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Contrasting feeding and agonistic behaviour of two blenny species on a small and remote island in the equatorial Atlantic Ocean

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Abstract

We investigated the feeding rates, agonistic behaviour and diet of two blenny species, *Entomacrodus vomerinus* and *Ophioblennius trinitatis*, by direct observation and gut content analysis. Both species coexist in small and shallow tide pools in the St Peter and St Paul's Archipelago, equatorial North Atlantic Ocean. The feeding rate of *O. trinitatis* was *c*. 55% higher than *E. vomerinus*. On the other hand, agonistic rate of *O. trinitatis* was negatively related to body size, whereas in *E. vomerinus* was positively related. Both species showed a high diet overlap, in which detritus was the most important food item (86% in *O. trinitatis* and 80% in *E. vomerinus*). Feeding activity was more intense during the morning for *O. trinitatis* but afternoon for *E. vomerinus*. These behavioural observations support the importance of temporal feeding partitioning as the main strategy allowing species co-existence in tide pools.

KEYWORDS

abundance, body size, diet, oceanic island, reef fish, territorial herbivores, tide pool

1 | INTRODUCTION

Herbivorous fishes are an important link between primary productivity and secondary consumers on tropical reefs (Choat *et al*., 2004). Owing to their role in algal population dynamics, understanding patterns of abundance and distribution of fishes that feed on primary producers is a paramount topic on the ecology of reef environments (Choat *et al*., 2004; Ferreira & Gonçalves, 2006; Floeter *et al*., 2005; Johansson *et al*., 2013). Previous studies on nominally herbivorous

fishes have revealed the importance of understanding the functional distinctions among different species and the mechanisms that regulate how food resources are acquired, processed and incorporated into their tissues (Clements *et al*., 2016; Hoey & Bonaldo, 2018; Siqueira *et al*., 2019). Most of these studies focused on large and abundant herbivores, such as parrotfishes (Labridae, Scarinae), surgeonfishes (Acanthuridae) and damselfishes (Pomacentridae; Bonaldo *et al*., 2006, Bonaldo *et al*., 2014; Bonaldo & Bellwood, 2009; Mendes *et al*., 2018; Ceccarelli *et al*., 2005; Ceccarelli, 2007; Green & Bellwood, 2009),

whereas small cryptobenthic groups, like blennies (Blenniformes) and gobies (Gobiidae), have received less attention (Depczynski & Bellwood, 2003; Mendes et al., 2009; Wilson, 2001). This is partly due to their small sizes, cryptic behaviour and the misconception that small herbivores do not play a significant role on regulating the structure of benthic algal communities (Robertson & Polunin, 1981). Nevertheless, given their high abundances, food intake and turnover rates, accounting for 60% of the consumed reef-fish biomass, cryptobenthic species are a crucial link in energy transfer in both grazing and detrital trophic pathways in coral reefs (Ackerman & Bellwood, 2000; Brandl et al., 2019; Depczynski & Bellwood, 2003; Hatcher, 1981; Wilson, 2004). In addition, the bulk of the net primary production in coral reefs is available as small benthic filamentous algae and microbial organisms, which are readily consumed by cryptobenthic fishes (Wilson, 2001, 2004). Although the diet and composition of a number of small cryptobenthic grazing fishes on reefs are well recognised (Hundt et al., 2014; Mendes et al., 2009; Townsend & Tibbetts, 2000), their contribution to reef trophodynamics remains poorly understood (Brandl et al., 2018).

The combtooth blennies are small (c. 5 cm) cryptobenthic species that live in close association with the substratum and represent an abundant component of fish assemblages in reefs worldwide (Townsend & Tibbetts, 2000). Many species ingest detritus from the epilithic algal matrix (EAM), which is a complex assemblage of filamentous algae and organic detritus colonised by several microorganisms, microalgae, smalls invertebrates and trapped sediments (Wilson & Bellwood, 1997), thus being considered herbivorous detritivores (Hundt & Simons, 2018). A number of combtooh blennies inhabit tide pools and must cope with the harsh environmental conditions typical of these habitats.

Tide pools are characterised by high variability in water temperature, salinity and dissolved oxygen that are mainly driven by an interplay between pool position (height and distance from the sea) and morphology (volume, surface area, depth; Pimentel et al., 2018). Resource limitation in tide pools (e.g., reduced space, low food availability, restricted number of shelters) usually promote the emergence of strong territorial disputes in order to gain access to the best refuges and feeding areas (Cheney, 2009). In this sense, the colonisation of new areas and the consumption of complementary items may would reduce the intraspecific competition (Clarke, 1999; Ord et al., 2017). For instance, amphibious blennies move into intertidal areas during high tide to avoid intraspecific competition (Ord et al., 2017), whereas tube blennies of the genus Acanthemblemaria Metzelaar 1919 consume complementary items reducing the competition (Clarke, 1999).

Territoriality or agonistic behaviour has been recognised as a key aspect of the social organisation in many reef-fish species, as it can determine the abundance of individuals as well as interactions between conspecifics and heterospecifics (Cantor et al., 2018). In this sense, territorial species have developed strategies to balance territorial defence energy expenditure with food intake (Ceccarelli et al., 2001). These strategies may vary according to fish species or habitat availability and may help understanding the species co-existence in restricted environments such as tide pools.

Besides the strategies developed by species to co-exist, different life-history traits, such as body size, group formation, period of activity or feeding behaviour have important ecological and evolutionary implications (Andrades et al., 2019; Murdoch, 1994). Maximum diversity and abundance occurs among smaller body sizes since these species have a higher speciation rate (Kulbicki et al., 2015; Robertson, 1998). Smaller individuals have higher feeding rates than larger ones because they have higher metabolic oxygen uptake (Clarke & Johnston, 1999; Yager & Summerfelt, 1994). Moreover, juveniles grow faster than adults, as they spend more energy on reproduction and territorial patrolling (Bonaldo et al., 2006). Thus, determining how life-history traits influence tide-pool assemblages is critical to understanding how species living in these harsh habitats are able to co-exist.

The Brazilian Province extends over 8000 km of coastline and harbours eight genera and 14 species of Blenniidae, half of these species are distributed across at least one of the four Brazilian oceanic islands (Pinheiro et al., 2018). Nevertheless, despite being key species for linking primary productivity to tertiary consumers (Ackerman & Bellwood, 2000; Depczynski & Bellwood, 2003), our ecological knowledge of blennies on remote oceanic islands is still scarce (Medeiros et al., 2014; Mendes, 2006, 2007). This is partly due to logistical constraints imposed by the remoteness of such islands, as well as difficulties in carrying out in situ observations on these small fishes. Here, we assessed the behaviour and diet of two nominally herbivorous species of Blenniidae, Ophioblennius trinitatis Miranda Ribeiro 1919 and Entomacrodus vomerinus (Valenciennes 1836), in the smallest and the most remote oceanic archipelago of the equatorial Atlantic Ocean to evaluate whether these species compete or partition the resources available in tide pools. By doing this, it will be possible to infer the trophic role performed by these blennies and their importance in local food webs.

2 | MATERIALS AND METHODS

All collections were performed under environmental and ethical permits of responsible agencies; ICMBIO collection permit 41,327–12.

2.1 | Study area

The St Peter and St Paul's Archipelago (SPSPA; 00° 55´ N, 29° 21´ W) comprises a small group of five rocky islets located 1010 km off the north-eastern coast of Brazil (Figure 1). With only c. 60 species registered to date, the SPSPA hosts the most depauperate reef fish fauna in the tropical seas (Feitoza et al., 2003; Luiz et al., 2015). Due to their isolation and reduced size, the fish fauna and ecological processes in the Brazilian oceanic islands differ from typical coastal reefs (Mendes et al., 2019; Pinheiro et al., 2018). Shallow reefs in the SPSPA are mainly covered by turf algae (EAM), the zoanthid Palythoa caribaeorum and macroalgae of the genera Bryopsis, Caulerpa and Dictyota (Magalhães et al., 2015). Tide pools occur exclusively on the main islet and are usually washed with seawater at high tide (Figure 1). Benthic communities in these tide pools consist mainly of P. caribaeorum and a thin EAM. Three herbivorous blennies occur in the tide pools of the
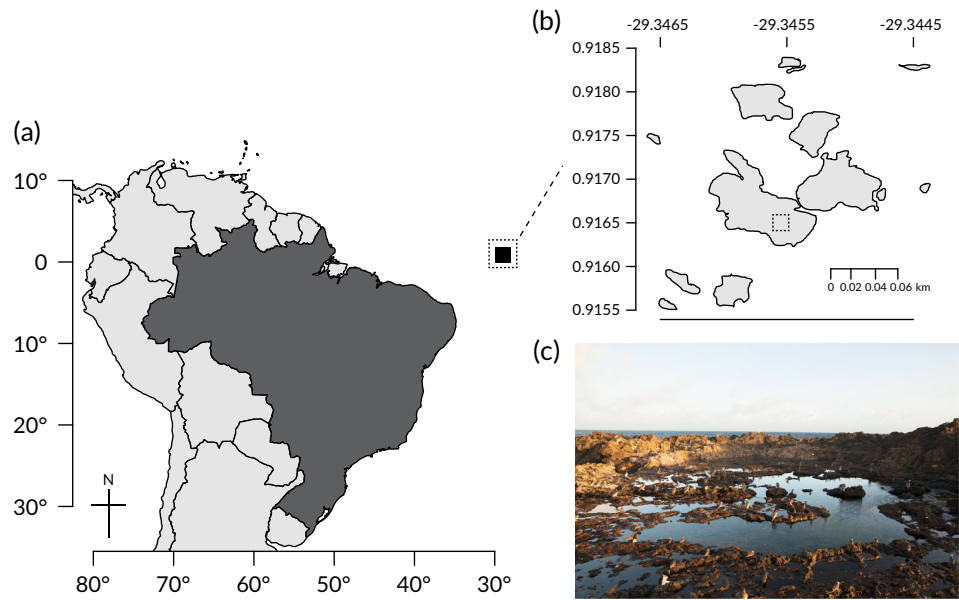
SPSPA: *O. trinitatis*, *E. vomerinus* and *Scartella itajobi* Rangel & Mendes, 2009. However, the latter has been reported only as a vagrant in the SPSPA (Lima-Filho *et al*., 2011).

2.2 | Data collection

Feeding (*i.e.* number of bites per minute) and agonistic rates (*i.e.* number of chases per minute) of both blenny species were recorded by direct observation during 3 min sessions in two periods of the day (07:00–09:00 h and 15:00–17:00 h) in November 2017. These observations were made in three connected shallow rocky tide pools (*c.* 30 cm deep). Observations were restricted to low tide because intense wave action prevents *in situ* observations during high tide. All observations were performed from outside the pools, as in many cases depth was less than 10 cm. The observer waited 1 min before recording information to reduce its effects on fish behaviour. The focal individual was then identified at the species level and had its body size estimated (total length, L_T, cm). Additionally, we estimated the abundance of all blennies around each focal individual within a 30 cm radius. In those cases where the individual was out of sight of the observer, the data was discarded. Although other species such as *Abudefduf saxatilis* (Linnaeus, 1758), *Stegastes sanctipauli* Lubbock & Edwards 1981, *Enneanectes smithi* Lubbock & Edwards 1981 and *Bathygobius soporator* (Valenciennes 1837) occur in the tide pools, no interaction between them and the blennies were registered. Therefore, these species were not recorded in our observations.

2.3 | Dietary analysis

We collected thirteen *E. vomerinus* and twelve *O. trinitatis* from the tide pools to test their dietary overlap. Specimens were collected
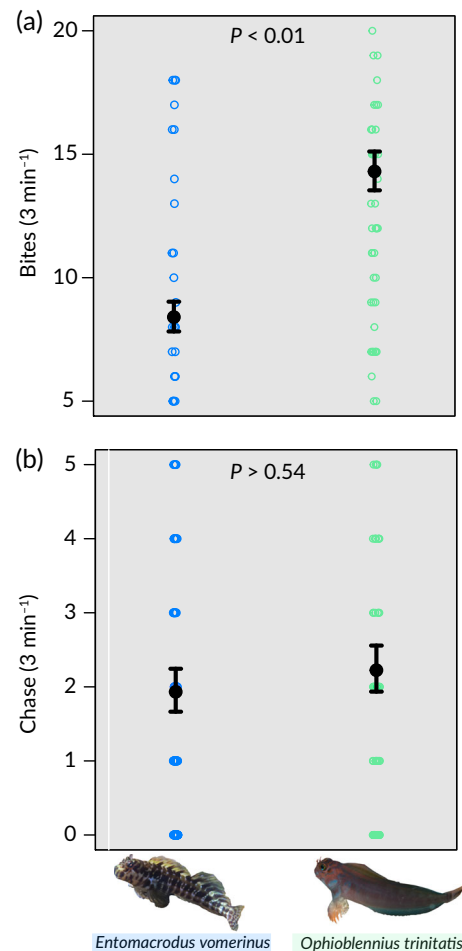

FIGURE 2 Comparison of (a) feeding rate and (b) agonistic behaviour of *Entomacrodus vomerinus* and *Ophioblennius trinitatis* in the St Peter and St Paul's Archipelago. O, Individual observation; (●), mean ± 95% CI

TABLE 1 Summary of the generalised linear model with Poisson distribution, showing the effect of the period of the day (morning or afternoon) during the low tide, body size, number of bites and chases, group size on the number of bites and chases in each blenny species. The significance of each factor was given by likelihood ratio test (LRT)
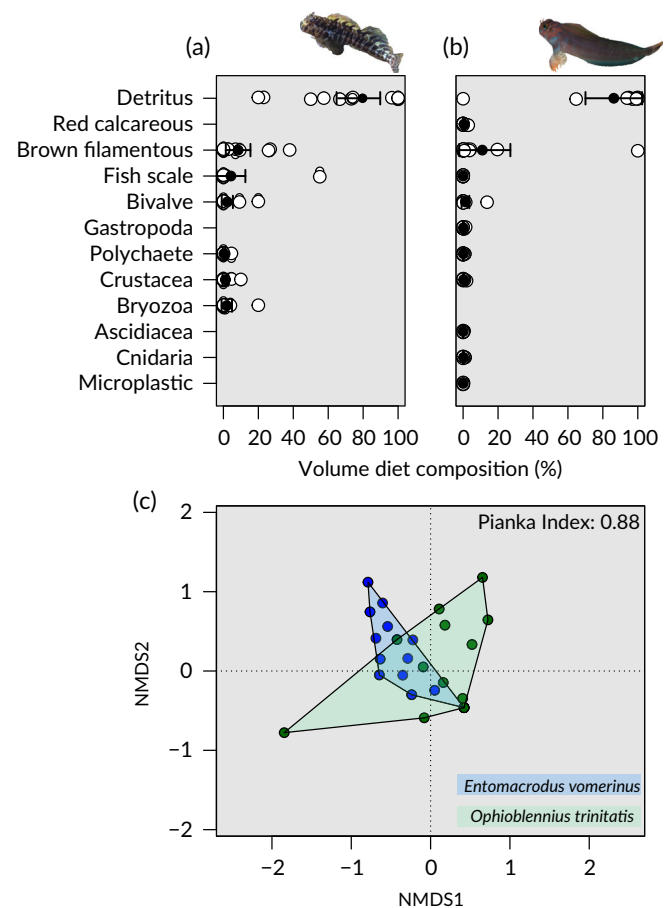
Predictor	*Entomacrodus vomerinus*				*Ophioblennius trinitatis*			
	Estimate	LRT	P	VIF	Estimate	LRT	P	VIF
Bites								
Period	2.76	17.15	< 0.01	1.01	2.75	53.14	< 0.01	1.05
Morning	−0.31				0.65			
Afternoon	2.45				2.75			
Body size	−0.06	8.79	< 0.01	1.07	−0.05	14.61	< 0.01	1.00
Group size	−0.17	2.34	< 0.01	1.07	0.22	61.07	< 0.01	1.05
Chases								
Period	−0.03	12.29	< 0.01	1.01	−2.99	53.49	< 0.01	1.05
Morning	−0.54				1.83			
Afternoon	−0.57				−4.82			
Body size	−0.11	1.89	< 0.01	1.07	0.11	6.40	< 0.01	1.00
Group size	0.86	58.31	< 0.01	1.07	0.81	82.67	< 0.01	1.15

Note: VIF, variance inflation factor.

using hand nets or hand spear and were immediately killed by pithing when necessary. We injected 10% formalin in filtered seawater into their gut cavities and fixed collected specimens by placing them in 10% formalin in seawater. In the laboratory, we dissected their entire guts and analysed the content under a stereoscopic microscope (×50 magnification). We identified the food items from each gut to the lowest possible taxonomic category (Table S1). The occurrence of each item was measured using graph paper (each cell comprising an area of 1 mm^2) as a counting grid beneath a Petri dish (Liedke *et al.*, 2016). The presence of each item was measured by counting the number of grid cells occupied by the item. Masses of seemingly unidentifiable organic material were analysed under an optical microscope (x40 magnification) to search for elements such as spicules and nematocysts that could not be identified at a lower magnification. Although detritus can be defined as 'dead and decaying primary producer material, which normally becomes detached from the primary producer after senescence' (Lartigue & Cebrian, 2012), it is often difficult to visually discriminate living components such as bacteria, diatoms and cyanobacteria from the non-living component (Wilson *et al.*, 2003). Thus, we applied this term broadly and identified detritus in the dietary analyses as any amorphic organic material found.

2.4 | Data analysis

To evaluate whether body size, feeding rate and agonistic behaviour varied between the two species, we used Student's *t*-test. To examine whether feeding rate and agonistic behaviour were influenced by the period of day (two levels: morning and afternoon), body size and density of individuals (*i.e.*, other blennies species), we used two generalised linear models (GLM) with Poisson distribution. We used the Poisson distribution because the number of bites and chases are positive and discrete (Zuur *et al.*, 2009). We checked collinearity among co-variables by simple correlations between pairs of variables prior to

FIGURE 3 Diet composition of (a) *Entomacrodus vomerinus* and (b) *Ophioblennius trinitatis* in the St Peter and St Paul's Archipelago: (o) Individual observation; (●), mean ± 95% CI. (c) Non-metric multidimensional scaling based on gut content of *E. vomerinus* (■) and *O. trinitatis* (■). O, Individual observation; convex hulls were drawn to emphasise the difference between the two species

analyses (Figure S1). We tested the significance of each factor by dropping each of them from the full models and performing likelihood ratio tests (LRT). Additionally, we estimated the variance inflation factor (VIF) after model fitting. The co-variables were not correlated to each other as VIF values in the final model were < 1.5 (Table 1), indicating no correlation among them (Dormann et al., 2013).

To compare the diet between the two species, we used a non-metric multidimensional scaling (nMDS) and estimated the Pianka index of niche overlap, in which values >0.6 suggest a strong diet overlap between the species (Pianka, 1973). All analyses were performed using the R environment (R Core Team, 2018).

3 | RESULTS

We observed 180 individuals of *E. vomerinus* and *O. trinitatis* (90 individuals of each species). The L_T differed between the blennies ($t = -2.53$, $df = 176$, $P < 0.01$), *O. trinitatis* being larger (mean ± SE $L_T = 5.02 \pm 0.19$ cm) than *E. vomerinus* ($L_T = 4.34 \pm 0.19$ cm). The feeding rate of *O. trinitatis* was 57.4% higher (mean ± SE 14.62 ± 1.45 bites 3 min^{-1}) than that of *E. vomerinus* (8.40 ± 1.30 bites 3 min^{-1}; $t = -3.02$, $df = 174.09$, $P < 0.01$; Figure 2(a)), while agonistic rate was similar between both species ($t = -0.61$, $df = 152$, $P > 0.05$; *O. trinitatis* 2.22 ± 1.45 chases 3 min^{-1}; *E. vomerinus* was 1.93 ± 0.26 chases 3 min^{-1}; Figure 2(b)).
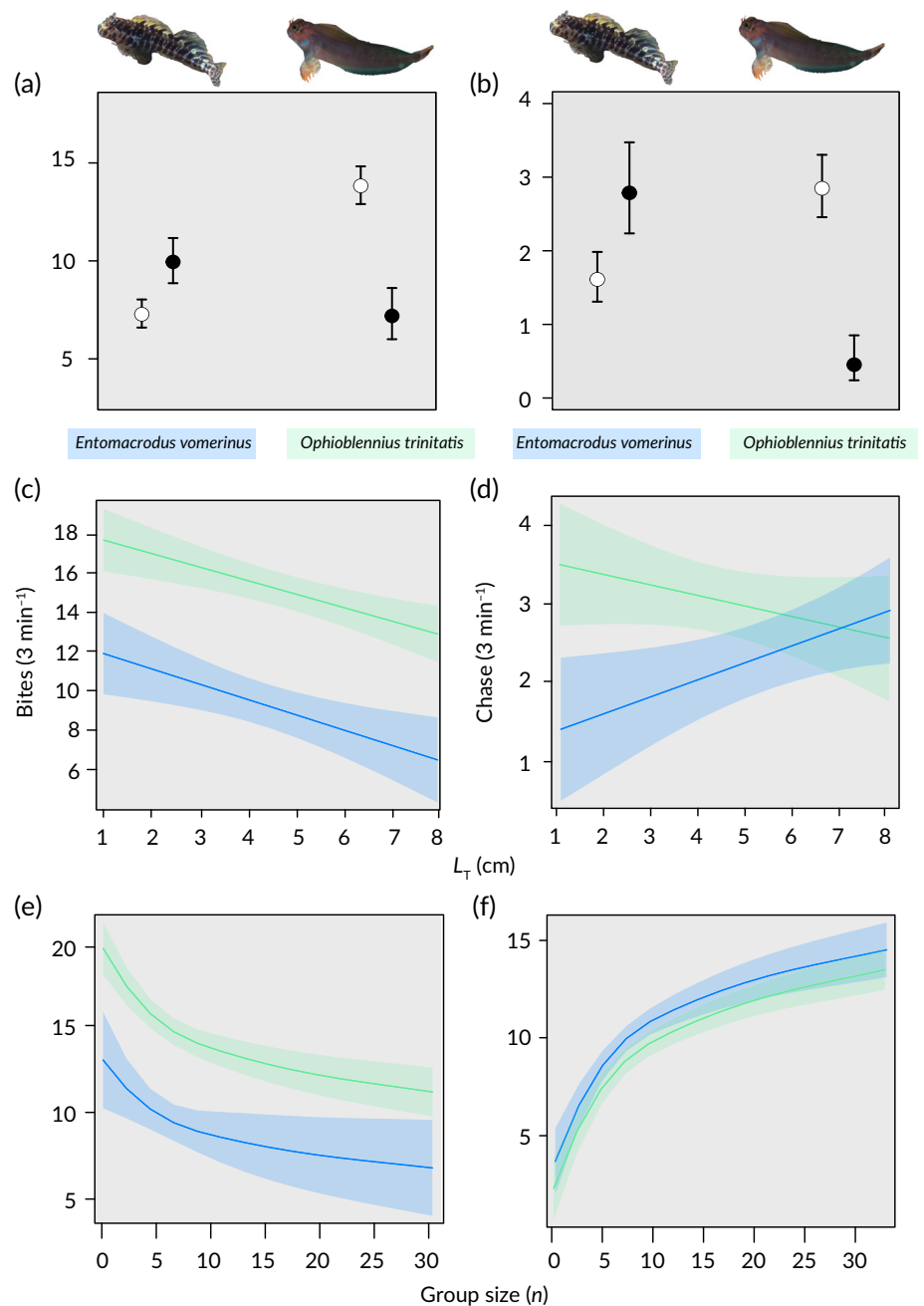

FIGURE 4 Comparison (mean ± 95% CI) of: (a), (c), (e) feeding rate and (b), (d), (f) agonistic behaviour (a), (b) in the morning (O) and afternoon (●) and the corresponding effect of (c), (d) total length (L_T) and (e), (f) group size of *Entomacrodus vomerinus* (——) and *Ophioblennius trinitatis* (——)in tide pools of the St Peter and St Paul's Archipelago

We identified 12 different food items in the diet of both species. Detritus was the most abundant item for both (86% in *O. trinitatis* and 80.1% in *E. vomerinus*), followed by brown filamentous algae (11% in *O. trinitatis* and 9.13% in *E. vomerinus*; Figure 3(a),(b)). Other items, such as fish scales and bivalves were less abundant dietary components of *E. vomerinus*, while *O. trinitatis* had a more variable diet, ingesting red calcareous algae, ascidians and various invertebrates (such as gastropods, cnidarians, polychaetes, crustaceans, bryozoans and bivalves) along with fish scales and microplastics (Figure 3(a)). Despite these differences, the two species presented a high dietary overlap as indicated by the Pianka Index of 0.88 (Figure 3(c)).

Feeding behaviour of both species varied according to the period of the day (Table 1).

Entomacrodus vomerinus increased its bite rate in the afternoon (9.95 ± 0.59 bites 3 min^{-1} in the afternoon; 7.27 ± 0.3 in the morning), while *O. trinitatis* feeding rate was higher in the morning (13.8 ± 0.49 bites 3 min^{-1} in the morning; 7.19 ± 0.66 bites 3 min^{-1} in the afternoon; Figure 4(a)). Likewise, the agonistic rate varied between the period of the day (Table 1). Chase frequency of *O. trinitatis* was higher in the morning (2.84 ± 0.21 chases 3 min^{-1} in the morning; 0.45 ± 0.15 chases 3 min^{-1} in the afternoon), while *E. vomerinus* presented a peak in chases in the afternoon (2.78 ± 0.31 chases 3 min^{-1} in the afternoon; 1.61 ± 0.17 chases 3 min^{-1} in the morning; Figure 4(b)). We detected a negative effect of L_T on the feeding rate of both species, with larger individuals showing lower feeding rates (Table 1 and Figure 4(c)). On the other hand, L_T only influenced the agonistic rate of *O. trinitatis*, with large individual exhibiting lower chases rates (Table 1 and Figure 4(d)). Finally, we observed a negative effect of the group size on the feeding rate of both species, with individuals decreasing their bite rate in the presence of large groups of potential competitors (Table 1 and Figure 4(e)) and a positive effect of group size on agonistic rate, with individuals of both species increasing chase in the presence of large groups (Table 1 and Figure 4(f)).

4 | DISCUSSION

The two blennies, *E. vomerinus* and *O. trinitatis*, exhibit behaviour consistent with a resource partitioning strategy (*i.e.* niche segregation). Although both species have a high degree of dietary overlap, their feeding and agonistic rates are divergent, which may allow their co-existence in tide pools. This niche segregation was observed with marked differences in feeding and agonistic rates throughout the day between the two species. Moreover, body size and abundance of other blennies had a strong influence on the feeding rate and agonistic behaviour of both species. Although the two species share several life-history traits such as maximum body size, trophic group, territoriality and habitat use, the temporal use of resources differed. This highlights the importance of studies on species biology and ecology to provide detailed information on their life-history traits and inferences about their functional role.

Feeding rate of *O. trinitatis* was nearly 55% higher than that of *E. vomerinus*. This difference can be attributed to factors like food processing modes (Choat *et al.*, 2004) and food quality. Both *E. vomerinus* and *O. trinitatis*, share some morphological features related to feeding and food processing; both have similar oral morphology with a number of premaxillary and dentary unattached teeth associated with a diet rich in detritus (Hundt & Simons, 2018). However, grazing fish ingesting similar amounts of detritus may differ substantially in their dietary nutritional profiles due to the inability of the observer to satisfactorily identify detrital components using traditional gut content methods (Clements *et al.*, 2016; Mendes *et al.*, 2018; Wilson *et al.*, 2003). Thus, the differences observed here may be associated with food quality, since detritus in the EAM is a highly heterogeneous food source (Crossman *et al.*, 2005; Wilson *et al.*, 2003). These species are apt to select detritus on a fine scale targeting different detrital components in the tide pools of the SPSPA as a way to avoid competition. This, however, deserves further evaluation using stable isotopes or fatty acid profile analyses.

The differences observed in the bite rate of both species may be associated with the period of feeding activity, since *O. trinitatis* concentrated its feeding activity in the morning and *E. vomerinus* in the afternoon. The high food intake of *E. vomerinus* in the afternoon can be explained by the fact that algae attain a higher nutritional value as measured by digestible starch content in this period (Townsend & Tibbetts, 2004; Zemke-White *et al.*, 2002). Although this pattern has been described for macroalgae (Zemke-White *et al.*, 2002), the photosynthetic microbial components of detritus (cyanobacteria, diatoms) may behave similarly increasing its nutritional value towards the afternoon. Thus, the higher feeding rate of *O. trinitatis* in the morning could be a strategy to compensate the intake of a relatively less nutritious detritus, while *E. vomerinus* would get the same amount of energy by eating less material in the afternoon. This strategy of modulating food intake with nutritional content has already been observed in herbivorous and omnivorous fish that require smaller amounts of material when their food has higher protein content (Goecker *et al.*, 2005; Mendes *et al.*, 2019; Raubenheimer *et al.*, 2005).

The most common food item found in the diet of *E. vomerinus* and *O. trinitatis* in SPSPA was detritus. This result corroborates the pattern described for others species of Blenniidae (Hundt *et al.*, 2014; Mendes *et al.*, 2009; Wilson, 2000) where most of them possess a specialised dentition for selectively graze detritus in the EAM (Christiansen *et al.*, 2010; Hundt & Simons, 2018). By ingesting a mixture of detritus, algae and invertebrates, both *E. vomerinus* and *O. trinitatis* can take advantage of several easily digestible and assimilable nutrients. It is likely that the consumption of fish scales by *E. vomerinus* is an occasional occurrence, as it was observed in only one individual. Ingestion of scales may have occurred from detached scales that accumulated in the EAM they feed on. This reinforces the idea that by consuming various components of the EAM in the tide pools of the SPSPA, these blennies play an important role in the local food webs. The microplastics found in the *O. trinitatis* diet possibly derived from local fishing activities for pelagic species that occur around the SPSPA.

We observed a negative effect of body size on feeding rate of both species and a positive effect on agonistic behaviour only in

E. vomerinus. This can be explained by the fact that smaller individuals present higher metabolic rates (Barneche *et al.*, 2008; Yager & Summerfelt, 1994), whereas the lower feeding rates observed in large individuals can be associated with the territorial behaviour of adults, which usually spend more time patrolling feeding and breeding territories. Our results highlight the importance of body size as a driver of feeding rate in small herbivorous detritivorous fish. At the same time, we observed contrasting and similar effects of group size on rates of feeding and agonistic behaviour for both species. As expected, bite rate decreased and aggressive behaviour increased given the abundance of potential competitors near the focal individuals. Although our observation was limited, we suggest that a strong competition occurs in the tide pools of the SPSPA, which is regulated by the number of individuals (Andrades *et al.*, 2019; Hixon *et al.*, 2012; Hixon & Carr, 1997).

The ecological differences between *E. vomerinus* and *O. trinitatis* described in this study allow the co-existence of the two species in a restricted environment and enable the species to perform better in some axes of their ecological niche, being necessarily less efficient under other axes (Chesson, 2000). These trade-offs are usually associated with differences in phenotypes or life-history traits (Brandl *et al.*, 2018), which often seems to be unknown in the case of cryptobenthic species. Finally, our results suggest that metabolic process and the abundance of individuals are key factors influencing cryptobenthic fish herbivory in tide pools in this remote oceanic archipelago.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

J.P.Q., V.J.G., T.C.M. conceived the idea. J.P.Q. analysed the data and T.C.M. contributed to coding and to interpreting results. J.P.Q., V.J.G. collected data. A.F. analysed the gut content. J.P.Q. wrote the paper and led the revisions and V.J.G., J.A.C.C.N., C.E.L.F., T.C.M. critically reviewed several versions of the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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