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Biocontrol agent selection under environmental change using functional responses, abundances and fecundities; the Relative Control Potential (RCP) metric

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Abstract

1. We currently lack the capacity to rapidly and reliably predict the efficacy of biological control agents due to inadequate consistency in derivations of functional and numerical responses and potential effects of context-dependencies.

2. Here, we propose and apply a novel metric, Relative Control Potential (RCP), which combines the functional response (FR, *per capita* effect) with proxies for the numerical response (NR, agent population response) to compare agent efficacies, where RCP = FR x Abundance (or other proxies e.g. Fecundity). The RCP metric is a comparative ratio between potential biocontrol agents, where values > 1 indicate higher relative control efficacy. Further, RCP can compare the efficacy of agents under environmental contexts, such as

temperature change. We thus derived the RCP for two predatory cyclopoid copepods, *Macrocyclops albidus* and *Megacyclops viridis*, towards larvae of the mosquito *Culex pipiens* under temperatures representative of current and future climate.

3. Both copepods exhibited potentially population destabilising Type II FRs, with increasing temperatures inducing greater magnitude functional responses through increased attack rates and decreased handling times. Attack rates by *M. albidus* were higher than *M. viridis*, yet handling times and maximum feeding rates were similar between the species across all temperatures.

4. The inclusion of abundance data drives an elevated RCP of *M. albidus* and the integration of fecundity drives greater RCP of *M. albidus* at peak temperatures. Q_{10} values are indicative of increased feeding activity by both copepods synonymous with temperature increases, however relative feeding level increases of *M. viridis* slowed towards the peak temperature. We present RCP calculations and biplots that represent the comparative efficacies of the two biological control agents across temperatures.

5. *Synthesis and applications*. The Relative Control Potential (RCP) metric provides a tool for practitioners to better assess the potential efficacy of biocontrol agents before their integration into management approaches for pests, vectors and invasive species.

Keywords: Functional response; Numerical response; Relative Control Potential; *Culex pipiens*; Mosquito; *Macrocyclops albidus*; *Megacyclops viridis*; Copepod

Introduction

Biological control has been applied to manage pest and invasive species in a variety of ecological systems (O’Neil, 1990; Marten and Reid, 2007; Van Driesche and Bellows, 2011; Calvo et al. 2016). However, attempts to reveal agent efficacy through the coupling of functional and numerical responses (FRs, NRs) are limited in practice, reducing our predictive capacity for population-level effects (but see Heisswolf et al. 2009; Costa et al. 2017). Further, natural systems are characterised by a number of abiotic and biotic context-dependencies that can alter species interaction strengths, including structural complexity (Barrios-O'Neill et al. 2014b), temperature (Wasserman et al. 2016; South et al. 2017), dissolved oxygen (Laverty et al. 2015), parasitism (Bunke et al. 2015; Laverty et al. 2017b) and multiple/higher predators (Alexander et al. 2013; Barrios-O'Neill et al. 2014a). Thus, rapid and reliable FR and NR derivations under context-dependencies are critical for the future of biocontrol strategies.

Climate change, coupled with urbanisation, is stimulating an unprecedented change in the population dynamics and status of mosquito vectors and their transmission of disease (Townroe and Callaghan, 2014; Medlock and Leach, 2015; Siraj et al. 2017), with mosquito invasions increasing with the transportation of goods and humans (e.g. Yee, 2016; Medlock et al. 2017). The *Culex pipiens* (Linneaus, 1758) complex is widespread globally and acts as the primary vectors of West Nile virus in the USA and continental Europe (Hubalek and Halouzka, 1999; Fonseca et al. 2004). Freshwater cyclopoid copepods exhibit marked potential for the biological control of mosquitoes (Marten and Reid, 2007; Baldacchino et al. 2017), and have been operationalised in large-scale field applications (Kay and Nam, 2005). However, we require rapid assessment of the relative biocontrol potential of such agents under changing climatic conditions. In this study, we therefore present and apply a new metric, based on FRs and NRs, to compare the efficacy of *Macrocyclops albidus* (Jurine, 1820) and *Megacyclops viridis* (Jurine, 1820) under current and predicted temperature regimes.

Functional responses (FRs) quantify consumption under differing resource densities, describing the key components of search, capture and handling time. Three broad FR types have been described: the linear Type I, hyperbolic Type II and sigmoidal Type III (Solomon, 1949; Holling, 1959). FR form and magnitude are both powerful predictors of the impacts of consumers on resource populations across taxonomic and trophic groups (Dick et al. 2014; 2017). However, as FRs only assess *per capita* impacts, incorporation of the Numerical Response (NR), that is the consumer population response, is also required to discern the Total Response (TR) of consumers, whereby:

$$\mathrm{TR} = \mathrm{FR} \; \mathrm{x} \; \mathrm{NR}$$

Eqn. 1.

In comparison to FRs, NRs are inherently more nebulous and difficult to quantify (Dick et al. 2017). Thus, simple consumer abundance (AB) has recently been proposed as a proxy for the numerical response, giving the ‘Impact Potential’ (IP) metric, which has proved robust in predicting ecological impact in the context of invasion biology (Dick et al. 2017; Laverty et al. 2017a):

$$\mathrm{IP} = \mathrm{FR} \times \mathrm{AB}$$

Eqn. 2.

where FR is the maximum feeding rate (reciprocal of handling time) and AB is a measure of consumer field abundance. In the context of biocontrol, we can express this as ‘Control Potential’, CP:

$$\mathrm{CP} = \mathrm{FR} \times \mathrm{AB}$$

Eqn. 3.

where FR is the maximum feeding rate as above. However, in addition, we propose that attack rate be used as a second measure of FR, as this parameter describes the slope of the FR curve at low prey densities and high attack rates can thus be particularly destabilising to prey populations. CP as an absolute measure is, however, rather meaningless, and needs a comparator, such as where two or more biocontrol agents require assessment as to their relative potential efficacies, hence 'Relative Control Potential' (RCP):

$$\mathrm{RCP} = \left(\frac{\text{FR agent A}}{\text{FR agent B}}\right) \times \left(\frac{\text{AB agent A}}{\text{AB agent B}}\right)$$

Eqn. 4.

Where RCP = 1, we predict no difference between biocontrol agents; for RCP < 1, we predict agent A to have lesser efficacy than agent B; whereas when RCP > 1, agent A is predicted to have greater efficacy than agent B. Further, increasing values above 1 indicate increasing relative efficacy of agent A compared to agent B.

Furthermore, we propose the use of fecundity as a second proxy for NR, which enables the incorporation into RCP of how quickly biocontrol agents can proliferate. Error can also be incorporated into the RCP metric depending on data availability, using a probability density function (pdf) to generate confidence intervals (CIs) and probabilities that RCP > 1 or > 10 (see Dick et al. 2017). Moreover, as contexts such as temperature can have profound impacts on consumer-resource interactions (Englund et al. 2011; Rall et al. 2012), RCP can be integrated to compare the efficacy of each biocontrol agent across environmental gradients. Here, we apply the RCP metric (Eqn. 4) to compare the biological control potentials of the copepods *M. albidus* and *M. viridis*, towards the mosquito complex *C. pipiens* over a temperature gradient reflective of current and future UK climate change scenarios. We also apply the Q_{10} coefficient to further illustrate feeding activity responses of the two agents across temperature variations (Bennett, 1990).

Materials and methods

Animal collection and rearing

M. albidus and *M. viridis* were collected at Glastry Clay Pit Ponds, Northern Ireland (54°29'18.5"N; 5°28'19.9"W) in January 2017 and kept in Queen's Marine Laboratory, Portaferry, N. Ireland, at 25 ± 2 ^{o}C under a 16:8 light:dark regime and 50 – 60% relative humidity. Cultures were initiated using ovigerous females, placed individually into 250 mL cups with dechlorinated tap water and fed *ad libitum* with *Chilomonas paramecium* and *Paramecium caudatum* to obtain nauplii. Starter cultures of these protozoans were available commercially (Sciento, Manchester, England) and cultured under the same laboratory conditions in 2 L glass beakers using autoclaved wheat seeds, with *C. paramecium* providing nourishment for nauplii and early copepodids and *P. caudatum* for late copepodids and adults. Adult copepods were identified by Maria Holyńska, Museum and Institute of Zoology, Warsaw, Poland. Copepods were mass-reared in 10 L tanks and fed *ad libitum* on the protozoan diet. At maturity, copepods were maintained at 12 ± 2 ^{o}C under a 12:12 light and dark regime and acclimatised for 7 days prior to experimentation in 5 L holding arenas of 22 cm diameter fed *ad libitum* on the protozoan prey.

Culex pipiens were obtained from a laboratory colony established at the University of Reading, originating from field-collected mosquitoes at the The Pirbright Institute, Surrey. The colony was sustained under the same conditions as the copepods in 32.5 x 32.5 x 32.5 cm cages (Bugdorm, Watkins and Doncaster, Leominster, England) and fed three times per week with defibrinated horse blood (TCS Biosciences, Buckingham, England) using a Hemotek® blood-feeding system (Hemotek Ltd., Accrington, England) and additionally provided with cotton pads soaked in a 10% sucrose solution. Cages contained black cups filled with 200 mL dechlorinated tap water for oviposition. Egg rafts were extracted three times per week and placed into larval bowls containing 3 L dechlorinated tap water, and fed *ad libitum* with ground guinea pig pellets (Pets at Home, Newtownabbey, Northern Ireland) until pupation.

Experimental procedure

Non-ovigerous adult female *M. albidus* and *M. viridis* (1.6 – 1.8 mm and 2.0 – 2.3 mm body length excluding caudal setae, respectively) were selected for experiments. We selected non-ovigerous females to standardise predators as cyclopoids are sexually dimorphic (Laybourn-Parry et al. 1988) and to eliminate cannibalism of hatching juveniles (Toscano et al. 2016). Prey used were recently hatched, first instar *C. pipiens* larvae (1.1 – 1.3 mm). Functional response experiments were undertaken in transparent polypropylene cups (42 mm dia.) containing 20 mL dechlorinated tap water from a continuously aerated source in a 12:12 light and dark regime over 24 h at 12 ^{o}C, 16 ^{o}C and 20 ^{o}C (Clifton NEIB water baths), representing diurnal temperature shifts and reasonable current autumn/winter, spring/summer and future spring/summer temperatures in the UK, respectively (Hulme et al. 2002; Hammond and Pryce, 2007). Dissolved oxygen was monitored using a YSI model 550A meter to ensure levels remained above 80% saturation. Both predators and prey were acclimatised to the two elevated temperatures over a two hour period prior to experiments; temperatures were increased every 30 minutes by either 1 ^{o}C or 2 ^{o}C (i.e. to 16 ^{o}C or 20 ^{o}C). Following the acclimatisation period, we added single adult females of either *M. albidus* or *M. viridis* to containers with prey densities of 2, 4, 8, 15, 30 and 60 (n = 4 per experimental group). Controls consisted of three replicates at each prey density and temperature in the absence of predators. Predators were individually starved for 24 h in containers of the same volume and diameter as the experimental arenas before being transferred to containers holding the corresponding prey density. Predators were removed from experimental arenas after 24 hours, with the numbers of prey alive counted to derive the numbers killed in each replicate.

Data manipulation and statistical analyses

Statistical analyses were undertaken in R v3.3.1. (R Core Team, 2015). Logistic regression of proportion of prey killed as a function of prey density was used to infer FR types; Type II FRs are characterised by a significant negative first-order term and Type III by a significant negative second order term following a significant positive first order term. To account for prey depletion, we fitted Rogers' random predator equation for conditions without prey replacement (Trexler et al. 1988; Juliano, 2001):

$$N_e = N_0(1 - \exp(a(N_e h - T)))$$

Eqn. 5.

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h is the handling time and T is the total experimental period. The Lambert W function was applied due to the implicit nature of the random predator equation (Bolker, 2008). Attack rates and maximum feeding rates '1/h' were non-parametrically bootstrapped (n = 30) to facilitate modelling of FR parameters with respect to 'predator' and 'temperature' factors and their interactions. Bootstrapped parameters were analysed using generalised linear models (GLMs) assuming a quasi-Poisson distribution. F-tests were used in a step-deletion process to compare residual deviances between models (Crawley, 2007). We applied Tukey's HSD method to infer specific pairwise differences using the 'multcomp' package in R (Hothorn et al. 2008).

Benthic survey data for *M. albidus and M. viridis* (as *Acanthocyclops viridis*) derived from Tinson and Laybourn-Parry (1986) were used to calculate RCP based on maximum field abundances using pooled bootstrapped mean maximum feeding and attack rates across all three temperatures. To calculate RCP using fecundity, we used results from Laybourn-Parry et al. (1988) to discern the proportion of total consumed energy devoted to reproduction across corresponding temperatures for the two copepods:

$$\text{Fecundity} = \left(\frac{P_r}{C}\right) \text{x}\, 100$$

Eqn. 6.

where P_r is the quantity of energy expended through the production of eggs and C is the total energy consumed at a given temperature (Table 1). Reproductive energy proportions at 16 ^{o}C were supplemented with those available for 15 ^{o}C.

We additionally calculated Q_{10} values to further quantify the effects of increased temperature on feeding rates and compare how these varied between predatory cyclopoids:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)}$$

Eqn. 7.

where Q_{10} is a coefficient without units, R_1 is the maximum feeding rate at temperature T_1 and R_2 is the maximum feeding rate at temperature T_2. The Q_{10} coefficient assesses how temperature increases of 10 ^{o}C affect the rate of biological processes (Bennett 1990); values of 1 – 1.5 are associated with a thermal plateau and values of 2 – 4 indicate substantive increases in activity as temperature increases (Huey, 1982; Bennett 1990). We generated ‘RCP biplots’ to present the RCP (see Laverty et al. 2017a) of the two predators using both the abundance (AB) and fecundity (FE) proxies for the numerical response.

Results

Prey survival in control treatments exceeded 98.5% across all temperatures, and thus experimental deaths were attributed to predation by copepods, which was also directly observed. Type II FRs were found in all predator and temperature combinations, as indicated by significantly negative first order terms (Table 2; Figure 1). Overall, attack rates (initial FR slopes; see Figure 1) for *M. albidus* were significantly higher than for *M. viridis* ($F_{1,178} = 7.25$, $p < 0.01$) and increased significantly with temperature ($F_{2,176} = 74.41$, $p < 0.001$). There were significant increases in attack rates between 12 °C and 16 °C ($z = 5.61$, $p < 0.001$), and 12 °C and 20 °C ($z = 6.75$, $p < 0.001$), but not between 16 °C and 20 °C ($z = 1.20$, p = NS). There was a significant ‘predator × temperature’ interaction ($F_{2,174} = 3.09$, $p < 0.05$), reflecting significantly greater attack rates by *M. albidus* only at the lowest temperature ($z = 3.42$, $p < 0.01$; Table 2; Figure 1). Overall, maximum feeding rates (asymptotes of FR curves; see Figure 1) did not differ significantly between the two predators ($F_{1,178} = 2.88$, p = NS), and increased significantly with temperature ($F_{2,176} = 110.29$, $p < 0.001$; Figure 1). There were significant increases in maximum feeding rates between all temperature levels (12 °C – 16 °C, $z = 4.23$, $p < 0.001$; 16 °C – 20 °C, $z = 4.79$, $p < 0.001$; 12 °C – 20 °C, $z = 8.81$, $p < 0.001$). There was a significant ‘predator × temperature’ interaction ($F_{2,174} = 3.46$, $p < 0.05$), reflecting an insignificant difference between maximum feeding rates of *M. viridis* at 16 °C and *M. albidus* at 20 °C ($z = 2.48$, p = NS) compared to a significant difference between *M. albidus* at 16 °C and *M. viridis* at 20 °C ($z = 6.24$, $p < 0.001$).

The RCP calculations integrating field abundances with maximum feeding and attack rates are presented in Table 3. These RCP scores exhibit high certainty and indicate strong comparative efficacy of *M. albidus*. It is evident from the biplots in Figures 2a and 2b that *M. albidus* populations display much higher densities than *M. viridis*, driving greater RCP using both FR parameters. The fecundity results in Table 1 reveal a general increase in the proportion of total consumed energy devoted to reproduction as temperature increases.

Anomalous to this is the response to warming of *M. viridis* at 20 ^{o}C, with fecundity here falling markedly. The ramifications of these fecundity variations for RCP are illustrated in Table 4 and Figures 2c and 2d, with relatively similar levels of efficacy for the two species illustrated at both 12 ^{o}C and 16 ^{o}C, followed by a substantial decrease in efficacy of *M. viridis* at 20 ^{o}C. The certainty of the RCP using fecundity strengthens at peak temperatures (Table 4). Under both NR proxies, differential efficacies were more pronounced using the attack rate parameter (Figure 2). The results for the Q_{10} coefficient for the two predators across the temperature gradient are illustrated in Table 5, and indicate that between 12 ^{o}C and 20 ^{o}C both the feeding rates of *M. albidus* and *M. viridis* were highly responsive to temperature increases (2.25 and 2.95 respectively). There was a marked difference between the predators in the incremental drivers of this response, with *M. viridis* exhibiting a rapid increase between 12 ^{o}C and 16 ^{o}C (4.70) which slowed between 16 ^{o}C and 20 ^{o}C (1.85). Conversely, *M. albidus* was consistent in its feeding response to increased temperatures (12 ^{o}C – 16 ^{o}C, 2.29; 16 ^{o}C – 20 ^{o}C, 2.22; Table 5).

Discussion

Biological control of pests, disease vectors and invasive species can be effective (e.g. Hajek, 2007; Nam et al. 2012; Veronesi et al. 2015), but efforts to predict the efficacy of natural enemies are limited when the functional response (FR) *per capita* effects are solely considered (Lester and Harmsen, 2002; Fernández-arhex and Corley, 2003). The complementary numerical response (NR) is, however, somewhat nebulous and difficult to derive, with proxies for the NR required to allow rapid assessment of the overall impact of a consumer (i.e. TR; Dick et al. 2017). Recent developments that combine functional and numerical responses (or their proxies) into a comparative metric (RIP; Dick et al. 2017) yield high explanatory and predictive power for the impacts of invasive species, and hence have potential in the assessment of the efficacy of biocontrol agents. Further value in the application of such metrics surrounds the integration of context-dependencies associated with environmental change, which can strongly affect interactions between consumers and their resources (e.g. oxygen availability: Laverty et al. 2015; habitat complexity: Barrios-O'Neill et al. 2014b). Thus, we present the Relative Control Potential (RCP) metric that uses *per capita* and consumer population responses to compare efficacy among biocontrol agents and can allow predictions of changes in such efficacies under context-dependencies.

The risk of mosquito-borne disease at continental scales has reached unprecedented levels in recent decades (Medlock and Leach, 2015). Arboviruses such as Zika, West Nile, dengue and chikungunya present enormous public health concern, with disease dynamics shifting rapidly under environmental change (Benelli and Melhorn, 2016; Siraj et al. 2017). Agricultural systems will additionally be impacted (Chevalier et al. 2013). This risk necessitates the formation of techniques to assess and compare the potential efficacies of biological control agents. Here, temperature was shown to mediate changes to the FR parameters of *M. albidus* and *M. viridis*, driving higher magnitude FRs through increasing attack rates and decreasing handling times. The temperature-dependence of attack rates reported here contrasts to suggestions that this FR parameter is temperature-independent (Rall et al. 2012; Dell et al.2014). We show that both predators exhibit high maximum feeding rates that exceed 30 of the West Nile virus vector *C. pipiens* per day at 20 ^{o}C. Critically, the Type II FRs found are indicative of a capacity to destabilise prey populations due to high proportional consumption at prey low densities (Long and Whitefleet-Smith, 2013). *M. albidus* and *M. viridis* show strong similarities in their *per capita* consumption, although the attack rates of *M. albidus* were significantly greater overall, illustrated by steeper gradients in the FR curves at low densities. As a result, *M. albidus* may be more effective in eliminating *C. pipiens* populations.

We demonstrate that integrating field abundances with RCP reveals far stronger control efficacies of *M. albidus* compared to *M. viridis*. The utility of abundance estimates lies in the projection of how many conspecifics may engage in the predator-prey (or other consumer-resource) interaction and it is thus a useful NR proxy. On the other hand, incorporating measures of fecundity estimates how rapidly biological control agents can reproduce when introduced. Using fecundity, we demonstrate temperature-dependencies of control efficacy. Stark fecundity variabilities are illustrated in the RCP biplots, with the reproductive devotion of *M. viridis* declining rapidly at 20 ^{o}C, whilst that of *M. albidus* continues to rise. The reduction in fecundity shown by *M. viridis* at 20 ^{o}C is concurrent with slowing foraging activity discerned through Q_{10} analysis, whereas *M. albidus* displays a consistent incremental increase with warming. Overall, *M. albidus* displays greater potential for the control of West Nile virus vector *C. pipiens* than *M. viridis*, particularly under climate change projections where our certainty for differential efficacy increases (e.g. Hulme et al. 2002). This differential efficacy is more pronounced when the attack rate parameter is applied. An increased metabolic demand could enable *M. albidus* to sustain efficiency in the consumption of *C. pipiens*, which proliferate more rapidly at higher temperatures, particularly in domestic and peri-domestic habitats in urbanised environments (Townroe and Callaghan, 2014).

In this study, temperature had a profound effect on predator-prey interactions. Temperature independence of ambush predators such as the benthic copepods examined here has been described (Awasthi et al. 2012; Novich et al. 2014), with strong dependencies driven, rather, in respect to prey foraging responses to temperature change. These interactions make predator-prey systems highly specific to both the species (Englund et al. 2011) and environment (Broitman et al. 2011), with optimal foraging patterns of ectothermic prey potentially peaking at intermediate temperatures (Englund et al. 2011; Kalinoski and DeLong 2016). In this study, feeding rates of candidate biocontrol agents peaked at the highest temperature, however the rate of increase slowed between 16 ^{o}C and 20 ^{o}C, as compared to between 12 ^{o}C and 16 ^{o}C; this trend was particularly marked for *M. viridis*. Temperature additionally has a substantial influence on the development of the focal prey, *C. pipiens*, driving significant reductions in development times under conditions of warming (Loetti et al. 2011; Ruybal et al. 2016), and necessitating increased foraging intensity. Yet, increases in *C. pipiens* mortality due to drivers outside of predation are also evident as temperatures rise (Ruybal et al. 2016). *M. albidus* has proved particularly effective against the invasive arbovirus vector *A. albopictus* following field trials (Marten, 1990; Veronesi et al. 2015). Previous research has suggested that copepods are more efficient consumers of *Aedes* spp. than *Culex* spp. as a result of morphological variations between the genera (Marten and Reid, 2007). However, laboratory trials have shown similar levels of overall predation by *M. albidus* towards both *A. albopictus* and *C. pipiens* (Veronesi et al. 2015), as well as by *Mesocyclops annulatus* (Micieli et al. 2002). Further field trials are required to elucidate whether their efficiencies towards *C. pipiens* translate empirically, particularly as it is the major West Nile virus vector in the USA and Europe (Hubalek and Halouzka, 1999; Fonseca et al. 2004) and part of one of the most widespread mosquito complexes in the world (Harbach, 2012).

This is the first study to develop and apply the RCP metric to biological control agent selection. We demonstrate that the integration of abundance and fecundity estimations can provide a means to differentiate between biocontrol agents that display similar *per capita* efficacies across temperature gradients. Adaptations of this metric have been applied successfully hitherto in the context of invasion biology to explain and predict the impact of invasive species (Dick et al. 2017; Laverty et al. 2017), yet similar fundamental principles enable its application to the selection of biocontrol agents. Overall, temperature increases will induce greater *per capita* predation pressure by predatory copepods towards *C. pipiens* and likely other mosquito species. Copepod applications to waterbodies can form an integral part of mosquito control efforts (Baldacchino et al. 2015), with large-scale field trials having proved successful (e.g. Kay and Nam, 2005), particularly given their ability to thrive in ranging natural and artificial waterbodies (Marten and Reid, 2007). Importantly, copepods can be augmented synergistically using existing control methods, such as the use of bacterial *Bacillus thuringiensis var. israelensis* (BTI; Kosiyachinda et al. 2003). Nanoparticles have additionally been founded to heighten predation (Murugan et al. 2015). The straightforward derivation of the RCP metric, and its visual representation in biplots, will allow comparisons of biological control agents across many ecological systems, and could increase cost-effectiveness of natural enemies in the long-term. Further proxies for numerical response, such as biocontrol agent longevity or biomass, can be integrated into the RCP metric as per the requirements of the assessed system or biocontrol approach, increasing the robustness and flexibility of the method. Moreover, the additional integration of a qualifier to account for target organism responses under matched environmental change scenarios could bolster the power of the RCP metric in reliably selecting biocontrol agents, and this is worth further consideration in future research.

Authors' contributions

Relative Control Potential (RCP) concept and framework: RNC, JTAD and JWED. Design and execution of experimental trials: RNC and JTAD. Fitting functional response models and

undertaking RCP calculations: RNC. First draft of the manuscript: RNC. Manuscript revisions: all authors.

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Data accessibility

Underlying functional response data will be made available on the Dryad Digital Repository.

References

Alexander, M.E., Dick, J.T.A., O'Connor, N.E., 2013. Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. Oikos 122(11), 1521–1531. http://dx.doi.org/10.1111/j.1600-0706.2013.00472.x.

Awasthi, A.K., Wu, C-W., Tsai, K-H., King, C-C., Hwang, J-S., 2012. How Does the Ambush Predatory Copepod *Megacyclops formosanus* (Harada, 1931) Capture Mosquito Larvae of *Aedes aegypti*? Zool. Stud. 51(7), 927–936.

Baldacchino, F., Caputo, B., Chandre, F., Drago, A., della Torre, A., Montarsi, F., Rizzoli, A., 2015. Control methods against invasive *Aedes* mosquitoes in Europe: A review. Pest Manage. Sci. 71(11), 1471–1485. http://dx.doi.org/10.1002/ps.4044.

Baldacchino, F. Bruno, M.C., Visentin, P., Blondel, K., Arnolid, D., Hauffe, H.C., Rizzoli, A., 2017. Predation efficiency of copepods against the new invasive mosquito species *Aedes koreicus* (Diptera: Culicidae) in Italy. Eur. Zool. J. 84(1), 43–48. http://dx.doi.org/10.1080/11250003.2016.1271028.

Barrios-O'Neill, D., Dick, J.T.A., Emmerson, M.C., Ricciardi, A., MacIsaac, H.J., Alexander, M.E., Bovy, H.C., 2014a. Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. J. Anim. Ecol. 83(3), 693–701. http://dx.doi.org/10.1111/1365-2656.12155.

Barrios-O'Neill, D., Dick, J.T.A., Emmerson, M.C., Ricciardi, A., MacIsaac, H. 2014b. Predator-free space, functional responses and biological invasions. Funct. Ecol. 29(3), 377–384. http://dx.doi.org/10.1111/1365-2435.12347.

Benelli, G., Melhorn, H., 2016. Declining malaria, rising of dengue and Zika virus: insights for mosquito vector control. Parasitol. Res. 115(5), 1747-1754. http://dx.doi.org/10.1007/s00436-016-4971-z.

Bennett, A.F., 1990. Thermal dependence of locomotor capacity. Am. J. Physiol. 259(2), 253–258.

Bolker, B.M., 2008. Ecological Models and Data in R. Princeton University Press, USA.

Broitman, B.R., Szathmary, P.L., Mislan, K.A.S., Blanchette, C.A., Helmuth, B., 2009. Predator-prey interactions under climate change: the importance of habitat vs body temperature. Oikos 118(2): 219–224. http://dx.doi.org/10.1111/j.1600-0706.2008.17075.x.

Bunke, M., Alexander, M.E., Dick, J.T., Hatcher, M.J., Paterson, R., Dunn, A.M., 2015. Eaten alive: cannibalism is enhanced by parasites. Open Sci. 2, 140369. http://dx.doi.org/10.1098/rsos.140369.

Calvo, F.J., Torres-Ruiz., A., Velázquez-Gonzále, J.C., Rodríguez-Leyva, E., Lomeli-Flores, J.R., 2016. Evaluation of *Dicyphus hesperus* for biological control of sweet potato whitefly and potato psyllid on greenhouse tomato. Biocontrol 61(4), 415-424. http://dx.doi.org/10.1007/s10526-016-9719-2.

Chevalier, V., 2013. Relevance of Rift Valley fever to public health in the European Union. Clin. Microbiol. Infect. 19(8), 705-708. http://dx.doi.org/10.1111/1469-0691.12163.

Costa, J.F., Matos, C.H.C., de Oliveira, C.R.F., da Silva, T.G.F., Lima Neto, I.F.A. 2017. Functional and numerical responses of *Stethorus tridens* Gordon (Coleoptera: Coccinellidae) preying on *Tetranychus bastosi* Tuttle, Baker & Sales (Acari: Tetranychidae) on physic nut (*Jatropha curcas*). Biol. Control 111, 1-5. https://doi.org/10.1016/j.biocontrol.2017.04.015.

Crawley, M.J., 2007. The R book. John Wiley & Sons, Chichester. http://dx.doi.org/10.1002/9780470515075.

Dell, A.I., Pawar, S., Savage, V.M., 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. J Anim Ecol 83(1), 70–84. http://dx.doi.org/10.1111/1365-2656.12081.

Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B., Kumschick, S., Weyl, O.L.F., Dunn, A.M., Hatcher, M.J., Paterson, R.A., Farnsworth, K.D., Richardson, D.M., 2014. Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biol. Invasions 16(4), 735–753. http://dx.doi.org/10.1007/s10530-013-0550-8.

Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill., D., Mensink, P.J., Britton, R., Médoc, V., Boets, P., Alexander, M.E., Taylor, N.G., Dunn, A.M., Hatcher, M.J., Rosewarne, P.J., Crookes, S., MacIsaac, H.J., Xu, M., Ricciardi, A., Wasserman, R.J., Ellender, B.R., Weyl, O.L.F., Lucy, F.E., Banks, P.B., Dodd, J.A., MacNeil, C., Penk, M.R., Aldridge, D.C., Caffrey, J.M., 2017. Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. J. Appl. Ecol. 54(4), 1259–1267. http://dx.doi.org/10.1111/1365-2664.12849.

Englund, G., Ohlund, G., Hein, C.L., Diehl, S., 2011. Temperature dependence of the functional response. Ecol. Lett. 14(9), 914–921. http://dx.doi.org/10.1111/j.1461-0248.2011.01661.x.

Fernández-arhex, V., Corley, J.C., 2003. The Functional Response of Parasitoids and its Implications for Biological Control. Biocontrol Sci. Technol. 13(4), 403–413. http://dx.doi.org/10.1080/0958315031000104523.

Fonseca, D.M., Keyghobadi, N., Malcolm, C.A., Mehmet, C., Schaffner, F., Mogi, M., Fleischer, R.C. and Wilkerson, R.C., 2004. Emerging vectors in the *Culex pipiens* complex. Sci. 303(5663), 1535–1538. http://dx.doi.org/10.1126/science.1094247.

Hajek, A., 2007. Introduction of a fungus into North America for control of gypsy moth, in: Vincent, C., Goettel, M.S., Lazarovits, G. (Eds.) Biological control: a global perspective. CAB International, Wallingford, pp. 53–62. http://dx.doi.org/10.1079/9781845932657.0000.

Hammond, D., Pryce, A.R., 2007. Climate change impacts and water temperature. Environment Agency Science Report SC060017/SR. Bristol.

Harbach, R.E., 2012. *Culex pipiens*: Species versus species complex - taxonomic history and perspective. J. Am. Mosq. Control Assoc. 28(4), 10–23. http://dx.doi.org/10.2987/8756-971X-28.4.10.

Heisswolf, A., Klemola, N. Ammunét, T., Klemola, T. 2009. Responses of generalist invertebrate predators to pupal densities of autumnal and winter moths under field conditions. Ecol. Entomol. 34(6), 709–717. http://dx.doi.org/10.1111/j.1365-2311.2009.01121.x.

Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91(7), 385–398. http://dx.doi.org/10.4039/Ent91385-7.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical J. 50(3), 346–363. http://dx.doi.org/10.1002/bimj.200810425.

Hubalek, Z., Halouzka, J., 1999. West Nile fever - a remerging mosquito-borne viral disease in Europe. Emerg. Infect. Dis. 5(5), 643–650. http://dx.doi.org/10.3201/eid0505.990505.

Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles, in: Gans, C., Pough, F.H. (Eds.), Biology of the Reptilia. Academic Press, New York, pp. 25–91. http://dx.doi.org/10.1093/icb/icq095

Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Lowe, J., Murphy, J.M., Hassell, D., Boorman, P., McDonald, R., Hill, S., 2002. Climate change scenarios for the United Kingdom. The UKCIP Scientific Report. Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich.

Juliano, S.A., 2001. Non-linear curve fitting: predation and functional response curves, in: Scheiner, S.M., Gurevitch, J. (Eds.), Design and Analysis of Ecological Experiments. Oxford University Press, Oxford, pp. 178–196. http://dx.doi.org/10.4319/lo.1995.40.8.1533.

Kalinoski, R.M. and DeLong, J.P., 2016. Beyond body mass: how prey traits improve predictions of functional response parameters. Oecol. 180(2), 543–550. http://dx.doi.org/10.1007/s00442-015-3487-z.

Kay, B.H. and V.S. Nam. 2005. New strategy against *Aedes aegypti* in Vietnam. Lancet 365(9459): 613-617. http://dx.doi.org/10.1016/S0140-6736(05)17913-6.

Kosiyachinda, P., Bhumiratana, A., Kittayapong, P., 2003. Enhancement of the efficacy of a combination of *Mesocyclops aspericornis* and *Bacillus thuringiensis var. israelensis* by community-based products in controlling *Aedes aegypti* larvae in Thailand. Amer. J. Trop. Med. Hyg. 69(2), 206–212.

Laverty C., Dick, J.T.A., Alexander, M.E., Lucy, F.E., 2015. Differential ecological impacts of invader and native predatory freshwater amphipods under environmental change are revealed by comparative functional responses. Biol Invasions 17(6), 1761–1770. http://dx.doi.org/10.1007/s10530-014-0832-9.

Laverty, C., Green, K.D., Dick, J.T.A., Barrios-O'Neill, D., Mensink, P.J., Médoc, V., Spataro, T., Caffrey, J.M., Lucy, F.E., Boets, P., Britton, J.R., Pegg, J., Callagher, C., 2017a. Assessing the ecological impacts of invasive species based on their functional responses and abundances. Biol. Invasion*s* 19(5),1653–1665. http://dx.doi.org/10.1007/s10530-017-1378-4.

Laverty, C., Brenner, D., McIlwaine, C., Lennon, J.J., Dick, J.T.A., Lucy, F.E., Christian, K.A., 2017b. Temperature rise and parasitic infection interact to increase the impact of an invasive species. Int. J. Parasitol. 47(5), 291–296. http://dx.doi.org/10.1016/j.ijpara.2016.12.004.

Laybourn-Parry, J., Abdullahi, B.A., Tinson, S.V., 1988. Temperature-dependent energy partitioning in the benthic copepods *Acanthocyclops viridis* and *Macrocyclops albidus*. Can. J. Zool. 66(12), 2709–2713. https://doi.org/10.1139/z88-397.

Lester, P.J., Harmsen, R., 2002. Functional and numerical responses do not always indicate the most effective predator for biological control: An analysis of two predators in a two-prey system. J. Appl. Ecol. 39(3), 455–468. http://dx.doi.org/10.1046/j.1365-2664.2002.00733.x.

Loetti, V., Schweigmanna, N., Burronia, N., 2011. Development rates, larval survivorship and wing length of *Culex pipiens* (Diptera: Culicidae) at constant temperatures. J. Nat. Hist. 45(36-36), 2207–2217. http://dx.doi.org/10.1080/00222933.2011.590946.

Long, W.C., Whitefleet-Smith, L., 2013. Cannibalism in red king crab: habitat, ontogeny, and the predator functional response. J. Exp. Mar. Biol. Ecol. 449, 142–148. http://dx.doi.org/10.1016/j.jembe.2013.09.004.

Marten, G.G., 1990. Elimination of *Aedes albopictus* from tire piles by introducing *Macrocyclops albidus* (Copepoda, Cyclopidae). J. Am. Mosq. Control Ass. 6(4), 689–693.

Marten, G.G., Reid, J.W., 2007. Cyclopoid copepods. J. Am. Mosq. Control Ass. 23(2), 65–92. http://dx.doi.org/10.2987/8756-971X(2007)23%5B65:CC%5D2.0.CO;2.

Medlock, J.M., Leach, S.A., 2015. Effect of climate change on vector-borne disease risk in the UK. Lancet Infect. Dis. 15(6), 721–730. http://dx.doi.org/10.1016/S1473-3099(15)70091-5.

Medlock, J.M., Vaux, A.G.C., Cull, B., Schäffner, F., Gillingham, E., Pfluger, V., Leach, S., 2017. Detection of the invasive mosquito species *Aedes albopictus* in southern England. Lancet Infect. Dis. 17(2), 140. http://dx.doi.org/10.1016/S1473-3099(17)30024-5.

Micieli, M.V., Marti, G. and García, J.J., 2002. Laboratory evaluation of *Mesocyclops annulatus* (Wierzejski, 1892) (Copepoda: Cyclopidea) as a predator of container-breeding mosquitoes in Argentina. Mem. Inst. Oswaldo Cruz. 97(6), 835–838. http://dx.doi.org/10.1590/S0074-02762002000600014.

Murugan, K., Benelli, G., Panneerselvam, C., Subramaniam, J., Jeyalalitha, T., Dinesh, D., Nicoletti, M., Hwang, J.S., Suresh, U., Madhiyazhagan, P., 2015. *Cymbopogon citratus*-synthesized gold nanoparticles boost the predation efficiency of copepod *Mesocyclops aspericornis* against malaria and dengue mosquitoes. Exp Parasitol 153, 129–138. http://dx.doi.org/10.1016/j.exppara.2015.03.017.

Nam, V.S., Yen, N.T., Duc, H.M., Tu, T.C., Thang, V.T., Le, N.H., Le Loan, L., Huong, V.T.Q., Khanh, L.H.K., Trang, H.T.T., Lam, L.Z.Y., Kutcher, S.C., Aaskov, J.G., Jeffery, J.A.L., Ryan, P.A., Kay, B.H., 2012. Community-based control of *Aedes aegypti* by using *Mesocyclops* in Southern Vietnam. Am. J. Trop. Med. Hyg. 86(5), 850–859. http://dx.doi.org/10.4269/ajtmh.2012.11-0466.

Novich, R.A., Erickson, E.K., Kalinoski, R.M., DeLong, J.P., 2014. The temperature independence of interaction strength in a sit-and-wait predator. Ecosphere 5(10), 1–19. http://dx.doi.org/10.1890/ES14-00216.1.

O'Neil, R.J., 1990. Functional response of arthropod predators and its role in the biological control of insect pests in agricultural systems, in: Dunn, P.E., Baker, R.R. (Eds.) New directions in biological control: alternatives for suppressing agricultural pests and diseases. Alan R. Liss, Inc., New York, pp. 83–96.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., Petchey, O.L., 2012. Universal temperature and body-mass scaling of feeding rates. Philos. Trans. R. Soc. Lond., Series B Biol. Sci. 367(1605), 2923–2934.

http://dx.doi.org/10.1098/rstb.2012.0242.

Ruybal, J.E., Kramer, L.D., Kilpatrick, A.M., 2016. Geographic variation in the response of Culex pipiens life history traits to temperature. Parasit. Vectors 9(116), 1–9. https://doi.org/10.1186/s13071-016-1402-z.

Siraj, A.S., Oidtman, R.J., Huber, J.H., Kraemer, M.U.G., Brady, O.J., Johansson, M.A., Perkins, T.A., 2017. Temperature modulates dengue virus epidemic growth rates through its effects on reproduction numbers and generation intervals. PLOS Negl. Trop. Dis. 11(7), e0005797. https://doi.org/10.1371/journal.pntd.0005797.

Solomon, M.E., 1949. The natural control of animal populations. J. Anim. Ecol. 18, 1–35.

South, J., Dick, J.T.A., McCard, M., Barrios-O'Neill, D., Anton, A., 2017. Predicting predatory impact of juvenile invasive lionfish (*Pterois volitans*) on a crustacean prey using functional response analysis: effects of temperature, habitat complexity and light regimes. Environ. Biol. Fish. http://dx.doi.org/10.1007/s10641-017-0633-y.

Tinson, S., Laybourn-Parry, J. 1986. The distribution and abundance of benthic cyclopoid copepods in Esthwaite Water, Cumbria. Hydrobiol. 131(3), 225–234. http://dx.doi.org/10.1007/BF00008858.

Toscano, B.J., Rombado, B.R., Rudolf, V.H.W., 2016. Deadly competition and life-saving predation: the potential for alternative stable states in a stage-structured predator–prey system. Proc. R. Soc. Biol., pii, 20161546. http://dx.doi.org/10.1098/rspb.2016.1546.

Townroe, S., Callaghan, A., 2014. British container breeding mosquitoes: The impact of urbanisation and climate change on community composition and phenology. PLoS ONE, 9(4), e95325. https://doi.org/10.1371/journal.pone.0095325.

Trexler, J.C., McCulloch, C.E., Travis, J., 1988. How can the functional response best be determined? Oecologia 76(2), 206–214. https://doi.org/10.1007/BF00379954.

Van Driesche, R., Bellows, T.S., 2011. Biological control. Springer, Berlin. https://doi.org/10.1007/978-1-4613-1157-7.

Veronesi, R., Carrieri, M., Maccagnani, B., Maini, S., Bellini, R. 2015. *Macrocyclops albidus* (Copepoda: cyclopidae) for the Biocontrol of *Aedes albopictus* and *Culex pipiens* in Italy. J. Am. Mosq. Control Assoc. 31(1), 32–43. https://doi.org/10.2987/13-6381.1.

Wasserman, R.J., Alexander, M.E., Weyl, O.J.F., Barrios-O'Neill, D., Froneman, P.W., Dalu, T., 2016. Emergent effects of structural complexity and temperature on predator-prey interactions. Ecosphere, 7(2), e01239. http://dx.doi.org/10.1002/ecs2.1239.

Yee, D.A. 2016. Thirty years of *Aedes albopictus* (Diptera: Culicidae) in America: An introduction to current perspectives and future challenges. J Med Entomol. 53(5), 989-991. https://doi.org/10.1093/jme/tjw063.

Tables

Table 1. Fecundity (%) calculations, entailing proportion of total consumed energy (C) devoted to production of eggs (P_r) in adult female *M. albidus* and *M. viridis* across 12 ^{o}C, 16 ^{o}C and 20 ^{o}C. Data relating to energetics adapted from Laybourn-Parry et al. (1988, n = 5, Eqn. 6).

Species	Temperature (^{o}C)	C (mJ)	P_r (mJ)	Fecundity (%)
M. albidus	12	31210	2355	7.55
	16	26150	2907	11.12
	20	29150	3691	12.66
M. viridis	12	34433	2851	8.28
	16	25311	3020	11.93
	20	24960	1671	6.70

Table 2. Results of logistic regression to denote functional response type across all predator and temperature treatments, alongside the starting attack rate (*a*) and handling time (*h*) parameter estimates generated using the Rogers' random predator equation (Eqn. 5).

Species	Temperature (^oC)	First order term	*p*	*a*	*p*	*h*	*p*
M. albidus	12	-0.024	< 0.001	1.276	< 0.001	0.065	< 0.001
M. albidus	16	-0.031	< 0.001	1.917	< 0.001	0.044	< 0.001
M. albidus	20	-0.037	< 0.001	2.373	< 0.001	0.035	< 0.001
M. viridis	12	-0.025	< 0.001	0.945	< 0.001	0.071	< 0.001
M. viridis	16	-0.030	< 0.001	1.896	< 0.001	0.039	< 0.001
M. viridis	20	-0.039	< 0.001	2.186	< 0.001	0.032	< 0.001

Table 3: Mean Relative Control Potential (RCP) using abundances for *M. albidus* and *M. viridis*, alongside uncertainties reflected through 60% confidence intervals (CI) and probability that the RCP output exceeds 1 using maximum feeding and attack rates. Asterisks denote significant levels of certainty that the RCP score is greater than 1 (* > 95%, ** > 99%, *** > 99.9%).

Comparators (agent A, agent B)	FR parameter (mean ± SD)	Abundance (mean ind. m^{-2} ± SD)	RCP	CI $p_{\mathrm{RCP}} > 1$ (%)
M. albidus, M. viridis	1/*h*: 22.80 (± 8.37), 24.41 (± 10.55)	6727 (± 1018.23), 562 (± 288.50)	16.77	6.79 – 23.78 99.97***
M. albidus, M. viridis	*a*: 1.98 (± 0.72), 1.77 (± 0.67)	6727 (± 1018.23), 562 (± 288.50)	19.34	8.18 – 27.35 99.99***

Table 4: Mean Relative Control Potential (RCP) using fecundities (%) across temperature change for *M. albidus* and *M. viridis* alongside uncertainties reflected through 60% confidence intervals (CI) and probability that the RCP output exceeds 1 using maximum feeding and attack rates. Asterisks denote significant levels of certainty that the RCP score is greater than 1 (* > 95%, ** > 99%, *** > 99.9%).

Comparators (agent A, agent B)	Temperature (°C)	FR parameter (mean ± SD)	Fecundity (%)	RCP	CI $p_{\mathrm{RCP}} > 1$ (%)
M. albidus, Me viridis	12	1/*h*: 15.88 (± 4.36), 13.99 (± 2.67)	7.55, 8.28	1.07	0.77 – 1.34 51.93
M. albidus, Me viridis	16	1/*h*: 22.12 (± 7.64), 25.98 (± 9.68)	11.12, 11.93	0.90	0.53 – 1.21 32.58
M. albidus, M. viridis	20	1/*h*: 30.42 (± 5.24), 33.25 (± 6.73)	12.66, 6.70	1.80	1.39 – 2.17 98.21*
M. albidus, Me viridis	12	*a*: 1.43 (± 0.52), 1.05 (± 0.34)	7.55, 8.28	1.37	0.82 – 1.83 66.71
M. albidus, Me viridis	16	*a*: 2.17 (± 0.51), 2.02 (± 0.39)	11.12, 11.93	1.04	0.77 – 1.28 49.04
M. albidus, M. viridis	20	*a*: 2.34 (± 0.75), 2.24 (± 0.54)	12.66, 6.70	2.09	1.39 – 2.69 95.34*

Table 5: Q_{10} coefficient (Eqn. 7) values associated with mean maximum feeding rates for both predators between temperature gradients.

Species	Temperature (ºC)	Mean max. feeding rate (1/*h*)	Q_{10} value
M. albidus	12 – 20	15.88 – 30.42	2.25
M. albidus	12 – 16	15.88 - 22.12	2.29
M. albidus	16 – 20	22.12 – 30.42	2.22
M. viridis	12 – 20	13.99 – 33.25	2.95
M. viridis	12 – 16	13.99 – 25.98	4.70
M. viridis	16 – 20	25.98 – 33.25	1.85

Figures

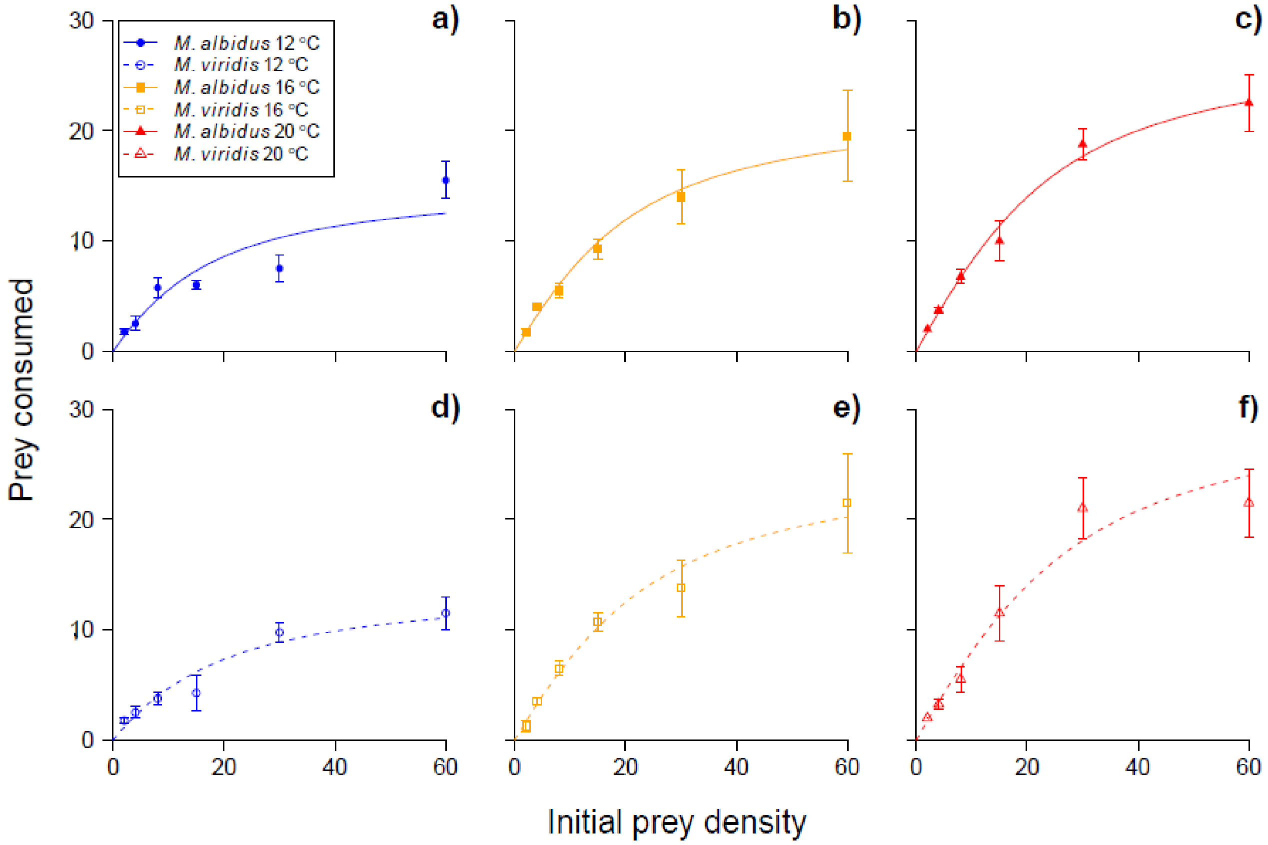

Figure 1. Functional responses of *M. albidus* (a, b, c) and *M. viridis* (d, e, f) towards first instar *C. pipiens* larvae at 12 ºC (a, d), 16 ºC (b, e) and 20 ºC (c, f) over the 24 hour experimental period. Means are ± SE at each prey density (*n* = 4).

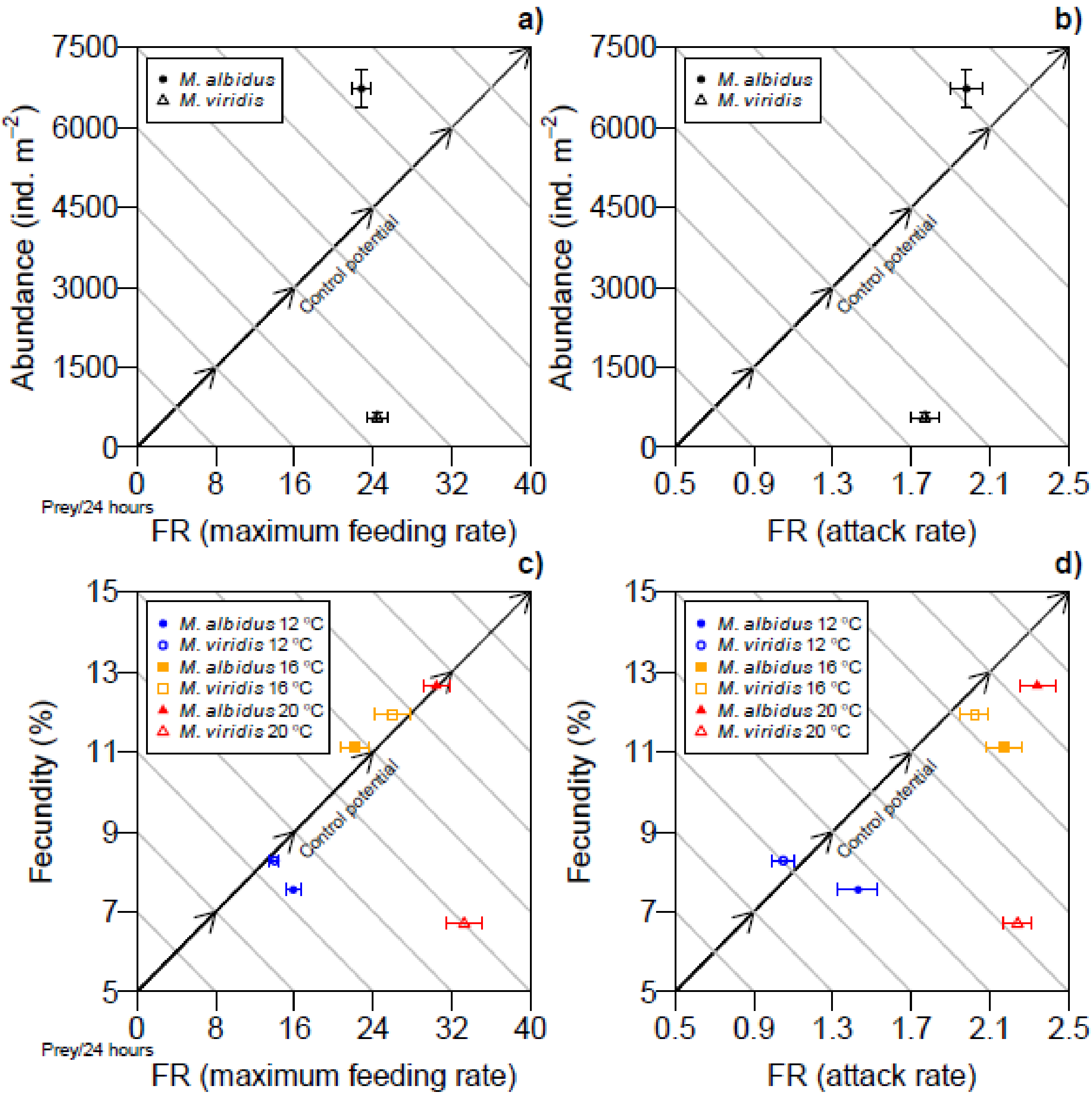

Figure 2. RCP biplots comparing *M. albidus* and *M. viridis* using abundance estimates (a, b; *n* = 8) and fecundity calculations (c, d; Table 1), with FR parameters of maximum feeding (a, c) and attack rate (b, d). FR parameters in abundance biplots are pooled bootstrapped estimates across all temperatures (*n* = 90); those in fecundity plots are temperature-specific estimates (*n* = 30). Increasing CP is read from bottom left to top right. Abundance and FR parameter means are ± SE.