



Multiple predator effects on juvenile prey survival

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Abstract

Predicting multiple predator effects (MPEs) on shared prey remains one of the biggest challenges in ecology. Empirical evidence indicates that interactions among predators can alter predation rates and modify any expected linear effects on prey survival. Knowledge on predator density, identity and life-history traits is expected to help predict the behavioral mechanisms that lead to non-linear changes in predation. Yet, few studies have rigorously examined the effects of predator–predator interactions on prey survival, particularly with marine vertebrate predators. Using an additive-substitutive design, we experimentally paired reef piscivores with different hunting mode [active predator, *Pseudochromis fuscus* (F); ambush predators, *Cephalopholis boenak* (B), *Epinephelus maculatus* (M)] to determine how behavioral interactions modified their combined impacts on damselfish prey. Results showed that behavioral patterns among predators matched those predicted from their hunting mode. However, it was the identity of the predators what determined the strength of any positive or negative interactions, and thus the nature and magnitude of MPEs on prey survival (i.e., risk-enhancing effects: treatments BB, MM and FM; risk-reducing: BM; and linear effects: FF, FB). Given the specificity of predator–predator interactions, none of the predators were fully functionally redundant. Even when two species seemed substitutable (i.e., predators F and M), they led to vastly diverse effects when paired with additional predator species (i.e., B). We concluded that knowledge of the identity of the predator species and the behavioral interactions among them is crucial to successfully predict MPEs in natural systems.

Keywords Predator identity · Predator hunting mode · Predator density · Additive-substitutive design · Mesopredators · Coral reef fish

Introduction

Food-web theory often assumes that ecologically similar species can be treated collectively as a single functional unit (e.g., Fretwell 1987; Hooper et al. 2005). However, due to differences in life-history traits (e.g., hunting modes, habitat domain), predator species within a functional unit

can have different effects on prey (e.g., Schmitz and Suttle 2001; Chalcraft and Reser 2003). Moreover, behavioral predator–predator interactions, as well as antipredator responses by prey, can lead to non-linear effects on mortality where the collective impact of multiple predators on prey cannot be predicted from the sum of their independent contributions (Sih et al. 1998; McCoy et al. 2012). While positive behavioral interactions among predators (i.e., facilitation, synergy) usually allows them to kill more prey than expected and lead to risk-enhancing effects (Soluk and Collins 1988; Losey and Denno 1998; Ford and Swearer 2012), antagonistic interactions (i.e., intraguild predation, interference competition) tend to reduce their joint impact on prey mortality and cause risk-reducing effects (Finke and Denno 2004; Vance-Chalcraft and Soluk 2005; Sitvarin and Rypstra 2014). Given that most food-webs include multiple predator species, studying predator–predator interactions and their ability to modify trophic links has been a critical step to understanding food-web ecology and community dynamics (Sih et al. 1998; Ives et al. 2005; Schmitz 2007; Golubski

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and Abrams 2011). Further, knowledge on the nature and magnitude of multiple predator effects (MPEs) can help us foresee the consequences of predator species loss and the cascading effects on ecosystem-level processes (Byrnes and Stachowicz 2009; Finke and Snyder 2010; Griffin et al. 2013).

Predator hunting mode (e.g., active, sit-and-wait, sit-and-pursuit) is often used to predict the nature of the MPEs as it can influence the prevalence and/or frequency of predator–predator interactions (Sokol-Hessner and Schmitz 2002; Schmitz 2007, 2009). In theory, two ambush predators should seldom see or interact with each other, thereby exerting predictable linear effects on prey mortality, while two active hunters should have high encounter rates with each other, and hence higher chances to engage in interference competition that leads to risk-reducing effects (Sih et al. 1998). Empirical tests on hunting mode are, however, often inconclusive as they require appropriate experimental designs to disentangle the effect of predator hunting mode from that of predator identity (e.g., including multiple predator species for each hunting mode; Newman 2008). Our understanding of MPEs has been further delayed by lack of research isolating the effects of predator density and predator identity through the simultaneous use of additive and substitutive experimental designs (Sih et al. 1998; Griffen 2006; Byrnes and Stachowicz 2009; McCoy et al. 2012). Additive experiments mainly test whether increases in total predator density (of the same or different predator species) lead to non-linear effects on prey mortality (Losey and Denno 1998; Vance-Chalcraft and Soluk 2005; Ford and Swearer 2012). Instead, substitutive designs (also known as replacement series) examine the effect of predator diversity by comparing how single-species and multi-species predator groups impact prey mortality (Sokol-Hessner and Schmitz 2002; Snyder et al. 2006; Straub and Snyder 2006). If the impact is equivalent between these predator groups it is often assumed that predator species have substitutable effects on the system (Sih et al. 1998; Sokol-Hessner and Schmitz 2002). Given the complexity of predator–predator interactions, robust experimental designs are required to fully unravel the effects of predator identity, predator hunting mode and predator density on MPEs. While invertebrate research has provided most of our knowledge on MPEs (e.g., Losey and Denno 1998; Sokol-Hessner and Schmitz 2002; Griffen 2006; Schmitz 2007, 2009; Griffin et al. 2013; Soomdat et al. 2014), little is understood about how behavioral predator–predator interactions influence MPEs in complex vertebrate systems.

Reef fish communities are ideal for examining MPEs. Mid-sized piscivores represent a diverse and abundant trophic guild, where predators exhibiting a wide variety of life-history traits (e.g., hunting strategies, sizes, habitat domains, ages, diurnal cycles) constantly interact while foraging on shared prey (Hixon 1991; Lukoschek and

McCormick 2002; Bshary et al. 2006; Stallings and Dingeldein 2012; Auster et al. 2016). Although reef mesopredators are known to exert a strong population bottleneck on recently settled reef fishes (Almany and Webster 2006; Stier et al. 2017), few studies have examined whether intraguild predator–predator interactions lead to non-linear effects on prey mortality. Research examining the effects of mesopredator diversity have shown that pelagic and benthic predators hunting in tandem can disproportionately increase the mortality of schooling fish than if hunting independently (risk-enhancing effects). In contrast, studies testing the effects of benthic predator density have found linear or risk-reducing effects depending on the species and number of predators involved (Stier et al. 2013; Stier and White 2014). Surprisingly, no study has simultaneously used additive and substitutive designs to effectively understand the role of reef mesopredator density and diversity on prey mortality. Further, the lack of behavioral data on marine predator–predator interactions prevents us from determining the mechanisms driving these MPEs. Given the ongoing exploitation of apex marine macro-carnivores (Jackson et al. 2001; Myers and Worm 2003), it is increasingly important to understand the cascading effects that changes within the mesopredator guild (e.g., increased density, reduced richness) might have on prey populations and ecosystem function (Stallings 2008).

In this study, we examined the combined effect that multiple benthic piscivores have on the survival of shared fish prey. Using three mesopredator fishes (active predator: *Pseudochromis fuscus*, ambush predators: *Cephalopholis boenak* and *Epinephelus maculatus*) and all the possible single and paired combinations, we explored how predator density, identity and hunting mode influence the nature and magnitude of MPEs. Specifically, we ran both additive (maintaining relative density but increasing total density) and substitutive (maintaining total density but increasing relative density) experimental designs to fully understand the combined effects of the three mesopredators. Additionally, we explored how mesopredators with different functional traits (hunting mode active vs. ambush predators) can influence the nature of MPEs.

Materials and methods

Study species and fish handling

The mesopredators *Pseudochromis fuscus*, *Cephalopholis boenak* and *Epinephelus maculatus* were selected as focal study species as they co-occur in shallow patch reefs, are highly site-attached, and voraciously forage on newly settled fish prey (Stewart and Jones 2001). The dottedback *P. fuscus* (family Pseudochromidae) is an active roaming carnivore which stalks and chases invertebrate and vertebrate

prey using mainly pursuit techniques (Feeney et al. 2012). Adults reach up to 7.0 cm standard length (SL), are predominantly solitary, have small home ranges ($< 2 \text{ m}^2$), and exhibit strong territorial behavior (Feeney et al. 2012). In contrast, the grouper species *C. boenak* and *E. maculatus* (family Serranidae) are cryptic piscivores with ambush and sit-and-wait hunting techniques. They often live in harems, display secretive behavior, and strike at prey only on their close vicinity (Hobson 1979; Shpigel and Fishelson 1989; Liu and Sadovy 2005). Although most groupers can reach large sizes during their adult life-stage ($> 20 \text{ cm SL}$; Beukers-Stewart and Jones 2004; Beukers-Stewart et al. 2011), juvenile-stage individuals tend to occupy the same mesopredator guild as adult dottybacks. Combinations of these mesopredators (adult dottybacks + juvenile groupers) have been widely used in coral reef research to examine predation on newly settled fish (Beukers and Jones 1998; Webster 2002; Webster and Almany 2002; Almany 2003). In this study, recruits of the damselfish *Pomacentrus amboinensis* were selected as focal prey given that they settle at high densities during the austral summer months and are frequently preyed upon by resident reef mesopredators (Webster 2002).

All fishes were collected from Lizard Island ($14^{\circ}40'S$, $145^{\circ}28'E$), northern Great Barrier Reef, Australia. At Lizard Island, adults of *P. fuscus* and juveniles of the groupers *C. boenak* and *E. maculatus* occur at high densities on the patch reefs of the lagoon (approx. 1 to 2 individuals of each species per patch reef), where they tend to aggregate in response to the high availability of newly settled fish (Beukers and Jones 1998; Webster 2002; Hixon and Jones 2005). Mesopredator fishes of similar size (adults of *P. fuscus*, $6.82 \pm 0.07 \text{ cm}$; juvenile *C. boenak*, $7.11 \pm 0.12 \text{ cm}$; juvenile *E. maculatus*, $6.69 \pm 0.08 \text{ cm}$; mean $SL \pm SE$) were captured using hand nets and an anaesthetic clove oil solution, while

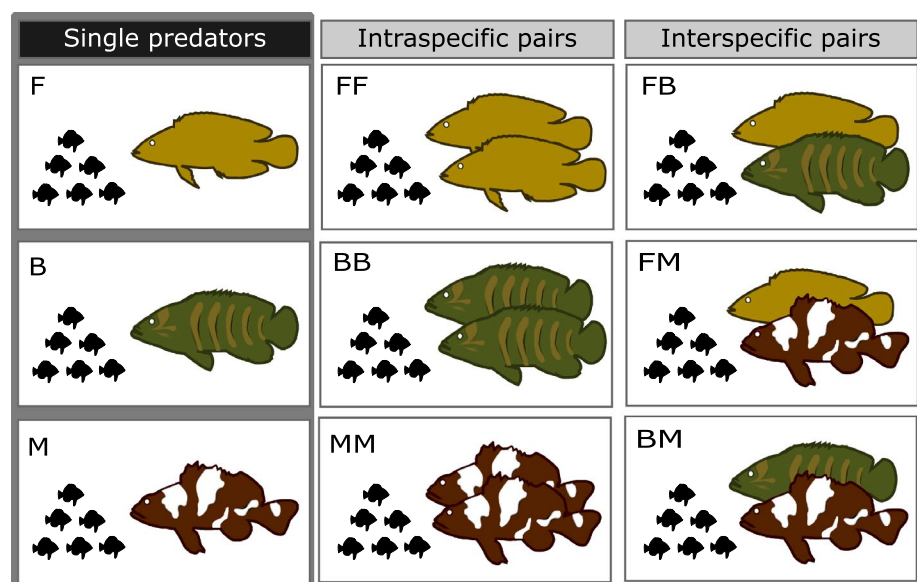
damselfish recruits ($1.29 \pm 0.003 \text{ cm}$, mean $SL \pm SE$) were collected as they came into the reef at the end of their larval phase using light traps. Fishes were transported to Lizard Island Research Station within 1 h of capture and maintained in individual aquaria with flow-through aerated seawater and ambient temperature and photoperiod. Mesopredators were fed squid daily, while damselfish were fed *Artemia* spp. twice a day. All fish were fed to satiation.

Experimental trials

Damselfish recruits (*P. amboinensis*) were exposed to nine predatory treatments including each single mesopredator on its own [*P. fuscus* (F); *C. boenak* (B); *E. maculatus* (M)] and all possible intraspecific (FF, BB, MM) and interspecific (FB, FM, BM) mesopredator pairs (Fig. 1). This experimental design comprised both additive and substitutive components to test for multiple predator effects (MPEs) on prey survival and the functional substitutability of mesopredator species. Preliminary trials showed a non-predator control treatment was unnecessary as prey survival was 100% in the absence of mesopredators.

Experimental trials were run in 368-L pools (1 m diameter \times 0.4 m depth; 0.8 m^2 surface area) with constant seawater flow. Each pool contained a 3 cm sand-layer as substrate, two large rubble heads to shelter predators (15 cm height \times 20 cm diameter), a small piece of the live bushy coral *Pocillopora damicornis* to shelter prey (5 cm height \times 10 cm diameter), and 5–7 pieces of PVC tube and rubble (standardized by total volume) randomly scattered in the arena to increase habitat complexity. Mesopredators were not fed for 24 h prior to being introduced into the pool at 17:00–18:00 h and allowed to acclimate for 13 h. The following morning (7:00–9:00 h), six damselfish prey were

Fig. 1 Experimental design including nine predatory treatments. Treatments comprise single mesopredators (*Pseudochromis fuscus*, F; *Cephalopholis boenak*, B; *Epinephelus maculatus*, M) foraging on their own and all possible intraspecific (FF, BB, MM) and interspecific pairs (FB, FM, BM). Predator(s) foraged on six damselfish recruits (*Pomacentrus amboinensis*) (color figure online)



introduced into each pool and protected within a clear bucket (38 cm height \times 24 cm diameter) while they acclimated to the experimental setup. After 10 min, the bucket was lifted, allowing the mesopredator(s) to access the prey for a total of 6 h (trial duration). Throughout the first hour of each trial, an observer recorded (1) the number of successful and non-successful feeding strikes by each mesopredator, and (2) the number of chases, bites and displays between mesopredators (as a measure of aggressive interactions). While mesopredator individuals were not tagged, the observer was able to separately track the behavior of each predator, using natural markings on the individuals. Each hour the number of damselfish surviving was recorded.

All the protocols used in this study were selected after preliminary trials and observations of the mesopredators and prey. For example, the 10-min prey acclimation period (i.e., time prior to removal of the clear bucket) was selected after initial assessments showed predators tended to retreat to their shelters after 10–20 min of failed strike attempts. As a result, once the bucket was lifted, predators took a long time to re-emerge and resume their foraging activity. This pattern was particularly evident for the ambush species which due to their secretive and sedentary behavior remained hidden for most of the time. Furthermore, most damselfish recruits were already using the coral head as shelter and defending it against conspecifics after 10 min. Preliminary trials also revealed that predator behavior (e.g., number of successful strikes) was best assessed *in situ* (live), given that video footage was of limited use because of the large size of the tanks (1 m diameter), small size of the prey (< 2 cm), and the presence of structures used to increase topographic complexity (shelters, rubble, PVC pipes). Finally, initial observations evidenced that most predator–prey and predator–predator interactions occurred within the first hour of trial as foraging activity tends to decrease over time due to predator satiation and/or prey depletion. Hence, the same observer (to maintain consistency in the behavioral measures) watched the first hour of all trials while recording predator behavior. Only three trials were run per day (1st trial began at 7:00 h, 2nd at 8:00 h, and 3rd at 9:00 h). Overall, each treatment had 10–12 replicates randomly assigned to different experimental pools ($n=5$), start-up times (7:00, 8:00, 9:00 h), and experimental days ($n=35$). Each individual fish (predator or prey) was used in only one trial.

Statistical analysis

Multiple predator effects

To examine the combined effect of multiple predators on damselfish prey, we computed for each predatory treatment the mean prey survival probabilities and 95% confidence intervals (CI) by analyzing the time-series of prey survival

with a Cox regression model (Cox and Oakes 1984). This ecological modelling approach allows the analysis of prey survival rates from time-dependent data and is able to handle functional responses of any shapes (Moya-Laraño and Wise 2000). The assumption that hazards were proportional across all treatments was successfully verified with a test on weighted residuals (Grambsch and Therneau 1994). Prey survivals calculated with Cox regressions were subsequently compared to predicted values from a null multiplicative risk model (MRM) which assumes independent-linear effects among predators (Soluk and Collins 1988). Following Soomdat et al. (Soomdat et al. 2014), we inferred a pair of predators had linear-effects on prey survival if the expected survival (calculated with the MRM) fell inside the 95% CI of the observed effects (calculated with Cox regressions). The MRM is the most common technique to analyze MPEs (e.g., Soluk and Collins 1988; Soluk 1993; Sih et al. 1998; Griffen 2006); however, given that it assumes constant per capita prey mortality through time (linear functional response) and/or no prey depletion, it can overestimate the occurrence of risk-enhancement effects in additive designs and risk-reduction effects in substitutive designs (see discussion by McCoy et al. 2012). To reduce any misinterpretation we analyzed our results in the light of both the additive and substitutive designs.

Predator density (additive model) We used the additive design and the probability of prey survival caused by each mesopredator species hunting independently (e.g., F, B, M), to examine whether increasing total mesopredator density (single predator vs. predator pairs) elicited non-linear effects. Analysis was made for both intraspecific and interspecific predator pairs. However, it must be noted that for interspecific pairs this model confounds the effects of increasing predator density to that of increasing predator richness. The expected survival for each of the intraspecific pairs (FF, BB, MM) was calculated as $E_{i,i} = P_i \times P_i$, where P_i is the probability of prey surviving when foraged on by a single predator i (i.e., F, B or M). The expected survival for each interspecific pair (FB, FM, BM) was estimated as $E_{i,j} = P_i \times P_j$, where P_i and P_j is the probability of prey surviving when foraged on by combinations of two different predators i and j .

Predator diversity (substitutive model) To examine the effects of mesopredator diversity (increase in richness) we employed the substitutive design. This approach experimentally controlled for total predator density, while comparing the effects of interspecific pairs to those observed on intraspecific pairs. The expected survival for interspecific pairs was calculated as $E_{i,j} = (P_{i,i} \times P_{j,j})^{0.5}$, where $P_{i,i}$ and $P_{j,j}$ is the probability of prey surviving when foraged on by pairs of intraspecific mesopredators (FF, BB or MM). Following

Sih et al. (1998), species were considered substitutable if the effect of an interspecific pair on prey survival (e.g., BM) was equivalent to the effects of each predator species in an intraspecific pair (e.g., BB and MM).

Predator behavior

We used one-way analyses of variance (ANOVA) to determine whether intra- and interspecific interactions affect mesopredator behavior (total strikes and successful strikes). For each mesopredator species (e.g., F) we compared: the mesopredator alone (i.e., F); the mesopredator in an intraspecific pair (e.g., FF); and the mesopredator in the two different interspecific pairs (i.e., FB and FM). All significant differences detected in the ANOVAs were subsequently explored using post hoc Tukey's HSD for unequal sample size. We further compared the total strikes and successful strikes between the dominant and subordinate individuals of each intraspecific pair (FF, BB, MM), using independent *t* tests with Bonferroni corrections. The dominant fish was considered the one that initiated most of the aggressive interactions and sheltered closest to the location of the prey. This approach was only used for intraspecific pairs, as the contrasting behavior of interspecific pairs hindered a correct distinction between dominant and subordinate fish (e.g., *P. fuscus* is usually more active and aggressive than *C. boenak* or *E. maculatus*, despite being the subordinate fish). Residual analyses were used to examine if the behavioral data satisfied the assumptions of normality and homoscedasticity. The strikes and successful strikes were square root transformed to meet the assumptions of parametric tests. The number of aggressive interactions was analyzed among treatments using a non-parametric Kruskal–Wallis one-way ANOVA given the heteroscedasticity of the data. All statistical analyses were performed in R version 3.2.2 (R Core Team 2015) using the packages survival (Therneau 2015) and rms (Harrell 2015).

Results

Acclimation to experimental arenas

All mesopredators acclimated well. The morning of the trial, mesopredators were seen regularly swimming through the rubble heads and making use of all the experimental arena and shelter provided. In the 10 min before the beginning of the trial (once prey was introduced into the clear bucket), mesopredators had already approached prey or even start striking at them through the clear bucket. Once the trial started all mesopredators foraged as expected according to their hunting mode. The active dottyback (*P. fuscus*) was constantly swimming and chasing the prey around the arena, while the ambush

groupers (*C. boenak* and *E. maculatus*) remained inside the shelter occasionally coming out to attack the prey. When in pairs, mesopredators displayed distinctive behaviors: either directly interacting (e.g., through displays and chases) or deliberately avoiding the location of the other mesopredator.

Multiple predator effects

Predator density (additive model)

The effect of mesopredator density on prey survival differed according to the identity of mesopredators paired (Fig. 2; blue lines). For intraspecific mesopredator pairs, prey survival either matched (for *P. fuscus* + *P. fuscus*) or was lower (for ambush predators; *C. boenak* + *C. boenak*; and *E. maculatus* + *E. maculatus*) than expected from the individual contribution of the predators involved. In contrast, each of the three interspecific predator pairs exerted a different effect on prey mortality; the pair *P. fuscus* + *C. boenak* met the expected capture success, the pair *P. fuscus* + *E. maculatus* caused lower prey survival, and the pair *C. boenak* + *E. maculatus* led to greater prey survival than expected.

Predator diversity (substitutive model)

Interspecific pairs of mesopredators killed less prey than intraspecific pairs (Fig. 2; for each interspecific pair, the mean survival is higher than the orange line predicted from the intraspecific pairs). Prey foraged on by *P. fuscus* + *C. boenak* or *C. boenak* + *E. maculatus* had higher survival probabilities than if foraged on by the same mesopredator species, but in intraspecific pairs. The interspecific pair *P. fuscus* + *E. maculatus* was the only case of mixed species where the observed prey survival overlapped with that predicted from the intraspecific pairs *P. fuscus* + *P. fuscus* and *E. maculatus* + *E. maculatus*.

Predator behavior

Mesopredator *P. fuscus* undertook approximately 6 times more strikes than *C. boenak* or *E. maculatus*; however, the capture success rate of the three predators was of a comparable magnitude (Fig. 3). The foraging behavior of the three mesopredators was differentially affected by the presence of intraspecific and interspecific species (Fig. 3). Predation by the active dottyback (*P. fuscus*) remained relatively constant independently of the presence of additional predators of the same or different species (Fig. 3i, iv; $P > 0.05$; Online resource 1). In contrast, the strikes and success of ambush groupers (*C. boenak* and *E. maculatus*) increased significantly when paired with the active species (*C. boenak* + *P. fuscus*, BF in Fig. 3ii and *E. maculatus* + *P. fuscus*, MF in Fig. 3iii, vi; Online resource

Fig. 2 Probability of prey survival (mean \pm 95% confidence intervals) for each predatory treatment. Treatments included single mesopredators (*Pseudochromis fuscus*, F; *Cephalopholis boenak*, B; *Epinephelus maculatus*, M) foraging each on their own and all possible intraspecific (FF, BB, MM) and interspecific pairs (FB, FM, BM). Horizontal lines indicate the expected level of prey survival according to the additive model (continuous black line) or the substitutive model (dashed grey line). *N* per treatment = 10 or 11

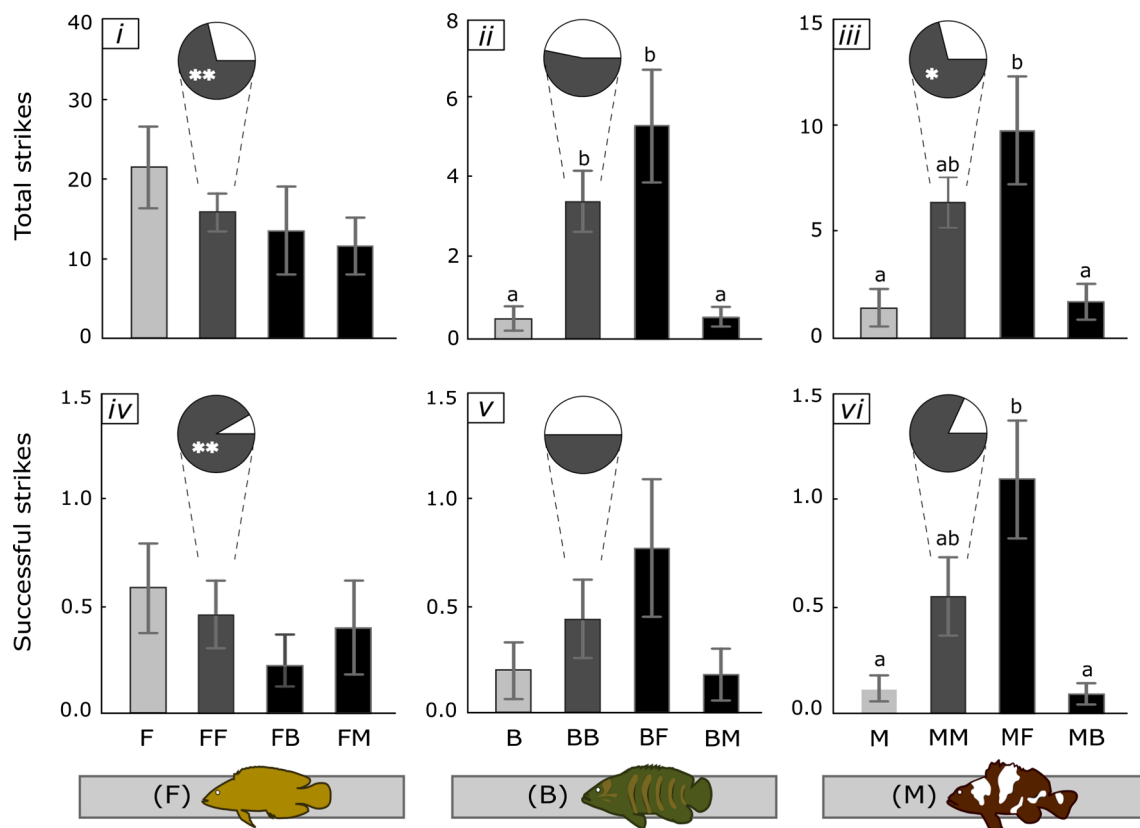
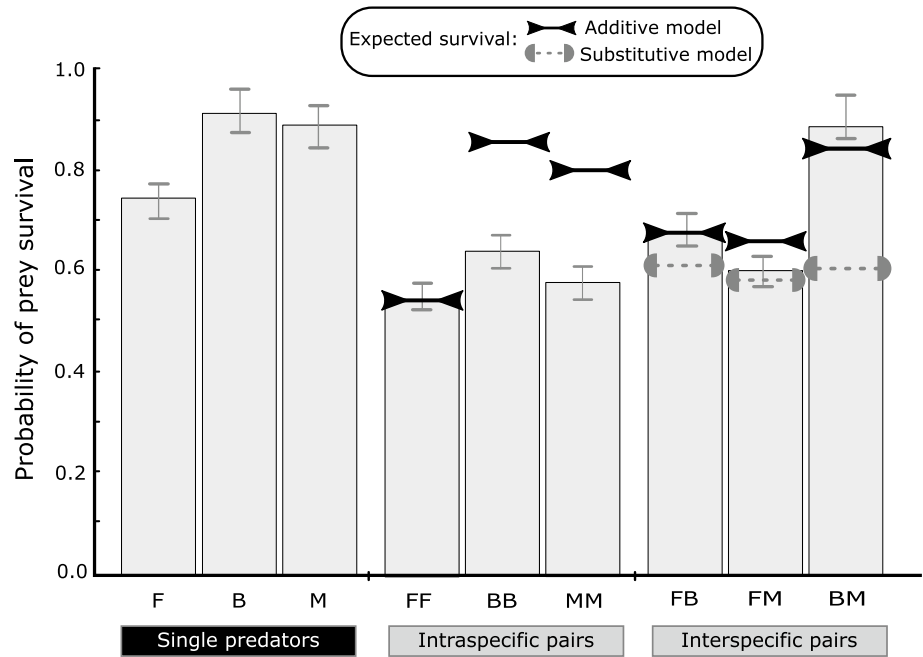


Fig. 3 Number of strikes (mean \pm SE, **i**, **ii**, **iii**) and successful strikes (**iv**, **v**, **vi**) for each mesopredator species *Pseudochromis fuscus* (**i**, **iv**), *Cephalopholis boenak* (**ii**, **v**), or *Epinephelus maculatus* (**iii**, **vi**) when foraging alone (light grey bars), on intraspecific pairs (dark grey bars) or on interspecific pairs (black bars). For intraspecific pairs, bars display the mean of the two individuals while the pie charts on top indicate the proportion of strikes (**i**, **ii**, **iii**) or successful strikes (**iv**, **v**,

vi) that the dominant (grey) and subordinate (white) individuals contributed to the total. Bars with the same lowercase letter correspond to the same homogenous group (Tukey's HSD; $P < 0.05$). Significant differences among the treatments (ANOVAs) were detected on panels **ii**, **iii**, and **vi**. Asterisks inside the pie represent significant differences according to the *t* tests (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, *N* per treatment = 10 or 11) (color figure online)

1) and improved marginally when foraging in intraspecific pairs (*C. boenak* + *C. boenak*, BB in Fig. 3ii and *E. maculatus* + *E. maculatus*, MM in Fig. 3iii, vi; Online resource 1). The only exception to this was the capture success of *C. boenak*, which remained relatively constant across all treatments (Fig. 3v). Interestingly, however, if both ambush species were placed together in an interspecific pair their predatory behavior (strikes and success) was relatively similar to when each one foraged alone (B and BM in Fig. 3ii, v; M and MB in Fig. 3iii, vi; Online resource 1).

Depending on the mesopredator species, dominant and subordinate individuals of intraspecific pairs had different contributions to the total strikes and success achieved by the pair. For example, in intraspecific pairs of *P. fuscus* + *P. fuscus* and *E. maculatus* + *E. maculatus* the dominant individual of the pair exerted most of the strikes and had the most success (pie charts in Fig. 3i, iii, iv, vi; *t* tests, $P < 0.05$; Online resource 2). In contrast, both individuals (dominant and subordinate) of *C. boenak* + *C. boenak* had very similar contributions to prey mortality (pie charts in Fig. 3ii, v; *t* tests, $P > 0.05$). Among the six pairs of mesopredators tested, aggressive interactions (i.e., display, chases, bites) were relatively low except for the intraspecific pair of active dottedbacks (*P. fuscus* + *P. fuscus*) which had significantly higher aggressive interactions than the rest (Fig. 4; Kruskal–Wallis; $H = 27.00$, $P < 0.001$).

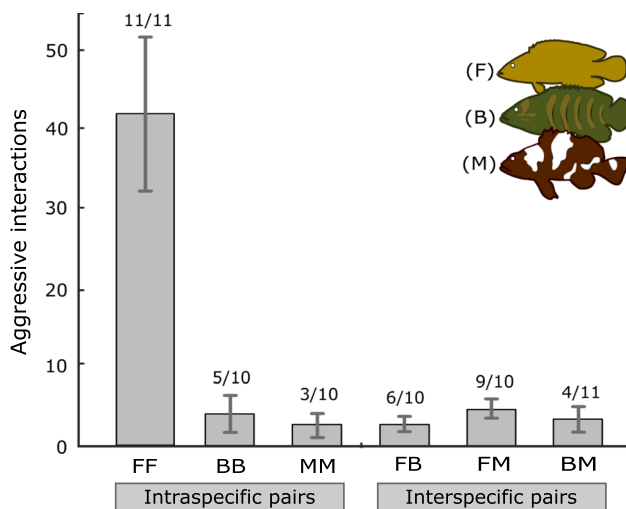


Fig. 4 Number of aggressive interactions (mean \pm SE) including chases, bites and displays recorded for intraspecific and interspecific mesopredator pairs. Mesopredators included *Pseudochromis fuscus* (F), *Cephalopholis boenak* (B), and *Epinephelus maculatus* (M). Numbers over the bars indicate the number of trials in which aggressive interactions occurred (N per treatment = 10 or 11) (color figure online)

Discussion

This study examined the behavioral interactions among three mesopredator species [active predator: *Pseudochromis fuscus* (F); ambush predators: *Cephalopholis boenak* (B), *Epinephelus maculatus* (M)] and their combined lethal effects on six fish prey. We found that although behavioral patterns within mesopredator pairs matched those predicted from their hunting mode, the identity of the mesopredator species determined the strength of any positive or negative interactions, and thus the nature and magnitude of MPEs on prey survival (i.e., risk-enhancing effects: treatments BB, MM and FM; risk-reducing: BM; and linear effects: FF, FB). Given the context-dependency of the predator–predator interactions, none of the mesopredators tested are expected to play substitutable roles on natural coral reefs. This results support recent studies underscoring the importance of predator species identity (e.g., Chalcraft and Reserits 2003; Straub and Snyder 2006; O’Connor et al. 2008; Stallings 2009; Sitvarin and Rypstra 2014), but highlight the complexity of predicting how disturbances to the abundance and richness of the mesopredator assemblage (e.g., mesopredator invasions and extirpations, top-predator loss and mesopredator release) will impact prey populations and ecosystems.

Can MPEs be predicted from predator hunting modes?

In alignment with the framework provided by Schmitz (2007) and empirical evidence from many terrestrial and aquatic systems (e.g., Sokol-Hessner and Schmitz 2002; Nilsson et al. 2008; Ramos and Van Buskirk 2012), this study demonstrates that knowledge of predator hunting mode can help predict the nature of the behavioral interactions among mesopredators (e.g., two active predators will exhibit aggressive behaviors). Nevertheless, our results also show that knowledge of such predator–predator interactions does not necessarily align with the nature or strength of MPEs encountered (e.g., aggressive behaviors of two active predators do not necessarily reduce prey mortality).

Predators with contrasting hunting modes

Predators with contrasting foraging behavior or habitat domain can often facilitate each other’s hunting success if a prey’s response to one predator increases its risk to the other predator (Soluk and Collins 1988; Soluk 1993; Losey and Denno 1998; Van Son and Thiel 2006; Ford and Swearer 2012). Consistent with these studies, we evidenced that predator pairs combining an active (*P. fuscus*) and an ambush mesopredator species (either *C. boenak* or

E. maculatus) tended to enhance the capture success of the ambush grouper. Prey escaping the chase of the active predator was more likely to approach the fixed position where the ambush predator was hiding, thus increasing their encounter and strike rates. Moreover, due to the distraction of the prey by the most imminent threat (the active predator), strikes by the ambush predator were more likely to be successful. Unexpectedly, although these behavioral patterns were consistent for the pairs *P. fuscus* + *C. boenak* and *P. fuscus* + *E. maculatus*, only the pair *P. fuscus* + *E. maculatus* caused higher prey mortalities than expected (risk-enhancing effects). Given that everything else in the experimental treatments remained the same, we hypothesize that the identity of the grouper species determined the strength of the behavioral interactions in the system and whether a positive MPE would occur or not.

Predators with equivalent hunting modes

Theory predicts that two sit-and-wait predators should rarely encounter each other, and hence lead to linear or weak risk-reducing effects (Sih et al. 1998; Schmitz 2007). Behavioral results for the three pairs of ambush predators (*C. boenak* + *C. boenak*, *E. maculatus* + *E. maculatus*, *C. boenak* + *E. maculatus*) revealed that groupers seldom interacted, remained stationary most of the time, and only left their shelter to attack prey. Although such shortage of direct predator–predator interactions (positive or negative) should have led to linear effects on mortality, we found opposing emergent MPEs depending on the nature of the interactions (either intraspecific or interspecific). Ambush predators engaged in intraspecific interactions (*C. boenak* + *C. boenak* and *E. maculatus* + *E. maculatus*) led to risk-enhancing effects, while pairs of different species (*C. boenak* + *E. maculatus*) led to risk-reduction. We hypothesize ambush predators altered each other's foraging behavior through indirect behavioral mechanisms, such as feeding facilitation (positive interaction) and passive interference (negative interaction). For example, given that many groupers are known to live in intraspecific harems (Liu and Sadovy 2005) it is not surprising that the presence of foraging conspecifics seems to encourage or enhance their feeding rates. Similar cases of feeding facilitation have been reported for species such as striped mullets and domestic chickens (Olla and Samet 1974; Keeling and Hurnik 1993). In contrast, we speculate that passive interference (e.g., a predator obstructing prey availability to the other; Maurer 1984) could have limited the killing success of groupers within interspecific pairs. Given that during the first hour of trial both species had levels of foraging activity similar to when hunting alone, interference likely arose later in the trial with the depletion of prey.

An equivalent case of incongruence between the behavioral patterns and the resulting MPE was evident with the pair

of active predators (*P. fuscus* + *P. fuscus*). As expected from their life-history traits, the pair of active predators engaged in very frequent and intense aggressive interactions (i.e., chases, bites, displays). Although such aggressiveness and interference should lead to reduced foraging effort and lower prey mortality (risk-reducing effects; Vance-Chalcraft and Soluk 2005; Griffen and Byers 2006) we instead found linear effects. Detailed behavioral observations revealed that although interference competition limited the foraging activity of the subordinate *P. fuscus*, the dominant individual significantly increased its foraging effort and strike success. This way, although the subordinate *P. fuscus* barely hunted, the expected prey mortality was met because the dominant *P. fuscus* drastically enhanced its foraging activity. Linear effects in which just one predator causes most of the prey mortality are usually detected in multi-species groups combining predator species with inherently distinct impact on prey [e.g., one species has high impact on prey, while the other low; reviewed by Sih et al. (1998)]. However, in this case the linear effects occurred due to the strong interference between conspecific predators with the same potential impact on prey.

Are predators substitutable?

Multiple predator species are often considered functional redundant (substitutable) if their impact on prey populations is similar to the single-species effect (Sih et al. 1998). Our substitutive model suggested that the dottyback *P. fuscus* (F) and the grouper *E. maculatus* (M) are functionally substitutable species given that the mortality caused by their interspecific pair (*P. fuscus* + *E. maculatus*, FM) was inherently similar to the average mortality caused by each species within an intraspecific pair ($FM = (FF/2 + MM/2)$). Despite these species seemed to have substitutable effects in this system, we do not consider mesopredators *P. fuscus* and *E. maculatus* to be functionally redundant because the pairing of each of these species with the grouper *C. boenak* produces different effects. While *P. fuscus* paired with *C. boenak* caused linear-effects on prey mortality, *E. maculatus* paired with *C. boenak* led to risk-reducing effects. Our work suggests that even when two predator species have substitutable effects on prey mortality (Evans 1991; Sokol-Hessner and Schmitz 2002; Straub and Snyder 2006) caution must be taken when assigning them into the same functional group as each one can have vastly diverse effects when interacting with additional species within the predator guild. Several studies already highlight how redundancy among species only holds for certain functional traits and tends to disappear when increasing the range of ecological conditions under consideration (Chalcraft and Reserairis 2003; Tylianakis et al. 2008). For instance, natural prey assemblages are composed by a number of interacting species

with different density and behavior. Thus, without the use of an ecologically relevant diversity of prey many important aspects of predator–prey and predator–predator interactions may be overlooked (e.g., resource complementarity among predator species; Snyder et al. 2006; Griffin et al. 2008). Although simplification is fundamental for the development of theory and the conceptualization of community structure and dynamics (Levin 1992), most evidence suggests functional redundancy seems to be rare in complex ecosystems (Chalcraft and Resetarits 2003).

The role of predator identity

Recent studies underscore the importance of predator identity on natural systems by demonstrating that even phylogenetically and morphologically related fishes (Stallings 2009), salamanders (Chalcraft and Resetarits 2003), crabs (O'Connor et al. 2008), spiders (Sitvarin and Rypstra 2014), and insects (Straub and Snyder 2006) can have substantially different lethal and sub-lethal effects on prey. Our results expand on these findings by showing that similar predators (e.g., from the same family and with common life-history traits) can also differ on the way they interact with each other, and hence on the type of MPEs they can trigger when in multi-species groups. For instance, although *C. boenak* and *E. maculatus* were both ambush groupers with narrow habitat domains, they interacted differently with *P. fuscus* and led to contrasting MPEs. Given the wide variety of traits that can influence the strength of prey suppression by predators (e.g., gape size, growth rate, hunting mode, diet breadth, prey preference, and capture rate) it seems unlikely that true redundancy is common.

The importance of mesopredator species identity suggests that the specific composition of the mesopredator guild (i.e., which species are present and who they interact with) determines the magnitude of predation on prey. This is important as it implies that most changes in the richness and density of mesopredators, through extirpations (e.g., the black-footed ferret *Mustela nigripes* Thorne and Williams 1988); invasions (e.g., the lionfish *Pterois volitans*; Schofield 2009) or lack of top-down control (e.g., mesopredator release of feral cats *Felis catus*; Crooks and Soulé 1999), are likely to alter the dynamics of predator–predator interactions, and hence the MPEs on prey. For instance, the widespread depletion of macro-carnivores from most terrestrial and marine ecosystems is triggering trophic cascades (Estes et al. 2011), whose outcome and magnitude might depend on the behavioral interactions that arise among mesopredator species. If positive mesopredator interactions are favored (e.g., synergies, facilitations), prey populations are likely to experience a dramatic increase of lethal and sub-lethal effects (e.g., enhanced mortality, reduced activity; Losey and Denno 1998; Ford and Swearer 2012). In contrast, if

negative interactions among mesopredators are favored (e.g., interference, intraguild predation) trophic cascades might be attenuated (Finke and Denno 2004; Sanders et al. 2011). Further research should explore how changes to the community composition of terrestrial and aquatic predators could favor one type of interactions or the other. Significant reductions of prey survival may have serious implications for the energy and trophic dynamics of entire food-webs.

As with most additive and substitutive experimental designs, the patterns here described should only be considered in the context of the trials and the study system employed (Sih et al. 1998; Griffen 2006; Schmitz 2007; McCoy et al. 2012). It must be taken into account that (a) MPEs can depend on the specific attributes of the predators (e.g., predator personality; Royauté and Pruitt 2015; Start and Gilbert 2017), the prey (e.g., prey density; Soluk 1993; Griffen 2006), and the habitats involved (e.g., topographic complexity; Swisher et al. 1998; Grabowski et al. 2008), and that (b) predator–predator interactions and predation risk can largely vary across spatial and temporal scales (Sih et al. 2000, Creel and Winnie 2005). For example, interactions among reef mesopredators may be favored during the summer months when many generalist piscivores target newly settled fish (Beukers-Stewart and Jones 2004; Feeney et al. 2012), but may be dampened on a daily basis by the opposing diel patterns of many mesopredators (e.g., dotty-backs mainly forage at midday, while groupers mostly hunt during crepuscular periods; Bosiger and McCormick 2014). Future research should build on our results to address how the MPEs we describe apply to more natural and complex scenarios (e.g., higher diversity of both predators and prey, longer time frames). To achieve this, it is important to use robust experimental designs that enable the disentangling of the roles of predator density, predator species identity and predator species traits. Many MPE studies may have overlooked the importance of predator identity if testing predator hunting modes or habitat domains represented by single predator species (e.g., Schmitz and Suttle 2001; Sokol-Hessner and Schmitz 2002; Nilsson et al. 2008; Ramos and Van Buskirk 2012).

Conclusion

This study demonstrates that knowledge of the identity of the mesopredator species involved, and the behavioral interactions among them is crucial to realistically predicting MPEs in biodiverse communities (Soluk 1993; Chalcraft and Resetarits 2003; Schmitz 2009). While the functional traits of the predators (e.g., hunting mode, habitat domain; Schmitz 2007) can help us understand the nature of the predator–predator interactions within the system, the strength of such interactions, and hence the actual

MPE on prey mortality will depend on the specific identity of the predators involved. In many systems, detailed information on the species composition and the biology, behavior, and ecology of predators may be difficult to obtain. However, this information will greatly contribute to predictive models that refine the mechanistic understanding of how ecosystems will respond to the changes in predator communities.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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