Friend or foe: Conflicting demands and conditional risk taking by opportunistic scavengers

F. Joel Fodrie [a,*], Michelle C. Brodeur [a,b], Benjamin J. Toscano [c,d], Sean P. Powers [b,c]

[a] Institute of Marine Sciences and Department of Marine Sciences, University of North Carolina at Chapel Hill, 3431 Arendell Street, Morehead City, NC 28557, USA
[b] Department of Marine Sciences, Life Sciences Building Room 25, University of South Alabama, Mobile AL 36688, USA
[c] Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, AL 36528, USA
[d] Department of Biological Sciences, University of South Carolina, 715 Sumter Street, Columbia, SC 29208, USA

ABSTRACT

To optimize individual fitness, prey should balance predation threats with their own foraging demands. For prey that have additional competitive or positive interactions with their predators, however, little is known about the dynamics that regulate risk management behaviors. Our study focused on common marine gastropods (oyster drills) and one of their major predators: stone crabs. Notably, stone crabs not only prey on drills, but also serve as an ally by breeching the shells of eastern oysters. Subsequently, the foraging success of drills on oysters can be enhanced in the presence of crabs via scavenging on damaged oysters. We manipulated predator (crab) presence, resource (oyster) availability and prey (drill) hunger to explore how complex food-web interactions affect the risk management of predatory and scavenging gastropods. In mesocosm trials, we found that: (1) drills selected habitat closer to a central risk-reward patch as resource availability increased, although the presence of a stone crab generally stifled this movement toward the risk-reward patch; (2) in treatments without any live oysters provided as a foraging resource, drills were attracted by the presence of stone crabs despite the lack of an obvious incentive for this risk-enhancing behavior; (3) drills starved for 14 days prior to entering mesocosms selected habitat without regard to predation threat, while drills that were not starved responded strongly to predator presence; and (4) drills became more aggregated as resource availability decreased, predation threat increased, or starvation level decreased. These results indicate that in resource-poor environments, drills demonstrate riskier behaviors than predicted by simple predator–prey models due to additional, positive interactions with their crab predators.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

The foraging behavior of an organism affects its habitat selection and distribution (MacArthur and Pianka, 1966), interactions with other species in food webs (Luttbeg and Sih, 2004), and even its anatomical form over evolutionary time (Wainwright et al., 2000). Combined with other fitness considerations such as risk-avoidance (Lima and Dill, 1990) and reproduction (Mangel and Clark, 1986), the foraging strategies of a species determine how time and energy are allotted among searching, feeding, resting and hiding behaviors. Indeed, there have been many behavioral studies to consider how species manage these potentially conflicting demands, particularly those involving acquisition of food resources and risk of predation (Dill and Fraser, 1997; Grabowski and Kimbro, 2005; Sih, 1980). In any given instance, the need to avoid being eaten generally takes precedence over the need to maximize energy intake (Grabowski and Kimbro, 2005; Heck et al., 2003). As a result, many potential predators themselves spend a large portion of their lives exhibiting defensive behaviors (vigilance) and avoiding risky circumstances (Sih, 1997).

Often, species that are linked via predator–prey relationships are also connected within food webs via facilitation (Fodrie et al., 2008), or, more commonly exploitative or interference competition (Polis and Holt, 1992). In these scenarios, it is likely that additional demands are placed on species to process and respond to the various rewards or penalties that follow from foraging or risk-avoidance strategies. For instance, intraguild prey, in the presence of an intraguild predator, may alter their distribution (predator-avoidance), diet (competition avoidance), or both in ways that could not be predicted from separate models of predator–prey games or competitive interactions (sensu Schmitt et al., 2009).

The primary goal of our study was to investigate how simultaneous negative (predation) and positive (facilitation of resource acquisition via opportunistic scavenging) interactions between species affected the foraging strategies of a common marine gastropod. Species with dual predatory-scavenging strategies, such as our focal gastropod, are partially supported by the provision of carcasses by other predatory and potentially more-dangerous species (Daleo et al., 2005). Therefore, their behavioral responses to the presence of

* Corresponding author. Tel.: +1 252 726 6841x149.
E-mail address: jfodrie@unc.edu (F.J. Fodrie).

other, dangerous species may be mitigated by the tendency of these higher predators to also attack the preferred prey of the gastropod. In highly modified food webs such as coastal estuarine systems, scavenging and kleptoparasitism (involving the theft of another predator's kill) are expected to be increasingly important drivers of overall community ecology (Wilson and Wolkovich, 2011). As such, there is a clear need to evaluate the potentially complex foraging and risk-avoidance strategies of species within these guilds.

Furthermore, many species can be described by fission–fusion social behaviors in which unrelated individuals can become aggregated based on a suite of intraspecific and environmental cues. Often, the aggregation of foraging individuals in to groups is a risk management response due to a "safety in numbers" strategy that increases predator detection or dilutes individual risk within the group (Bednekoff and Lima, 1998). In particular, many scavenging or kleptoparasitic species are characterized by group foraging strategies — likely in response to risky behaviors that bring them in close proximity to more dangerous predators (Heithaus and Dill, 2002; Trinkel and Kastberger, 2005). However, group foraging is not without some costs. For instance, group size among foraging predators is understood to be limited by intraspecific competition for resources (Janson and Goldsmith, 1995). At present, however, we have comparatively little understanding of the relative importance of predation risk and intraspecific competition across gradients in resource availability in determining the group foraging behaviors of scavenging gastropod species.

Tri-trophic interactions among oyster drills (*Stramonita haemastoma*), their eastern oyster prey (*Crassostrea virginica*), and stone crabs (*Menippe adina*), which prey upon both drills and oysters (Fig. 1A), provide a model for examining how complex food-web interactions affect risk management and foraging behavior. Throughout the northwestern Gulf of Mexico, these species co-occur within oyster reef habitat over large (among reefs) and small (<1 m within reefs) scales (Lindberg and Marshall, 1984; Butler, 1985). Recently, Fodrie et al. (2008) demonstrated that crabs facilitated the foraging activities of drills on oysters within field enclosures via the cracking/chipping of shells. This occurred even though crabs also killed some drills during experimental trials (see also: Powell and Gunter, 1968), resulting in enhanced mortality for oysters due to the increased foraging rates of crabs in response to drills stealing oyster tissue made available by earlier crab attacks. Following these results, several questions remain regarding how drills manage risk in the presence of a stone crab — which is both an enemy and an ally. Can drills recognize situations in which the risk presented by crabs is low, such as when oysters, the preferred prey of crabs (Powell and Gunter, 1968; Brown and Haight, 1992), are abundant (Luttbeg et al., 2003; Holt and Huxel, 2007)? Furthermore, how does risk management regulate the dynamics of group foraging behaviors among drills (Brown and Alexander, 1994)?

To investigate the regulatory mechanisms and patterns of risk management by drills, we designed a manipulative experiment to address the following questions: (1) what are the relative roles of resource availability, predator presence and individual condition on the risk management of a common estuarine gastropod? And (2) do opportunistically scavenging prey utilize a safety-in-numbers strategy to mitigate risk in the presence of a stone crab, and is this foraging behavior mediated by resource availability or hunger?
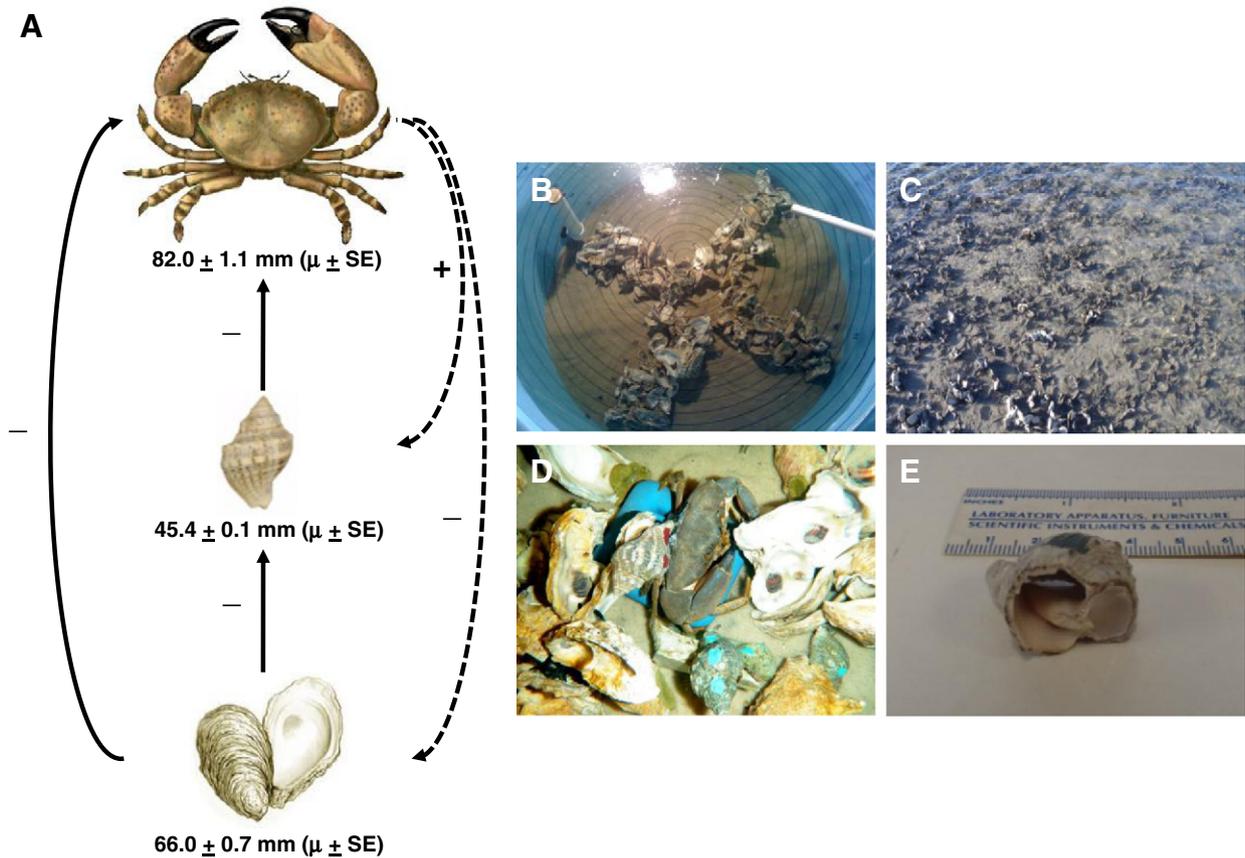
Fig. 1. (A) The tri-trophic food web within oyster reef communities examined in this study. Positive (+) and negative (−) direct (solid lines) and indirect (dashed lines) interactions are shown between species. The arrows go from prey toward predators for direct interactions, following the flow of energy. Conversely, the arrows go from predators toward prey for indirect interactions, in this case arising from behavioral modifications of drills, which steal tissues of oysters breeched by crabs. Also shown are a series of images demonstrating: (B) the spatial arrangement of oyster reef habitat within our laboratory mesocosms; (C) the natural mosaic of oyster habitat we intended to mimic, defined by interspersed oyster clumps and soft bottom; (D) the close proximity of several drills to a stone crab during a trial in which drills were starved 14 days and then presented no live oysters to feed upon; and (E) characteristic shell fragment remaining following stone crab predation on oyster drills during our experiments.

2. Materials and methods

2.1. Experimental design

We conducted a series of mesocosm trials to assess how predation threat, resource availability, and individual condition (starvation period) interactively determine the foraging behaviors of a marine gastropod (drills). The behavioral responses of drills were quantified as habitat selection (distance from a central risk-reward patch) and intraspecific social interactions (aggregation). To accomplish this, we mimicked the conflict scenario of Sih (1980) by manipulating live oyster density and stone crab presence within a centrally located risk-reward patch inside laboratory mesocosms (Fig. 1B). Our trials were run with 0, 3 or 15 live oysters placed inside the central resource patch, and drills were allowed to forage either with or without a stone crab in the same central patch where we placed live oysters. We also manipulated the starvation level of our focal prey species during these trials, as drills were either held without food for 1 or 14 days before being placed inside our experimental mesocosms where they could then forage for live oysters. Thus, we conducted a $3 \times 2 \times 2$ orthogonal design with 12 unique treatments. We ran 16 replicates of each treatment combination, resulting in 192 trials in which we observed the foraging and risk-avoidance behaviors of drills. Additional trials of each unique treatment were also run with prey habituation included as a fourth manipulation (i.e., drills were either held in 60-L aquaria with a stone crab – claws banded – for 1 day before being introduced to our mesocosm trials, or not). Habituation was later shown to have no statistically significant effects ($\alpha = 0.05$; $P \gg 0.05$) on drill behavior (habitat selection and aggregation), either independently or via interactions with other factors, and therefore we largely exclude it from further discussion.

2.2. Collections

This experiment was conducted during June–August, 2009, at the Dauphin Island Sea Lab (DISL). All oysters, oyster drills and stone crabs were collected from fringing oyster reefs around Dauphin Island, Alabama, and immediately returned to holding tanks at DISL. Drills and crabs were collected 1–2 days before experiments began, while live oysters were collected <1 week before mesocosm trials and scraped to remove loose epifauna. Prior to experiments, oyster drills and stone crabs were held without food in separate 60-L Plexiglas holding tanks (59.7-cm long × 30.5-cm deep × 33.0-cm wide) and subjected to an artificial photocycle (12-h light: 12-h dark). Oysters were held in bags deployed off the end of the DISL vessel dock before use in experimental trials. The sizes of oysters (66.0 ± 0.7 mm [$\mu \pm 1$ SE], length of main growth axis), drills (45.4 ± 0.1 mm along longest dimension) and crabs (82.0 ± 1.1 mm carapace width) were measured to ensure consistency among treatments, and only small differences (<5%) were observed.

2.3. Experimental mesocosm trials

Following a conditioning phase in which drills were starved for either 1 or 14 days, drills were placed in experimental mesocosms under a range of resource (live oyster density) and threat (predator presence) scenarios. During conditioning, drills were held in groups of 10 within 23-cm long × 5-cm deep × 23-cm wide VEXAR pens placed inside the Plexiglas holding tanks (separate treatments in separate tanks). Experimental mesocosms consisted of 6 cylindrical 665-L (110-cm diameter, 70-cm deep) tanks filled with seawater to a depth of 50 cm (maintained at 25 °C and a salinity of 24 ppt). Each mesocosm contained an X-shaped oyster reef (4 arms, each 55 cm long by 10 cm wide by 10 cm tall) over a 5-cm layer of sand, with a gap between reef arms for a resource patch at the center of the tank (Fig. 1B). Oysters used in the construction of artificial reefs were collected from nearby

marshes, shucked, bleached, rinsed, sun dried for approximately 2 weeks, and then anchored together using cable ties. This design mimicked natural reefs (Fig. 1C) and allowed us to more readily track the position of drills throughout the experiment.

Since we did not have enough tanks to include every unique treatment during each experimental run, we completely randomized treatments among the 6 tanks and 32 cycles. During each trial, we first added live oysters to the central resource patch. Although the number of live oysters differed among treatments, we maintained a constant shell volume by adding dead shell in the '0' and '3' oyster treatments as needed. Next, we placed a 10-kg weight within the resource patch, on which we tethered a stone crab in the 'predator-present' treatment (Fig. 1D). Tethers were 12 cm long, and restricted the crab to a nearly stationary position. Because stone crabs spend most of their time in burrows and are typically observed to be stationary when outside their burrows (Powell and Gunter, 1968; Lindberg and Marshall, 1984), we think this manipulation was appropriate. Finally, we placed 10 individually marked drills (2 or 3 drills on each oyster reef arm) 30-cm away from the center of the mesocosm (i.e., risk-reward patch). The numbers of oysters, crabs and drills used in these trials reflect natural densities in the northern Gulf of Mexico (Gregalis et al., 2008).

Drills were allowed to acclimate in the tank for 1 h before observations were made. Then, we recorded the position of each drill every 60 min for 8 h. To quantitatively document the position of drills, we used a clear Plexiglas sheet on which we drew concentric circles at every 2.5 cm radiating out from the central risk-reward patch. During each observation period, we place this sheet over mesocosm tanks so that the center of the Plexiglas and tank were aligned (Fig. 1B). Using this circular grid, observations were made by looking down a weighted string to record the position of each drill relative to (distance from) the central patch. We also recorded whether each drill was on live oyster, the artificial reef matrix, sand, the tank walls, or within 2.5 cm of another drill. After the eighth observation of drill locations, we stopped the experiment and returned all animals to a nearby marsh.

2.4. Statistical analyses

Our experiment produced 15,360 observations on the foraging behavior of 1,920 drills. We collapsed these data by averaging the position data from each set of 10 drills run together to produce a single behavioral (distance) measure for each mesocosm during each observation period. Subsequently, we ran a 3-way repeated-measures analysis of variance (ANOVA) to determine how predator presence, resource availability, and starvation affected the foraging decisions of drills over time (distance to central patch). We utilized a repeated-measure design since we did not assume that serial measurements were independent of each other. These data passed tests of normality and homoscedasticity, so no data transformations were required prior to analyses. However, our data failed the assumption of sphericity regarding the overall variance–covariance data matrix. Therefore, we used the Greenhouse–Geisser epsilon correction to adjust the degrees-of-freedom allowed in our statistical model (Quinn and Keough, 2002). Similarly, we utilized a 3-way repeated-measures analysis of variance (ANOVA) to determine how predator presence, resource availability, and starvation affected the social behaviors of drills over time (aggregation). For this analysis, we tallied the number of drills found within 2.5 cm of another drill during each time interval of each trial. Again, we were able to conduct these analyses on untransformed data, and utilized a repeated-measure design. As before, we used epsilon-adjusted model outputs due to the lack of variance–covariance sphericity. Statistical tests were conducted using JMP 9.0.0 software (SAS Institute Inc.). Because each statistical analysis applied to separate and easily distinguishable hypotheses, we made no corrections to experiment-wise alpha (Moran, 2003).

3. Results

3.1. Foraging behaviors

The foraging behavior (i.e. habitat selection) of drills was interactively determined by resource availability, predation threat, and starvation level (Table 1; 3-way interaction $P = 0.007$, without further interaction with time). Additional interactions were observed between time, resource availability and predation threat ($P = 0.001$) as well as between time, resource availability and starvation level ($P = 0.009$). Although we acknowledge these two higher-order interactions with time, the magnitude of differences in the response of drills among treatments generally increased linearly through time (e.g. Fig. 2), strengthening statistical arguments regarding the importance of resource availability, predation threat, and starvation as determinants of drill behavior.

To streamline our presentation, we explain our interaction results among resource, predation and starvation factors as a series of pairwise descriptions that then build toward 3-way effects. Although all drills began our trials 30 cm away from the central risk-reward patch, drills presented some level of resource reward moved toward the center of the mesocosm by 4–15 cm while those presented no resource reward moved 3–10 cm away from the central patch over the course of the 8-hour experiment (Fig. 2A). Notably, these patterns held regardless of crab presence, although there was an important interaction between resource availability and predation threat. In treatments with some level of resource provided, drills responded to crab presence by selecting habitat 5–7 cm farther away from the central risk-reward patch relative to the crab absent treatments (measured after 8 h). Conversely, when no oysters were provided in the mesocosm, drills were notably closer to the central risk-reward patch (~33 cm away after 8 h) in the treatments that included a stone crab, relative to the treatments that did not (~40 cm away after 8 h; Fig. 2A).

The manipulation of starvation level further mediated the response of drills across gradients in resource availability and predation threat. When crabs were absent in mesocosms, drills moved toward the central patch if some oyster resource was provided, and by the end of the experiment were, on average, approximately 25 cm from the center of the mesocosm. Conversely, unstarved drills moved slightly away from the central patch when a crab was present in mesocosms, averaged across all treatments in which no live oysters were provided. This risk-avoidance behavior was not observed in treatments in which a crab was present and drills were starved for 14 days, regardless of resource provision (Fig. 2B). Rather, those drills
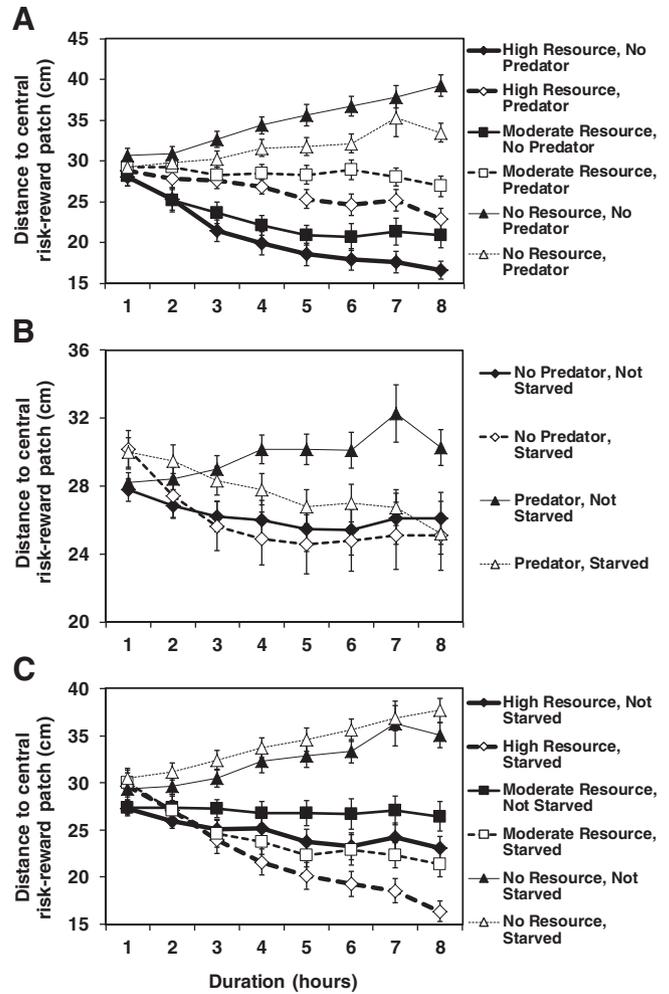
Fig. 2. Distribution of oyster drills in relation to a central risk-reward patch. Data represent the means ($\mu \pm 1$SE) of 16 replicate runs in which the positions of 10 oyster drills within experimental mesocosms were recorded every 60 min during 8-hour trials. We manipulated resource availability (live oyster density), predation threat (stone crab presence) and prey condition (starvation time) during these trials. Data are presented in a series of panels with respect to manipulations (within a 3-way design) of (A) resource availability*predation threat, (B) predation threat*prey condition, or (C) resource availability*prey condition.

Table 1
Results of a three-way repeated-measures ANOVA testing for effects of resource availability (live oyster density), predation threat (presence/absence of a stone crab) and prey condition (starvation time) on the foraging and risk-avoidance behaviors of oyster drills.

| Factor	DF	SS	MS	F-value	P-value
Resource	2	27,216.32	13,608.16	59.52	**<0.001**
Predator	1	2696.64	2696.64	11.79	**<0.001**
Starvation	1	569.89	569.89	2.49	0.116
Resource*predator	2	6316.07	3158.03	13.81	**<0.001**
Resource*starvation	2	1592.48	796.24	3.48	**0.033**
Predator*starvation	1	339.19	339.19	1.48	0.225
Resource*predator*starvation	2	2320.93	1160.47	5.08	**0.007**
Residuals	168	39,462.79	234.90		
Time	2.82	847.79	121.11	6.31	**<0.001**
Time*resource	5.633	7056.73	504.05	26.28	**<0.001**
Time*predator	2.82	529.09	75.58	3.94	**0.010**
Time*starvation	2.82	1169.82	167.12	8.71	**<0.001**
Time*resource*predator	5.633	1014.98	72.50	3.78	**0.001**
Time*resource*starvation	5.633	788.97	56.36	2.94	**0.009**
Time*predator*starvation	2.82	279.71	39.96	2.08	0.106
Time*resource*predator*starvation	5.633	153.73	10.98	0.57	0.742
Residuals	473.17	23,104.26	19.646		

Significant values ($P \leq 0.05$) and shown in **bold**.

selected habitat as if no crab was present, and by the end of the experiment were, on average, approximately 25 cm from the central risk-reward patch (25% closer than unstarved drills in the presence of a crab). We note, however, that the advance of starved drills toward the central patch was slower in treatments that included a crab relative to those that did not (Fig. 2B).

Finally, the presence of live oysters attracted drills toward the central patch over the course of 8-hour experimental runs, and this was true regardless of starvation level among drills (Fig. 2C). By the conclusion of the experiment, however, starved drills had moved nearly twice as close (i.e., 5–8 cm closer) to the central patch relative to unstarved drills when some level of resource was provided. In treatments with no live oysters, however, starved drills moved slightly farther away from the central patch (~37 cm) than did drills that were not starved, although the differences between group means were negligible based on standard error terms (Fig. 2C).

3.2. Social behaviors

Unlike our habitat selection results, we recorded few interactions among factors that regulated the social behaviors of drills (number aggregated) (Table 2). We did detect a significant ($P = 0.050$) interaction between all factors included in the repeated-measures ANOVA (Table 2). However, because time could have interacted with other treatments in a manner not interesting ecologically (i.e., the drills were most likely to be aggregated at time 1 because of how they were originally positioned in the mesocosms regardless of treatment type; Fig. 3A–B), we focus our results and discussion on the response(s) of drills to the independent experimental factors. Resource availability significantly affected drill behavior, as more individuals tended to aggregate as resources became less abundant (Fig. 3A,C; $P < 0.001$; no resource $= 0.92 \pm 0.04$ individuals aggregated, medium resource $= 0.77 \pm 0.15$ individuals aggregated, high resource $= 0.56 \pm 0.01$ individuals aggregated). In general, the presence of a predator also increased aggregation ($P = 0.022$), although the differences were numerically small on a raw scale (Fig. 3A–B; predator-present $= 0.82 \pm 0.12$ individuals aggregated, predator-absent $= 0.68 \pm 0.10$ individuals aggregated) Lastly, starvation level had a significant effect on aggregation ($P = 0.047$), as drills starved for 14 days tended to be somewhat less aggregated than drills starved for only 1 day (Fig. 3B–C; starved $= 0.67 \pm 0.12$ individuals aggregated, not starved 0.83 ± 0.16 individuals aggregated).
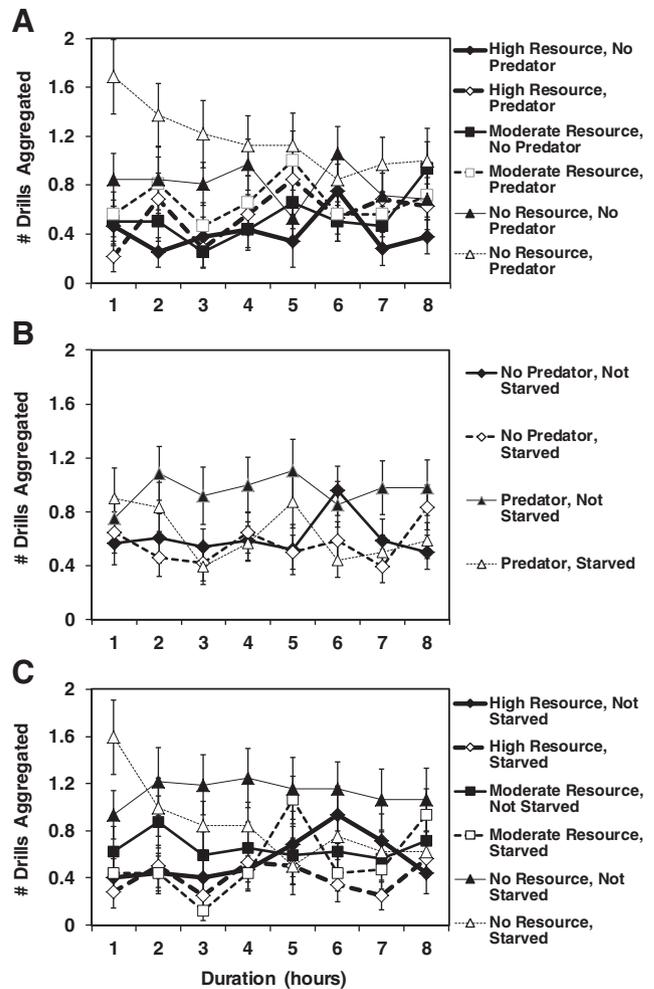
Fig. 3. Aggregation of oyster drills in relation to manipulations of resource availability (live oyster density), predation threat (presence/absence of a stone crab) and prey condition (starvation time). Data represent the means ($\mu \pm 1$ SE) of 16 replicate runs in which all drills within 2.5 cm of another drill were considered "aggregated". Drill positions were recorded every 60 min during 8-hour trials. Data are presented in a series of panels with respect to manipulations (within a 3-way design) of (A) resource availability*predation threat, (B) predation threat*prey condition, or (C) resource availability*prey condition.

Table 2
Results of a three-way repeated-measures ANOVA testing for effects of resource availability (live oyster density), predation threat (presence/absence of a stone crab) and prey condition (starvation time) on the social behaviors of oyster drills.

Factor	DF	SS	MS	F-value	P-value
Resource	2	71.80	35.90	10.91	**<0.001**
Predator	1	17.51	17.51	5.32	**0.022**
Starvation	1	13.13	13.13	3.99	**0.047**
Resource*predator	2	4.09	2.04	0.62	0.539
Resource*starvation	2	1.92	0.96	0.29	0.747
Predator*starvation	1	7.32	7.32	2.22	0.138
Resource*predator*starvation	2	1.73	0.86	0.26	0.770
Residuals	168	580.56	3.46		
Time	6.02	5.64	0.81	0.80	0.569
Time*resource	12.03	21.90	1.56	1.56	0.098
Time*predator	6.02	11.78	1.68	1.67	0.123
Time*starvation	6.02	9.73	1.39	1.38	0.217
Time*resource*predator	12.03	13.40	0.96	0.95	0.492
Time*resource*starvation	12.03	26.69	1.91	1.90	0.086
Time*predator*starvation	6.02	5.69	0.81	0.81	0.563
Time*resource*predator*starvation	12.03	26.55	1.90	1.89	**0.050**
Residuals	1011.36	1201.69	1.02		

Significant values ($P \leq 0.05$) and shown in **bold**.

4. Discussion

How prey balance the conflicting demands of predator-avoidance and successful foraging is of major interest to ecologists and behaviorists for its role in determining individual fitness and life-history strategies (Werner and Hall, 1988). To better understand how opportunistic scavenging affects these behaviors, we designed an experiment to assess the foraging tactics of oyster drills in the presence of a stone crab — a known predator and facilitator (Fodrie et al., 2008). In trials that included either a high or moderate abundance of live oysters, the foraging behavior of drills was predictable from previous studies of predator–prey games (e.g., Sih, 1980): drills shifted significantly farther away from a central risk-reward patch in the presence of predatory stone crabs. However, in trials run without live oysters for drills to forage on, drills in the predator-absent trials positioned themselves, on average, significantly farther from the central risk-reward patch than drills in the trials that included a stone crab. Notably, this complete reversal of behavior occurred despite the lack of an obvious incentive for drills to accept higher risk (i.e., proximity to a predator) in no-resource trials.

While drills in trials run without any live oysters moved slightly away from the central patch regardless of other factors, a null model would predict this outward drift in the absence of incentives to move inward due to the relative abundance of bottom habitat nearer (30% of total mesocosm habitat was inside the 30-cm radius) versus farther (70% of total mesocosm habitat was between the 30-cm and 55-cm radii) from the starting position of drills. Indeed, drill movements in the no-resource*no-predator treatments confirm this expectation. With this in mind, our most important result is the qualitative difference in drill behavior between predator-present and predator-free treatments.

Understanding the counterintuitive behavior of drills in low-resource trials requires accounting for the multiple interactions among drills and stone crabs. In particular, previous experimental work has demonstrated that stone crabs are among a suite of potential predators that also facilitate the foraging activities of drills by breeching the shells of shellfish (crabs and bivalves), thereby enhancing resource acquisition by opportunistic drills via scavenging (Daleo et al., 2005; Fodrie et al., 2008). Similar results have been observed with hungry flatworms that move towards cues from an Odonate (dragonfly larvae) predator in the absence of other food resources, perhaps exploring scavenging opportunities (Collins and Gerald, 2009). Although likely chemical in nature, we are uncertain whether drills were responding to cues indicative of crab presence *per se*, or perhaps residues on or digestive excretions from the stone crab indicative of prey resources.

Notably, we expected to see drills adopt more risky behaviors as live oyster density increased (a shared resource for drills and crabs) potentially due to diminished aggressiveness of stone crabs within food-rich patches (Berger-Tal et al., 2010) or due to greater opportunities of 'messy feeding' by crabs (Fodrie et al., 2008). Rather, our results suggest that drills rely on crabs more for resource provision as resource availability decreases or as time since last feeding increases, and that prey condition (Lima, 1988) was likely a more important determinant of foraging behaviors than was predator condition in our mesocosm experiments.

The foraging behaviors of oyster drills and stone crabs are a model marine system for examining how opportunistic scavenging affects the behavioral interactions among potential prey and predators. Scavenging behaviors (including kleptoparasitism) are likely more common in food webs than previously anticipated, and accounting for these energy-flow pathways can dramatically change our understanding of food-web dynamics in increasingly disturbed ecosystems (Wilson and Wolkovich, 2011). In our study system, drills and other gastropods are able to switch feeding modes from predation to scavenging by feeding on shellfish that have already been attacked and killed by crabs or shorebirds (e.g., Daleo et al., 2005). In terrestrial systems, similar dynamics exist between ungulate or feline prey, spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*). Hyenas compete with lions for food, but may also be attacked and killed by lions (Hunter et al., 2007). Furthermore, hyena groups are attracted to and benefit from carcasses (as are drills, Fodrie et al., 2008), which may bring them in to close contact with lions or other natural enemies (Trinkel and Kastberger, 2005). While our mesocosm experiments are among the first to specifically address how scavenging may lead to deviations from predicted risk-avoidance strategies of prey (i.e., movement toward potential predators in the absence of readily available food), the generality of our results should be tested within analogous scenarios such as the hyena–lion system. This is particularly true as it relates to our 'lower resource – enhanced risk behavior' finding. Moreover, examination of these disparate systems elucidates several additional factors that must be explored to better understand how combined predation and facilitation (i.e., provision of carcasses) affect prey behaviors. For example, the behavioral responses (perceived safety distance, fleeing, vigilance) of large mammalian carnivores to attempted kleptoparasitism is heavily impacted by the group size of each species, age structure of each species and past experiences of individuals with their enemies (Cooper, 1991; Durant, 2000; Pangle and Holekamp, 2010). At present, the roles these factors play in determining the risk-avoidance strategies of oyster drills are unknown.

Mesocosm results indicate that drills also utilized a 'safety in numbers' strategy to mitigate some of the risk they experienced by foraging in the vicinity of stone crabs, as drills were significantly more aggregated in treatments that included the predatory crab. Previously, Brown and Alexander (1994) documented that drills, which must excavate small holes in oyster shells to feed, routinely attack large (>70 g wet mass) individual oysters in groups even though the per capita feeding of individual drills decreases during group foraging (measured as tissue consumed per oyster attacked). To explain these findings, Brown and Alexander (1994) suggested several possible mechanisms, but did not consider the role that vigilance and predator-avoidance may play in group foraging behaviors. During attacks on larger oysters, which can take more than a day to complete (Brown and Richardson, 1987), drills are exposed to a host of predators including stone crabs (sensu Wirsing et al., 2007) over scales often less than 1 m (as used in our mesocosm tanks). We hypothesize that group foraging allows each individual drill to maximize the ratio between energy return and time investment (as well as reduce variability in acquisition time under low/no resource conditions; Caraco, 1981), and therefore, group foraging represents a predator-avoidance strategy (Skilleter and Peterson, 1994; Soto et al., 2005). Additionally, group foraging may aid in the detection of predators or resources (as aggregation increased as resource availability decreased) through the social transmission of chemical or mechanical cues, as well as a means of spreading risk within the group (Heithaus, 2005; Skilleter and Peterson, 1994). Whereas group size is ultimately a balance between reduced risk and increased intraspecific competition, it was notable that starved drills were somewhat less aggregated than drills that were not starved for 14 days — perhaps indicating that the behaviors of hungry drills were determined by the immediate need to maximize individual resource acquisition and accept an even riskier foraging strategy (sensu Janson, 1988).

Given that oyster drills and stone crabs co-occur over small scales (~1 m²) and have daily ranges over similarly small distances, we expect that our press-style mesocosm trials are representative of typical predator–prey encounter rates in the wild. Furthermore, the magnitude of differences in drill habitat selection (5–25 cm) are highly relevant for assessing predation risk for animals that typically move only a few body lengths per minute. However, we also acknowledge several potential biases. For instance, our trials were run with predatory stone crabs tethered within a central reward patch. Several studies

have noted how the distribution of species pairs differs in trials with or without the location of the predator fixed (reviewed in Luttbeg and Sih, 2004). Conversely, theoretical treatments suggest that predators should be distributed to match the abundance of the resource (oysters) sought by their prey (drills and oysters). As such, our manipulation was a logical simplification of nature by placing crabs within the single, central resource patch (Sih, 1998). Furthermore, stone crabs are often sedentary for long (hours-days) periods (Beck, 1995), and are therefore amendable to tethering. A second notable concern we acknowledge relates to the transmission and potential saturation of olfactory cues within enclosed, recirculating mesocosm tanks. Olfactory cues are critically important for the detection and tracking of prey by predatory crabs and gastropods (Ferner et al., 2008; Smee and Weissburg, 2008). These cues are significantly affected by both water flow (Finelli et al., 2000; clearly, mesocosm tanks wouldn't permit wind- or tide-driven currents) and bottom habitat complexity (Ferner et al., 2008; which we did not vary, but attempted to use representative habitat structure). Particularly if cue saturation became a problem, drills may have had difficulty gauging spatial gradients in risk and resource levels. We expect this is a conservative error that would have resulted in statistically weaker, rather than stronger, results. Lastly, drills were clearly still responding to the mesocosm conditions they encountered even at the conclusion of our 8-hour experiments, as patterns of habitat selection had not yet stabilized. This suggests that the responses of drills to pulsed (i.e., roving finfishes) and pressed (stone crabs) predation threats could be qualitatively different, and therefore predator identity is important for understanding the risk-avoidance behaviors of these gastropods. We do think that 8-hour press experiments are a relevant time scale for examining oyster drill–crab encounters within oyster reefs based on the general mobility of these species and the scales over which they are distributed on oyster reefs (Gregalis et al., 2008). We also note that we observed no differences in the response of drills either preconditioned for 24 h with a stone crab, or not preconditioned, prior to their introduction in to mesocosm tanks (see methods). Therefore, it is unlikely that we would have observed fundamentally different results had we allowed the experiment to run longer.

Our manipulations and findings also contribute to the debate regarding the relative importance of consumptive (CE) and nonconsumptive effects (NCE) as top-down drivers of community ecology. Some recent reviews have concluded that due to the strong fitness incentive for prey to avoid risky behaviors, the mere threat of predation in the ambit of prey can have impacts that are stronger than direct consumption (Dill et al., 2003; Preisser et al., 2005). However, past studies and our new data indicate that hungrier, more desperate prey accept more risky foraging behaviors as revealed by their distance to predators, or via decreased vigilance (Kotler et al., 2004; Lima, 1995). In our mesocosm trials, the potential for behavior suppression of drill foraging decreased as resource abundance decreased (Luttbeg et al., 2003). Furthermore, drills starved for 2 weeks actually behaved as though they were in a predator-free environment regardless of whether treatments included a stone crab or not (i.e., as resource acquisition became more important to the prey, fear of predation became relatively less important). In this scenario, there appeared to be little behavioral suppression (NCEs) of drill foraging, as well an enhanced likelihood for direct encounters between oyster drills and stone crabs (CEs). With this in mind, we expect that short-term, press experiments could overestimate the importance of NCEs if they fail to account for changes in prey behaviors that can result from temporal shifts in prey condition (i.e., hunger). More broadly, Luttbeg et al. (2003) also found that behavioral compensation of prey over extended periods of time (weeks-seasons) can diminish or completely negate the relative importance of NCEs measured during an experiment or a portion of the year.

Enacting ecosystem-based management to conserve natural resources will require renewed focus on quantifying natural mortalities

(e.g., predator–prey dynamics), and this includes analyses of the sophisticated foraging games performed by species pairs (Tyrell et al., 2011). For instance, calculating natural mortality of eastern oysters remains difficult because we do not yet fully understand the numerically or behaviorally mediated indirect effects on oyster mortality that result from complex interactions among a diverse suite of competing or synergistic predators (e.g., oyster drills and stone crabs, among others). Because oyster reefs are highly modified and stressed systems worldwide (Beck et al., 2011), complex behaviors related to opportunistic scavenging are likely to be important for understanding population fitness within the reef community (Wilson and Wolkovich, 2011). Drawing from our manipulative experiments, field-based data are critical to better understand exactly how drills manage the conflicting demands of prey acquisition and predator-avoidance in the presence of stone crabs (a potential predator, but also a facilitator), and over what temporal and spatial scales can we draw correlations between stone crab density, oyster drill density, oyster drill mortality, and eastern oyster mortality. This is particularly important in order to account for flow-mediated olfactory cues among species that were absent in our mesocosm experiments. Lastly, our data highlight how even species engaged in predatory or competitive exchanges may simultaneously be connected through positive interactions that significantly affect behavioral and trophic ecology (Bruno et al., 2003). Although applied to an estuarine reef ecosystem here, this is broadly applicable to many other environments to understand the mechanisms driving risk allocation of opportunistic scavengers and subsequent ecosystem effects.

References

Beck, M.W., 1995. Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. Ecology 76, 968–980.

Beck, M.W., et al., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61, 107–116.

Bednekoff, P.A., Lima, S.L., 1998. Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. Procl. R. Soc. Lond. B Biol. Sci. 265, 2021–2026.

Berger-Tal, O., Mukherjee, S., Kotler, B.P., Brown, J.S., 2010. Complex state-dependent games between owls and gerbils. Ecol. Lett. 13, 302–310.

Brown, K.M., Alexander Jr., J.E., 1994. Group foraging in a marine gastropod predator: benefits and costs to individuals. Mar. Ecol. Prog. Ser. 112, 97–105.

Brown, K.M., Haight, E.S., 1992. The foraging ecology of the Gulf of Mexico stone crab *Menippe adina* (Williams et Felder). J. Exp. Mar. Biol. Ecol. 160, 67–80.

Brown, K.M., Richardson, T.D., 1987. Foraging ecology of the southern oyster drill *Thais haemastoma* (Gray): constraints on prey choice. J. Exp. Mar. Biol. Ecol. 114, 123–141.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18, 119–125.

Butler, P.A., 1985. Synoptic Review of the Literature on the Southern Oyster Drill, *Thais Haemastoma* Floridana. National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Caraco, T., 1981. Risk sensitivity and foraging groups. Ecology 62, 527–531.

Collins, A.M., Gerald, G.W., 2009. Attraction of flatworms at various hunger levels toward cues from an Odonate predator. Ethology 115, 449–456.

Cooper, S.M., 1991. Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyenas. Afr. J. Ecol. 29, 130–136.

Daleo, P., Escapa, M., Isacch, J.P., Ribeiro, P., Iribarne, O., 2005. Trophic facilitation by the oystercatcher *Haematopus palliatus* Temminick on the scavenger snail *Buccinanops globulosum* Kiener in a Patagonian bay. J. Exp. Mar. Biol. Ecol. 325, 27–34.

Dill, L.M., Fraser, A.H.G., 1997. The worm re-turns: hiding behavior of a tube-dwelling marine polychaete, *Serpula vermicularis*. Behav. Ecol. 8, 186.

Dill, L.M., Heithaus, M.R., Walters, C.J., 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84, 1151–1157.

Durant, S.M., 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. Behav. Ecol. 11, 624–632.

Ferner, M.C., Smee, D.L., Weissburg, M.J., 2008. Habitat complexity alters lethal and non-lethal olfactory interactions between predators and prey. Mar. Ecol. Prog. Ser. 374, 13–22.

Finelli, C.M., Pentcheff, N.D., Zimmer, R.K., Wethey, D.S., 2000. Physical constraints on ecological processes: a field test of odor-mediated foraging. Ecology 81, 784–797.

Fodrie, F.J., Kenworthy, M.D., Powers, S.P., 2008. Unintended facilitation between marine consumers generates enhanced mortality for their shared prey. Ecology 89, 3268–3274.

Grabowski, J.H., Kimbro, D.L., 2005. Predator-avoidance behavior extends trophic cascades to refuge habitats. Ecology 86, 1312–1319.

Gregalis, K.C., Powers, S.P., Heck Jr., K.L., 2008. Restoration of oyster reefs along a bio-physical gradient in Mobile Bay, Alabama. J. Shellfish. Res. 27, 1163–1169.

Heck Jr., K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser. 253, 123–136.

Heithaus, M.R., 2005. Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. Mar. Biol. 147, 27–35.

Heithaus, M.R., Dill, L.M., 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83, 480–491.

Holt, R.D., Huxel, G.R., 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. Ecology 88, 2706–2712.

Hunter, J.S., Durant, S.M., Caro, T.M., 2007. To flee or not to flee: predator avoidance by cheetahs at kills. Behav. Ecol. Sociobiol. 61, 1033–1042.

Janson, C.H., 1988. Intra-specific food competition and primate social structure: a synthesis. Behaviour 105, 1–17.

Janson, C.H., Goldsmith, M.L., 1995. Predicting group size in primates: foraging costs and predation risks. Behav. Ecol. 6, 326–336.

Kotler, B.P., Brown, J.S., Bouskila, A., 2004. Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. Ecology 85, 917–922.

Lima, S.L., 1988. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. Oikos 53, 3–11.

Lima, S.L., 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim. Behav. 49, 11–20.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Lindberg, W.J., Marshall, M.J., 1984. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida): Stone Crab. Biological Report 82. US Department of the Interior, Fish and Wildlife Service.

Luttbeg, B., Sih, A., 2004. Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk. Isr. J. Zool. 50, 233–254.

Luttbeg, B., Rowe, L., Mangel, M., 2003. Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. Ecology 84, 1140–1150.

MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. Am. Nat. 100, 603–609.

Mangel, M., Clark, C.W., 1986. Towards a unified foraging theory. Ecology 67, 1127–1138.

Moran, M.D., 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100, 403–405.

Pangle, W.M., Holekamp, K.E., 2010. Age-related variation in threat-sensitive behavior exhibited by spotted hyenas: observational and experimental approaches. Behaviour 147, 1009–1033.

Polis, G.A., Holt, R.D., 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol. Evol. 7, 151–154.

Powell, E.H., Gunter, G., 1968. Observations on the stone crab, *Menippe mercenaria* Say, in the vicinity of Port Aransas, Texas. Gulf Res. Rep. 2, 285–299.

Preisser, E.L., Bolnick, D.I., Benard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86, 501–509.

Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Lape, J.C.P., 2009. Intraguild predation in a structured habitat: distinguishing multiple-predator effects from competitor effects. Ecology 90, 2434–2443.

Sih, A., 1980. Optimal behavior: can foragers balance two conflicting demands? Science 210, 1041–1043.

Sih, A., 1997. To hide or not to hide? Refuge use in a fluctuating environment. Trends Ecol. Evol. 12, 375–376.

Sih, A., 1998. Game theory and predator–prey response races. In: Dugatkin, L.A., Reeve, H.K. (Eds.), Advances in Game Theory and the Study of Animal Behavior. Oxford University Press, Oxford, pp. 221–238.

Skilleter, G.A., Peterson, C.H., 1994. Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. Oecologia 100, 268–278.

Smee, D.L., Weissburg, M.J., 2008. Heightened prey responses in risky habitats: predation pressure increases prey sensitivity to predation risk. Mar. Ecol. Prog. Ser. 363, 39–50.

Soto, R.E., Castilla, J.C., Bozinovic, F., 2005. The impact of physiological demands on foraging decisions under predation risk: a test with the whelk *Acanthina monodon*. Ethology 111, 1044–1049.

Trinkel, M., Kastberger, G., 2005. Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. Afr. J. Ecol. 43, 220–224.

Tyrrell, M.C., Link, J.S., Moustahfid, H., 2011. The importance of including predation in fish population models: implications for biological reference points. Fish. Res. 108, 1–8.

Wainwright, P.C., Westneat, M.W., Bellwood, D.R., 2000. Linking feeding behavior and jaw mechanics in fishes. In: Domenici, P., Blake, R. (Eds.), Biomechanics in animal behavior. BIOS Scientific, Oxford, pp. 207–221.

Werner, E.E., Hall, D.J., 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69, 1352–1366.

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: how carnivores and carrion structure communities. Trends Ecol. Evol. 26, 129–135.

Wirsing, A., Heithaus, M., Dill, L., 2007. Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger. Anim. Behav. 74, 1085–1091.