

Research Article

Shell shocked: high potential impacts on native prey by non-native turtles irrespective of benthic habitat context

Ross N. Cuthbert^{1,2,*}, Neil E. Coughlan¹, James W.E. Dickey¹, Michael Rea¹, Ciaran Laverty¹, Josie South^{1,2}, Kate Crane¹, Monica McCard¹ and Jaimie T.A. Dick¹

¹Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, BT9 5DL, United Kingdom

²South African Institute for Aquatic Biodiversity (SAIAB), Makhandla, 6140, South Africa

Author e-mails: rcuthbert03@qub.ac.uk (RNC), ncoughlan02@qub.ac.uk (NEC), jdickey03@qub.ac.uk (JWED), michael.rea.bsc@gmail.com (MR), claverty14@qub.ac.uk (CL), j.south@saiab.ac.za (JS), kcrane02@qub.ac.uk (KC), mmccard01@qub.ac.uk (MMC), j.dick@qub.ac.uk (JTAD)

*Corresponding author

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Abstract

The poorly-regulated pet trade is a major source of potential invasive species, with deliberate release often resulting in introductions of non-native species without invasion histories. Predicting the potential impacts of species with no invasion history is particularly difficult. Functional responses (FRs; resource use as a function of resource density) have proven useful in the quantification of ecological impacts of invasive species, and may be used to screen likely impacts of species which lack invasion histories. Here, we used laboratory experiments to quantify the FRs of four freshwater turtles commonly traded as household pets: *Trachemys scripta scripta*, the yellow-bellied slider; *T. s. troostii*, the Cumberland slider; *Sternotherus odoratus*, the common musk turtle; and *Kinosternon subrubrum*, the Eastern mud turtle, towards representative chironomid and gammarid prey under eight densities in the presence and absence of substrate. All turtles exhibited potentially population destabilising Type II (hyperbolic) FRs towards each prey type, irrespective of the presence of substrate, characterised by high predation rates at low prey densities. Magnitudes of FRs were generally higher for *T. s. scripta* and *T. s. troostii* compared to *S. odoratus* and *K. subrubrum*. The presence of substrate reduced the magnitude of FRs towards both prey types overall, however, these effects were modest and most pronounced for the two *T. scripta* subspecies. We demonstrate marked and sustained predatory impacts of non-native turtles on native prey, irrespective of benthic habitat contexts. We conclude that commonly traded turtles that lack invasion histories could precipitate substantial ecological impact, particularly in freshwater ecosystems where there are no native analogues.

Key words: habitat complexity, functional response, predation, context-dependence, pet trade

Introduction

Aquatic invasive species (AIS) have adversely impacted the biodiversity, community dynamics, ecological functioning, and the economic and social value of many freshwater ecosystems (Dick et al. 2013, 2017a, b; Simberloff et al. 2013; Courchamp et al. 2017; Hussner et al. 2017). Although many potential invaders fail to establish for a variety of ecological and evolutionary reasons, with 74% of invaders experiencing a reduction in

relative performance in novel ranges (Colautti et al. 2014), AIS continue to spread and establish (Seebens et al. 2017), further imperilling freshwater ecosystems (Darwall et al. 2018). Although the mechanisms that underpin overland transport of AIS are frequently unknown (Caffrey et al. 2016; Coughlan et al. 2017), a variety of species are undoubtedly transported by anthropogenic activities (Gallardo and Aldridge 2013). Accordingly, biosecurity protocols designed to inhibit further spread of invasive species are now a key component of management strategies (Coughlan et al. 2018a, b; Cuthbert et al. 2018a, 2019b; Crane et al. 2019). Despite the major benefits of spread-prevention protocols (Piria et al. 2017), there remains a substantial risk of accidental and deliberate introductions due to the inappropriate disposal of unwanted pets, and the misconceptions surrounding the ethics and potential consequences of “mercy” release (i.e., freeing captured animals) (Rixon et al. 2005; Gertzen et al. 2008; Liu et al. 2013; Dickey et al. 2018; Patoka et al. 2018; Wasserman et al. 2019). In particular, AIS frequently present a substantial and complex management burden that often must be addressed with only minimal resources (Piria et al. 2017; Coughlan et al. 2019).

Effective evidence-based management protocols that can enable the most efficacious distribution of limited resources towards AIS are needed (Booy et al. 2017; Roy et al. 2018; Dick et al. 2017a, b). In particular, methodologies that enhance understanding of current invaders, and accurately predict the consequences of novel introduced species, are essential to AIS management strategies (Dick et al. 2017a, b, c; Laverty et al. 2017a; Dickey et al. 2018; Cuthbert et al. 2019c). Forecasting the ecological impacts of invaders remains a challenge for invasion biologists (Dick et al. 2014; 2017a,b; Cuthbert et al. 2019c). However, the approach of assessing the functional response (FR) of an invader within a novel ecosystem has been identified as a useful tool to quantify and predict ecological impacts (Alexander et al. 2014; Dick et al. 2013, 2017a, b; Cuthbert et al. 2019c). Functional responses examine the relationship between resource use and resource availability, such as between predators and prey (Holling 1959). Three broad forms of FR can emanate from this relationship: the linear Type I, where consumption increases linearly with prey density; inversely density-dependent Type II, whereby consumption rates fall asymptotically as prey density increases; and positively density-dependent Type III, where proportional prey consumption initially increases before again falling to reach an asymptote (Hassell 1978). Importantly, the Type of FR can facilitate different outcomes for prey populations. Whilst consumers exhibiting Type II FRs are more likely to destabilise prey populations due to high proportional intake at low prey densities, Type III FRs may impart stability through provisioning of low density refugia for prey (Murdoch and Oaten 1975; Hassell 1978; Colton 1987).

Using the comparative functional response (CFR) approach to compare invaders to native trophic analogues has been shown to be a reliable predictor of invader impacts across different consumer-resource systems (Alexander et al. 2014; Dick et al. 2014, 2017a, b, c; Lavery et al. 2017a; Dickey et al. 2018; Cuthbert et al. 2019c). For example, the invasive mysid *Hemimysis anomala* has been shown to exhibit a higher FR than trophically analogous natives, corroborating known field impacts among prey types (Dick et al. 2013). However, where native analogues for comparison with invaders are absent, CFRs could still be used to predict ecological impact. That is, among multiple existing and emerging invaders, CFR may be used to identify those potentially most-damaging. Comparative functional response further facilitates the prediction and understanding of ecological impacts across a plethora of context-dependencies and interactive effects (Dick et al. 2017a, b, c; Lavery et al. 2017a), such as dissolved oxygen (Lavery et al. 2015), habitat complexity (Wasserman et al. 2016; Cuthbert et al. 2018b), higher order predators (Barrios-O'Neill et al. 2014), parasites (Lavery et al. 2017b) and temperature (Cuthbert et al. 2018c; Wasserman et al. 2018). However, in many instances, traditional FR and CFR studies have not accounted for simple biotic or abiotic conditions that can likely modulate the *in situ* predator-prey relationship. For instance, the simultaneous presence of multiple food resources can affect interaction strengths through processes such as prey preferences and prey switching (Médoc et al. 2018; Cuthbert et al. 2018d, 2019a). Moreover, the complexities and possible differential spatial use of habitats are not often replicated within experimental arenas when assessing predator impact (but see Barrios-O'Neill et al. 2017). For example, the presence of benthic substrate complexity may impair detection of certain prey, resulting in reduced predatory impacts. In turn, the presence of benthic habitat complexity has been shown to create a more stabilising FR form (e.g., Alexander et al. 2012), but can also increase FR magnitudes due to prey clumping (e.g., Alexander et al. 2013).

Recently, geopolitical entities such as the European Union (EU) and United States (US), have begun to legislate against the trade and possession of selected invasive species (e.g., EU Species of Union Concern; Safeguarding the Nation from the Impacts of Invasive Species – amendment to US Executive Order) (Tollington et al. 2017). However, although commendable, the banning of species may inadvertently result in their introduction to novel ecosystems as current owners seek to dispose of unwanted living specimens (Hulme 2015; Patoka et al. 2018). For example, the freshwater turtle *Trachemys scripta elegans* (Wied-Neuwied, 1839), known as the red-eared slider, is listed as an EU Species of Union Concern, having invaded 73 countries (García-Díaz et al. 2015; Capinha et al. 2017) across all continents but Antarctica (Rödger et al. 2009). However, following a 1977 EU trade ban on this species, owners were prompted to release illegal red-eared sliders into the wild (Hulme 2015). Accordingly, there is an urgent

requirement to examine the potential ecological effects of turtle species frequently purchased as pets, especially those that currently lack invasion histories. Although a popular pet species worldwide, *T. s. elegans* has been shown to negatively impact the growth of native turtles, and may compete for food and basking habitat with natives (Teillac-Deschamps et al. 2009; Polo-Cavia et al. 2011; Pearson et al. 2015). In Europe, *T. s. elegans* negatively impacts native turtle species, such as the European pond turtle (*Emys orbicularis galloitalica* Fritz 1995) and Spanish terrapin (*Mauremys leprosa* (Schweiger 1812)) through both exploitative and interference competition (Cadi and Joly 2003). However, knowledge of many existing and emerging invasive turtle impacts on multiple prey species remains limited (but see Dickey et al. 2018). Dietary patterns are also known to shift across ontogeny in freshwater turtles, with individuals particularly carnivorous during juvenile stages (Ernst and Lovich 2009). Yet, there remains a distinct lack of quantification of ecological impacts of existing and emerging invasive turtles with native prey, impeding the identification and targeting of the most-damaging turtle species for management.

Here, we use the CFR approach to examine impacts of four commonly traded turtles originating from North America: *Trachemys scripta scripta* (Thunberg in Schoepff 1792), the yellow-bellied slider; *T. s. troostii* (Holbrook 1836), the Cumberland slider; *Sternotherus odoratus* (Latreille in Sonnini and Latreille 1801), the common musk turtle; and *Kinosternon subrubrum* (Lacépède 1788), the Eastern mud turtle. Functional responses are assessed separately for each species upon two common benthic invertebrate prey items, chironomids and gammarids, under eight different densities, all with and without the presence of substrate complexity (i.e., benthic sand coverage; see later). Within freshwater ecosystems, chironomids are one of the most diverse and abundant groups (Nicacio and Juen 2015), and are useful bioindicators of water quality, whilst gammarids are widespread and functionally-important shredders (Kelly et al. 2002).

Materials and methods

Organisms and husbandry

Nine juvenile individuals of each turtle species were provided by Maidenhead Aquatics, Northern Ireland, and size-matched as closely as possible (carapace lengths 35–50 mm; mixed sexes). Turtles were housed by species in holding tanks (60 × 45 × 60 cm; Exo Terra, UK) containing dechlorinated tap water at 16 °C under a natural light regime. Each holding tank contained two basking platforms and basking lights to create a hot spot of 23 °C, controlled by an automatic temperature controller (Habistat Classic, England). Substrate (0.8 mm grainsize sand, JBL, Germany) was added to the bottom 30 mm of each holding tank. Specimens were individually quarantined for one week prior to experiments. During both

the quarantine and experimental periods, no illness or mortality was recorded, and animals were fed daily with commercial floating turtle food (JBL, Germany). Turtles were fed as much as they could consume individually within approximately 10 minutes (as per JBL instructions).

Two prey types were utilised in the experiment. First, live chironomid larvae (> 20 mm total length) were purchased from Maidenhead Aquatics, Northern Ireland. Second, the amphipod crustacean *Gammarus pulex* (Linnaeus, 1758) (> 15 mm body length; unparasitised) were collected from the Minnowburn River, Northern Ireland (54.548N; 5.952W). Both prey types were acclimated to the experimental temperature regime for two days before use in glass aquaria. These represent typical, widespread freshwater invertebrate groups that could be impacted by turtle predation. During pilot experiments, all predators readily fed on both prey types. Freshwater turtles are known to be opportunistic at different life stages, feeding on a variety of aquatic invertebrate, vertebrate and vegetation species (Balzani et al. 2016).

FR Procedure

Prior to experimental FR trials, turtles were unfed for 24 hours to standardize hunger levels. Prey species were independently added to glass experimental tanks (250 mm × 120 mm × 90 mm; 16 °C), either with or without 30 mm of substrate (0.8 mm grainsize), *circa* 15 minutes before the introduction of turtles. Prey densities of 2, 4, 8, 16, 32, 64, 128, 256 were utilised ($n = 6$ per experimental trial group), and predators were introduced singularly. Individual predators were reused systematically, following a recovery period of at least three days. Each turtle species was examined separately, with individuals being randomly selected and assigned to a random prey density and allowed to feed for a 30-minute period. After this period, turtles were removed and remaining live prey counted to quantify those killed. To quantify prey mortality in the absence of turtle predators, controls were performed for each prey density ($n = 3$ each) under the same experimental conditions. In total, excluding controls, 128 groups were tested (4 turtle species × 2 prey species × 2 substrate types × 8 prey supplies) with 6 replicate trials per group, resulting in 768 trials overall.

Statistical analyses

We analysed raw prey consumption using generalised linear models (GLMs) assuming a Poisson error distribution, with “predator” (4 levels), “prey” (2 levels), “substrate” (2 levels) and “prey supply” (8 levels) included factorially as explanatory variables. Insignificant terms and interactions were removed stepwise backwards from models to generate the most parsimonious fit (Crawley 2007), with model selection performed *via* analysis of deviance, and χ^2 reported to communicate the effect size of a

factor on the dependent variable. Where a factor yielded significance at the 95% confidence level, we used Tukey's comparisons to generate pairwise estimates with Holm-Bonferroni adjustment of P values (*lsmeans::lsmeans*; Lenth 2016).

For each predator, prey and substrate combination, we determined FRs phenomenologically using logistic regression of proportional prey consumption as a function of prey density (*frair::frair_test*; Pritchard et al. 2017). Where a significantly negative first-order term was detected, a categorical Type II FR was inferred (Juliano 2001). Based on these analyses, each FR was deemed to be Type II. Therefore, and as prey were not replaced as they were consumed, we fitted Rogers' random predator equation (Rogers 1972), which accounted for prey depletion during the experiment, using maximum likelihood model fitting and parameter estimation (*frair::frair_fit*; Pritchard et al. 2017):

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

where N_e is the number of prey killed or consumed, N_0 is the starting prey supply, a is the attack rate, h is the handling time and T is the total time allowed for predation (here, 30-minutes). The *Lambert W* function was incorporated in order to make the random predator equation solvable (Bolker 2008). Maximum feeding rates were then calculated over the total experimental period ($1/h$). Functional responses were non-parametrically bootstrapped ($n = 2000$) to generate 95% bias-corrected and accelerated confidence intervals (CIs) around attack rate (a) and handling time (h) estimates (*frair::frair_boot*; Pritchard et al. 2017). Estimates were therefore derived and visualised from the original data, and effects examined through comparison of CI overlaps across prey densities supplied (see Barrios-O'Neill et al. 2014, 2015). Statistical analyses were performed using R v3.4.4 (R Development Core Team 2018).

Results

Prey survival in controls always exceeded 98%, and thus we assumed most prey deaths in FR trials to result directly from predation by turtles, which we also observed. Overall consumption was significantly affected by turtle identity (Table 1). *Trachemys scripta scripta* consumed significantly more prey than the other three turtle types (all $P < 0.001$), whereas *T. s. troostii*, in turn, consumed significantly more prey than *K. subrubrum* and *S. odoratus* (both $P < 0.001$). However, consumption did not differ significantly between *K. subrubrum* and *S. odoratus* ($P = 0.17$). Significantly more chironomids were consumed than gammarids, and significantly less prey were consumed in the presence of substrate overall (Table 1). Furthermore, prey consumption increased with greater levels of prey supply under the non-replacement design, and particularly towards chironomids as the “prey \times prey supply” interaction was significant (Table 1). Prey-dependence

Table 1. Poisson generalised linear model coefficients considering prey consumption as a function of predator, prey, substrate and prey supply, and their interactions.

Term	χ^2	df	P-value
Predator	89.00	3	< 0.001
Prey	4656.00	1	< 0.001
Substrate	170.10	1	< 0.001
Prey supply	21883.60	7	< 0.001
Predator:Prey	75.00	3	< 0.001
Predator:Substrate	69.60	2	< 0.001
Prey:Substrate	23.50	1	< 0.001
Predator:Prey supply	18.60	21	0.61
Prey:Prey supply	1741.20	7	< 0.001
Substrate:Prey supply	12.20	7	0.10
Predator:Prey:Substrate	5.70	3	0.13
Predator:Prey:Prey supply	14.20	21	0.86
Predator:Substrate:Prey supply	17.30	21	0.69
Prey:Substrate:Prey supply	6.90	7	0.44
Predator:Prey:Substrate:Prey supply	12.00	21	0.94

of differential predator consumption rates was demonstrated by a significant “predator \times prey” interaction (Table 1), wherein *T. s. troostii* and *T. s. scripta* exhibited greater magnitude consumptive differences relative to *K. subrubrum* and *S. odoratus* towards gammarid prey. Furthermore, differential consumption rates between predators were substrate-dependent (“predator \times substrate”: Table 1), with the relative consumption by *T. s. scripta* and *T. s. troostii* reduced to a greater extent in the presence of substrate overall. However, chironomids exhibited significantly greater consumptive risk reductions than gammarids where substrate was present (“prey \times substrate”: Table 1). All other terms were non-significant and were thus removed stepwise from the model.

All turtles demonstrated Type II FRs towards both prey types as evidenced by significantly negative first-order terms, irrespective of substrate treatment (Table 2). With chironomid prey, substrate caused significant reductions to the FR magnitude of *T. s. scripta* and *T. s. troostii* as FR CIs were divergent, but affected *K. subrubrum* and *S. odoratus* to a lesser extent. The two *T. scripta* subspecies exhibited the highest magnitude FRs when prey were presented in the absence of substrate, with attack rates being considerably higher (Table 2; Figure 1a–d). Functional response CIs of *T. s. scripta* were divergent across all except maximal prey supplies when compared to *K. subrubrum*, and at higher densities when compared to *S. odoratus*, reflecting lower handling times and greater maximum feeding rates (1/h) compared to *S. odoratus*. On the other hand, *T. s. troostii* only exhibited significantly higher FR magnitudes compared to *K. subrubrum* at intermediate, and *S. odoratus* at high, chironomid supplies (Figure 1). Conversely, where substrate was present with chironomids, differential impacts of *T. s. scripta* were reduced, with maximum feeding rates substantially lower than in the absence of substrate and FR CIs overlapping across all prey supplies when compared to both *K. subrubrum* and *S. odoratus* (Figure 1). This reflects greater similarities in FR magnitudes and parameters

Table 2. First-order terms and P -values resulting from logistic regression of proportional prey consumption under differing supplies, alongside rounded initial and bootstrapped ($n = 2000$; 95% confidence intervals (CIs)) functional response parameters (attack rate, a ; handling time, h) of *Trachemys scripta scripta* (Tss), *Trachemys scripta troostii* (Tst), *Sternotherus odoratus* (So) and *Kinosternon subrubrum* (Ks) under different prey and substrate treatments.

Species	Prey	Substrate	1 st order term, P	a	95% CIs (a)	h	95% CIs (h)	Maximum feeding rate (1/ h)
Tss	Chironomid	No	-0.009, $P < 0.001$	3.296	2.864–4.015	0.003	0.003–0.004	301.68
Tst	Chironomid	No	-0.008, $P < 0.001$	2.790	2.216–3.497	0.004	0.003–0.004	274.74
So	Chironomid	No	-0.009, $P < 0.001$	2.411	2.088–2.956	0.005	0.004–0.005	209.91
Ks	Chironomid	No	-0.005, $P < 0.001$	1.738	1.440–2.170	0.003	0.002–0.004	318.95
Tss	Chironomid	Yes	-0.006, $P < 0.001$	1.607	1.343–1.909	0.005	0.003–0.005	217.17
Tst	Chironomid	Yes	-0.004, $P < 0.001$	1.228	1.08–1.424	0.005	0.004–0.005	218.91
So	Chironomid	Yes	-0.005, $P < 0.001$	1.541	1.341–1.845	0.004	0.003–0.005	273.06
Ks	Chironomid	Yes	-0.006, $P < 0.001$	1.807	1.472–2.221	0.004	0.003–0.005	232.72
Tss	Gammarid	No	-0.013, $P < 0.001$	3.723	3.104–4.688	0.023	0.022–0.025	42.68
Tst	Gammarid	No	-0.012, $P < 0.001$	3.209	2.620–4.039	0.026	0.024–0.028	38.30
So	Gammarid	No	-0.011, $P < 0.001$	2.244	1.858–2.629	0.039	0.037–0.042	25.45
Ks	Gammarid	No	-0.012, $P < 0.001$	2.819	2.375–3.395	0.040	0.038–0.042	24.99
Tss	Gammarid	Yes	-0.011, $P < 0.001$	2.581	2.134–3.222	0.027	0.026–0.028	37.02
Tst	Gammarid	Yes	-0.011, $P < 0.001$	2.088	1.693–2.639	0.028	0.026–0.030	35.27
So	Gammarid	Yes	-0.011, $P < 0.001$	1.869	1.520–2.281	0.039	0.036–0.041	25.52
Ks	Gammarid	Yes	-0.011, $P < 0.001$	2.234	1.827–2.753	0.037	0.035–0.039	27.30

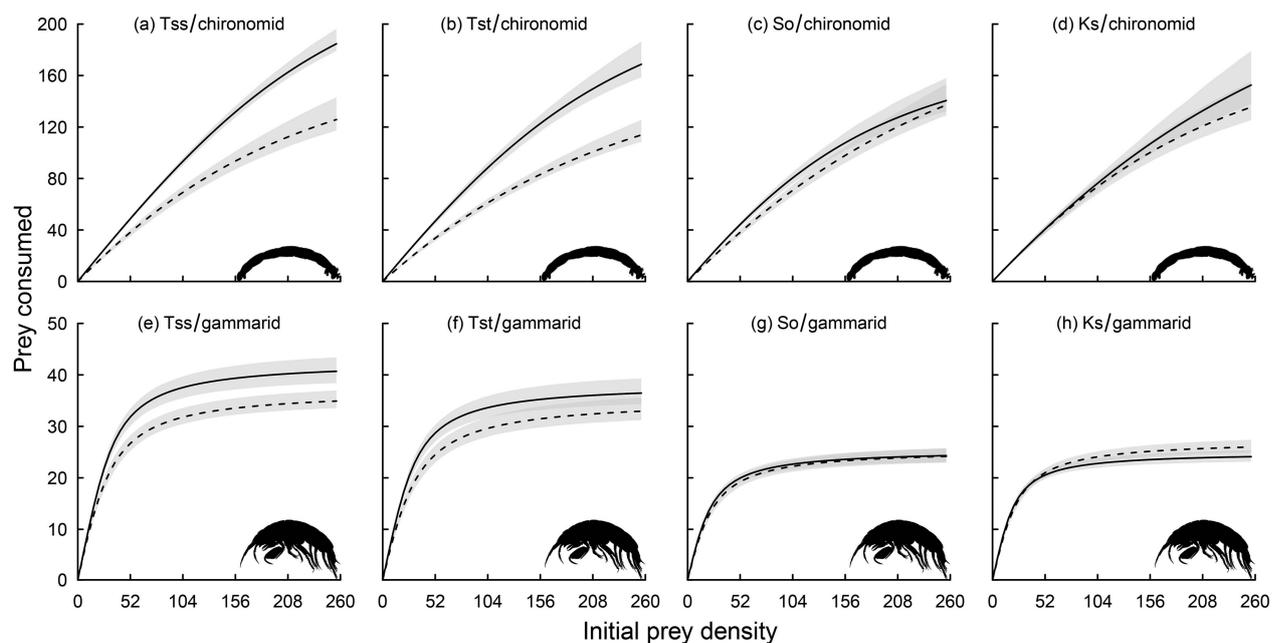


Figure 1. Functional responses of *Trachemys scripta scripta* (Tss), *Trachemys scripta troostii* (Tst), *Sternotherus odoratus* (So) and *Kinosternon subrubrum* (Ks) towards chironomid (a–d) and gammarid (e–h) prey in the presence (dashed line) and absence (solid line) of substrate. Shaded areas are bootstrapped ($n = 2000$) 95% confidence intervals (CIs).

here (Table 2; Figure 1). Trends were also reversed for *T. s. troostii*, with FRs in the presence of substrate significantly lower than both *K. subrubrum* and *S. odoratus* at intermediate-high prey densities, with FR CIs divergent and maximum feeding rates lower (Table 2).

With gammarid prey, the FRs of *T. s. troostii* and *T. s. scripta* were again more affected by substrate presence than *K. subrubrum* and *S. odoratus* (Figure 1e–h), with the two *T. scripta* subspecies showing substantial FR magnitude reductions. Handling times of *T. s. scripta* were significantly

greater, and maximum feeding rates thus lower, where substrate was present as opposed to absent (Table 2), reflected in divergence of FR CIs (Figure 1). For all turtles, attack rates were generally higher towards gammarid prey than towards chironomids (Table 2). Where substrate was absent, FRs of *T. s. scripta* and *T. s. troostii* were again significantly higher than both *K. subrubrum* and *S. odoratus* (Figure 1), with higher attack rates and lower handling times (Table 2). Accordingly, maximum feeding rates were substantially higher by the two *T. scripta* subspecies here (Table 2). This overall trend was sustained towards gammarids in the presence of substrate, however reduced differences in attack rates, handling times and maximum feeding rates among the turtle species were demonstrated with substrate present (Table 2).

Discussion

Globally, invasive species are continuing to emerge and spread at unprecedented rates (Seebens et al. 2017, 2018). The global trade of reptiles and amphibians has resulted in a number of high-profile invaders with serious ecological impacts (Kraus 2015; Nori et al. 2017). Further, “mercy” release of captured animals has been identified as a major pathway for non-native species introductions which lack invasion histories, for example by religious groups or pet owners (Dickey et al. 2018; Wasserman et al. 2019). However, understanding and quantifying the impact of species that lack known invasion histories remains notoriously problematic (Ricciardi et al. 2013; Dick et al. 2017a, b, c). Recently, the CFR approach between invasive and native species has yielded excellent explanatory and predictive power of invader impact on native prey populations (Alexander et al. 2014; Dick et al. 2013, 2014, 2017a, b, c; Laverty et al. 2017a; Cuthbert et al. 2019c). As such, the CFR approach can aid in the identification of potentially impactful species amongst those without previous invasion histories. Furthermore, the CFR approach is especially informative when examined in relation to a suite of context-dependencies that may potentially modulate ecological interaction strengths (Barrios-O’Neill et al. 2014; Wasserman et al. 2016; Laverty et al. 2017b; South et al. 2017). Whilst the context-dependency of invader impacts (e.g., habitat complexity) can make predictions difficult, simple laboratory experiments can produce meaningful comparative results pertaining to interaction strengths (Laverty et al. 2017a). Herein, we demonstrated interspecific differences in non-native turtle impacts, yet also show how a single environmental context (substrate) can differentially remediate impacts among species. In turn, this enables identification of the most-damaging species based on *per capita* effects.

As shown in our study, the CFR approach can be extended to assess the predatory impact of multiple species that lack an invasion history and native analogues. All of the study species examined displayed a sustained and destabilising Type II FR, which suggests that these species could

rapidly eliminate low density prey species. Functional response Type was unaffected by the presence of benthic substrate, which has been shown to modulate FR forms to more stabilising sigmoidal Type IIIs in other consumer-resource systems (e.g., Alexander et al. 2012, 2013). As such, even where there is potential for physical refuge, all four turtle types in our study were able to effectively target and kill high proportions of both benthic native prey types, even when the prey were present at low densities in the environment. The combination of high maximum feeding and attack rates of turtles with both prey species highlights an ability to exert high impact at both high and low prey densities (Dick et al. 2014). Assessing the maximum feeding rate in relation to the reproductive output of the prey is often overlooked, however the maximum feeding rate of *T. s. scripta* on *G. pulex* both with and without substrate, ~ 40 individuals per thirty minutes, is particularly significant when one considers that individual *G. pulex* have a maximum brood size of 14.79 and only one generation per year (Grabowski et al. 2007). Furthermore, attack rates were particularly high towards gammarid prey in our study by all turtle species, indicating substantial predatory impacts at low prey densities.

Our results display clear differential impacts among the four turtle species examined. With both prey types and in the absence of substrate, *T. s. scripta* and *T. s. troostii* demonstrated the strongest *per capita* effects, with greater attack rates and lower handling times as compared to *S. odoratus* and *K. subrubrum*. Therefore, these subspecies, and particularly *T. s. scripta*, have the greatest potential for impact amongst those examined, and will likely exert the greatest top-down pressure on underlying trophic groups if introduced. Although predatory impacts were still marked in the presence of substrate, FR magnitudes were affected through changes to attack rates and handling times with substrate. However, the effects on consumption arising from the presence of substrate were also different between species. Generally, FRs of *K. subrubrum* and *S. odoratus* were less affected by the presence of substrate than the two *T. scripta* subspecies, suggesting that these species may be most resilient to changes in benthic habitat structure in aquatic ecosystems. Indeed, substrate presence reduced maximum feeding rates of *T. s. scripta* and *T. s. troostii* by 13.26% and 7.91%, respectively, towards gammarid prey, whilst maximum feeding rates of *S. odoratus* and *K. subrubrum* increased in substrate. As always, caution should be exerted when paralleling simplified laboratory experiments with real-world environments. In particular, whilst we present considerable interspecific differences in the effects of substrate on predatory turtles, only one type of substrate addition was applied in our study, and other substrates may have different effects on interaction strengths towards specific prey. Nevertheless, the CFR approach has been shown to yield high predictive power for invader impacts (Dick et al. 2014; Cuthbert et al. 2019c), as well as the influence of context-dependencies on *per capita* impacts in other simplified study systems.

In essence, these potential invaders could have a profound impact within a naive native community, and particularly in the case of *T. scripta* subspecies within simplified habitats. The introduction of predators such as turtles to novel environments which lack analogous trophic groups has the potential for drastic consequences on native communities through processes such as predation. In particular, across northern Europe, there are no native turtle species with comparative ecological functional roles, and therefore a lack of competition following introduction could accentuate ecological impacts (Dickey et al. 2018). Elsewhere in Europe and around the World, non-native turtles have adversely affected native turtle species through competitive interactions (e.g., Cadi and Joly 2003). Indeed, on the Iberian Peninsula, aggressive and competitive interactions with invaders are thought to be a major cause of displacement of native Spanish turtles (Polo-Cavia et al. 2011). Hybridisation between turtle species poses a further threat to native populations when in contact with invaders (Parham et al. 2013), potentially bolstering effects related to interference and exploitative competition. Moreover, even if environmental conditions prevent reproduction within an introduced range, the longevity associated with these species can result in sustained impact on prey populations over time, e.g., *K. subrubrum* can live for up to 46 years (Frazer et al. 1991). The impact of these species may be exacerbated if global climate change and/or adaptation leads to these populations becoming reproductively viable, particularly as different species have different temperature requirements for reproduction, combined with the potentially destabilising predatory behaviours exhibited by freshwater turtle species (Bugter et al. 2011; Dickey et al. 2018). We thus advocate that further regulation and monitoring of these and other high-risk traded pet species is necessary to reduce the spread of potential invaders, particularly in light of climate change which may affect the reproductive status of introduced populations. Although, even if reproduction is impeded by climate, increasing biomass associated with growth could result in greater consumption by turtles, and perhaps non-linearly. The integration of this information could further bolster the impact projections based on the CFR approach (see Dick et al. 2017c; Dickey et al. 2018).

Although our study demonstrates considerable predatory impact of all four turtles in their juvenile stage, other environmental contexts may further alter the interaction strengths between these species and native biota. In the natural environment, introduced turtles will be exposed to a range of resource types which may affect interactions towards specific prey *via* processes such as prey preference and switching (e.g., Cuthbert et al. 2018d, 2019a). Therefore, further research should seek to elucidate the effects of choice between resources on the impacts of non-native turtles on focal prey, given their omnivorous feeding traits (Bouchard and Bjorndal

2006; Rawski et al. 2018). Indeed, omnivory has been shown to influence the impact derivations of invasive species within the CFR framework (e.g., Médoc et al. 2018). Many freshwater turtles undergo ontogenic shifts in dietary preferences, wherein a greater degree of carnivory is exhibited in juvenile stages (Ernst and Lovich 2009). Further, the development and inclusion of measures for numerical response (population-level response to resources) and propagule pressure in the comparative assessments of turtles and other emerging invasive species would be of substantial value, given that the CFR approach is grounded in examinations of *per capita* effects alone (but see Dick et al 2017a; Dickey et al. 2018). As such, the additional consideration of population abundances and life history traits such as fecundity could greatly enhance the predictive power of the CFR approach applied here (see Dickey et al. 2018). Nevertheless, the ease of use of the CFR approach, coupled with its predictive power, make the methodology highly informative to stakeholders involved in invasive species management in different study systems (Dick et al. 2014, 2017a; Cuthbert et al. 2019c). Examinations of impact across different turtle life stages, sexes and sizes would be additionally informative as to the effects of population demographics on interaction strengths of emerging invaders. However, increased regulation of the international pet trade is required to ultimately limit the potential for introduction, spread and impact of traded turtles and other potential invaders in new geographic ranges.

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Authors' contributions

MR, CL, JTAD: research conceptualisation; MR, CL, JS, KC, JTAD: sample design and methodology; MR: investigation and data collection; RNC: data analysis and interpretation; MR: ethics approval; JTAD: funding provision; RNC, NEC, JWED: original draft; all authors: review & editing.

Conflict of interest

Declarations of interest: none.

Ethics and permits

Ethical approval for work with turtles was granted by the School of Biological Sciences Animal Research Ethics Committee, Queen's University Belfast.

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