Luanda: O, F plates  $p: 0.18$  with 82.7 of similarity between treatments; O, C plates  $p: 0.1$  with 64.6 of similarity between treatments and F, C plates  $p: 0.10$  with 94.5 of similarity between treatments; Lobito: O, F plates  $p: 0.30$  with 86.4 of similarity between treatments; O, C plates  $p: 0.11$  with 42.8 of similarity between treatments and F, C plates  $p: 0.11$  with 51.2 of similarity between treatments ).

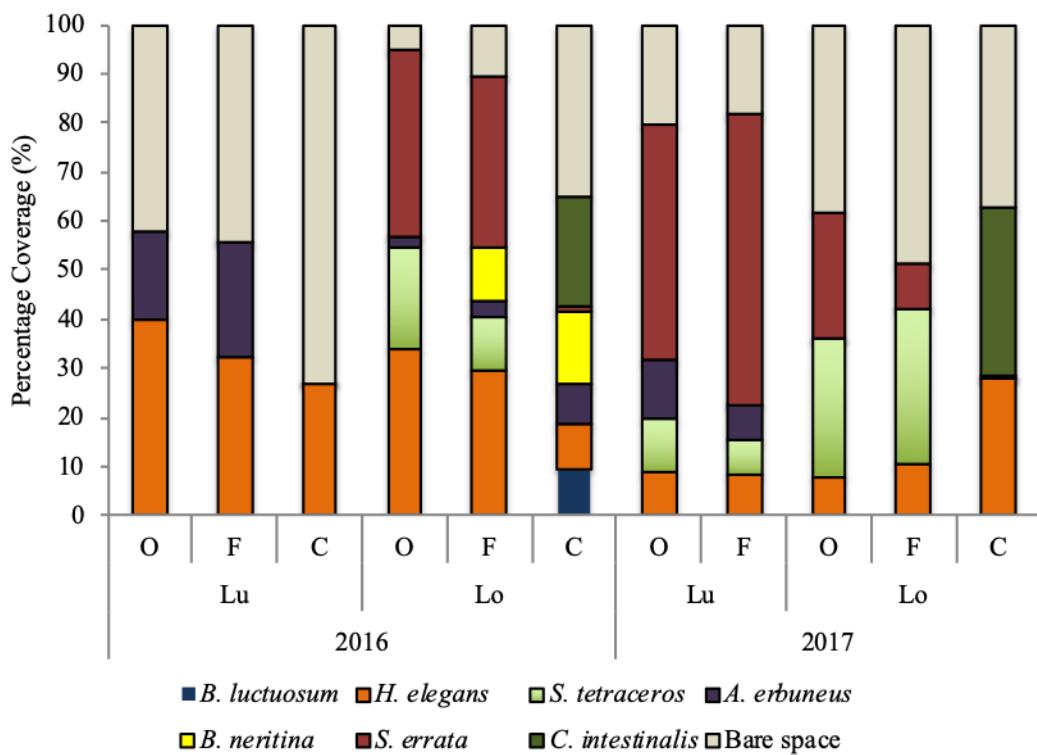


Figure 2 – Cover percentage of the most abundant species occurring during the two seasons sampled at each treatment tested. Lu: Luanda; Lo: Lobito; O: “Open”, F: “Fenced”; C: “Caged”.

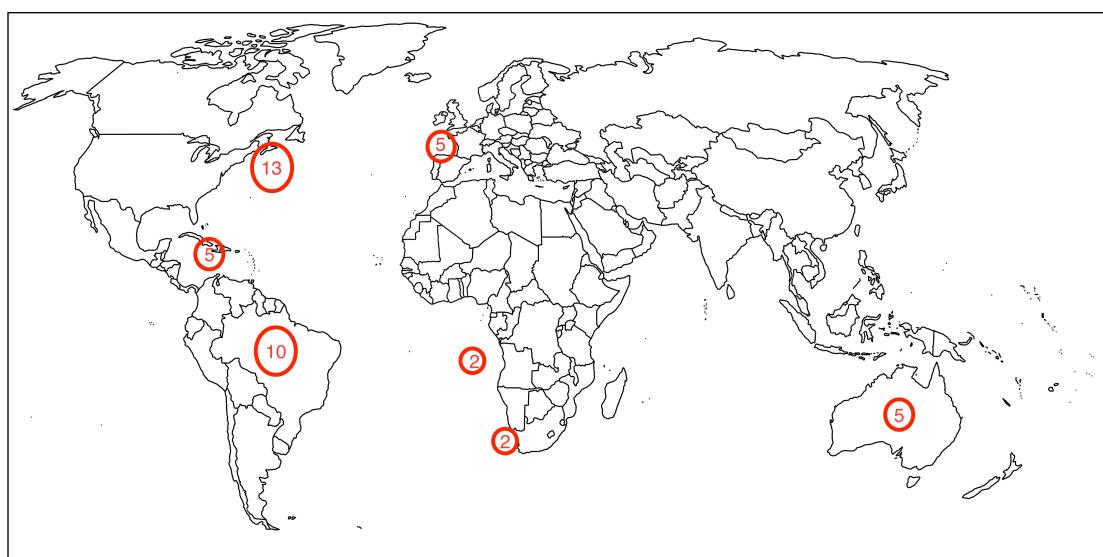


Figure 3 – Map indicating the regions of the world with experiments testing the influence of biotic factors in incrusting communities. (Numbers in circles: number of sampling sites in each region).

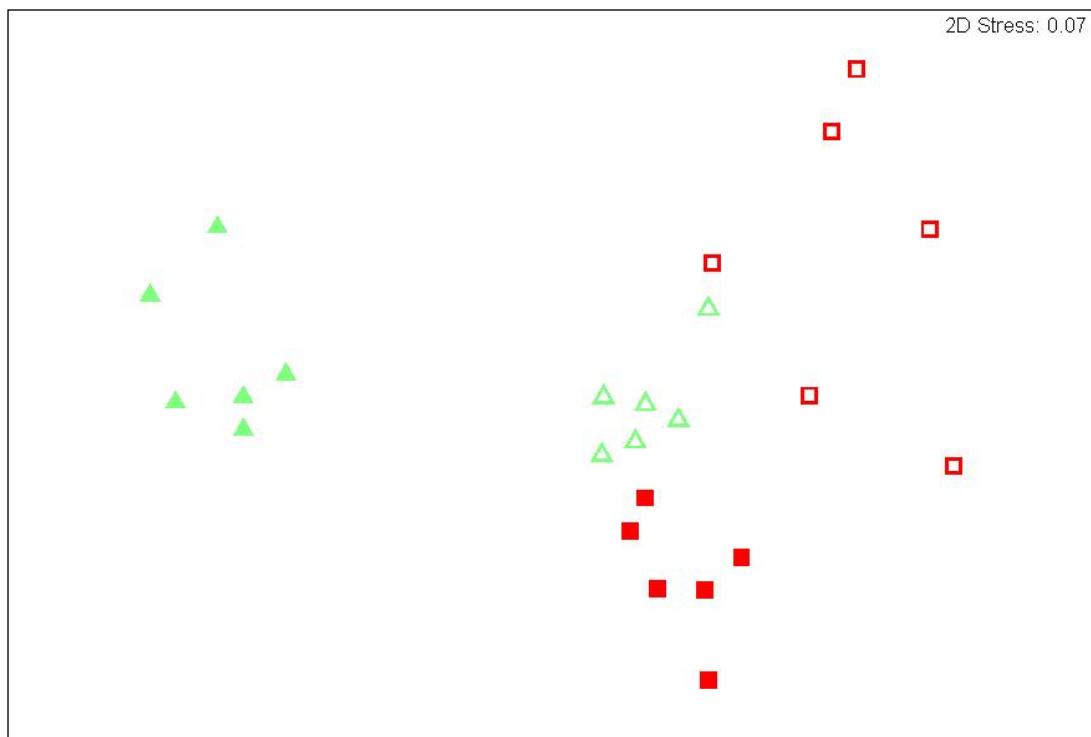


Figure 4 – Comparison of species' cover percentage area in predicated plates between Luanda and Lobito based on nMDS across the two seasons sampled. (Solid triangle: Luanda 2016; Solid square: Luanda 2017; Blanc triangle: Lobito 2016; Blanc square: Lobito 2017).

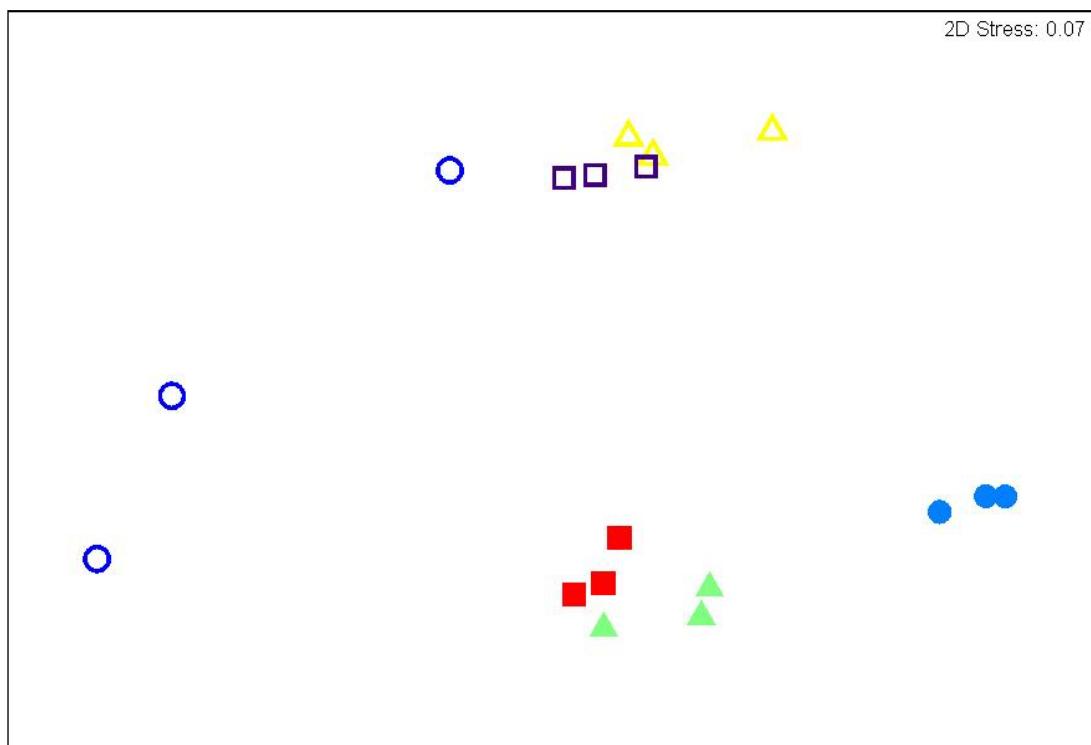


Figure 5 – Comparison of the species' cover percentage area between Luanda and Lobito based on nMDS across season 2016 and the three treatments tested. (Solid triangle: Luanda open; Solid square: Luanda fenced; Solid circle: Luanda caged; Blanc triangle: Lobito open; Blanc square: Lobito fenced; Blanc circle: Lobito caged).

Table 1 – PERMANOVA analyses of the effects of sampling sites and season in predated plates (Site: Si; Season: Se); *p*-values were obtained using 999 permutations; \**p* < 0.05.

	Df	MS	F
Si	1	6908.9	39.6*
Se	1	7211.2	41.4*
SixSe	1	1977.7	11.36*
Error	20	174	

Table 2 – Results of SIMPER analysis comparing predated plates in the both sites and seasons sampled. The average dissimilarities, as well as taxa contributing most to these dissimilarities, are presented. Seasons: 2016 and 2017.

	2016	2017
Average dissimilarity comparing sites in each season (%)	44.25 9	38.2 9
Contributions of taxa (%)		
<i>Schizoporella errata</i>	43.88 2	34.2 2
<i>Bugula neritina</i>	5.87	-
<i>Spirobranchus tetraceros</i>	21.49 2	23.4 2
<i>Amphibalanus erubaneus</i>	23.11 2	27.9 2

Table 3 – PERMANOVA analyses of the effects of sampling sites and treatment in season 2016. (Site: Si; Treatment: Tr); *p*-values were obtained using 999 permutations; \**p* < 0.05.

	df	MS	F
Si	1	8013.1	53.3*
Tr	2	1946.3	12.9*
SixTr	2	2563.7	8*
Error	17	269	

Table 4 – Results of SIMPER analysis, comparing sites in each treatment tested for season 2016. The average dissimilarities, as well as taxa contributing most to these dissimilarities, are presented (see text for more details). Treatments: O (Open); F (Fenced) and C (Caged).

	O	F	C
Average dissimilarity comparing sites in each treatment (%)	49.3 6	39.5 5	72.8 9
Contributions of taxa (%)			
<i>Schizoporella errata</i>	39.1 0	49.3 9	12.2 0
<i>Bugula neritina</i>	-	10.8 9	17.6 1
<i>Spirobranchus tetraceros</i>	27.8 6	14.2 1	-
<i>Amphibalanus erbuneus</i>	22.4 9	23.6 7	12.0 0
<i>Hydroides elegans</i>	8.93	-	9.74
<i>Branchiomma luctuosum</i>	-	-	16.5 7
<i>Ciona intestinalis</i>	-	-	26.4 7

## Discussion

The majority of the work dealing with predation driving sessile communities was conducted in the northern hemisphere, and in Africa the only published study was carried out in a subtropical region. The studies dealing with biotic factors are fragmentary in relation to the magnitude of the existing marine environments, and consequently there is a lack of knowledge about biotic factors and its influence on fouling communities with non-native species, especially in Africa and Asia. In this study it is shown the existence of a temporal variation of the communities, even in a typically tropical region, where it could be expected greater stability of the conditions, but predation can influence non-native species diversity in fouling communities on these region.

Considering only communities exposed to predators, temporal variation was more intense in Luanda, a site under strong anthropogenic pressure. Luanda was dominated by *H. elegans* and *A. erbuneus*, while Lobito by *S. errata* and *S. tetraceros*. Although *A. erbuneus* occurred in both sites, its coverage percentage was higher in Luanda. These patterns may be related to differences among the two sites,

like (1) variable availability of resources, (2) distinctive assemblage of species, (3) distinctive vulnerability to predation, (4) unique communities of predators, and (5) environmental pressures.

Differences in community composition among sites along with anthropogenic impact probably played an important role in determining the temporal turnover of species. Species adopting exploitative competition that quickly occupy available space via recruitment or growth (e.g., *S. errata* and *A. erburneus*) were observed at both sites, but in distinct seasons. In 2016, communities from Luanda were dominated by *H. elegans* and *A. erburneus*, but in 2017, *S. errata* replaced those species as dominant species. In Lobito, *S. errata* and *H. elegans* dominated the plates, and in 2017 *S. tetraceros* replaced *H. elegans*. The three species share the non-native status and structural defenses, and so, besides differences in species traits, physical factors could be involved in this temporal turnover, like changes in water temperature between seasons. It is well known that *H. elegans*, for instance, is common and can easily dominate artificial substrates in subtropical and tropical waters (ten Hove, 1974; Hadfield *et al.*, 1994; Bastida-Zavala & ten Hove, 2002; Schwan *et al.*, 2015). Regarding *S. errata*, the high reproduction and settlement of this species during the warmer months in the Western Mediterranean (Italy) (Montanaro & Tursi, 1983), corroborating its presence in Luanda in 2017 (plates were also set in the warmer months). The abundance of the species in Lobito in 2016 could be explained by the production of gametes throughout the year, although its larval production could be interrupted by some breaks (Sokolover *et al.*, 2018). Larvae of *A. erburneus* can successfully settle one to three days following the final naupliar moult, at 26°C (Costlow & Bookhout, 1957). Besides, the species also settles better in outer surfaces under good water flow (e.g., Gibbons, 1988; Soniat & Burton, 2005; Johnson *et al.*, 2017), which can explain the percentage coverage in open and fenced plates, with better water circulation. Based on its native range, the species survives in estuaries, from winter ice cover to warm tropical temperatures (Henry & McLaughlin, 1975), which explains its presence in both seasons, but with different percentage coverage.

The results obtained in this study corroborate that predation in tropical sites control several dimensions of diversity (Freestone *et al.*, 2011), in which total percent cover was also reduced in exposed communities in a tropical sampling site. On the other hand, the results in the study for the caged and uncaged plates presented similar species richness in a subtropical region (Vieira *et al.*, 2016), opposite to a temperate

region, on which predation increased diversity by removing dominant competitors in an intertidal community (Paine, 1966). At the end of the experiment, the observed patterns of dominance (barnacles in the predated plates and ascidians in the caged plates) indicate that predation has redirected the successional process, leading to the formation of differentiated communities. Predation influenced the species composition in both sites by reducing the number of dominant competitors susceptible to predation, like *Ciona intestinalis* and *Branchiomma luctuosum*, and allowing the increase of less competitive species with more efficient defense against predators, like the armored species of bryozoans (*Schizoporella errata*) and barnacles (*Amphibalanus erbuneus*). This pattern is evidenced by the high dominance of ascidians in the predator-free communities (cf. Dumont, 2011; Kremer & Rocha, 2016; Dias *et al.*, *in prep*). Despite this, the presence of *C. intestinalis* did not provide an increase in coverage area by other species, contrary to what happened in other studies, where the dominance of ascidians in caged plates corresponded to a greater species richness (e.g. Osman & Whitlatch, 2004).

This study contributes to a better understanding of the ecological processes driving colonization at the local scale in two Angolan systems. Biotic interaction in the form of predation promoted the replacement in dominance of non-native species and prevented high densities of common species of invasive fouling communities, such as ascidians, like *Ciona intestinalis* and bryozoans like *Bugula neritina*. Caged (= non predated) plates were generally more similar to each other within the two sites, corroborating that this biotic factor is determinant in the formation and structure of fouling communities. The experiment was performed as a 3-month submersion, which could limit our findings and conclusions, but our results corroborate that predation is an important structuring force for tropical regions (Freestone *et al.*, 2013; Kremer & Rocha, 2016). We highlight some mechanisms beneath biotic interactions that affect and promote invasions in fouling communities, and the demand for upcoming studies to obtain responses about biotic interactions and physical disturbance as important drivers involved in marine bioinvasions in the tropics.

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### Supplementary material

SI – Non-native benthic invertebrate species occurring in both marinas and seasons. ‘Clube Naval de Luanda’ (Luanda) and ‘Clube Náutico do Lobito’ (Lobito); August/2016 (Aug16) and January/2017 (Jan17); “Caged” (C), “Fenced” (F); “Open” (O).

Species	Status	Luanda		Lobito	
		Aug16	Jan17	Aug16	Jan17
<i>Obelia cf. dichotoma</i>	I	X	X	X	X
<i>Clytia cf. gracilis</i>	I			X	
<i>Calycella gracilis</i>	I			X	
<i>Turritopsis nutricula</i>	I			X	
<i>Branchiomma luctuosum</i>	I	X	X	X	X
<i>Spirobranchus tetraceros</i>	I	X	X	X	X
<i>Hydroides elegans</i>	I	X	X	X	X
<i>Balanus trigonus</i>	I	X	X	X	X
<i>Amphibalanus eburneus</i>	I	X	X	X	X
<i>Bugula neritina</i>	I	X	X	X	X
<i>Bugulina stolonifera</i>	I	X		X	X
<i>Amathia verticillata</i>	I	X	X	X	X
<i>Schizoporella errata</i>	I	X	X	X	X
<i>Watersipora subtorquata</i>	I		X	X	
<i>Buskia socialis</i>	I	X			
<i>Styela plicata</i>	I	X			
<i>Styela canopus</i>	I				X
<i>Polyclinum constelatum</i>	I			X	
<i>Ciona intestinalis</i>	I	X		X	X
<i>Symplegma cf brakenhielmi</i>	I		X	X	X

## **CONSIDERAÇÕES FINAIS**

Neste estudo apresentamos a primeira avaliação sobre alguns grupos de invertebrados bentônicos sésseis introduzidos na costa Angolana. Constatou-se que a costa oeste da África é amplamente ignorada do ponto de vista científico, estando entre as regiões menos conhecidas do mundo, sendo imprescindível informações sobre a distribuição das espécies e sua biodiversidade, tanto das nativas como das introduzidas.

A nossa revisão histórica da biodiversidade marinha em águas angolanas, baseada em registros da literatura científica (incluindo a cinzenta), coleções de museus, e levantamentos faunísticos não publicados (tendo por base informação de substratos naturais e artificiais), resultou na classificação de 29 espécies não-nativas para a costa Angolana. Do estudo realizado nas marinas escolhidas em duas baías de Angola, 35 táxons foram catalogados, sendo 21 espécies introduzidas, 2 criptogênicas, 2 nativas e 10 não identificadas. Treze táxons (introduzidos ou criptogênicos) são registados pela primeira vez em águas angolanas, viz. *Clytia cf. gracilis*, *Calycella gracilis*, *Branchiomma luctuosum*, *Spirobranchus tetraceros*, *Amphibalanus eburneus*, *Bugulina stolonifera*, *Amathia verticillata*, *Biflustra perambulata*, *Buskia socialis*, *Watersipora subtorquata*, *Ascidia cf. multotentaculata*, *Styela canopus* e *Symplegma cf. brackenhielmi*. A presença destes 13 novos registros de espécies introduzidas ou criptogênicas indica lacunas de conhecimento sobre bioinvasões em Angola, demonstrando que estudos de fauna ampla, incluindo substratos naturais e artificiais, são obrigatórios, corroborando também, o papel proeminente das marinas e portos como principais vias de introdução, bem como demonstrando a vulnerabilidade das baías de Luanda e Lobito às invasões biológicas. A caracterização de espécies nativas e introduzidas dentro de marinas com diferentes características ambientais e físicas deverá ser o próximo passo para futuros estudos no continente africano em geral, e em Angola, particularmente, uma vez que prevemos que haverá introduções continuadas. Para além disso, estudos na costa rochosa perto das marinas podem revelar a disseminação de espécies não nativas para substratos naturais.

Foi igualmente avaliado como os fatores bióticos, no caso a predação, afetam o sucesso de povoamento de espécies não-nativas e, consequentemente, determina a sua composição nos dois locais de estudo. Os poliquetas *Branchiomma luctuosum*, *Hydroides elegans*, *Spirobranchus tetraceros*, a craca *Amphibalanus eburneus*, os briozoários *Bugula neritina* e *Schizoporella errata* e a ascídia *Ciona intestinalis* foram as espécies mais abundantes (> 9% em cobertura) em pelo menos um dos

## **CONSIDERAÇÕES FINAIS**

tratamentos (placas abertas, placas semi fechadas e placas fechadas) e/ou nos locais estudados. Essas espécies foram utilizadas para se discutir a influência do fator biótico de predação contrastando-se com variáveis espaciais e temporais. Do levantamento bibliográfico sobre influência de fatores bióticos em comunidades incrustantes, constatamos que o conhecimento sobre os mesmos é fragmentado em relação à magnitude dos ambientes marinhos existentes e, consequentemente, há uma falta de conhecimento sobre os fatores bióticos e sua influência nas comunidades de incrustação com espécies não-nativas, especialmente na África e na Ásia. O estudo da predação nos dois locais, com o uso de placas de colonização, contribuiu para uma melhor compreensão dos processos ecológicos que conduzem a colonização à escala local em dois sistemas angolanos. A interação biótica na forma de predação promoveu a substituição na dominância de espécies não-nativas e previu altas densidades de espécies não-nativas comuns em comunidades incrustantes, tais como *Ciona intestinalis* e *Bugula neritina*. As placas protegidas pela predação foram em geral mais semelhantes entre si dentro dos dois locais, corroborando que a predação é determinante na formação e estrutura de comunidades incrustantes. Destacou-se, desta forma, alguns mecanismos de interações bióticas que afetam e promovem invasões em comunidades incrustantes, e a necessidade por estudos futuros para obter respostas sobre interações bióticas e distúrbios físicos, como importantes fatores envolvidos nas bioinvasões marinhas nos trópicos.

A África está entre as regiões menos conhecidas do mundo e há carência em informações sobre distribuição de espécies e biodiversidade de espécies nativas e não-nativas. Este desconhecimento básico surge como o maior problema para se compreender melhor o enorme impacto que as invasões marinhas exercem sobre os ecossistemas marinhos neste continente. Porém, apesar dos estudos em bioinvasões marinhas no continente africano serem incipientes, são decisivos para se conseguir obter uma visão global do problema e adoptar ações para a conservação dos habitats marinhos.

## RESUMO

A bioinvasão é amplamente reconhecida como a segunda principal causa de perda de biodiversidade. A maior parte do comércio mundial ocorre por transporte marítimo entre portos, concentrados em baías e estuários, criando oportunidades para transferências de espécies associadas a cascos de navios e materiais de lastro. Considerando o grande número de espécies não-nativas reportadas para a região do Atlântico Sul e o intenso tráfico de escravos que ligaram os continentes americano e africano desde o século XVI, é esperado que a pouco conhecida costa ocidental de África esteja exposta à intensa introdução de espécies não-nativas. A falta de avaliação ecológica e estudos das espécies não-nativas marinhas em Angola criou uma lacuna em relação à sua distribuição atual e impacto nas comunidades nativas. Os principais objetivos deste estudo foram revelar e avaliar o estado atual das espécies costeiras marinhas bentônicas não-nativas registradas em duas baías angolanas e compreender alguns dos fatores que podem afetar a sua abundância e distribuição. Da revisão bibliográfica realizada, 29 espécies foram classificadas como introduzidas e 7 como criptogênicas. A coleta realizada nos dois pontos, Luanda e Lobito, teve como resultado a identificação de 21 espécies introduzidas e 2 criptogênicas, das quais, 13 são novos registros para a costa Angolana. Considerando apenas as comunidades expostas aos predadores, a variação temporal foi mais intensa em Luanda, local sob forte pressão antrópica. Ao final do experimento, os padrões observados de dominância (cracas nas placas predadas e ascídias nas placas protegidas) indicam que a predação redirecionou o processo sucessional, levando à formação de comunidades diferenciadas. Neste estudo, foi apresentada a primeira avaliação sobre alguns grupos de invertebrados bentônicos sésseis introduzidos na costa angolana. Constata-se que a costa oeste da África é amplamente ignorada do ponto de vista científico, estando entre as regiões menos conhecidas do mundo, sendo imprescindível informações sobre a distribuição das espécies e sua biodiversidade, tanto para nativas como introduzidas. Destacamos alguns mecanismos de interações bióticas que afetam e promovem invasões em comunidades incrustantes, e a necessidade por estudos futuros para obter respostas sobre interações bióticas e distúrbios físicos, como fatores importantes envolvidos nas bioinvasões marinhas nos trópicos.

**Palavras-chave:** espécies marinhas não-nativas, organismos incrustantes, fatores bióticos, Atlântico Sul, Angola.

## **ABSTRACT**

Bioinvasion is widely recognized as the second leading cause of biodiversity loss. Most of the world trade occurs through maritime transport between ports, concentrating on bays and estuaries, creating opportunities for species transfers associated with ship hulls and ballast materials. Considering these large numbers of non-native species reported for the South Atlantic region, and the intense traffic of slaves that connected American and African continents since the XVI century, it is expected that the poorly known Western Coast of Africa would be exposed to intense introduction of exotic species. The lack of ecological assessment and studies of non-native marine species in Angola has created a gap in relation to its current distribution and impact on native communities. The main objectives of this study were to reveal and evaluate the current status of non-native benthic marine coastal species recorded in two Angolan bays and to understand some of the factors that may affect their abundance and distribution. From the literature review, 29 species were classified as introduced and 7 as cryptogenic. The collection of the two sites, Luanda and Lobito, resulted in the identification of 21 introduced species and 2 cryptogenic species, of which 13 are new records for the Angolan coast. Considering only the communities exposed to predators, the temporal variation was more intense in Luanda, a place under strong anthropic pressure. At the end of the experiment, observed patterns of dominance (barnacles on the predatory plates and ascidians on the protected plates) indicate that predation redirected the successional process, leading to the formation of differentiated communities. In this study, the first evaluation of some groups of introduced sessile benthic invertebrates on the Angolan coast was presented. It is noted that the west coast of Africa is largely ignored from a scientific point of view, being among the least known regions in the world, and information on the distribution of species and their biodiversity, both native and introduced, is essential. We highlight some mechanisms beneath biotic interactions that affect and promote invasions in fouling communities, and the demand for upcoming studies to obtain responses about biotic interactions and physical disturbance as important drivers involved in marine bioinvasions in the tropics.

**Keywords:** marine non-native species, incrusting organisms, biotic factors, South Atlantic, Angola.