

Consumers that are not ‘ideal’ or ‘free’ can still approach the ideal free distribution using simple patch-leaving rules

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Summary

1. The ideal free distribution (IFD) has been widely used to determine whether consumers distribute themselves optimally. However, this theory is based on three assumptions that are clearly violated in many systems. The theory assumes that all individuals know the quality of each available site, are equally free to move between all sites, and have equal competitive abilities.
2. I examine the utility of this theory to predict the distribution of the invasive European green crab *Carcinus maenas*, a species that likely violates all of these assumptions. I demonstrate three main findings.
3. First, understanding how density-dependent interference and size alter individual foraging behaviour is important for understanding the density and biomass distribution of *C. maenas* in invaded habitats.
4. Second, once behavioural mechanisms of crab foraging are accurately included in the model, the IFD does a good job of predicting the distribution of *C. maenas*, even though *C. maenas* violates the theory’s fundamental assumptions.
5. Third, *C. maenas*’ distribution can be obtained using simple decision rules and reasonable movement patterns.

Key-words: *Carcinus maenas*, decision rule, ideal free distribution, optimal foraging theory, predator interference

Introduction

Determining what controls the spatial distributions of species is a fundamental goal of ecology, and yet can be one of the more difficult aspects to investigate. Numerous factors contribute to species distributions, including environmental characteristics, refuge availability, resource distribution and intra- and interspecific interactions. Recognizing that all species consume resources, studies have often focused on the distribution of species relative to the distribution of their required resources. This has often been done using optimality models. A broad class of optimality/game theoretical models that presumes consumers distribute themselves spatially so as to maximize per capita resource uptake, are models based on the ideal free distribution (Fretwell & Lucas 1970), hereafter abbreviated as IFD. (For a recent review of IFD theory from a game theoretic perspective, see Krivan, Cressman & Schneider 2008.)

Two main types of IFD models have been explored. Continuous input models assume that resources are added continuously, although at different rates to different habitats,

and are immediately consumed. The IFD predicts that consumers in this scenario should partition their numbers across patches so that their distribution is proportional to the distribution of incoming resources (i.e. the ‘input matching rule’, Parker 1978). Numerous studies provide support for this prediction (reviewed in Parker & Sutherland 1986; Tregenza 1995). However, constant rates of resource input are indicative of only a minority of systems. The majority of systems may be more closely approximated by standing stock models (also called interference models), which presume a standing stock of resources that varies in densities across patches (Tregenza, Parker & Thompson 1996). In this case, the predicted distribution of consumers depends on the intensity of interference. When interference is weak or non-existent, the IFD predicts that consumers will aggregate in the patch with the highest resource density (Comins & Hassel 1979). When interference is strong among equal competitors, the IFD predicts that interference will cause some consumers to move to poorer patches, with the ultimate consumer distribution yielding consumption rates that are approximately equivalent across all patches (van der Meer & Ens 1997). Empirical studies provide only limited support for interference models, possibly because model predictions often do not incorporate

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system-specific relationship between interference effects and consumer density (reviewed in Parker & Sutherland 1986; Tregenza 1995; Tregenza *et al.* 1996). Ideally, interference models should be based on a mechanistic understanding of this relationship derived from experimental manipulations of prey and predator densities under semi-natural conditions (van der Meer & Ens 1997).

While intuitively appealing and widely used, the IFD is based on assumptions that are clearly violated in many, if not most, systems. First, consumers are assumed to have ideal knowledge of the resource levels in each available patch and to make accurate assessments of potential consumption rates in each, thus allowing them to choose the best patch. Second, consumers are assumed to move equally between all patches. Third, all consumers are assumed to have equal competitive abilities. However, in reality, consumers often have a limited range over which they can detect resource levels, are limited in their ability to migrate between patches by distance, habitat configuration, etc., and differ in competitive ability. Cressman & Krivan (2006) recently demonstrated that the IFD is robust and can still emerge even when its assumptions are violated, such as when movement is random and when migrants move into patches with lower payoff. However, the IFD has been criticized for these unrealistic assumptions, leading some to suggest that this theory may have limited application to field conditions and particularly to species distributions at landscape scales (Ranta, Lundberg & Kaitala 1999). Here I examine the value of the IFD when these assumptions are not met by inspecting the distribution of a consumer that violates each of these assumptions.

The European green crab *Carcinus maenas* is an invasive predator to North America, occurring on both the Atlantic and Pacific coasts (Grosholz & Ruiz 1996). I examine its distribution across coves along a kilometre of beach at Odiorne Point State Park on the New Hampshire coast. *Carcinus maenas* has a ravenous appetite for bivalve mollusks, and its density is positively correlated with mussel (*Mytilus edulis*) density at Odiorne Point (Griffen, Guy & Buck 2008). However, while *C. maenas* is known to aggregate to areas with lots of mussels, assumptions of the IFD are as untenable for this species as they are for many others. First, coves at Odiorne Point are spaced over more than a kilometre of coastline (Fig. 1), and individual *C. maenas* are unlikely to have an ideal knowledge of mussel density across these coves. Second, given the linear arrangement of coves (Fig. 1), crabs are not likely to disperse between them equally; rather, crabs are more likely to move between adjacent coves. Finally, competitive ability among *C. maenas* differs widely, with dominance determined largely by the size of interacting individuals (Smallegange & van der Meer 2007). Interference between crabs takes the form of fighting and threat displays that result in loss of time spent foraging (Smallegange, van der Meer & Kurvers 2006).

Consumers such as *C. maenas* with incomplete habitat knowledge may choose where to forage by implementing simple patch leaving rules. However, the rich literature on the use of optimal patch leaving rules is based primarily on the

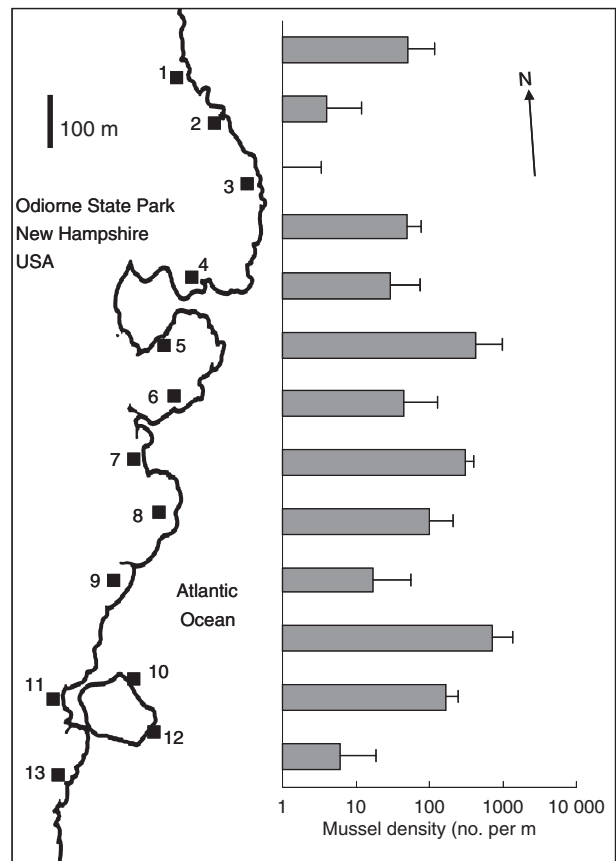


Fig. 1. Map of Odiorne Point, NH demonstrating the relative locations of 13 separate sampling areas. The bar graph indicates the density of mussels at each of these sites (mean \pm SD, $n = 6$). Bars represent the sites sequentially from top to bottom. Note log scale.

Marginal Value Theorem (Nonacs 2001), which, as with the IFD, also assumes broad information on patch quality. Yet knowing the quality of distant patches may be unrealistic in many instances when density-dependent interference occurs between mobile consumers. This is because patch quality is dynamic, depending on shifting consumer densities. Thus, even prior experience in each available patch does not ensure ideal knowledge.

I compared observed crab densities across sites to densities predicted by the IFD. I also used simulation models based on crab interference to determine whether simple patch leaving rules that do not meet IFD assumptions can nevertheless allow crabs to achieve the IFD. I developed these interference models using empirically demonstrated changes in *C. maenas* consumption rates with changes in conspecific density, mussel prey density, and size-specific consumptive abilities (Elner & Hughes 1978; Griffen & Delaney 2007; Griffen & Williamson 2008). Finally, I use these models to explore how efficiently crabs may be able to distribute according to IFD expectations, and thus how well crabs can track temporally variable resource densities.

I demonstrate that, although it violates IFD assumptions, *C. maenas* is indeed distributed approximately according to ideal free expectations at Odiorne Point. I also demonstrate that adherence to unrealistic IFD assumptions is not neces-

sary to produce this distribution. Rather, crabs can achieve this distribution by following simple decision rules that are based only on current consumption rates of individuals (i.e. these rules assume no knowledge of consumption rates in distant habitats), combined with migration only between adjacent sites.

Materials and methods

I first briefly describe my study system. I then describe the simulation model used to derive the predicted IFD (the 'IFD model'), and two simulation models in which I relax the IFD assumptions. In the 'equal competitor model', I relax both the ideal knowledge and the free movement assumptions. In the 'unequal competitor model', I relax these same two assumptions and also the assumption of equal competitors. All models were implemented using MATLAB (v. 7.7.0) and statistical comparisons were made using R (v. 2.7.1).

STUDY SYSTEM

I examined *C. maenas* distribution at Odiorne Point State Park, a semi-exposed rocky intertidal site located on the New Hampshire coast. This site is characterized by a series of coves, each with extensive boulder fields that provide excellent crab habitat. Coves are separated by bedrock outcroppings or stretches of sandy beach that provide poor habitat for crabs, and crabs were never found in these 'divider' areas during low tide sampling (Fig. 1). I sampled within each of these coves in July 2005 and previously reported a positive correlation between *C. maenas* density and mussel density across coves (see Griffen *et al.* 2008 for a full description of the site and the sampling methods). I use that same data here to examine whether *C. maenas* is distributed across 13 coves at Odiorne Point according to expectations of the IFD. (Griffen *et al.* 2008 included two sites at Rye Harbor, NH, which is located just south of Odiorne Point State Park. However, these two sites are separated by approximately 0.5 km of sandy beach that crabs are unlikely to traverse. I therefore did not include the two sites at Rye Harbor in this study.) At each site, the observed density and size (carapace width, CW) of crabs was measured. Crab wet biomass was calculated using an empirical relationship between CW and biomass (biomass = $0.0009 \times CW^{2.6441}$, $R^2 > 0.99$, author, unpublished data). At each site, the observed density and size (shell length, divided into seven categories: < 5, 5–10, 11–15, 16–20, 21–25, 26–35 and > 35 mm) of mussels was also determined. Mussels are only consumed in large numbers by *C. maenas* with CW ≥ 20 mm (Ropes 1989). This is also the size that migration in and out of intertidal habitats is observed (although migration is greatest for individuals > 30 mm CW, migration begins when individuals reach 20 mm CW, see table 5 of Hunter & Naylor 1993). I therefore used separate regressions to examine how large (≥ 20 mm CW) and small (< 20 mm CW) crab density changed with log-transformed mussel density across coves. For the remainder of this paper, I then focus only on the 288 large crabs observed during sampling within the 13 coves at Odiorne Point.

ARE CRABS DISTRIBUTED ACCORDING TO IFD EXPECTATIONS?

The IFD of equal competitors predicts that consumers should select sites where their consumption rates are highest and that, at equilibrium, this results in consumers being distributed so that all individuals have similar, maximized consumption rates. I simulated this

process using an individual based, deterministic, simulation model to generate a predicted IFD which I then compared to the observed crab distribution at Odiorne Point. I determined the IFD of crabs across these coves by simulation rather than by numerical calculation (for example, using methods in van der Meer & Ens 1997) to facilitate direct comparison with results of the patch leaving rule simulation models described below. Thus the IFD model described here and the patch leaving rule models described below were all based on the same functional response calculations that incorporate prey density and predator interference.

Potential consumption rates of crabs within a particular cove will vary depending on the density of mussel prey and the density of competing crabs within that cove. I accounted for these factors in calculating potential consumption rates for crabs in each cove using a modified Holling's (1959) type III functional response:

$$C = \frac{aN^2T}{1 + aN^2T_h}, \quad \text{eqn 1}$$

where N is total mussel density, T is time (day, set to one for all models), a is searching efficiency and T_h is handling time (days). I used a type III functional response because *C. maenas* is omnivorous, and with many other food types naturally available (Ropes 1969), may switch to alternative food when mussels become scarce. I modified a and T_h in eqn 1 to include previously demonstrated changes in these parameters with crab density, P :

$$a = k_1 P^{k_2}, \quad \text{eqn 2}$$

$$T_h = k_3 e^{k_4 P}, \quad \text{eqn 3}$$

where $k_1 = 0.18$, $k_2 = -0.98$, $k_3 = 0.03$, and $k_4 = 0.07$. Values for these coefficients were estimated using nonlinear regression ($P < 0.01$ for each) on data from an experiment where *C. maenas* density and mussel density were orthogonally altered and consumption rates were measured (Griffen & Delaney 2007). These model-estimated changes in a and T_h with increases in P are consistent with behavioural observations for *C. maenas* (Smallegange *et al.* 2006; Smallegange & van der Meer 2007). As with other behaviour-based models (e.g. Stillman, Goss-Custard & Caldwell 1997), the strength of this modified functional response is that it incorporates changes in the per capita strength of interference with changes in predator density, rather than assuming interference is a linear function of predator density, as is assumed by using a constant interference coefficient in interference models.

The simulation proceeded as follows. I assumed that the observed mussel density in each cove reflected a standing stock of mussel prey. The simulation was initiated with all sampled crabs aggregated into a single pool, and no crabs in any of the 13 coves. Individuals were then randomly selected from this pool and sequentially 'placed' into the cove that offered the highest consumption rate. Potential consumption rates in each cove were calculated with the addition of each crab, and were based on the density of mussel prey and the density of competing crabs already in that cove, using eqns (1–3). This simulation therefore incorporated the ideal knowledge, free movement and equal competitor assumptions inherent in the IFD. Thus, the simulation predicted the distribution of crabs if they follow the IFD perfectly, resulting in a crab distribution where the consumption rate of all crabs was approximately equal and no crab could improve its mussel consumption by being placed into another cove (Cressman & Křivan 2006). I will refer to this model as the IFD model. I compared the density distribution predicted by the IFD model to the observed densities across all coves using mean percent deviation, defined as the

mean of $\Sigma|\text{observed} - \text{predicted}| / \text{observed} \times 100$. I did not compare biomass using the IFD model because it assumes all crabs are identical and average biomass would therefore be an artefact of the order in which crabs were drawn from the pool of crabs.

EQUAL COMPETITOR MODEL

As explained above, IFD assumptions are each likely violated in this system. I therefore constructed stochastic, individual based simulation models for crab movement that eliminated these assumptions. My purpose was to determine whether simple patch leaving rules and realistic movement patterns that do not invoke these assumptions could yield a crab distribution similar to the IFD and/or the observed distribution. I first constructed a model, referred to as the equal competitor model, that eliminates the ideal knowledge and free movement assumptions, but maintains the equal-competitors assumption.

The equal competitor model was initiated with the 288 sampled crabs randomly distributed across coves so that the initial crab densities in all coves were approximately equal. During each daily time step, the model then performed the following three steps.

1. The model calculated the consumption rate of each crab based on the density of prey and the density of crabs in the cove where it was located using eqns (1–3).
2. The model then used a simple rule to determine if crabs moved out of a cove. I assumed that the probability (p) that crabs would leave a cove was related to consumption in that cove, as follows:

$$p = 1 - \frac{c}{c_{\max}}, \quad \text{eqn 4}$$

where c is the consumption rate of the focal crab, and c_{\max} is the maximum daily consumption rate of a single crab foraging alone on an abundance of mussels (28 mussels day^{-1} at this site, Griffen & Delaney 2007). Thus, crabs are more likely to leave a site as their consumption rate decreases. Functionally, crabs left their current site when p exceeded the value of a random variable, x , drawn from a uniform distribution from 0 to 1.

3. If crabs did leave their current site, the model randomly chose whether they moved to the cove just to their north, or the one just to their south (boundaries were reflective so that crabs in end coves could only move in one direction).

These movement decisions were made for each crab during each time step, and the model was updated (i.e. individuals migrated) synchronously. I iterated the model for 150 time steps, which is approximately the length of the actively foraging summer season for these crabs (May–October), assuming that crabs can only move once per day. Values reported are means of 500 model iterations. This model overcame both the ideal knowledge and the free movement assumptions that are included in the IFD by using a patch leaving rule that is based only on a crab's consumption rate in its current site and by allowing crabs to move only to adjacent sites.

I separately compared both the density and biomass distributions predicted by the equal competitor model to the observed distributions across coves at Odiorne Point using the mean percent deviation.

UNEQUAL COMPETITOR MODEL

I next constructed a model that eliminated all three IFD assumptions (ideal knowledge, free movement, equal competitors), referred to as the unequal competitor model. This model was identical to the equal competitor model, except that it incorporated differential ability of specific crabs to consume mussels of different sizes. Mussels at this

site occur over a wide range of sizes from < 1 mm to > 60 mm shell length. The ability and efficiency of *C. maenas* in consuming mussels depends on both crab size and mussel size (Elnor & Hughes 1978). I obtained data on handling time (T_h , the time to crack open and consume mussels) for different sized individual crabs consuming different sized mussels from Figs 1 and 2 of Elnor & Hughes (1978) (individual data points estimated by eye). I then used nonlinear regression ($P \ll 0.001$) to determine the relationship in this data between handling time and the ratio of mussel shell length (cm) to crab carapace width (cm):

$$T_h^* = 0.34 \left(\frac{\text{mussel length}}{\text{crab width}} \right)^3. \quad \text{eqn 5}$$

Equation 5 provides an estimate of changes in handling time independent of changes associated with crab density described in eqn 3. I therefore used T_h^* from eqn 5 as the y -intercept in the relationship between handling time and predator density, by substituting the right hand side of eqn 5 for k_3 in eqn 3:

$$T_h^* = 0.34 \left(\frac{\text{mussel length}}{\text{crab width}} \right)^3 e^{k_4 P}. \quad \text{eqn 6}$$

I assumed that mussels in each of the size classes (i) given previously were accurately represented by the median value ($i = 0.3, 7.5, 13, 18, 23, 30$ and 40 mm). I therefore simultaneously incorporated the effects of predator density on a and T_h and the effects of crab and mussel size on T_h by calculating consumption of each of these seven mussel size classes separately, as follows:

$$C_i = \frac{aN^2T}{1 + aN^2T_h^*}. \quad \text{eqn 7}$$

Different size mussels provide different sizes of meals and can therefore not be compared simply as the number of mussels consumed. I thus converted the number of mussels consumed in each size class (C_i) to the kilojoules of energy (E_i) consumed using a relationship between mussel length and energy from Elnor & Hughes (1978): $\ln(\text{energy}) = 3.03 \times \ln(\text{length}) - 2.34$ ($R^2 = 0.95$). I then determined the overall consumption rate of energy (kJ day^{-1}) per gram of crab biomass by summing the proportional contributions of each mussel size class:

$$\sum_{i=1}^j \frac{E_i f_i}{m}, \quad \text{eqn 8}$$

where f_i is the frequency of mussel size class i , j is the number of mussel size classes (7), and m is the mass of the focal crab. Expressing consumption per unit crab biomass accounts for the fact that larger crabs need to consume more energy, and may therefore be more likely to leave a site than would a smaller crab obtaining the same consumption rate at that site.

I separately compared both the density and biomass distributions predicted by the unequal competitor model to the observed distributions across coves at Odiorne Point using mean percent deviation.

The model simulations described above used 150 time steps, or approximately the length of the summer foraging season for crabs, assuming that crabs move once per day. An additional question of ecological importance is whether crabs could feasibly track temporally variable resource densities using the patch leaving rule modelled here. I repeated simulations using the unequal competitor model with varying numbers of time steps to track how long it takes crabs to go from a random distribution across sites to matching the IFD. I

started with a single time step and increased the number of time steps in intervals of 1 from 1 to 10, intervals of 2 from 10 to 20, intervals of 5 from 20 to 50, and intervals of 25 from 50 to 150. For each of these, I determined the means square error between the IFD (from the IFD model) and the mean predicted density across coves from 100 replicates of the unequal competitor model.

SENSITIVITY ANALYSES

I examined the sensitivity of both the equal and unequal competitor models. I performed two tests to verify that the predicted distribution resulted from changes in crab foraging because of density-dependent predator interference and was not 'hardwired' into the model. First, I compared the observed distributions to predictions of a random model (crab movement based on random 'decisions' that were independent of consumption rates). Second, I compared the observed distribution to predicted distributions from both the IFD model and the equal competitor model when the influence of crab density on prey handling times and searching efficiencies was removed [instead using constants in eqn 1 for these functional response parameters, taken from Griffen & Delaney 2007].

The equal and unequal competitor models that relaxed IFD assumptions both produced predicted crab density distributions that were similar to the expected IFD. I determined whether this ability of these models to reflect the IFD was a result of specific idiosyncrasies of the study system as follows. I varied the relative order of the 13 sites to determine if altering the relative order of high and low mussel sites influenced results. I varied the total number of sites included from 0.5 to 2X the number of actual sites (through eliminating end sites or creating additional artificial sites). I varied the total number of mussels found in the system from 0.5 to 2X the observed number by randomly adding or reducing the number of mussels at sites. I varied the number of crabs modelled from 0.5 to 2X the number of sampled crabs. After each of these alterations, I re-examined the ability of both the equal competitor and unequal competitor models to replicate the expected IFD crab density. I did this by comparing the predicted crab density from the altered equal or unequal competitor model to the predicted distribution from the IFD model with the same alterations (the IFD model was deterministic and provided the IFD of crabs under any conditions).

Finally, I examined the sensitivity of the equal and unequal competitor model results to the patch leaving rule. Both models assumed that the probability (P) that a crab would leave a cove was directly proportional to the decrease in consumption rate, relative to the maximum consumption rate as described by eqn 4. I tested the ability of each of these models to predict the observed density and biomass across coves when the patch leaving rule was considerably more or less stringent. Specifically, I added a constant to the right hand side of eqn 4, ranging from -1 to 1 in steps of 0.05. Addition of negative values make p less likely to exceed the random variable x , making movement less likely, even when consumption rates are low. Conversely, addition of positive values makes p more likely to exceed the random variable x , making movement more likely even at small decreases in consumption. For each variation on the decision rule, I determined the percent deviation of the mean of 100 replicates of density and biomass from the observed density and biomass. Using percent differences put density and biomass on the same scale and facilitated comparison.

Results

The distribution of large and small *C. maenas* across coves at Odiorne Point differed strongly. The mean density of large *C.*

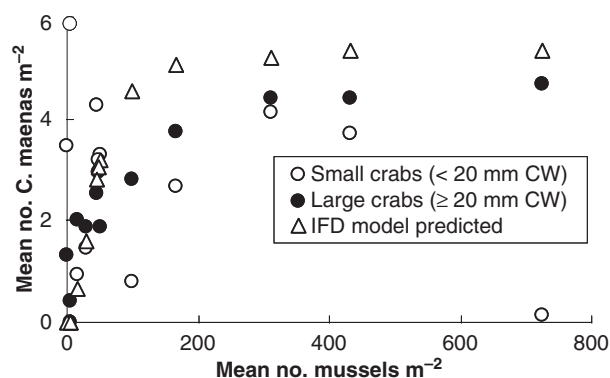


Fig. 2. Mean number of large and small *Carcinus maenas* observed across sites with different mussel densities at Odiorne Point, and predicted densities of large *C. maenas* based on the ideal free distribution model.

maenas increased logarithmically with mussel density (regression on log-transformed mussel density, $F_{1,11} = 4.28$, $P \ll 0.001$, $R^2 = 0.82$, Fig. 2), reaching a maximum density around five crabs per m². In contrast, small crabs were not correlated with mussel density (regression on log-transformed mussel density, $F_{1,11} = 0.14$, $P = 0.72$, $R^2 = 0.14$, Fig. 2).

ARE CRABS DISTRIBUTED ACCORDING TO IFD?

The distribution of large crabs at Odiorne Point is described fairly well by the IFD. Specifically, the IFD model predicted that the density of large crabs should increase asymptotically, maxing out at just over five crabs per m². The observed mean distribution of large crabs closely matched this predicted distribution across coves (mean percent deviation = 39.8%, Fig. 2). However, the observed density was slightly lower than predicted in good sites and slightly higher than predicted in some poorer sites, suggesting 'undermatching'.

EQUAL COMPETITOR MODEL

The densities of crabs predicted by the equal competitor model matched the densities predicted by the IFD model (mean percent deviation = 38.9%) and provided an even better match to the observed crab densities (mean percent deviation = 27.8%, Fig. 3a). However, while the biomass of crabs predicted by the equal competitor model across coves was correlated with the observed crab biomass, there was a substantial amount of deviation between observed and expected (mean percent deviation = 42.6%).

UNEQUAL COMPETITOR MODEL

The densities of crabs predicted by the unequal competitor model also matched the densities predicted by the IFD model (mean percent deviation = 44.7%) and the observed crab densities (mean percent deviation = 33.4%, Fig. 3b). Additionally, the unequal competitor model did a much better job than the equal competitor model of predicting the observed

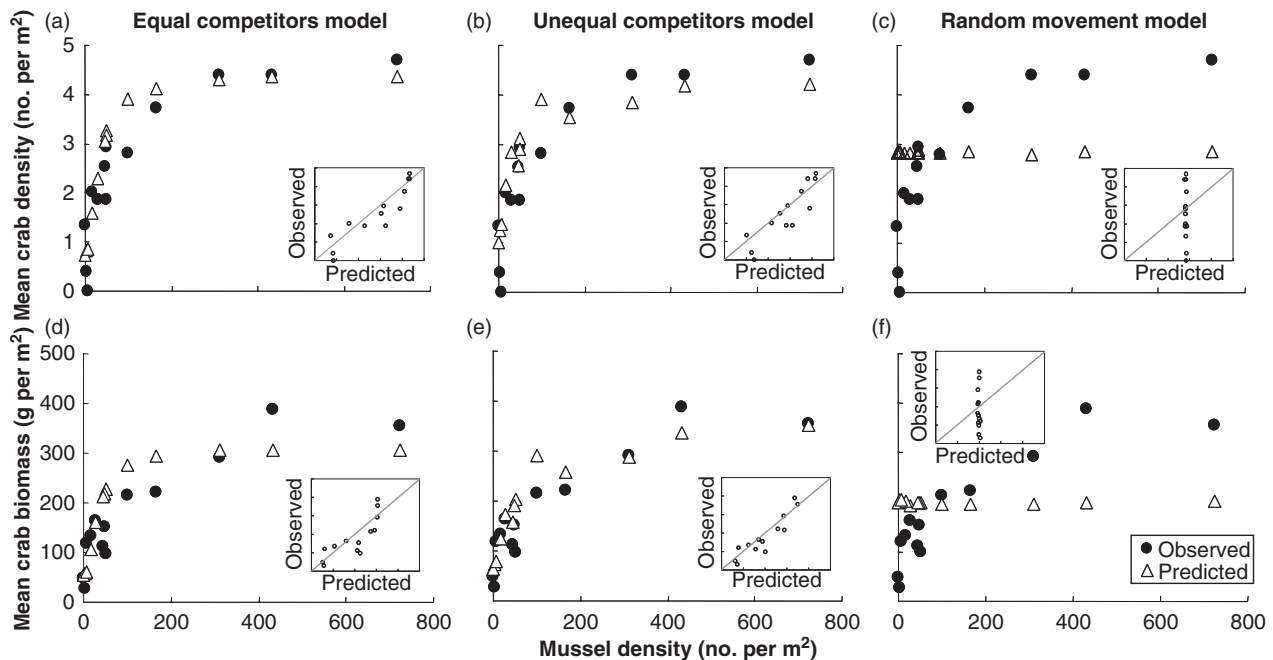


Fig. 3. Comparison of observed crab densities with the mean model predicted densities from 500 runs of the equal competitor model (a), the unequal competitor model (b), and a random movement model (c) across 13 sites at Odiorne Point, NH. Also comparison of observed crab biomass with the mean model-predicted biomass from 500 runs of the equal competitor model (d), the unequal competitor model (e) and a random movement model (f). Inset graphs show observed vs. model predicted values to demonstrate deviation from 1 : 1 relationship (grey line).

crab biomass across coves (mean percent deviation = 26.9%, Fig. 3e).

Using the assumed patch leaving rule implemented here allowed modelled crabs to track differences in mussel density across coves very efficiently. Simulations conducted with different numbers of model time steps showed that crabs could go from a random distribution across coves to closely matching the IFD density across coves in just five time steps (Fig. 4).

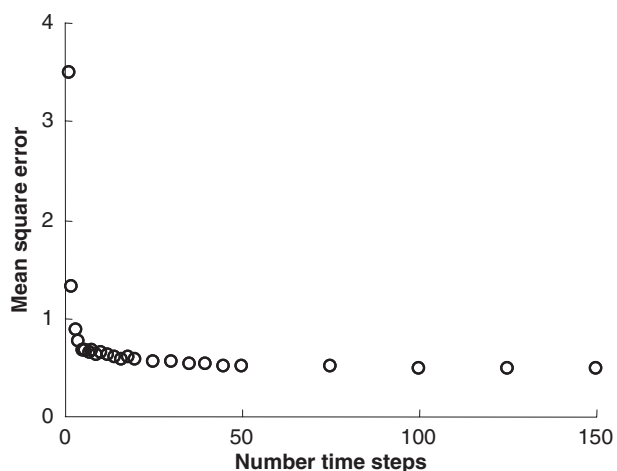


Fig. 4. Number of time steps required for crabs to go from a random distribution across sites to matching the ideal free distribution (IFD) expected densities when crabs use the patch leaving rule implemented in the unequal competitor model. Y-axis is mean square error between the mean of 100 replicates at each number of time steps and the deterministic IFD.

SENSITIVITY ANALYSES

Results were not an artefact of model formulation, and removing density-dependent foraging mechanisms yielded non-sensical results. When the equal competitor model was altered so that crabs randomly chose to leave a site, the model predicted that crab density and biomass should be approximately equal across all sites (mean percent deviation for random vs. observed density = 78.8%, Fig. 3c; mean percent deviation for random vs. observed biomass = 110.4%, Fig. 3f). Qualitatively similar results were obtained when random movement was implemented in the unequal competitor model (not shown). When the effects of crab density on handling time and search efficiency were removed from the models, all crabs in the simulations aggregated to the single site with the highest mussel density.

Results here are not an artefact of idiosyncrasies of this study system. Specifically, these models were insensitive to the relative order of different quality sites, the total number of sites, the total number of mussels included in the simulations, or the total number of crabs. When each of these factors was modified in model simulations, the crab density predicted by both the equal and unequal competition models always closely matched predictions of the deterministic IFD model with the same modifications.

Finally, model results here are sensitive to the patch leaving rule. Both the equal and unequal competition models most accurately predicted observed crab densities and biomass using the decision rule given in eqn 4. The accuracy of these models declined when crabs were either more or less likely to leave a cove as consumption rates decreased (Fig. 5).

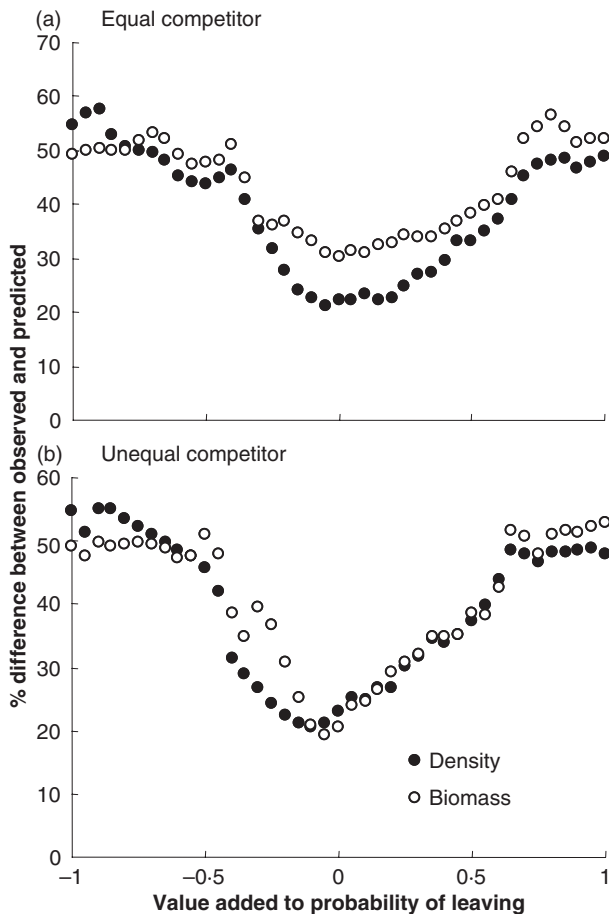


Fig. 5. Sensitivity analysis for the patch leaving rule for both the equal (a) and unequal (b) competitor models. Negative values on the *x*-axis indicate lenient leaving rules, where consumption rates can decrease substantially before crabs are likely to leave a site. Positive values on the *x*-axis indicate stringent leaving rules, where crabs are likely to leave a site even at small decreases in consumption rate.

Discussion

The IFD has accurately predicted consumer distributions in numerous small scale experiments, but its effectiveness for predicting landscape scale consumer distributions has been questioned (Ranta *et al.* 1999). I examined the distribution of *C. maenas* across a stretch of beach that was large in scale relative to crab movement. The observed crab density across Odiorne Point matched IFD predictions fairly well (Figs 2 and 3), indicating both that *C. maenas* is nearly optimally distributed, and that the IFD can be applicable over large spatial scales. Further, the poor correlation between the density of small crabs and the density of mussels across sites suggests that the distribution of large crabs does not simply reflect greater larval settlement into areas with lots of mussels, but rather, likely reflects the movement of larger crabs to profitable prey patches (Fig. 2).

The equal competitor model relaxed the IFD assumptions of ideal knowledge and free movement. The close match of predicted densities derived from this model to observed densities reinforces the previous finding that the IFD is robust to

violations of assumptions of ideal knowledge and free movement (Cressman & Krivan 2006). However, crab biomass across coves predicted by the equal competitor model provided a poor estimate of observed biomass compared to the prediction by the unequal competitor model (Fig. 3). This suggests that fully understanding crab distribution requires inclusion of not only density-dependent effects that are included in the IFD, but also size-specific prey consumption abilities.

A key aspect of both the equal and unequal competitor models was the use of a patch leaving rule. The high sensitivity of the model to the formulation of this rule (Fig. 5) suggests that crabs are likely highly sensitive to consumption rates and will readily emigrate in search of better foraging grounds when consumption rates decline. Further, the efficiency of the patch leaving rule even with very minimal movement (Fig. 4) and under a wide range of conditions (see sensitivity analysis above) suggests that patch leaving rules will allow crabs to track gradually changing mussel densities very efficiently throughout the summer foraging season, and to quickly redistribute themselves in response to pulsed prey recruitment. However, while the rule used here is a plausible candidate based on known foraging mechanisms for *C. maenas* (Elner & Hughes 1978; Smallegange *et al.* 2006; Griffen & Delaney 2007; Griffen & Williamson 2008), other rules may also be plausible, and determining the actual decision rule used by foraging crabs is an exercise left for future experimental investigations.

Whatever the precise rule is, the ability of consumers to achieve complex patterns (Fig. 3) using simple decision rules is an example of self organization. Self organization, where complex broader-scale patterns and processes emerge from simple individual-level behaviours based only on local information, is also seen in colony behaviours of social insects (Bonabeau *et al.* 1997), schooling in fish (Viscido, Parrish & Grunbaum 2004), flocking in birds, and artificial intelligence in robotics (Nolfi & Floreano 2000).

The models here included five simplifying assumptions regarding *C. maenas* foraging ecology. These assumptions reflect a lack of sufficient data for this study system and may have contributed to the deviation between observed and model predicted densities and biomass. Each of these assumptions is discussed below.

1. The unequal competitor model assumed that unequal competition was manifested only through the differential ability of crabs of different sizes to consume mussels of different sizes. In reality, unequal competition in shore crabs may also influence foraging efficiency, as interference-induced reductions in foraging are greatest when crabs are paired with a larger or similar sized crab (Smallegange & van der Meer 2007). However, this pattern may not hold when many crabs interact simultaneously. Under these conditions, the amount of time spent in aggressive behaviour, and therefore not foraging, increases with relative crab size (author, unpublished data). It is therefore unclear how foraging efficiency of

unequal competitor scales with predator density when high densities are comprised of crabs of various sizes interacting simultaneously. Ultimately, the effect of crab size and mussel size on handling times may far outweigh the effect of differences in foraging efficiency because of relative competitor size. Smallegange & van der Meer (2007) report 13–23% changes in foraging time due to relative competitor size, whereas Elnor & Hughes (1978) report that handling time alone changed by more than a factor of 24 depending on crab and mussel size.

- Models here assumed that the observed crab distributions that were determined at low tide reflect distributions at high tide when crabs are foraging. The density of foraging crabs at high tide may in fact be greater than that observed at low tide, as large crabs are known to move from subtidal to intertidal areas to feed at high tide (Hunter & Naylor 1993). Sensitivity analysis indicated that increasing the overall number of crabs in the model did not alter the ability of either the equal or unequal competitor model to predict IFD densities. However, if tidal migratory crabs only move into coves with high mussel abundance, this may account for the undermatching in coves with the highest mussel densities (Fig. 3d).
- The models assume that mussels are the only food source for *C. maenas*. In reality *C. maenas* is omnivorous, and frequently consumes a wide range of plant and animal prey (Ropes 1969; Griffen & Byers 2009). This fact is reflected in the decision to use a type III functional response as described above. The availability and utilization of alternative food within a given cove likely also contributes to an individual's decision to leave in search of better foraging. Explicitly including omnivory may, for example, reduce the likelihood that crabs will leave a site with low mussel abundance if alternative food sources are abundant.
- Equation 8 assumes that *C. maenas* consumes mussels of different sizes in proportion to their relative frequency in the environment. However, *C. maenas* commonly selects mussels based on mussel size (Mascaro & Seed 2001), the presence of epibionts (Enderlein *et al.* 2003), and whether mussels are present singly or in groups (Burch & Seed 2000). Differences across coves in any of these factors may explain lower or higher than expected crab abundance.
- The IFD assumes that individuals are equally free to move to any available patch; in contrast, the equal and unequal competitor models only allowed individuals to migrate into adjacent sites. However, these models still retain an assumption of no travel costs. In reality, crabs could incur a travel cost were they to migrate for the purpose of increasing consumption, only to move into an adjacent site that offered lower consumption rates than the original site. If such costs limit the ability of individuals to repeatedly migrate to maximize consumption rates, then this may explain some of the deviation between observed and predicted crab distributions. However, such costs may be minimal in this system because *C. maenas*

can survive for several weeks without eating (Mente 2003).

In summary, the IFD represents a steady state that may be naturally achieved when organisms migrate to maximize consumption rates. As demonstrated by the equal and unequal competitor models, the IFD may still be achieved when IFD assumptions are violated, as long as individuals are able to repeatedly migrate until this steady state is reached. Despite the inherent assumptions, the models here accurately predicted > 80% of variation in crab density and biomass across coves within a very minimal number of time steps (Figs 3 and 4). This suggests that *C. maenas* actively migrates to maximize foraging efficiency and that the processes modelled here capture essential aspects of these foraging movements.

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