

Ectoparasite infection levels differ between fish from upwelling-exposed and sheltered rocky reefs areas in Brazil

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ABSTRACT

Ubiquitous and abundant within marine ecosystems, parasites play essential ecological roles such as shaping host population dynamics, altering competition between species, and influencing energy flows through communities. Their diversity and population dynamics are demonstrably shaped by both seasonal and geographic variations. These variations have been often explored at broad spatial scale. However, parasite communities can exhibit significant disparities even at small spatial scales, driven by factors such as wave exposure, temperature fluctuations, and benthic habitat composition. We investigated how crustacean parasites of fish – caligids and gnathiids - differed between two distinct habitats, which are separated solely by a few kilometres, at Arraial do Cabo, Brazil. These two habitats are characterised by a sheltered embayment (hereinafter referred to as “inside”) or an exposed upwelling habitat (hereinafter referred to as “outside”). Individual fish from four species were examined in both habitats. We found that the infestation rate of caligids varied among fish species and, gnathiids varied between the two sampling sites. Gnathiids were absent from fish outside, while they were present on fish inside the embayment. This disparity suggests a critical role of local environmental factors in shaping gnathiid distribution. Potential drivers include temperature fluctuations, substrate composition, and wave exposure, which differed markedly between the two sites. Conversely, caligid parasites infected fish in both locations. While environmental factors may also influence caligid abundance, they appear to exhibit greater tolerance compared to gnathiids. These findings emphasize the importance of incorporating fine-scale environmental heterogeneity when investigating parasite distribution patterns.

1. Introduction

In the marine environment, parasites are widespread, abundant and have crucial functional roles in the ecosystems they inhabit. Parasites can affect the surrounding community of free-living organisms by, for

example, regulating host populations (i.e., keeping it near an equilibrium; Poulin, 1999; Lafferty, 2013), and facilitating the transfer of energy through food webs (Lafferty et al., 2006; Lafferty, 2013). Parasites are often characterised by their dynamic assemblages as they can vary drastically according to a multitude of factors, including host behaviour

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and environmental conditions (Poulin, 2007).

Ectoparasites, defined as those that infect fish skin and external orifices, are extremely diverse and have evolved complex adaptations to attach to their hosts, feed and reproduce (e.g., Kim, 1985; Guerenstein et al., 2000; Mikheev et al., 2015). They can be permanently attached, spending their entire life on the skin of the host, or transient, possessing both free-living and infective stages (Van As and Van As, 2019). Ectoparasite populations can fluctuate depending on various factors such as host density (Wood et al., 2014), host immune response (Kar et al., 2016), and the presence of predators (Grutter, 1999; Paula et al., 2021). Ectoparasites can cause skin irritation and inflammation, which can also induce secondary infections (Johnson et al., 2019). They can weaken their host's immune system, drain their energy (Sikkel and Welicky, 2019) and, in some cases, even cause the death of their hosts (Johnson et al., 2019).

Crustacean ectoparasites represent a major portion of all ectoparasites infecting fish (over 7000 species, Boxshall and Hayes, 2019) displaying a remarkable diversity in shape and function (Smit et al., 2019). Crustaceans from the group Isopoda, Copepoda, and Amphipoda, encompass diverse families and species of ectoparasites, targeting and infecting a wide range of vertebrate and invertebrate hosts (Smit et al., 2019). Caligidae (Copepoda), often referred to as 'sea lice', is a diverse group of ectoparasites, with more than 500 species described (Boxshall and Hayes, 2019). Caligids are parasitic while pre-adults and adults (Maran et al., 2013) and they graze on the host epidermis feeding on mucus, skin, and underlying tissue of fish hosts (Whelan, 2010). After hatching, the naupliar stages are non-parasitic and remain in the water column until reaching their first parasitic stage on the host. Despite their widespread distribution in tropical (e.g., Byrnes, 1987; Soler-Jiménez et al., 2019) and subtropical (e.g., Catalano and Hutson, 2010) marine environments, research on caligids has primarily focused on their threats to farmed salmon in temperate regions of Northern Europe (e.g., Revie et al., 2002; Igboeli et al., 2014).

Gnathiidae (Isopoda), also referred as the "tick of the sea" (Artim and Sikkel, 2016) are another group of crustacean ectoparasites. They are hematophagous, i.e., feeding on fish blood and plasma. Gnathiids are parasitic solely during larval stages, and are therefore referred to as 'micropredators' (Lafferty and Kuris, 2002). The non-feeding adults live on the benthos to reproduce (Smit and Davies, 2004). After hatching, the larvae swim from the benthos to a fish host, feed and drop off to reach the benthos again and moult to the next larval stage (Smit and Davies, 2004). Gnathiids have three parasitic larval stages, that is, after the first moult, the second stage larvae repeat this feeding procedure and moult again into the third and final larval stage. After the feeding of the third larval stage, gnathiids metamorphose into a non-feeding and non-parasitic adult (Smit and Davies, 2004). Both moulting larvae and adults gnathiid require appropriate substrate to moult in between each stage and to reproduce, respectively (Tanaka, 2007). Gnathiids are ubiquitous ectoparasites (Poore and Bruce, 2012), have a broad host range (Hendrick et al., 2023), and are mostly studied in tropical reefs (e.g., Grutter and Poulin, 1998; Grutter and Hendrikz, 1999; Sikkel et al., 2019), but occurring in diverse marine habitats, for instance, deep ocean (e.g., Svavarsson, 1999; George, 2003), temperate habitats (e.g., Arnal and Morand, 2001; Narvaez et al., 2015) and even in Antarctic environments (e.g., Wägele, 1987).

Ectoparasites distribution and abundance are influenced by seasonal variations (Sikkel et al., 2019; Jemi Job et al., 2022), with temperature fluctuation being considered as a major factor influencing parasite life cycles and their abilities to infect their hosts (Groner et al., 2014; Brazenor et al., 2020). For caligids, warmer temperatures can benefit certain species; with some increasing their reproductive success and development (Groner et al., 2014; Montory et al., 2018). However, other ectoparasites such as gnathiids, exhibit thermal susceptibility. For example, high mortality rates were observed for gnathiids when the temperature exceeds the average seasonal sea surface temperature in tropical systems such as the Great Barrier Reef in Australia and in the

Philippines (Sikkel et al., 2019; Shodipo et al., 2020).

Temporal variabilities induced by local factors such as wind-driven upwelling systems can also influence local marine communities. Upwelling systems are defined as areas in the ocean where cooler, nutrient-rich water from deeper layers rises to the surface (Barber, 2001). Brazil is exposed to several upwelling systems along its coastline (Coelho-Souza et al., 2012), which play a crucial role in the local marine productivity (Souza et al., 2020). The Cabo Frio Upwelling System, located off the coast of the state of Rio de Janeiro, is mainly driven by the prevailing northeasterly winds that blow along the coast for most of the year, especially in the spring and summer (Valentin, 2001; Cordeiro et al., 2020). The influence of this upwelling system exhibits spatial heterogeneity along the surrounding coastline (Valentin, 1984). Indeed, the region of Arraial do Cabo is characterised by the presence of two distinct and contrasting habitat types: one experiences the direct influence of the Cabo Frio Upwelling System bringing cold water, while the second habitat is located within a large embayment and thus only occasionally affected by upwelling. The occurrence of these two different water masses is responsible for a diverse scenario with subtropical and warm temperate organisms within a few kilometres of each other (from 1 to 5 km) with several organisms shown to be affected by these two distinctive environments. The assemblage of roving fish herbivores, for example, varies considerably between each habitat type (Cordeiro et al., 2016). On the eastern side, the sheltered side (hereinafter referred to as "inside"), detritivorous and herbivorous fish species are more abundant while on the western side, the exposed upwelling side (hereinafter referred to as "outside"), omnivorous fish species are the most abundant (Cordeiro et al., 2016). Fish species that are characteristic from deep temperate water along the Brazilian coast are also found to inhabit the shallow depths of this upwelling region (Anderson et al. 2015; Ferreira et al., 2001).

In this study, we investigated how small-scale variation could influence the abundance of two groups of fish parasites, Gnathiidae and Caligidae. These parasitic groups have been previously investigated in Brazil; however, studies were mostly focusing on their respective taxonomy (e.g., Boxshall and Montú, 1997; Luque et al., 2013; Morales-Serna et al., 2016) rather than their ecological role and importance. We sampled within the two distinct habitats, inside and outside the embayment (see Fig. 1). To do so, we first examined the abundance of gnathiids and caligids on four common fish species on both habitats during the upwelling season. We then explored the emergence of gnathiids from the benthos to understand if the benthic availability was a potential limiting factor for presence of gnathiids. Based on both gnathiids and caligids ecology and susceptibility to their environment, we hypothesised that gnathiid will be less abundant outside the embayment, in the upwelling system, knowing that temperature might be a limiting factor for their presence/absence (e.g., Tanaka, 2007). On the other hand, we hypothesised that caligids, that are generally more resilient to temperature changes, will be present in both habitats.

2. Methods

2.1. Sampling area

This study was carried out in Arraial do Cabo (22° 57' S; 41° 01' W; Fig. 1) in December 2014. The coastal waters of this region are characterised by two main distinct habitats, the exposed side – outside the embayment, on the west side (Fig. 1), is affected directly by the upwelling system, bringing cold water (mean temperature < 18°C), but also by higher wave exposure and deeper habitat (Cordeiro et al., 2016). The sheltered side – inside the embayment on the eastern side (Fig. 1), is protected by the position of Cabo Frio Island, creating a large embayment characterised by shallower depth, less influenced by upwelling waters, with the surface layer of the water remaining warmer and stable at ~ 22°C (Cordeiro et al., 2016). Additionally, the geography of the

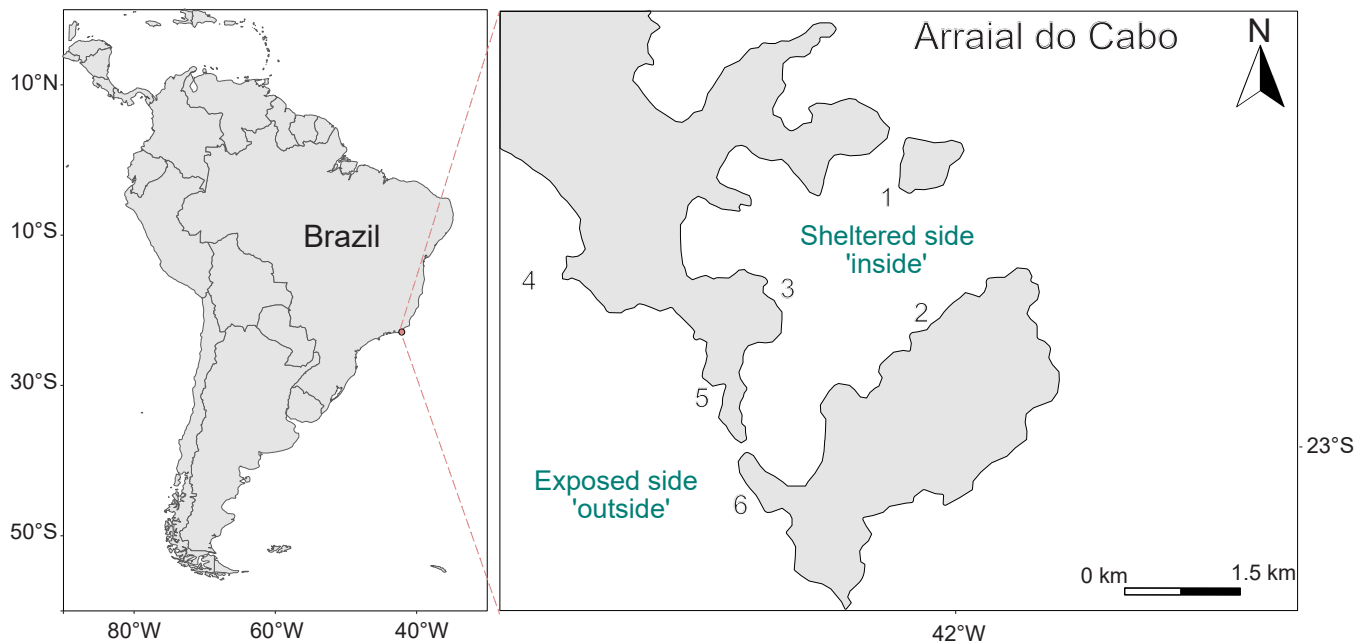


Fig. 1. Study area in Arraial do Cabo, Brazil. The exposed side, called ‘outside’, represents the area that is directly affected by the upwelling system, bringing cold water (mean temperature $< 18^{\circ}\text{C}$). The sheltered side, called ‘inside’, represents the embayment that is protected by the upwelling system (mean temperature 22°C). Data collection sites: 1 – Ilha dos Porcos; 2 – Abobrinha; 3 – Saco do Gato; 4 – Ilha dos Franceses; 5 – Some-tudo; 6 – Saco dos Ingleses. Abobrinha (inside) and Saco dos Ingleses (outside) were the two sites used for the gnathiid emergence traps.

area causes reefs on the western side to be more exposed to waves compared to those on the eastern side, which are more sheltered from the prevailing winds.

2.2. Fish collection

Four species of fish were investigated for their caligid and gnathiid abundance. These fish occur on both inside and outside the embayment and were collected over 10 days using a speargun while scuba diving between 07h00 and 10h00 in a depth ranging from 3 to 8 m at six different sites; three inside and three outside the embayment (see Fig. 1). A total of 54 fish were collected from the following species: the doctorfish *Acanthurus chirurgus* ($n = 14$; mean body size Total Length \pm SD: $26.8\text{ cm} \pm 3.1\text{ cm}$), the squirrelfish *Holocentrus adscensionis* ($n = 14$; $25.7\text{ cm} \pm 4.6\text{ cm}$), the chub *Kyphosus vaigiensis* ($n = 14$; $28.1\text{ cm} \pm 3.7\text{ cm}$) and the seabream *Diplodus argenteus* ($n = 12$; $21.8\text{ cm} \pm 2\text{ cm}$).

2.3. Fish ectoparasite infestation assessment

Directly after capture, each fish was quickly transferred into an individual hermetically sealed plastic bag to prevent loss of parasites and were euthanised using an ice slurry with the fish still inside their individual bags. In the laboratory, fish were transferred into individual freshwater baths for 10 min and brushed to dislodge any remaining ectoparasites. Fish were measured (cm, Total Length, Standard Length) and weighed (g, wet weight). All fluids (i.e., from the sealed plastic bag and the freshwater bath) were then filtered with a plankton net ($60\text{ }\mu\text{m}$ mesh size) and the remaining material were preserved in 70 % alcohol for further analysis. Both gnathiids and caligids were identified to the family level (Gnathiidae and Caligidae) using dissecting microscope and kept in 5 mL vials with 70 % alcohol.

2.4. Gnathiids emergence from the benthos

Parasitic stages of gnathiids emerge from the benthos to infect fish (Tanaka, 2007). But this is not the case for caligids, that can be present anywhere in the water column before finding a fish host. For this reason,

only gnathiids were considered. Gnathiid larvae were collected over night for approximately 16 hours (between 17h00 and 10h00) using eight emergence traps at two sites, inside ($n = 4$; Abobrinha site, see Fig. 1) and outside ($n = 4$; Saco dos Ingleses site, see Fig. 1), at similar depth (between 5 and 8 m). Traps were placed haphazardly by scuba divers on the substratum. The traps were identical and made of $100\text{ }\mu\text{m}$ plankton mesh. They measured 1 m^2 at the base (PVC pipe base) and were 0.85 m high. At the top of the trap, an upside-down funnel was fixed to the mesh and a jar lid was attached to the narrow part of the funnel. The 500 mL collecting bottle was placed at dusk and retrieved at dawn. To secure the traps to the substratum, weight was added into the PVC tubes (the foundation of the trap) with sand. Each corner of the trap was also attached to the nearby rocks with ropes to remain stable. The collecting bottle was added when the traps were settled. After overnight samplings, the bottles were retrieved and closed (Chambers and Sikkell, 2002). Back to the laboratory, gnathiids were counted using a dissecting microscope and preserved in 70 % alcohol.

2.5. Statistical analysis

The intensity of infestation by caligid copepods and gnathiid isopods were compared among sides (inside and outside) and species using separate zero-inflated negative binomial Generalized Linear Models (GLM) with negative binomial distribution due to data properties (i.e. non-normal and over dispersed). The GLM models were run using the *glmmTMB* function from the package *glmmTMB* (Brooks et al., 2017). The response variable was the ectoparasite group (number of caligid or gnathiid per fish) and side (inside/outside) and fish species were added as fixed effects in the model with an interaction between the two variables. The log-transformed weight in grams of each fish was applied as offset in the analysis to account for differences in sample units (i.e. fish with different size). This approach allows fitted values to be only positive, as well as their confidence interval, which permits the natural heterogeneity in data to be better fitted by the negative binomial distribution (Zuur et al., 2009). Weight was preferred to length as measure to better represent the available space for parasites to settle in more than one dimension, and also may account for side effects of infection such as

weight loss (Britton et al., 2011). Model selection was performed by comparing the Akaike Information Criterion (AIC) and derived Δ AIC of the different GLMM models tested. Statistical values from GLMM models were extracted using the function *Anova* (package *car*, Fox and Weisberg, 2018), and model validation was conducted using the permuted residuals calculated with the function *simulateResiduals* (package *DHARMA*, Hartig, 2019). Significant differences found in tested factors were investigated through pairwise comparisons between their levels using the function *emmeans* (package *emmeans*, Lenth, 2020). The predicted number of both caligids and gnathiids on each fish species were calculated using the function *ggpredict* (package *ggeffects*, Lüdtke, 2018).

The abundance of each planktonic group captured in traps was compared between sides (inside vs. outside) using the Kruskal-Wallis test due to non-normality of data distribution using the function *kruskal.test* (*stats* package, R Core Team, 2021). All statistical analyses were conducted using the software R v4.1.2 (R Core Team, 2021).

3. Results

3.1. Fish ectoparasite infestation assessment

From all the fish captured (n = 54), 44 showed signs of caligid and/or gnathiid infestation. The prevalence of total ectoparasite infestation varied from 42.9 % to 87.5 % inside, whereas it varied from 50 % to 100 % outside (Table 1).

Diplodus argenteus and *Holocentrus adscensionis* specimens had lower prevalence of infestation inside and outside the embayment compared to *Acanthurus chirurgus* and *Kyphosus vaigiensis* (Table 1; Fig. 2). On both sides, individual *A. chirurgus* had higher number of parasites (maximum 43 and 41 ectoparasites inside and outside, respectively).

We found caligid copepods on the body surface of fishes captured on both sides whereas gnathiid isopods were solely found on fishes captured inside (Fig. 3). Caligid infestation varied significantly between fish species ($X^2 = 17.79$; p-value = 0.004) but not between sides ($X^2 = 2.64$; p-value = 0.10; Table S1). These contrasts were particularly due to the differences between high caligid infestation of *A. chirurgus* and *K. vaigiensis* and low caligid infestation of *D. argenteus* and *H. adscensionis* (Fig. 3A; Fig. S1; Table S2, S3).

Overall, gnathiid infestation was lower with 44 % of fish infected. Individual *A. chirurgus* were the most infected with gnathiids (max number 17; median = 2; lower-quartile = 0; upper-quartile = 8). Individual *D. argenteus* was infected with a median of 0.5 gnathiids (lower-quartile = 0; upper-quartile = 1.75), and individual *K. vaigiensis* with a median of 1 gnathiid (lower-quartile = 0; upper-quartile = 3.5). Only one individual *H. adscensionis* was found infected with one gnathiid

Table 1

Total prevalence (% of fish infected) and intensity (median number of parasites per fish species) of infestation for both gnathiids and caligids on four species of fish collected in Arraial do Cabo (Brazil). Numbers in brackets represent the range (minimum and maximum number of parasites infestation per fish). Prevalence in bold indicate significant differences in prevalence of infestation (X^2 , p < 0.05) between habitats (inside vs outside) for each species.

Species	Inside		Outside	
	Prevalence (%)	Intensity of infestation (n)	Prevalence (%)	Intensity of infestation (n)
<i>Acanthurus chirurgus</i>	87.5	4 (1–43)	100	17 (1–41)
<i>Diplodus argenteus</i>	66.7	1.5 (1–4)	50	0.5 (1–2)
<i>Holocentrus adscensionis</i>	42.9	0 (1–6)	85.7	2 (1–7)
<i>Kyphosus vaigiensis</i>	86.7	10 (2–27)	100	8 (6–27)

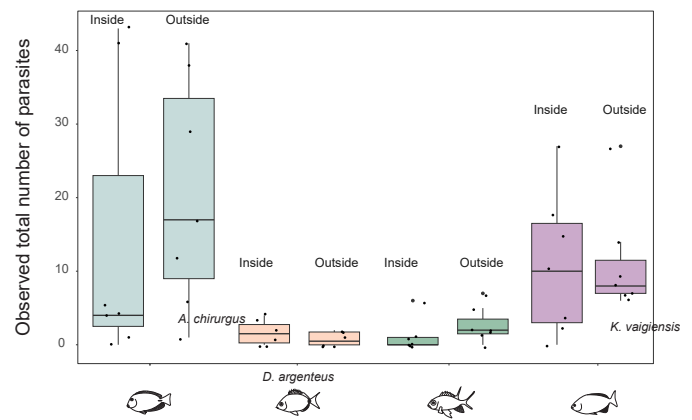


Fig. 2. Total number of observed ectoparasites (caligid and gnathiid) on the four species of fish *Acanthurus chirurgus*, *Diplodus argenteus*, *Holocentrus adscensionis* and *Kyphosus vaigiensis* sampled inside and outside. Boxplot representation with the lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles). Each box colour represents a fish species and each dot represents a fish individual.

inside. The predicted number of gnathiids varied between 0.12 (95 % CI = 0.01–1.46) for *H. adscensionis* to 1.5 (95 % CI = 0.35–6.39) for *A. chirurgus* (Fig. 3; Table S4). But no significant difference was found between the infestation rate of gnathiid between species ($X^2 = 2.95$; p-value = 0.4) inside.

3.2. Gnathiid emergence from the benthos

Gnathiid larvae were found only inside (Fig. 4), where they were the dominant group among all planktonic groups collected in the traps (50.9 % of total abundance, Table 2). Two other free-living groups, amphipods and copepods were collected from the traps in both sides (Fig. 4).

Free-living copepods were the most abundant group captured in the traps outside the embayment (92.4 %, Table 2), and significant differences were found between sides for copepods ($X^2 = 5.33$; p-value = 0.02) while amphipods were present with relatively similar abundance in each side (Table 2).

4. Discussion

Our results revealed that the infestation rate of two crustacean ectoparasites – caligids and gnathiids – differ between fish hosts and also differ between the two habitats studied, which are separated by only a few kilometres. This was particularly true for gnathiid ectoparasites, which were found to infect fish inside the embayment in Arraial do Cabo, but no infestation was recorded outside, in the upwelling exposed habitats. Similarly, gnathiids emerging from the substrate were only found inside, highlighting this habitat as suitable for this group of parasites.

The absence of gnathiids outside suggests that some environmental factors may be precluding them from establishing or surviving in this area. Temperature could be a limiting factor for the absence of gnathiid outside the embayment. Most species of gnathiid have been recorded in tropical environment, where most studies have been done regarding the ecology of gnathiids (Sikkel and Welicky, 2019). However, gnathiids are also present in subtropical, temperate and even polar environments (Wägele, 1987; Arnal and Morand, 2001; Narvaez et al., 2015), which indicate that some species are tolerant to low temperatures. Here, because we did not find any individual outside and the identification of the gnathiid was done at the family level only, no clear conclusions could be drawn regarding their tolerance to lower temperature from outside. Furthermore, clear effects of temperature fluctuation on

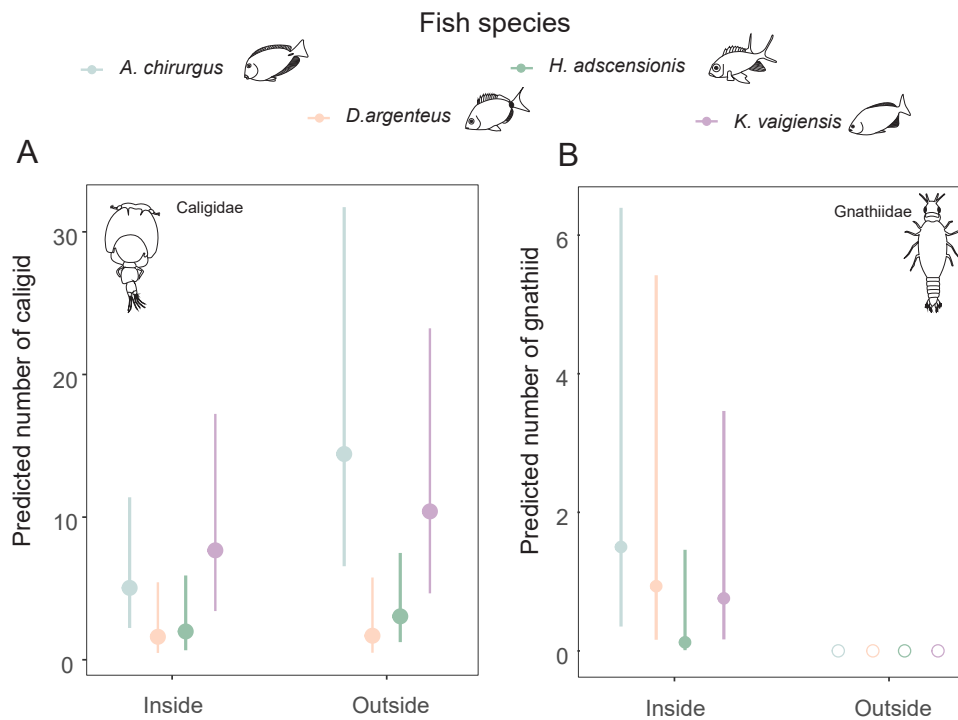


Fig. 3. Predicted number of (A) Caligidae and (B) Gnathiidae for the four species of fish (presented with the different colours and silhouettes) in both habitats: inside and outside. The dots represent the predicted number of parasites, and the lines represent the 95 % Confidence Interval.

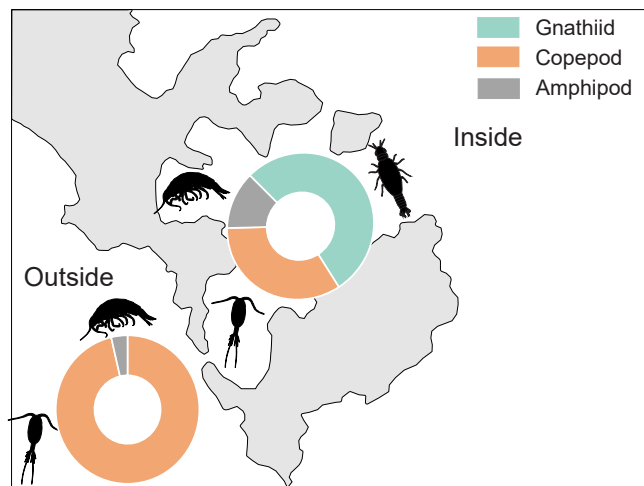


Fig. 4. Abundance of planktonic groups collected from the emergence traps on both sides. Inside (right) represents the sheltered habitat and the outside habitat (left) represents the upwelling environment.

Table 2

Abundance (total, median, minimum and maximum) of planktonic groups captured in the emergence traps (n total = 8). Different letters indicate significant differences in number of individuals (Kruskal-Wallis X^2 , $p < 0.05$) between habitats (inside vs outside) for each planktonic group.

Groups	Inside			Outside		
	n	Median	Min-max	n	Median	Min-max
Gnathiid larvae	149	39	19–52	0	-	-
Copepods	95	21 a	9–44	632	116.5 b	97–302
Amphipods	35	6 a	3–20	24	6 a	1–11
TOTAL	279	-	-	656	-	-

gnathiid abundance and survivorship were found in tropical regions. For instance, gnathiid numbers in emergence traps dropped significantly during warm-water months in the Great Barrier Reef (Australia), which coincided with or followed a coral bleaching event. However, these populations bounced back to average levels in cooler months later that year (Sikkel et al., 2019). Gnathiids were also found to die after long exposure to high water temperature (mimicking heat wave) under laboratory conditions (Shodipo et al., 2020) and were not tolerant to temperature fluctuations in temperate environments (Tanaka and Aoki, 2000). Inside, where gnathiids were found, the temperature is constant (~22 °C). However, outside, temperature can fluctuate from 16 °C to 23 °C, depending on wind regimes (Cordeiro et al., 2016). Therefore, a possible constraint for gnathiids establishment outside could be the high fluctuation of temperature. Gnathiids are also substantially associated with the benthos, particularly for moulting and reproducing (Smit and Davies, 2004). In tropical reefs, gnathiid larvae were found to be more abundant in coral rubble than in live coral habitats (Santos and Sikkel, 2019; Paula et al., 2021), potentially avoiding predation by live coral (Artim and Sikkel, 2013; Paula et al., 2021). In temperate systems, gnathiid larvae are also site-selective, being more abundant, for example, where the benthic habitats were composed mainly of red algae and sessile organisms, associated with rugose rocks (Ventura et al., 2018). Hence, substrate composition might be an important factor limiting the presence of gnathiids. In Arraial do Cabo, the substrate varies substantially between the inside and outside (Cordeiro et al., 2016; Mello-Fonseca et al., 2021). Inside, where the gnathiids were found, the benthic cover is mostly composed of epilithic algal matrix (i. e., turfing algae, detritus, sediment, and invertebrate; Kramer et al., 2012) and sessile organisms such as sponges, anemones, ascidians and bryozoans (Ferreira et al., 2001; Rogers et al., 2014; Cordeiro et al., 2016; Mello-Fonseca et al., 2021) whereas outside, macroalgae and articulated coralline algae are more abundant (within the same depth range of our study; Cordeiro et al., 2016; Mello-Fonseca et al., 2021). The substrate preference of gnathiids in this area remains unclear, but sessile organisms such as sponges may create suitable microhabitats for gnathiids, aligning with the findings of Ventura et al. (2018). Finally,

gnathiid abundance might also be contingent with the presence of predators, such as cleaner fish (Grutter, 1996). However, in Arraial do Cabo, the main cleaner fish, a specialised cleaning goby – *Elacatinus figaro*, is only present inside (Mazzei et al., 2021) where the gnathiids were present. Therefore, predation may not be the main factor driving the observed presence/absence patterns of gnathiids inside/outside. While incidental consumption of gnathiid is also observed from non-cleaner fish (e.g., herbivores fish that target algae and inadvertently consume gnathiid as well; Nicholson et al., 2024), their consumption is almost negligible comparing to the amount consumed by the cleaner fish (Nicholson et al., 2024). Caligids were present on fish inside and outside and in higher number than gnathiids. While caligids might also be impacted by temperature fluctuations, especially in terms of development (Groner et al., 2014), it seems that generally, caligids are more resilient to temperature fluctuations than gnathiids (Groner et al., 2014; Ventura et al., 2018). It is important to consider that multiple species may inhabit the coastal waters of Arraial do Cabo, which differ on their tolerance for water temperature fluctuations. Indeed, marine parasitic copepods, which include caligids, are the second largest group of ectoparasite in Latin America (including Brazil; Luque and Poulin, 2007), and the diversity of caligid species has been documented in Neotropical regions, with over 115 species reported from various hosts (Morales-Serna et al., 2016). Future studies investigating lower taxonomical assignment (species level) will be necessary to explore the possibility of multiple caligid species with distinct temperature tolerances in Arraial do Cabo. While water movement and currents can significantly impact caligid naupliar larvae (Brooks, 2005; Ventura et al., 2018), to the best of our knowledge, no studies have investigated the impact of wave exposure on gnathiid abundance. In Arraial do Cabo, wave exposure is higher outside, where the upwelling is also stronger (Cordeiro et al., 2016), suggesting that hydrodynamic regime can be a limiting factor for both caligid and gnathiid abundance. However, no differences in caligid infestation rates were found for fish inside and outside suggesting that this might not be a limiting factor for caligid. On the other hand, wave exposure could be another limiting factor for the presence/absence of gnathiid, but additional studies are necessary to investigate this further.

Caligid infestation varied between species with *K. vaigiensis* and *A. chirurgus* individuals being the most infected. However, overall gnathiid infestation did not differ between fish species. Fish use different strategies to avoid ectoparasite infestation. These strategies include migration (e.g., migratory escape from infected locations or individuals: Shaw and Binning, 2016; diel migrations: Hendrick et al., 2024), mucous cocoon self-protection (Grutter et al., 2011), having a pelagic larval phase (Duong et al., 2019), and seeking out cleaner fish (Grutter, 1999). Beyond these behavioural strategies, fish possess traits that can influence their susceptibility to parasite infestation. For instance, their feeding habits and daily activity patterns (Luque et al., 2004) can impact their vulnerability. Ectoparasites, on the other hand, also show preference for certain fish species or families based on various factors. These factors include the abundance of the fish (Nagel and Grutter, 2007), the chemical cues emitted by the fish (Mikheev et al., 2004), and the behaviour and immunological traits of fish (Coile and Sikkell, 2013). Although our focus fish species differ in terms of mobility, feeding mode and activity, a larger sample will be necessary to build any strong correlations between their ecological attributes and infestation rate. For instance, only a single gnathiid was found infecting an individual *Holocentrus adscensionis*. This species is a nocturnal species, feeding away from the reef at night (Greenfield and Carpenter, 1981; Froese and Pauly, 2019), and nocturnal migration performed by some fish can reduce exposure to gnathiids, which have peaks of activity during this period (Sikkell et al., 2017). Therefore, the observed low infestation rate on *H. adscensionis* could be associated with its nocturnal activity. Generally, *A. chirurgus* was more infected by caligid and gnathiid ectoparasites. It is possible that *A. chirurgus*, like many other surgeonfish species, is particularly susceptible to both ecto- and endoparasites (e.g.,

Coile and Sikkell, 2013; Sikkell et al., 2009; Bernal et al., 2016). However, further data is necessary to confirm these hypotheses. This study was also conducted over a limited duration, covering only a single season. Consequently, it would also be valuable to perform these surveys across multiple seasons to determine whether infestation patterns exhibit consistency over time. The unique geography of Arraial do Cabo, characterised by distinct abiotic conditions of tropical/subtropical to warm-temperate habitats existing in proximity and separated only by a narrow channel, makes it a valuable natural laboratory for scientific studies (Mendes et al., 2009; Cordeiro et al., 2016). Our research sheds light on the role of local environmental factors in shaping the infestation patterns of ectoparasites observed in four reef fish species. Our findings support the influence of temperature fluctuations, benthic substrate composition, and possibly hydrodynamics on the population dynamics of both gnathiid and caligid parasites. To gain a deeper understanding of these patterns, further experimental research could explore habitat selection by gnathiids in Arraial do Cabo and the impact of temperature fluctuations for gnathiid abundance. Investigating how currents influence the dispersal of caligid nauplii larvae in their natural environment (*in situ*) can be another crucial step for understanding caligid population dynamics. Finally, considering the ongoing global impacts of climate change on marine ecosystems and the susceptibility of these crustacean parasites and their hosts to these stressors (e.g., Löhmus and Björklund, 2015; Shodipo et al., 2020; Narvaez et al., 2021), it is likely that infestations patterns might be affected in a near future.

Ethical note

Fish were collected with permit approval from the granting agency IBAMA/SISBIO (Permit number: 46271–4) under the project: "Influência de fatores ecológicos e antropogênicos no comportamento, fisiologia e saúde dos peixes recifais".

CRedit authorship contribution statement

Pauline Narvaez: Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Cesar Cordeiro:** Writing – review & editing, Investigation, Formal analysis. **Marta Soares:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Vinicius Giglio:** Writing – review & editing, Investigation, Formal analysis. **Miguel Furtado:** Writing – review & editing, Methodology, Investigation. **Renata Mazzei:** Writing – review & editing, Methodology. **Carlos Ferreira:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests Carlos Eduardo Leite Ferreira reports financial support was provided by FAPERJ (proc.E-26/111.293/2013). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.rsma.2024.103909](https://doi.org/10.1016/j.rsma.2024.103909).

Data availability

The data will be share on a open access platform (Zenodo)

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