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Corresponding Author	Family Name	<b>Nagelkerken</b>	
	Particle		
	Given Name	<b>Ivan</b>	
	Suffix		
	Division	Southern Seas Ecology Laboratories, School of Biological Sciences, and The Environment Institute	
	Organization	The University of Adelaide	
	Address	Adelaide, SA, 5005, Australia	
	Phone		
	Fax		
	Email	ivan.nagelkerken@adelaide.edu.au	
	URL		
	ORCID	<a href="http://orcid.org/0000-0003-4499-3940">http://orcid.org/0000-0003-4499-3940</a>	

---

Author	Family Name	<b>Coni</b>	
	Particle		
	Given Name	<b>Ericka O. C.</b>	
	Suffix		
	Division	Southern Seas Ecology Laboratories, School of Biological Sciences, and The Environment Institute	
	Organization	The University of Adelaide	
	Address	Adelaide, SA, 5005, Australia	
	Phone		
	Fax		
	Email		
	URL		
	ORCID		

---

Author	Family Name	<b>Booth</b>	
	Particle		
	Given Name	<b>David J.</b>	
	Suffix		
	Division	Fish Ecology Lab, School of Life Sciences	
	Organization	University of Technology Sydney	
	Address	Ultimo, NSW, 2007, Australia	
	Phone		
	Fax		
	Email		
	URL		
	ORCID		

Email  
URL  
ORCID

---

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Abstract	<p>Poleward range extensions of coral reef species can reshuffle temperate communities by generating competitive interactions that did not exist previously. However, novel environmental conditions and locally adapted native temperate species may slow tropical invasions by reducing the ability of invaders to access local resources (e.g. food and shelter). We test this hypothesis on wild marine fish in a climate warming hotspot using a field experiment encompassing artificial prey release. We evaluated seven behaviours associated with foraging and aggressive interactions in a common range-extending coral reef fish (<i>Abudefduf vaigiensis</i>) and a co-shoaling temperate fish (<i>Microcanthus strigatus</i>) along a latitudinal temperature gradient (730 km) in SE Australia. We found that the coral reef fish had reduced foraging performance (i.e. slower prey perception, slower prey inspection, decreased prey intake, increased distance to prey) in their novel temperate range than in their subtropical range. Furthermore, higher abundance of temperate fishes was associated with increased retreat behaviour by coral reef fish (i.e. withdrawal from foraging on released prey), independent of latitude. Where their ranges overlapped, temperate fish showed higher foraging and aggression than coral reef fish. Our findings suggest that lower foraging performance of tropical fish at their leading range edge is driven by the combined effect of environmental factors (e.g. lower seawater temperature and/or unfamiliarity with novel conditions in their extended temperate ranges) and biological factors (e.g. increased abundance and larger body sizes of local temperate fishes). Whilst a future increase in ocean warming is expected to alleviate current foraging limitations in coral reef fishes at leading range edges, under current warming native temperate fishes at their trailing edges appear able to slow the range extension of coral reef fishes into temperate ecosystems by limiting their access to resources.</p>
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Keywords (separated by '-')	Range extensions - Tropical vagrants - Ocean warming - Behavioural interference - Foraging performance - Aggressive interactions - Temperate reefs
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1 REPORT

2 **Novel species interactions and environmental conditions reduce**  
3 **foraging competency at the temperate range edge**  
4 **of a range-extending coral reef fish**

5 **Ericka O. C. Coni<sup>1</sup> · David J. Booth<sup>2</sup> · Ivan Nagelkerken<sup>1</sup>**

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14 and shelter). We test this hypothesis on wild marine fish in  
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18 actions in a common range-extending coral reef fish  
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22 reef fish had reduced foraging performance (i.e. slower  
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27 increased retreat behaviour by coral reef fish (i.e. with-  
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resources. 44

**Keywords** Range extensions · Tropical vagrants · Ocean 45  
warming · Behavioural interference · Foraging 46  
performance · Aggressive interactions · Temperate reefs 47

**Introduction** 48

Climate change is a major force driving global redistribu- 49  
tion of species on land and in the ocean (Poloczanska et al. 50  
2013; Pecl et al. 2017). However, the successful estab- 51  
lishment and ecological impacts of range-extending species 52  
(i.e. species that change their distribution limits to keep 53  
pace with their shifting temperature niches, Doak and 54  
Morris 2010) on recipient communities will strongly 55  
depend on interaction strength with local species (Mas- 56  
ciocchi et al. 2010; Gilman et al. 2010). It is common 57  
knowledge that the structure of natural communities is 58  
shaped by biological interactions (Bolker et al. 2003; Wisz 59  
et al. 2013) and such interactions are one of the pillars 60  
maintaining ecosystems in equilibrium. Thus, disruption of 61  
species interactions that have established over long evo- 62  
lutionary periods may lead to disruption of key ecosystem 63  
functions (Bascompte et al. 2006; Ives and Carpenter 2007; 64

A1 Topic Editor Alastair Harborne

A2 ✉ Ivan Nagelkerken  
A3 ivan.nagelkerken@adelaide.edu.au

A4 <sup>1</sup> Southern Seas Ecology Laboratories, School of Biological  
A5 Sciences, and The Environment Institute, The University of  
A6 Adelaide, Adelaide, SA 5005, Australia

A7 <sup>2</sup> Fish Ecology Lab, School of Life Sciences, University of  
A8 Technology Sydney, Ultimo, NSW 2007, Australia

65 O’Gorman and Emmerson 2009). For example, the pole-  
66 ward influx of tropical species has already caused regime  
67 shifts in native temperate ecosystems in which recovery to  
68 the previous natural stage has become difficult (Wernberg  
69 et al. 2016). In Japan, the arrival of tropical herbivorous  
70 fishes caused the depletion of the principal habitat-forming  
71 species (kelp forests), opening up space for the colonisation  
72 of corals (Nagelkerken and Simpson 2013). There is evi-  
73 dence that this phenomenon is rapidly occurring as well  
74 along the Australian temperate coasts, as the abundance of  
75 tropical and subtropical herbivorous fishes and corals has  
76 increased in the last few decades (Bennett et al. 2015;  
77 Booth and Sear 2018; Monaco et al. 2021). Yet, few studies  
78 incorporate novel ecological interactions into predictions  
79 of species range shifts and their establishment in novel  
80 ranges.

81 Without considering species interactions, it remains  
82 difficult to accurately forecast the impacts of range-ex-  
83 tending species (e.g. they may be more aggressive or have  
84 higher foraging performance) on local species, and evalu-  
85 ate whether they are therefore likely to increase their  
86 abundances at higher latitudes to the detriment of local  
87 species under global warming (Shinen and Morgan 2009;  
88 Callaway and Ridenour 2004). Invasion theory postulates  
89 that competition is one of the main mechanisms driving  
90 successful invasion of alien species, because they are  
91 usually superior competitors compared to native species  
92 (Sakai et al. 2001; Vila and Weiner 2004). Similar to alien  
93 species, the influx of range-extended species can reshuffle  
94 species dominance in temperate systems or displace native  
95 species with lower competitive performance (Nagelkerken  
96 and Simpson 2013; Milazzo et al. 2013). Although the pace  
97 of invasion by range-extending species is typically slower  
98 than that of introduced species (Sorte et al. 2010), the  
99 consequences and magnitude of their establishment might  
100 be very similar (Kola and Lodge 2001; Sorte et al. 2010).  
101 Thus, given the potential emergence of competitive inter-  
102 actions among range-extending and native species, there is  
103 a pressing need to understand how native species might  
104 alter the establishment and persistence of range-extending  
105 species.

106 Whilst many invasive species are superior competitors,  
107 this is not always the case (Kimbrow et al. 2013; Levine  
108 et al. 2004; Parker and Gilbert 2007). The biotic resistance  
109 theory postulates that native species sometimes exhibit  
110 higher competitive ability than invaders, reducing estab-  
111 lishment and persistence of invaders (Levine et al. 2004; de  
112 Rivera et al. 2005; Von Holle 2005; Von Holle and Sim-  
113 berloff 2005; Fridley et al. 2007). Nevertheless, only few  
114 studies on marine and terrestrial range extensions have  
115 focussed on success or failure of local species to resist the  
116 establishment of novel species into their communities  
117 (Paini et al. 2008). Hence, competitive effects of invaders

as well as natives are critical to understand potential 118  
changes to community structures under future climate (Vilá 119  
and Weiner 2004; Paini et al. 2008). Alternatively, species 120  
might change their behaviour through phenotypic plasticity 121  
and avoid or reduce direct conflicts and enable coexistence 122  
(Perri and Randall 1999; Wilson et al. 1999; Lambert 123  
2002). For example, avoidance of dominant species and 124  
adjusted retreat and escape behaviours can facilitate the 125  
coexistence of some species by decreasing their risk of 126  
injuries and agonistic-related stress (Rychlik and Zwolak 127  
2005). However, such adaptive behaviours might create 128  
trade-offs and incur costs to individual fitness (Chesson 129  
2000; Liancourt et al. 2005). Therefore, it is expected that 130  
range-extending species that exhibit subordinate beha- 131  
vioural responses to native species may have lower likeli- 132  
hood to colonise non-native communities than range- 133  
extending species that are stronger competitors. However, 134  
coexistence may occur if these new arrivals occupy a dif- 135  
ferent niche than local species, or display conflict-avoid- 136  
ance behaviours that are not to the detriment of other 137  
fitness-related behaviours. 138

139 Over the last two decades, hundreds of coral reef fish  
140 species have been recruiting in temperate Australia during  
141 summer (Booth et al. 2007; Feary et al. 2013). These  
142 tropical fish species have not yet established breeding  
143 populations at temperate latitudes, because the winter  
144 temperatures there are still below their minimum thermal  
145 tolerance. Each year, new pulses of tropical recruits arrive  
146 in temperate ecosystems, where they persist for several  
147 months until seawater temperatures drop too low (Eme and  
148 Bennett 2008; Figueira and Booth 2010). However, ongo-  
149 ing intensification of ocean warming and strengthening of  
150 poleward ocean currents is likely to relax these abiotic  
151 thresholds and facilitate the permanent establishment of  
152 tropical species in the near future (Figueira and Booth  
153 2010; Booth et al. 2018). Under current warming, other  
154 factors such as species interactions with temperate fishes  
155 are also of importance, and these might buffer or retard the  
156 invasion of tropical range-extending species at higher lat-  
157 itudes (e.g. Pigot et al. 2013; Coni et al. 2021). Whilst  
158 some tropical and temperate fishes seem to positively  
159 interact (Smith et al. 2018) and co-exist in their trophic  
160 niches (Kingsbury et al. 2019), competitive exclusion  
161 might still exist, especially if tropical fishes have a reduced  
162 body condition due to environmental stress (Poulos and  
163 McCormick 2014). Additionally, the unknown environ-  
164 ment of recipient communities (e.g. reduced water tem-  
165 perature and novel habitats, prey and predators) can affect  
166 some aspects of species behaviour, leading to a competitive  
167 disadvantage in range-extending species, which in turn  
168 would affect their behavioural interactions with local spe-  
169 cies (Figueira and Booth 2010; Figueira et al. 2019).  
170 Hence, understanding the competitive ability (ability to

171 respond to the inhibitory effects of co-existing species)  
 172 between tropical invader and temperate species may give  
 173 insights into the competitive hierarchies that are emerging  
 174 due to climate change (Lauchlan et al. 2019), and the  
 175 identification of potential “winners” and “losers” (e.g.  
 176 Liancourt et al. 2005; Poulos and McCormick 2014) that  
 177 could compromise novel communities at high latitudes.

178 Native species could resist range-extending species  
 179 through a variety of behaviours, including aggressive  
 180 interactions and behavioural interference during feeding  
 181 (see Table S1). Such behaviours are strongly mediated by  
 182 body size (Robertson 1995; Munday et al. 2001). At the  
 183 current early stages of warming, most tropical range-ex-  
 184 tending fishes still only occur as recruits and early-juve-  
 185 niles, with relatively small body sizes compared to co-  
 186 shoaling temperate species, which creates a body-size  
 187 disadvantage that can mediate the colonisation of these  
 188 tropical range-extending species into novel environments  
 189 where the native species are bigger on average. Yet, very  
 190 little attention has been given to the question of how dif-  
 191 ferences in body size might mediate the behavioural  
 192 interactions of tropical range-extending species with native  
 193 species, and if such biological effects are stronger or  
 194 weaker than abiotic stressors (Louthan et al. 2015).

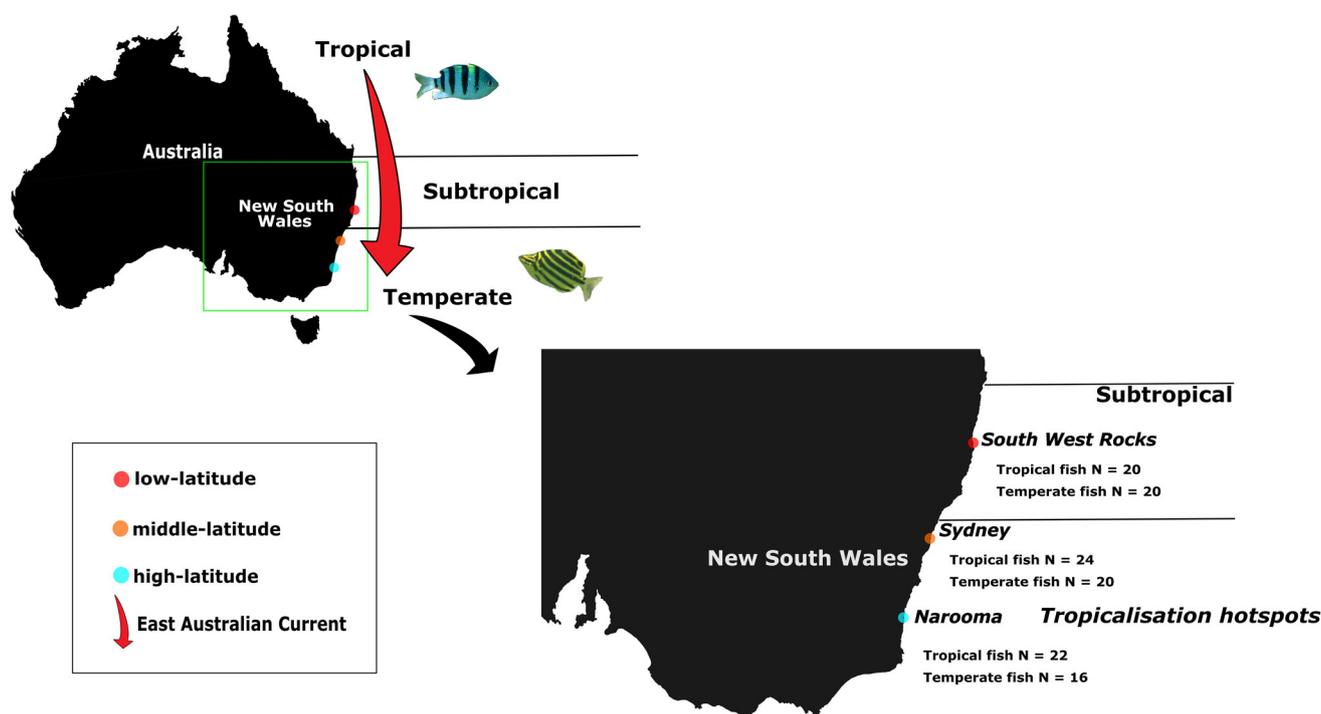
195 Here we test three hypotheses: (1) at cold-water leading  
 196 edges where tropical fishes are invading novel temperate  
 197 ecosystems their aggressiveness and foraging efficiency is  
 198 lower than that of native temperate species, (2) tropical  
 199 fishes exhibit reduced foraging ability and aggressive  
 200 interactions as a function of increasing latitude, and (3)  
 201 temperate species do not alter their foraging ability and  
 202 aggressive interactions at their trailing warm-water edges  
 203 where tropical species are invading. We test these  
 204 hypotheses by comparing the foraging ability and aggres-  
 205 sive interactions of a common tropical range-extending  
 206 species (*Abudefduf vaigiensis*—Pomacentridae) and co-  
 207 shoaling native temperate fish (*Microcanthus strigatus*—  
 208 Microcanthidae) along a latitudinal temperature gradient  
 209 (6° latitude, 730 km of coastline) under current ocean  
 210 warming. These species were chosen as a model for novel  
 211 species interactions, because they are commonly observed  
 212 using the same habitat and forming mixed-species shoals,  
 213 suggesting a strong overlap in their ecological niches  
 214 (Smith et al. 2018). Such comparative approaches involv-  
 215 ing potential invaders and native species have often been  
 216 useful in explaining what increases invader success in  
 217 recipient communities (Daehlet 2003). To evaluate whether  
 218 foraging competency of tropical and co-shoaling temperate  
 219 fishes is altered along a latitudinal temperature gradient  
 220 (from subtropical to temperate waters) in a climate  
 221 warming hotspot, we quantified their aggressive interac-  
 222 tions (chasing and escaping rates) and foraging perfor-  
 223 mance in terms of perceiving, inspecting, and consuming

224 prey in situ. Additionally, to reveal whether altered for-  
 225 aging performance and aggressive interactions were related  
 226 to composition of local species communities, we also  
 227 quantified the abundance of all temperate and tropical  
 228 range-extending fishes that shared the same habitat and  
 229 belonged to the same trophic guild (omnivorous), and that  
 230 could potentially interact behaviourally with invading  
 231 vagrants. Understanding whether interactions with native  
 232 species might act in synchrony with changing abiotic  
 233 conditions is crucial to predict the likelihood of tropical  
 234 fish invasions in temperate environments, and their  
 235 potential effects on temperate fish communities under  
 236 ongoing climate change.

## 237 Materials and methods

### 238 Study area and species

239 The study was conducted at six sites ranging from low to  
 240 high latitudes along the south-eastern Australian coast  
 241 (Fig. 1) during the summers of 2017 and 2018 when  
 242 recruitment of tropical fishes peaks (January to May). The  
 243 lower latitude (two sites at South West Rocks) is consid-  
 244 ered to be the most similar environment to the tropical  
 245 fish’s native range, comprising subtropical reefs where the  
 246 abundance of tropical fish species is highest among the  
 247 three latitudes studied (Fig. S1), and the mean seawater  
 248 winter temperature (Table S1) does not surpass their lower  
 249 thermal tolerance (i.e. ~ 18–22 °C; Djurichkovic et al.  
 250 2019). At this latitude, the benthic environment is mostly  
 251 composed of bare rocks (site 1) or a mosaic of sparse oyster  
 252 reefs and rocks (site 2). The middle latitude is situated  
 253 around Sydney, and included three sites which reflect  
 254 tropicalisation hotspots (Booth et al. 2007): Shelly Beach,  
 255 Little Manly, and Narrabeen. The benthic reef community  
 256 at Shelly Beach and Little Manly is composed of a mosaic  
 257 of macroalgae (e.g. kelp), turf-forming algae, bare rock and  
 258 sea urchin barrens, while at Narrabeen it is mainly com-  
 259 prised of bare rock, turf algae and sparse oyster reef. The  
 260 high latitude site (Narooma) represented the coldest studied  
 261 site (Table S2), and comprised the most unfamiliar and  
 262 hostile environment for tropical fishes where the abun-  
 263 dance of temperate fish species is highest among the sites  
 264 (Fig. S1). At this site, tropical fishes were found on shallow  
 265 bare rocks and patches of sparse oyster reefs. The sites at  
 266 the low and middle latitudes were chosen based on an 18-yr  
 267 study of ongoing tropical fish settlement on shallow rocky  
 268 reefs along the coast of south-east Australia (Booth et al.  
 269 2007, 2018), while the site at the high latitude has been  
 270 only recently monitored (~ 3 years). For each latitude,  
 271 sites (if more than one sampled) were pooled due to the low  
 272 number of replicate fishes found at some sites.



**Fig. 1** Map showing the sites of the in situ manipulative experiments and the tropical (*Abudefduf vaigiensis*—top photo) and temperate (*Microcanthus strigatus*—bottom photo) fishes studied. Red circle indicates the low latitude region: two sites at South West Rocks (30° 52' 34" S, 153° 4' 2" E and 30° 53' 0" S, 153° 2' 17" E). Orange

circle indicates the middle latitude region: Shelly Beach (33° 48' 1.13" S, 151° 17' 31.23" E), Little Manly (33° 48' 23" S, 151° 17' 8" E) and Narrabeen (33° 42' 7" S, 151° 18' 21" E). Blue circle indicates the high latitude region: Narooma (36° 12' 54" S, 150° 7' 51" E). N = sample size of fishes

273 We selected one model species for each temperature  
 274 affinity (tropical vs temperate): (1) the most common  
 275 tropical range-extending species *Abudefduf vaigiensis*, and  
 276 (2) the common co-shoaling temperate species *Microcan-*  
 277 *thus strigatus*. The tropical species is a common inhabitant  
 278 of warm Indo-Pacific reefs including the Coral Sea (Fish-  
 279 Base—Froese and Pauly 2016), but is also a vagrant that  
 280 occurs every summer along the south-eastern Australian  
 281 temperate coast (Booth et al. 2007). The temperate species  
 282 occurs throughout subtropical (Central Queensland) and  
 283 temperate (southern New South Wales) Australian reefs.  
 284 These two species have coexisted for longer periods of  
 285 time at our subtropical site at the low latitude (during all  
 286 seasons) than at the high latitude sites where they only co-  
 287 occur on a seasonal-basis, i.e. January to May (Feary et al.  
 288 2013). They often form mixed-species shoals, usually share  
 289 the same habitat, and belong to the same trophic guild  
 290 (omnivorous feeders). They were also the two species most  
 291 attracted to the in situ experimental prey releases, allowing  
 292 for sufficient replication within each latitude (*Abudefduf*  
 293 *vaigiensis*: low = 20, middle = 24, high = 22 and *Micro-*  
 294 *canthus strigatus*: low = 20, middle = 20, high = 16).  
 295 Most of the tropical fishes observed from the low to high  
 296 latitudes are recruits and early-juveniles. Juvenile individ-  
 297 uals also occur, however, in a smaller quantity.

## Data collection and experimental design

298  
 299 For each fish species, we (1) quantified aggressive inter-  
 300 actions with all directly surrounding species, and (2) tested  
 301 their foraging performance based on various foraging  
 302 behaviours, as a function of latitude (ranging from warmer  
 303 to cooler sea temperatures) and abundance of all species  
 304 attracted to the released prey. Abundance of species was  
 305 separated into three groups: (1) abundance of conspecifics  
 306 (individuals of the same species) of each studied species,  
 307 (2) abundance of all native-temperate fishes, and (3)  
 308 abundance of all tropical range-extending fishes. The last  
 309 two groups do not include individuals of the focal species.

310 As tropical fish are commonly found in shallow waters  
 311 (water depth ranging from 50 cm to 2 m) along the  
 312 shoreline of embayments, sampling was carried out by a  
 313 maximum of two divers on snorkel. Seven behaviours, five  
 314 as a proxy of foraging performance and two as a proxy of  
 315 aggressive interactions (see Fish Behaviour section below),  
 316 were quantified in situ for each fish species using a maxi-  
 317 mum of 5 min. of video (GoPros) recording. A manipula-  
 318 tive underwater experiment was performed to attract fish  
 319 and instigate species interactions (foraging arena experi-  
 320 ment) (Fig. S2). At each site, foraging arenas (low = 40,  
 321 middle = 44, high = 38) were deployed over three days.

On a day to day basis, data collection was carried out in different areas to avoid filming the same individuals. The experiment comprised artificial release of dead prey (brine shrimp, *Artemia*). Prey were delivered through a tube of 2.5 cm in diameter and 1 m in length attached to a dive weight that was positioned on the reef substratum at approximately 50 cm from a fixed camera (GoPro) with the camera lens directed toward the prey released point. This distance was chosen to best observe the tropical fish recruits that were usually < 5 cm in body size. A two-minute period was incorporated as acclimation time to the experimental devices before releasing prey. The observer maintained a distance of at least 2 m from the experimental prey release site during the entire video recording, only briefly approaching when release of fresh prey through the tube was needed. Recruits and early-stage individuals of tropical and temperate species are relatively site-attached, minimising the chance that the same individual was repeatedly recorded across replicate recordings. To allow for independent observations, foraging arena experiments were randomly performed with a distance of at least 2 m of each other for both tropical and temperate species. The prey were constantly released through the tube via a 60-ml syringe. Each syringe contained ~ 1.25 g of brine shrimp (*Artemia*) mixed with ~ 60 ml of salt water, but only half of the syringe content was released each time. At the start of each foraging arena experiment, half of the syringe content was released at a constant rate through the tube to attract fish and aggregate them within the field of view of the camera. Once all released prey had been consumed by the fishes or had dissipated due to water currents, an additional release of prey (i.e. another half of a syringe content) was performed. This procedure was repeated until the end of each 5-min recording (~ 10 releases of ~ 12.5 g of brine shrimp each per recording). Recordings were performed under the wide angle setting with a resolution of 1080p at a speed of 25 frames/sec.

The results should be interpreted within the context of experimental food provision, as patterns may differ when natural prey are considered. Nevertheless, our study provides experimental support from the wild of the inherent capacity of temperate fish to affect the performance of tropical vagrants through interference behaviours.

### 365 Fish behaviour

The video recordings were evaluated using VLC media player 2.1.3 on a desktop computer. The following behaviours were quantified for each focal individual in each recording (Table S1): (1) prey attraction time, measured as the time (seconds) it took for the fish to swim towards the tube (i.e. prey release point) and take a bite at the prey upon their first release, (2) minimum distance to prey,

measured as the shortest distance (cm) (i.e. visually estimated using a ruler) that the fish approached the prey release point during its observation time, (3) prey inspection rate, measured as the number of times an individual approached (distance of  $\leq 5$  body lengths) the prey release point as soon as the prey was released, (4) bite rate, continuously counted during the observation and measured as the total number of successful bites taken at the released prey, (5) retreat rate, continuously counted during the observation and measured as the number of times a fish approached the prey release point within 5 body lengths but decided to abruptly return to its previous position, (6) chasing rate, continuously counted during the observation and measured as the number of times that the focal individual swam aggressively (e.g. attacking an individual and forcing it away from the released prey) towards another individual, and (7) escaping rate, continuously counted during the observation and measured as the total number of times that the focal individual fled from an aggressor. The behaviours that were measured as continuous counts (prey inspection, bites, retreats, chasing, and escaping) were then expressed as rates per unit of time (e.g. bite rates/sec.). These were calculated by dividing the respective behavioural counts of each individual by its total observation time. When a chasing event was observed, the body size of the individuals involved in this interaction was registered to check if this behaviour could be related to differences in body size. For example, when a temperate fish chased the focal tropical individual, the size of the aggressor (if it was larger or smaller) was registered in comparison with the size of the focal fish.

To avoid pseudo-replication only one individual of each species was randomly chosen (e.g. the first individual seen in the group was selected) and analysed for each video recording, especially when they were shoaling with individuals of the same species. All behaviours of an individual were analysed from the same recording. The video recordings were a maximum of 5 min, but as fishes were mobile, the time that they were within the view of the camera ranged between 20 s and 5 min (average observation time ~ 2 min). Short observation times have been found to be sufficient to obtain a representative estimate of our focal behaviours (Figueira et al. 2019; Biro et al. 2010; Francini-Filho et al. 2010; Beck et al. 2016). The life stage (recruit, early-juvenile, juvenile) of the tropical fishes was recorded for each focal individual.

In each video where we recorded the behaviours of a single focal fish, we also quantified the abundance of all tropical and temperate fishes, and other individuals of *A. vaigiensis* and *M. strigatus* (i.e. their respective conspecific abundances) present within the field of view, and that were attracted to the released prey. For each individual section of the recording, the abundances of these three fish groups

426 were quantified in intervals of 10 s. These replicate abundances  
427 estimates were afterwards averaged for each individual  
428 recording.

## 429 Statistical analyses

430 As tropical range-extending species were more abundant at  
431 lower latitudes and the opposite was true for the temperate  
432 species, first a permutational multivariate analysis of  
433 covariance (MANCOVA) was used to examine the effect  
434 of latitude (three levels of categorical and fixed factors—  
435 “low”, “middle”, “high”) on the behaviour (dependent  
436 variables: all seven behaviours) of the tropical and temperate  
437 species (species as a fixed factor— “*A. vaigiensis*”  
438 and “*M. strigatus*”) using the total abundance of temperate  
439 fishes, total abundance of tropical fishes, and total abundance  
440 of conspecific individuals of *A. vaigiensis* and *M. strigatus*  
441 across latitudes as covariates. This analysis was  
442 performed only to evaluate if the effect of latitude on  
443 species behaviour was related to abundances of local species  
444 (covariate). Observation time was also included in this  
445 analysis as a covariate, because the observation time varied  
446 among the observed fishes (ranging from 20 s to 5 min);  
447 not including it could provide a bias of the mean behavioural  
448 responses between latitude and species. Interactions  
449 between the categorical factors (latitude and species) and  
450 the four covariates were removed from the final model  
451 (MANCOVA), because their initial inclusion did not show  
452 a significant effect (i.e. meaning that the effect of latitude  
453 on species behaviour is independent of temperate, tropical,  
454 conspecific abundances and observation time) (Table S3),  
455 and maintaining them in the final model could lead to  
456 misinterpretation of the results (Engqvist 2005; Beck and  
457 Bliwise 2014). Univariate permutational analysis of  
458 covariance (ANCOVA) was then performed for each  
459 behaviour in order to clarify the interpretation of the  
460 MANCOVAs and evaluate the individual behaviours that  
461 were responsible for any latitudinal differences as revealed  
462 by the MANCOVAs. Fish life stage was also included as  
463 an explanatory variable with three levels of categorical and  
464 random factors: recruits ( $\leq 3$  cm), early-juveniles  
465 ( $> 3$ – $4.5$  cm), and juveniles ( $> 4.5$ – $7$  cm). However, only  
466 the tropical species could be grouped in these three categories.  
467 Most of the temperate fish in the view of the camera  
468 were juveniles. Thus, the effect of the factor life stage is  
469 tested only for tropical fish.

470 Because the behaviours were measured using different  
471 units (which could bias the analyses), prior to all analyses,  
472 all behavioural data were standardised (i.e. scaling technique  
473 used for standardising scores on the same scale by dividing  
474 a score’s deviation by the standard deviation in a data set).  
475 As a result, all behaviours are transformed to the same scale.  
476 A posteriori pairwise comparison of the means

477 was used to evaluate differences among latitudes, species,  
478 and species within latitude when a significant interaction  
479 was present.

480 All analyses were performed on square root transformed  
481 data, and used Euclidian resemblance matrices. Where the  
482 number of permutations was low, a Monte Carlo test was  
483 used and post-hoc pooling of interaction terms was performed  
484 to enable a more powerful test of the main effect (only if their  
485  $p$  value was  $> 0.25$ ; Winer et al. 1991). For significant effects  
486 ( $p < 0.05$ ) pairwise tests were used to compare the respective  
487 means (Anderson 2001).

488 For the behaviours that showed a significant effect of the  
489 covariates in the ANCOVAs, we calculated their adjusted  
490  $R^2$  (also known as the coefficient of determination) to evaluate  
491 the strength of their relationships for each species separately.  
492 The  $R^2$  can indicate to what extent (expressed in %) the  
493 variance of the covariate (abundance of temperate or tropical  
494 fishes, or individuals of the same species) explains the  
495 variance of dependent variables (behaviour) (Miles 2014).

497 The MANCOVAs, ANCOVAs, and a posteriori pairwise  
498 comparisons of the means were performed using the software  
499 Primer version 6.

500 Differences in density between species per body sizes,  
501 measured as small (individuals  $< 5$  cm), medium (5–10 cm)  
502 and large ( $> 10$  cm) individuals during field surveys (see  
503 details in Booth et al. 2007) conducted at the same sites and  
504 years as for the videos recordings, were compared between the  
505 focal tropical and temperate fishes using permutational ANOVA.  
506 This analysis was performed to evaluate if differences in body  
507 size between tropical and temperate species across latitude  
508 could explain the differences detected in species behaviours.  
509

## 510 Results

511 The behavioural repertoire (all seven behaviours combined)  
512 differed significantly across latitudes (Table S4, MANCOVA,  
513  $F = 3.809$ ,  $p = 0.033$ ) and between tropical (*A. vaigiensis*)  
514 and temperate (*M. strigatus*) species (MANCOVA,  $F = 17.804$ ,  
515  $p = 0.0002$ ). Pairwise tests revealed that the behavioural  
516 repertoire differed between low and middle latitudes, but  
517 not from high latitude, respectively, for both species. Only  
518 the abundance of temperate fishes (MANCOVA,  $F = 3.972$ ,  
519  $p = 0.004$ ) had a significant effect on the species behaviours.  
520 Overall, the behaviours of the tropical fish were not affected  
521 by different life stage (recruits, early-juveniles, juveniles)  
522 (MANCOVA,  $F = 0.836$ ,  $p = 0.559$ ). The observation time  
523 of individuals was significantly related to the species  
524 behaviour (MANCOVA,  $F = 3.972$ ,  $p = 0.004$ ), but the  
525 interactions with latitude and species did not show a  
526 significant effect, meaning that the latitudinal differences of  
527

528 species behaviour were not influenced by the time of  
529 observation (Table S3).

### 530 Tropical fish species

531 Four out of seven behaviours that acted as proxies for  
532 foraging and aggressive performance differed as a function  
533 of latitude at least in one of the life stage categories (re-  
534 cruit, early-juvenile, juvenile). Bite rates (ANCOVA, lati-  
535 tude:  $p = 0.0002$ ) and prey inspection rates  
536 (latitude  $\times$  species interaction:  $p = 0.039$ ) were lower at  
537 middle and high latitudes than at low latitude, while prey  
538 attraction time (latitude  $\times$  species interaction:  $p = 0.009$ )  
539 and, minimum distance to prey for recruits of *A. vaigiensis*  
540 (latitude  $\times$  life stage:  $p = 0.023$ ) all increased from low to  
541 middle and high latitudes. Additionally, recruits showed a  
542 shorter distance to prey than juveniles at the low latitude  
543 (Fig. 2, Fig S3, Table S5). The behaviours that indicate  
544 direct aggressive interactions (chasing and escaping rates)  
545 did not differ as a function of latitude or among individuals  
546 of each species, heterospecific tropical and temperate fish  
547 species (Fig. S4). Only two behaviours of the tropical fish  
548 were significantly related to the abundance of temperate  
549 fishes and conspecifics: retreat rates were positively related  
550 to the total abundance of temperate fishes ( $R^2 = 0.28$ ;  
551 ANCOVA,  $p = 0.0002$ , Fig. 3a and Table S5) but nega-  
552 tively related to the abundance of conspecific individuals  
553 ( $R^2 = 0.24$ ,  $p = 0.032$ , Fig. 3b), whilst bite rates were  
554 negatively related to the abundance of temperate fishes  
555 ( $R^2 = 0.08$ ,  $p = 0.016$ , Fig. 3c), but positively related to the  
556 abundance of conspecifics ( $R^2 = 0.20$ ,  $p = 0.013$ , Fig. 3d).

### 557 Temperate fish species

558 Temperate fishes differed in three out of seven behaviours  
559 as a function of latitude. Bite rates (ANCOVA, latitude:  
560  $p = 0.0002$ ) and chasing rates (latitude:  $p = 0.003$ ) were  
561 higher at low latitude than middle and high latitudes,  
562 respectively, while prey attraction time (ANCOVA, lati-  
563 tude:  $p = 0.0002$ ) was higher at middle latitude than at high  
564 latitude, but the low latitude did not differ from middle and  
565 high latitudes (Fig. 2, Table S5). Unlike the tropical fish,  
566 *M. strigatus* exhibited higher chasing behaviour against  
567 individuals of the same species and tropical fishes at low  
568 latitude than at middle and high latitudes, while they  
569 escaped more from heterospecific temperate fish at the high  
570 latitude (Fig. S4). Retreat rate was positively related to  
571 abundance of other temperate fishes ( $R^2 = 0.41$ ;  
572 ANCOVA,  $p = 0.0002$ , Fig. 3a and Table S4). A weak  
573 negative relationship was observed between retreat rates  
574 and abundance of conspecific individuals ( $R^2 = 0.06$ ,  
575  $p = 0.032$ , Fig. 3b), and bite rate and abundance of other  
576 temperate fishes ( $R^2 = 0.11$ ,  $p = 0.016$ , Fig. 3c). Bite rate

also had a weak positive relationship with the abundance of  
conspecifics ( $R^2 = 0.09$ ,  $p = 0.013$ , Fig. 3d).

### Tropical versus temperate fish species

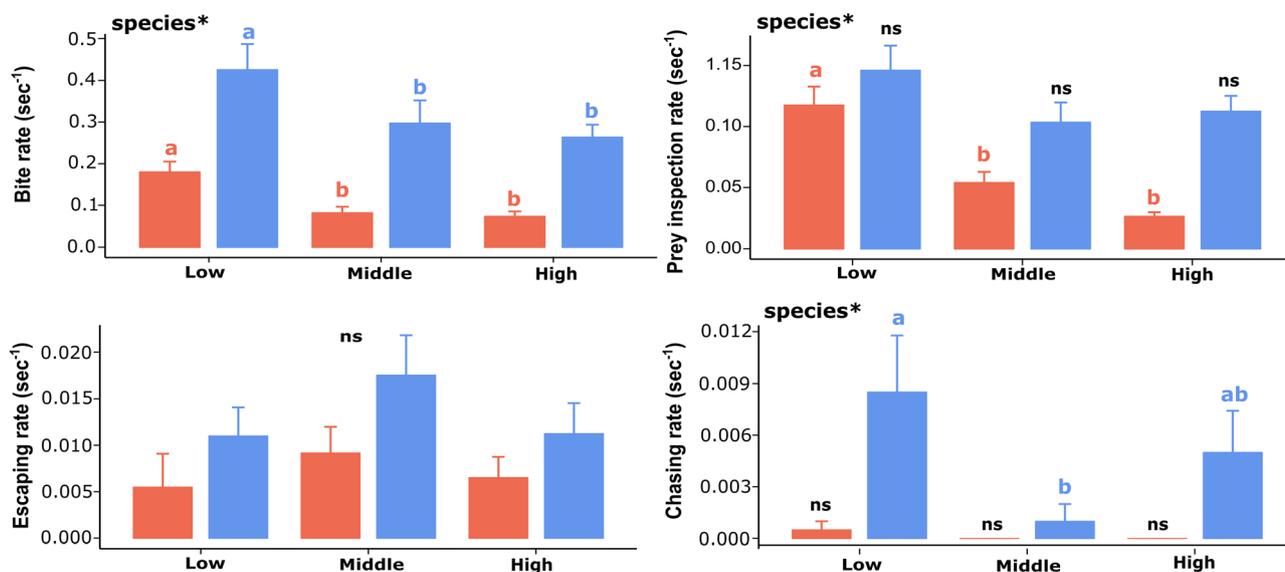
In five out of seven behaviours, the temperate fish showed a  
higher foraging performance than the tropical species at  
least in one of the latitudes: higher bite rate ( $p = 0.029$ ),  
higher prey inspection ( $p = 0.039$ ), higher chasing rate  
( $p = 0.006$ ), prey attraction time ( $p = 0.009$ ), and a shorter  
distance to prey (ANCOVA,  $p = 0.002$ ), respectively  
(Fig. 2, Table S5).

Whilst the density of small, medium and large sizes of  
individuals of the focal tropical (*A. vaigiensis*) and tem-  
perate (*M. strigatus*) species were higher at the low latitude  
than at middle and high latitudes, the densities of large  
individuals of the focal temperate fish (*M. strigatus*) were  
higher than the densities of large individuals of *A.*  
*vaigiensis* independent of the latitude, and the tropical fish  
showed higher densities of small individuals than their co-  
shoaling temperate species, irrespective of latitude  
(Fig. S5, Table S6).

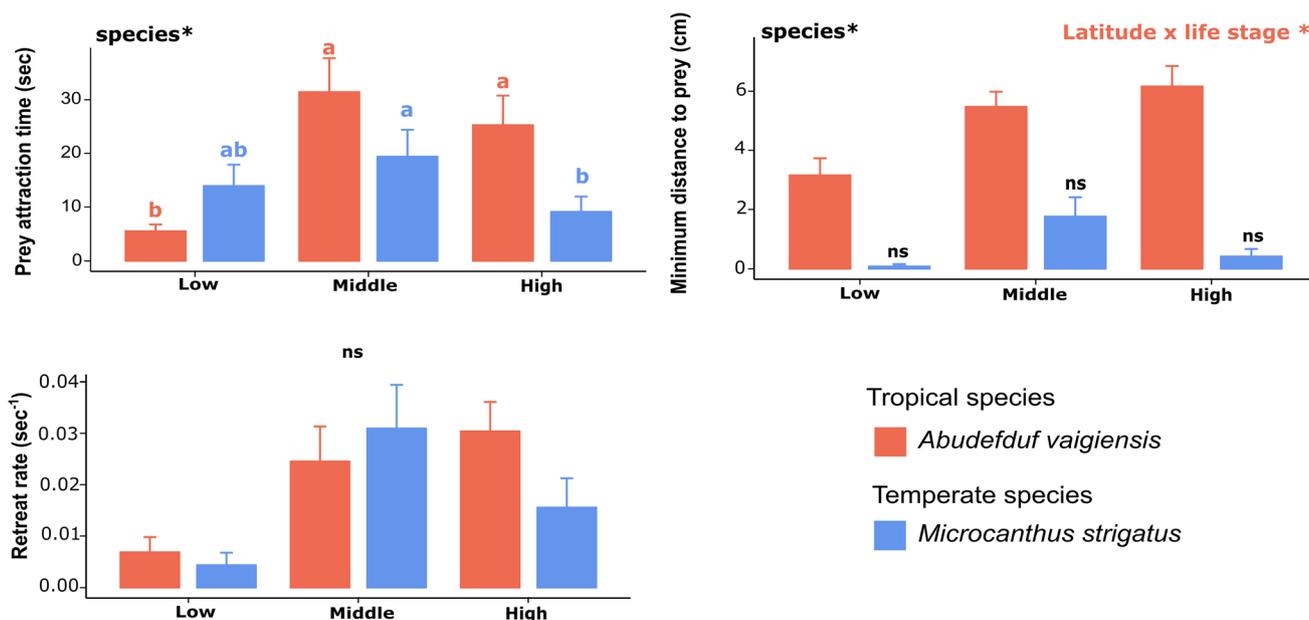
### Discussion

The central tenet of biological invasion theory is that alien  
species are often competitively stronger than non-native  
species and therefore experience successful invasions with  
substantial impacts on the communities in their novel  
environments (Carlton et al. 1999; Branch and Steffani  
2004; Davis 2003; Vila and Weiner 2004). However, we  
here show that the foraging competency (using various  
foraging behaviours as a proxy) of a common tropical  
range-extending fish, regardless of life stage (i.e. recruit,  
early-juvenile, or juvenile), is lower in its novel temperate  
range than in its native subtropical range and lower than  
that of its co-shoaling temperate fish species, which may  
compromise its fitness in its novel invaded range. Reduced  
foraging performance of tropical fish at their high-latitude  
range edges was expressed through (1) increased prey  
attraction time, (2) increased distance to prey (for recruits),  
(3) reduced prey inspection rates, and (4) reduced bite  
rates, respectively, compared to their native ranges. In  
contrast, the aggressive interactions with local temperate  
fish (chasing and escaping behaviours) during foraging did  
not increase in their novel ranges. Although for coral reef  
fishes the expectation is that feeding rates reduce in cold-  
temperate waters (Barneche et al. 2009; Kingsbury et al.  
2020), we observed that other behaviours related to for-  
aging performance were also compromised (i.e. increased  
distance and attraction time to prey, reduced prey inspec-  
tion rates). Thus, the reduced foraging performance as a

### A decrease from low to high latitude indicates reduced performance



### An increase from low to high latitude indicates reduced performance

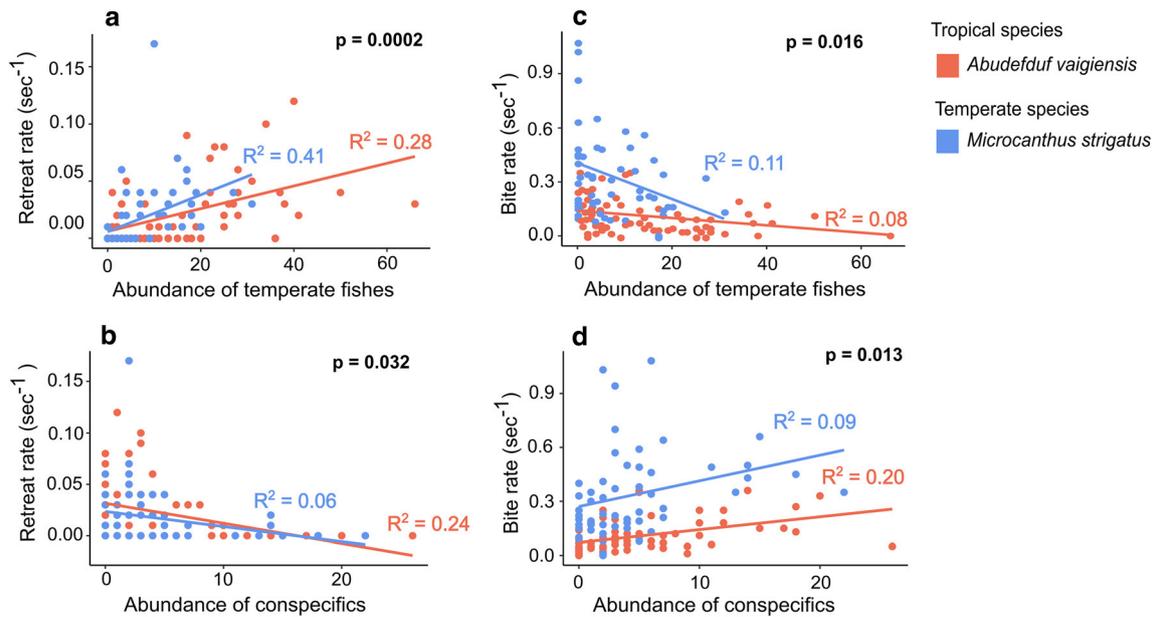


**Fig. 2** Behavioural proxies (mean + SE) of foraging competency in tropical and temperate fishes across a latitudinal gradient (see Fig. 1) based on the food acquisition and on aggressive interactions (escaping and chasing rates). The graphs are grouped into behaviours that show reduced performance when they decrease (above 4 panels) or when they increase (lower 3 panels) from low to high latitudes,

respectively. Letters indicate significant latitudinal differences within species ( $p < 0.05$ ; see Tables S5). ns = no significant differences. Significant difference between the tropical and temperate fish species within latitudes are indicated as 'species\*' and life stage among latitude is indicated as 'Latitude  $\times$  life stage\*' (only for the tropical fish as indicated by the orange colour) (see Table S5)

625 function of latitude suggests that tropical fishes are still  
626 poorly behaviourally adapted to either lower temperatures  
627 and the novel biological conditions (e.g. surrounding  
628 habitats), which might increase their vulnerability to local  
629 competitors and predators (Figueira et al. 2019). Cooler-  
630 temperate waters are known to cause lower metabolic rates

and foraging performance in *Abudegduf vaigiensis* and this  
is linked to a reduced energy allocation towards somatic  
growth (Kingsbury et al. 2020). Our observed decline from  
low to high latitude in foraging performance by tropical  
range-extending fishes may be restricting their growth,



**Fig. 3** Relationship between behaviours (a, b retreat rates; c, d bite rates) of *Abudedefduf vaigiensis* and *Microcanthus strigatus* and the abundance of temperate fishes and conspecific individuals (average of total number of temperate fishes and same individuals of each focal

species per sample). Adjusted  $R^2$  shows the proportion that the respective covariate contributed to the variability of the model. Model  $p$  values for the covariates are shown inside each panel

636 survival, and consequent permanent establishment in temperate ecosystems under current ocean warming.

637  
638 Species composition at high latitudes can alter the foraging performance of tropical species in their novel temperate ranges. We show that tropical fishes were more efficient in approaching (decreased retreat rates) and consuming (increased bite rates) prey with increased abundances of conspecifics (irrespective of latitude), but contrastingly an increased abundance of temperate fishes increased their retreat rates. At sites with higher abundances of typically larger temperate fishes, these aggregated around the released prey and formed a physical barrier, preventing tropical fishes from approaching the released prey (Fig. S2). Such physical displacement has also been observed in native vs invasive terrestrial organisms (Masciocchi et al. 2010). Density-dependent competition is often observed among fishes. For example, at elevated abundance, coral-dwelling damselfishes become more aggressive and interference competition for refuge increases, leading to inferior competitors being more susceptible to predation (Holbrook and Schmitt 2002).  
654  
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656  
657 Unexpectedly, a higher abundance of temperate fishes was not related to an increased aggression (escaping and chasing rates) between the tropical and temperate species.  
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659  
660 No signs of aggressive interactions between tropical and temperate species have been reported before. Instead, Smith et al. (2018) revealed that *A. vaigiensis* increased their growth rates at temperate reefs when schooling with temperate species. Additionally, Kingsbury et al. (2019)

665 found that these tropical and temperate species occupied segregated trophic niches that did not overlap significantly probably due to their generalist feeding strategies. Nevertheless, in our experiment we observed *M. strigatus* and other temperate fishes (e.g. mado, *Atypichthys strigatus*; sweep, *Scorpius lineolatus*; yellow bream, *Acanthopagrus australis*) all to be aggressively interacting with *A. vaigiensis* and interfering in their performance by inhibiting their access to food resources during their feeding, indicating that native temperate fishes were capable of interfering in the performance of tropical fishes by inhibiting their access to food resources. Although *A. vaigiensis* are considered diet generalists (zooplankton, algae and invertebrates) and thus experience less competition for specific prey species (Anderson et al. 2017; Kingsbury et al. 2019), such food items differ in nutritional values. This means that temperate fishes can still limit the foraging performance and fitness of generalist tropical fishes on temperate reefs by restricting their access to more nutritious food items. With accelerating ocean warming, a higher diversity and abundance of tropical fishes is expected in temperate ecosystems (Fowler et al. 2017).  
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687 Whilst under current warming, larger-sized native temperate fishes may slow the pace of tropical invasions through behavioural interference during feeding, increasing abundances and body sizes of tropical fishes under future warming can counter these species interaction effects through increased foraging performance when shoaling with their own species.  
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694 Tropical fishes appear to have a lower competency than  
 695 temperate fishes in cool-water environment, as indicated by  
 696 an overall lower foraging and aggressive performance (four  
 697 out of seven behaviours) in their novel ranges (mid and  
 698 high latitudes) than the temperate species. Inferior com-  
 699 petitors often suffer high mortality rates by being more  
 700 susceptible to predation and competition (Forrester and  
 701 Steele 2000; Holbrook and Schmitt 2002; Almany 2003).  
 702 In addition to low temperatures, this reduced competency  
 703 compared to the temperate fish may be related to differ-  
 704 ences in body size. Most of the tropical fishes at temperate  
 705 latitudes were smaller than the temperate fishes and are  
 706 therefore likely to be behaviourally subordinate to larger  
 707 juvenile or adult local temperate fishes in terms of feeding  
 708 competency (Persson 1985; Young 2003; Poulos and  
 709 McCormick 2014). For instance, 91% of the escaping  
 710 events registered for the tropical species were from tem-  
 711 perate fish species, and all of the temperate fishes (100%)  
 712 were larger than the tropical ones, indicating the propensity  
 713 of tropical range-extending fish to be competitively  
 714 excluded from native fishes in at least the initial stage of  
 715 tropicalisation. However, shoaling with temperate fishes  
 716 (including *M. strigatus*) can sometimes also facilitate the  
 717 performance of tropical fishes in temperate ecosystems by  
 718 enhancing access to resources and hence increasing growth  
 719 (Smith et al. 2018) and survival rates (Paijmans et al.  
 720 2020). Under current warming, temperate fishes still seem  
 721 to have a behavioural advantage at their trailing edges over  
 722 range-extending tropical fishes through larger body sizes,  
 723 higher foraging and aggressive performance and higher  
 724 abundances.

725 As expected, the performance of the temperate fish  
 726 species was largely similar across latitude. Only three out  
 727 of seven behaviours were affected by latitude (i.e.  
 728 increased bite rate and chasing rate at the warmer low-  
 729 latitude and increased prey attraction time at the middle  
 730 than high latitudes). Such higher foraging and aggressive  
 731 performance at low latitude might be explained by the fact  
 732 that the natural range of *M. strigatus* covers all sites that we  
 733 studied across the latitudinal gradient (Tea et al. 2019), and  
 734 that they perform best at subtropical-warmer temperatures  
 735 in the centre of their distributional range (Payne et al.  
 736 2016). A similar pattern was found in other temperate  
 737 marine fish species in the Tasman Sea (Neuheimer et al.  
 738 2011). As temperate species have a wider thermal niche  
 739 than tropical species (Tewksbury et al. 2008; Perez et al.  
 740 2016), current ocean warming initially has positive rather  
 741 than negative effects on some of the performance traits of  
 742 temperate fishes at their trailing edges.

743 We demonstrate that at higher latitudes (in novel tem-  
 744 perate environments) and at elevated abundance and larger  
 745 body sizes of temperate fishes, the foraging performance of  
 746 range-extending tropical species is currently compromised.

747 This suggests that both physical and biological factors  
 748 might be acting in synchrony to restrict the establishment  
 749 of tropical species in temperate ecosystems under current  
 750 warming. Behavioural interference for prey resources by  
 751 larger temperate fishes can limit resource access and might  
 752 force tropical species to use less desirable resources  
 753 slowing the initial stages of tropicalisation of temperate  
 754 ecosystems during which tropicals are overrepresented by  
 755 small recruits. However, when the thermal stress of tem-  
 756 perate environments is relaxed under future warming and  
 757 the performance and survival of vagrant tropical fishes is  
 758 no longer affected by low water temperatures, they will  
 759 persist until adulthood and the likelihood of stronger  
 760 behavioural interactions with native species may increase  
 761 in temperate ecosystems.

762 **Supplementary Information** The online version contains  
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 764

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770 **Declarations**

771 **Conflict of interest** On behalf of all authors, the corresponding  
 772 author states that there is no conflict of interest.

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