



## Original Articles

# Combining resource population dynamics into impact assessments of native and invasive species under abiotic change

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## ABSTRACT

Predicting future changes in interspecific interactions continues to be a challenge for environmental managers. This uncertainty is exacerbated by increasing biological invasions and the likelihood that the strength of trophic interactions among native species will change. Abiotic variables influence predator resource utilisation and abundance as well as resource population dynamics. Currently no practical metric or impact prediction methodology can adequately account for all of these factors. Functional Response (FR) methods successfully incorporate resource utilisation rates with regards to resource density to quantify consumer-resource interactions under varying abiotic contexts. This approach has been extended to create the Relative Impact Potential (RIP) metric to compare invader vs native impact. However, this does not incorporate resource abundance dynamics, which clearly can also change with abiotic context. We propose a Resource Reproduction Qualifier (RRQ) be incorporated into the RIP metric, whereby RRQ is the reciprocal of the fraction or proportion to which reproduction (e.g. of prey species) changes under an environmental context. This modifies the RIP score to give a more informative  $RIP_q$  value, which may be contextually increased or decreased. We empirically demonstrate the utility and benefits of including RRQ into impact potential predictions with an invasive species (the lionfish *Pterois volitans*) and two European native species (shanny fish *Lipophrys pholis* and lesser spotted dogfish *Scyliorhinus canicula*) under different abiotic contexts. Despite high FR and abundance, lionfish impacts were reduced by increasing prey recruitment at higher temperatures, however, remained high impact overall. Shanny predatory impact increased with increasing temperature and was exacerbated by decreasing prey fecundity. Two population increase scenarios (50% and 80%) were assessed for lesser spotted dogfish under predicted temperature increases, preying upon *E. marinus*. Both scenarios indicated heightened predatory impact with increasing predator FR and decreasing prey fecundity. Our new metric demonstrates that accounting for resource reproductive responses to abiotic drivers, in tandem with the consumer per capita and abundance responses, better estimate the magnitudes of predicted inter-species interactions and ecological impacts. This can be used in stock assessments and predictions, as well as invasive species risk assessments in a comprehensive yet user-friendly manner.

## 1. Introduction

Trophic interactions and their likely changes in the face of abiotic perturbations are understudied, commensurate with the severity of drivers such as climate change (Gilman et al., 2010; Rosenblatt &

Schmitz, 2014; Gunderson et al., 2017). This is due to the difficult nature of modelling a suite of abiotic variables and experimentally manipulating conditions to deliver robust predictions (Dawson et al., 2011), coupled with the prohibitive nature of the long time series data needed to assess changes in trophic interactions in the field. There is a

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considerable lack of empirical understanding of the way changes in abiotic parameters can mediate important interspecific interactions, and thus they cannot be effectively incorporated into future scenario predictions (Gilman et al., 2010; Uszko et al., 2017). It is widely accepted that prediction of climate change impacts, and the various abiotic factors this affects (e.g. temperature, pH, dissolved oxygen), over numerous scales (both trophic and temporal), is essential for future biodiversity management and conservation (Kumschick et al., 2015; Urban et al., 2016). However, most models and frameworks proposed have focused on species range shifts (Thomas et al., 2004; Graham et al., 2006; Ruegg et al., 2006) and the responses of one species towards one or more abiotic variables (Donelson et al., 2014; Gilbert et al., 2014). These studies have disseminated important information as to the likely persistence of species and the structuring of ecosystems, but they generally do not consider the effect of biotic processes, such as predation, explicitly (Gunderson et al., 2016; Gunderson et al., 2017). This leaves a large gap in the knowledge of how abiotic contexts may mediate the dynamics that underpin whole community population changes (Sutherst et al., 2007; Van der Putten et al., 2010).

A considerable amount of work has been focused on invasive species impact prediction and the role of both biotic and abiotic context dependence (Rahel and Olden, 2008; Dick et al., 2014; Laverty et al., 2017; Dick et al., 2017a; b; Dickey et al., 2020). This is in part due to the large cost of invasive alien species to economies (Cuthbert et al., 2021; Diagne et al., 2021), biodiversity (Meyerson et al., 2019; Tickner et al., 2020), and due to many impacts being exacerbated by abiotic variables (Walther et al., 2010; Crooks et al., 2011). Further, climate change may allow species range expansions into novel areas, resulting in extralimital dispersal (Kaustuv et al., 2001). It is also possible that native species may develop traits akin to invaders as environmental conditions become more optimal for certain species and less optimal for others simultaneously, depending on the physiology of the species in question (Valéry et al., 2009; Carey et al., 2012; South & Dick, 2017). In particular, climatic variation (i.e. temperature) is likely to drive changes in metabolism, predation and behaviour (Dell et al. 2014; Iacarella et al., 2015; Uiterwaal & DeLong, 2020). Accordingly, climate-induced movements towards thermal optima could heighten ecological impacts of invasive species via enhanced consumer performance; however, the responses of their resources must be considered in parallel.

Practical metrics that allow understanding and prediction of multiple elements of global change in terms of ecological impacts across study systems are thus urgently required (Dick et al., 2017a; Dickey et al., 2020). This is particularly acute as the wider implications of anthropogenic disturbance to both biotic and abiotic factors are emerging threats to food security and human health (Mazza et al., 2014; Plagányi, 2019; Fujimori et al., 2019). This evidence all points to the necessity of developing a comprehensive, rapid, and reliable framework for predicting the population impacts of abiotic change (Williams et al., 2008; Van der Putten et al., 2010; Monaco et al., 2016). Such a framework must allow for: (1) predator and other consumer abundances (Baum & Worm, 2009; Dick et al., 2017b); (2) resource availability (Baum & Worm, 2009; Thomsen et al., 2011); and, (3) empirical quantification of species interaction strengths (Monaco et al., 2016; Dick et al., 2017a; b). Within this framework, the prediction mechanism would ideally be standardised and universally applicable across trophic and taxonomic systems to allow rapid identification and prediction of ecological impact (Dickey et al., 2020).

Functional responses (FR) and their derivative metrics (Dick et al., 2017a; b; Dickey et al., 2018; Cuthbert et al., 2019; Dickey et al., 2020) are proven reliable and powerful tools to predict and understand invasive species impacts. The merit in the FR approach is that it is simplistic yet reliable, and that it provides stakeholders and policy makers with a rapid impact assessment method (Dick et al., 2017a; b; Dickey et al., 2020). Notably, it allows prediction of impact for species with no prior invasion history. Moreover, by integrating consumer FR and abundance (i.e. numerical response proxies), the Relative Impact Potential (RIP)

metric (see Dickey et al., 2020 for review) can be used to derive impact potential of predator–prey (and other consumer–resource) systems, as well as competitive interactions, under various abiotic scenarios (Laverty et al., 2017; Cuthbert et al., 2019; Mofu et al., 2019; Dickey et al., 2020).

Here, we propose and demonstrate how the RIP metric lends itself to a further modification to assess the impacts of consumer species under differing abiotic contexts and climate change scenarios, such as increased temperature (Dickey et al., 2020). We thus further develop the RIP metric to consider abiotic context and climate effects on the consumer, through effects on the FR, but also to crucially incorporate resource (e.g. prey) responses to abiotic/climate effects, and hence overall prediction of ecological impact of consumers under varying abiotic conditions.

## 2. Methods

### 2.1. Metric development

In order to assess the ecological impact of a consumer species under abiotic contexts such as climate change scenarios, rather than comparing an invader and a native species (i.e. as in Dick et al., 2017a; b and Laverty et al., 2017), the metric is adjusted to a comparison of a single species of consumer under higher or lower temperature conditions (or other abiotic variables), that is, **Equations (1) and (2)**. We illustrate this with FR (i.e. Functional Response) and AB (i.e. Abundance) estimates for one consumer species under different thermal scenarios to produce an RIP score as:

$$RIP = \left( \frac{FR_{HigherTemp.}}{FR_{LowerTemp.}} \right) \times \left( \frac{AB_{HigherTemp.}}{AB_{LowerTemp.}} \right) \quad (1)$$

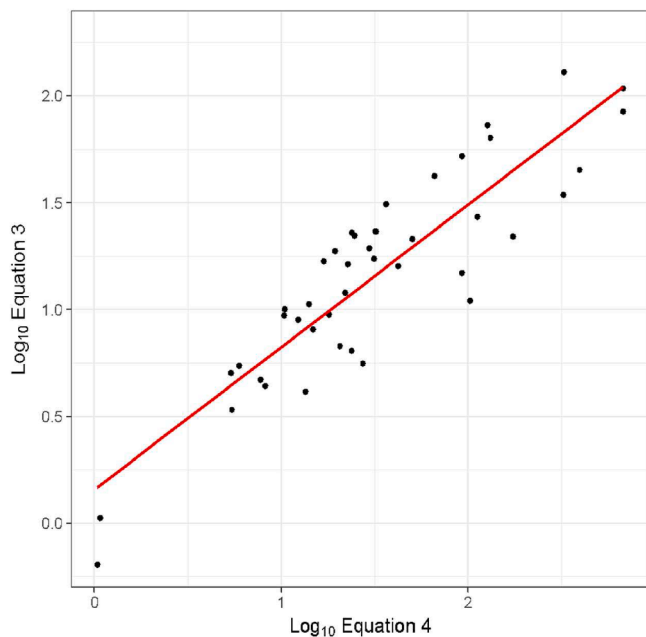
$$f(RIP) = \left( \frac{f(FR_{HigherTemp.})}{f(FR_{LowerTemp.})} \right) \times \left( \frac{f(AB_{HigherTemp.})}{f(AB_{LowerTemp.})} \right) \quad (2)$$

**Equation (1)** can simply utilise estimates or means of FR and AB, whereas **Equation (2)** uses the means and SDs to find the uncertainty around the RIP score using the probability density function method (see Dick et al., 2017b; Laverty et al., 2017; Dickey et al., 2020). However, this latter method is a somewhat laborious and complex process that requires information that is often difficult to obtain (especially SDs; see Dick et al., 2017b). Therefore, using the data in **Table S1** in Dick et al. (2017b), we demonstrate here that the simplified RIP estimates are closely correlated with the more complex RIP estimates incorporating the probability density function ( $r^2 = 0.78$ , intercept = 0.15, slope = 0.66,  $p < 0.001$ ; **Fig. 1**). This justifies the use of the simpler **Equation (1)** throughout this paper, and in future studies.

However, prey (or other resource) abundance has the potential to change with temperature (and other abiotic variables) and it is therefore important to assess whether there will be an increase or decrease in prey population size with the variables investigated. As such, this change in prey abundance has the potential to either increase or decrease the RIP value, as an increase in prey abundance could offset an increase in predator FR and/or AB, while a decrease in prey abundance could increase overall consumer impact. We thus propose a modifier to **Equation (1)** that we call the “Resource Reproductive Qualifier” (RRQ), defined as the reciprocal of the fraction or proportion to which reproduction (e.g. of prey species) changes with temperature (or other environmental variable – see Dickey et al. (2020); **Equation (3)**):

$$RRQ = 1 / \left( \frac{ReproductiveOutputAtHigherTemperature}{ReproductiveOutputAtLowerTemperature} \right) \quad (3)$$

For example, if a prey species doubles its reproductive output at a higher temperature, then this will halve the RIP value as it is multiplied by  $\frac{1}{2}$  (i.e. multiply RIP by  $1/2 = 0.5$ ); alternatively, a prey species that halves its reproductive output at a higher temperature will double the



**Fig. 1.** Log<sub>10</sub> regression of Equation (1) and Equation (2) (data from Table S1 in Dick et al., 2017b) demonstrating that the results obtained from incorporating the PDF (eqn (2)) into impact assessments are significantly correlated with the results obtained from the simpler RIP equation (eqn (1)) that does not incorporate the PDF.

RIP value (i.e. multiply RIP by 1/0.5 = 2); and a prey species that has its reproduction reduced to 75 % will have the RIP increase by a factor of 1.33 (i.e. multiply RIP by 1/0.75 = 1.33). Equation (4) thus captures both the original RIP value and its modification by RRQ:

$$RIP_q = \left( \frac{FROfInvaderAtHighTemp.}{FROfInvaderAtLowTemp.} \right) \times \left( \frac{ABOfInvaderAtHighTemp.}{ABOfInvaderAtLowTemp.} \right) \times RRQ \quad (4)$$

which now balances the temperature change effects on both consumer and resource to predict ecological impact.

Below, we develop the metric and then demonstrate its utility across three study systems. We use data from South et al. (2017) to show how the ecological impact of the notorious invasive fish *Pterois volitans* (red lionfish) predating on the shrimp *Palaemonetes varians* changes under a low and high temperature regime, representing current temperatures at the lionfish invasion front in the Atlantic and Mediterranean invasions. We also use two widely distributed European native species combinations to illustrate how native species interactions can be affected by temperature regimes and potentially develop adverse ecological impacts. For this, data were derived from South and Dick (2017) on juvenile *Scyliorhinus canicula*, the lesser spotted dogfish (hereafter referred to as dogfish) predating upon a crustacean, the amphipod *Echinogammarus marinus* under a current and predicted raised temperature regime, and the second between an intertidal blenniid *Lipophrys pholis* (hereafter referred to as shanny) and *E. marinus* under a predicted temperature regime with data derived from South et al. (2018).

## 2.2. Data visualisation

Biplots are used in a similar manner to Laverty et al. (2017) and Dickey et al. (2020) to demonstrate how RIP can be driven by changes in both *per capita* effect i.e. FRs, and numerical response proxies i.e. abundance and density. This also allows for the incorporation of uncertainty (SE) around the estimation. As such, the RIP should be read from bottom left to top right. We then show how RRQ affects the initial RIP value, to give a better impact metric, i.e. the RIP<sub>q</sub>.

## 3. Results

### 3.1. Lionfish *Pterois volitans* predator & shrimp *Palaemonetes varians* prey

We demonstrate here an impact assessment of lionfish using their invasion front under cooler temperatures in the Atlantic Ocean at Cape Hatteras, USA, compared to their invasion core under the warmer temperatures of the Atlantic Ocean around The Bahamas. This allows a direct estimate of abundance at different temperatures by way of using the invasion gradient as a proxy. In addition this could be used to forecast differences in impact along future invasion gradients, and associated warming scenarios, such as the incumbent lionfish invasion of the Mediterranean. Lionfish data on FR maximum feeding rate were taken from South et al. (2017), using the data from 22 °C (low temperature) and 26 °C (high temperature). The prey species used in this study was the grass shrimp, *Palaemonetes varians*. At 22 °C there was a lionfish maximum feeding rate (hr<sup>-1</sup>) of 4.34 ± 0.55 SE, and at 26 °C a maximum feeding rate (hr<sup>-1</sup>) of 8.34 ± 0.65 SE. Abundance for the invaded range was 21.20 ± 5.1 SD ha<sup>-1</sup> at the lower temperature (20 °C at Cape Hatteras; Whitfield et al., 2007) and 393.00 ± 144.4 SD ha<sup>-1</sup> (Green & Côté 2009) at high temperature (28.68 ± 0.02 SE °C in The Bahamas; Cure et al., 2012). While the experimental temperature treatment (26 °C) in South et al. (2017) is lower than the higher temperature here, the temperatures reported in Cure et al. (2012) are from the June-September warm periods and can be taken as summer seasonal means (S1). Therein, the feeding rate data presented here are likely to be conservative relative to the higher temperatures. Thus we find:

$$RIP = \left( \frac{8.34}{4.34} \right) \times \left( \frac{393}{21.2} \right) = 35.6 \quad (5)$$

Data on *P. varians* reproduction and fecundity were variable, where development time was faster with fewer instars at higher temperatures, but overall fecundity did not change (Oliphant et al., 2014). Successful development from larval stage to juvenile stage can increase by 10.75 % when increased from 25 °C to 30 °C (25 °C: 86.50 %, 30 °C: 95.80 %) (Oliphant et al., 2014). We chose to use the survival rates from Oliphant et al. (2014) as our proxy for RRQ (i.e. a conservative 10 % prey increase), despite being a slightly different range than our experimental treatment temperatures, i.e. 22–26 °C, and thus:

$$RRQ = \frac{1}{\left( \frac{110}{1} \right)} = 0.91 \quad (6)$$

Consequently, the RIP<sub>q</sub> value can be calculated as:

$$RIP_q = \left( \frac{8.34}{4.34} \right) \times \left( \frac{393}{21.2} \right) \times 0.91 = 32.4 \quad (7)$$

There is a marked difference in RIP of lionfish at their invasion core (i.e. The Bahamas and the Atlantic) compared to the invasion front (i.e. North Carolina, Cape Hatteras) (Fig. 2a). High RIP in the invasion core is driven by elevated maximum feeding rates coupled with high abundance at the higher temperature (Fig. 2a). The RIP score is 35.62, indicating a particularly high relative impact potential, but due to the RRQ of 0.91 the impact is reduced by prey population dynamics which result in an RIP<sub>q</sub> of 32.4 (Fig. 2b).

### 3.2. Shanny *Lipophrys pholis* predator & amphipod *Echinogammarus marinus* prey

We determine possible change in a native predator impact under a warming scenario from 15 °C to 19 °C. This represents the 2017 summer high and highest predicted summer water temperature increase in the Irish Sea (Sokolov et al., 2009; South et al., 2018).

Data on shanny (*L. pholis*) FR maximum feeding rates on the amphipod *Echinogammarus marinus* were taken from South et al. (2018).

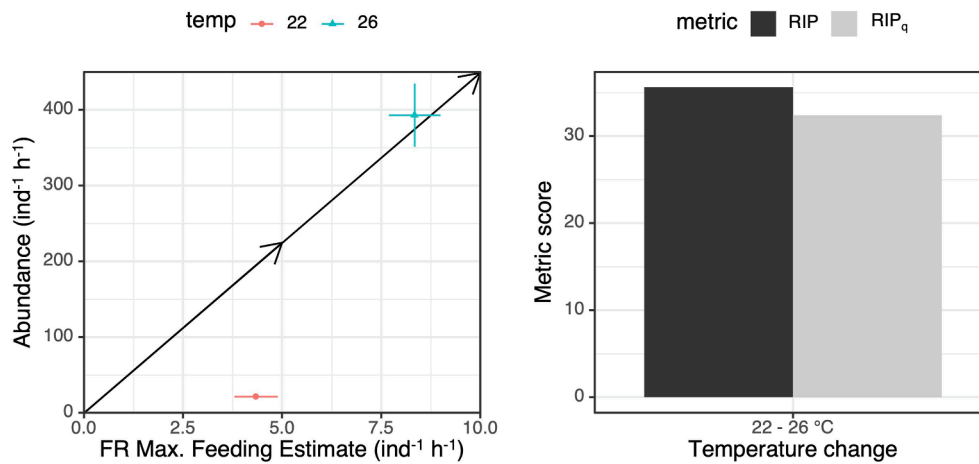


Fig. 2. a) Biplots showing RIP (with SE where available) of invasive lionfish (*Pterois volitans*) predating on grass shrimp (*Palaemonetes varians*) at 22 °C at the invasion front in Northern Carolina and 26 °C at the invasion core in The Bahamas, b) RIP metric value and RIP<sub>q</sub> metric value after RRQ (0.91) is applied for lionfish at 22 °C–26 °C. Impact increases from bottom left to top right.

At 15 °C, *L. pholis* had a maximum feeding rate (hr<sup>-1</sup>) of 17.28 ± 2.21 SE and at 19 °C a maximum feeding rate (hr<sup>-1</sup>) of 7.61 ± 2.12 SE.

Data on shanny abundance were collected via a survey at Ballyhenry Bay, Portaferry, Northern Ireland in August 2017 (54.39 N, -5.57 W). Transects (n = 5) of 10 m were carried out vertically down the shore line at low tide, whereby a search area of 1 m each side of the transect line was maintained to allow a total search area of 20 m<sup>2</sup> for each transect. Searching involved lifting cobbles and large rocks and searching under seaweed to count the total number of fish found. All searching was exhaustive and carried out by the same surveyor to avoid observation bias. Overall, *L. pholis* had an abundance of 0.33 ± 0.30 SD m<sup>-2</sup>. This population estimate is aligned with the 15 °C temperature treatment due to it representing the current population abundance.

Shannys have a wide distribution in the Northern Hemisphere and spawn in the cooler months of the year at their southern limits in Portugal (Almada et al., 1990). Data are varied on the physiological and environmental cues and constraints of shanny breeding ecology. At their southern limit in Portugal breeding takes place in November-February at temperatures of 9.5 °C–17 °C (Qasim 1957; Almada et al., 1990; Faria et al., 2002), whereas the population in Great Britain and Ireland breeds from April-August (Zander 1986; Qasim 1957). Embryo development time decreases with increasing temperature and latitudinal differences in temperature affect settlement of pelagic larvae, where increased temperature reduces pelagic duration (Carvalho et al., 2017; Faria et al., 2002; Qasim, 1957; S1). Almada et al. (1990) postulate that the differences in breeding time could be due to genetic differences in population or due to physiological requirements, however, this remains unresolved. What was defined as common between the two population breeding habits, though, is that the cue for breeding starting is at the end of the minimum sea temperature for the region, but regardless of the region a temperature rise to around 17 °C curtails breeding activity (Almada et al., 1990). For illustrative purposes, and due to warming temperatures of up to 19 °C (Sokolov et al., 2009), we speculate that the shanny breeding season in the British Isles may potentially be shortened from a five-month period to a two-month period, resulting in a 60 % loss of breeding season (Conover 1992; S1). Therefore, it could be inferred that at 19 °C there is a potential 60 % shanny population decrease due to lack of suitable breeding temperature over the year. This scenario would result in a hypothetical reduction in shanny abundance from 0.33 m<sup>-2</sup> to 0.13 m<sup>-2</sup>.

Consequently, the RIP for an increase in temperature from 15 °C to 19 °C is calculated as:

$$RIP = \left(\frac{7.61}{17.28}\right) \times \left(\frac{0.13}{0.33}\right) = 0.17 \quad (8)$$

For *E. marinus*, warming caused females to be less fecund at 20 °C (mean ± SD: 7 ± 1 juveniles released per female) compared to 15 °C (mean ± SD: 16 ± 2 juveniles released per female) resulting in 56 % lower reproductive output (Maranhão & Marques 2003; see S1). Thus the RRQ is:

$$RRQ = \frac{1}{\left(\frac{7}{16}\right)} = 2.28 \quad (9)$$

Therefore, the RIP<sub>q</sub> is calculated as:

$$RIP_q = \left(\frac{7.61}{17.28}\right) \times \left(\frac{0.13}{0.33}\right) \times 2.28 = 0.39 \quad (10)$$

The ecological impact of shanny decreased under predicted warming trends from 15 to 19 °C due to both maximum feeding rate and abundance decreasing (Fig. 3a). The RIP score is below 1, indicating lesser ecological impact than baseline temperatures (0.17; Fig. 3a). The RRQ score increases the RIP<sub>q</sub> when temperatures are raised to 19 °C as a result of decreasing prey population, however, the RIP<sub>q</sub> remains below 1 (0.39; Fig. 3b).

### 3.3. Lesser-spotted dogfish *Scyliorhinus canicula* predator & amphipod *Echinogammarus marinus* prey

We calculate the impact of native and non-commercial elasmobranch predator dogfish, under current water temperatures in the Irish Sea (11.3 °C) and predicted summer mean temperature (16.3 °C) (Sokolov et al., 2009; South & Dick 2017).

Data on juvenile lesser-spotted dogfish *S. canicula* (34.82 ± 2.77 SD cm total length) and FR maximum feeding rate estimates were taken from South & Dick (2017). Prey species used in this study, again, were the amphipods *E. marinus*. At 11 °C there was a maximum feeding rate (hr<sup>-1</sup>) of 12.37 ± 1.67 SE, whilst at the 16 °C treatment there was a maximum feeding rate (hr<sup>-1</sup>) of 29.42 ± 4.23 SE (South & Dick 2017).

Data on dogfish abundance were collected over March 2015 as part of the bi-annual Agri-Food Bioscience Institute (AFBI) March groundfish survey of the Irish Sea (See S2 for locations). Dogfish abundance was 29.63 ± 41.82 SD M<sup>-2</sup> (nautical mile); this abundance estimate was used for the baseline 11.3 °C treatment. Data on dogfish gestation time and fecundity were then used to estimate a potential dogfish population change under a raised temperature regime. In UK waters, gestation time is around 273 days, but in waters 10 °C and under, eggs can be retained for up to a week longer (Ballard et al., 1993). In warmer waters (16 °C) gestation time is 145–175 (range) days (Ballard et al., 1993). This is a decrease of 35.89–46.88 % in gestation time (S1). Dogfish fecundity is

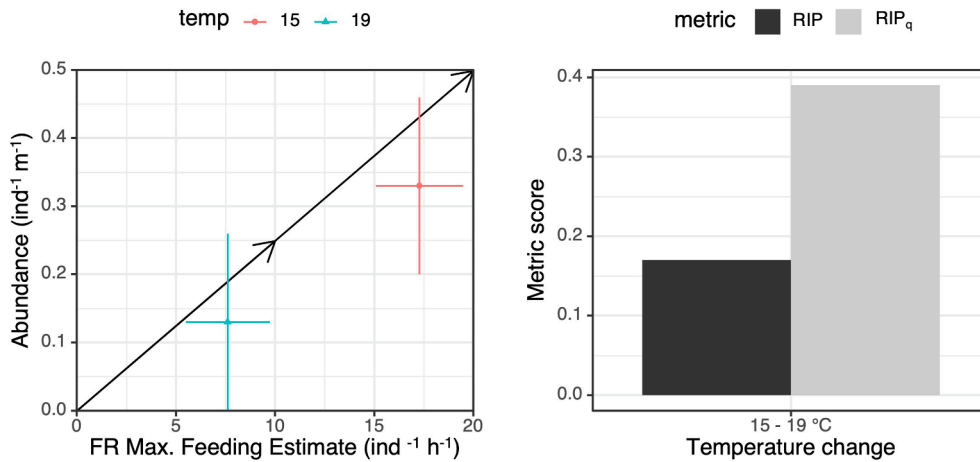


Fig. 3. a) Biplots showing RIP (with SE) of shanny (*Lipophrys pholis*) predating on *E. marinus* at 15 °C current summer high in the Irish Sea and 19 °C highest predicted summer high, b) RIP metric value and RIP<sub>q</sub> metric value after RRQ (2.28) is applied for shannys at 15 °C–19 °C. Impact increases from bottom left to top right.

estimated 26–62 eggs a year in the North East Atlantic (Ellis & Shackley 1997) and estimates of 40–240, 96–115 and 45–190 eggs per female a year in Northern Tunisia, Tunisia and the Gulf of Lion, respectively (Capapé 1977; Capapé et al., 1991; Capapé et al., 2014; S1), where temperatures are higher. Estimates of fecundity were variable due to high inter-individual variation and multiple drivers alongside temperature, such as female age, body size and body condition all affecting egg production (Capapé et al., 2014). In these calculations it was assumed that fishing pressure stayed the same. With this information in mind, it was estimated that there could feasibly be a dogfish population increase of 50–80 % with increased temperature due to decreasing gestation time (S1). As a result we considered both a 50 % (44.44 individuals<sup>-1</sup> M<sup>-2</sup>) and an 80 % (53.33 individuals<sup>-1</sup> M<sup>-2</sup>) abundance increase scenario (S1). Where RIP is calculated as:

$$50\%IncreaseScenarioRIP = \left(\frac{29.42}{12.37}\right) \times \left(\frac{44.44}{29.63}\right) = 3.56 \quad (11)$$

$$80\%IncreaseScenarioRIP = \left(\frac{29.42}{12.37}\right) \times \left(\frac{53.33}{29.63}\right) = 4.28 \quad (12)$$

Prey population data were collated from Maranhão & Marques (2003), wherein reproductive output dropped from 24 ± 4 SD juveniles released per female at 10 °C to 16 ± 2 SD juveniles released per female at 15 °C. Therefore, there is a decrease in the prey population at the higher

temperature (16.3 °C) investigated by South & Dick (2017), making the RRQ:

$$RRQ = \frac{1}{\left(\frac{16}{24}\right)} = 1.5 \quad (13)$$

Thus the RIP<sub>q</sub> values for a 50 % increase in dogfish abundance is:

$$50\%IncreaseScenarioRIP_q = \left(\frac{29.42}{12.37}\right) \times \left(\frac{44.44}{29.63}\right) \times 1.5 = 5.35 \quad (14)$$

and the RIP<sub>q</sub> under an 80 % increase in dogfish abundance scenario is calculated as:

$$80\%IncreaseScenarioRIP_q = \left(\frac{29.42}{12.37}\right) \times \left(\frac{53.33}{29.63}\right) \times 1.5 = 6.42 \quad (15)$$

There is a clear shift towards a higher RIP when temperature is increased as a result of increasing predator maximum feeding rates and predator population abundance (Fig. 4a). The RIP score is above 1 for both 50 % and 80 % population increase at the raised temperature (3.56 & 4.28, respectively; Fig. 4b). When the RRQ (1.5) is incorporated, taking into account the decreasing fecundity of *E. marinus*, the resulting RIP<sub>q</sub> is higher than the RIP, 5.35 for the 50 % predator increase scenario and 6.42 for the 80 % predator increase scenario (Fig. 4b). All results here suggest increased temperatures will enhance the magnitude of trophic interactions by dogfish in the Irish Sea.

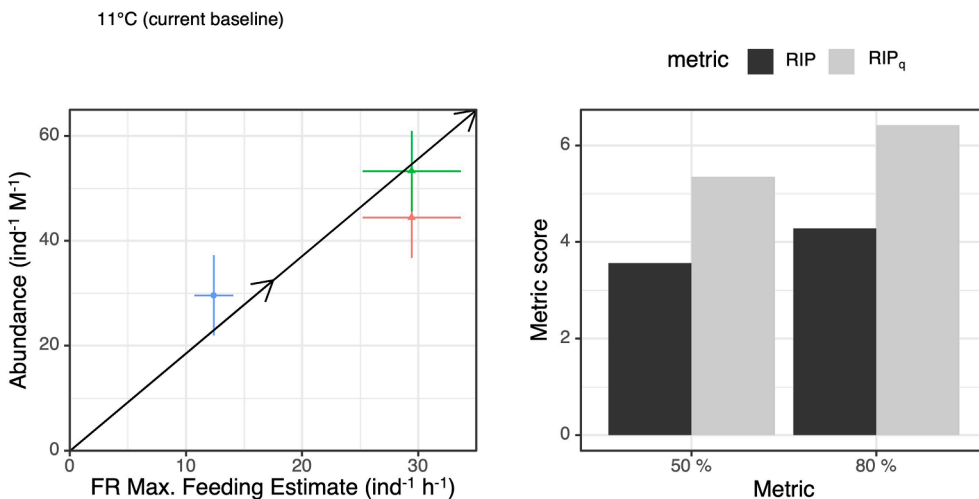


Fig. 4. a) Biplots showing RIP (with SE) of dogfish (*Scyliorhinus canicula*) predating on *E. marinus* at the current mean temperature in the Irish Sea 11 °C and predicted summer mean temperature 16.3 °C under a 50 % dogfish population increase and 80 % dogfish population increase, b) RIP metric value and RIP<sub>q</sub> metric value when RRQ (1.5) is applied for dogfish at 11.3 °C–16.3 °C under a 50 % population increase scenario, and 11.3 °C–16.3 °C under a 80 % population increase scenario. Impact increases from bottom left to top right.

### 3.4. General discussion

Community dynamics and species interactions are mediated by the environmental drivers they are exposed to; therefore, the prediction of the strength and direction of such interactions relies upon gathering an understanding of how these factors affect community levels (Denny & Helmuth 2009; Le Quesne & Pinnegar 2012; Davidson et al., 2021). To create an overarching prediction framework, it is necessary to ensure that we take into account consumer-resource interactions and contextual variables (Van der Putten et al., 2010; Gunderson et al., 2016; Gunderson et al., 2017). These are two inter-linked drivers of ecological impact and it is important to consider them in concert if we are to develop early and effective management systems (Dickey et al., 2020). Furthermore, an integral piece of information is often omitted: resource abundance, which can be manipulated and assessed on its effect upon predatory behaviour under varying abiotic conditions. A sound understanding of resource dynamics is essential for both stock assessments and predictions, as well as invader impact predictions (Beaury et al., 2020). This is due to high resource availability potentially offsetting environmental stress (i.e. increased metabolic rate and the associated behavioural trade offs) (Thomsen et al., 2011; Gilman, 2017). It is towards providing a solution to this theoretical gap, that we demonstrate in our results how resource abundance can be incorporated into overarching impact assessments, with an applicability to resource management as well as risk assessments.

Using the metric conceived by Dick et al. (2017b) and Laverty et al. (2017), and since developed by Dickey et al. (2020), we provide an illustration of the changes expected in the predatory impact of an invasive species under potential temperatures experienced along an invasion gradient (lionfish) and of two native predator-prey combinations under expected future temperatures (shanny and dogfish). It is possible to use the methods and results presented here to triage and horizon scan where species may exert further ecological impacts in the future, for example, through application to the burgeoning lionfish (both *P. volitans* and *P. miles*) invasion in the Mediterranean (Gürlek et al., 2016; Bariche et al., 2017; Turan et al., 2017). By adapting this metric to assess the intraspecific effects of climatic change rather than a specifically invader/native comparison, we provide a method to rapidly quantify ecological impacts of consumer species on prey populations, which can be applied to any trophic and taxonomic group under any relevant abiotic variable. With the incorporation of changes in resource reproduction, our metric takes into account the way in which thermal changes are expected to affect prey as well as predator populations. This then allows us to represent the effect (or lack of effect) of changing dynamics in prey abundance on the RIP score, resulting in an adjusted value (i.e. the  $RIP_q$ ). Taking both predator and prey population dynamics into account is essential when trying to predict change in interaction strength, due to differing effects of abiotic variables on each species (South & Dick 2017). In this way, we demonstrate a prediction metric that accounts for (1) predator abundance (Baum & Worm 2009; Dick et al., 2017b); (2) resource availability (Baum & Worm 2009; Thomsen et al., 2011); (3) and empirical quantification of species interaction strength (Monaco et al., 2016; Dick et al., 2017a; b; Dickey et al., 2020) under varying abiotic perturbations.

### 3.5. Lionfish (*Pterois volitans*) & *Palaemonetes varians*

Lionfish ecological impact at the invasion front is vastly constrained by lower temperature. Temperature increase did facilitate an increase in prey abundance as a result of juvenile survival, however, the  $RIP_q$  value for lionfish at these temperatures suggests that the impact at the invasion core will be higher than at the invasion front due to a coupling of high abundance and high maximum feeding rates in this area. It should be noted here that the densities used for the Atlantic invaded range are described as “record densities” (Green & Côté 2009) and therefore are on the extreme side (but see Bejarano et al., 2015). In defence of using

this estimation, it provides an upper estimate limit and shows the possible extremes of lionfish colonisation and settlement and hence impact in the Atlantic invaded range. However, using our method presented here, it is relatively simple to calculate context dependent (i.e. location specific) values for RIP and  $RIP_q$ , which may prove helpful for the ongoing local management of these damaging invaders. This is especially useful as abundance estimates and thus impact can be constantly re-assessed and updated to follow trends in removal efforts, or as a result of climate facilitated bridgehead colonisation and establishment (Grieve et al., 2016). Further, our results mirror known field trends depicting the high ecological impact of lionfish but can be applied on a case study basis to resolve dispute around actual conferred impacts (see Hackerott et al., 2017).

It would also be possible to use our method to compare the RIP and  $RIP_q$  of lionfish native ranges in the Pacific Ocean ( $1.70 \pm 2.27$  SD  $ha^{-1}$ ) and Indian Ocean ( $28.80 \pm 1.75$  SD  $ha^{-1}$ ) (Kulbicki et al., 2012). There are comparatively similar temperatures within the Atlantic invaded range and the native range (Cure et al., 2012; Kulbicki et al., 2012) but highly disparate population densities between them. This, again, highlights the effect of predator abundance on the RIP and  $RIP_q$  as it emphasises the importance of the incorporation of abundance into prediction metrics as well as creating location specific impact assessments (Dick et al., 2017a; b; Hackerott et al., 2017; Laverty et al., 2017; Dickey et al., 2020). This example was not completed in this study due to recent work identifying population level differences in species FRs (Boets et al., 2019; Grimm et al., 2020) and data on the FR of lionfish in their native range currently unavailable. Thus, the predictive capacity of laboratory experiments can be enhanced by incorporating different populations as well as prey switching capacity (see McCard et al., 2021). Nonetheless, if compared between native and invaded range, the overall impact (RIP and  $RIP_q$ ) is likely to be lower even if the effect of temperature on FR is the same (per the environmental matching hypothesis: Iacarella et al., 2015), purely due to the massive invasive range abundance of lionfish.

### 3.6. Shanny (*Lipophrys pholis*) & *Echinogammarus marinus*

Increasing temperatures decreased the RIP of the shanny by dampening predator *per capita* response (FR) and numerical response (AB), and the prey species also experienced a concomitant decrease in fecundity. Overall, the RIP and  $RIP_q$  values were below 1 which is considered as conveying lower impact on the prey species than at present (Dick et al., 2017b; Dickey et al., 2020). This is concordant with ecological theory that co-evolved sympatric native species should not exert damaging predation pressure on prey populations. Negative trends in both FR and abundance under predicted warming scenarios go against the metabolic theory of ecology (Brown et al., 2004; Englund et al., 2011) and indicate that there should be further investigation into the mechanics of thermal responses (but see Uiterwaal and DeLong 2020). This compounds the importance of considering specific predator and prey dynamics as well as life history changes under thermal regimes when assessing and forecasting possible changes in ecological impact, of either native or invasive species, as excluding variables can cause confounding interpretations. Especially when considering intertidal species that are physiologically predisposed to being resilient against environmental variation, as there is growing evidence that organisms exposed to such preconditioning or chronic thermal stress develop protective physiological traits (Hawkins & Warner 2017; Marigómez et al., 2017).

In our worked example we speculated a 60 % decrease in breeding season but acclimation, changes in developmental time, phenological shifts or range shifts may occur in response to temperature increases (Visser et al., 2006; Carvalho et al., 2017; Davidson et al., 2021). While not able to predict the population response currently, the possible outcomes of range shifts or phenological shifts would probably result in trophic interaction changes which makes the  $RIP_q$  method even more applicable for forecasting impact, should either occur.

Furthermore, we used *E. marinus* fecundity data as the proxy for RRQ, but there are also data available for embryonic development times of *E. marinus*. At 20 °C ( $17 \pm 0.3$ ) there is a shorter embryonic development compared to 15 °C ( $32 \pm 0.5$  days), resulting in a 48 % decrease in development time (Maranhão & Marques 2003). These data suggest that warming, despite reducing fecundity, can increase generational turnover time which may, to some degree, confound the inferences made when considering an RRQ value reflecting fecundity alone. Future developments towards incorporating resource population dynamics into impact assessment should identify ways in which to integrate multiple resource proxies.

### 3.7. Lesser-spotted dogfish (*Scyliorhinus canicula*) & *Echinogammarus marinus*

The RIP biplot schematics show a clear increase in dogfish impact with increasing temperature, driven by both the increase in FR and increasing consumer population abundance. The temperatures used here reflect the potential 3–5 °C global sea surface temperature increase in the future (Sokolov et al., 2009). Temperature has a clear effect on the *per capita* impact of dogfish (South and Dick 2017) and, when combined with the potential population abundance increase, it is thus evident that higher temperatures may cause a substantial increase in the RIP and  $RIP_q$  of dogfish on prey populations, given the reduction in *E. marinus* fecundity. At these temperatures, the rate of embryonic development of *E. marinus* was found to have no significant difference between 10 °C and 15 °C (mean  $\pm$  SD:  $33 \pm 0.7$  days and  $32 \pm 0.5$  days respectively) (Maranhão & Marques 2003). As such, if embryonic development was used instead as a proxy it may be considered that the RRQ would be fixed at 1 and therefore would not cause the ultimate  $RIP_q$  calculation to differ from the RIP value. Further, feeding rates are driven by body size in addition to contextual factors (Gillooly et al., 2002; Rall et al., 2012; Barrios-O'Neill et al., 2016). In South & Dick (2017), the dogfish used were juveniles, therefore reducing the body mass ratio, the true maximum feeding rate of adult dogfish on this prey should be higher due to allometric scaling (Vucic-Pestic et al., 2010; Rall et al., 2012; Uiterwaal & DeLong 2020).

Dogfish make an unusual case study as elasmobranchs are generally classed as “K-strategists”, referring to the long gestation times, low fecundity, large body size, and delayed maturation times (King & McFarlane 2003). Usually K-selected species are at risk to over exploitation by predation, fishing, and abiotic perturbations due to their life history traits (Gallucci et al., 2006), but dogfish pose an anomaly to this generalisation. Populations of lesser spotted dogfish are stable and increasing in the Irish Sea (Richardson 2016) and have a higher fecundity than other teleosts (Capapé 1977; Spencer & Collie 1995). This is because they are not a targeted fishery in the Irish Sea (Richardson 2016) and have a >90 % survival rate when discarded (Kaiser & Spencer 1995; Revill et al., 2005; Rodríguez-Cabello et al., 2005). Therefore, with slow warming scenarios and lack of predation pressure and exploitation they have increased hugely in abundance (Sguotti et al., 2016; Richardson 2016). They are potentially exerting a considerable top down pressure on the Irish Sea system, which is set to only increase in the future, especially if fishing pressure and practices remain the same. These results suggest that under predicted climatic scenarios, dogfish may be capable of exerting a predatory impact value comparable to that of the highly invasive Chinese mitten crab (*Eriocheir sinensis*; Dick et al., 2017b). Wherein, the magnitude of relative impact potential value exerted by native dogfish on their native prey communities system is similar to that of the invasive Chinese mitten crab upon native freshwater prey. This supports the hypothesis that projected climate change could cause native species to develop traits associated with invasive species (Valéry et al., 2009; Carey et al., 2012) and drives home the necessity of case by case assessments of potentially damaging species.

### 3.8. Conclusion

The present study demonstrates the utility of the RIP metric to assess differences in impact under changing environmental variables, but most importantly improves upon the integrity of the impact prediction through incorporating resource abundance. While the RIP metric has been used previously to successfully predict potential impacts of a variety of species under a variety of contexts (Dick et al., 2017a; b; Dickey et al., 2020), we add value by including a resource reproduction qualifier (RRQ) and exhibiting the ways in which prey population dynamics can enhance or dampen the initial impact prediction in response to climatic variables (Dickey et al., 2020). Abiotic drivers can affect metabolism (Brown et al., 2004), fecundity (Raak-van den Berg et al., 2017), development time (Carvalho et al., 2017) and trophic interaction strength (Uiterwaal & DeLong 2020; Davidson et al., 2021) in a variety of directions depending on the species. In the present study we elucidate on how temperature change can cause myriad effects on both predator and prey population dynamics and therefore impact potential. The differential effects of this are captured here wherein the RRQ (i.e. prey reproduction dynamics) was higher than 1 in the lionfish example (*P. varians*), was lower than 1 in the shanny example (*E. marinus*), and had the potential to be fixed at 1 in the dogfish example depending on which RRQ proxy was chosen for *E. marinus* and the focal temperature. We emphasise the fact that density dependent resource utilisation, predator abundance and resource abundance must be considered in tandem in order to understand the way in which the strength of trophic interactions may change in the future but acknowledge that further additions and alterations need to be considered in consequent method developments. For example, the method can also be used to quantify changes in trophic interactions under the host of abiotic changes associated with climate change, such as salinity change, dissolved oxygen levels and ocean acidification (Dickey et al., 2021a; b).

Future developments towards user friendly metrics should consider that while abiotic context is an important determinant of interaction strength there are usually multitudes of interacting stressors and dynamics (Jackson et al., 2016; Birk et al., 2020; Orr et al., 2020). Accordingly, this would involve looking at multiple stressor effects on systems (Craig et al., 2017; Guiden et al., 2019; Orr et al., 2020). Although, at this point, in order to successfully assess these interactions we rely upon having a solid knowledge base of basic species ecology and life history dynamics under current conditions as well as under predicted climatic change, which are unfortunately lacking for a vast number of potentially threatening and threatened species in all ecosystems. For example, many species experience a reduction in body size with increasing temperature/decreasing oxygen (Baudron et al., 2014), which would then reduce the biomass available for predators to consume and thus may cause an increased total *per capita* response on the prey community. Although, these dynamics can also induce early, and growth independent, maturation and thus reproduction and indeed some species do not experience size reduction at all (Audzijoynyte et al., 2020). Further, changes in climate are forcing shifts in species phenology, which will further affect the way in which ecological impact is actualised due to mis-matches in resource abundance patterns (Renner & Zohner 2018). This, again, would need to be assessed on a case-by-case basis but it would be more poignant when assessing specialist species rather than generalist species which have a higher aptitude for resource switching (Dickey et al., 2020). We therefore advocate that there is huge value in maintaining ecological research priorities of monitoring baseline population abundances, distributions and basic ecology (fecundity, growth rates, trophic interactions etc). Nonetheless, the methodology presented here can deliver a succinct and standardised way of quantifying relative impact potential while considering many environmental variables with the information that is currently available (Dickey et al., 2020).

Policy makers can use this as a tool to understand how invasive and native species may become ecologically and economically damaging in

the future, and as this method facilitates forecasting for predicted impacts it could be incorporated into horizon-scanning/pre-emptive methods (Gallardo et al., 2016; Beaury et al., 2020). Our methods and results substantiate the assertion by Dick et al. (2017b) that low impact or native species would have RIP and RIP<sub>q</sub> scores <1 and establish that the simpler method for calculating RIP is a robust technique (Laverty et al., 2017; Cuthbert et al., 2019; Mofu et al., 2019). Therefore, this method lends itself as a framework for localised impact predictions, allowing contextually informed mitigation plans to be created.

#### 4. Open research statement

Data are already published and publicly available, with those items properly cited in this submission. Raw data for *Lipophrys pholis* abundance and *Scyliorhinus canicula* abundance are provided publicly at: <https://doi.org/10.6084/m9.figshare.18550346.v1> and <https://doi.org/10.6084/m9.figshare.18550709.v1>.

#### CRedit authorship contribution statement

**Josie South:** Conceptualization, Methodology, Data curation, Writing – original draft. **James W.E. Dickey:** Conceptualization, Methodology, Writing – review & editing. **Ross N. Cuthbert:** Conceptualization, Methodology, Writing – review & editing. **Jaimie T.A. Dick:** Conceptualization, Methodology, Writing – review & editing, Supervision.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data are available from published literature and at <https://doi.org/10.6084/m9.figshare.18550346.v1> and <https://doi.org/10.6084/m9.figshare.18550709.v1>

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109260>.

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