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Multiple dimensions of habitat selection: how the combined effects of food density and detectability drive forager distributions

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ABSTRACT

Habitat structure has profound effects on foraging animals: it affects prey abundance, while at the same time influencing a forager's searching efficiency. For example, in marine systems, foundation species (e.g coral reefs and seagrass beds) have a strong habitat-structuring effect by increasing prey densities, but simultaneously also creating spatial refuges causing negative effects on searching efficiency of consumers. These two dimensions of habitat quality, which are rarely studied in concert, were experimentally investigated for red knots (*Calidris c. canutus*) foraging in the intertidal seagrass ecosystem of Banc d'Arguin (Mauritania). The mudflats here covered by a gradient of seagrass densities from sparse with low densities of prey (that should be relatively easy to find) to dense with high densities of prey (that should be harder to detect). Intake-rate maximizing red knots would have to find an optimum at intermediate seagrass densities. We tested this inference in a unique experimental setting by bringing indoors natural habitat patches that ranged from no to dense seagrass, on which we measured intake rates, searching efficiencies, prey handling times and patch preferences. As predicted, red knots showed high searching efficiencies at low prey densities in patches with little or no seagrass, and low searching efficiencies at high prey densities in dense seagrass. Red knots gained the highest intake rate in patches of degrading seagrass with intermediate total prey- and seagrass densities. Using field observations on forager densities, we confirmed the preferred use of mudflats with intermediate seagrass densities. Thus, we conclude that to accurately predict the habitat choice of a consumer, habitat-modifying effects by foundation species should be considered.

INTRODUCTION

Prey density is an important factor determining forager distributions. Moreover, it is generally assumed that foragers will try to maximize their intake rates, and that this will occur at the highest (harvestable) prey densities (Holling 1959, Stephens and Krebs 1986, Zwarts and Wanink 1993). Students of foraging ecology have typically consider harvestable food density to be the most important predictor of intake rates and forager distributions (MacArthur and Pianka 1966). However, the world is obviously more complex, and an increasing number of studies has shown that other factors should not be ignored (e.g. Brown 1988, Piersma 2012). Habitat complexity, for example, can obstruct the detectability of prey, influencing the behaviour of foragers and their prey, as well as their interaction (Ryer 1988, Anderson 2001, Lannin and Hovel 2011). Habitat complexity is a function of abiotic structures (e.g., rock crevices, ship wrecks), but also of biotic structures such as plants, trees and woody debris in terrestrial systems, and macro algae, submerged plants, coral reefs and shellfish beds in aquatic ecosystems (e.g. Ryer 1988, Ripple et al. 2001, Arthur et al. 2005, Hopcraft et al. 2005, Loarie et al. 2013, Toscano and Griffen 2013).

Marine foundation species, like coral reefs, seagrass and mussel beds, are classic examples of species which have a strong structuring role through modification of resource availability, reduction of physical stress and enhancement of habitat complexity (Jones et al. 1994, Stachowicz and Hay 1999, van der Heide et al. 2007, van der Zee et al. 2012). On the other hand, by enhancing spatial complexity, they also create spatial refuge from predation (Orth et al. 1984, Bruno et al. 2003), thereby negatively affecting the per capita success rate of the forager (i.e. its searching efficiency, defined as the density-corrected prey encounter rate; Beddington 1975). Yet, despite the importance of habitat-modification by foundation species for consumer-resource interactions, the net outcome for consumers of the balance between prey density enhancement on the one hand and increased habitat complexity on the other hand has rarely been studied experimentally (Olf et al. 2009).

Here, we investigated how the combined effect of prey density and habitat complexity in an intertidal seagrass bed explains the intake rate and habitat choice of an avian forager, the red knot (*Calidris canutus canutus*). This medium-sized shorebird mainly spends its nonbreeding season at Banc d'Arguin, Mauritania (West Africa), where it feeds on molluscs buried in intertidal seagrass beds (Onrust et al. 2013, van Gils et al. 2013). In general, seagrass has a positive effect on species richness and abundance (Orth et al. 1984, Honkoop et al. 2008, van Gils et al. 2015). In our study area, for example, seagrass and the Lucinid bivalve (*Loripes lucinalis*) densities are tightly linked due to a mutualistic relationship (van der Heide et al. 2012b). While at first sight the increase in prey density should be an advantage for knots, local prey depletion in high seagrass densities by red knots was far less than expected based on earlier experiments on bare mudflats (Piersma et al. 1995, chapter 6). Moreover, on average red knots were not found at the highest densities of *Loripes* available in our study area (van Gils et al. 2015). Although, red knots

possess a unique sensory organ in the tip of the bill to detect hard-shelled prey buried in soft wet sediments without direct contact ('remote touch') (Piersma et al. 1995, Piersma et al. 1998). Recent experimental work, however, revealed that in seagrass red knots 'lose their sixth sense' and can only detect their prey by direct touch rather than remotely (chapter 6). Therefore, in seagrass intake rate and habitat choice by foraging red knots may not be simply a function of prey density but also of habitat complexity created by seagrass.

We hypothesize that red knots need to find an optimum where the positive effect of high prey densities (at high seagrass densities) becomes cancelled out by low searching efficiencies at high seagrass densities. We first experimentally investigated this idea in captive red knots foraging on patches taken from a seagrass gradient in the field, namely bare sediment, colonizing-, long term healthy and degrading seagrass habitat. We experimentally scored intake rates, searching efficiencies, prey handling time and the preference for certain habitats. We predicted that the highest intake rates would be found at the intermediate seagrass densities (colonizing and degrading patches), and that these patches would also be most preferred. To investigate whether our experimental outcomes relate to field observations, we reanalyse data on red knot distributions collected in the field by van Gils et al. (2015) and relate these to prey densities and NDVI (Normalized Difference Vegetation Index, as proxy for seagrass cover).

METHODS

Study area

The intertidal area of the Parc National du Banc d'Arguin (PNBA), Mauritania, West Africa (19°53'N, 16°17'W), covers about 500 km² of mudflat dominated by mixed meadows of *Zostera noltii*, *Halodule wrightii* and *Cymodocea nodosa* (Wolff et al. 1993). The shallow intertidal seagrass beds accumulate large amounts of organic matter-rich sediment by attenuating currents and waves (Folmer et al. 2012, van der Heide et al. 2012b). The decomposition of organic matter is primarily controlled by anaerobic sulphate-reducing bacteria that produce sulphide, which is toxic to seagrass (Lamers et al. 2013). In combination with drought events sulphide toxicity forces seagrass beds to go through successional dynamics alternating between low and high seagrass biomass yielding mosaics of different developmental stages (chapter 3 & 4). Based on NDVI satellite images and observation on the ground we could distinguish four habitats: bare sandy mudflat with no seagrass (bare from here on), sandy habitat recently colonized by seagrass (colonized), long term healthy seagrass with thick silt layer (~1 m, > 37 year-old meadows) (healthy) and degrading seagrass habitat (degrading). Degrading seagrass was very patchy at a fine spatial scale that could not be detected by satellite images, therefore, classification of this habitat type was mainly done by observations on the ground. These four habitats were used as habitat treatment during the experiments.

Birds

The experiment was conducted in January 2012 at the Iwik research station PNBA. Five red knots were caught with mist nets on 20 January 2012 on the Abelgh Eiznaya high-tide roost, 2.5 km from the research station. Birds were housed as a group in an aviary (2.0×0.6×0.4 m) with sand on the floor, fresh water *ad libitum* and on a natural day-light cycle. Birds were fed hard shelled bivalves (*Loripes* and *Dosinia isocardia*) to keep natural gizzard size and in addition minced *Anadara senillis* collected on a daily basis. To keep birds motivated to feed during the experimental trials, daily rations were adjusted to keep body mass just above ca. 100 g (e.g. Oudman et al. 2014).

Experimental design

Experimental trials were conducted in the birds aviary. We conducted the experiments with intact sediment cores (experimental patch) which were collected in PVC columns from four habitat types (bare, colonizing-, healthy- and degrading seagrass) at the Abelgh Eiznaya mudflats (19°53.54' N, 16°18.85'W). The PVC cores (ø: 15 cm) were taken to a depth of 10 cm, sealed at the bottom, and transported to the research station. Here, cores were kept submerged in buckets filled with seawater to prevent dehydration. Each habitat treatment was offered in five times to each bird, every individual core was used once and the order of the birds and treatment were chosen randomly.

Each trial was conducted with one individual bird at the time, with each bird being involved in one trial per treatment per day. Unfortunately, one bird died after four experimental days, leading to a total of 96 trials suitable for analyses. During trials the other birds were waiting in a separated part of the aviary such that they were in vocal and visual contact with the experimental bird. A trial stopped after 3 min. of active foraging time, which included probing, pecking in the sediment, and handling seagrass on the experimental patch. Each trial was digitally recorded with a camera (Canon VIXIA HG21). Search- and handling time for each prey encounter and ingested prey were scored by slowing down the video tape to one-fourth of the recording speed by using Observer package (Noldus Information Technology 1997). Intake rates (preys s^{-1}) were calculated by dividing the total accepted preys by the total active search time. Average searching efficiency ($cm^2 s^{-1}$) was calculated per trial by $1/T_s \times D$, where D is the initial prey density (m^{-2}) and was calculated by adding accepted preys (swallowed) and leftover preys (not eaten in patch, see below for details) and T_s is the average search time per prey per trial.

After a trial had ended, above and belowground seagrass and the benthic animals were collected following a standard procedure (Honkoop et al. 2008, van Gils et al. 2012): cores were sieved over a 1-mm mesh, in the laboratory all molluscs in the sample were counted and identified to species level and their shell length were measured to the nearest 0.1 mm. Individual species ash-free dry mass (AFDM) was determined by using length-specific AFDM curves (Onrust et al. 2013; unpub. data van Gils, van der Geest and de Fouw) The top (0–4 cm) and the bottom (4–10 cm) were separated to distinguish between prey items which were accessible for red knots from those that were not. Two

gastropod species (*Gibbula divaricata* and *Gibberula* sp.) and a thick-shelled bivalve (*Senilia senilis*) were omitted from the data because they were not eaten by red knots. Total dry mass (DM in gram) of the seagrass was determined after drying (48 hours at 60°C). In addition a sediment subsamples was taken from the top of 5 cm and frozen after collection (-10°C). Subsamples were freeze-dried in the laboratory, after which we determined median grain size using a particle size analyser with auto sampler (Coulter LS 13 320).

To determine the habitat preference of the red knots we carried out a second experiment in which we offered the habitats in a dichotomous preference setting (following van der Meer 1992). Individual habitat patches were used once and offered pairwise to the experimental birds. Each bird received all six combinations of the four different habitat types once a day over two days. Unfortunately, one bird died after two experimental days the second day, leading to 56 experimental trials. The order of the birds, habitat treatment combinations and position of the habitat (left or right) was chosen randomly. Prior to the trial a bird was placed in front of the two habitat treatment combination and separated by a netting panel through which the focal bird could visually inspect the two patches. This panel was lifted after we made sure that the bird had given both patches a close look. A trial was ended when the bird switched three times between the two habitat treatments. Each trial was digitally recorded with a camera. The total time spend on each treatment was used in the analysis and the habitat where most time was spend was used as preference, resulting in a binomial distribution.

Statistical analysis

All statistical analyses were conducted using the software program R (R Development Core Team 2014). Seagrass biomass, prey density, sediment median grain size were analyzed using one-way ANOVA with habitat treatment as a fixed factor and Tukey HSD for post-hoc comparisons. Searching efficiency, prey handling time and intake rate were tested using mixed-effect model with habitat treatment as fixed factor and bird as random factor (function *lmer*). Seagrass biomass versus prey density and searching efficiency were analyzed with a nonlinear model based on least-squares estimates (function *nls*). We used a Generalized Linear Model (function *glm*) with Binomial distribution for preference test. All statistical analyses were done in R (R Development Core Team 2014), mixed model with Sattertwiate corrected degrees of freedom (package *lmerTest* for mixed-effect models) (Bolker et al. 2009, Mun and Chun 2014).

RESULTS

Total prey densities differed significantly between habitat treatments (Figure 7.1A, ANOVA, $F_{3,92} = 42.79$, $P < 0.001$). This was also detected in the top 4 centimetres (ANOVA, $F_{3,92} = 20.33$, $P < 0.001$), however, here only bare sediment differed significantly from the other habitat treatments (Figure 7.1A). We could not detect a difference

for prey flesh AFDM between habitat treatments (ANOVA, $F_{3,92} = 1.94$, $P = 0.12$). Total and shoot seagrass biomass differed significantly between habitat treatments (Figure 7.1B, $F_{3,91} = 123.2$, $P < 0.001$ and $F_{3,91} = 65.63$, $P < 0.001$) and prey density increased with seagrass biomass (Figure 7.1C, total: $b_0 = 55.46 \pm \text{SE } 1.74$, $P < 0.001$, $b_1 = 0.60 \pm 0.1$, $P < 0.001$, $R^2 = 0.58$, top 4 cm: $b_0 = 256.61 \pm 1.88$, $P < 0.001$, $b_1 = 0.24 \pm 0.12$, $P < 0.05$, $R^2 = 0.37$). Sediment median grain size differed between treatments ($F_{3,16} = 91.27$, $P < 0.001$). Post-hoc test grouped degrading and healthy seagrass ($P = 0.1$; mean $\pm \text{SE} = 57.7 \pm 1.34 \mu\text{m}$) and bare and colonizing seagrass together ($P = 0.08$, $243.1 \pm 12.7 \mu\text{m}$).

Intake rates differed significantly between habitats, with the highest intake rates being achieved on the degrading habitat treatments (Figure 7.2A, GLMM, $F = 10.09$, $P < 0.001$). Searching efficiency differed between habitat treatments (GLMM, $F = 12.34$, $P < 0.001$) and decreased exponentially with seagrass biomass (Figure 7.2B, $b_0 = 0.79 \pm \text{SE } 1.10$, $P < 0.05$, $b_1 = -0.004 \pm 0.0009$, $P < 0.001$). Prey handling time did not differ between

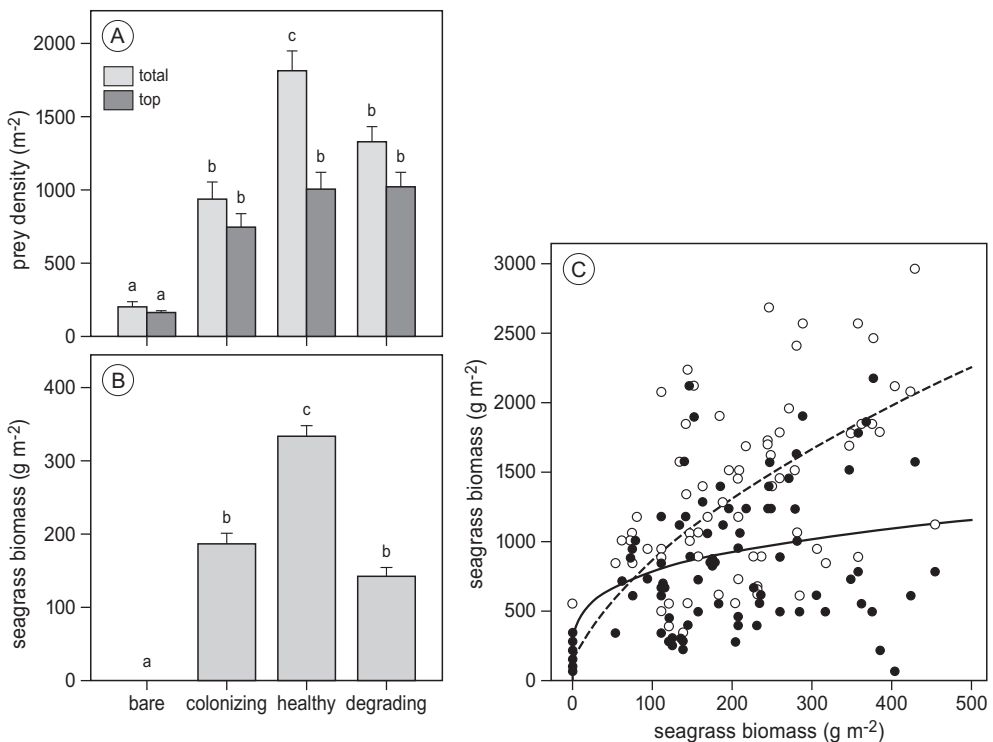


Figure 7.1 (A) Prey densities differed significantly between the four habitats, both concerning all prey and the ones living in the top 4 centimetres. (B) Total seagrass densities (sum of above and below ground biomass) differed significantly between habitats. Letters indicate post-hoc groups and error bars depict standard error. (C) Total prey density (dotted line through open dots, $y = 55.46x^{0.60}$) and the top 4 centimetres prey density (solid line through closed dots, $y = 256.61x^{0.24}$) increased with total seagrass biomass.

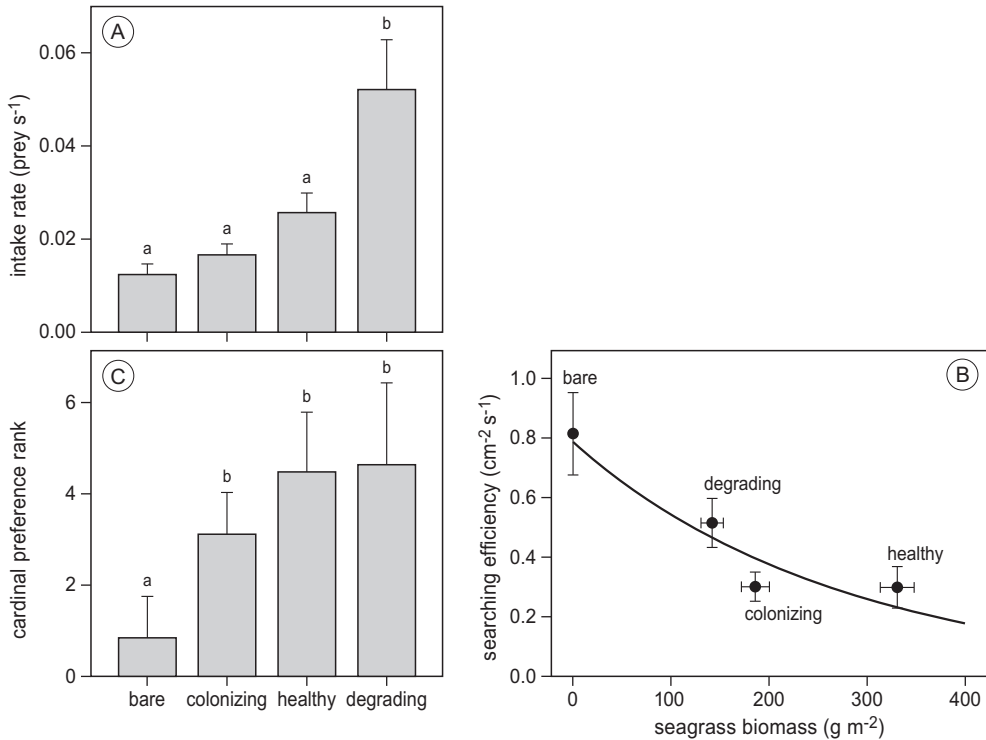


Figure 7.2 (A) Observed intake rates differed significantly between habitats, with intake rates in degrading habitat being higher than in the other habitats. (B) Searching efficiency decreased with seagrass biomass ($y = 0.79e^{-0.004x}$). (C) Preference of the red knots for the habitat differed between bare and all other habitats, with an equal preference for all seagrass-covered habitats. Letters indicate post-hoc groups and error bars depict standard error.

treatment habitats (mean \pm SE = 1.35 ± 0.14 s, (GLMM, $F = 1.21$, $P = 0.31$ Preference of the red knots for the habitat differed between bare and all other habitats (Figure 7.2C, GLMM, $P < 0.05$), post-hoc test showed that there was an equal preference for all seagrass-covered habitats (degrading versus colonizing: $P = 0.20$, healthy versus colonizing: $P = 0.07$, healthy versus degrading: $P = 0.84$).

DISCUSSION

Although there are multiple studies showing that foundation species increase habitat complexity thereby providing refuge for prey and mediating consumer-resource interactions (for example: Meerhoff et al. 2007, Lannin and Hovel 2011, van der Zee et al. 2012), relatively few studies have examined the direct effect on searching efficiency (but see Ryer 1988, Lannin and Hovel 2011). In this study we show that habitat complexity increases prey density and simultaneously decreases searching efficiency. In turn, affect-

ing the intake rate and habitat choice of the consumer, red knots in this case, when foraging on seagrass covered mudflats. This study confirms that red knots cannot rely on their remote prey detection when foraging in seagrass (see for details: chapter 6). As a consequence, the high prey densities in dense seagrass which should be an advantage for knots are 'hidden' within the seagrass rhizome layer. So, it falsely suggests there is a high prey density availability for red knots in Banc d'Arguin and predictions on carrying capacity based on feeding conditions in the past have taken this into account (e.g. Zwarts et al. 1990). Obviously, this needs further investigation to put this in perspective.

We found that red knots need to find an optimum where high encounter rates begin to be cancelled out by low searching efficiencies at increasing seagrass densities. In addition, the preference test showed that red knots preferred seagrass rich habitat over bare sand. However, based on their high intake rates gained on degrading seagrass, one may expect that red knot would have a strong preference for intermediate seagrass (degrading habitat), but this was not the case. Apparently there are other factors playing an important role in habitat preference of red knots. For example, red knots use patch sample information to get to know the value of their surrounding (van Gils et al. 2003). As the red knots did not have unlimited time on the experimental patches, the duration may have not been sufficient to get to know the value of the patch accurately. However, results from both experiments suggest that the combined effects of prey density and seagrass biomass are important predictors to understand intake rate and habitat choice of red knots.

To get insight in the habitat choice of red knots in the field we combined field data on individual red knot positions, available prey densities and NDVI (Landsat image taken on 14 April 2007, within the bird observation period) as a proxy for seagrass cover (see for details: van Gils et al. 2015). We calculated intake rates based on functional response type II with searching efficiency and handling time from our first experiment, shown as lines of equal intake rate in a state space of prey densities vs. NDVI (curved lines in Figure 7.3). The intake rate lines show that red knots potentially gain the highest intake rates at low seagrass biomass and high prey densities. However, looking at the frequency distribution of the NDVI values and the positive relationship between prey density and NDVI we see that such sites hardly existed (Figure 7.3). The positive relation between prey density and seagrass found here was consistent with our experimental data and other studies (Honkoop et al. 2008, Folmer et al. 2012, van der Heide et al. 2012b). In line with the predictions and the experimental results, this analysis shows that also in the wild, red knots aim for the optimum, intermediate seagrass density where their intake rate is maximized (between 0.01 and 0.025 prey s^{-1}) (Figure 7.3). Note that the predicted numerical intake rates match the intake rates observed on free-ranging red knots at Banc d'Arguin (van Gils et al. 2015).

Recently, there has been an increasing amount of attention for how the interplay between habitat modification and trophic interactions affect ecosystem functioning (Olff et al. 2009, van der Heide et al. 2012a, van der Zee et al. 2012, Sanders et al. 2014). Foundation species, like coral reefs and seagrass, strongly modify habitat structure creating spatial refuge from predation (Peterson 1982, Orth et al. 1984, Stachowicz and Hay

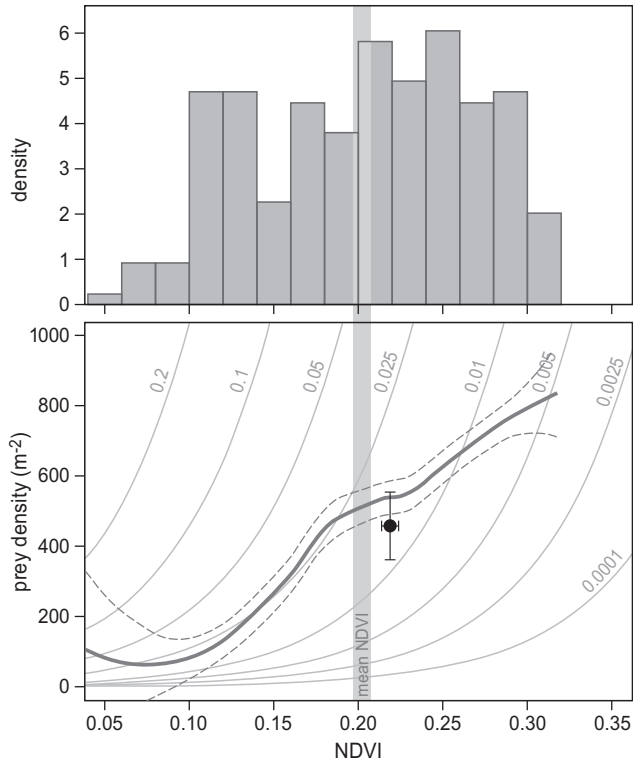


Figure 7.3 The available prey density against NDVI in the environment in April 2007 (fitted with non-linear regression model, LOESS function (R Development Core Team 2014) (dotted lines depict standard error) and the average prey densities and average NDVI at the red knot positions (dot with error bars depict standard errors). Curved lines give equal intake rate (prey s^{-1}) predicted by the functional response based on the parameters estimated in this study.

1999, Bruno and Bertness 2001, Stachowicz 2001). As a consequence, this will affect the searching efficiency of the consumer. Nevertheless, how foundation species quantitatively affect searching efficiency through habitat modification is poorly studied (Olf et al. 2009). Our study shows that foraging success and habitat choice of red knots is mediated by the habitat modifying properties of seagrass, which provide habitat (boosting prey density) but also refuge for prey (hampering prey detectability). Therefore, the combined effects of prey density and detectability are important factors and should be considered when predicting the distribution of foragers in ecosystems with foundation species.

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