

Contrasting ecological impacts of native and non-native marine crabs: a global meta-analysis

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ABSTRACT: Concern about the impacts of invasive species on invaded communities is often linked to the expectation that invasive consumers will be more effective at using resources than native ones. Many invasive marine crabs (infraorder Brachyura) are regarded as particularly capable consumers; however, native crabs can also exert significant influence on community structure. We used marine crabs as a focal group to test whether non-native consumers have greater impacts than native consumers on native prey populations by conducting a systematic review and meta-analysis of 834 crab foraging experiments. In addition to the effect of crab origin (non-native or native) on prey abundance, we examined the effects of interaction type (direct or indirect), prey type, and experimental design. Overall, direct consumption by non-native crabs did not reduce prey abundance more than predation by native crabs, although the magnitude of reductions in prey abundance varied with prey type and experimental design. Indirect interactions with crabs (i.e. through trophic cascades with crabs as the initiators) generally increased the abundance of native species. The direct and indirect impacts of non-native crabs were significantly greater than those of native crabs on primary producers and in simplified experiments with low species diversity. Thus, detecting differences between native and non-native crabs may be heavily influenced by experimental design. Importantly, we found few studies that considered direct interactions (competitive or predatory) between native and non-native crabs. These interactions should be a focus of future research because they could greatly alter consumption rates and overall prey mortality in the wild.

KEY WORDS: Aquatic invasive species · Marine crustaceans · Meta-analysis · Ecological impact · Taxonomic distinctiveness hypothesis

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INTRODUCTION

Invasions by non-native species are a leading cause of population declines and biodiversity loss worldwide (Sala et al. 2000, Clavero et al. 2009, Butchart et al. 2010). Impacts can occur due to changes in species interactions, including competition (Kenward & Holm 1993, Martin et al. 2010, Shochat et al. 2010), parasitism (Daszak et al. 2000), and disease (Prenter et al. 2004), with the direct and indirect trophic effects of invasive consumers probably the best-studied mechanism for these declines (Lockwood et al. 2007). For example, the introduction of the brown tree snake *Boiga*

irregularis to the island of Guam, which previously lacked any predatory mammals or reptiles, resulted in massive population declines of the island's avifauna due to predation by this novel predator species (Rodda et al. 1992, Wiles et al. 1995). Similar case studies, including the invasion by Indo-Pacific lionfish *Pterois volitans* in the Caribbean (Green et al. 2012) and feral cats *Felis silvestris catus* in New Zealand (Dowding & Murphy 2001), reinforce the popular narrative of the 'voracious invasive' (Salo et al. 2007).

However, non-native consumers are not universally detrimental to native prey biodiversity. Some non-native consumers have negligible or undetect-

able effects on native prey populations (Parker et al. 1999). For instance, the predatory impacts of invasive cane toad *Rhinella marina* in Australia have been largely imperceptible, despite the species' formidable reputation as a predator (Shine 2010). Invasive rats (*Rattus* spp.) can have highly variable impacts on seabird colonies depending on the life history traits of the prey species (Jones et al. 2008). In other cases, non-native species may have minimal impact if they behave similarly to native ecological equivalents (Greenlees et al. 2006, Lepori et al. 2012).

Two of the most prominent mechanisms underpinning the observed variability in impacts of invasive consumers are naïveté by both prey and predators and species distinctiveness (Ricciardi & Atkinson 2004, Lockwood et al. 2007, Sih et al. 2010). Native prey might not recognize non-native consumers as being dangerous (i.e. prey naïveté), but conversely non-native consumers might not perceive native prey as being edible (i.e. predator naïveté), because of a lack of co-evolutionary history (Sih et al. 2010). Both native prey and non-native consumers might therefore exhibit inappropriate responses of avoidance/escape and attack, respectively, during encounters, leading to variable impacts. In addition, the extent to which naïveté influences the impact of non-native predators on native prey will often be mediated by distinctiveness, which describes how novel an introduced species is in a recipient ecosystem (Ricciardi & Atkinson 2004). Typically, the more distinctive an introduced consumer is, either taxonomically or functionally, from native consumers, the greater its impacts (Ricciardi & Atkinson 2004, Thomsen et al. 2014). The variability in impacts of invasive consumers on prey abundance and/or biodiversity makes predicting the effects of new and emerging invasive species a significant challenge (Parker et al. 1999, Byers et al. 2002, Leung et al. 2012).

One group of invasive consumers of growing concern is marine crabs (infraorder Brachyura; Breen & Metaxas 2012). International shipping has been a vector for crab invasions since the 1800s (Carlton & Cohen 2003). A survey of publicly accessible invasive species databases and select publications shows that the frequency of new introductions and detections of non-native marine crabs continues unabated (Fig. 1; see Table S1 linked from the Supplement at www.int-res.com/articles/suppl/m577p093_supp.pdf), creating a need for a better understanding of their potential impacts (Grosholz & Ruiz 1996, Breen & Metaxas 2012). Non-native crabs can have significant negative direct and indirect effects on native populations. For example, the globally invasive European green

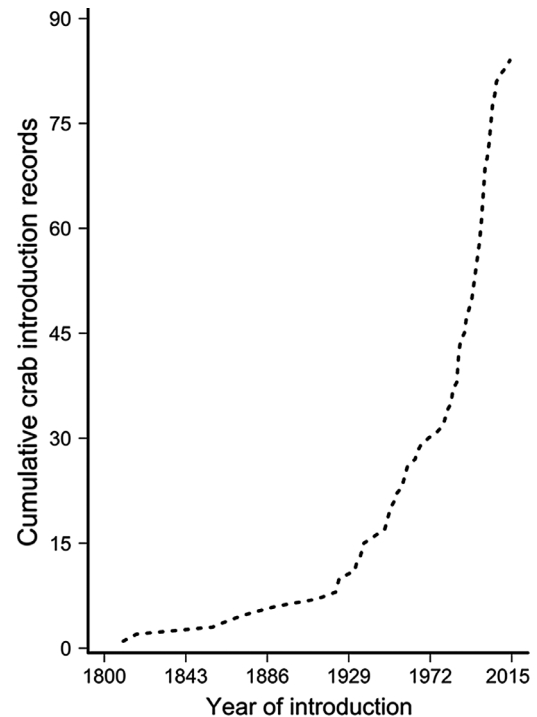


Fig. 1. Cumulative number of newly recorded introductions of marine and euryhaline crab species worldwide. Data from national (Australia, New Zealand, USA, South Africa, UK), regional (Europe), and international (IUCN/SSC Invasive Species Specialist Group) online databases for invasive species monitoring as well as select publications (see Table S1 for details)

crab *Carcinus maenas* is recognized as an effective shellfish predator and has been implicated in large declines of some shellfish populations (Glude 1955, Welch 1968, Grosholz et al. 2000). Similarly, the Asian shore crab *Hemigrapsus sanguineus* both preys upon and competes with native crab species (e.g. fiddler crab *Uca pugilator* and flatback mud crab *Eurypanopeus depressus*) along the east coast of the USA and has been implicated in large declines in native crab abundances (Jensen et al. 2002, Kraemer et al. 2007, Peterson et al. 2014, Griffen & Riley 2015). While the indirect effects of non-native species, including marine crabs, are not as well studied (White et al. 2006), there is some evidence for trophic cascades. For example, the European green crab can indirectly reduce mortality of sessile invertebrates (i.e. barnacles and mussels) and primary producers (i.e. cordgrass *Spartina alterniflora*) through direct consumption of intermediate consumers (Trussell et al. 2003, 2006, Griffen & Byers 2009, Bertness & Coverdale 2013).

While studies support the general notion that non-native crabs can negatively impact prey populations,

they do not address how these effects compare to those of native crabs. Recent meta-analyses have found that invasive consumers tend to have a greater negative impact on prey abundance than native consumers (Salo et al. 2007, Paolucci et al. 2013). However, the majority of studies in these meta-analyses were derived from terrestrial and freshwater ecosystems (100% in Salo et al. 2007; 85% in Paolucci et al. 2013), where the impact of predators on their prey is usually less marked than in marine systems, especially intertidal areas (Sih et al. 1985). Marine crabs in particular are known to play important roles in structuring intertidal and near-shore marine communities (Boudreau & Worm 2012). For example, within its native range, the European green crab can significantly reduce bivalve abundances and has a strong effect on temporal variation in these populations (Richards et al. 1999). Similarly, on the US east coast, the native blue crab *Callinectes sapidus* is considered a keystone predator, having population-level effects on native mud crab *Panopeus herbstii*, oyster *Crassostrea virginica*, and cordgrass through both direct and indirect trophic interactions (Silliman & Bertness 2002, Grabowski et al. 2008, Hill & Weissburg 2013). Thus, native crabs might have both direct and indirect ecological effects that are as large as (or larger than) those of non-native crabs, despite the general expectation that non-native species will have larger impacts.

To estimate the relative ecological impacts of native and non-native crabs, we conducted a systematic review and meta-analysis of the substantial experimental literature on crab foraging. We asked 3 main questions. First, do crabs have different effects on the abundance (as a proxy for survival) of species with which they interact directly (i.e. prey) and indirectly (i.e. via potential trophic cascades)? We expected that prey abundance would decrease in direct interactions and increase in indirect interactions with predatory crabs. Second, do native and non-native crabs differ in their effects on the abundance of species with which they interact? If the narrative of the 'voracious invasive' holds, then non-native crabs should have larger negative effects on their prey than native species (Salo et al. 2007), but it is not clear whether this difference will reverberate across multiple trophic levels (i.e. in indirect interactions) (White et al. 2006). Third, are certain prey types more susceptible to predation by non-native than native crabs? Assuming no difference among prey in capacity to recognize non-native predators, we predicted that prey, especially those with limited escape abilities, might be more vulnerable to non-native crab predation (e.g. Sih et al. 2010, Grason & Buhle 2016).

METHODS

Literature search, selection criteria, and data extraction

We searched the ecological literature for experiments quantifying the direct and indirect impacts of crabs on their prey. Two online databases, the Web of Science (WOS; 'all years' ending December 2016) and the Aquatic Sciences and Fisheries Abstracts (ASFA; 'all years' ending December 2016), were searched using keyword combinations of crab* + predat* (to capture predation, predatory, predator) + compet* (to capture competition, competitor, competitive) + marine. In addition, we looked at relevant cited literature from the papers we found. A total of 5429 abstracts were returned. After removing duplicates, conference proceedings, and irrelevant search results, the remainder (556 abstracts) were systematically reviewed (Fig. S1 in the Supplement, Table S2 linked from the Supplement).

To be included in our meta-analysis, each study was required to meet the following criteria. (1) The focal crab species was a true crab (infraorder Brachyura) in its adult form and was a near-shore or intertidal species. (2) The study examined the interspecific effect of crab presence (i.e. studies of cannibalism were excluded). (3) Crab presence had a potential direct or indirect effect on the survival of another species through consumption (i.e. parasitic interactions were excluded). (4) Crab presence was manipulated (either directly or using spatial/temporal gradients) so there was a 'no-crab' control. (5) The response of the species affected by crabs was measured in terms of abundance (e.g. density, biomass, percent cover) either removed or remaining by the end of the experiment (prey abundance at the start of experiments was always assumed or shown to be equal across treatments). Finally, (6) the study reported the required data to calculate an effect size for each species affected by crabs.

We considered each responding species' abundance reported in a study as an individual experiment (see section on non-independence below). For each experiment, the mean abundance of responding species, standard deviation, and sample size for both with- and without-crab treatment groups were recorded. When the data required were only available from figures, we used the program GraphClick v 3.0.2 (www.arizona-software.ch/graphclick) to extract values for the parameters needed. When standard errors or confidence intervals were provided, we converted them to standard deviations.

We recorded as potential moderators of the ecological effect of crabs whether the crab species was native or non-native, whether the interaction was direct or indirect, the functional group of the responding species, and details about the experimental design (Table S3 in the Supplement). Responding species were categorized into 1 of 5 functional groups based on habitat and mobility: (1) primary producers, including seaweeds, seagrasses, and phytoplankton; (2) sessile invertebrates, including mussels, oysters, barnacles, and encrusting epifauna; (3) mobile epifauna, including other decapods, gastropods, scallops, and echinoderms; (4) mobile infauna, including clams, marine worms, and infaunal crustaceans (amphipods and isopods); and (5) vertebrates, which was limited to birds and fish (Table S3). Because experimental design can strongly affect the results of a study (Fernandes et al. 1999), we categorized designs based on similarity to natural conditions. The 5 categories ranged from 'natural experiments,' which used spatial or temporal variation in crab presence to measure effects on responding species abundance in the field, to increasingly precisely manipulated laboratory experiments where a crab predator interacted with a single responding species (Table S3).

Two additional factors could be important in determining the impacts of non-native species. First, time since arrival in a new area has been proposed as a predictor of the potential impacts of marine invaders (Rosson et al. 2012, Byers et al. 2015). Unfortunately, there was insufficient information on the timing of marine crab introductions at the precise locations at which experiments were conducted to consider this variable in our analyses. Second, body size is an important determinant of both predatory and competitive interactions in crabs (Boudreau et al. 2013, Hill & Weissburg 2013, Tina et al. 2015). To address whether there was a bias towards larger non-native marine crabs rather than native ones, we compiled information on average crab carapace width (mm) for every species in the dataset from a variety of sources (Table S4 in the Supplement) and compared mean sizes of native and non-native species with a Mann-Whitney test.

Data analysis

We generated individual effect sizes for each comparison using the standardized mean difference (i.e. Hedge's g) of the responding species' abundance at the end of an experiment, weighted by the inverse of the variance for each. Hedge's g was calculated as

the mean difference in abundance at the end of an experiment between treatments without and with crabs, divided by the pooled standard deviation across groups (Viechtbauer 2010). This metric is preferable to ratios when means can have values of 0 (Hedges et al. 1999), which was the case here. Abundance at the end of each experiment was reported either as number remaining or number consumed. If crabs have an effect on a responding species, the former measure would yield a positive value, while the latter would yield a negative one. For consistency and to make the results more intuitive, we reversed the sign of the effect size for experiments reporting remaining abundance so that across all studies, negative values denoted a decline in responding species abundance in the presence of crabs. For all mean effect sizes, we calculated 95% confidence intervals (CI). Mean effect sizes are considered to be significant when the CI does not overlap 0.

The direct and indirect interactions of crabs with responding species are expected to have opposite effects on species abundance, i.e. decreasing the abundance of prey consumed, and increasing the abundance of species released from interactions with those prey. We first tested the effect of interaction type (fixed factor: direct or indirect) on Hedge's g using a mixed-effects model, with the source publication (study ID) included as a random effect to control for multiple experiments from individual studies. Because the results supported our expectation (see 'Results'), we considered direct and indirect interactions separately for all subsequent analyses, including testing for publication bias (see next sub-section). We conducted all analyses in R, using the `rma()` function within the *metafor* package to generate models (R Development Core Team 2008, Viechtbauer 2010).

We conducted a 2-step analysis (e.g. Magrath et al. 2014, Stein et al. 2014, Gallardo et al. 2016). We first ran a set of single-moderator mixed-effect models to estimate how the effect of crab presence on Hedge's g varied with (1) crab origin (fixed factor: native or non-native), (2) responding species' functional group (fixed factor: 5 categories described in the previous sub-section), and (3) experimental design (fixed factor: 5 categories, Table S3). Source publication (study ID) was included as a random effect. Then we used a new set of mixed-effects models to assess the difference between native and non-native crabs specifically by examining interactions between crab origin and, separately, prey functional group and experimental design (with study ID included as a random effect in all cases). For all models we estimated residual heterogeneity using the restricted maximum-

likelihood estimator τ^2 and used Q_E to test for significance. To determine if there were significant differences between the levels of the categorical moderators, we used Cochran's Q -test (Q_M) with the 'mods' argument in *metafor* to ignore the intercept (Viechtbauer 2010). To determine whether the effect of native and non-native crabs differed in the interaction models, we used Wald-type chi-squared tests (Viechtbauer 2010).

Testing for non-independence and publication bias

A common problem with meta-analyses is non-independence. In our study, non-independence arose from 3 main sources, which we tried to minimize. First, in some studies, the same control group was used as the baseline for multiple experimental treatments. On average, there were 1.9 (\pm 2.3 SD) experiments per control treatment in our dataset. In such cases, we used only the lowest and highest density treatments (and their shared control) to ensure that the minimum and maximum impacts were captured, and disregarded all intermediate treatments (Romero et al. 2015). Second, in longitudinal studies, abundance was reported as time-series. In these instances, we used only the last point of the series (Romero et al. 2015). Third, studies often contributed more than 1 experiment to the dataset. Studies in our dataset contributed an average of 6.1 (\pm 7.5 SD) experiments. The first and third sources of non-independence were largely attributed to a few large enclosure studies that examined the response of multiple species to crab presence and did not use fully factorial experimental designs. We therefore cross-validated our data using a leave-one-out approach to see if any individual experiments or entire studies significantly influenced the overall effect size of direct and (separately) indirect interactions. To do so, we systematically removed each study and each individual experiment from the direct and indirect datasets and recalculated the overall effect size of the random-effects model. An influential experiment or study should change the overall effect size significantly when left out.

Another problem with meta-analyses is the disproportionate publication of significant results leading to overestimates of the overall effect size. Publication is expected to be biased against smaller studies, which are more likely to find non-significant results (Borenstein et al. 2009). We tested for potential publication bias in the direct and indirect interactions datasets separately. We first examined funnel plot

asymmetry, which suggested a dearth of non-significant, small studies in both datasets (Fig. S2 in the Supplement). Instead of using a trim-and-fill method (Duval & Tweedie 2000), which can be unduly influenced by 1 or 2 anomalous experiments (Borenstein et al. 2009), we ran cumulative meta-analyses where studies were added sequentially from most to least precise, based on variance (Fig. S3 in the Supplement). As variance typically increases as studies become smaller (i.e. less within-study replication), variance can be used to identify the threshold at which small studies start to influence the overall effect size (Borenstein et al. 2009). These thresholds were estimated visually to be at variance values of 0.73 for studies of direct effects of crabs, and 1.02 for studies of indirect effects. Studies with variances smaller than these thresholds ($n = 394$, or 61% of the complete dataset, for direct effects; $n = 148$, or 79% of the complete dataset, for indirect effects) were then retained in 'large-studies-only' datasets, and all analyses were repeated on these restricted datasets (Borenstein et al. 2009). Given that the results from analyses of the full and 'large-studies-only' datasets were similar (Table S5 in the Supplement), and that Rosenthal's fail-safe numbers (direct: 321 152; indirect: 20 412) were large relative to sample sizes for the full datasets, we present the results from the full datasets here. However, we caution that if the funnel plot asymmetries are due to bias, the effect sizes we report might be slightly inflated.

Finally, because studies of European green crab contributed more than one-third (38%) of experiments on non-native crabs, we repeated the analyses omitting this species. There were few differences in results between the restricted and full datasets, which we attribute mainly to increased variance owing to smaller sample sizes (Table S6 in the Supplement).

RESULTS

Overview

A total of 137 papers, published between 1977 and December 2016, met all selection criteria, contributing 834 individual estimates of the effect of non-native (35%) and native (65%) crabs on the survival of responding species (Table S2). The most commonly studied crab species was the European green crab (38%). It was also the only species to have experiments conducted in both its native and non-native range. The most commonly studied prey types

were sessile invertebrates (32%) and infauna (29%). All experimental designs were well represented (between 18 and 31%), with the exception of natural field experiments (3%). Experiments originated from all continents except Asia and Antarctica. However, northern temperate latitudes ($>23^{\circ}\text{N}$; 88%) and North America (65%) had the greatest representation in the dataset. The majority of experiments tested the direct (consumptive) effect of crabs (78%).

There was no significant difference in mean carapace width between native (mean \pm 1 SD: 60.5 ± 49.7 mm) and non-native crab species in the database (34.4 ± 21.3 mm; Mann-Whitney test, $U = 132.0$, $n = 55$, $p = 0.37$).

Direct ($n = 647$) and indirect ($n = 187$) interactions between crabs and responding species had significantly different effects on the abundance of responding species ($Q_M = 176.72$, $df = 1$, $p < 0.01$). As expected, direct interactions (i.e. consumption by crabs) had a significant, negative effect on prey abundance ($g = -1.06$, 95% CI = -1.25 to -0.88 , $p < 0.01$) while indirect interactions had a significant, positive effect ($g = 0.34$, 95% CI = 0.11 to 0.58 , $p < 0.01$).

The sequential omission of 2 large enclosure studies reporting direct interactions increased the magnitude of the overall effect size (without Griffin et al. 2008: $g = -1.26$, 95% CI = -1.45 to -1.07 ; without Fernandes et al. 1999: $g = -1.25$, 95% CI = -1.44 to -1.06), but the confidence intervals in both cases still encompassed the overall effect size of the complete dataset. The same was observed for 2 large studies of indirect interactions (without Tyrrell et al. 2006: $g = 0.77$, 95% CI = 0.40 to 1.15 ; without Matassa & Trussell 2011: $g = 0.67$, 95% CI = 0.34 to 1.00). However, because the direction and statistical significance of the models were not changed in either case, we chose to leave these studies in the datasets for further analyses.

Direct interactions

Overall, non-native crabs did not significantly reduce the abundance of responding species any more than native crabs ($Q_M = 0.25$, $df = 1$, $p = 0.61$; Fig. 2). Prey abundance was significantly reduced by crabs in all

experiments, with the strongest effects occurring in laboratory-based experiments (i.e. mesocosms and single-species predation experiments) ($Q_M = 46.96$, $df = 4$, $p < 0.01$; Fig. 2). Mesocosm experiments were the only design type where native and non-native crabs had significantly different effects, with non-native crabs reducing prey abundance more than native crabs (Table 1).

Although all prey types were significantly negatively affected by crab predation (Fig. 2), there were significant differences in effect sizes among prey functional groups ($Q_M = 19.96$, $df = 4$, $p < 0.01$). Direct predation by non-native crabs reduced the abundance of primary producers significantly more than direct predation by native crabs, while direct predation by native crabs reduced the abundance of mobile epifauna and vertebrates significantly more than by non-native crabs (Table 1). However, the effect on vertebrates arises from very small sample sizes (Table 1). There were no other differences between native and non-native crabs in consumption of other prey types (Table 1).

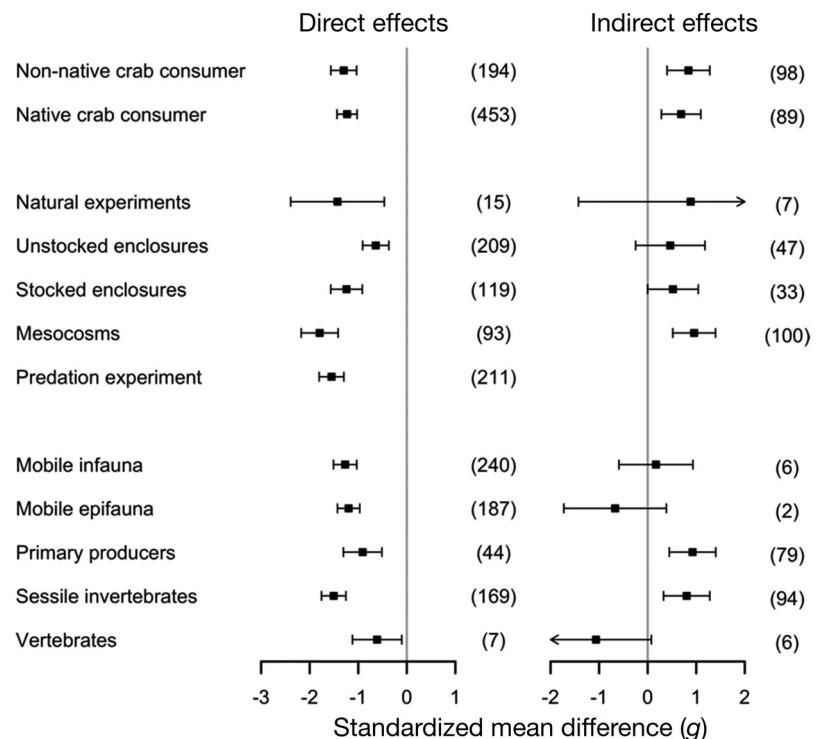


Fig. 2. Weighted average effect sizes (Hedge's g) and 95% confidence intervals from models of relative abundance of species involved in direct and indirect interactions with crabs. The number of individual experiments included for each effect size is indicated in parentheses. Effect sizes for each level of 3 moderators are shown: crab origin, experimental design, and prey type. Negative effect sizes indicate lower abundance of responding species in treatments with crabs than in treatments without crabs. Effect sizes are considered significant when confidence intervals do not overlap 0

Table 1. Results of mixed-effects models of species abundance after direct (i.e. consumptive) interactions with crabs. All models considered crab origin (non-native or native), one of either experimental design or prey type, and the interaction between origin and the focal moderator as fixed factors, and study ID as a random factor. Weighted average effect sizes (Hedge's g), i.e. the standardized mean difference in prey abundance when a crab consumer was present vs. absent in an experiment, are considered significant when confidence intervals (CI) do not overlap 0. p -values refer to pairwise Wald-type chi-squared (Q_M) comparisons between non-native and native crabs for each moderator level; significant values ($p < 0.05$) are shown in **bold**

Moderator		g	CI _{lower}	CI _{upper}	n	Q_M	p
Model: Crab origin × Experimental design							
Natural experiments	Non-native	-1.67	-3.31	-0.03	4	0.13	0.72
	Native	-1.30	-2.48	-0.12	11		
Unstocked field enclosures	Non-native	-0.59	-0.96	-0.23	57	<0.01	0.95
	Native	-0.61	-0.93	-0.28	152		
Stocked field enclosures	Non-native	-1.46	-1.88	-1.05	59	0.59	0.44
	Native	-1.29	-1.69	-0.88	60		
Lab mesocosms	Non-native	-2.34	-2.95	-1.73	8	4.96	0.03
	Native	-1.53	-1.99	-1.06	85		
Lab predation experiment	Non-native	-1.52	-1.88	-1.16	66	0.04	0.84
	Native	-1.56	-1.87	-1.25	145		
Model: Crab origin × Prey functional group							
Mobile infauna	Non-native	-1.40	-1.74	-1.06	82	3.14	0.08
	Native	-1.06	-1.33	-0.78	158		
Mobile epifauna	Non-native	-0.75	-1.11	-0.39	31	9.45	<0.01
	Native	-1.35	-1.60	-1.10	156		
Sessile invertebrates	Non-native	-1.71	-2.06	-1.37	70	1.35	0.25
	Native	-1.50	-1.79	-1.21	99		
Primary producers	Non-native	-1.37	-1.94	-0.79	10	4.80	0.03
	Native	-0.48	-1.04	0.08	34		
Vertebrates	Non-native	0.00	-0.62	0.63	1	11.62	<0.01
	Native	-1.94	-2.88	-1.00	6		

Indirect interactions

Overall, the abundance of species interacting indirectly with crabs increased in the presence of crabs (i.e. g was positive); however, there was no significant difference in effect sizes between native and non-native crabs ($Q_M = 0.45$, $df = 1$, $p = 0.50$; Fig. 2).

The impact on responding species abundance did not differ significantly among experimental designs ($Q_M = 5.63$, $df = 3$, $p = 0.13$; Fig. 2). Mesocosm experiments yielded the largest and only statistically significant indirect effect on responding species abundance ($p < 0.01$; Fig. 2). It was not possible to compare the indirect effects of non-native and native crabs in natural field experiments because of the absence of such studies for native crabs. The only difference in indirect effects between native and non-native crabs was for unstocked field enclosures, where non-native crabs increased the abundance of responding species significantly more than native crabs (Table 2).

The indirect effect of crabs varied among prey types ($Q_M = 18.43$, $df = 4$, $p < 0.01$; Fig. 2). The abundance of both sessile invertebrates (e.g. barnacles; $p < 0.01$) and primary producers ($p < 0.01$) increased the most in the presence of crabs, compared to treatments without crabs (Fig. 2). There was a significant difference between the indirect effects of native and non-native crabs on the abundance of primary producers, with non-native crabs having a larger positive effect than native crabs (Table 2).

DISCUSSION

Non-native consumers were expected to have larger negative impacts on native prey abundance than native consumers (Salo et al. 2007, Paolucci et al. 2013, Thomsen et al. 2014, Alexander et al. 2015). In general, our meta-analysis does not support this expectation. Regardless of whether the interactions between crabs and prey species were direct

(e.g. predation) or indirect (e.g. via trophic cascades), we could not detect an overall difference in abundance of responding species between native and non-native crabs. Although some differences between native and non-native crabs arose in experiments with specific experimental designs and prey types, they did not consistently point to non-native crabs having greater impacts.

We had predicted that the abundance of species that interact directly with predatory crabs would decrease, but that species interacting indirectly with a crab predator would benefit. These predictions were supported. Direct effects were always strongly negative, regardless of crab origin, prey type, or experimental design (Fig. 2), which is consistent with our understanding of marine crabs as important generalist predators in nearshore and intertidal ecosystems (Boudreau & Worm 2012). Overall indirect effects on the abundance of responding species were positive, but were more variable among experimental designs

Table 2. Results of mixed-effects models of species' abundance after indirect (i.e. via trophic cascade) interactions with crabs. All models considered crab origin (non-native or native), one of either experimental design or prey type, and the interaction between origin and the focal moderator as fixed factors, and study ID as a random factor. Weighted average effect sizes (Hedge's g), i.e. the standardized mean difference in prey abundance when a crab consumer was present vs. absent in an experiment, are considered significant when confidence intervals (CI) do not overlap 0. p -values refer to pairwise Wald-type chi-squared (Q_M) comparisons between non-native and native crabs for each moderator level; significant values ($p < 0.05$) are shown in **bold**. (–) No data available to test the interaction for that particular level of the moderator and origin combination

Moderator		g	CI _{lower}	CI _{upper}	n	Q_M	p
Model: Crab origin × Experimental design							
Natural experiments	Non-native	0.89	–1.20	2.97	7	–	–
	Native	–	–	–	0	–	–
Unstocked field enclosures	Non-native	1.66	0.75	2.57	24	12.16	<0.01
	Native	–0.67	–1.61	0.27	23		
Stocked field enclosures	Non-native	0.57	0	1.16	21	2.96	0.09
	Native	–0.09	–0.79	0.62	12		
Lab mesocosms	Non-native	0.83	0.32	1.33	46	0.86	0.36
	Native	1.06	0.61	1.51	54		
Model: Crab origin × Prey functional group							
Mobile infauna	Non-native	0.23	–0.81	1.26	4	0.86	0.35
	Native	0.91	–0.21	2.02	2		
Mobile epifauna	Non-native	–0.33	–1.43	0.77	2	–	–
	Native	–	–	–	0		
Sessile invertebrates	Non-native	1.06	0.55	1.57	60	0.5	0.47
	Native	1.24	0.65	1.82	34		
Primary producers	Non-native	1.95	1.21	2.69	28	13.65	<0.01
	Native	0.16	–0.43	0.76	51		
Vertebrates	Non-native	–0.99	–2.38	0.40	4	<0.01	0.95
	Native	–1.08	–3.44	1.28	2		

and prey types than direct effects (Fig. 2). This is consistent with the notion that indirect effects are typically harder to predict, test, and detect than direct effects (White et al. 2006). Furthermore, indirect impacts are not always manifested as changes in prey survival or abundance, which was the metric used here. Indirect effects of consumers are sometimes detectable as size shifts (Peterson et al. 2014) and in phenotypic and behavioral adaptations of prey (Freeman & Byers 2006, Brookes & Rochette 2007, Flynn & Smee 2010, Whitlow 2010), neither of which could be examined here.

Generally, the impact of non-native crabs on the abundance of responding species was similar to that of native crabs, regardless of whether the interaction was direct or indirect. This is contrary to recent meta-analyses comparing other taxa of non-native and native consumers. These studies found that the effects of

non-native species were consistently 2 to 3 times larger than those of native species, and invoked prey naïveté and novelty of the non-native consumer as potential explanations (e.g. Salo et al. 2007, Paolucci et al. 2013). The converse mechanisms, i.e. limited prey naïveté and low distinctiveness of non-native crab species in recipient communities, may explain why non-native and native crabs appear to have similar impacts. Most nearshore marine communities, except at the most polar latitudes, have co-evolved alongside crab-like consumers (Aronson et al. 2015). This ubiquity may make it less likely for a non-native crab to be taxonomically or functionally distinct from native crab species. From the native prey's perspective, a novel crab consumer may therefore not represent a particularly significant adaptive challenge. Indeed, the rapid responses of formerly naïve prey species to novel crab predators have been demonstrated experimentally for both European green crab (Edgell et al. 2009) and Asian shore crab (Freeman & Byers 2006).

Prey type influenced the effect of direct interactions with crabs. The abundance of all prey groups was significantly reduced by direct predation from crabs, but with some variation among groups. Within prey groups, the extent of these reductions was similar regardless of crab origin, with the exception of primary producers and mobile epifauna. Primary producers were disproportionately affected by non-native crabs, although this result is based on a relatively small sample size. In contrast, the abundance of mobile epifauna was more negatively affected by native crabs. Due to the wide variety of prey species encompassed in the 'mobile epifauna' functional group, it is unlikely that this pattern is driven by a single mechanism. However, it could suggest predator naïveté, where non-native crabs are unfamiliar with the anti-predator defenses and escape responses of novel prey species and therefore can consume less than na-

tive crabs (Sih et al. 2010). Our prediction that sessile prey would be the most vulnerable to non-native crab predation due to lack of an active behavioral escape response (Vermeij 1987) was not supported. The similarity in direct effects of native and non-native crabs on this group may indicate that sessile prey, particularly those that rely on shells as a mechanical defense (e.g. mussels), are adapted to crushing predators, regardless of crab origin.

Prey type also influenced the effect of indirect interactions with crabs. In contrast to direct interactions, the effects of indirect interactions with crabs were more variable, with some prey types responding positively to the presence of predatory crabs and others not responding at all. Primary producers and sessile invertebrates benefited the most from crab presence. This result is probably explained by the fact that sessile species are particularly susceptible to consumers (Sih et al. 2010), and they were often included in studies focusing on tri-trophic cascades where crabs preyed upon an intermediate consumer, thus relaxing consumption on sessile species at the lowest trophic level. As with direct effects, there was a significant difference between native and non-native crabs in their indirect effect on primary producers, with non-native crabs associated with a larger increase in abundance of primary producers than native crabs (Table 2). It is possible that the intermediate predators used in tri-trophic cascade experiments are more responsive to non-native than native crabs, thus releasing primary producers more effectively from herbivory (Sih et al. 2010). However, it is not clear why the same larger indirect impact of non-native crabs is absent when sessile invertebrates are the basal prey (Table 2).

The magnitude of the effect of predatory crabs on other species also varied significantly among experimental designs. For direct interactions, laboratory-based experiments on crab predation resulted in the largest reductions in prey abundance, undoubtedly because of the absence of alternative prey and/or the limited biotic interactions experienced by predators. The direct effects of native and non-native crabs were generally similar, except in laboratory mesocosms where non-native crabs reduced prey abundance more than native crabs. This result should be interpreted with some caution, however, given the very small number of mesocosm experiments using non-native crabs (Table 1). For indirect interactions, the presence of crabs was associated with increased abundance of responding species, but this effect was only significant in mesocosm experiments, supporting the notion that interactions

are easier to detect in simpler systems. However, in contrast to direct interactions, non-native crabs exerted significantly larger, positive indirect effects on responding species abundance than native crabs in unstocked field enclosures but not in any other type of experiment. It is notable that most unstocked field enclosures included primary producers as the basal responding species, and plants and algae responded strongly (negatively for direct interactions, positively for indirect interactions) to the presence of non-native crabs.

Our review has revealed several important research gaps. We found marked geographic and taxonomic biases in the studies available, which reflect a need for more research on non-native crabs outside of North America and Europe. Studies of non-native crabs could also be biased towards species suspected of having strong negative impacts (e.g. green crabs). If this is the case here, then non-native crabs could in fact have smaller impacts than we estimated. The indirect impacts of crab consumers are generally understudied, especially for mobile fauna and vertebrates. The few studies that have attempted to demonstrate indirect linkages between crab consumers and vertebrates (e.g. wading birds or juvenile fish) suggest potentially important competitive interactions (Table 1; Estelle & Grosholz 2012). We also noted that there are very few natural field experiments. This is unfortunate because, although such experiments do not offer the same level of control as mesocosm and other laboratory designs, ecosystem-wide studies are among the best tools available for understanding the impacts of native and non-native species over large spatial and temporal scales (Carpenter et al. 1995, Sagarin & Pauchard 2010). Most importantly, we found few studies that placed native and non-native crabs in direct competition for single or multiple prey items. Thus, while non-native predators might have different functional responses and impacts on native prey abundance than native predators when held on their own (Dick et al. 2013, Dunoyer et al. 2014, Alexander et al. 2015), these measures of predatory impact might be greatly modified by ecological interactions. Experiments that consider both non-native and native species together will help determine whether mortality imposed by non-native predators simply replaces mortality imposed by native predators, or whether it is additive. The implications of such studies for understanding the effect of non-native predators in the wild are critical and can inform risk assessments and management efforts.

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