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ORIGINAL ARTICLE

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Inter-specific differences in invader and native fish functional responses illustrate neutral effects on prey but superior invader competitive ability

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Abstract

1. Inter-specific interactions are key factors in the structuring and functioning of ecological communities. Therefore, it is necessary to assess species interactions, such as predator–prey dynamics and competitive exclusion, within the context of continuing global species introductions. The aim of the present study was to assess ecological impacts and competitive exclusion dynamics involving co-occurring introduced and native fish species, using the multiple predator functional response (FR) approach.
2. We use comparative FR analysis (resource uptake as a function of resource density) to assess inter-specific interactions between the invasive western mosquitofish *Gambusia affinis* and the native freshwater river goby *Glossogobius callidus* towards chironomid larvae. The FR was derived for each fish species as individuals and when in heterospecific pairings. Data from single individuals were used to predict the expected FR of individuals when in heterospecific multiple predator combinations. Expected FRs were then compared to the observed FRs of each predator in combination trials, enumerated using prey items in their gut contents.
3. Both fish species displayed Type II FRs, however, in single fish trials, invasive mosquitofish had significantly higher FRs (curve asymptotes; i.e. shorter handling times and higher maximum feeding rates) than native river gobies. Heterospecific mosquitofish-river goby combinations revealed that the FR of the river goby was reduced (i.e. longer handling times and lower maximum feeding rates) by the presence of mosquitofish, whereas this combination greatly enhanced mosquitofish FR magnitudes (i.e. shorter handling times and higher maximum feeding rates). The heterospecific treatments resulted in neutral impacts on prey and there were clear inter-species interference in favour of the non-native mosquitofish.
4. This study demonstrates how multiple predators can alter the shape of individual FRs, with neutral effects on prey but superior invader competitive ability. This has implications for predicting the naturalisation success of invasive predators, as predatory and competitive interactions with native predators and prey may facilitate rather than impede establishment.

KEYWORDS
competition, fish, gut content, multi-predator effects, predator–prey dynamics

1 | INTRODUCTION

Human-mediated vectors and pathways have increased the introduction of non-native species into new environments and, in particular, freshwater fishes are one of the most commonly introduced taxa (Gozlan, 2008). While introduction pathways for fishes are fairly well understood (e.g. Copp et al., 2005), establishment success appears to be context dependent, and mediated by a variety of influences including abiotic factors such as temperature (Jeschke & Strayer, 2006; Kolar & Lodge, 2001), biotic factors such as predatory and competitive interactions (Latombe et al., 2017; Marchetti, Moyle, & Levine, 2004), and propagule pressure (Woodford, Hui, Richardson, & Weyl, 2013). Thus, understanding the drivers of establishment success or failure is of conceptual and practical importance (Sato et al., 2010). Of particular importance in this regard are biotic interactions between native and non-native species, which can have strong implications for community dynamics, as both consumptive and non-consumptive interactions will have direct effects on a predator's fitness and prey biomass (Barrios-O'Neill, Dick, Emmerson et al., 2014; Britton, Davies, & Harrod, 2010; Lopez, Davis, & Wong, 2018; Médoc & Spataro, 2015).

A classic method used to understand predator–prey interactions and competition is the quantification of the functional response (FR) (Holling, 1959; Murdoch & Oaten, 1975). The FR of a consumer describes the relationship between *per capita* prey (or other resource) consumption and prey (or other resource) density (Holling, 1959, 1965; Solomon, 1949). Functional responses are thus a critical determinant in the outcome of interacting consumer-resource populations (Holling, 1959). The types and magnitude of FRs quantify whether consumers will regulate, stabilise, or destabilise the resources in a population (Juliano, 2001; Murdoch & Oaten, 1975). Further, differential FRs may reveal inter-specific competitive asymmetries (Dick et al., 2017).

The relationships between consumer resource uptake and resource densities result in three FR *types*: linear Type I, hyperbolic Type II, and sigmoidal Type III (Holling, 1959; Jeschke et al., 2004). Functional responses have been applied to various aspects of ecology (Abrams, 1982; Englund & Harms, 2001; Faria, Godoy, & Trinca, 2004; Feldman, 2006), such as assessing adaptive behaviours (Abrams, 1982) and how resource abundance influences the *per capita* effects of individual predators under a number of environmental variables such as temperature (Stephens & Krebs, 1986), but only more recently have comparative FR analyses been used to assess invasive species impacts on resources such as prey, whereby the impact of an invader is contrasted with functionally similar native and/or non-native species (Dick et al., 2014; Gebauer, Veselý, Kouba, Buřič, & Drozd, 2018; Xu et al., 2016).

In this regard, Dick et al. (2014) highlighted that FRs provide a rapid, reliable, inexpensive and readily applicable tool to assess invader ecological impacts across taxonomic and trophic groups. A similar approach has also been applied to quantify multiple predator effects (MPEs), by comparing predicted and observed FRs based on single predator and multiple predator combinations and their consumption of prey (Barrios-O'Neill, Dick, Ricciardi, MacIsaac, & Emmerson, 2014; Soluk, 1993; Wasserman, 2016). As such, there is much potential for the use of comparative FRs for assessment of dynamics between invasive and native species.

Introduced species enter ecological interaction networks and interact with resident communities, resulting in novel heterospecific interactions, which can include interactions among predators that have no co-evolutionary relationships (Jackson et al., 2017). Consequently, there is a need to better understand the effects of multiple species interactions in invasion and biotic resistance contexts (Barrios-O'Neill, Dick, Ricciardi et al., 2014; Wasserman, 2016). These interactions are fundamental to the structure and functioning of ecological communities and are well-known regulators of predator–prey dynamics (Barrios-O'Neill, Dick, Emmerson et al., 2014).

In a food web context, predator–predator interactions are mediated by intermediate species and these are termed indirect effects and, furthermore, when one species modifies how the other species interacts, this is called trait-mediated indirect effects (Abrams, Menge, Mittelbach, Spiller, & Yodzis, 1996; Schmitz, 1998; Werner & Peacor, 2003). These interactions can lead to emergent MPEs. Quantifying and qualifying MPEs are necessary to understand how interactions between predator and prey may be altered by the addition of another predator, and how one predator may interfere with the predatory success of another (Sokol-Hessner & Schmitz, 2002; Soluk, 1993).

The present study thus aims to determine the individual-level FRs of the alien invasive western mosquitofish *Gambusia affinis* (Poeciliidae), hereafter referred to as *mosquitofish*, and the native freshwater river goby *Glossogobius callidus* (Gobiidae), towards a readily consumed prey, under multi-predator scenarios using the multiple predator FR approach (see Barrios-O'Neill, Dick, Emmerson et al., 2014; Wasserman, 2016). To do this, we use a novel approach of quantifying individual prey consumption from gut contents to assess the predator FR of the introduced and native predators under multi-predator scenarios. This approach bridges a major gap, whereby previous MPE research has not been able to assign predator consumption rate to individuals, but has rather focussed on the overall effects by determining prey consumption from counts of prey surviving (Barrios-O'Neill, Dick, Emmerson et al., 2014; Wasserman, 2016). This latter approach has the potential to mask the presence of MPEs if respective predatory facilitation and disruption occur simultaneously between two predator species, with no observed non-additive effects on prey. As such, chironomid larvae, a prey source that is easily quantified in gut content analyses as their heads are relatively resistant to digestion, were used in experiments to test the hypotheses that: (1) invasive mosquitofish will have significantly higher FRs (curve asymptotes) than native river goby; (2) MPEs will be observed for both predator species through differences in individual and multi-predator scenario FRs; and (3) MPEs may not be detectable based on surviving prey counts, but revealed by gut content analysis.