University of Reading

Sex-skewed trophic impacts in ephemeral wetlands

Article

Accepted Version

Cuthbert, R. N., Dalu, T., Wasserman, R. J., Weyl, O. L. F., Callaghan, A. ORCID: https://orcid.org/0000-0002-2731-3352, Froneman, W. and Dick, J. T. A. (2019) Sex-skewed trophic impacts in ephemeral wetlands. Freshwater Biology, 64 (2). pp. 359-366. ISSN 0046-5070 doi: 10.1111/fwb.13228 Available at https://centaur.reading.ac.uk/81537/

It is advisable to refer to the publisher's version if you intend to cite from the work. See Guidance on citing.

To link to this article DOI: http://dx.doi.org/10.1111/fwb.13228

Publisher: Wiley

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the End User Agreement.

www.reading.ac.uk/centaur

CentAUR

University of Reading

Central Archive at the University of Reading

Reading's research outputs online

Sex-skewed trophic impacts in ephemeral wetlands

Biotic interactions in temporary ponds

Ross N. Cuthbert[*1, 2, 3], Tatenda Dalu[4, 5], Ryan J. Wasserman[5, 6], Olaf L. F. Weyl[2], Amanda Callaghan[3], P. William Froneman[7], Jaimie T. A. Dick[1]

[1]*Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, Medical Biology Centre, Belfast BT9 7BL, Northern Ireland*

[2]*DST/NRF Research Chair in Inland Fisheries and Freshwater Ecology, South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown 6140, South Africa*

[3]*Ecology and Evolutionary Biology, School of Biological Sciences, University of Reading, Harborne Building, Reading RG6 6AS, England*

[4]*Department of Ecology and Resource Management, University of Venda, Thohoyandou 0950, South Africa*

[5]*South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown 6140, South Africa*

[6]*Department of Biological Sciences and Biotechnology, Botswana International University of Science and Technology, P. Bag 16, Palapye, Botswana*

[7]*Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa*

[*]*Corresponding author: address, Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, Medical Biology Centre, Belfast BT9 7BL, Northern Ireland; e-mail, rcuthbert03@qub.ac.uk; orcid ID, https://orcid.org/0000-0003-2770-254X*

Keywords

predator-prey; functional response; zooplankton; population impact; *Lovenula raynerae*

Abstract

1. Predation can have marked impacts on ecosystem structure, function and stability. However, quantifications of biotic interactions frequently overlook demographic variabilities within populations which can modulate interaction strengths, such as sex and reproductive status. Compositional population ratios between males and females, alongside reproductive status, are highly variable temporally in ephemeral aquatic systems, and may profoundly mediate levels of ecological impact and thus stability of trophic groups.

2. In the present study, we apply functional responses (resource intake as a function of resource density) to quantify predatory impacts of adult males, non-gravid females and gravid females of the calanoid copepod *Lovenula raynerae* (Diaptomidae), an abundant ephemeral pond specialist, on larvae of the *Culex pipiens* (Culicidae) mosquito complex. We then develop a novel metric to forecast population-level impacts across different population sex ratio scenarios.

3. *Lovenula raynerae* demonstrated prey population destabilising Type II functional responses irrespective of sex and reproductive status, yet variable functional response magnitudes were found. While male and non-gravid female copepods exhibited similar functional response maximum feeding rates, gravid female feeding rates were substantially higher, implying higher resource demands for progeny development. Ecological impacts of *L. raynerae* on lower trophic groups increased markedly where their abundances increased but, crucially, also as population sex ratios became more biased towards gravid female copepods.

4. We demonstrate that population-level impacts do not only correlate tightly with abundance, but may be further modulated by reproductive status variations. Thus, the development of sex-skewed ratios in favour of gravid females during the hydroperiod likely heightens ecological impacts on lower trophic groups. The implications of these results for prey population stability are discussed in the context of freshwater ecosystems.

1. Introduction

Predation profoundly affects prey population stability and the overall structuring and functioning of communities at the ecosystem level (Brooks & Dodson, 1965; Carpenter et al., 1975; Wasserman et al., 2013). In particular, invertebrate population dynamics in aquatic systems are heavily influenced by predation (Brooks & Dodson, 1965; Sih et al., 1985; Brendonck et al., 2002; Wasserman et al., 2013), with population demographics in freshwaters highly changeable due to a plethora of biotic and abiotic variables (e.g. Wasserman et al., 2018). Temporal differences in population demographics of resident predators can, in turn, affect interaction strengths towards basal prey (e.g. Alexander et al., 2013), and the nature of these interactions can influence population persistence of many trophic groups (Murdoch, 1969; Dick et al., 2014, 2017). Classical models concerning predator-prey interactions have, however, often assumed equivalence between individual predators irrespective of intraspecific life history variabilities (Volterra, 1928; Lotka, 1956; Rosenzweig & MacArthur, 1963). Consequently, effects related to sex ratios or ontogeny have largely been overlooked, undermining our capacity to reliably predict the total impacts of predators on prey groups within ecosystems.

Ephemeral wetlands are idealised model systems for testing ecological theories that are broadly applicable to ecology, evolutionary biology and conservation biology, particularly given their small size, relatively simple trophic structuring and clear physical boundaries (De Meester et al., 2005; Dalu et al., 2017b). Further, in contrast to permanent freshwaters, their characteristically short wet phases enable observations of ecological processes over the entire duration of the hydroperiod (Dalu et al. 2017b; Wasserman et al., 2018). As they are internally drained, wet phases in ephemeral systems rely entirely on periodic rainfall. Crustacean groups such as copepods are often numerically abundant in the early-middle stages of hydroperiod as they hatch

from dormant eggs *in situ*, and have been reported to occupy the top trophic level in these simple ecosystems for parts of the hydroperiod (Dalu et al., 2017b, c). Indeed, mass-hatching of predatory zooplankton can occur as a once-off event, and may elicit enormous predation pressure on lower trophic groups over short timescales (Brendonck & De Meester, 2003).

Sex ratios within ephemeral aquatic systems can be highly varied through the hydroperiod, and sex-skewed ratios in favour of female copepods may manifest over time due to selective processes such as predation (see male predation hypothesis: Kiørboe, 2006; Gusmão et al., 2013; Wasserman et al., 2018). However, ephemeral aquatic systems remain poorly understood as a result of their spatial and temporal heterogeneity, with interaction strengths between trophic groups very poorly quantified (though see Wasserman et al., 2016a, 2018; Cuthbert et al. 2018a). Indeed, in many arid locations, ephemeral wetlands are not even mapped, let alone studied (see Dalu et al. 2017a). This is despite the fact that these systems often act as hotspots for threatened and endemic species that are unable to persist in more permanent waters due to greater predation pressures (De Meester et al., 2005). Ephemeral ecosystems also often lack intensive higher-order vertebrate predation (Kerfoot & Lynch, 1987; Brendonck et al., 2002) and, moreover, exhibit rapid ecological succession through the restricted wet phases. As environmental change implications for biotic interactions are the most challenging to predict with certainty, quantifying interaction strengths between species is crucial to understanding ecosystem stability (Daufresne et al., 2009; Gilbert et al., 2014), and this is particularly important in ephemeral wetlands where there is a high degree of specialist adaptation and endemism (De Meester et al., 2005; Dalu et al. 2017a).

Functional responses have been a staple method in elucidating consumer-resource interactions, and have been frequently used to examine biotic context-dependencies of interaction strengths

within ecosystems (e.g. Alexander et al., 2013; Barrios-O'Neill et al., 2014; Wasserman et al., 2016b). In a predation context, functional responses depict the predation rate as a function of prey density. Three common functional response forms have been described (Holling, 1959): (1) Type I, specific to filter-feeders (Jeschke et al., 2004), wherein the consumption rate increases linearly with the quantity of resources supplied up to a sharply defined maximum (Holling, 1959; Hassell, 1978); (2) Type II, where the consumption rate falls asymptopically with prey density; (3) Type III, characterised by a sigmoidal form wherein the predation rate increases at low prey densities, before once again falling asymptopically (Holling, 1959; Hassell, 1978). Both the form and magnitude of the functional response can be used to quantify *per capita* ecological impacts of consumers in ecosystems (Dick et al., 2014), and, in turn, predict ecosystem-level stability outcomes arising from predator-prey interactions (e.g. Rosenzweig & MacArthur, 1963). In this respect, Type II forms have been frequently characterised as destabilising due to high levels of resource consumption at low resource (e.g. prey) densities, whereas Type III forms may facilitate stability within communities due to refuge provisioning at low prey densities (e.g. Murdoch, 1969; Dick et al., 2014).

The present study thus aimed to quantify interaction strengths within ephemeral wetlands across variable population sex ratios. Although functional responses have shown to be robust in quantifications of *per capita* biotic interaction strengths between consumers and resources, assimilations of population-level effects are often lacking, reducing our capacity to project interaction strengths holistically between trophic groups (though see Dick et al., 2017; Cuthbert et al., 2018b, c). Furthermore, methodological advances which address consumer impact implications resulting from changing population demographics temporally have yet to be developed fully. Here, we examine the effects of emergent and field-validated sex-skewed

populations on predatory impacts within ephemeral aquatic systems at the *per capita* and then population-level. First, we use comparative functional responses to quantify the ecological impacts of adult males, non-gravid females and gravid females of the calanoid copepod *Lovenula raynerae*, a top predator in ephemeral wetlands, towards larval prey of the vectorially-important *Culex pipiens* mosquito complex. Such large copepod species have been previously demonstrated to be voracious consumers of mosquito larvae which colonise ephemeral ecosystems (e.g. Cuthbert et al., 2018a). We then quantify and illustrate population-level trophic impacts of *L. raynerae* using scenarios of sex ratio dynamics within ephemeral aquatic ecosystems. Therein, we develop novel metrics to elucidate how changing population demographics and abundances may drive trophic impacts in such ecosystems.

2. Methods

2.1. Animal collection and maintenance

During the 2017–2018 austral summer, adult *L. raynerae* (Suárez-Morales et al., 2015) were collected from an ephemeral pond in the Eastern Cape province of South Africa (33° 16' 47.8" S, 26° 35' 39.8" E) by towing a zooplankton net through the upper water column, and were then transported in source water to a controlled environment (CE) room at Rhodes University, Grahamstown, Eastern Cape. Adult males, non-gravid females and gravid females (males, 4.71 mm ± 0.11 mm; females, 4.77 mm ± 0.14 mm; gravid females, 4.88 mm ± 0.08 mm) were maintained in the CE room at 25 ± 1 °C in 25 L aquaria and fed *ad libitum* with larval mosquito prey. The focal prey, *C. pipiens* larvae (3.14 mm ± 0.19 mm) were cultured using egg rafts collected from artificial containers on the Rhodes University campus, and reared to the desired

size class in the laboratory using a diet of crushed rabbit pellets (Agricol, Port Elizabeth), supplied *ad libitum*. Mosquitoes were identified in accordance with Jupp (1996). Experimentation and acclimation were undertaken under a 12:12 light:dark laboratory photoperiod.

2.2. Functional responses

To derive the effects of sex and reproductive status variations on the *per capita* predatory impact of focal copepods, we employed a 3 × 6 experimental design with respect to copepod group (3 levels) and prey density (6 levels). Adult males, non-gravid females and gravid females of *L. raynerae* were provided larvae of *C. pipiens* at six prey densities (2, 4, 8, 16, 32, 64; $n = 4$ per experimental group) in 80 mL arenas of 5.6 cm diameter containing dechlorinated tapwater from a continuously aerated source. Prey were allowed to settle for 2 h prior to the addition of predators, which subsequently fed undisturbed for 5 h. Following the experimental period, predators were removed and remaining live prey counted. Predators were starved for 48 h before use to standardise levels of hunger. Controls consisted of three replicates at each prey density without the addition of predators.

2.3. Statistical analyses and impact projections

All statistical analyses were undertaken in R v3.4.4 (R Core Team, 2018). Generalised linear models (GLMs) assuming a Poisson error distribution were used to analyse overall prey consumption with respect to the ‘copepod group’ and ‘prey density’ factors, and their interaction. Residual deviance did not exceed degrees of freedom and so thus counts were not deemed to be overdispersed here. Non-significant terms were removed stepwise from the model to obtain the

most parsimonious fit, with χ^2 used for model simplification *via* analysis of deviance parameter selection (Crawley, 2007).

Several approaches have been developed for the analysis of functional responses, with model selection dependent on whether a particular study design is phenomenological or mechanistic in its aims (Jeschke et al., 2002). As mechanistic applications of attack rate and handling time parameters are reliant on empirical validations of parameter estimates, however, here we employ a phenomenological approach to examine comparatively the functional response types and parameter estimates in a factorial design (see also Alexander et al. 2012; Dick et al. 2014). Functional response analyses were thus undertaken using the 'frair' package in R (Pritchard et al., 2017). Logistic regression of the proportion of prey consumed as a function of prey density was used to infer functional response types. A Type II functional response is characterised by a significantly negative first order term, whilst a Type III functional response is characterised by a significantly positive first order term followed by a significantly negative second order term (Solomon, 1949; Holling, 1959). As prey were not replaced as they were consumed, we fit Rogers' random predator equation which accounts for depleting prey densities over the experimental period (Trexler et al., 1998; Juliano, 2001):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \qquad \text{Eqn. 1.}$$

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 used to make the random predator equation solvable (Bolker, 2008). Initial functional response fits were non-parametrically bootstrapped 2000 times to generate bias-corrected and accelerated 95%

confidence intervals, enabling the functional responses to be considered in population terms across prey densities (e.g. Barrios-O'Neill et al., 2014).

We then used handling time (*h*) estimates from Eqn. 1 to quantify maximum feeding rates over the experimental period (1/*h*) for each copepod group, before calculating ecological impacts of *L. raynerae* across varied intraspecific sex ratios, where impact with gravid females *g* is derived as:

$$g = ((1/h_m) \times p_m) + ((1/h_f) \times p_f)$$

Eqn. 2.

where 1/*h* is the maximum feeding rate of males ($_m$) or gravid females ($_f$), and *p* is the proportion of males or gravid females within a given population. As handling times and, inversely, maximum feeding rates of males and non-gravid females were highly similar, we used the mean initial estimate of maximum feeding rate (1/*h*) between these groups to derive a baseline null impact level using Eqn. 2, unchanged across sex ratio variabilities. We thus created an impact index aligned with gravid female copepods by dividing their proportioned impact score against this null baseline, where impact index *I* is:

$$I = (g/b)$$

Eqn. 3.

resulting from the division of the proportioned impact with gravid females *g* by the baseline impact between non-gravid and male copepods *b*. Then, using proportional abundance estimations as a multiplier, Eqn. 3 can be modified to project population-level impacts, where *PI* is:

$$PI = I \times p_{ab}$$

Eqn. 4.

where p_{ab} is the proportion of maximum population abundance at a given time. We then used biplots to display *PI* graphically for different sex ratio scenarios, given varied copepod population compositions.

3. Results

No prey mortality was observed in control treatments and thus all experimental deaths were attributed to predation. This was further evidenced visually and by partially consumed remains of culicid prey. Type II functional responses were observed for each predator treatment as evident from significantly negative first order terms (Table 1; Figure 1). Overall consumption was significantly affected by the sex and reproductive status of copepods ($\chi^2 = 7.55$, $df = 2$, $p = 0.02$), driven by greater predation levels by gravid females compared to males and non-gravid females. Overall consumption also increased significantly as prey densities increased ($\chi^2 = 136.55$, $df = 5$, $p < 0.001$), and this effect was consistent across different copepod groups as there was no significant 'sex × prey density' interaction effect ($\chi^2 = 2.12$, $df = 10$, $p = 0.99$). Gravid females displayed a substantially higher functional response magnitude, with considerably lower handling times corroborating with greater maximum feeding rates than males or non-gravid females (Table 1; Figure 1). Conversely, functional response magnitudes of male and non-gravid female *L. raynerae* were highly similar (Figure 1).

Impact index values increased substantially where intraspecific proportions became sex-skewed in favour of gravid females, driven by the marked maximum feeding rates of gravid female *L. raynerae* relative to males and non-gravid females (Table 2). Generally, population-level impacts increased as copepods approached maximal abundances and with skewed populations in favour

of gravid females (Figure 2). Where sex ratios were relatively stable, population impacts increased concurrently only with abundance (Figure 2a). However, where populations became increasingly sex-skewed towards gravid females under higher abundances, population-level impacts at maximal abundances were greater than under the stable sex ratio scenario (Figure 2b), and, inversely, where proportions of gravid females decreased with increasing overall abundance (Figure 2c).

4. Discussion

Demographics within species populations can be highly variable across spatiotemporal gradients, and such variations can have significant implications for biotic interactions within ecosystems, such as predation (Alexander et al. 2013; Wasserman et al., 2018). Given the important role of predation in the structuring and functioning of aquatic ecosystems (Brooks & Dodson, 1965; Carpenter et al., 1975; Wasserman et al., 2013), understanding the implications of demographics, such as sex ratio variabilities, is critical for robust interaction strength quantifications between trophic groups. Further, the development of measures to predict ecological impacts is crucial. The present study demonstrates biotic context-dependencies in interaction strengths between the freshwater calanoid copepod *L. raynerae* and basal culicid prey, wherein maximum feeding rates were similar between male and non-gravid female copepods, but were elevated in gravid female copepods. Thus, the effects of sex demographics on ecological impacts are in turn dependent on reproductive status. Further, given their highly dynamic communities (Wasserman et al., 2018), we demonstrate that trophic impacts may exhibit marked variations over the course of the hydroperiod in ephemeral freshwater ecosystems, with these impacts in turn dependent on the structuring of sex ratios relative to abundances within populations. Our results demonstrate how quantifications of demographic variations in consumptive traits can be used to help predict

ecological impacts, with our approach equally applicable to consumer-resource interactions in other ecosystems.

Functional responses have been widely applied to quantify the impacts of predators on prey populations (see for example Dick et al., 2014; Cuthbert et al., 2018b). However, studies often standardise predator characteristics, such as sex or size (e.g. Laverty et al., 2015; Wasserman et al. 2016a; South et al., 2017). Whilst this is important with respect to trophically-analogous species comparisons, this approach may reduce our capacity to derive holistic accounts of ecological impact for species with complicated population demographics. In our model system, we show that *L. raynerae* exhibits a Type II functional response irrespective of sex or reproductive status. This functional response form is associated with destabilising pressures towards prey populations (see Dick et al., 2014) and thus may drive localised extinctions of prey. Indeed, *L. raynerae* adult males have previously been shown to exert a similar functional response towards daphniid prey (Wasserman et al., 2016a). This contrasts with other calanoid species which demonstrate a sigmoidal functional response, conducive to greater potential for prey population stability due to low density prey refugia (Wasserman et al., 2016a). Moreover, *L. raynerae* has been shown to be a top predator and a particularly strong competitor with other copepods in ephemeral ponds, with greater prey capture efficiencies and shorter handling times (Wasserman et al,. 2016a; Dalu et al., 2017c). Thus, the predatory impact of *L. raynerae* may be particularly high towards low density basal prey populations irrespective of sex demographics. The feeding niche of *L. raynerae* has also been shown to be relatively small, and fluctuates with relative resource availabilities, with zooplankton forming a large dietary component (Dalu et al., 2016). For this species, consumptive traits have additionally been shown to be similar between sexes (Dalu et al., 2017c), particularly during the early pond stage when mosquitoes are most

abundant. It is therefore likely that such predatory traits drive substantial impacts upon lower trophic groups in these systems, especially given the recurrent destabilising Type II functional responses of *L. raynerae* (Wasserman et al., 2016a; Cuthbert et al., 2018a). However, quantifications of variations in biotic interaction strengths driven by processes such as prey preferences and switching across predator demographic variabilities could further enhance predictive efforts surrounding interaction strengths and cascade effects to prey through ecosystems (e.g. Murdoch, 1969; Cuthbert et al., 2018d).

Although the functional response form of *L. raynerae* was similar through their sex and reproductive demography, there were substantial variations in functional response magnitude. Handling times were lowest for gravid female copepods, resulting in the highest maximum feeding rates across copepod groups. In turn, there were no significant differences between males and non-gravid females, indicating that a greater nutritional uptake is driven in line with reproductive status in copepods. The elevated feeding rates of gravid females shown here likely translates into greater *per capita* pressures on basal prey when this group is abundant. Globally, copepods are a highly diverse and widespread group, forming substantial components of aquatic ecosystems (Dussart & Defaye, 2001). Given sexual dimorphism is prevalent in many copepod species, with females often more voracious due to heightened energy demands associated with size and reproduction, it is likely our results would be paralleled in other ecosystems (e.g. Laybourn-Parry et al., 1988; Marten and Reid, 2007). The application of functional responses holds great potential in the quantification of demographic implications for consumer-resource interactions across ecosystems. Standardised laboratory experiments may yield high explanatory power in comparing interactions, both between and within species, and have been shown to

correlate tightly with known ecological impacts in the field and with independent impact measures (Dick et al., 2014; 2017).

Sex ratios can be particularly dynamic through time due to selective processes such as predation, and have been shown to change markedly over the hydroperiod in ephemeral aquatic ecosystems (e.g. Wasserman et al., 2018). In turn, interaction strengths between trophic groups also vary substantially over the course of the hydroperiod (Schneider & Frost, 1996; O' Neill & Thorp, 2014), with predation pressures characteristically dominated by invertebrates in these systems. Although recent advances have sought to integrate population-level impacts with *per capita* effects in order to derive comprehensive ecological impact predictions in the context of invasive species (Dick et al., 2017) and biological control (Cuthbert et al., 2018b), there has been little consideration hitherto for population demographic variabilities which may further modulate impact. Such quantifications could provide improved insights into population-level consumer-resource interactions across ecosystems. In our study system, we demonstrate that the integration of sex ratios, and particularly reproductive status, may further enhance predictions for population-level impacts on lower trophic groups in ephemeral ponds and other ecosystems. Thus, here, as female *L. raynerae* have been shown to dominate zooplankton assemblages in the middle and late hydroperiod within ephemeral aquatic ecosystems (Wasserman et al., 2018), ecological impacts during this period are likely elevated if large proportions of copepods are gravid and present in high abundances. We postulate that this may indeed be the case, given the necessity of dormant egg production towards the end of the hydroperiod, coupled with frequent mass-hatching events (Brendonck & De Meester, 2003). Indeed, the high consumption rates demonstrated in the present study may promote high fitness and gravidity within populations while prey are abundant, thus further exacerbating ecological impacts through feedbacks. Given

that ephemeral aquatic ecosystems remain poorly studied despite their ecological significance (Dalu et al., 2017a), our displayed derivations of population-level impacts are based on hypothetical sex ratio scenarios across the course of the hydroperiod. However, extreme sex ratio variations have indeed been demonstrated in these systems through field observations (see Wasserman et al., 2018).

In conclusion, the results of the present study show that sex-skewed population demographics can profoundly influence predation rates, which ultimately may drive fluctuations in population-level ecological impacts temporally. We present a novel approach which could improve the forecasting of ecological impacts in ecosystems through the integration of *per capita*, abundance and compositional effects within populations. Here, although female copepods are more voracious, this effect is dependent on their state of gravidity, with only gravid and ovigerous females exhibiting significantly higher feeding rates than males. Accordingly, we expect impacts on lower trophic groups to be greatest where gravid females disproportionately dominate zooplankton populations across the hydroperiod. To this end, further research should seek to elucidate the effects of multiple con/interspecific predators on predatory impact in these atypical aquatic systems, in order to ascertain the direct effects of multiple predators on consumption rates, alongside variations in ecological impacts across life history stages. Further examinations of temporal demographics across a multitude of ecosystems would be highly informative in identifying large-scale implications of sex ratio variations for interaction strengths.

Acknowledgements

This study forms part of a PhD studentship funded by the Department for the Economy, Northern Ireland. We extend gratitude to Rhodes University for the provision of laboratory facilities. We acknowledge use of infrastructure and equipment provided by the SAIAB Research Platform and

the funding channelled through the NRF-SAIAB Institutional Support system. This study was partially funded by the National Research Foundation – South African Research Chairs Initiative of the Department of Science and Technology (Inland Fisheries and Freshwater Ecology, Grant No. 110507).

Conflicts of interest

The authors declare no conflicts of interest.

Data accessibility

Underlying functional response data are available in the online supplementary information.

References

Alexander, M. E., Dick, J. T. A., O'Connor, N. E., Haddaway, N. R., & Farnsworth K. D. (2012). Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey supply, model selection and habitat complexity. *Marine Ecology Progress Series*, 468, 191–202.

Alexander, M. E., Dick, J. T. A., & O'Connor, N. E. (2013). Born to kill: Predatory functional responses of the littoral amphipod *Echinogammarus marinus* Leach throughout its life history. *Journal of Experimental Marine Biology and Ecology*, 439, 92–99.

Barrios-O'Neill, D., Dick, J. T. A., Emmerson, M. C., Ricciardi, A., MacIsaac, H. J., Alexander, M. E., & Bovy, H. C. (2014). Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. *Journal of Animal Ecology*. 83, 693–701.

Bolker, B. M. (2008). Ecological models and data in R. Princeton University Press, Princeton.

372 Brendonck, L., & De Meester, L. (2003). Egg banks in freshwater zooplankton: evolutionary and
373 ecological archives in the sediment. *Hydrobiologia,* 491, 65–84.

374 Brendonck, L., Michels, E., De Meester., L., & Riddoch, B. (2002). Temporary pools are not
375 'enemy-free'. *Hydrobiologia,* 486, 147–159.

376 Brooks, J. L., & Dodson, S. I. (1965). Predation, body size, and composition of plankton.
377 *Science,* 150, 28–35.

378 Carpenter, S. R., Kitchell, J. F., & Hodgson, J. R. (1985). Cascading trophic interactions and lake
379 productivity. *BioScience,* 35, 634–639.

380 Crawley, M. J. (2007). The R book. John Wiley & Sons, Chichester.

381 Cuthbert, R. N., Dalu, T., Wasserman, R. J., Callaghan, A., Weyl, O. L. F., & Dick, J. T. A.
382 (2018a) Calanoid copepods: an overlooked tool in the control of disease vector mosquitoes.
383 Journal of Medical Entomology, online.

384 Cuthbert, R. N., Dick, J. T. A., Callaghan, A., & Dickey, J. W. E. (2018b). Biological control
385 agent selection under environmental change using functional responses, abundances and
386 fecundities; the Relative Control Potential (RCP) metric. *Biological Control,* 121, 50–57.

387 Cuthbert, R. N., Dick, J. T. A., & Callaghan, A. (2018c). Interspecific variation, habitat
388 complexity and ovipositional responses modulate the efficacy of cyclopoid copepods in disease
389 vector control. *Biological Control*, 121, 80–87.

390 Cuthbert, R. N., Dickey, J. W. E., McMorrow, C., Laverty, C., & Dick, J. T. A. (2018d)
391 Resistance is futile: lack of predator switching and a preference for native prey predict the
392 success of an invasive prey species. *R. Soc. Open Sci.* **5**, 180339.

393 Dalu, T., Weyl, O. L. F., Froneman, P. W., & Wasserman, R. J. (2016). Trophic interactions in
394 an austral temperate ephemeral pond inferred using stable isotope analysis. *Hydrobiologia*, 768,
395 81–94.

396 Dalu, T., Wasserman, R. J., & Dalu, M. T. B. (2017a). Agricultural intensification and drought
397 frequency increases may have landscape level consequences for ephemeral ecosystems. *Global*
398 *Change Biology*, 23, 983–985.

399 Dalu, T., Wasserman, R. J., Froneman, P. W., & Weyl, O. L. F. (2017b). Trophic isotopic carbon
400 variation increases with pond's hydroperiod: Evidence from an Austral ephemeral ecosystem.
401 *Scientific Reports*, 7, 7572.

402 Dalu, T., Wasserman, R. J., Vink, T. J. F., & Weyl, O. L. F. (2017c). Sex and species specific
403 isotopic niche specialisation increases with trophic complexity: evidence from an ephemeral
404 pond ecosystem. *Scientific Reports*, 7, 43229.

405 Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in
406 aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of*
407 *America*, 106, 12788–12793.

408 De Meester, L., Declerck, S., Stoks, R., Louette, G.,Van De Meutter, F., De Bie, T., …
409 Brendonck, J. (2005). Ponds and pools as model systems in conservation biology, ecology and
410 evolutionary biology. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15, 715–725.

411 Dick, J. T. A., Alexander, M. E., Jeschke, J. M., Ricciardi, A., MacIsaac, H. J., Robinson, T. B.,
412 Kumschick, S., … Richardson, D. M. (2014). Advancing impact prediction and hypothesis
413 testing in invasion ecol- ogy using a comparative functional response approach. *Biological*
414 *Invasions*, 16, 735–753.

Dick, J. T. A., Laverty, C., Lennon, J. J., Barrios-O'Neill, D., Mensink, P. J., Britton, R., … 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. *Journal of Applied Ecology*, 54, 1259–1267.

Dussart, B. H., & Defaye, D. (2001). Introduction to the Copepoda. guides to the identification of the microinvertebrates of the continental waters of the World. Backhuys Publishers, Leiden.

Gilbert, B., Tunney, T. D., McCann, K. S., DeLong, J. P., Vasseur, D. A., Savage, V., … O'Connor, M. I. (2014). A bioenergetics framework for the temperature dependence of trophic interactions. *Ecology Letters*, 17, 902–914.

Gusmão, L. F. M., McKinnon, A. D., & Richardson, A. J. (2009). No evidence of predation causing female-biased sex ratios in marine pelagic copepods. *Marine Ecology Progress Series*, 482, 279–298.

Hassell, M. P. (1978). The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton.

Holling, C. S. (1959). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91: 293–320.

Jeschke, J. M., Kopp, M., & Tollrian, R. (2002). Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs*, 72, 95–112.

Jeschke, J. M., Kopp, M., & Tollrian, R. (2004). Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biological Reviews of the Cambridge Philosophical Society*, 79, 337–349.

436 Juliano, S. A. (2001). Nonlinear curve fitting: predation and functional response curves. In
437 Scheiner, S. M., & Gurevitch, J. (Eds). Design and analysis of ecological experiments. (pp. 178–
438 196). Oxford University Press, Oxford.

439 Jupp, P. G. (1996). Mosquitoes of southern Africa: Culicinae and Toxorhynchitinae. Ekogilde
440 Publishers, Hartebeespoort.

441 Kerfoot, W. C., & Lynch, M. (1987). Branchiopod communities: associations with planktivorous
442 fish in space and time. In Kerfoot, W. C. & Sih, A. (Eds.), Predation: Direct and indirect impacts
443 on aquatic communities (pp. 367–378). University Press of New England, New Hampshire.

444 Kiørboe, T. (2006). Sex, sex-ratios, and the dynamics of pelagic copepod populations.
445 *Oecologia,* 148, 40–50.

446 Laverty C., Dick, J. T. A., Alexander, M. E., & Lucy, F. E., (2015). Differential ecological
447 impacts of invader and native predatory freshwater amphipods under environmental change are
448 revealed by comparative functional responses. *Biological Invasions,* 17, 1761–1770.

449 Laybourn-Parry, J., Abdullahi, B. A., & Tinson, S. V. (1988). Temperature-dependent energy
450 partitioning in the benthic copepods *Acanthocyclops viridis* and *Macrocyclops albidus*.
451 *Canadian Journal of Zoolo*gy, 66, 2709–2713.

452 Lotka, A. J. (1956). Elements of mathematical biology (2nd ed.). Dover Publications, New York.

453 Marten, G. G. & Reid, J.W. (2007). Cyclopoid copepods. *Journal of the American Mosquito*
454 *Control Association,* 23, 65–92.

455 Murdoch, W. W. (1969). Switching in general predators: experiments on predator specificity and
456 stability of prey populations. *Ecological Monographs,* 39, 335–354.

457 O'Neill, B. J., & Thorp, J. H. (2014). Untangling food-web structure in an ephemeral ecosystem.
458 *Freshwater Biology*, 59, 1462–1473.

459 Pritchard, D. W., Paterson, R. A., Bovy, H. C., & Barrios-O'Neill, D. (2017). Frair: an R
460 package for fitting and comparing consumer functional responses. *Methods in Ecology and*
461 *Evolution*, 8, 1528–1534.

462 R Core Team (2018). R: A language and environment for statistical computing. R Foundation for
463 Statistical Computing, Vienna.

464 Schneider, D. W., & Frost, T. M. (1996). Habitat duration and community structure in temporary
465 ponds. *Journal of the North American Benthological Society*, 15, 64–86.

466 Sih, A., Crowley, P., McPeek, M., Petranka, J. & Strohmeier, K. (1985). Predation, competition
467 and prey communities: a review of field experiments. *Annual Review of Ecology, Evolution and*
468 *Systematics*, 16, 269–311.

469 Solomon, M. E., (1949). The natural control of animal populations. *Journal of Animal Ecology*,
470 18, 1–35.

471 South, J., Dick, J. T. A., McCard, M., Barrios-O'Neill, D., & Anton, A. (2017). Predicting
472 predatory impact of juvenile invasive lionfish (*Pterois volitans*) on a crustacean prey using
473 functional response analysis: effects of temperature, habitat complexity and light regimes.
474 *Environmental Biology of Fishes*, 100, 1155–1165.

475 Suárez-Morales, E., Wasserman, R.J., & Dalu, T. (2015). A new species of *Lovenula* Schmeil
476 (Copepoda, Calanoida, Diaptomidae) from the Eastern Cape Province of South Africa.
477 *Crustaceana*, 88, 324–342.

Trexler, J. C., McCulloch, C. E., & Travis, J. (1988). How can the functional response best be determined? *Oecologia,* 76, 206–214.

Volterra, V. (1928). Variations and fluctuations of the number of individuals in animal species living together. *ICES Journal of Marine Science,* 3, 3–51.

Wasserman, R. J., Noyon, M., Avery, T. S., & Froneman, P. W. (2013). Trophic level stability-inducing effects of predaceous early juvenile fish in an estuarine mesocosm study. *PLoS ONE,* 6, e61019

Wasserman, R. J., Alexander, M. E., Barrios-O'Neill, D., Weyl, O. L. F., & Dalu, T. (2016a). Using functional responses to assess predator hatching phenology implications for pioneering prey in arid temporary pools. *Journal of Plankton Research,* 38, 154–158.

Wasserman, R. J., Alexander, M. E., Dalu, T., Ellender, B., Kaiser, H., & Weyl, O. L. F. (2016b). Using functional responses to quantify interaction effects among predators. *Functional Ecology,* 30, 1988–1998.

Wasserman, R. J., Weston, M., Weyl, O. L. F., Froneman, P. W., Welch, R. J., Vink, T. J. F., & Dalu, T. (2018). Sacrificial males: the potential role of copulation and predation in contributing to copepod sex-skewed ratios. *Oikos,* 127, 970–980.

Table 1. First order terms and significance levels resulting from logistic regression of the proportion of prey killed as a function of prey density, and rounded functional response parameter estimates across differing predator treatments resulting from Rogers' random predator equation.

Predator	First order term, *p*	Attack rate (*a*), *p*	Handling time (*h*), *p*	Maximum feeding rate (1/*h*)
Male	-0.02, < 0.01	0.42, < 0.001	0.10, < 0.001	9.96
Female	-0.02, < 0.001	0.73, < 0.001	0.11, < 0.001	9.44
Gravid female	-0.02, < 0.001	0.60, < 0.001	0.06, < 0.001	16.37

513

514

515

516

517

518 Table 2. Impact index scores for *Lovenula raynerae* across different sex ratios, where
519 proportioned impacts with gravid females are indexed relative to a null baseline comprised of
520 non-gravid females and males (see Eqns. 2, 3).

Proportion male and non-gravid female	Proportion gravid female	Non-gravid female (null) baseline impact (*b*)	Gravid female impact (*g*)	Impact index (*g*/*b*)
0.9	0.1	9.70	10.37	1.07
0.8	0.2	9.70	11.03	1.14
0.7	0.3	9.70	11.70	1.21
0.6	0.4	9.70	12.37	1.28
0.5	0.5	9.70	13.03	1.34
0.4	0.6	9.70	13.70	1.41
0.3	0.7	9.70	14.37	1.48
0.2	0.8	9.70	15.04	1.55
0.1	0.9	9.70	15.70	1.62

521

Figure 1. Functional responses of adult male, non-gravid female and gravid female *Lovenula raynerae* towards common culicid prey. Shaded areas represent bootstrapped (n = 2000) confidence intervals and points are raw data (n = 4 per experimental group).

Figure 2. Scenarios of differential impacts of *Lovenula raynerae* (Eqns. 3, 4), using functional response results, associated with changing hypothetical sex ratios and proportion (prop.) of maximal abundances, where: a) sex ratios remain balanced; b) sex ratios become increasingly skewed towards gravid females; and c) sex ratios become increasingly skewed towards male or non-gravid females. Population-level impacts are read diagonally, from bottom-left to top-right.