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# Multiple predator effects are modified by search area and prey size

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**Abstract** The strength of trophic and non-trophic interactions in predator–prey dynamics may be modified by predator density/diversity and prey size characteristics. In aquatic environments, multi-dimensional scaling of search areas (water depth and surface area) may mediate interactions among predators, with implications for prey risk. Here, we used a comparative functional response (FR) approach to investigate the effects of search area, predator composition and prey size on the strength of trophic and non-trophic interactions in freshwater habitats. A model system comprising two predatory notonectids (*Anisops breddini* and *Anisops sardeus*) was examined consuming four larval instar prey of *Culex quinquefasciatus*

mosquitoes at nine different arena sizes, consisting of three crossed levels of surface area and water depth. Type II FRs were most common among predator groups, with 2nd instar prey consumed the most overall. Here, *A. sardeus* exhibited significantly higher feeding rates as compared to *A. breddini*, particularly in shallow waters. Non-trophic interactions in conspecific *A. breddini* and heterospecific pairs were mostly negative, indicating reduced prey risk. Further, predator–predator antagonisms were most pronounced in the heterospecific pairs. Strength of trophic and non-trophic interactions is thus dependent on complex interplays between the characteristics of predator–prey participants in combination with environmental heterogeneities.

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## Introduction

Consumer-resource interactions underpin many basic and applied questions in ecology (Rall et al., 2012; Dick et al., 2014; Laverty et al., 2015; Uiterwaal & DeLong, 2018). In this regard, the functional response (FR; Types I, II and III), which describes the relationship between prey densities and predator feeding rates (or other consumer-resource systems), is a central tool in quantifying consumer-resource interactions, ranging from fundamental food web dynamics

(Vucic-Pestic et al., 2010; Barrios-O’Neil et al., 2014), to applied evaluations of biocontrol agents (Uiterwaal & DeLong, 2018; Dalal et al., 2019; Cuthbert et al., 2019, 2020a) and invasive species impacts (Bollache et al., 2008; Lavery et al., 2015, 2017). Discernment of FR Types can inform predictions of ecosystem stabilities. In Type I FRs, the consumption rate increases linearly with resource density up to a threshold, beyond which it remains constant. Type I FRs are relatively uncommon, except for filter-feeders (Jeschke et al., 2004). For hyperbolic Type II FRs, consumption rates are highest at low resource densities, with this form more likely to extirpate resources where they are rare. Type III FRs, on the other hand, are defined by a logistic curve with low resource consumption at low and high prey densities, and high consumption at intermediate densities, possibly indicating the presence of habitat refugia for prey at low densities (Holling, 1959; Murdoch & Oaten, 1975). Type II and III functional responses are usually defined in predator–prey systems (Holling, 1959).

In addition to resource density-dependencies, consumer density-dependencies are also often pervasive. Ecosystems typically comprise multiple consumers sharing the same resources (Barrios-O’Neill et al., 2014; Wasserman et al., 2016a; Cuthbert et al., 2020a). This leads to interactions among consumers, such as predators (i.e., intraguild predation, competition or cooperation), which may drive ‘multiple predator effects’ (MPEs; Polis & Holt, 1992; Sih et al., 1998; Vance-Chalcraft & Soluk, 2005; Schmitz, 2009). Several studies have applied FRs in assessing MPEs across resource density gradients (e.g., Wasserman et al., 2016a; Sentis et al., 2017; Veselý et al., 2019; Cuthbert et al., 2020a). Multiple predator species can broadly interact in three different ways: (1) synergistically, where prey risk is enhanced (Losey & Denno, 1998; Sih et al., 1998); (2) antagonistically, where prey risk is reduced, typically through predator–predator interference (Sih et al., 1998; Vance-Chalcraft & Soluk, 2005); or (3) additively, or independently, where predation rates combine independently to heighten prey risk (Cuthbert et al., 2020a).

Predator–predator interactions can take place in the form of interspecific or intraspecific competition. In interspecific cases, competition occurs between individuals of two different species for the shared resources. On the other hand, intraspecific

competition is when two or more individuals of the same species compete for the use of resources (Wilson, 1975). Studies on food webs generally focus on trophic interactions (i.e., predator–prey interactions), and their strength is often measured in terms of paired predator–prey systems. However, recent studies have suggested the high importance of non-trophic effects (i.e., predator–predator interaction) for predictions of community outcomes and understandings of ecological dynamics (Preisser et al., 2005; McCoy et al., 2012; Okuyama & Bolker, 2012; Hammill et al., 2015; Sentis et al., 2017; Veselý et al., 2019). This is particularly pertinent in aquatic ecosystems, where trait-mediated effects are widespread in the form of waterborne cues, which can influence entire populations of species across their life histories (Peacor & Werner, 2001).

While the implications of predator–predator dynamics for non-trophic interactions have been quantified across both terrestrial and freshwater habitats (Losey & Denno, 1998; Schausberger & Walzer, 2001; Sentis et al., 2017; Veselý et al., 2019), environmental context-dependencies may further modify the strength of these interactions. However, there has been a lack of consideration for the influence of such context-dependencies on multiple predator effects, particularly at varied habitat conditions (but see Hughes & Grabowski, 2006; Sentis et al., 2017; Veselý et al., 2017, 2019). In single predator–prey systems, multiple factors such as structural complexity, temperature and prey size have been shown to combine non-linearly in their influence on the strength of trophic interactions (Sentis et al., 2012; Wasserman et al., 2016b; Kolar et al., 2019; Kreuzinger-Janik et al., 2019), complicating predictions of interaction strengths under changing environments.

Freshwater systems are heterogeneous environments (Urban, 2004; Palmer et al., 2010), with climate warming and increased drought likely to alter the physical characteristics of inland waterbodies and their food webs (Adrian et al., 2009; Amundrud & Srivastava, 2019; Amundrud et al., 2019). In particular, the size of any habitat (or ecosystem) influences the overall food web structure (McHugh et al., 2015). In this context, alterations of water volumes may have direct implications for predator–prey and predator–predator dynamics through changes in the encounter and capture rates with prey, particularly in ephemeral habitats that experience periodic wet

and dry periods (Cuthbert et al., 2021). Reductions in search area associated with lowered water volume may potentially intensify interference among predators in three-dimensional spaces, with implications for predator antagonisms and prey risk. As such, the dimensionality of the consumer search area is a major driver of trophic interaction strengths that drives or limits species co-existence (Pawar et al., 2012). Nevertheless, while the effects of search area on the parameters of single predator–prey FRs have been observed previously (Uiterwaal et al., 2017, 2018; Uiterwaal & DeLong, 2018; Dalal et al., 2019), no studies have yet examined the influence of search area on the strength of non-trophic interactions across varying interspecific predator compositions.

The strength of predator–prey interactions also differs with relative body sizes of predator and prey (Yodzis & Innes, 1992; Emmerson & Raffaelli, 2004; Brose et al., 2006; Brose, 2010). The strongest interactions have been demonstrated at intermediate predator–prey size ratios, as predators are often less efficient at handling resources above or below specific size thresholds (Suchman & Sullivan, 1998; Yamaguchi & Kishida, 2016; Cuthbert et al., 2020b). In a recent study, Dalal et al. (2020a) showed that prey size and search areas interacted to mediate levels of prey risk, with refuge effects in small prey exacerbated in larger habitats. Accordingly, for prey growing fast and reproducing in transient aquatic environments, predation risk may vary spatiotemporally as water volumes and predator composition change quickly. Understanding these context-dependent processes is critical, given that predator–prey interactions underpin ecosystem structure and function (Paine, 1980). Therefore, should search areas shift due to e.g., climate change or other contexts, there could be consequences for wider ecosystem integrity and stability. Moreover, in an applied sense, understanding these interactions could be informative for the selection and deployment of biological control agents, if the resource is a pest, invasive or vector species (Buxton et al., 2020).

Mosquitoes develop rapidly and colonise a vast range of natural and artificial water bodies, including habitats in urban areas (Townroe & Callaghan, 2014) where they can be important prey for aquatic predators. Lentic water bodies are also breeding habitats of aquatic insect orders such as Hemiptera, Odonata, and Coleoptera that often dominate higher

trophic levels in the absence of higher-order vertebrates (Batzer & Wissinger, 1996; Dalal & Gupta, 2016). These groups structure aquatic communities via trait- and density-mediated trophic interactions in both natural and artificial ephemeral systems (Peckarsky et al., 1993; Eubanks & Denno, 2001). In particular, notonectids (Hemiptera: Notonectidae; commonly called “backswimmers”) are voracious predators that often occupy the highest trophic level in ephemeral aquatic ecosystems where mosquitoes successfully colonise (Blaustein, 1998; Wasserman et al., 2016a; Dalal & Gupta, 2018). Their diet includes all four larval instars of mosquitoes, but predation efficiencies and preferences vary according to the ontogenic stages of their prey (Dalal et al., 2019, 2020a).

With a lack of studies into multiple predator effects in aquatic systems where search areas can influence the trophic/non-trophic interaction strengths across varied predator combinations and prey stages, the present study therefore aims to unravel the context-dependencies of predator–predator and predator–prey combinations under different prey sizes. We used a manipulated search area comprising three different, crossed surface areas and water depths. This study will address the ecological complexities and aquatic environmental heterogeneities which underpin trophic and non-trophic interaction strengths. Specifically, we used comparative FRs to quantify the strength of non-trophic interactions between conspecific and heterospecific pairs of two common notonectid species, *Anisops breddini* Kirkaldy, 1901 (Heteroptera: Notonectidae) and *A. sardeus* Herrich-Schaeffer, 1849, and larval *Culex quinquefasciatus* Say, 1823 (Diptera: Culicidae). *C. quinquefasciatus* is a member of *C. pipiens* complex that exhibits a widespread distribution and breeds in diverse aquatic systems, including wetlands, rice fields and artificial containers (Miyagi et al., 1992; Jacob et al., 2006; Okiwelu & Noutcha, 2012). We experimentally manipulated search area by systematically altering surface areas and depths of aquaria and examined emergent effects of different predator densities and diversities for mosquito prey risk. We combined experimental and modelling approaches to determine whether the strength of trophic and non-trophic interactions relate to water volumes, prey size and the composition of predator assemblages. We hypothesised that with increasing search areas and mosquito prey instars, the trophic interaction (predation risk) decreases and non-trophic

interaction increases. We also hypothesised that heterospecific predator pairs show different predatory behaviour (i.e., additive, synergistic or antagonistic) than conspecific pairs in varying search areas.

## Materials and methods

### Animal collection and husbandry

Size-matched notonectid predators, adult *A. breddini* (mean length  $\pm$  SE:  $7.06 \pm 0.04$  mm) and *A. sardeus* ( $7.27 \pm 0.05$  mm) were collected from fishery ponds in Irongmara, Cachar, Assam, India ( $24^{\circ}41'15.78''\text{N}$ ,  $92^{\circ}45'12.21''\text{E}$ ) during the summer-monsoon season of 2017 by pulling a kick net (mesh size 60  $\mu\text{m}$ ) through the water column. Notonectids were transported in source water to a laboratory in the Department of Ecology and Environmental Science, Assam University, Silchar campus. This laboratory was maintained at  $30^{\circ}\text{C}$  ( $\pm 2^{\circ}\text{C}$ ) and under a 12:12 h light:dark photoperiod. The species were acclimatized separately in glass aquaria holding 25 L dechlorinated tap water with continuous aeration for at least one week prior to experimentation. Aquaria water was changed every 10 days and notonectids were fed ad libitum with 3rd and 4th instar mosquito larvae and all sizes of chironomid larvae.

Egg rafts of *C. quinquefasciatus* prey were collected on-site by sampling container habitats filled with a jaggery (i.e., organic cane sugar; Arya Farm Products Pvt. Ltd, Bengaluru, India) and water mixture in outdoor locations. The mosquito egg rafts were transferred and reared in the same laboratory as notonectids (see before), where upon hatching, larvae were fed ad libitum with crushed jaggery in order to obtain the four instar stages (mean length  $\pm$  SE: 1st instar,  $1.10 \pm 0.02$  mm; 2nd instar,  $2.22 \pm 0.04$  mm; 3rd instar,  $3.97 \pm 0.02$  mm; 4th instar,  $4.91 \pm 0.05$  mm).

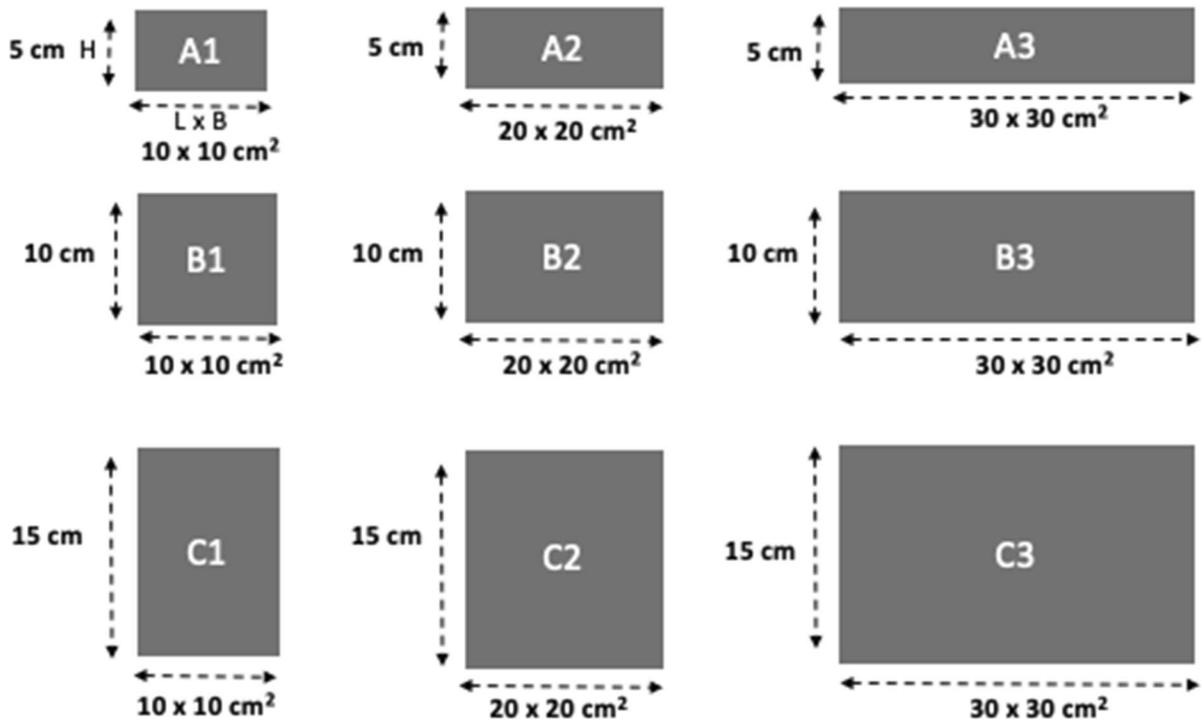
### Experimental design

Feeding trials were conducted in nine different types of glass aquaria, fully crossing three different levels of surface area [length ( $L$ )  $\times$  width ( $B$ ): 10, 20 and 30  $\text{cm}^2$ ] and three different levels of water depths (5, 10 and 15 cm) (Fig. 1). Water depth levels were selected based on natural observations and surface

area levels were selected based on feasibility and laboratory space. Here, five predator treatments consisted of either individuals of each species, conspecific pairs or heterospecific pairs (i.e., individual: 1 *A. breddini* or 1 *A. sardeus*; conspecific: 2 *A. breddini* or 2 *A. sardeus*; and heterospecific: 1 *A. breddini* + 1 *A. sardeus*), which were starved for 24 h to standardize hunger prior to experimental trials. Individual or paired predator species were separately provided with four different larval instars of *C. quinquefasciatus* under six prey densities (5, 10, 25, 50, 75, 100). Controls consisted of prey without predators at each glass aquaria size, instar stage and prey density ( $n=3$  per experimental group). Fresh mosquito larvae were used in each experimental trial. Remaining excess mosquito larvae after the experiment were used as a food for the reared predators in the aquarium. We thus employed a factorial “ $3 \times 3 \times 5 \times 4 \times 6$ ” experimental design to discern the effects of “surface area”, “water depth”, “predator treatment”, “prey instar” and “prey density”, respectively, on notonectid-mosquito interaction strengths. We conducted 3 replicates for each combination of these treatments leading to a total of 3240 trials, excluding predator-free control trials. Individual notonectids were introduced following the addition of prey to each arena and were allowed to feed for 24 h. The predators were then removed and numbers of remaining live prey were counted to quantify numbers killed. Experimental trials were fully randomised according to batches of experimental treatment groups (54 trials  $\text{day}^{-1}$ ). Out of 1944 multiple predator trials (3 predator pairs  $\times$  3 surface area  $\times$  3 water depth  $\times$  4 prey instar  $\times$  6 prey densities  $\times$  3 experimental trials = 1944), 41 trials displayed intraguild predation, and these replicates were repeated and replaced.

### Prey consumption

Prey killed in individual predator trials (i.e., single *A. breddini* or single *A. sardeus*) were analysed with respect to “surface area”, “water depth”, “predator” and “prey instar”, along with their interactions, using a generalised linear model (GLM) assuming a quasi-Poisson family to correct for overdispersion in the R base ‘stats’ package. “Prey density” was also included as an individual continuous variable in the GLM, owing to its importance in FR derivations. Main effect sizes and significance levels were



**Fig. 1** Diagrammatic illustration of nine different sized containers used in the functional response and multiple predator effect experiment. The three different surface areas are coded

1, 2 and 3, while the three different depths are A, B and C. Here,  $L$  and  $B$  are the length and widths of the aquarium, and  $H$  is the depth of the water

derived through  $F$ -tests with Type III sums of squares using the ‘car’ package in R (Fox & Weisberg, 2018). Effects throughout are reported from ‘full models’, and therefore are over and above the other terms included in the models. *Post-hoc* Tukey tests were conducted for the significance of pairwise comparisons using the ‘emmeans’ R package (Lenth, 2018).

### Functional responses (FRs)

In the present study, FRs were interpreted “phenomenologically” rather than “mechanistically” in order to compare different factorial treatments under matched experimental conditions (Jeschke et al., 2002; Dick et al., 2014). Logistic regression of the proportion of prey (from 1st to 4th instar) killed as a function of “prey density” (continuous predictor) was used to categorise FR types across each experimental group (i.e., for both single and multiple predators) under the three levels of surface area and water depth (Juliano, 2001; Pritchard et al., 2017). Here, a significantly

negative first-order term indicates a Type II FR, while a significantly positive first-order term followed by a significantly negative second order term indicates a Type III FR. Conversely, a non-significant first and second order term is considered to be a Type I FR. A generalised FR model to account for the non-replacement experimental design (i.e., prey depletion) was computed (Rogers, 1972; Real, 1977; Pritchard et al., 2017):

$$N_e = N_0(1 - \exp(bN_0^q(hN_e - T))), \quad (1)$$

where  $b$  is the attack or capture rate, which, combined with the scaling exponent  $q$ , gives the density-dependent capture rate ( $bN_0^q$ ),  $h$  is the handling time,  $T$  is the total experimental time,  $N_0$  is the initial prey density and  $N_e$  is the number of prey eaten. Here,  $q$  was optimized to provide a means to examine fits for categorical or flexible Type II or III forms. We used maximum likelihood estimation for model fitting (Bolker, 2010). Where FR types were equivocal, i.e., when evidence for a particular FR Type is not

indicated through logistic regression, we compared candidate models using Akaike's Information Criterion (AIC) (with different scaling components) and selected the models that minimised information loss (Wasserman et al., 2016c). Following model selection, we non-parametrically bootstrapped FRs 2000 times to produce 95% confidence intervals (CIs) for each experimental treatment combination across prey densities. The bootstrapped FR parameters (i.e., capture rate and handling time) and scaling exponents were analysed along with their interactions against the predictors using analysis of variance (ANOVA). Functional response analyses were conducted in the 'frair' package in R (Pritchard et al., 2017) and ANOVA in the base 'stats' package in R.

### Species interaction strength (IS)

Species interaction strength ( $IS$ ) is the sum of both trophic ( $IS_T$ ) and non-trophic ( $IS_{NT}$ ) interaction strengths. Here,  $IS(C,R)$  can be expressed as the total flux from resource (R) to consumers (C), measured as the relative change in resource density after the introduction of the consumers (Berlow et al., 1999):

$$IS(C, R) = 1 - \frac{N_{RIC}}{N_R}, \quad (2)$$

where  $N_R$  and  $N_{RIC}$  are observed densities of a resource (R) in the absence and presence of consumers (C), respectively.  $IS$  was calculated using Eq. 2 for each experimental trial of both conspecific and heterospecific pairs, which gives the proportion of prey killed in each trial. The effects of "surface area", "water depth", "predator pair" (both con- and heterospecific combinations) and "prey instar", and their interactions on  $IS$  were analysed using a binomial generalised linear model (GLM) with a 'logit link' function. "Prey density" (continuous predictor) was included as a covariate in the GLM. Main effect sizes and significance levels were derived through Chi-squared test with Type III sums of squares using 'car' package in R (Fox & Weisberg, 2018). Post-hoc Tukey tests were then conducted for the significance of pairwise comparisons using the 'emmeans' R package (Lenth, 2018).

We statistically compared the  $IS$  and  $IS_T$  values using a binomial GLM, accounting  $IS_T$  as an offset. A significant positive or negative intercept value

indicates  $IS_T$  values underestimate or overestimate  $IS$ , respectively.

### Multiple predator effects (MPEs)

To detect emergent MPEs, we visually compared CIs of observed FRs (see before) with those of predicted FRs. Predicted FRs were generated using a population-dynamic model of prey depletion over time using individual predator FR parameter estimates (i.e., capture rate and handling time) (McCoy et al., 2012; Sentsis & Boukal, 2018):

$$\frac{dN}{dt} = - \sum_{i=1}^n f_i(N)P_i, \quad (3)$$

where  $N$  is the prey density,  $P_i$  ( $i = 1, 2, \dots, n$ ) are the population densities of predators  $i$  and  $f_i(N)$  is the FR of predator  $i$ . To generate predictions of expected prey survival in both conspecific and heterospecific predator trials across all prey instars and search area, initial values of  $N_0$  and  $P_i$  ( $i = 1, 2, \dots, n$ ) were set at the experimental initial prey and predator densities. The population-dynamic model (Eq. 3) was then integrated over the experimental time (i.e., 24 h) for each predator treatment and prey density to predict prey survival. Following Sentsis et al. (2017), the 95% CIs around the predictions were estimated using global sensitivity analysis that used the CIs of each FR parameter estimate along with their variance-covariance matrix (covariance is assumed to be zero when not known) to generate a number of random parameter sets using a Latin hypercube sampling algorithm (Soetaert & Petzoldt, 2010). Equation 3 was then integrated over time (24 h) for each parameter set and expected prey survival was calculated using the 'sensRange' function in the R package 'FME' (Soetaert & Petzoldt, 2010). These simulations provided the 2.5% and the 97.5% quantiles of the survival values that were used as the 95% CIs around the predicted consumption values.

The expected trophic interaction strengths  $IS_T$  were also calculated for each predator pair by supplementing Eq. 2 with the predicted number of surviving prey from Eq. 3. Here, we can distinguish  $IS_T$  from  $IS$  as  $IS$  values were calculated from observed consumption values of con- and heterospecific predator pairs, whereas  $IS_T$  values were calculated from predictions

not including non-trophic interactions among multiple predators.

#### Non-trophic species interaction strength ( $IS_{NT}$ )

Non-trophic interaction strengths ( $IS_{NT}$ ) among the competing predators towards the shared prey were calculated by deducting  $IS_T$  (i.e., mean predicted proportion of prey eaten) from  $IS$  (i.e., observed experimentally). That is, negative  $IS_{NT}$  would confer antagonistic predator–predator interactions (and vice-versa), as predictions in the absence of non-trophic effects would be higher than experimental observations that included these interactions. The effects of “surface area”, “water depth”, “predator pair”, and “prey instar”, along with their interactions, on  $IS_{NT}$  were then assessed using an analysis of covariance (ANCOVA). “Prey density” (continuous predictor) was included as the covariate. As residuals suggested a hump-shaped effect of prey density, we also included a quadratic term for prey density. We compared the models with quadratic and linear prey density effects using an analysis of deviance and found that the best model was the one with a quadratic prey density effect. *Post-hoc* comparisons were then computed as mentioned above. All the statistical analyses were computed in R version 3.5.2 (R Core Team, 2020).

## Results

### Individual raw consumption

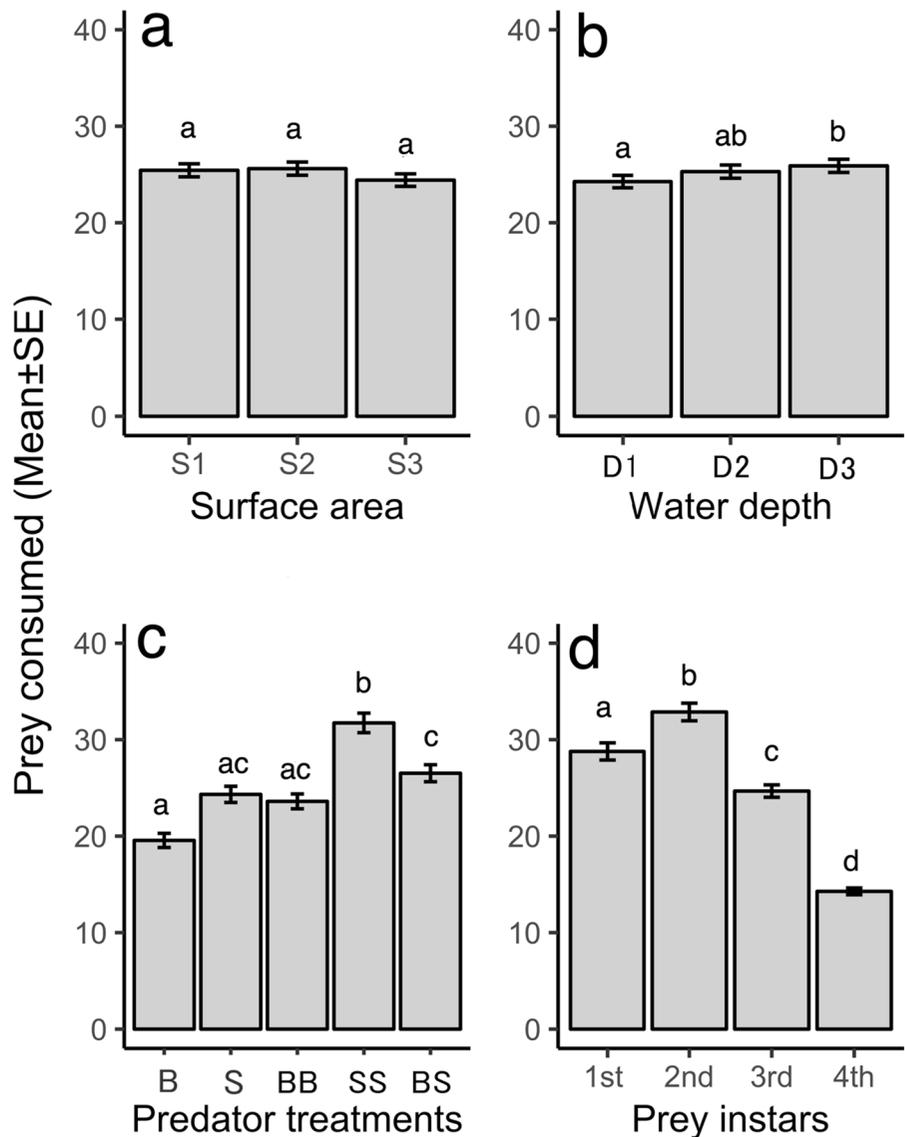
Mosquito prey survival exceeded 99% in predator-free controls across all arena sizes and prey instars. Consumption data thus were not adjusted for background mortality rates. Overall, the raw consumption was not significantly different among the surface area levels, but significantly differed among the water depth levels ( $P < 0.01$ , Table S1; Fig. 2a, b). Raw consumption by individual notonectids increased significantly with increasing prey density overall (Table S1). A significant three-way “surface area  $\times$  water depth  $\times$  predator” interaction indicated that differential predator killing efficiencies were dependent on search areas (Table S1). Under low water depths, consumption by *A. sardeus* was significantly greater than *A. breddini*

at small and large surface areas (both  $P < 0.05$ ), but not at the medium surface area ( $P > 0.05$ ). Under intermediate water depths, consumption of *A. sardeus* was significantly more than *A. breddini* only at the small surface area ( $P < 0.001$ ). Under high water depths, no significant differences in consumption between the predator species were observed among the three surface areas (all  $P > 0.05$ ). Thus, predatory performance of individual *A. sardeus* was generally most enhanced relative to *A. breddini* in shallow waters (Table S1; Figs. 2c, S1–S2). Among the five predator treatments, highest mean prey consumption was observed in conspecific *A. sardeus* followed by heterospecific combinations, while lowest mean consumption was observed in individual *A. breddini* (Fig. 2c). Raw consumption of mosquitoes was significantly affected by prey instar stage (Table S1; Fig. 2d), with 2nd instar prey being consumed significantly more than all other instar stages (all  $P < 0.001$ ). This was followed by 1st instar prey, which were significantly consumed more than either 3rd or 4th instar prey (both  $P < 0.001$ ), while 4th instar prey was consumed least (all  $P < 0.001$ ).

### Functional response (FRs) overall trends

Type II FRs were most prevalent (137 out of 180 FR types), followed by Type III FRs (43 out of 180 FR types) across both individual and paired predator treatments. Type III FRs were observed mostly in consumption of 1st instar mosquito prey, followed by 3rd and 2nd instar stages (Table S2). Individual FRs revealed *A. sardeus* consumed more prey than *A. breddini* at lower and intermediate prey densities, particularly at low to medium search areas. Whereas, at higher search areas no such differences were observed (Fig. 3). Individual and multiple predator FR parameters (i.e., capture rate, handling time) of both *A. breddini* and *A. sardeus* were dependent on search area (i.e., surface area and water depth) and mosquito prey instar stages ( $P < 0.001$ , Tables S3 and S4; Figs S1–S8). Mean capture rates decreased as surface area and water depth increased, while handling time did so marginally overall (Fig. 4a, b, e, f). For predator treatments, higher capture rates and shorter handling times were typically displayed by multiple predators compared to individual predators. Here, conspecific *A. sardeus* displayed highest

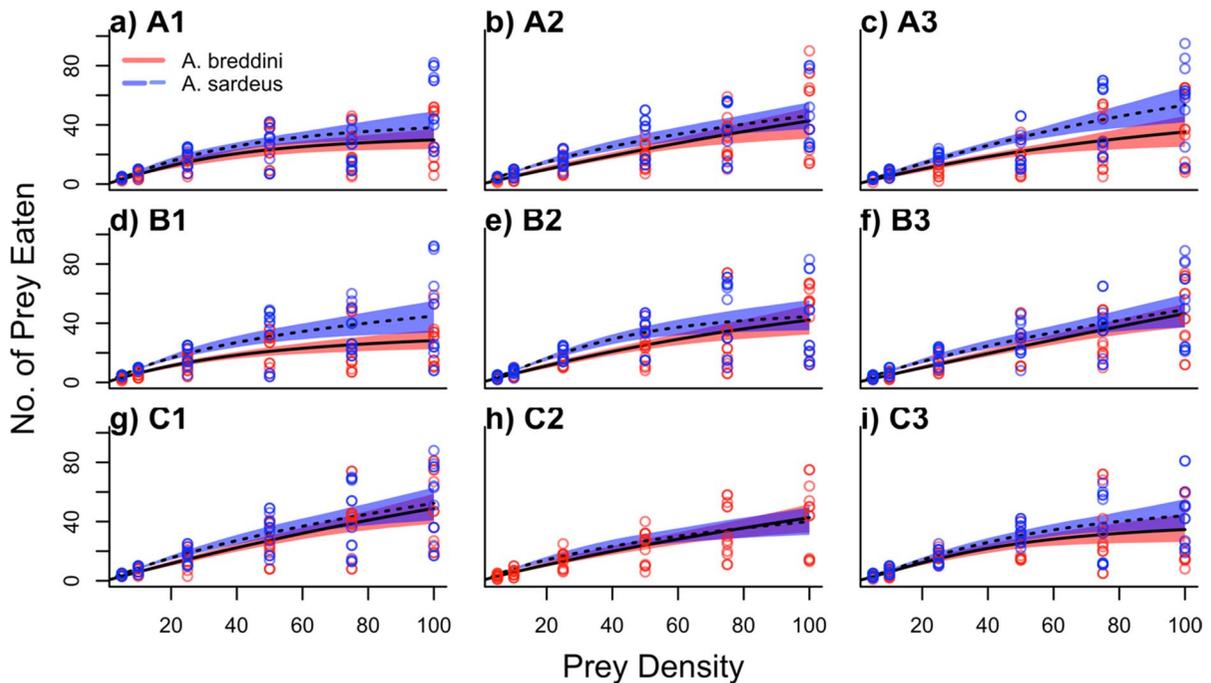
**Fig. 2** Mosquito prey consumed (Mean  $\pm$  SE) across **a** surface area (S1 = small, S2 = medium, S3 = large), **b** water depth (D1 = low, D2 = intermediate, D3 = high), **c** predator treatments (B = individual *Anisops breddini*, S = *A. sardeus*, BB = conspecific *A. breddini*, SS = conspecific *A. sardeus*, BS = heterospecific *A. breddini* + *A. sardeus*) and **d** prey instars (1st instar, 2nd instar, 3rd instar and 4th instar). Bars with different letters are significantly different from one another (at least  $P \leq 0.05$ )



capture rates and lowest handling times (Fig. 4c & g). Predators also showed the highest mean capture rate for 3rd instar prey and lowest for 1st instar prey, whereas mean handling time was highest for 4th instar prey and lowest for 1st instar (Table S2; Fig. 4d, h). Mean scaling exponents showed varied results across the four predictors (Fig. 4i–l). Differences in bootstrapped capture rates, handling times and scaling exponents were statistically significant across all four predictors (surface area, water depth, predator combinations and prey instars) and their interactions (Table S3–S5).

#### Multiple predator effects (MPEs)

The strength and nature of MPEs differed across search areas, predator pairings, and prey sizes (Figs. S3–S8). For conspecific *A. breddini*, antagonistic MPEs were observed mainly in trials with 1st (7 out of 9 arena types) and 2nd (8 out of 9 arena types) instar prey, followed by 3rd (4 out of 9 arena types) and 4th (1 out of 9 arena types) instar prey, where CIs of predicted FRs were significantly higher than those observed. The remaining treatments exhibited additive MPEs; however, one synergistic MPE was observed for consumption of 3rd instar prey under



**Fig. 3** Functional responses of individual *Anisops breddini* and *A. sardeus* towards *Culex quinquefasciatus* larvae across water depth and search area variations. The three increasing surface areas are coded 1 (a, d, g), 2 (b, e, h) and 3 (c, f, i),

while the three increasing depths are A (a, b, c), B (d, e, f) and C (g, h, i). The shaded areas are 95% confidence intervals from bootstrapping ( $n=2000$ ) and the points are raw observations

intermediate surface areas and depths (Fig S4). For conspecific *A. sardeus*, antagonistic MPEs were similarly observed for consumption of 1st (8 out of 9 arena types), 2nd (2 out of 9 arena types), 3rd (5 out of 9 arena types) and then 4th (1 out of 9 arena types) instar prey. The remaining arenas exhibited additive MPEs, while emergent synergistic effect was observed only once (for consumption of 1st instar prey at the medium surface area and high water depth arena) (Figs. S5–S6). For heterospecific notonectid pairs, emergent antagonistic MPEs were mainly observed in trials with 1st (8 out of 9 arena types), 2nd (8 out of 9 arena types) and 3rd (7 out of 9 arena types) instar prey, but rarely with 4th (3 out of 9 arena types) instar prey. The remaining heterospecific MPEs were additive in nature (Figs. S7–S8).

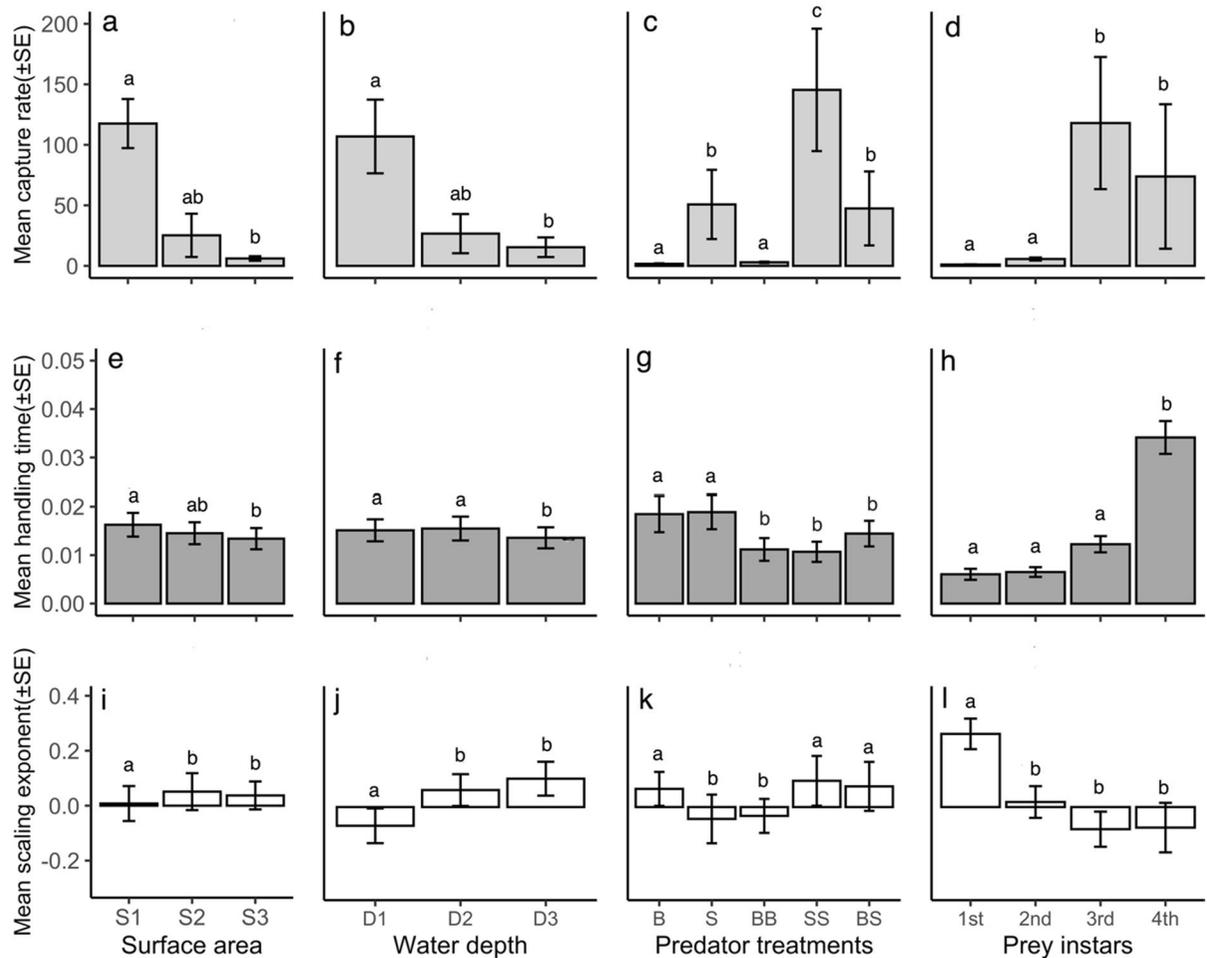
#### Species interaction strength ( $IS$ )

The model selection indicated that  $IS$  in treatments with multiple predators was not significantly influenced by surface area or water depth (Table 1). The

best candidate model indicated that  $IS$  significantly differed among predator pairs and prey instars, and significantly decreased with increasing prey density overall (Table 1; Figs. S9–S14). The strongest  $IS$  was significantly exhibited in conspecific *A. sardeus* pairs, followed by heterospecific notonectid pairs, while the significantly weakest  $IS$  was observed in conspecific *A. breddini* pairs irrespective of arena type (Fig. 5, all  $P < 0.01$ ). Overall, the significantly highest  $IS$  was observed towards 2nd instar prey compared to other instars (Fig. 5, all  $P < 0.01$ ). This was followed by 3rd instar prey which had significantly higher  $IS$  than 4th instar prey ( $P < 0.001$ ), but was, in turn, not significantly different from 1st instar prey ( $P > 0.05$ ). The lowest  $IS$  was significantly observed for consumption of 4th instar mosquito larvae (all  $P < 0.01$ ) (Table 1; Fig. 5).

#### Non-trophic interaction strength ( $IS_{NT}$ )

The best candidate model indicated significant three-way “surface area  $\times$  water depth  $\times$  prey instar” and



**Fig. 4** Mean ( $\pm$ SE) bootstrapped parameters of functional response i.e., capture rate (light grey bar; **a–d**) and handling time (dark grey bar; **e–h**) along with scaling exponent (white bar; **i–l**) towards three surface area (**a**, **e**, **i**), three water depth (**b**, **f**, **j**), five predator treatments (**c**, **g**, **k**) and prey instars (**d**,

**h**, **l**). Note: B=individual *Anisops breddini*, S=individual *A. sardeus*, BB=conspecific *A. breddini*, SS=conspecific *A. sardeus*, BS=heterospecific *A. breddini*+*A. sardeus*. Bars with different letters above are significantly different from one another (at least  $P \leq 0.05$ )

“water depth  $\times$  predator pair  $\times$  prey instar” interactions, with the effects of search area components dependent on the composition of predator pairs and prey instar stages (Table 2). Additionally,  $IS_{NT}$  showed a unimodal dependence on mosquito prey density, indicating higher antagonism at intermediate prey density while weaker antagonism was observed at low and high prey densities, particularly for *A. sardeus* (Table 2). For conspecific *A. breddini*, antagonism was mostly observed at intermediate and high prey density in consumption of 1st and 2nd instar prey (Fig. S15). For consumption of 3rd instar prey,

conspecific pairs of *A. breddini* showed antagonism either in intermediate or high prey densities, particularly in low and high water depth arenas. Conversely, they showed synergistic behaviour in medium surface area and medium water depth arena (Fig. S16i–ix). On the other hand, consumption of 4th instar prey showed a lack of  $IS_{NT}$  in most cases (Fig. S16x–xviii). Unlike *A. breddini*, conspecific pairs of *A. sardeus* did not display clear indication of antagonism in consumption of all four prey instars (Fig. S17 and S18). In heterospecific combinations of *A. breddini* and *A. sardeus*, antagonistic behaviour was observed either

**Table 1** Analysis of deviance from binomial generalised linear model (GLM) considering species interaction strength ( $IS$ ) with respect to ‘surface area’, ‘water depth’, ‘predator pair’ and ‘prey instar’, and their interactions, with ‘prey density’ as a continuous covariate

Predictors	Df	Deviance	Resid. Df	Resid. dev	$Pr(> Chi)$	Sig
Surface area	2	1.889	643	197.144	0.3889	–
Water depth	2	0.096	645	199.033	0.9532	–
Predator pair	2	17.089	641	180.055	0.0001	***
Prey instar	3	35.253	638	144.802	1.08E–07	***
Prey density	1	46.553	637	98.249	8.92E–12	***
Surface area:water depth	4	2.848	633	95.401	0.5835	–
Surface area:predator pair	4	0.29	625	94.843	0.9904	–
Water depth:predator pair	4	0.268	629	95.133	0.9917	–
Surface area:prey instar	6	0.467	613	93.725	0.9982	–
Water depth:prey instar	6	0.651	619	94.192	0.9954	–
Predator pair:prey instar	6	0.874	607	92.851	0.9899	–
Surface area:water depth:predator pair	8	1.428	599	91.423	0.9938	–
Surface area:water depth:prey instar	12	0.757	587	90.666	0.9999	–
Surface area:predator pair:prey instar	12	0.894	563	87.642	0.9999	–
Water depth:predator pair:prey instar	12	2.13	575	88.537	0.9991	–
Surface area:water depth:predator pair:prey instar	24	2.445	539	85.197	1	–
NULL	647	199.129				

Significance levels: \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$

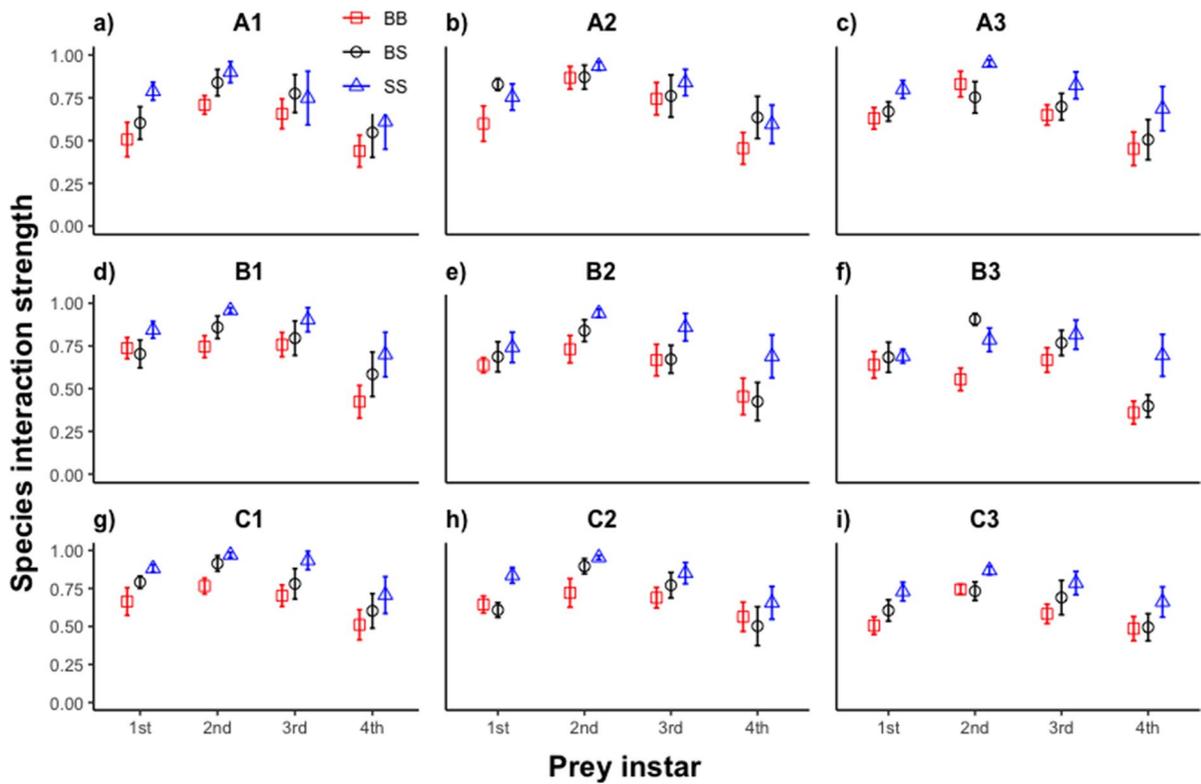
at intermediate or high prey densities in all four prey instars (Figs. S19 and S20). Overall, heterospecific notonectid pairs displayed significantly lowest  $IS_{NT}$  and thus the greatest antagonistic effects as compared to either conspecific *A. breddini* or *A. sardeus* (all  $P < 0.01$ ). Here, with medium surface areas and water depths, significantly lower  $IS_{NT}$  (i.e., higher antagonism) was observed as compared to other search areas. On the other hand, conspecific *A. sardeus* displayed significantly higher  $IS_{NT}$ , indicating synergistic effect as compared to the rest of the predator pairs (all  $P < 0.001$ ) (Fig. 6). Under low and high surface areas or water depths, both conspecific *A. breddini* and heterospecific notonectid pairs displayed significantly higher antagonism than conspecific *A. sardeus* (all  $P < 0.001$ ; Fig. 6).

## Discussion

Understanding the effects of search area, predator composition and prey size effects on species interactions is critical to predict community structure and dynamics (Duffy et al., 2007; Sentis et al., 2014; Dalal et al., 2019, 2020a, b). However, little is known

about how the search area and prey size interact to influence the strength of trophic and non-trophic interactions, particularly in aquatic ecosystems characterised by dynamic water volume and colonisation processes (Sentis et al., 2017; Dalal et al., 2019, 2020b). In three-dimensional aquatic ecosystems, alterations to water volume may scale non-linearly according to surface area and water depth, necessitating understandings for biotic interactions within and between these search area gradients. The present study demonstrates the implications of changes in search area for interaction strengths in an aquatic predator–prey system. In particular, the strength of non-trophic interactions conferred among multiple predators were dependent on search area scaling, predator composition and prey size, indicating complex interactions mediating predatory effects.

Differential *per capita* predator performance was observed in the present study, with superior feeding rates of *A. sardeus* relative to *A. breddini* dependent on search area characteristics. Shallow waters facilitated significantly greater feeding rates by *A. sardeus* compared to *A. breddini*, however these differences became less clear as water depth increased. While previous research has identified *A. sardeus*



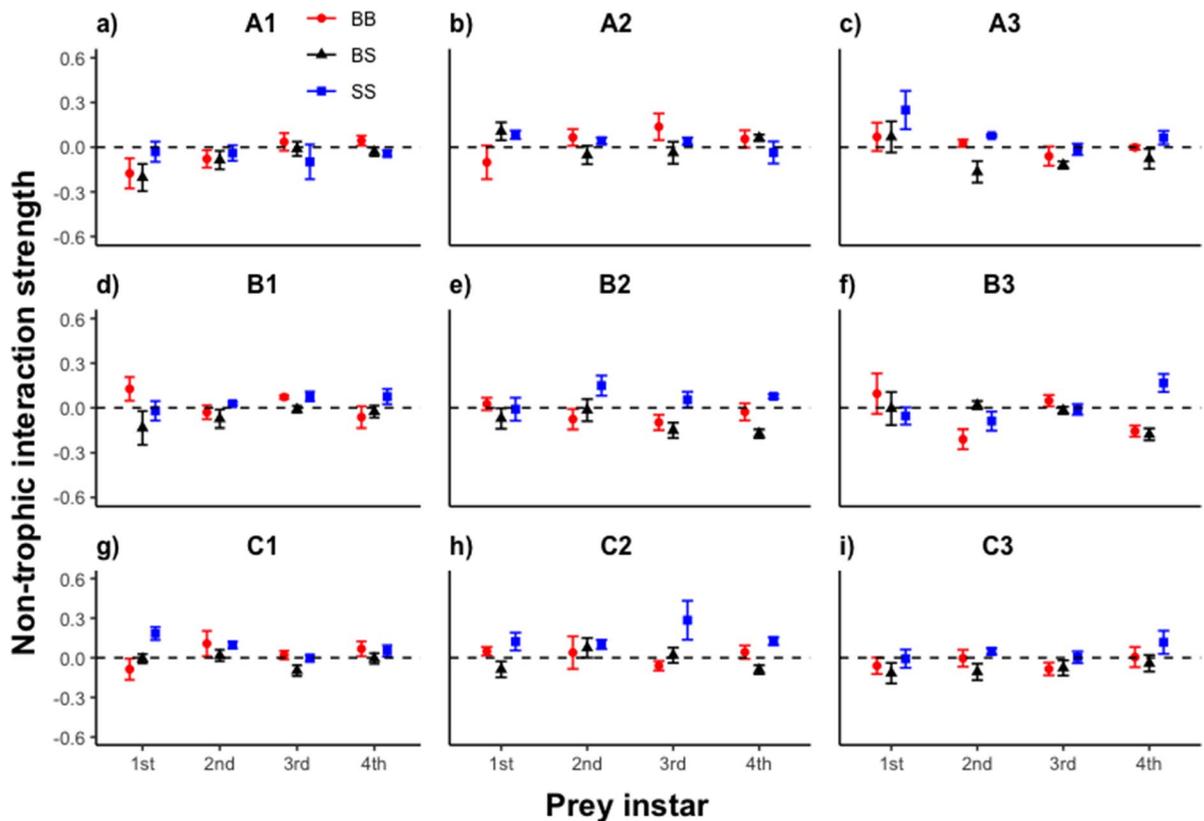
**Fig. 5** Mean ( $\pm$ SE) interaction strength (*IS*) among predator pairs (*BB*—conspecific *Anisops breddini*; *BS*—1 *Anisops breddini*+1 *Anisops sardeus*; *SS*—conspecific *Anisops sardeus*)

towards four prey instars (1st to 4th) of *Culex quinquefasciatus* larvae across three surface areas (1—**a, d, g**; 2—**b, e, h**; 3—**c, f, i**) and water depths (**A**—**a–c**; **B**—**d–f**; **C**—**g–i**)

**Table 2** Analysis of covariance (ANCOVA) considering non-trophic interaction strength ( $IS_{NT}$ ) with respect to ‘surface area’, ‘water depth’, ‘predator pair’ and ‘prey instar’, and their interactions, with ‘prey density’ was included as a continuous covariable

Predictors	Sum Sq	Df	F value	Pr(>F)	Sig.
Surface area	0.1512	2	3.3675	0.0352	*
Water depth	0.1501	2	3.342	3.61E-02	*
Predator pair	1.1859	2	26.4108	1.14E-11	***
Prey instar	0.0055	3	0.0813	0.9702	–
Prey density	0.9133	1	40.6806	3.86E-10	***
Surface area:water depth	0.4539	4	5.054	0.0005	***
Surface area:predator pair	0.0851	4	0.9476	0.4360	–
Water depth:predator pair	0.1083	4	1.2057	0.3073	–
Surface area:prey instar	0.2587	6	1.9206	0.0755	–
Water depth:prey instar	0.149	6	1.1059	0.3575	–
Predator pair:prey instar	0.0427	6	0.317	0.9281	–
Surface area:water depth:predator pair	0.2875	8	1.6009	0.1215	–
Surface area:water depth:prey instar	0.6301	12	2.339	0.0062	**
Surface area:predator pair:prey instar	0.3443	12	1.2779	0.2274	–
Water depth:predator pair:prey instar	1.0189	12	3.782	1.54E-05	***
Surface area:water depth:predator pair:prey instar	0.6299	24	1.1691	0.2639	–
Residuals	12.1008	539			

Here, ‘prey density’ was tested with quadratic model  
 Significance levels:  
 \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ;  
 \* $P < 0.05$



**Fig. 6** Mean ( $\pm$ SE) non-trophic interaction strength ( $IS_{NT}$ ) among predator pairs (BB—conspecific *Anisops breddini*; BS—1 *Anisops breddini*+1 *Anisops sardeus*; SS—conspecific *Anisops sardeus*) towards four prey instars (1st to 4th) of *Culex*

*quinquefasciatus* larvae across three surface areas (1—a, d, g; 2—b, e, h; 3—c, f, i) and water depths (A—a–c; B—d–f; C—g–i)

as a particularly voracious predator (Dalal et al., 2019, 2020a), both species belong to the Anisopinae notonectid sub-family which, unlike all other diving insects, are able to exploit the pelagic zone and achieve near-neutral buoyancy (Matthews & Seymour, 2008). Accordingly, water depth alterations directly mediate encounter rates between *Anisops* species and their prey, and our results suggest *A. sardeus* performs better in shallow conditions. For both predators, however, interactions were strongest towards 2nd instar mosquito stages, corroborating other studies considering similar species in the context of optimal foraging (Pastorok, 1981; Fischer et al., 2012; Dalal et al., 2020a, b). Contrastingly, feeding rates were generally lowest toward 4th instar prey stages, likely owing to handling constraints associated with this larger prey type. This demonstrated strong interactions of notonectids towards intermediate prey sizes,

which are better-handled as compared to small- or large sized prey (Suchman & Sullivan, 1998; Yamaguchi & Kishida, 2016).

Destabilising Type II FRs, characterised by high proportional predation rates at low prey densities, were most prevalent by notonectids in the present study, both as individuals and multiple predator groups. Similar results have been observed for other notonectid predators against mosquito larvae (Saha et al., 2007; Mondol et al., 2017; Cuthbert et al., 2019; Dalal et al., 2019, 2020b). Type III FRs were, however, most prevalent towards early instar prey, suggesting that the focal notonectids may impart a size refuge to this instar stage when scarce (Holling, 1959; Murdoch & Oaten, 1975; Williams & Martinez, 2004; Dalal et al., 2019). *Anisops sardeus* generally displayed higher search efficiencies and lower handling times than *A. breddini*, indicating higher

predatory impacts towards both low and high mosquito prey densities. Likewise, conspecific pairs of *A. sardeus* displayed greater capture rates and shorter handling times than either heterospecific pairings or conspecific *A. breddini* groupings. Accordingly, among multiple predator groups, *A. sardeus* displayed significantly higher interaction strength irrespective of search area variations, while heterospecific pairs or conspecific *A. breddini* groups were less effective in regulation of mosquito populations. Multiple predator interaction strengths also peaked towards 2nd instar pairs, and were weakest towards 4th instar stages. Interaction strengths thus appeared to scale unimodally towards intermediate prey sizes, which have been identified as most profitable for these predator size classes (see Fischer et al., 2012; Dalal et al., 2020a). Taken in combination, our results suggest that, in both individual and conspecific treatments, *A. sardeus* exerts the greatest degree of biotic resistance towards larval mosquito prey and that 2nd prey instar was the most consumed instar.

Emergent MPEs were dependent on search area, predator composition and prey size characteristics in the present study. Within food webs, negative MPEs associated with predator interferences are common and drive higher antagonism among predators (Vance-Chalcraft & Soluk, 2005; Griffen & Williamson, 2008; Sentis et al., 2017; Veselý et al., 2019). While antagonisms (i.e., negative MPEs) were commonly observed across all predator pairings, these effects were most consistent towards early instar prey stages (i.e., 1st–2nd instars) overall. However, multiple *A. sardeus* interactions were either synergistic or additive towards all prey stages, in contrast to other predator groups. Multiple predator effects tended, conversely, to manifest additively towards later instar stages, irrespective of predator composition. This might be caused by predators spending longer handling prey items rather than engaging in non-trophic interactions which result in interference (Woodward & Warren, 2007). Synergistic and additive MPEs were more evidenced in the present study, with prey risk reductions documented in all treatment groups, indicating the high predatory potential of tropical notonectid species against the mosquito larvae. Additionally, negative non-trophic interactions between conspecific *A. breddini* and heterospecific predator pairs were also observed, indicating actively

antagonistic or passive interactions in a group where *A. breddini* was present.

The prevalence of antagonistic MPEs was further evidenced by generally negative non-trophic interaction strengths across search areas, predator groups and prey instar stages. Heterospecific predator pairs exhibited the most negative predator–predator interactions. Strong interspecific competition between *A. breddini* and *A. sardeus* could thus act to increase antagonistic effects. Similar antagonistic behaviours in heterospecific predator combinations have also been observed among fish, crab and odonate nymph groupings (Wasserman et al., 2016a; Gunderson et al., 2017; Sentis et al., 2017). While the behavioural traits which underpin this antagonism require further elucidation, *A. sardeus* were anecdotally observed to display asymmetrical aggression towards *A. breddini* which reduced overall feeding rates. However, the strength of non-trophic interactions was further mediated by water depth, surface area and prey instar variations. While non-trophic interactions between conspecific *A. sardeus* were always significantly less negative than heterospecific predator groupings, conspecific *A. breddini* were also significantly more antagonistic than *A. sardeus* under low and high search areas. The strength of negative non-trophic interactions was also mediated by prey instar stage in conspecific predator groups, with antagonisms most pronounced for small 2nd instar prey. Given a greater quantity of small prey is required to reach predator satiation (Griffiths, 1980), there is a greater potential for competition and antagonistic interactions towards these prey types via searching processes. It is interesting to note that both trophic and non-trophic interaction strengths peak for predators preying on 2nd instar prey which might indicate that the relationship between prey size and both interaction types have a similar concave shape. On the other hand, non-trophic interaction strengths also displayed a hump-shaped relationship towards prey density, with higher predator–predator interactions at intermediate prey densities than either lower or higher prey densities. Similar results have also been observed for predatory odonates and dipterans feeding on *Daphnia magna* (Sentis et al., 2017).

Overall, notonectids were highly voracious in consuming mosquito larvae, particularly in shallow to medium search areas where 2nd instar larva was the most favourable prey stage. Accordingly, an optimum

prey size (2nd instar) and prey density (intermediate) was identified for notonectid predators where predation was higher. Here, *A. sardeus* and its conspecific pair were more voracious against the prey as compared to conspecific pairs of *A. breddini* or heterospecific pairs. Conspecific pair of *A. sardeus* thus showed more evidence of synergistic behaviour, which leads to more prey being eaten than expected across the different search areas. On the other hand, the heterospecific combination led to higher antagonisms, particularly in medium search areas, which led to a lower prey mortality. This thus revealed higher trophic and non-trophic interactions in low or medium search areas, which may reflect a concentration effect for both predators and prey that bolstered their encounters and interactions. These results also have implications for practitioners aiming to improve the efficiency of biological control agents, by identifying the aquatic contexts in which mosquitoes will be more effectively regulated.

In natural ecosystems, species are often engaged in complex communities where interaction strengths between multiple species are widespread and have considerable effects on prey survival, as well as the transfer of energy and nutrients across trophic levels (Denny and Benedetti-Cecchi 2012; Kéfi et al., 2012; McCoy et al., 2012; Okuyama and Bolker, 2012; Vázquez et al., 2015; Sentis et al., 2017). Hence, both trophic and non-trophic interactions have direct influence on food web stability and overall ecosystem dynamics. In particular, trophic interactions alone cannot provide clear picture of species interaction strength, and non-trophic interaction strengths must be increasingly considered since they can differ firmly among predator assemblages (Hammill et al., 2015; Sentis et al., 2017). Given the interacting influence of search area and prey size on non-trophic interactions have remained unexplored, the present study provides novel insights into key contexts which modulate interaction strengths within dynamic aquatic ecosystems. In particular, the effects of search area on interaction strengths are dependent on the characteristics of predator–prey participants, with predator–predator antagonisms most pronounced towards smaller prey sizes and by heterospecific predator groupings. The present study is limited to two predator species and two predator combinations, and therefore, further studies should be considered for multiple predator effects having more than two predator combinations and

higher predator species diversity. Also, studies are required to better understand predator–predator and predator–prey interactions among other taxonomic groups and different environmental contexts, such as under climatic warming and deoxygenation.

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**Data availability** Data available from figshare, <https://doi.org/10.6084/m9.figshare.10058375>

**Declarations**

**Conflict of interest** All the authors declare no conflict of interest.

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