Body size and vigilance mediate asymmetric interference competition for food in fish larvae

Shinnosuke Nakayama and Lee A. Fuiman
Department of Marine Science, Marine Science Institute, the University of Texas at Austin,
750 Channel View Drive, Port Aransas, TX 78373, USA

Interference competition for food is difficult to measure because feeding rates altered by behavioral interactions of competitors are confounded by exploitative competition, the depletion of food over time. We quantified the magnitude of interference competition between individuals using a combination of experiments and computer simulations, which allowed us to remove the effect of exploitative competition. We used this approach to test the hypothesis that interference competition reduces feeding rates of young red drum (*Sciaenops ocellatus*) and that the magnitude of interference competition is related to phenotypic traits, such as the sizes of competitors and behavioral interactions between them. In laboratory experiments, we measured prey consumption and behavioral interactions between 2 fish of different sizes (7- to 25-mm standard length). We used computer simulations to remove the effects of exploitative competition and found that prey consumed by focal individuals decreased in the presence of competitors due to interference competition and that the decrease was stronger when focal individuals were smaller than competitors and when the competing individuals were generally larger. We also found greater impairment of prey consumption by focal individuals when they were more vigilant (more reactive) to the presence of competitors. A better understanding of the magnitude of asymmetry in interference competition has important implications for understanding population dynamics, spatial distribution, and reproductive strategies of many organisms. This is the first study to quantify the asymmetry in interference competition when prey density changes over time. *Key words:* aggression, body size, exploitative competition, interference competition, red drum, *Sciaenops ocellatus*, vigilance. *[Behav Ecol 21:708–713 (2010)]*

Interference competition is defined as direct interactions between organisms that decrease use of the common resources (Park 1954). In most organisms, interference competition takes place through agonistic behavioral interactions (Kotrschal et al. 1993; Smallegange et al. 2006). In food competition, these behavioral interactions reduce feeding rates by sacrificing the time allocable to feeding (Smallegange et al. 2006) and result in additional energetic costs from agonistic interactions (Briffa and Sneddon 2007). However, when individuals compete for food, feeding rates depend not only on interference with competitors but also on an individual's feeding efficiency in the absence of a competitor. Individuals utilizing a common finite food resource can also affect feeding rates of other individuals indirectly by decreasing food availability, and individuals with higher feeding efficiencies (e.g., higher search rate, higher capture success, shorter food handling time) can obtain more food without interference. This exploitative competition is inevitable unless food does not deplete over time.

Interference competition is ubiquitous in nature (Schoener 1983), and hence, its significance should be considered when attempting to understand and predict population dynamics and the spatial distribution of organisms. Many theoretical studies have tried to incorporate interference competition into the ideal free distribution (IFD) models to find its effects on the spatial distribution of consumers either when competitors have equal competitive weights (Sutherland 1983; Moody and Houston 1995; Tregenza, Parker, and Thompson 1996; van der Meer and Ens 1997) or when competitive weights

differ among consumers (Parker and Sutherland 1986; Sutherland and Parker 1992; Tregenza, Hack, and Thompson 1996; van der Meer 1997; Grand and Dill 1999; Humphries et al. 2001). To test the effects of interference competition, we need to know relative competitive weights of consumers for all possible interfering phenotypes within the habitat. However, we are aware of no study that has measured them adequately because of the difficulty in disentangling direct (interference) competition and indirect (exploitative) competition.

Differences in feeding efficiency among competitors cannot be neglected in organisms that span a wide range of body sizes and compete for common food because body size is a key determinant of feeding efficiency in many animals (Persson et al. 1998). Therefore, body size, size-related feeding efficiency, and the magnitude of exploitative competition must be taken into account in order to detect interference competition when competitors vary in size. Few studies have separated the 2 kinds of competition. Smallegange et al. (2006) accomplished this for shore crabs (*Carcinus maenas*) of a single size class by replenishing consumed prey. However, previous studies have failed to adequately separate interference competition from exploitative competition when competition is asymmetric and resources decrease over time, leading to uncertainty about the magnitude of asymmetry in interference competition (Werner 1994; Post et al. 1999).

Here, we developed a method to separate interference competition from exploitative competition using a combination of experiments and computer simulations and investigated whether the size relationship and behavioral interactions between competitors explain the magnitude of interference competition in larval red drum (*Sciaenops ocellatus*). Red drum is a subtropical and temperate coastal fish. Its larvae settle in structured habitats, such as sea grass meadows or oyster beds. They mainly prey upon copepods and mysids (Soto et al. 1998). Because it spawns many times over a 2-month

reproductive season, various sizes of young red drum (about 7- to 25-mm standard length) co-occur in settlement habitats, where the density of settlers can be locally high (Rooker et al. 1999). These conditions may negatively affect the feeding rates of small larvae through interference competition because larger larvae are aggressive to smaller larvae (Nakayama et al. 2009). Specifically, we hypothesized that the size relationship with conspecific competitors and behavioral interactions between them explain the magnitude interference competition, measured as the decrease of prey consumed by a fish. To quantify the magnitude of interference competition, we measured the number of prey consumed by a focal fish in the presence of a conspecific competitor and removed the effect of exploitative competition using numerical simulations based on the feeding efficiencies of 2 competing fish. This method allowed us to test any size combination of competing individuals and, thus, to see more clearly the effects of body size and behavioral interactions between competitors on the magnitude of interference competition.

MATERIAL AND METHODS

We studied interference competition by combining computer simulations with results from laboratory experiments. First, we obtained the relationship between foraging efficiency and body size by measuring prey search rate and handling time of an individual fish in the absence of a competitor. Second, in the presence of a competitor, we measured the number of prey consumed by a focal fish and behavioral interactions between them. Then, we simulated the expected number of prey consumed by the focal fish in the absence of interference from the competitor using size-dependent foraging efficiencies of the focal fish and the competitor. We compared the observed and simulated number of prey consumed by the focal fish to assess the magnitude of interference competition and examined how the size relationship and behavioral interactions between the focal fish and competitors affected the magnitude of interference competition.

Foraging efficiency without competition

Red drum eggs were collected from wild-caught captive-spawned adults at the Coastal Conservation Association/Central Power and Light Marine Development Center (Corpus Christi, TX). Three batches of eggs were collected (12 and 24 September 2007 and 22 October 2007) and reared under the same conditions, resulting in a wide variety of sizes of larvae for the experiment due to the different ages of fish among batches and different growth rates among individuals within batches. Spawning was induced naturally by manipulating temperature and photoperiod. Eggs were spawned at night, collected the next morning, and transported to the University of Texas Marine Science Institute (Port Aransas, TX).

Approximately 5000 viable eggs from each batch were put into a 60-l fiberglass rearing tank (60 cm in diameter at maximum). Mean temperature and salinity (± standard deviation [SD]) were 26.9 ± 0.3 °C and 27.5 ± 0.7 ppt, respectively, and illumination was set to a daily cycle of 12:12 light:dark. Eggs hatched the next day. Fish were fed 400 000 rotifers (*Brachionus* spp.) from days 2–11 after hatching and 60 000 *Artemia salina* nauplii from day 10 onward within 2 h after lights on, following a feeding protocol based on the density of red drum larvae (Lazo et al. 2000). Both diets were enriched with Algamac-2000 (Aquafauna Bio-Marine, Inc., Hawthorne, CA) for 12 h prior to feeding.

The experiment was designed under the hypothesis that intervals of prey captures by isolated individual fish were explained by their body size (developmental state) and the number of prey remaining in the tank. At 1800 h on the day before the experiment, 6 fish were taken randomly from the 3 rearing tanks using a dip net; fish with apparently abnormal behavior were avoided. The selected fish were put individually into 1-l plastic containers without food overnight to ensure an equivalent feeding state among all fish at the beginning of the experiment. Temperature was kept at 27.0 ± 0.5 °C (mean ± SD) using a water bath, and salinity was 26.9 ± 0.7 ppt.

The following day, 1 fish was put into a 15-l glass tank (50 × 20 cm and 15-cm high), which contained a heater and weak aeration. After 10 min, *Artemia* nauplii were delivered over the surface of the water using a pipette. The number of prey introduced was 45, 60, 90, 150, 600, or 1200 (density: 3, 4, 6, 10, 40, and 80 l^{-1}, respectively). Aeration quickly dispersed the *Artemia* evenly through the water after they were introduced. For each initial prey density, the intervals of prey captures (s) were recorded from the 1st to 10th capture (9 intervals). After the 10th capture, the fish was removed from the tank using a dip net and put back into the 1-l plastic container without food. This procedure was repeated for the same individual with 6 different prey densities at 1-h intervals. The sequence of prey density offered was randomized for each fish, and no fish showed signs of satiation during the experiment. The experiment was conducted from 0900 to 1900 h local time. Temperature and salinity in the tank were kept at 26.8 ± 0.6 °C and 26.1 ± 1.1 ppt, respectively.

In all, 76 fish were used for the experiment, ranging in standard length from 6.1 to 25.7 mm and ranging in age from 18- to 63-day posthatching. The interval between prey captures was described as a function of body size (standard length) and the number of prey remaining in the tank using a generalized linear mixed model (glmmPQL in MASS package ver7.35 of R; Venables and Ripley 2002). Individuals were specified as a random effect in the model. The dependent variable was assumed to have a Gamma distribution and was linked to the linear predictors with a logarithmic function. Body size and the number of prey remaining in the tank were log transformed to achieve a better fit to the model. Coefficients were evaluated using penalized quasi-likelihood estimation.

Competition experiment

Red drum eggs were collected and raised in the same way as in the previous experiment (6 batches spawned from 10 October to 24 November 2007). Each batch of eggs was raised in a separate rearing tank. At 1800 h on the day before the experiment, 12 fish were selected from the 2 rearing tanks, 6 fish from each. Fish were kept individually in a 1-l plastic container in the same way as the individual foraging efficiency experiment (26.8 ± 0.4 °C and 27.1 ± 0.7 ppt).

The following day, 2 fish were paired up so that each fish came from a different rearing tank and thus from a different batch. One fish was randomly assigned as a focal fish and the other as a competitor. A pair of fish was gently put into a 15-l glass tank (50 × 20 cm and 15-cm high), which contained a heater and weak aeration, and the interactive behavior of the focal fish was recorded for 15 min. Interactive behavior was categorized as 1) aggression performed, 2) aggression received, or 3) vigilance. We defined aggression performed as a focal fish displacing or attacking a competitor from behind with a rapid acceleration. In all cases, a competitor responded by accelerating away from the focal fish. Aggression received was recorded when a focal fish received aggressive behavior from the competitor. Vigilance was defined as a focal fish accelerating away from a nearby competitor without being chased or attacked.

After 15 min, 45 prey (*Artemia* nauplii) were gently added to the tank using a pipette, and the number of prey captured by

the focal fish and interactive behavior of the focal fish were recorded for 15 min. Aeration dispersed the prey evenly through the water quickly after they were introduced. The number of prey was chosen so that 2 fish could keep foraging without being satiated during the experiment. More than a half of the prey were consumed by the 2 fish within 15 min (26.3 ± 0.6 prey, mean ± SD).

In all, 120 pairs of fish were tested. Focal fish used for the experiment ranged from 6.0- to 24.7-mm standard length and from 16- to 56-day posthatching. The difference in length of the 2 fish (focal fish minus competitor) ranged from −15.1 to +13.4 mm and the difference in age ranged from −28 to +28 days old.

Isolation of interference competition

We estimated the number of prey a focal fish would capture in the absence of interference competition (i.e., exploitative competition only) by numerical simulation using the Gillespie algorithm (Gillespie 1977). First, assuming that prey were evenly distributed in the water, we calculated for both a focal fish and a competitor the expected interval (time) to encounter the first prey, using the number of prey remaining in the tank (45) and their body sizes (see "Foraging efficiency without competition"). Then, the inverse of the expected interval was taken as the instantaneous prey capture rate (r_f and r_c for a focal fish and the competitor, respectively). From the prey capture rates of each fish (r_f and r_c), the probability of the focal fish capturing the first prey earlier than the competitor (P_f) was calculated as:

$$P_f = \frac{r_f}{r_f + r_c}.$$

A random number between 0 and 1 was generated from a uniform distribution, and the first prey capture was assigned to the focal fish if P_f was greater than that random number; if not, the competitor encountered prey first. The time to the first prey capture was drawn randomly from an exponential distribution with $\lambda = r_f + r_c$. When either the focal fish or the competitor captured the prey, r_f and r_c were updated with the decreased number of prey remaining in the tank (now 44), and the updated P_f was compared with a new random number to decide whether the focal fish or the competitor captured the second prey. The time from the first to the second prey capture was drawn randomly from an exponential distribution with the updated λ.

The simulation was continued until either all prey were captured or 15 min of simulation time elapsed by updating r_f and r_c every time the number of prey remaining in the tank was decreased. The simulation was repeated 1000 times for each pair, and the average number of prey consumed by each focal fish was calculated. We simulated the expected number of prey captured by a focal fish in all 120 pairs used in the food competition experiment.

Statistical analysis

A multivariate linear regression was applied to explore the effects of body size and behavioral interactions on the observed number of prey captured by focal fish. The same approach was adopted to see the effects of body size and interactive behavior on the magnitude of interference competition that the focal fish experienced. The magnitude of interference competition was quantified as the decrease in the number of prey captured by focal fish due to interference competition, calculated by subtracting the observed number of prey captured by focal fish from the simulated number (Figure 1).
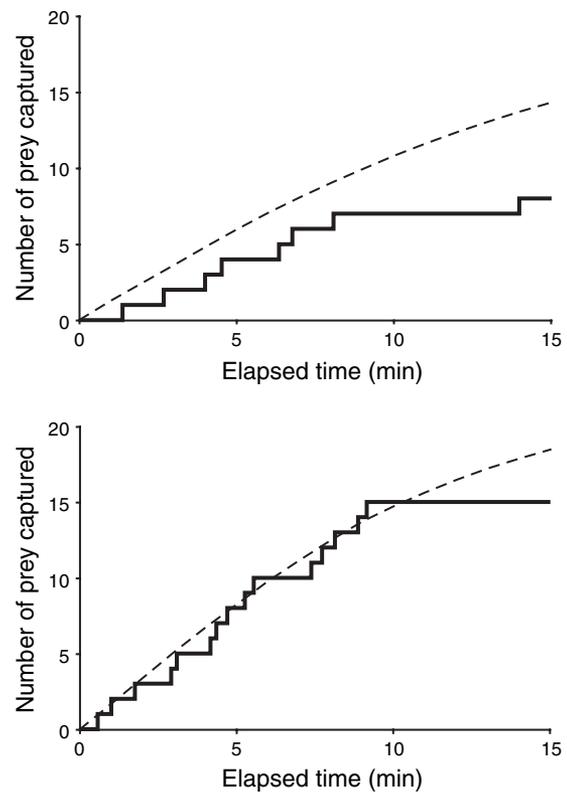

Figure 1
Representative change in number of prey captured by a focal fish over time. Dashed lines indicate the mean of 1000 numerical simulations (exploitative competition only). Solid lines indicate the observed number of prey captured by a focal fish (exploitative plus interference). Upper: focal = 8.7 mm and competitor = 13.4 mm. Lower: focal = 13.6 mm and competitor = 9.4 mm. The magnitude of interference competition was calculated as the simulated number of prey consumed minus the observed number.

Five explanatory variables were used to understand variations in the observed number of prey captured and the magnitude of interference competition. Two of them were morphological traits: difference in standard length between the 2 fish (focal fish minus competitor) and mean length of the 2 fish (indicative of developmental state; Fuiman et al. 1998). The other 3 explanatory variables were counts of interactive behavior of a focal fish during 30 min of observation (aggression performed, aggression received, and vigilance). Behavioral variables (counts) were normalized by log transformation after adding 1. The statistical interactions of these 5 explanatory variables (all possible combinations) were also included. The number of parameters in the multivariate model was reduced using the Akaike information criterion (Akaike 1974). All statistical analyses were performed using R (v2.10.1; http://www.r-project.org). Statistical significance was determined at $\alpha = 0.05$. Numerical simulations were performed using Fortran programming language.

RESULTS

The generalized linear mixed model showed that the interval between prey capture was explained by the body size of a fish and the number of prey remaining in the tank (Table 1). The interval decreased as the body size increased ($P < 0.001$) and increased as the number of prey in the tank decreased ($P < 0.001$).

Table 1

Generalized linear mixed model for the interval between consecutive prey captures

Source	Coefficient	SE	df	t	P
Intercept	7.58	0.43	4027	17.71	<0.001
Log_e(length)	−0.72	0.17	74	−4.19	<0.001
Log_e(number of prey remaining)	−0.59	0.02	4027	−39.21	<0.001

df, Degrees of freedom; SE, standard error. Individual fish were included as a random effect. The model describes the natural logarithm of interval.

The numerical simulation (exploitative competition only) showed that the number of prey consumed by a focal fish was explained by the size difference, mean size, and the interaction between size difference and mean size ($F_{3,116} = 206.5$, $P < 0.001$, adjusted $R^2 = 0.838$). The observed number of prey consumed by a focal fish, which was affected by both exploitative competition and interference competition, was explained by the size difference, mean size, and vigilance ($F_{4,115} = 31.37$, $P < 0.001$, adjusted $R^2 = 0.505$; Table 2). The statistical interaction between size difference and mean size was retained in the model after applying parameter reduction by the Akaike information criterion, but it was not significant ($P = 0.071$).

Five variables were retained in the model to explain the magnitude of interference competition, after parameter reduction by the Akaike information criterion ($F_{3,116} = 19.72$, $P < 0.001$, adjusted $R^2 = 0.321$; Table 2). The magnitude of interference competition became stronger when the focal fish were smaller than their competitors ($P < 0.001$) and when both fish were developed more (i.e., mean length of the focal fish and competitors increased, $P = 0.007$). The magnitude of interference competition also became stronger when they exhibited more vigilance ($P < 0.001$). All other variables were excluded from the model.

DISCUSSION

Our results demonstrate the presence of asymmetric interference competition for food among red drum during their early life. This is the first study to quantify the asymmetry in interference competition when prey density changes over time. The magnitude of interference competition was mediated by morphological traits and behavioral interactions of competing individuals. Size differences between competitors led to asymmetric interference competition (different magnitude of interference competition depending on body size relative to a competitor), and the degree of the asymmetry changed with mean body size (developmental state) of competing individuals. Vigilant behavior negatively affected food consumption in addition to the effects of mean size and size difference. Focal fish suffered more from interference competition when 1) they were smaller than competitors, 2) both competing individuals were larger, and (3) they were more vigilant against competitors.

What causes asymmetry in the magnitude of interference competition? If interference competition were caused by agonistic interactions alone, both participants would lose an equal amount of time allocable to feeding during the interactions. As a result, individuals with higher feeding efficiencies (shorter intervals between prey captures) would forfeit more prey than those with lower feeding efficiencies during the same amount of time lost to behavioral interaction. Under these circumstances, larger individuals should be deprived of more prey than smaller individuals because they have higher feeding efficiencies. However, our results showed the opposite trend: smaller individuals were deprived of more prey through interference competition than larger individuals (Table 2). These results indicate that the lost time allocable to feeding was asymmetric among competitors (van der Meer 1997), with more lost time for smaller individuals. Although a pair of larger individuals experienced the stronger interference competition than a pair of smaller individuals (Table 2), the larger reduction in prey capture in a pair of larger individuals would be simply because they can capture more prey without interference competition due to the shorter interval between prey captures (Table 1).

One possible cause of asymmetric lost time between competing individuals would be the difference in time to resume feeding behavior after aggressive interactions. Individuals that received aggressive behavior may take longer to resume feeding behavior than those that performed aggressive behavior. Our results of stronger interference experienced by smaller individuals would be because smaller individuals tend to receive aggressive behavior from the larger individuals more frequently than vice versa (Nakayama et al. 2009). The alternative cause could be differences among individuals in the degree of vigilance because vigilance is a one-way interaction, and no kleptoparasitism was observed during the experiment. Our finding that interference competition affects more vigilant individuals more strongly supports the idea that the

Table 2

Analysis of variance for the effect of size and behavioral interactions on the observed number of prey captured by a focal fish and the magnitude of interference competition using multivariate linear regressions

Source	Coefficient	df	SS	F	P
Observed number of prey captured by a focal fish					
Intercept	9.70				
Difference in length	1.31	1	1310.7	82.01	<0.001
Mean length	0.14	1	98.5	6.16	0.014
Vigilance	−3.48	1	543.2	33.99	<0.001
Difference in length × mean length	−0.05	1	53.1	3.33	0.071
Residuals		115	1837.9		
Interference competition					
Intercept	0.31				
Difference in length	−0.24	1	352.4	27.49	<0.001
Mean length	0.46	1	98.1	7.65	0.007
Vigilance	2.83	1	307.7	24.00	<0.001
Residuals		116	1486.9		

df, Degrees of freedom; SS, sum of squares. Model parameters were reduced using the Akaike information criterion.

magnitude of vigilance is the cause of asymmetric interference competition. Vigilance is known to affect feeding rates of wading birds by reducing time allocable to feeding (Vahl et al. 2005). When competitors differ in competitive ability, subordinate individuals become more vigilant to avoid fighting, which is associated with a higher risk of injury (Leimar et al. 1991) and more time lost for feeding (Smallegange et al. 2006). Whereas larger individuals in our experiments may have been less concerned about threats, smaller individuals may have spent more time for vigilance to avoid fights rather than foraging. Previously, we demonstrated that smaller individuals show vigilant behavior more often than larger individuals in this species (Nakayama et al. 2009). Fish may be able to assess a competitor's threat by detecting subtle hints of a competitor's aggressiveness, such as aggressive display (Ros et al. 2006) or chemical signals (Giaquinto and Volpato 1997), to avoid agonistic physical interactions. Although vigilance reduced prey consumed by the fish, individuals with high vigilance may benefit in growth if aggressive interactions have a higher energetic cost than the loss of foraging time. On the other hand, individuals that often exhibit escape behavior without being attacked or chased by conspecifics may increase predation risk because their elevated activity would attract predators (Fuiman and Magurran 1994; Minderman et al. 2006).

Our method of combining experiments and simulations allows us to investigate the magnitude of interference competition in pairs of any size combinations. Smith (1990) successfully separated interference competition from exploitative competition in larval salamanders by dividing the tank with a mesh that only allowed the prey to pass through but prevented physical interactions between salamanders. However, this method is difficult to apply when interference competition takes place through nonphysical interactions, such as vigilance or chemical substances. Our methods, on the other hand, can be applied to any mechanism of interference competition, such as the effects of competitor density and prey density, because the competing individuals interact freely in any manner. Several studies have measured interference competition using the Hassell and Varley (1969) model (Dolman 1995; Flaxman and deRoos 2007), but measuring the magnitude of interference competition is difficult when resource densities are changing within a patch over time, which may be common in nature (Tregenza, Parker, and Thompson 1996). Also, this method is difficult to apply when competitors differ in competitive weights. Our method of measuring the magnitude of interference competition should be more accurate when prey density changes over time.

The number of prey captured by individuals can also change in the absence of interference if individuals change their feeding efficiencies in the presence of competitors. Such changes would alter the magnitude of exploitative competition from the levels estimated by the simulations. Still, we can conclude that the presence of the competitor decreased the feeding rate of an individual as a net effect of interference competition and possibly a change in the magnitude of exploitative competition. The change in feeding efficiency and the magnitude of exploitative competition in the presence of other individuals may be considered as a form of interference because interference competition has been defined as "any kind of interaction between competitors that reduces searching efficiency" (Sutherland 1983).

Our behavioral results are applicable to broader topics in ecology, such as spatial distribution of organisms. Tregenza, Parker, and Thompson (1996) mentioned, "The ideal free distribution (IFD) under unequal competitors can only be described accurately if the relative ability of all individuals are known." The IFD models with asymmetric interference

competition have led to different conclusions on how competitor density and competitive weights affect distributions (Parker and Sutherland 1986; Tregenza, Hack, and Thompson 1996; van der Meer 1997), and these models need to be tested with adequate weighting of the competitors' effects on feeding rates. Also, understanding the magnitude of asymmetry in interference competition could answer how asymmetric interference competition affects population dynamics by altering individual growth. If interference competition negatively affects growth of smaller individuals more strongly than larger individuals, interference competition would expand the initial size difference. On the other hand, if the advantage in prey consumption for larger individuals does not compensate their higher metabolic demands, the size difference in the population would decrease. In Arctic charr (*Salvelinus alpinus*), for example, larger fish require a higher density of macroinvertebrates to maintain basal metabolism because the increasing prey capture efficiency does not keep pace with the increasing metabolism during development, which results in an advantage for smaller fish under exploitative competition in terms of growth and starvation (Byström and Andersson 2005). Including change in feeding rate by asymmetric interference competition in models for population distribution and dynamics would significantly improve the model quality, and we believe that our approach and findings can contribute to that improvement.

In conclusion, red drum exhibited interference competition, and the magnitude of this competition was related to the size relationship between competing individuals and the frequency of vigilant behavior. If food resources are routinely limited in nursery habitats, asymmetric competition among different sizes of young could play an important role in their survival. If larger individuals are favored for growth and survival, the cohorts spawned early in the spawning season will have an advantage when small individuals from later cohorts arrive in the nursery habitats. Further investigations on how interference competition affects growth, mortality, and distribution are required to understand differential survivorship, population dynamics, and reproductive strategy in this and other species. Also, our findings suggest that large size in the population is not necessarily advantageous in competition when the size distribution in the local microhabitat differs from that of the whole population (Parker and Sutherland 1986; Bautista et al. 1995). Rather, we need to take into account both absolute and relative sizes in these microhabitats to estimate the competitive advantage of individuals because competition occurs at the individual level on a local scale.

FUNDING

REFERENCES

Akaike H. 1974. A new look at the statistical model identification. IEEE Trans Automat Contr. 19:716–723.

Bautista LM, Alonso JC, Alonso JA. 1995. A field test of ideal free distribution in flock-feeding common cranes. J Anim Ecol. 64: 747–757.

Briffa M, Sneddon LU. 2007. Physiological constraints on contest behaviour. Funct Ecol. 21:627–637.

Byström P, Andersson J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). Oikos. 110:523–536.

Dolman PM. 1995. The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrohenax nivalis*. Oecologia. 102:511–514.

Flaxman SM, deRoos CA. 2007. Different modes of resource variation provide a critical test of ideal free distribution models. Behav Ecol Sociobiol. 61:877–886.

Fuiman LA, Magurran AE. 1994. Development of predator defences in fishes. Rev Fish Biol Fish. 4:145–183.

Fuiman LA, Poling KR, Higgs DM. 1998. Quantifying developmental progress for comparative studies of larval fishes. Copeia. 1998: 602–611.

Giaquinto PC, Volpato GL. 1997. Chemical communication, aggression, and conspecific recognition in the fish Nile tilapia. Physiol Behav. 62:1333–1338.

Gillespie DT. 1977. Exact stochastic simulation of coupled chemical reactions. J Phys Chem. 81:2340–2361.

Grand TC, Dill LM. 1999. Predation risk, unequal competitors and the ideal free distribution. Evol Ecol Res. 1:389–409.

Hassell MP, Varley GC. 1969. New inductive population model for insect parasites and its bearing on biological control. Nature. 223:1133–1136.

Humphries S, Ruxton GD, van der Meer J. 2001. Unequal competitor ideal free distributions: predictions for differential effects of interference between habitats. J Anim Ecol. 70:1062–1069.

Kotrschal K, Hemetsberger J, Dittami J. 1993. Food exploitation by a winter flock of greylag geese: behavioral dynamics, competition and social status. Behav Ecol Sociobiol. 33:289–295.

Lazo JP, Holt GJ, Arnold CR. 2000. Ontogeny of pancreatic enzymes in larval red drum *Sciaenops ocellatus*. Aquacult Nutr. 6: 183–192.

Leimar O, Austad S, Enquist M. 1991. A test of the sequential assessment game: fighting in the bowl and doily spider *Frontinella pyramitela*. Evolution. 45:862–874.

van der Meer J. 1997. The ideal free distribution when predators differ in competitive abilities. Oikos. 80:301–310.

van der Meer J, Ens BJ. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. J Anim Ecol. 66:846–858.

Minderman J, Lind J, Cresswell W. 2006. Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. J Anim Ecol. 75:713–723.

Moody AL, Houston AI. 1995. Interference and the ideal free distribution. Anim Behav. 49:1065–1072.

Nakayama S, Ojanguren AF, Fuiman LA. 2009. To fight, or not to fight: determinants and consequences of social behaviour in young red drum (*Sciaenops ocellatus*). Behaviour. 146:815–830.

Park T. 1954. Experimental studies of interspecies competition. II. Temperature, humidity and competition in two species of *Tribolium*. Physiol Zool. 27:177–238.

Parker GA, Sutherland WJ. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Anim Behav. 34:1222–1242.

Persson L, Leonardsson K, de Roos AM, Gyllenberg M, Christensen B. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. Theor Popul Biol. 54:270–293.

Post JR, Parkinson EA, Johnston NT. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. Ecol Monogr. 69:155–175.

Rooker JR, Holt SA, Holt GJ, Fuiman LA. 1999. Spatial and temporal variability in growth, mortality, and recruitment potential of post-settlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. Fish Bull. 97:581–590.

Ros AFH, Becker K, Oliveira RF. 2006. Aggressive behaviour and energy metabolism in a cichlid fish, *Oreochromis mossambicus*. Physiol Behav. 89:164–170.

Schoener TW. 1983. Field experiments on interspecific competition. Am Nat. 122:240–285.

Smallegange IM, van der Meer J, Kurvers RHJM. 2006. Disentangling interference competition from exploitative competition in a crab-bivalve system using a novel experimental approach. Oikos. 113:157–167.

Smith CK. 1990. Effects of variation in body size on intraspecific competition among larval salamanders. Ecology. 71:1777–1788.

Soto MA, Holt GJ, Holt SA, Rooker J. 1998. Food habit and dietary overlap of newly settled red drum (*Sciaenops ocellatus*) and Atlantic croaker (*Micropogonias undulatus*) from Texas seagrass meadows. Gulf Res Rep. 10:41–55.

Sutherland WJ. 1983. Aggregation and the 'ideal free' distribution. J Anim Ecol. 52:821–828.

Sutherland WJ, Parker GA. 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. Anim Behav. 44:345–355.

Tregenza T, Hack MA, Thompson DJ. 1996. Relative competitive success of unequal competitors changes with overall density. Oikos. 77:158–162.

Tregenza T, Parker GA, Thompson DJ. 1996. Interference and the ideal free distribution: models and tests. Behav Ecol. 7:379–386.

Vahl WK, van der Meer J, Weissing FJ, van Dullemen D, Piersma T. 2005. The mechanisms of interference competition: two experiments on foraging waders. Behav Ecol. 16:845–855.

Venables WN, Ripley BD. 2002. Modern applied statistics with S. 4th ed. New York: Springer.

Werner EE. 1994. Ontogenic scaling of competing relations: size-dependent effects and responses in two anuran larvae. Ecology. 75:197–213.