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Crab wars: testing the ideal free distribution with invasive *Carcinus maenas* and native *Hemigrapsus nudus*

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Abstract

Invasive species can cause changes in community composition, native species' habitat acquisition and reduce abundance of native species. The Ideal Free Distribution (IFD) provides a conceptual framework for describing intraspecific distributions of individuals and can be modified for interspecific interactions to correct for differing competitive ability. We examined whether the IFD of *Hemigrapsus nudus (H. nudus)*, native to the west coast of North America, varies with the introduction of invasive *Carcinus maenas (C. maenas)* with respect to food availability. We tested this experimentally by constructing artificial habitats with patches of high and low food availability and monitoring the distributions and feeding rates of *H. nudus* and *C. maenas* among these food patches. *C. maenas* was six times more competitive in acquiring food than *H. nudus*. Based on this foraging discrepancy, spatial distributions between food patches did not follow those predicted mathematically by the IFD. *H. nudus* did not distribute ideally in terms of food, while *C. maenas* did. Thus, the ability of *C. maenas'* to ideally distribute combined with its high food acquisition rate, has the potential to affect *H. nudus* survival with the spread of *C. maenas* in the Pacific Northwest.

Keywords — *Carcinus maenas*, Ideal Free Distribution, *Hemigrapsus nudus*, interference model, marine invasions

1. Introduction

Human activities such as trade and transport have caused unprecedented rates of change in biotic systems in part by facilitating the spread of invasive species. Introduced species that become invasive can cause "invasional meltdowns" where invasive species can shift community composition and displace native species [1, 2, 3, 4]. One such mechanism by which these shifts may occur is by increased competitive pressure from invasive species [5]. In particular, invasive geckos have been shown to monopolize clumped resources thereby displacing native species [6]. As well, invasive species across taxa – plants, crustaceans, and vertebrates – often show superior competitive ability and use this ability to exclude native species from resources [7, 8, 9] In these scenarios, unequal competitive ability is shown to be an important driver in predicting invasion success.

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Animals distribute themselves across landscapes as they attempt to optimize their access to spatially distributed resources [10]. These distributions are commonly described with models, such as the Ideal Free Distribution (IFD) [11], which describes how individuals distribute based on intraspecific competition between habitats of varying resource availability [12, 13]. The IFD assumes individuals move "ideally", such that they are optimizing for a resource (assuming complete environmental knowledge), and "freely", are not hindered in their movement by territoriality or physical barrier [11]. The model predicts that individuals are optimally distributed between good and poor habitats such that individuals have equal fitness when the number of individuals in a patch matches the resource abundance in said patch [11].

Traditionally, the IFD only predicts distributions based on intraspecific competition among individuals with equal competitive ability – often it is only this simpler model that is verified ecologically [10, 12, 14, 15]. However, the basic IFD can be expanded into an interference model where, in the absence of predatory interactions or physical interference, unequal competitors from different species can still distribute in an ideal free manner. In order to expand the model to include species of differing competitive ability, individuals are defined as competitive units (how likely an individual is to monopolize resources), where competitive units, rather than the number of individuals, are matched to resource abundance [16]. This expansion allows the IFD to be used as predictive framework to model how invasive species with greater competitive ability may affect distributions of native species [17, 18].

One particularly successful invasive species in coastal marine communities is *Carcinus maenas* (European green crab), which has been introduced globally and is responsible for drastic changes in community composition among bivalves and crustaceans [3, 19, 20]. In their native range off the Atlantic coasts of Europe and North Africa, green crabs grow 6-10 cm across their carapace and may eat bivalves, gastropods, crustaceans, and seaweeds [21, 22, 23]. In their invasive range, *C. maenas* follow the IFD [24], colonize intertidal habitats with mud, sand, or rocky substrate [21] and often show higher competitive ability than native species [20]. As an invasive species, *C. maenas* contributed to the crash of the *Mya arenaria* (soft-shell clam) fishery [21] and McDonald et al. [3] found that increasing abundance of *C. maenas* corresponded to decreased recruitment and habitat displacement of the native *Metacarcinus magister* (Dungeness crab).

Due to the global expansion of *C. maenas*, researchers have examined their competitive ability and their impacts on native species. One study in Newfoundland experimentally examined *C. maenas* competition with the native *Cancer irroratus* and showed the presence of green crabs reduced *C. irroratus* foraging time, especially in competitive interactions between smaller individuals [25]. Other studies showed that juvenile lobsters spend significantly less time foraging in the presence of *C. maenas* [26] and that *C. maenas* have the potential to outcompete *Callinectes sapidus* (blue crabs) and *Hemigrapsus sanguineus* (Japanese shore crab) during competition experiments over food [3]. These studies, however, lack direct evaluations of *C. maenas*' competitive advantage over native species under variable food availability and do not examine how competitive advantage of *C. maenas* affects distributions of native species across rich and poor habitats [27].

We tested how the IFD of native *Hemigrapsus nudus* Dana 1851 (purple shore crabs) change in the presence of *C. maenas*. *H. nudus* are native from Alaska to Baja California, inhabit rocky substrate in the mid to high intertidal [28]. They are dietary generalists that mainly feed on diatoms, green algae as well as scavenged prey [29, 30]. Although *C. maenas* and *H. nudus* ranges do not directly overlap at the present in British Columbia, as *C. maenas* continues to spread the two species will come into direct contact [31].

We predicted that *C. maenas* are more efficient at monopolizing resources than *H. nudus* and attempted to quantify this difference. We then used an interference IFD model to predict the most probable distribution of *C. maenas* and *H. nudus* between good and poor quality patches and tested the model experimentally in an artificial laboratory setting to see if empirical results matched theoretical IFD predictions. These experiments highlight the potential impacts of *C. maenas* on the ability of *H. nudus* to access resources and will provide further insight into the IFD's effectiveness at predicting interspecific distributions.

2. RESULTS

2.1. Crab Wars: Determining the relative competitiveness of *H. nudus* and *C. maenas*

We determined that *C. maenas* spent significantly more time eating than *H. nudus* (p-value < 0.001; Figure 1). On average *C. maenas* spent 27.1% of their time feeding, six times more than *H. nudus* (Figure 1). We confirmed this 6:1 ratio with observations in artificial habitats used in later experiments and got a comparable ratio of 5:1.

2.2. Interference Model

We used our results from determining the relative competitive ability to express *C. maenas* in terms of competitive units of *H. nudus*. We then constructed an IFD interference model predicting the most probable distribution of individuals between patches of high and low quality. With three *C. maenas* and six *H. nudus*, the model predicted the most probable distribution would be two *C. maenas* and six *H. nudus* in the good patch, and one *C. maenas* and no *H. nudus* in the poor patch (Table 1). Thus, with repeated trials, we expected this to be our average distribution. This is not what we saw, instead observing an average of one *C. maenas* and two *H. nudus* in the good patch and two *C. maenas* and four *H. nudus* in the poor patch (Table 1).

Table 1: *Model predictions and experimental observations of C. maenas and H. nudus distributions among good and poor patches (N = 3, averages ±0.33 absolute error).*

	Number of *C. maenas* in good patch	**Number of *C. maenas* in poor patch**	**Number of *H. nudus* in good patch**	**Number of *H. nudus* in poor patch**
Predicted	2	1	6	0
Observed*	1	2	2	4

*rounded to nearest whole number averages

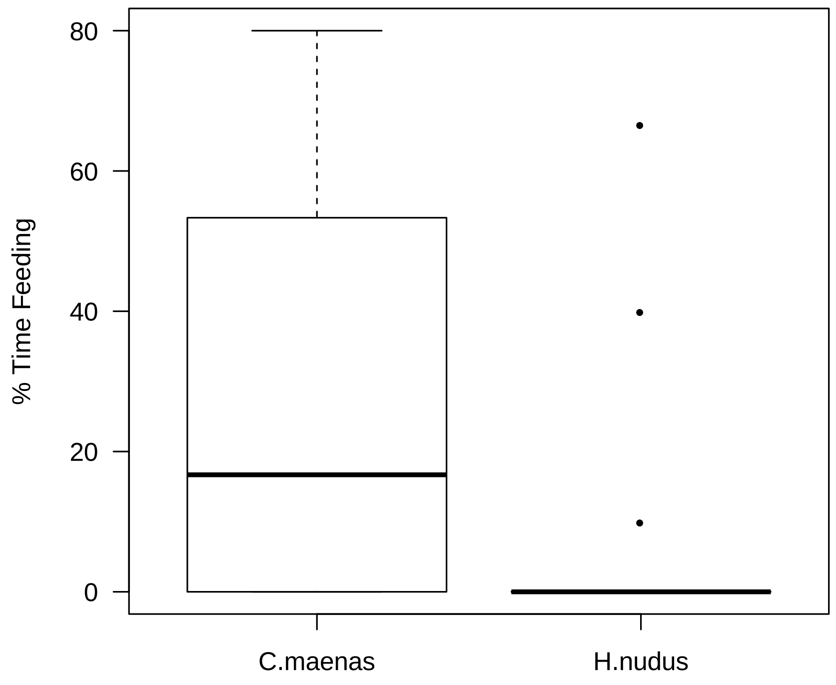

Figure 1: *Comparison of percent time feeding in C. maenas* ($N = 30$) *and H. nudus* ($N = 30$) *(t-test:* $t = 3.95$, $df = 41.81$, *p-value* < 0.001*).*

2.3. Determining the distribution of *H. nudus* and *C. maenas* between resource patches

To verify the "free" assumption of the IFD, we examined the distribution of *C. maenas* and *H. nudus* in the good resource patches from our experimental results. We compared the relationship between the number of *C. maenas* and *H. nudus* in a given good patch (Figure 2) over the course of our experiments. As predicted by the IFD, there is no relationship between *C. maenas* and *H. nudus* distributions ($r^2 = 0.042$) and they do not distribute with respect to each other.

To determine if both species of crab distributed based on food availability, we compared the ratio of crabs in the good to poor patches (Figure 3). There was no significant difference in the ratio of *H. nudus* or *C. maenas* present in the good patches across the varying densities of *C. maenas* and constant levels of food (p-value $= 0.41$ and p-value $= 0.256$ respectively; Figure 3). The ratio of *H. nudus* in the good to poor patch was unchanging across trials and was about 1:1 – 50% of *H. nudus* were in the good patch and 50% were in the poor patch – implying they did not distribute based on food availability (Figure 3A). As well, note that this ratio matches that observed when there are zero *C. maenas* in the experimental system, which is our null model and mimics a natural system in which there are no *C. maenas*. This reaffirms that *H. nudus*

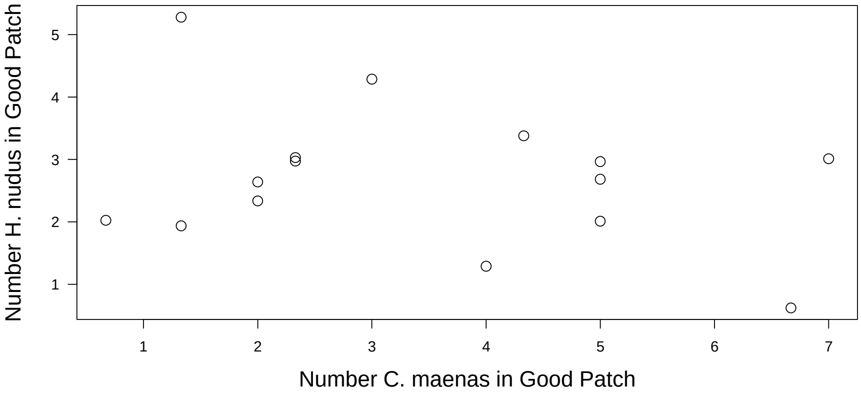

Figure 2: *The relationship between the number of C. maenas and H. nudus in the good patch (linear regression:* $y = -0.1761x + 3.4403$, $r^2 = 0.042$, $N = 15$*).*

do not change their distribution based on the presence *C. maenas*. This was counter to our prediction that increasing the number of *C. maenas* would shift the IFD of *H. nudus* based on the relative competitive ability of the two species.

However, the ratio of *C. maenas* in the good versus poor patch was significantly lower in trials with excess food than with limiting food (p-value $= 0.034$; Figure 4). Since the amount of food was constant, the number of *C. maenas* in the system determined whether food was limiting (six, seven, or nine *C. maenas*) or in excess (three and nine *C. maenas*). In treatments with excess food, the ratio of *C. maenas* in the good to poor habitat is about 1:1. In treatments with limiting food, the ratio of *C. maenas* in the good to poor habitat is about 2.5:1, thus showing that, depending on food availability, *C. maenas* will distribute based on food as predicted by the model.

3. DISCUSSION

As has been suggested by other research, *C. maenas* shows higher competitive ability than species in the ranges in which it invades [3, 20]. As we showed in our results, *C. maenas* also shows higher competitive ability than *H. nudus* and is better able to monopolize resources. This suggests that when both species are size-matched and are directly competing for the same food source *C. maenas* will be able to outcompete *H. nudus*. However, both *C. maenas* and *H. nudus* are dietary generalists [21, 22, 23, 30, 31]. This suggests that under high *C. maenas* density, if *H. nudus* is faced with direct competition from *C. maenas*, then *H. nudus* is likely to find alternate sources of food that are less preferable to *C. maenas*. This could have potential impacts on *H. nudus* populations if individuals are forced to spend more time foraging or consuming food of poorer nutrient quality.

We evaluated how the IFD of *H. nudus* changed under varying numbers of *C. maenas* and observed that *H. nudus* were freely distributed with respect to the number of *C. maenas* in a patch. We concluded this because increasing the number of *C. maenas* present in a trial did not effect *H. nudus* distribution: over all trials *H. nudus*

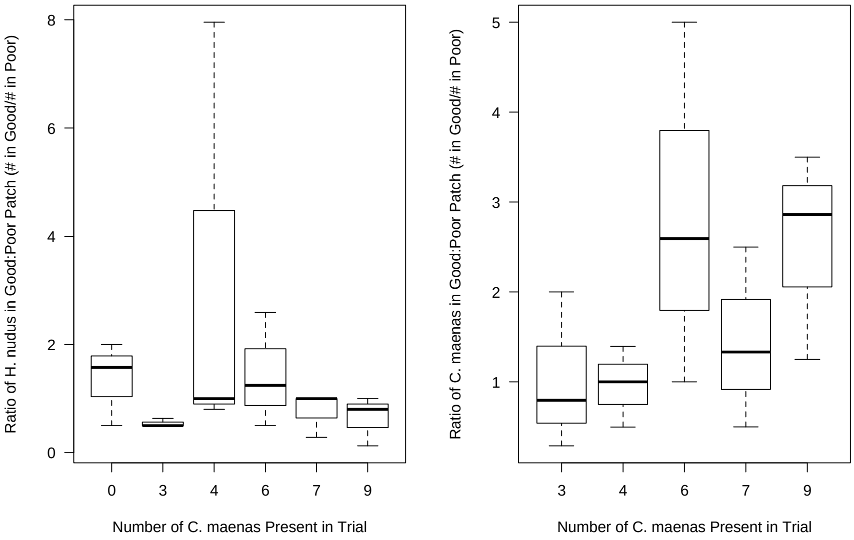

Figure 3: *The ratio of H. nudus and C. maenas in good versus poor patches and variance across trials (Fig. 3A: ANOVA with log transformation:* $F = 1.11$, $df = 5.12$, *p-value* $= 0.41$, $N = 3$; *Fig3B: ANOVA:* $F = 1.57$, $df = 4, 10$, *p-value* $= 0.256$, $N = 3$*).*

randomly assorted between the two good and poor quality patches. This implies that not only were *H. nudus* non-territorial to member of their own species, but also non-territorial with *C. maenas*. We are confident in our interpretation of this result, as we did not observe any defensive action or direct interaction between individuals within or between species that would have indicated territoriality.

While in our trials *H. nudus* did not distribute themselves based on the presence of *C. maenas*, behaviour of *H. nudus* might change with more exposure to *C. maenas* as a potential competitor and ultimately predator. Although we sized matched *H. nudus* and *C. maenas* in the experiments, adult *C. maenas* are more than 1.67 times as large as *H. nudus* [20] and are known to prey on juvenile *C. magister* and other crustaceans [21, 22, 23]. Thus, adult *C. maenas* could conceivably prey on *H. nudus*, but since these two species ranges to no yet overlap *H. nudus* has not developed a fear response. A predator response could shift the "free" nature of the IFD and cause *H. nudus* to distribute based on *C. maenas* avoidance. Further experiments should be conducted to evaluate this potential response and how it may limit *H. nudus* access to resources.

Although *H. nudus* distributed freely among patches, they were not distributed ideally: they did not distribute based on food availability and patch quality as predicted by the IFD. The interference IFD model did not accurately predict the distribution of *C. maenas* and *H. nudus* among good and poor patches because *H. nudus* did not distribute based on food availability, which skewed observed patterns away from the model's theoretical predictions. In our experiments, *H. nudus* were evenly distributed among good and poor patches, thus suggesting *H. nudus* did not distribute based on food availability. During our experiments, we observed that *H. nudus* preferentially associated with corners and cover. Thus, our results indicate that *H. nudus* is sensitive

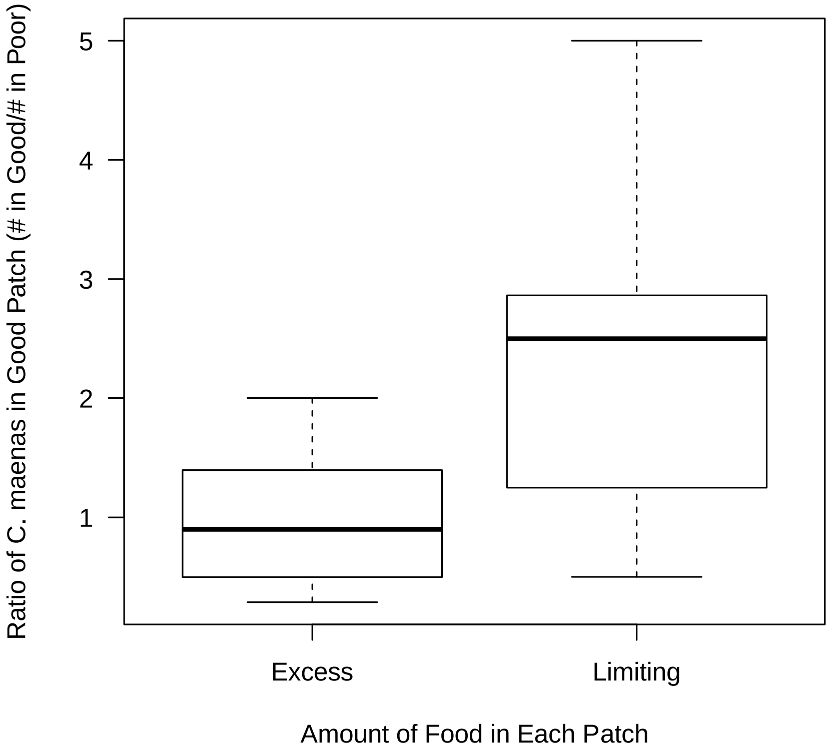

Figure 4: *The ratio of C. maenas in good verus poor patches under scenarios with excess food (3 and 4 C. maenas) and limiting food (6, 7, and 9 C. maenas; t-test:* $t = -2.39$, $df = 11.742$, *p-value* < 0.034, $N = 6$ *for excess,* $N = 9$ *for limiting).*

to stressful laboratory environments and optimizes shelter over food, thus creating an IFD based on shelter availability. Given that a variety of stressors, such as increased oceanic temperatures, decreased pH, noise pollution, and habitat loss, are expected to increase [32, 33, 34], further research should examine directly how these disturbances will change *H. nudus* distributions among various types of resources. As well, we only ran experiments at one density of *H. nudus* and with one size class of *H. nudus* and *C. maenas*, as such we suggest future research examine how general our results are across varying sizes of individuals and densities of *H. nudus*.

From previous studies, we know that *C. maenas* distributes according to the IFD [24]. Our experiments confirmed this result: *C. maenas* distributed based on food availability only in resource-limited conditions. This makes ecological sense; there are no fitness benefits to distributing based on relative patch quality if food is not limiting in any patch. This highlights a potential mechanism by which *C. maenas* is successful invader. Given that *C. maenas* was able to distribute according to the IFD in a potentially stressful lab environment as it does in its natural setting, we suggest that this implies *C. maenas* is less sensitive to changes in its environment. If this is true, this implies that *C. maenas* is able to be a successful invader over wide range of new habitats and environments. This lack of sensitivity combined with a high competitive ability suggests that in situations where the environment changes, *C. maenas* will be able to outcompete more sensitive species, perhaps such as *H. nudus*.

4. METHODS

4.1. Animal Care

All animals were collected in Barkley Sound, BC and experiments were conducted at Bamfield Marine Sciences Centre (BMSC). Thirty-four *C. maenas* were collected from the head of Pipestem Inlet, British Columbia (49°1′41"N 125°14′42"W), in an area sheltered from waves with muddy and sandy substrate. 37 *H. nudus* were collected from Dixon Island (48°51′ 10"N, 125°7′ 11"W) and 54 *H. nudus* from Seppings Island (48°50′ 24"N, 125°12′ 28"W). Both *H. nudus* collection sites consisted of large cobblestone beaches with sheltered wave exposure in the mid and high intertidal respectively. All individuals of both species were approximately 2-6cm long (carapace).

In the lab, three sea-tables (2.5 by 0.75m troughs filled with circulating sea-water) were used to create artificial habitats for each of our three crab populations. Cover was created by placing rocks and macroalgae (*Fucus sp*) within sea-tables. In order to ensure equal hunger levels, and thus motivation to eat, we starved crabs outside the experimental trials. Unfortunately, standardizing the length of starvation was not possible due to the limited time frame of this project and limited number of crabs. We used a mixture of *Mytilus sp.* collected from beneath the dock of the BMSC in Bamfield inlet as prey items during our experiments. We kept these in a separate sea table also filled with circulating seawater and crushed them immediately prior to use. Mussels were used within 24 hours of collection. Pieces, roughly one cm in diameter, were used as a single unit of food. All use and maintenance of crabs followed BMSC animal care guidelines and protocols (AUP# UP15-MBE-01).

4.2. Crab Wars: Determining the relative competitiveness of *H. nudus* and *C. maenas*

To determine the relative competitiveness of *H. nudus* versus *C. maenas*, we set up 30 small tanks each containing one size-matched individual from *C. maenas* and *H. nudus* [9]. We placed one mussel in each tank beneath a plastic enclosure with holes that prevented access to the mussel, but allowed the crabs to sense it. The crabs had 10 minutes to habituate, based our field observations and experiments conducted by MacDonald et al. (2001). After the habituation period, we removed the cover protecting the mussels and recorded which of the two species in each tank ate the mussel. We recorded this information at 1-minute intervals for 15 minutes. We used this information to estimate the percent of time that each individual of each species spent eating.

4.3. Building the IFD interference model

We used relative rates of consumption to express *C. maenas* in terms of *H. nudus* by constructing a conversion ratio based on food consumed by individuals of the two species. Given that *C. maenas* ate six times more than *H. nudus*, we defined one relative food unit for *C. maenas* as six pieces of mussel while one mussel piece was a food unit for *H. nudus*. This ratio allowed us to create a theoretical system in which a good patch (18 mussel pieces) had three times as many food units as a poor patch (six mussel pieces). Thus, there were enough food units in the poor patch to be sufficient for either one *C. maenas* or six *H. nudus*. The good patch had enough food units for three *C. maenas* or eighteen *H. nudus*.

We chose the 3:1 ratio between good and poor patch resource availability for both mathematical and practical purposes. Mathematically, any ratio between the good and poor patch could haven been used to predict distributions. However, we excluded some possible ratios due to small effect size, or because they predicted randomness which we would not be able to distinguish from an insignificant result. We also excluded ratios that required more individuals than to which we had access in the lab. Thus the 3:1 ratio was the only ratio that was experimentally plausible as well as having a single outcome that was vastly more probable than other outcomes.

From this, we constructed a mathematical model to determine all the possible combinations of the distributions of three *C. maenas* and eighteen *H. nudus* among good and poor patches where each individual would have access to a single relative food unit. We used combinatorics to determine the number of ways all possible distributions could be constructed when individuals maintain access to one single relative food unit (six mussel pieces for *C. maenas*, one mussel pieces for *H. nudus*). Thus, the most probable outcome expected under the IFD is the one that had the most possible ways to be constructed.

4.4. Formula for determining the combination model:

$$n(\textit{C. maenas}\text{ total})Cn(\textit{C. maenas}\text{ in good}) \cdot n(\textit{H. nudus}\text{ total})Cn(\textit{H. nudus}\text{ in good})$$

4.5. Experimentally testing the IFD interference model

We designed and set up a lab system with three sea-tables (troughs filled with circulating sea-water) to test both the distributions predicted by the interference model and those theorized by the IFD. We created good and poor quality patches by placing crushed mussel (one piece of mussel was one food unit) in trays at either end of the sea-tables, approximately 2.25m apart. We covered the food with a porous plastic container so the crabs could sense the food, but not eat it, and waited for a 10-minute habituation period before removing the covering. We placed three *C. maenas* and six *H. nudus* (equivalent to one green crab's feeding capacity), in the center of each sea-table. We then recorded the distribution of the crabs in the good and poor patches every twenty minutes for one hour, for each of the three tanks. This generated an average distribution of individuals for each of the three replicated tanks. We compared these experimental distributions to the theoretical predictions generated by the IFD interference model.

4.6. Testing how the distribution of *H. nudus* changes with variable *C. maenas* density

We repeated the above experiment five times with varying numbers of *C. maenas*. We ran the experiment with zero, three, four, six, or nine *C. maenas*, each replicated three times, to gain an understanding of how the animals would distribute under a gradient of *C. maenas* densities. Zero *C. maenas* was our control: it represented an environmental system without the introduction of *C. maenas*. We chose to run the experiment with six *C. maenas* to mimic a scenario with equal numbers of both species and nine to mimic a system with the high green crab densities observed in some areas of the PNW. The other numbers of *C. maenas* were chosen to fill out the gradient from zero to nine. With four, six, or nine *C. maenas* there was less total food in a sea-table than competitive units of crabs. At zero or three *C. maenas* the food was in excess. We kept the number of *H. nudus* constant at six individuals and did not vary the amount of food present. In the final trial, in which there were nine *C. maenas*, we also recorded how many of each species were feeding in each patch. This allowed us to confirm the relative competitiveness determined from our prior experiments.

4.7. Statistical Analysis

All our statistical analysis was done in R, version 3.1.2.

To determine the relative competitiveness of *C. maenas* and *H. nudus* and their percent time feeding, we tallied the number of times each individual ate during the 15 scans and divided this number by the total number of minutes in each scan sample. A two-sample Welch's t-test was then used to compare the percent of time spent feeding of *H. nudus* and *C. maenas*.

To test whether *H. nudus* were distributing freely we used simple linear regression to show how the number of *H. nudus* in a patch changed with number of *C. maenas* in a patch. If individuals were distributing freely we predicted no trend.

To determine the proportion of individuals of each species present in a good patch, we divided the number of *individuals of that species* found in the good patch by the number of *individuals of that species* in the poor patch. We used ANOVA with log transformation to test whether the ratios of *each species* in a good patch varied across the trials of differing numbers of *C. maenas*. We also aggregated our data based on treatments with excess and limiting food. We used a two-sample Welch's t-test to compare the ratios of *C. maenas* between the trials with limited and excess resources.

5. CONCLUSION

Although the IFD failed to predict the distributions of *H. nudus*, ecologically, our results still have implications for how *C. maenas* could affect the survival of *H. nudus*. Based on our results in stressful lab conditions, *C. maenas* distributed based on food availability whereas *H. nudus* did not. Even if this result is an artefact of *H. nudus* taking longer to acclimate to lab conditions or preferring to forage under different light or temperatures, our result still indicates that *H. nudus* are more sensitive to change than *C. maenas*. This implies that in natural environments with added stressors, such as habitat disturbance or climate change, *H. nudus* potentially prioritize shelter, not food, while *C. maenas* prioritize food. As well, *C. maenas* consume available food faster than *H. nudus*. Thus, based on our data we expect that in resource-limited conditions with high densities of *C. maeanas*, they will outcompete *H. nudus* for food with which both species have dietary overlap. Our results indicate that that *C. maenas* is less sensitive to change than *H. nudus* and so have more access to food and will eat it quicker, which has potential ramifications for survival of *H. nudus* populations as coastal systems continue to change.

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