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On the context-dependent scaling of consumer feeding rates

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On the context-dependent scaling of consumer feeding rates

Abstract
The stability of consumer–resource systems can depend on the form of feeding interactions (i.e. functional responses). Size-based models predict interactions – and thus stability – based on consumer–resource size ratios. However, little is known about how interaction contexts (e.g. simple or complex habitats) might alter scaling relationships. Addressing this, we experimentally measured interactions between a large size range of aquatic predators (4–6400 mg over 1347 feeding trials) and an invasive prey that transitions among habitats: from the water column (3D interactions) to simple and complex benthic substrates (2D interactions). Simple and complex substrates mediated successive reductions in capture rates – particularly around the unimodal optimum – and promoted prey population stability in model simulations. Many real consumer–resource systems transition between 2D and 3D interactions, and along complexity gradients. Thus, Context-Dependent Scaling (CDS) of feeding interactions could represent an unrecognised aspect of food webs, and quantifying the extent of CDS might enhance predictive ecology.

Keywords
Body size, density dependence, functional response, habitat complexity, invasive species, population stability, predator–prey dynamics, scaling, Type II, Type III.

INTRODUCTION
In ecology, complexity and contingency are pervasive, and so the notion that many patterns and processes can be unified by considering organisms as consumers and processors of energy – embodied within the metabolic theory of ecology (MTE; Brown et al. 2004) – is appealingly parsimonious. Because MTE offers a mechanistic link between temperature, body size and metabolic rate, it follows that the feeding rates of consumers (i.e. their energy acquisition) should reflect intrinsic metabolic demand. However, generalising consumer feeding rates to metabolic first principles remains problematic, particularly for two reasons: (1) because feeding rates emerge from the relative performance of at least two agents – the consumer and the resource (Ohlund et al. 2014); and (2) because historical energy acquisition and storage can dictate the necessity for feeding interactions when consumers encounter resources (Maino et al. 2014).

In its most basic form, the interaction between consumer and resource can be formalised as the functional response (Holling 1959; Real 1977), defining the relationship between resource acquisition by a single consumer and resource density:

\[ N_c = hN \]  

\[ N_c = \frac{hN^{q+1}}{1 + bhN^{q+1}} \]

where \( N_c \) is the per capita rate of resource consumption (individuals s\(^{-1}\)), \( h \) is the capture rate or search coefficient of the consumer (m\(^2\) s\(^{-1}\) or m\(^3\) s\(^{-1}\)) – for simplicity, we treat capture rates and search coefficients as synonymous (but see Kalinkat et al. 2013) – \( N \) is the resource density (individuals m\(^2\) or m\(^3\), constant in time), \( h \) (s) is consumer handling time, strictly incorporating the processes of subjugation and ingestion (but often reflecting digestion: see supplementary materials) and \( q \) is the scaling exponent, defining the extent to which the functional response departs from a decelerating hyperbola (Type II) towards a sigmoidal (Type III) form. Where \( q = 0 \) capture rates are independent of \( N \). Where \( q > 0 \) capture rates depend explicitly on \( N \), often reflecting consumer learning, whereby capture rates increase with \( N \), resulting from: (1) increased encounters (e.g. switching from passive to active searching), or (2) an increased ratio of captures to encounters.

Across the biosphere, capture rates scale positively with consumer mass (Fig. 1), but there are layers of complexity nested within this trend (Pawar et al. 2012; Rall et al. 2012). For example, consumers often exhibit lower capture rates towards relatively large or small resources (Osenberg & Mittelbach 1989; Persson et al. 1998; Aljeltlawi et al. 2004; Vonesh & Bolker 2005). As a result, at the local scale, capture rates often distribute unimodally along a spectrum of consumer (\( M_c \)), resource (\( M_r \)), body mass ratios (\( \frac{M_c}{M_r} \)), delineating a series of ‘sub webs’ nested within the general trend (Fig. 1, blue and orange; Woodward et al. 2005; Rall et al. 2012). Isolating the dependence of capture rates on \( \frac{M_c}{M_r} \) yields a general scaling for capture rates with consumer mass (Pawar et al. 2012):

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Non-linear feeding interactions (eqn 1b, where $h$ and/or $q > 0$) are a crucial component of the scaling of consumer feeding rates for two reasons: (1) because measuring interactions at fixed resource densities can underestimate or overestimate feeding rates, which are rarely linear in nature (Jeschke et al. 2004); and (2) because the size dependencies of non-linear feeding interactions – in terms of shape (that is, functional response Type – primarily $q$ and $b$) and magnitude (primarily $h$) – are critical for the coexistence of consumer–resource pairs (Murdock 1969; Kalinkat et al. 2013), and promote stability in tri-trophic food chains or complex food webs (Williams & Martinez 2004; Brose et al. 2006). In particular, small consumer–resource mass ratios can result in destabilising Type II functional responses ($q = 0$) due to high resource exploitation at low resource densities. As ratios increase, responses systematically transition ($q > 0$) towards stabilising Type III sigmoid curves typified by low resource exploitation at high resource densities (Kalinkat et al. 2013). Size-based approaches to defining interactions are not without limitations, but their value is manifest in linking MTE with local-scale community dynamics and in making useful predictions at these scales, for example, describing the consequences of species loss from food webs (Schneider et al. 2012).

We argue that understanding the community-level consequences of extinctions, invasions and the impacts of anthropogenic stressors will depend acutely on resolving local scaling within subwebs. Generalisations of consumer feeding around temperature and body mass constitute only part of the means to this end, particularly because resources (i.e. prey) utilise refuge space (Barrios-O’Neill et al. 2015), employ defensive adaptations (Osenberg & Mittelbach 1989) and may not consistently co-occur with consumers (Englund & Leonardsson 2008) – any of which can force suboptimal consumer feeding rates. In addition, consumer capture rates depend on how consumers and resources converge across the landscape (i.e. relative velocity) and the dimensionality and size of their respective detection regions (Pawar et al. 2012). Detection region size, in particular, increases substantially when consumers switch from searching over a surface (2D interactions) to searching through a volume (3D interactions). Such switches are likely pervasive in benthic-pelagic aquatic systems where consumers migrate within and between habitats (Barrios-O’Neill et al. 2014b). Indeed, relative velocity and detection region are also independently modified by habitat structure (Manatunge et al. 2000), which may or may not covary with dimensionality. At local scales, the magnitude and shape of consumer–resource interactions can therefore vary with context in space and time – primarily through the modification of capture rates. Thus, some degree of systematic variability is intrinsic to the size scaling of consumer feeding rates; yet attempts to understand and quantify this variability are lacking, resulting in a substantial knowledge gap. Moreover, addressing this gap empirically requires the simultaneous incorporation of consumer size, resource density and contexts such as dimensionality and complexity – together representing a considerable logistical challenge.

Here, in the largest empirical study of its kind, we resolve the functional responses of a range of aquatic ectotherm vertebrate and invertebrate predators – covering four orders of magnitude in body mass between ~4 and ~6400 mg (Table 1) – feeding upon a successful invasive Ponto-Caspian prey species, the corophiid amphipod *Chelicorophium curvispinum* Sars 1895. In 1347 laboratory trials, we quantified the size scaling of functional response parameters across different spatial contexts reflecting the constantly shifting distribution of *C. curvispinum* in lacustrine systems: swimming in the water column – a structurally simple 3D context – and established on a range of structurally simple and complex 2D substrates. We hypothesised that: (1) 2D contexts would yield reductions in consumption concomitant with reductions in capture rates when compared to the 3D context; (2) that structural complexity would further reduce consumption by the same mechanism and (3) that, given a unimodal distribution of capture rates (Fig. 1), reductions would be largest for consumers with optimal capture rates in relation to resource size. Population dynamical simulations parameterised with context-specific functional response models further illustrate how stability regimes might shift with interaction context, whereby increasing substrate complexity eliminates extinction and reduces instability in prey populations across the entire spectrum of
Table 1 Body masses (wt weights in mg) for each predator/size treatment and predator–prey body mass ratios (R) with *Chelicorophium curvispinum*

<table>
<thead>
<tr>
<th>Predator</th>
<th>Rank mass (small &gt; large)</th>
<th>No. trials (all contexts)</th>
<th>Mean mass (mg)</th>
<th>SD</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gammarus d. celticus</td>
<td>1</td>
<td>63</td>
<td>4.38</td>
<td>0.55</td>
<td>1.12</td>
</tr>
<tr>
<td>Gammarus pulex</td>
<td>2</td>
<td>63</td>
<td>4.56</td>
<td>0.5</td>
<td>1.17</td>
</tr>
<tr>
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<td>3</td>
<td>63</td>
<td>8.13</td>
<td>1.81</td>
<td>2.08</td>
</tr>
<tr>
<td>Gammarus pulex</td>
<td>4</td>
<td>63</td>
<td>8.59</td>
<td>1.87</td>
<td>2.2</td>
</tr>
<tr>
<td>Hemimysis anomala</td>
<td>5</td>
<td>91</td>
<td>17.49</td>
<td>2.94</td>
<td>4.49</td>
</tr>
<tr>
<td>Mysis salemaai</td>
<td>6</td>
<td>34</td>
<td>19.15</td>
<td>1.56</td>
<td>4.91</td>
</tr>
<tr>
<td>Gammarus d. celticus</td>
<td>7</td>
<td>63</td>
<td>22.43</td>
<td>5.16</td>
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</tr>
<tr>
<td>Gammarus pulex</td>
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<td>24.03</td>
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<td>54.78</td>
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<td>12.58</td>
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<tr>
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<td>91</td>
<td>83.88</td>
<td>12.69</td>
<td>21.51</td>
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<tr>
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<td>13</td>
<td>91</td>
<td>156.68</td>
<td>36.64</td>
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<tr>
<td>Gasterosteus aculeatus</td>
<td>14</td>
<td>63</td>
<td>402.87</td>
<td>50.98</td>
<td>103.3</td>
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<tr>
<td>Gasterosteus aculeatus</td>
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<td>63</td>
<td>664.73</td>
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<td>Perca fluviatilis</td>
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<td>1118.97</td>
<td>284.95</td>
<td>286.91</td>
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<tr>
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<td>69</td>
<td>1225.64</td>
<td>217.53</td>
<td>314.27</td>
</tr>
<tr>
<td>Salmo trutta</td>
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<td>69</td>
<td>1865.42</td>
<td>217.65</td>
<td>478.31</td>
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<tr>
<td>Barbatula barbatula</td>
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<td>63</td>
<td>2694.05</td>
<td>505.52</td>
<td>690.78</td>
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<tr>
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<td>54</td>
<td>6433.96</td>
<td>1568.49</td>
<td>1649.73</td>
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</tbody>
</table>

We then go on to develop a framework outlining the Context-Dependent Scaling (CDS) of consumer feeding rates.

**MATERIAL AND METHODS**

**Animal collection and maintenance**

We used five species of predatory fish and four predatory crustaceans – and several size classes of some of these predators – resulting in twenty discrete predator–prey body mass ratio pairings, with overlapping body mass distributions covering body mass ratios of ~1 to ~1600 (Table 1). *Chelicorophium curvispinum* was used as prey in all trials and was collected from Lough Derg, Co. Tipperary (52.92583° N, 8.27913° W). Nine-spined stickleback *Pungitius pungitius* (Linnaeus 1758) and the mysid shrimps *Mysis salemaai* (Sars 1870) were collected from the Lagan tributary, which was changed every 2–3 days. Although *C. curvispinum* can survive for long periods of time under laboratory conditions (Barrios-O’Neill, personal observation), we ensured negligible background mortality during feeding trials by collecting new batches of *C. curvispinum* from the field at 10 day intervals.

**Experimental trials**

*Chelicorophium curvispinum* is found swimming in the water column and also established in mud tubes among the benthos (Van den Brink *et al.* 1993; Noordhuis *et al.* 2009). It can achieve very high abundances on spatially complex substrates such as biogenic mussel reefs, and will also establish on simple substrates, particularly on muddy sediments and on anthropogenic structures (Barrios-O’Neill, personal observation; van Riel *et al.* 2006). Therefore, we aimed to derive the functional responses of the resident predators across three spatial contexts reflecting the distribution and behaviour of *C. curvispinum*: swimming in the water column (a 3D context), established in mud tubes on simple substrates and established in mud tubes on complex substrates (2D contexts). Here, although complexity effects in 2D contexts can be isolated, changes in prey behaviour and arena edge effects prevent the explicit isolation of dimensionality.

Prey *C. curvispinum* were initially coarsely sorted for size, yielding experimental individuals with a mean wet weight of 3.9 mg ± 0.05 SE. All trials were conducted in circular arenas of 11.5 cm Ø filled with 700 mL of filtered (25 µm) Lough Derg source water. Arena treatments were designed to reflect three aforementioned contexts: ‘swimming’ containing only water, ‘simple’ containing ~20 g of 250–500 µm diameter (Ø) sediment particulates and ‘complex’ containing 20 g sediment particulates and 20 artificial black pebbles (18.6 mm Ø, maintained under an identical temperature and lighting regime in 40 L aquaria and continuously aerated unfiltered water from the Lagan tributary, which was changed every 2–3 days. Although *C. curvispinum* can survive for long periods of time under laboratory conditions (Barrios-O’Neill, personal observation), we ensured negligible background mortality during feeding trials by collecting new batches of *C. curvispinum* from the field at 10 day intervals.
6.1 mm tall). Prey were introduced into arenas over a minimum density range of 2, 4, 6, 10, 25, 40 and 100 individuals and with replication of $n \geq 3$. In instances where predator feeding did not become prey saturated, the density range was increased, particularly for some larger predators with higher feeding rates, where densities of up to 300 prey were used. Maximum prey density in experimental trials translates to a maximum field abundance of ~ 29 000 individuals per m$^2$, which is commonly observed in the Rhine River and its tributaries, although during invasion peaks maximum actual field abundance can be an order of magnitude greater (Van den Brink et al. 1993).

To allow C. curvispinum in spatially simple and complex 2D treatments time to construct tubes from sediment particulates, a period of 4 h elapsed before the introduction of single starved predators into all treatments. Trials ran for 24 h and were terminated on the removal of predators, after which surviving prey were counted. Refer to supplementary materials for further details on setup and behavioural observations. Here, we retain data from all experimental trials regardless of whether consumption occurred for three reasons: (1) because predation was naturally infrequent with the smallest consumers; (2) because non-consumption at low prey densities can result in Type III functional responses and (3) because disregarding natural variation (e.g. Toscano & Griffen 2014) in consumption is tantamount to subsampling.

Predator-free controls ($n \geq 3$) across all densities and treatments indicated that background prey mortality was negligible and did not affect our results.

**Functional response model**

Eqn 1b assumes that prey density remains constant in time – an assumption that is violated over the course of an experimental trial unless consumed prey are immediately replaced. Therefore, we adopt a generalised functional response model that accounts for the non-replacement of prey as they are consumed (Real 1977; Vucic-Pestic et al. 2010):

$$N_c = N_0(1 - \exp(bN_0^q(hN_c - T)))$$  \hspace{1cm} (3)

where $N_c$ is the number of prey eaten, $N_0$ is the initial prey density, $b$ is the search coefficient or capture rate (arena volume/footprint day$^{-1}$) which, in combination with the scaling exponent, $q$, gives the density-dependent capture rate ($bN_0^q$). $h$ is the handling time (day$^{-1}$) and $T$ is the total time. Note that units reflect experimental scale and time. We used maximum likelihood (Bolker 2010) to estimate modal parameters for each predator–treatment combination and prevented negative estimates of $q$ (Vucic-Pestic et al. 2010); for Type II functional responses, where $q = 0$ eqn 3 collapses to the random predator equation (Rogers 1972).

**Scaling relationships**

Following the quantification of individual predator–prey functional responses, we tested for systematic relationships across three experimental contexts between predator–prey body mass ratios and the capture rates, handling times and scaling exponents derived from eqn 3. We treat predator–prey body mass ratios as the focal explanatory variable to appropriately scale relationships with consumer feeding parameters; where predators are close in size to their prey, small changes in predator mass result in large changes to predator–prey mass ratios. Being constrained by a single-prey species study system, we are unable to explicitly isolate the effects of predator–prey mass ratios from predator mass as in eqn 2 and, therefore, cannot address general scaling beyond the subweb level.

Based on the search space model of Pawar et al. (2012), we hypothesised that context-driven differences in consumption would manifest through changes in consumer capture rates (Introduction: hypothesis (1) and hypothesis (2)). For rigour, however, we initially explored global data sets (of $h$, $b$ and $q$ respectively: eqn. 3) by comparing polynomial models including experimental context as an explanatory variable against models retaining only body mass ratio as explanatory. Throughout model selection and fitting, we opt to transform independent and dependent variables by $\log_{10}(x + 1)$ to avoid problems at 0. ANOVAs between models provided initial justification for splitting capture rates by context ($F_{2,55} = 12.01$, $P < 0.001$) and amalgamating handling times ($F_{2,45} = 0.10$, $P = 0.906$) and scaling exponents ($F_{2,45} = 0.70$, $P = 0.501$). We further hypothesised that reductions in capture rates would be most pronounced for those consumers with the highest rates (Introduction: hypothesis (3)). Therefore, we tested capture rate scaling for deviations from linearity via removal of quadratic terms for each context: ‘swimming’ ($F_{1,17} = 42.10$, $P < 0.001$); ‘simple’ ($F_{1,17} = 0.70$, $P = 0.077$) and ‘complex’ ($F_{1,17} = 0.12$, $P = 0.730$). The contexts ‘swimming’ and ‘simple’ exhibited non-linear unimodal distributions, therefore we used generalised Ricker functions to describe these data (Persson et al. 1998):

$$\log_{10}(b + 1) = \beta \left( \frac{\log_{10}(R + 1)}{\gamma} \right) \exp \left( 1 - \frac{\log_{10}(R + 1)}{\gamma} \right)$$  \hspace{1cm} (4)

where $b$ is the capture rate, $R$ is the predator–prey body mass ratio and $\beta$, $\gamma$ and $\alpha$ are constants. We fitted eqn 4 using a non-linear least-squares regression approach. In contrast, the context ‘complex’ exhibited a power law relationship. Therefore, we fitted a linear model to $\log_{10}$ transformed data using a least-squares approach and did not extrapolate below the body mass ratio at which predation did not occur ($b = 0$).

Global cross-context consumer handling times were described by an exponentially declining function – primarily as a simple means to capture observed data – but also reflecting the mechanistic impossibility of negative handling times, and previously observed exponential declines with consumer mass or consumer–resource mass ratios (Aljetlawi et al. 2004; Kalinkat et al. 2013). We fitted the following using non-linear least-squares regression:

$$\log_{10}(h + 1) = \delta \exp(z \log_{10}(R + 1))$$  \hspace{1cm} (5)

where $h$ is the handling time, $R$ is the predator–prey body mass ratio and $\delta$ and $z$ are constants.

For scaling exponents, we retain the cross-context polynomial function, describing a $u$-shaped relationship with
predator–prey body mass ratios (refer to the legend of Fig. 2 for details).

Population dynamics

Context-specific functional response models (i.e. context-specific capture rates combined with cross-context handling time and scaling exponent models) were used to modify the Rosenzweig-MacArthur model of predator–prey dynamics (Rosenzweig & MacArthur 1963):

\[
\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) - \left( \frac{bN^{q+1}}{1 + bhN^{q+1}} \right) P
\]

(6a)

\[
\frac{dP}{dt} = \left( \frac{bN^{q+1}}{1 + bhN^{q+1}} \right) eP - mP
\]

(6b)

where \( P \) and \( N \) are predator and prey population sizes (number of individuals), respectively, \( t \) is time, \( r \) is the growth rate of the prey, \( K \) is the prey carrying capacity, \( e \) is predator assimilation efficiency and \( m \) is predator mortality. Functional response parameters are modified by body mass ratios according to global handling time and scaling exponent models, \( h \) and \( q \), whereas capture rate models, \( b \), are specific to contexts ‘swimming’, ‘simple’ and ‘complex’. Here, we focus on the local minima and maxima of prey population size, and resulting population instability (coefficient of variation) in the context of the invasion success of \( C. \) curvispinum.

RESULTS

Scaling relationships

Predator capture rates exhibited unimodal relationships (eqn 4) with predator–prey body mass ratios for swimming prey in 3D environments (Fig. 2a: all model parameters significant at \( P < 0.05 \); refer to figure legend) and prey established on simple 2D substrates (Fig. 2b: all model parameters significant at \( P < 0.05 \); refer to figure legend). On simple 2D substrates predation by the smallest size classes of predators was suppressed \((b = 0)\), whereas the optimum capture rate was lowered and upshifted along the body mass ratio axis, supporting hypothesis (1) (Fig. 2b as compared with Fig. 2a). In contrast, the presence of habitat structure – i.e. prey established on complex 2D substrate – resulted in a marked flattening of the relationship between capture rates and predator–prey body mass ratios into a shallow power law relationship (Fig. 2c as compared with Fig. 2b, linear coefficient \( = 0.05 \pm 0.01, P < 0.001 \), supporting
hypothesis (2) and hypothesis (3). Despite pronounced differences at low and intermediate body mass ratios, capture rates tended to converge at the highest mass ratios among all contexts (Fig. 2a–c).

Consumer handling times declined exponentially with increasing predator-prey body mass ratios, and relationships were qualitatively similar among contexts (Fig. 2d: orange, blue and green points). The global exponential model (eqn 5) described this trend appropriately ($\delta = 0.38 \pm 0.14$, $P = 0.012$ and $\varepsilon = -1.25 \pm 0.40$, $P = 0.003$), but tended to overestimate handling times (Fig. 2d: model line and data points).

Scaling exponents were notably variable (Fig. 2e: orange, blue and green points), with absolute Type II functional responses ($q = 0$) occurring across the range of body mass ratios, and among all predatory contexts. Despite this inherent variability, the tendency for higher scaling exponents – for increasingly Type III functional responses – to correlate with small and large predator–prey body mass ratios was evidenced by the u-shaped cross-context polynomial model (Fig. 2e: model line, all model parameters significant at $P < 0.05$; refer to figure legend).

Model parameters $b$, $h$ and $q$ (eqn 3) combine to yield context-specific functional response models (Fig. 3a–c), which demonstrate that interactions on substrates – both simple and complex – are suppressed at small predator–prey body mass ratios (Fig. 3d, $R = 1$). Generalising handling times across contexts results in identical maximum feeding rates ($1/hT$) and, therefore, leads to a convergence of predicted consumption at high prey densities (Fig. 3d, $R = 10$). However, context-specific capture rates models ensure that predicted consumption at critical low prey densities was markedly different among contexts, except at the highest mass ratios (Fig. 3d: all panels)

**Population dynamics**

For prey populations swimming in 3D (Fig. 4a) stability and coexistence occurred only at high and low predator–prey body mass ratios, with prey maintaining higher stable equilibria when interacting with small predators (low ratios) as compared to large predators (high ratios). As ratios increase, the stable equilibria associated with low ratios abruptly bifurcate to chaotic dynamics and/or complete population crashes, only coalescing to stability and coexistence again above body mass ratios of 1000. For prey established on simple 2D substrates (Fig. 4b), population dynamics were superficially similar to those of prey in 3D (Fig. 4a). However, the coefficient of variation (CV) – reflecting population instability – reveals that prey populations established on simple 2D substrate exhibit increased stability (i.e. a lower CV) when compared to 3D, notably at intermediate body mass ratios (Fig. 4d: orange trace vs. Fig. 4d: blue trace). For prey on complex 2D substrates (Fig. 4c), coexistence ($N > 0$) occurred across the entire spectrum of predator–prey body mass ratios and, whereas populations destabilised to some degree at intermediate body mass ratios, they remained consistently stable across a greater range of body mass ratios than comparative contexts (Fig. 4d: green trace as compared with orange and blue traces). Supplementary materials detail how sensitive these differences are to $K$ (eqn 6a) and $q$ (eqn 4).

**DISCUSSION**

Our findings suggest that the scaling of consumer feeding rates can be context dependent – potentially at small spatiotemporal scales – and are largely congruent with hypotheses (1–3), supporting the contention that capture rates mediate this variation. Thus, interactions can vary within the confines of metabolic limits, simultaneously with key extraneous drivers and consumer body mass. Consequently, we propose a conceptual progression that moves away from framing feeding rates primarily around temperature and body size at the local scale, while still recognising that these remain fundamental predictors. We envisage a Context-Dependent Scaling (CDS) of feeding rates as consumer-resource systems move between contexts that systematically modify a consumer’s search space and encounter rate with resources.

**Beyond metabolic scaling**

Evidence suggests that the form and magnitude of a consumer’s functional response is size and temperature dependent (Englund et al. 2011; Rall et al. 2012). In turn, these dependencies dictate consumer–resource coexistence and population stability (Vucic-Pestic et al. 2011; Kalinkat et al. 2013). Functional responses also change systematically with, among other things, habitat structural complexity (Barrios-O’Neill et al. 2015) and dimensionality of search space (Pawar et al. 2012). Drivers such as these may operate equally across a range of consumer body sizes, and vary predictably in space and time (e.g. light), or instead act disproportionately on specific consumer sizes and/or vary in myriad ways in space and time (e.g. structural complexity).

Stability and coexistence between consumers and resources depends on more than temperature and body mass, as feeding rates are also demonstrably coupled to extraneous drivers including – but not limited to – dimensionality and structural complexity. For this reason, our reductive comparisons of prey population stability regimes between experimental contexts are primarily illustrative. Even if interactions within the wider community are not considered, simple consumer–resource population stability will result from the contributions of each context to modifying interactions and resultant population dynamics. Indeed, intra- and interspecific interference are particularly critical modulators in this respect because interference may scale with dimensionality and consumer size (Barrios-O’Neill et al. 2014a; DeLong 2014) and because higher predator cues are likely to universally modify feeding rates (Paterson et al. 2013). Nevertheless, these results do imply that some degree of structural complexity can be a critical determinant of coexistence and stability.

Our results suggest that intermediate predator–prey body mass ratios are aligned with both high capture rates and low scaling exponents, translating to a large – potentially destabilising – consumptive impacts where prey populations are small. The reductions in capture rates at intermediate ratios associated with complex habitat structure (Fig. 2c) – and concomitant coexistence in simulations (Fig. 4e) – suggest that structural complexity modulates destabilising interactions. In addition to this context dependency, the natural
invertebrate–vertebrate transition with increasing consumer mass highlights the importance of species identity in determining the scaling of capture rates (Rall et al. 2011), particularly because species assemblages can vary in space and time (Hutchinson 1961).

**Dimensionality and complexity of consumer search space**

Pawar et al. (2012) suggest that feeding rates scale superlinearly in 3D and sublinearly in 2D, and that differences in scaling are driven by the size of consumer and resource detection regions. Although the size of our largest consumer’s (Salmo trutta) detection region likely exceeds the size of the arena in our 3D habitat, this does not necessarily preclude detection region as the mechanism underpinning the relative differences in capture rates among our treatments due to the effects of prey cryptis and obstructed line of sight on consumer detection region in 2D habitats.

We find that interactions are broadly strongest towards swimming prey and, here, they are also acutely size structured, with larger variations in capture rates over the same range of body mass ratios. On spatially complex substrates the opposite is true, where capture rates are generally lower for a given consumer body mass, and vary less with body mass ratios. Together, these observations suggest that interactions might systematically vary beyond the 2D/3D binary. In 3D pelagic systems, feeding rates are often strongly size structured (Wahlström et al. 2000) and characterised by large aggregations of predators and prey. The latter is a characteristic shared by 2D carnivore-ungulate systems in open, structurally

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**Figure 3** Functional response surfaces as defined by context-specific (Fig. 2a–c) and global parameters (Fig. 2d–e) for: (a) swimming prey; (b) prey on simple substrate and (c) prey on complex substrate. $N_e$ is prey consumption rate, $N_0$ is initial prey density and $R$ is the predator–prey body mass ratio. Points are log-transformed consumption data (open points are above model surface, filled points are below). Lines are residual distances from actual consumption rate data to predicted consumption rates defined by model surfaces. (d) Highlights differences between surfaces (a–c) across four orders of magnitude in $R$: 1 (0.30 log transformed), 10 (1.04 log transformed), 100 (2.00 log transformed) and 1000 (3.00 log transformed).

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simple grasslands (Fryxell 1995). Thus, interaction strengths may also vary continuously along gradients of environmental heterogeneity and structural complexity. Many studied 3D systems are less structurally complex than 2D systems, suggesting that the observed correlations of Pawar et al. might also be underpinned by complexity. However, although our experimental treatments reflect the real-world transitions of *C. curvispinum*, the link to dimensionality remains weak because refuge availability is restricted to our 2D treatment. Altogether, a deeper understanding of the relative contributions of complexity and dimensionality represents an important next step towards making tractable generalisations of consumer feeding rates.

**CDS and the limits of body mass dependencies**

Understanding the causes and consequences of extinctions, invasions and a range of other processes will depend acutely on resolving the scaling of consumer feeding rates: from a global-scale delineation according to MTE (Brown *et al.* 2004), through to the local-scale incorporating body mass ratios (Vucic-Pestic *et al.* 2010, 2011; Rall *et al.* 2012), towards finely resolved CDS.

The constituent parts of consumer feeding rates – capture rates and handling times – present several issues where the objective is to relate consumer feeding rates to stability in food webs. Handling times often exhibit a negative power law with increasing consumer mass (Vucic-Pestic *et al.* 2010; Pawar *et al.* 2012), but here we find an exponential decline similar to Aljetlawi *et al.* (2004). In part, this could result from the fixed experimental time and subsequent handling to digestion limitation transition with consumer size (see supplementary materials). Also, at small predator–prey body mass ratios aspects of interactions are not necessarily aligned with metabolic demand – for example, due to interference competition and intraguild predation (Barrios-O’Neill *et al.* 2014a).

Capture rates are widely observed – or assumed – to exhibit unimodal associations with consumer–resource body mass ratios (Persson *et al.* 1998; Vucic-Pestic *et al.* 2010; Pawar *et al.* 2012; Kalinkat *et al.* 2013). But we show here that the form of these unimodal associations can be context dependent (Fig. 2a–b), and disappear in certain contexts (Fig. 2c). In contrast, scaling exponents – as critical determinants of functional response shape (i.e. Type II or Type III) – often exhibit equivocal body mass dependency (Brose 2010; Vucic-Pestic *et al.* 2010), and we find evidence for Type II responses throughout our data (Fig. 2e). Because the link between functional response type and population stability can also be tenuous (Uszko *et al.* 2015), translating mass-based generalisations of consumer feeding to whole-community dynamics could be problematic. Despite this, CDS posits that defined changes in capture rate scaling – as opposed to ambiguous changes in functional response shape – remain a quantifiable modulator of consumer–resource coexistence.

Changes in capture rate scaling among contexts imply that CDS is inherently spatiotemporal, and suggest that scaling might even be inherently dynamic, but our non-sequential experiments cannot explicitly demonstrate this. Nevertheless, Fig. 5 qualitatively illustrates how local scaling might change if and when contexts change. Critically, the spatiotemporal consistency of dimensionality, structural complexity and other drivers will determine the degree to which size and temperature can act as standalone predictors of feeding rates. The corollary of this assertion is that CDS will be more prevalent where systems are characterised by changing consumer search strategies and associated heterogeneity, or where search strategies shift with ontogeny (Pawar *et al.* 2013). Even where heterogeneity typifies a system, CDS may not necessarily operate at a timescale relevant to population dynamics.

We propose that an underlying mechanism of CDS is the modification of consumer capture rates (Fig. 5), in the first instance via modification of the detection region (A_D) available...
to consumers and their resources (Fig. 5: blue regions) and, secondarily, through modification of the relative velocity \( V_r \) of consumer–resource pairs. \( A_D \) has already been mechanistically linked to dimensionality (Pawar et al. 2012) and structural complexity is known to modify both \( A_D \) and \( V_r \) (Manatunge et al. 2000), whereas other factors – such as dimensionality – may act primarily on \( A_D \) (Fig. 5).

A key empirical result of our study is the collapse of oft-observed unimodal distribution of capture rates (Figs 1 and 2a–c). In the extreme, resources are either too large or too small for consumers – meaning that resources are never consumed, regardless of encounter rate. At optimum ratios, however, a large proportion of encounters result in capture, implying that reductions in \( A_D \) will disproportionately reduce the capture rates of consumers foraging on optimally sized resources. Thus, hump-shaped scaling relationships can collapse in complex habitats where \( A_D \) is reduced (Fig. 2c).

Concluding remarks

Despite the long-recognised importance of body size in ecology (Elton 1927; Peters 1986; Woodward et al. 2005), it is only relatively recently that ecologists have begun to comprehensively resolve the body mass dependencies of consumer feeding rates (Vucic-Pestic et al. 2010; Pawar et al. 2015). We advance this area of inquiry by demonstrating the acute context dependency of capture rate scaling, and thus advocate the explicit consideration of CDS as a potentially important structuring mechanism in ecological networks.

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