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INTRASPECIFIC COMPETITION AMONG EARLY LIFE STAGES

AND THE OPTIMAL SPAWNING STRATEGY OF RED DRUM

(*SCIAENOPS OCELLATUS*)

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(*SCIAENOPS OCELLATUS*)

by

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INTRASPECIFIC COMPETITION AMONG EARLY LIFE STAGES AND THE OPTIMAL SPAWNING STRATEGY OF RED DRUM (*SCIAENOPS OCELLATUS*)

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This collection of studies was designed to understand the mechanisms and consequences of competition among early life stages of red drum (*Sciaenops ocellatus*), with a special attention to asymmetric competition and multiple-breeding strategy of parents. The overall hypotheses were that (1) red drum larvae show behavioral interactions, and the magnitude of these interactions is explained by the sizes of the competing individuals, (2) red drum larvae compete for food and habitat use, and the competition is asymmetric as determined by size and behavioral interactions, and (3) the parents can reduce negative effects of competition among larvae and increase larval survival by altering their multiple-spawning traits. The laboratory experiments showed the existence of sociality in red drum larvae. The magnitudes of aggressive behavior, vigilant behavior and shoaling behavior were explained by a combination of absolute and relative phenotypes of competing individuals, such as body lengths and body condition.

A new method of combining the laboratory experiments and the foraging theory disentangled interference competition for food from exploitative competition, revealing that both absolute and relative body lengths of competing individuals influence feeding efficiencies. In addition, vigilant behavior decreased feeding efficiency regardless of body sizes. The competitor size and behavioral interactions between individuals had different effects on competition for habitat use: the existence of larger individuals prevented the newly settled larvae from entering preferred habitats, whereas the aggressive behavior from the occupants of preferred habitats moved newly settled larvae to the unpreferred habitats. Finally, computer simulations using an individual-based model revealed that as interference competition among larvae increased, the number of spawning events and the spawning interval of the parents increased to lessen competition and maximize total survival of offspring.

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Chapter 1: General introduction

Species maximize fitness through adaptation, including adaptation of life histories to prevailing environments (Stearns 1992). Reproductive strategy is one of the key components that determine the success of species. Various reproductive traits can be adaptive, such as energy allocated to reproduction, time to maturation, timing and frequency of breeding, and selection of breeding sites. These traits have evolved to maximize population growth within the constraints of the ambient environment, a species' physiology, and trade-offs with other life-history traits (Gould and Lewontin 1979; Stearns and Koella 1986; Roff and Fairbairn 2007).

Some organisms allocate all excess energy to reproduction and die after reproduction, whereas others reproduce multiple times during their lifetime to increase their reproductive success. Semelparity (reproducing once in lifetime) is usually favored when future survival of the parents is low or uncertain, whereas iteroparity (reproducing over several reproductive seasons) is usually favored when post-reproductive survival of parents is high relative to offspring survival and fecundity increases with age (Murphy 1968; Charnov and Schaffer 1973; Schaffer 1974; Philippi and Seger 1989; Zeineddine and Jansen 2009). Some organisms distribute their reproductive energy into multiple batches during a single reproductive season (multiple breeding) to diversify the risk and avoid catastrophic loss of offspring when the environment for offspring survival is uncertain over shorter time scales (Bell 1976; Wilbur and Rudolf 2006). So far, the question about how parents spread their reproductive efforts over time has been explored

as a bet-hedging strategy in time to cope with environmental uncertainty for offspring survival. However, the success of each offspring may be affected not only by environmental predictability, but also by the success of other offspring through intraspecific competition.

Competition is a behavioral adaptation through which each individual tries to increase fitness. Competition can affect growth by altering feeding efficiency in two ways. Individuals with better feeding performance can disproportionately exploit food, which reduces food availability for individuals with poorer feeding performance (exploitative competition). Also, individuals can compete for a common resource through direct behavioral interactions with other individuals, which prevents resource utilization of competitively inferior individuals (interference competition). Competition can also affect patterns of habitat use. Subordinate species often shift to suboptimal niches to avoid a reduction in fitness (Werner and Hall 1976; Maitz and Dickman 2001; Jonsson *et al*. 2008).

Competition among offspring that increases their individual fitness can conflict with the reproductive strategy of parents that maximizes total offspring survival. Multiple breeding potentially affects the social environment of offspring by altering the density and size distribution of offspring in nursery habitats. Multiple breeding can decrease intra-cohort competition by reducing the instantaneous density of offspring when resources for offspring are scarce. On the other hand, multiple breeding can create inter-cohort competition due to temporal and spatial overlap between cohorts if the interval between cohorts is short or the cohorts stay long in nursery habitats, whereas parents may

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miss the period of suitable conditions for offspring survival if the reproductive interval is too wide. If competition among offspring has a significant impact on offspring survival, it could feed back to the reproductive strategies of the parents, specifically, the optimal multiple-breeding traits that maximize total offspring survival.

Selection for optimal reproductive traits would become complicated if the competitive abilities of cohorts vary over time. Multiple breeding can create temporal overlap between cohorts that may be disadvantageous for the later cohort through exploitative or interference competition, since individuals from early cohorts would have better feeding performance and be stronger in direct behavioral interactions due to their larger size when the later cohorts appear. Understanding the effects of intraspecific competition on survival and the degree of asymmetry between cohorts will enable us to comprehend how parents finance their reproductive efforts in time from an evolutionary point of view when multiple spawning creates asymmetric intraspecific competition.

Many fishes spawn numerous small eggs to deal with uncertainty in offspring survival due to stochastic environments (Winemiller and Rose 1993). High fecundity increases the chance of encountering conspecifics and amplifies the impact of competition on survival. Also, many fishes experience a massive increase in body size with development over a short period of time (Fuiman *et al*. 1998), which has significant effects on asymmetric competition for food and habitat use, since competitive ability is often related to body size (Wilson 1975). However, the importance of competition during the early life of fishes has not received much attention. Considering their high fecundity

and their high mortality during early life a slight change in survivorship during early life would result in a large increase in the number of recruits (Houde 2002).

Red drum (*Sciaenops ocellatus*) is an iteroparous, multiple-spawning fish and a good model with which to investigate competition and the adaptation of reproductive traits. Social behavior has not been studied in this species. In the northwestern Gulf of Mexico, red drum spawn near shore multiple times over 2 to 3 months during Fall, when water temperature decreases by about 5–9°C (Rooker *et al.* 1999). After a brief pelagic period, larvae are transported into the bays by tidal currents and settle into seagrass beds at about 4–8 mm in total length (Rooker *et al.* 1999). Cohorts of larvae arrive at the nursery habitats in successive waves. The density of red drum larvae in seagrass beds sometimes exceeds 11 individuals m^{-2}, and larvae of various sizes (about 8–25 mm in total length) co-occur (Rooker *et al.* 1999). These conditions create the potential for competition for food during early life, which could affect the growth and survival of larvae in the nursery habitat. Red drum larvae may also compete for habitat that serves as a shelter from predators. Stunz and Minello (2001) found higher survival of newly settled red drum larvae in structurally complex habitats than in unvegetated habitats. Therefore, competition could have a significant impact on survival when resources, such as food and shelter, are scarce relative to larval density, and one could expect that the spawning traits (specifically, spawning interval, batch fecundity) of red drum have adapted to the potential impact of competition during early life on larval survival.

The aim of this set of studies is to understand competition among fish larvae and the effect of competition on multiple-spawning strategy of the parents. The overall

hypotheses are that (1) red drum larvae show behavioral interactions, and the magnitude of these interactions is explained by the sizes of the competing individuals, (2) red drum larvae compete for food and habitat use, and the competition is asymmetric as determined by size and behavioral interactions, and (3) parents can reduce the negative effects of competition among larvae and increase offspring survival by altering multiple-spawning traits. Chapter 2 demonstrates the presence of behavioral interactions among red drum larvae and explores the determinants of behavioral interactions. Chapter 3 disentangles the magnitude of interference competition for food from exploitative competition, and examines the effects of body sizes of competing individuals and behavioral interactions on the asymmetry in interference competition. Chapter 4 examines competition for habitat use, specifically the effects of the presence of a competitor, behavioral interactions, and habitat quality on competition for habitat use. Chapter 5 explores the relationship between offspring competition and multiple-spawning reproductive traits using an individual-based model. This work explored how the magnitude of asymmetric interference competition for food and subsequent habitat competition affects multiple breeding when parents attempt to maximize offspring survival.

Chapter 2: Determinants and consequences of social behavior in young red drum

ABSTRACT

Social behavior is critical for survival and fitness in many organisms. The aim of this study was to examine the effects of developmental state, physiological state and their differences between individuals on the intensities of aggressive and grouping behaviors in red drum (*Sciaenops ocellatus*) larvae. Body size was used as a proxy for developmental state and body condition (i.e., residual of wet weight from the relationship between body size and wet weight) as a measure of physiological condition. Social interactions between two fish were observed for 30 min in a 9-L tank. We found that the duration of grouping behavior increased as body size increased, but aggressive behavior was less frequent as body size and condition increased. The larger fish in a trial tended to be aggressive to the smaller one, and fish of similar sizes tended to show grouping behavior. Fish that more frequently displayed aggressive behaviors tended to occupy the lower part of the water column. Our results suggest a competitive disadvantage for larvae from late cohorts when they recruit to nursery habitats where larger larvae from early cohorts already reside. This work demonstrated the significant roles of body size and condition in social interactions, and the importance of looking at both absolute traits and traits relative to the other individuals to explain the magnitude of social behaviors.

INTRODUCTION

Social behavior, such as aggression and cooperation, has evolved in many organisms to increase fitness. Organisms try to maximize individual fitness by competing for resources, such as food, territories, or mates, or by cooperating with other individuals (Krebs and Davies 1993). Although social behavior may improve an individual's fitness, it often has costs. For example, territoriality can result in exclusive access to resources that are critical for fitness, such as food, shelter and mates (Maher and Lott 2000), but engaging in fighting is costly in terms of energy and time (Briffa and Sneddon 2007). Grouping behavior can increase fitness as well, by decreasing predation pressure, increasing foraging efficiency, and increasing mating success (Dugatkin 2002). In migratory animals, grouping behavior also increases the accuracy of choosing migratory routes (Couzin *et al.* 2005). On the other hand, large group size increases conspicuousness to a predator (Krause and Godin 1995), competition for food (Johnsson 2003), and risk of disease transmission (Côté and Poulin 1995). Therefore, the balance between the costs and benefits of social behavior determines whether it is better to be aggressive or cooperative in a particular environment (Komdeur 2006).

An individual's developmental state and its physiological condition play a critical role in social behavior. For example, American lobster (*Homarus americanus*) become aggressive with the development of claws (Lang *et al.* 1977), and chub mackerel (*Scomber japonicus*) first begin to display shoaling behavior during metamorphosis (Nakayama *et al.* 2007). Food may be more valuable to animals in poor physiological condition than to those in good condition. In dark-eyed junco (*Junco hyemalis*),

individuals in poor condition are more aggressive (Cristol 1992). Also, to avoid food competition, hungry three-spined stickleback (*Gasterosteus aculaetus*) spend less time in a shoal than satiated individuals (Krause 1993). Growth rate and age may also affect social behavior (Jönsson *et al.* 1998; Côté 2000; Vøllestad and Quinn 2003), but the published results lack consistency. Phenotypic differences between competing animals also help determine the nature of interactions. Many studies have reported the effect of differences in body size and condition on social behavior. Fighting intensity in male jumping spiders (*Euophyrys parvula*) escalated when the difference in carapace length between the two individuals was smaller (Wells 1988). In female house finch (*Carpodacus mexicanus*), aggressive interaction was also escalated when the difference in body condition (ratio of body mass to body length) was smaller (Jonart *et al.* 2007). However, smaller difference in body size is also known to facilitate shoaling behavior in many fishes (Pitcher *et al.* 1986; Ward and Krause 2001).

Social behavior is mutual and cannot be performed by individual decision because behavior of one individual affects that of others (Maynard Smith 1982). Also, a complex suite of phenotypes, such as developmental state and physiological condition, affects social behavior. Therefore, it is important to measure the effect of individual phenotypic traits on social behavior as well as the effect of differences in these traits between interacting individuals in order to understand the mechanism of decision-making in social behavior. However, there are few studies that combine both the developmental state and physiological condition of a focal animal and their relationship to the opponent's traits (e.g., Jonart *et al.* 2007).

We used larval red drum (*Sciaenops ocellatus*) to investigate the relationship between body traits and social behavior. Depending on conditions, larval red drum show both aggressive and cooperative (grouping) behavior with conspecifics. Their synchronous batch-spawning reproductive strategy over a 2–3 month period during Fall (Peters and McMichael 1987), when water temperature decreases by 7–9°C from about 31°C (Rooker *et al.* 1999), results in co-occurrence in the nursery habitat of conspecific larvae that differ in size, age, and physiological condition. In the early season, the nursery habitat is occupied only by the first cohort, and thus the variability in size and condition is relatively narrow. As the season progresses, however, successive cohorts overlap thereby increasing size variability in the nursery habitat. Also, the seasonal decline in water temperature lowers the growth rate and alters the condition of larvae from late cohorts, which exaggerates the phenotypic variability among red drum in the nursery habitat. The high density of red drum larvae in the seagrass meadows (sometimes > 11 individuals m^{-2}) and wide range of sizes (8 to 25 mm standard length, Rooker *et al.* 1999) represent ideal conditions for a variety of social interactions among conspecifics. If interactions are aggressive and smaller individuals are disadvantaged, social behavior could interfere with growth and survival of larvae depending on their arrival to the nursery habitat.

We experimentally investigated how social behavior is determined by the individual's developmental state (measured as a body size), physiological condition (measured as a body condition), and differences in these states between two individuals that interact with each other. We tested whether social behavior affects the vertical

position of fish by comparing the average vertical position of a fish before and after encountering a conspecific.

MATERIAL AND METHODS

Life history of red drum

Red drum inhabit subtropical to temperate coastal waters in the Gulf of Mexico and western Atlantic Ocean (Hoese and Moore 1998). Males mature in 3 years and females in 5 years, which is about 70 cm and 75 cm fork length, respectively (Hoese and Moore 1998; Beckman *et al.* 1988). There is no difference in length-weight relationships between adult males and females (Beckman *et al.* 1988). Females spawn multiple times synchronously during Fall (Comyns *et al.* 1991) near estuaries (Holt *et al.* 1983). During a 2-week pelagic stage, larvae are transported into estuaries mainly by tidal currents and settle at about 7 mm standard length (Holt *et al.* 1983). In Texas bays, red drum larvae settle mainly on shallow (0–1.5 m in depth) seagrass meadows (Pérez-Domínguez 2004), in which seagrass heights range from 12 to 26 cm (Holt *et al.* 1983). Red drum spanning a wide range of sizes (about 7 to 25 mm standard length) are found in the centre of seagrass meadows, but only smaller individuals (8 to 12 mm standard length) occur in the deeper edges of these habitats (Pérez-Domínguez 2004).

Husbandry and experimental procedures

Red drum eggs were obtained from captive spawning of wild-caught adults at the Coastal Conservation Association / Central Power and Light Marine Development Center

(Corpus Christi, Texas, USA). Spawning was induced by manipulating photoperiod and temperature. Eggs of two batches (October 27 and November 9, 2005) were obtained from a single pair of adults and transferred to a laboratory at The University of Texas Marine Science Institute (Port Aransas, Texas) within 18 h after spawning. After treating eggs with 1×10^{-5} % formalin for 30 min to prevent fungal infections, approximately 5,000 viable eggs from the same spawn were put into each of two 60-L fiberglass conical tanks (60 cm maximum diameter). Temperature and salinity in both tanks were kept at an average of 26.9 °C and 27.4 ppt, respectively. Daily photoperiod was set for a 12-h light and 12-h dark cycle. Eggs hatched on the next day. Beginning the day after hatching, fish were fed 400,000 rotifers (*Brachionus* spp.) enriched with nutrients for 45 min (Algamac-2000, Aquafauna Bio-Marine, Inc., Hawthorne, USA) in each tank daily until 11 d after hatching. From 12 d after hatching, fish were fed 60,000 enriched *Artemia salina* nauplii.

Behavioral interactions were observed for pairs of individuals from the same spawn but separate rearing tanks. Therefore, individuals tested were reared under the same conditions but never encountered each other before. From 18 to 34 d after hatching, one individual was netted randomly from each of two rearing tanks; fish that showed obviously abnormal behavior were avoided. At 1800 h, each fish was put into one side of a 9-L Plexiglas tank (40 × 15 × 15 cm), which was divided into two compartments by an opaque plastic partition, and the two fish were allowed to acclimate overnight. Three walls of the tank were covered with neutral grey paper with grids at 5-cm intervals for the convenience of observation, and behavior of the fish was observed through the fourth wall. The bottom of the tank was covered with sand and a single piece of artificial

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seagrass (5 cm tall, 3 cm wide) was placed in the centre of the bottom for shelter. Water temperature and salinity in the experimental tanks were about 23.5°C and 27.0 ppt, respectively.

Observations were performed between 1300 and 1800 h on the next day. First, one of the two fish was randomly assigned as a focal fish, and its vertical position from the bottom of the tank (in cm) was recorded once per minute for 5 min. Then, the partition was gently removed, and vertical position of the focal fish was recorded every 2 min for 20 min, and then once at 25 and 30 min. Meanwhile, the number of behavioral interactions (aggression and avoidance) and duration of grouping behavior between the two individuals was recorded. Aggression was the sum of the number of displacements and attacking behaviors. Displacement was defined as one fish approaching the other from behind without an abrupt increase in swimming speed and displacing it to another position. Attacking behavior was defined as one fish approaching the other with rapid acceleration. In most cases attacking behavior was from behind, but sometimes it occurred face-to-face followed by staring at each other for a few seconds without moving. Avoidance was defined as one fish accelerating rapidly without receiving apparent aggressive behavior from the other fish. Grouping behavior was defined as two individuals swimming closely (arbitrarily established as within 5 cm of each other, approximately 2–6.6 body lengths) at approximately the same speed and direction. During grouping behavior, two individuals usually swam side-by-side, and demonstrated no preference for being ahead of or behind the other. After the observation period, digital pictures of the fish were taken using a microscope, and total length of each individual

was measured to the nearest 0.01 mm using an image analysis software (Image J; National Institutes of Health, http://www.nih.gov), and wet weight was measured to the nearest 1 mg.

Trials were conducted from 15 November to 14 December 2005, with 3 to 6 pairs of fish per day, 101 trials in total (63 pairs from the first batch, 38 pairs from the second batch). Length-specific instantaneous growth coefficient of each individual (g) was calculated using an exponential growth model:

$$\text{Total length} = 2.0 \cdot e^{gt}$$

where t was days after hatching. The initial total length (2.0 mm) was used from our unpublished data on newly hatched red drum larvae (A. F. Ojanguren, unpublished data). Body condition was estimated for each fish as the residual from a log length – log wet weight regression of 202 fish used in the experiment (see Froese 2006). It was impossible to identify sex of the fish at larval stages; sex was not inspected.

Statistical analysis

Using a generalized linear model, total number of aggressive events, total number of avoidance events, and total duration of grouping behavior were analyzed with respect to traits of the focal fish and the difference of these traits between the two fish. The independent variables were total length, condition, and growth coefficient of the focal fish as well as the differences in total length and condition between the two fish in each

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trial. A batch identifier was also included in the analyses. Differences in length and condition between the two fish were calculated by subtracting length or condition of the opponent from that of the focal fish in a pair when analyzing the number of aggressive events and avoidance. For analyzing the duration of grouping behavior, differences were calculated as the absolute value of the difference between the two fish because grouping behavior is a mutual behavior. Age was omitted from the model because it was mostly explained by total length and growth coefficient of the focal fish ($R^2 = 0.95$). Difference in growth coefficient between the focal fish and opponent was not included in the model because the two fish tested were always at the same age, giving such a calculation no more information than total length alone. For the analyses of the numbers of aggressive and avoidance events, Poisson distribution for the response variables and log link function were specified in the models taking into the attributes of the response variables. This allows us to deal with the heteroscedasticity of response variables without transformation. For the analysis of the duration of grouping behavior, gamma-Poisson distribution and log link function were specified (McCullagh and Nelder 1989). Parameters for the explanatory variables were estimated using maximum likelihood estimation and models were simplified by removing the least significant explanatory variables from the models until the Akaike information criterion did not decrease further (Akaike 1974).

A general linear model was applied to the mean vertical position of the focal fish, measured from the bottom of the tank, before encounter and after encounter. Dependent variables were total number of aggressive events performed by the focal fish, total

number of aggressive events received by the focal fish, total number of avoidance events, total duration of grouping behavior, mean vertical position of the focal fish before encounter, and batch identifier. The model was then simplified using backward elimination method. All statistical analyses were performed with SPSS 16.0 (SPSS Inc., Chicago, USA) using the $\alpha = 0.05$ level of significance.

RESULTS

Of 101 trials, total lengths of the focal fish ranged from 7.5 to 23.5 mm, and the difference in length between two individuals ranged from 0.1 to 10.7 mm. Body conditions of the focal fish and the difference in condition ranged from −0.19 to 0.16 and 2.5×10^{-4} to 2.0×10^{-1}, respectively. Growth coefficients of the focal fish were from 0.036 to 0.101, ages ranging from 18 to 34 days after hatching.

Total number of aggressive events performed by a focal fish was negatively related to total length and condition of the focal fish and positively related to differences in total length and condition between the focal fish and opponent (Table 2.1). Growth coefficient was removed from the model because it did not decrease the Akaike information criterion. Condition and difference in total length were negatively related to total number of avoidance events, but other variables (growth coefficient, difference in condition, total length) did not affect the number of avoidance events and were removed from the model (Table 2.2). Total duration of grouping behavior increased with total length of the focal fish and decreased with increasing absolute value of the difference in total length and absolute value of the difference in condition (Table 2.3).

A focal fish's mean vertical position from the bottom after encounter was negatively related to total number of aggressive events performed by the focal fish ($F_{1, 98}$ = 5.04, p = 0.027, Fig. 2.1), and was positively related to mean vertical position before encounter ($F_{1, 98}$ = 26.03, $p < 0.001$). These two variables significantly explained the mean vertical position of a focal fish after encounter ($F_{2, 98}$ = 17.43, $p < 0.001$). Total duration of grouping behavior (p = 0.891), total number of avoidance events (p = 0.525), and total number of aggressive events received by a focal fish (p = 0.551) did not have significant effects and thus were removed from the model. There was no significant effect of batch in any of the analyses ($p > 0.05$).

DISCUSSION

A fish displayed aggressive behavior more frequently when (1) it was small (earlier developmental state), (2) it was bigger than the opponent with which it was paired, (3) it was in poor condition, and (4) its condition was better than that of the opponent with which it was paired. Those aggressive fish moved to the lower part of the water column after encountering an opponent. Avoidance occurred more often when (1) the focal fish was smaller than the opponent with which it was paired, and (2) it was in poor condition. Grouping behavior lasted longer when the two fish were (1) similar in size, (2) large (later developmental state), and (3) of similar condition. Growth coefficient did not contribute in any predictable way to interactions as measured here. These results show that phenotypic traits of an individual, especially length (developmental state),

Table 2.1. Generalized linear model for total number of aggressive events. The overall model is statistically significant ($\chi^2_4 = 190.31$, $p < 0.001$).

Variable	Parameter	Standard error	Wald χ^2	p
Constant	2.29	0.27	71.08	< 0.001
Total length	−0.10	0.02	23.85	< 0.001
Difference in total length	0.26	0.03	103.66	< 0.001
Condition	−7.10	1.67	18.00	< 0.001
Difference in condition	7.51	1.29	34.15	< 0.001

Table 2.2. Generalized linear model for total number of avoidance. The overall model is statistically significant ($\chi^2_2 = 16.13$, $p < 0.001$).

Variable	Parameter	Standard error	Wald χ^2	p
Constant	−0.38	0.13	8.95	0.003
Difference in total length	−0.10	0.03	11.97	0.001
Condition	−4.81	2.15	4.98	0.026

Table 2.3. Generalized model for total duration of grouping behavior. The overall model is statistically significant ($\chi^2_3 = 152.49$, $p < 0.001$).

Variable	Parameter	Standard error	Wald χ^2	p
Constant	−2.21	4.10	29.12	< 0.001
Total length	0.29	0.03	109.83	< 0.001
| Difference in total length |	−0.42	0.05	75.72	< 0.001
| Difference in condition |	−8.24	2.96	7.75	0.005

Figure 2.1. Total number of aggressive events performed by a focal fish during 30 min observation and mean vertical position of a focal fish from the bottom after encounter. Mean vertical position was adjusted with the effect of mean vertical position before encounter ($r^2 = 0.048$, $p = 0.027$).
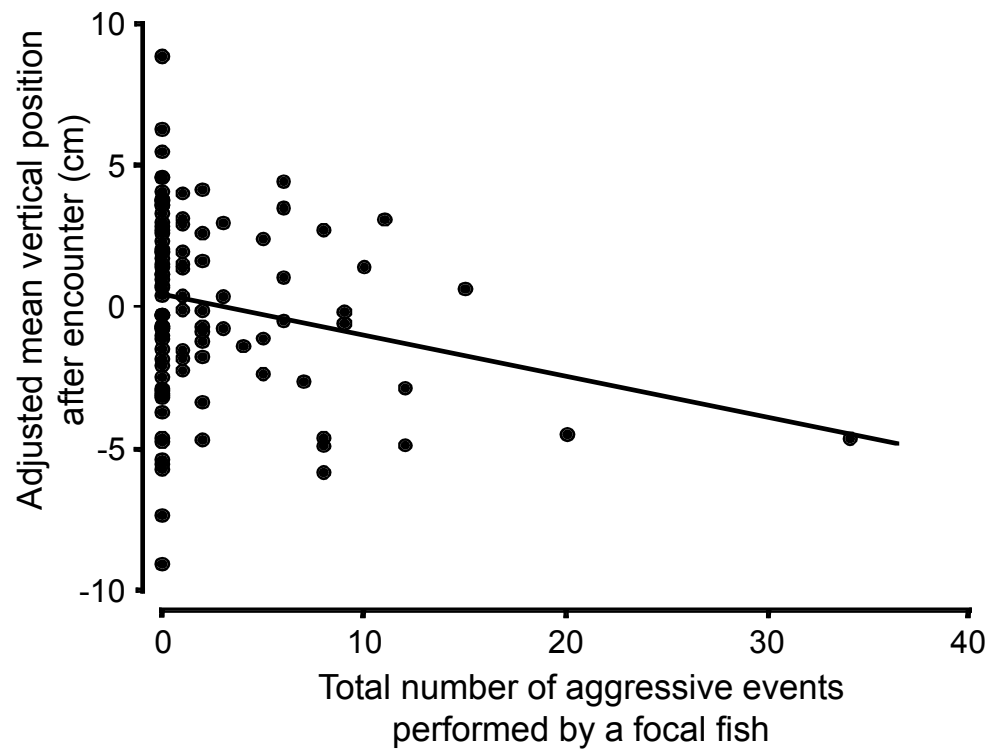
body condition, and how they differ between two individuals are determinants of social behavior in larval red drum.

Since size and size difference are important determinants of the nature and degree of social interactions, the variability in size found on nursery grounds through the season should influence the social interactions, and possibly survival of larvae. Fish from the early cohorts may be aggressive to fish from later cohorts and interfere with their feeding and predator avoidance. Also, fish from later cohorts may become more vigilant to avoid interactions with fish from early cohorts, resulting in less time for foraging and reduced growth. Aggressive behavior by larger red drum directed to smaller individuals may affect the settlement of the small ones. In coral reef fishes, Almany (2004) reported that prior residents use aggressive behavior to prevent the settlement of newly arriving fish. Therefore, the synchronous batch-spawning strategy in red drum, which increases size variability of offspring in the nursery grounds compared to a single synchronous spawning strategy, may be disadvantageous for fish from the late cohorts.

Aggressive behavior occurred in the smallest fish examined (7.5 mm total length), suggesting that onset of aggressive behavior in red drum is before or around the beginning of the settlement stage. Phenotypic differences between interacting individuals seem to be important for aggressive behavior. Larger individuals within a pair tend to show more frequent aggressive behavior toward smaller individuals. Likewise, individuals in a pair that are in better condition tend to show more frequent aggressive behavior toward the individuals in poorer condition. These individuals of larger body size or better condition relative to the opponents are more likely to win the contest and

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individuals of smaller body size or poorer condition are more likely to pay a cost for fighting (Huntingford and Turner 1987). As a consequence, the competitively inferior fish may choose to avoid encounters that would expose them to aggressive behavior and thereby reduce the risks of increased energy expenditure (Wilson *et al.* 1990), decreased time available for foraging (Ruzzante and Doyle 1991), decreased vigilance to predators (Jakobsson *et al.* 1995), and increased risk of injury by retaliation (Leimar *et al.* 1991). One way of avoiding such encounters in nature is for smaller red drum to occupy different parts of the nursery habitat. Observations that smaller red drum larvae are in greater abundance around the edges of seagrass bed (Pérez-Domínguez 2004) support this idea.

Aggressive behavior was displayed more frequently when individuals were in generally poor condition. This may result from a difference in the value of particular resources depending on physiological condition; individuals in poor condition might place more value on certain resources for their survival than individuals in good condition (McNamara and Houston 1990; Dugatkin and Ohlsen 1990). Even though no food was provided in this experiment, the display of aggression may affect the relationship between two individuals and therefore acquisition of future resources. In a pair, aggression was displayed more frequently by the individual that was in better condition than its poorer condition opponent. This implies that physiological condition relative to an opponent is also important for the aggressive behavior, as well as the absolute physiological conditions of the individuals. Thus, aggressive behavior might escalate when individuals are in poor condition and the opponents are in even poorer

condition. Food abundance relative to fish density would likely change the physiological condition of individuals and subsequently affect the nature and intensity of aggressive behavior in the wild.

Young red drum are known to be cannibalistic when reared in tanks at elevated densities (Chang and Liao 2003). The aggressive behavior observed in our trials were, however, not solely an attempt at cannibalism because aggressive behavior was also observed when the two fish were at similar sizes, or even from smaller to larger individuals. If this is the case, aggressive behavior should have been observed only from larger individuals to smaller individuals because red drum can only eat conspecifics that are smaller due to the limitation of gape size (Fuiman 1994; Krebs and Turingan 2003). However, we cannot entirely exclude the possibility of cannibalism, considering that individuals with poorer condition were more aggressive.

Many fish species develop schooling behavior sometime during the larval period (Hunter and Coyne 1982; Gallego and Hearth 1994; Nakayama *et al.* 2007). The ontogenetic increase we observed in the duration of grouping behavior in red drum larvae may reflect an increasing benefit of grouping behavior. When they are small, their strategy might be to grow out of a period of high size-based vulnerability to predators, whereas when they are big enough to sacrifice growth for survival, they may begin using grouping behavior to increase survival. It seems unlikely that a group of only two individuals could create a confusion effect to increase survival (Landeau and Terborgh 1986; Krause 1994), but a group of two could increase survival by increasing vigilance against a predator (Brown and Warburton 1999) or increased time available for other

activities by cooperative predator inspection (Dugatkin and Alfieri 1991). The cost of resource competition within a group (Grand and Dill 1999) would also affect grouping behavior. Our results suggest that fish can benefit most from grouping behavior by associating with others of similar size and condition. This may be because fish of smaller size or poorer condition would be competitively inferior (Metcalfe and Thomson 1995), and therefore association with individuals of larger size or better condition would impair their survival.

Avoidance can be interpreted as vigilance or an action that reduces costs of fighting. Avoidance was observed more frequently in the smaller individuals in a pair; the opposite trend was observed for aggressive behavior. This indicates that fish change their behavior from avoidance to grouping to aggression as their size relative to their opponent increases. The decision between aggressive and grouping behavior would change depending on resource abundance and predation pressure (Huntingford and Turner 1987; Krause and Ruxton 2002). Scarce resources would create an agonistic environment, whereas high predation pressure should favor grouping behavior.

We did not expect that the intensity of aggression received by a focal fish would not change its vertical position in the water column. Assuming that the lower part of the tank was a preferable habitat, individuals that received more aggressive behavior should have been displaced to the less preferred upper part of the tank. Instead, more aggressive individuals moved to the lower part of the tank. One possible explanation is that the posturing of aggressive behavior prefers lower position in the water column. Moving down the water column may be advantageous in aggressive interactions. Another possible

explanation is that a balance between costs and benefits for resources changes depending on the presence of the opponents. For example, in migratory birds, the competitively superior males arrive at the nesting sites earlier regardless of the higher risk of predation so that they can be competitively superior (Kokko 1999). When red drum are alone, they may not need to remain in the habitat with low predation risk if it is not the best foraging site, whereas competitive environments would change the relative value of the habitat. The depth of the experimental tank (15 cm) was enough to reflect their vertical positions in the wild because the height of seagrass meadows they inhabit in was about 12-26 cm (Holt *et al.* 1983).

Would the relationships observed in our experiments be different if the experiment were conducted with genetically unrelated individuals or with different batches of eggs? Firstly, kin discrimination by odor and subsequent aggression toward non-kin has been studied intensively in salmonids (e.g., Brown and Brown 1993; Brown and Brown 1996), but kin discrimination would be less likely under field conditions (Griffiths and Armstrong 2000). It might be advantageous for nest-building, demersal spawning species to possess the ability to discriminate kin to increase parental fitness, but it would be unreasonable to expect the same ability in marine pelagic species, whose eggs are scattered and dispersed over a very large area. The probability of encountering siblings must be negligible compared to the probability of encountering non-siblings. To our knowledge, there is no example of kin discrimination in marine pelagic species (reviewed by Griffiths 2003). Secondly, although the magnitude might be different, we believe that the trends in relationships between size and observed behavioral traits would

not change if the same experiments were conducted on genetically unrelated individuals or on different batches. In addition, all the fish tested for behavioral interactions were reared in different tanks and had not met each other before the test.

The behavioral interactions we observed could be operating on nursery grounds to alter mortality, and therefore, recruitment success. The effects of these interactions would vary with resource availability. Stunz and Minello (2001) found higher survival of newly settled red drum larvae in structurally complex habitats than in non-vegetated habitats. Aggressive behavior and vertical segregation are unlikely to affect survival of subdominant individuals when resources, such as food and shelter, are abundant because they can swim to find other available resources. However, these interactions might have a significant impact on survival when resources are scarce. Aggressive behavior would lead to asymmetric resource acquisition among individuals, which would result in promoting greater survival of large individuals from early batches as compared to later cohorts.

Chapter 3: Body size and vigilance cause asymmetric interference competition for food in red drum larvae

ABSTRACT

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 hypothesized that interference competition reduces feeding rates of young red drum (*Sciaenops ocellatus*) and that the magnitude of the effect is related to phenotypic traits, such as the sizes of competitors and behavioral interactions between them. We conducted laboratory experiments to measure prey consumption and behavioral interactions between two fish of different sizes (7–25 mm standard length) and estimated the magnitude of interference competition. After removing the effects of exploitative competition through computer simulations, we found that prey consumption of 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 was 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.

INTRODUCTION

Interference competition can be defined as direct interactions between organisms that decrease utilization of common resources (Park 1954, 1962). This type of competition is assumed to occur commonly in nature (Schoener 1983), and it can be a key factor in population dynamics (Sibly and Hone 2002), niche segregation (van der Meer and Ens 1997; Humphries *et al.* 2001) and life history traits (Fielding 2004). 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 results 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 with a high search rate, high capture success, and/or short handling time can indirectly reduce the feeding rate of individuals with lower efficiencies by obtaining more food per unit time without interference. This exploitative competition is inevitable unless food does not deplete over time.

Many studies have tried to find and quantify interference competition, but they have rarely succeeded in separating interference competition from exploitative competition because food was depleted over time. Smallegange *et al.* (2006) successfully separated interference competition from exploitative competition between shore crabs (*Carcinus maenas*) by replenishing consumed prey. However, this approach is difficult to

apply when competitors have different feeding efficiencies, since it confounds the effect of interference competition on feeding rates.

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, we need to take into account body size, size-related feeding efficiency, and the magnitude of exploitative competition in order to detect interference competition when competitors vary in size. Previous studies failed to separate interference competition from exploitative competition, leading to uncertainty about which type of competition was important (Werner 1994; Post *et al.* 1999).

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 seagrass meadows or oyster beds. Because it spawns many times over a 2-month reproductive season, various sizes of young red drum (about 7 mm 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 large larvae are aggressive to smaller larvae (Nakayama *et al.* 2009). Specifically, we hypothesized that the size relationship with conspecific competitors and behavioral interactions

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between them explain the magnitude of the decrease in the number of prey consumed by a fish attributable to interference competition. We measured prey consumption of 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 two competing fish to quantify the magnitude of interference competition. 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. Care and experimental work with animals were conducted in compliance

with Institutional Animal Care and Use Committee, the University of Texas at Austin (protocol number 07102301).

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, Texas, USA). Three batches of eggs were collected (September 12, 24, and October 22, 2007) and reared to produce a wide variety of sizes of larvae for the experiment. 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, Texas, USA).

Approximately 5,000 viable eggs from each batch were put into a 60-l fiberglass conical rearing tank ($\varnothing$60 cm at maximum). Temperature and salinity were kept at 26.9 ± 0.3°C and 27.5 ± 0.7 ppt, respectively (mean $\pm$ SD), and illumination was set to a daily cycle of 12-h light and 12-h dark. Eggs hatched the next day. Fish were fed 400,000 rotifers (*Brachionus* spp.) from days 2 to 11 after hatching, and 60,000 *Artemia salina* nauplii from day 10 onward within 2 h after lights on. Both diets were enriched with Algamac-2000 (Aquafauna Bio-Marine, Inc., Hawthorne, California, USA) for 12 hours prior to feeding.

The experiment was designed to describe the relationship between foraging efficiency (prey search rate and handling time) of isolated individual fish and their body size (developmental state). At 1800 h on the day before the experiment, six fish were

taken randomly from the three 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 $\pm$ SD) using a water bath, and salinity was 26.9 ± 0.7 ppt.

The following day, one fish was put into a 15-l glass tank (50×20 cm $\times 15$ cm high), which contained a heater and weak aeration. After 10 min, *Artemia* nauplii were provided using a pipette over the surface of the water. The number of prey introduced was chosen from 45, 60, 90, 150, 600, and 1200 (density: 3, 4, 6, 10, 40, and 80 l^{-1}, respectively). Aeration dispersed the *Artemia* evenly through the water quickly after they were introduced. The elapsed time until each of the first 10 prey captures was recorded, but only the time from the fifth to tenth prey capture was used to calculate prey capture rate (s^{-1}) because the time interval for the first five prey captures fluctuated widely (coefficient of variation for the first to fifth 0.88 ± 0.31, the fifth to tenth 0.63 ± 0.19, mean $\pm$ SD). After the tenth capture, the fish was removed from the tank using a dip net and put back to the 1-l plastic container without food. This procedure was repeated for the same individual with six 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 h 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 d post-hatching. For each fish, prey search rate and prey handling time were estimated by fitting Holling's type II functional response function (Holling 1959) with the six prey densities and the corresponding observed prey capture rates:

$$R_c = \frac{aD}{1 + aDT_h}$$

where R_c is capture rate (prey s^{-1}), a is prey search rate (ml s^{-1}), D is prey density (ml^{-1}) and T_h is prey handling time (s prey^{-1}). Since the capture success of *Artemia* by red drum was virtually 100% for the entire size range of fish tested, the calculated handling time was the time from encountering a prey, through attacking and ingesting the prey, to resuming searching behavior. The decrease in prey density through the experiment was ignored because the trial was terminated after 10 prey captures, at which time the decrease in prey density was negligible; D was set at the initial prey density.

The relationship between body size (standard length) and search rate was obtained using linear regression. Body size was log-transformed to achieve a better fit to the regression. The effect of fish size on handling time was fitted using the empirical function (Walton *et al.* 1992):

$$T_h = \exp\left(b \cdot 10^{(c/\text{length})}\right)$$

where *b* and *c* are constants. These constants were estimated using a non-linear least-squares estimation method. When exploring the effects of fish size on search rate and handling time, each data point was weighted by the coefficient of determination (R^2) from Holling's type II functional response function so that better estimates of search rate and handling time had a greater weight in the regression.

Competition experiment

Red drum eggs were collected and raised in the same way as in the previous experiment (total of six batches, spawned from October 10 to November 24, 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 two rearing tanks, six 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, 27.1 ± 0.7 ppt).

The following day, two 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 × 15 cm high), which contained a heater and weak aeration, and the interactive behavior of a 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 feeding activities of a 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 two fish could keep foraging without being satiated during the experiment. Most of the prey were consumed within 15 min.

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 days post-hatching. The difference in length of the two fish (focal fish − 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 consume in the absence of interference competition (i.e., exploitative competition only) by numerical simulation. Search rates and handling times were assigned to a focal fish and a competitor based on their standard lengths (see *Individual foraging efficiencies without competition*). Assuming that prey were evenly distributed in the water, we calculated for both a focal fish and a competitor the time to encounter the first prey, using the size-dependent search rate and the initial prey density:

$$t_{f,1} = \frac{V}{a_f N} \qquad \text{(focal fish)}$$

$$t_{c,1} = \frac{V}{a_c N} \qquad \text{(competitor)}$$

where $t_{f,i}$ and $t_{c,i}$ denote the time for a focal fish and a competitor to encounter the i-th prey, V is a volume of water (15,000 ml), a_f and a_c are the search rates (ml s^{-1}) of a focal fish and a competitor based on their lengths, and N is an initial number of prey (45). From the time to first prey encounter by each fish ($t_{f,1}$, $t_{c,1}$), the probability of the focal fish encountering the first prey earlier than the competitor ($P_{f,1}$) was calculated as:

$$P_{f,1} = \frac{t_{f,1}}{t_{f,1} + t_{c,1}}$$

A random number between 0 and 1 was generated from a uniform distribution, and the first prey encounter was assigned to a focal fish if $P_{f,1}$ was greater than that random number; if not, a competitor encountered prey first.

If a focal fish encountered the first prey, then prey density decreased (now 44 in 15 l), assuming that prey capture success was 100%. Next, we calculated the time for a focal fish from the start of the experiment to encountering its second prey and the time for the competitor to encounter its first prey as:

$$t_{f,2} = t_{f,1} + T_{h,f} + \frac{V}{a_f(N-1)} \qquad \text{(focal fish)}$$

$$t_{c,1} = \frac{V}{a_c(N-1)} \qquad \text{(competitor)}$$

where $T_{h,f}$ is the size-dependent prey handling time for a focal fish (s prey^{-1}). A focal fish encountered the second prey before the competitor encountered the first prey with a probability of:

$$P_{f,2} = \frac{t_{f,2}}{t_{f,2} + t_{c,1}}$$

The higher probability decided whether a focal fish or a competitor encountered the next prey. The routine was switched if a competitor encountered the first prey before a focal fish did ($P_{f,1} \leq$ random number). In this simulation, the time to encounter the next prey increased as the simulation went on because of the decreasing prey density. The simulation was continued until either all prey were captured or 15 min of simulation time elapsed. 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 consumed by a focal fish in all 120 pairs used in the food competition experiment.

Statistical analysis

A multiple regression approach was applied to explore the effects of body size and behavioral interactions on the magnitude of interference competition between two fish. Interference competition was quantified in two ways from the observed and simulated number of prey consumed by focal fish: (1) The interference difference (observed − simulated), or (2) the interference ratio (observed / simulated). The interference difference (I_d) represents the change in the number of prey consumed in the presence of a competitor. The interference ratio (I_r) shows the proportion of prey consumed under interference competition to that under no interference competition.

Five explanatory variables were used to understand variations in the magnitude of interference competition. Two of them were morphological traits: difference in standard length between two fish (focal fish − competitor) and mean length of the two fish. The other three explanatory variables were counts of behavioral interactions between two individuals (aggression performed, aggression received, and vigilance). Behavioral variables were normalized by log-transformation after adding one. The statistical interactions of these five 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 (v2.9.0, http://www.r-project.org). Statistical significance was determined at $\alpha = 0.05$. Numerical simulations were performed using Fortran programming language.

RESULTS

The coefficients of determination (R^2) for Holling's type II functional response function fitted to the observed data for each of 76 fish ranged from 0.41 to 0.99, with an average of 0.73. Search rate increased as fish length increased ($F_{1, 74} = 34.6$, $P < 0.001$; Fig. 3.1a). Handling time showed a steep decrease as fish length increased for fish smaller than about 10 mm, but it did not change at larger sizes. All parameters of the model that described this trend were statistically significant ($b = 0.772$, $t = 4.126$, $df = 74$, $P < 0.001$; $c = 3.087$, $t = 3.77$, $df = 74$, $P < 0.001$; Fig. 3.1b).

The numerical simulation (exploitative competition only) showed that the number of prey consumed 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 $R^2 = 0.838$; Fig. 3.2a). The observed number of prey consumed (exploitative competition + interference competition) was explained by the size difference, mean size and vigilance ($F_{4, 115} = 31.37$, $P < 0.001$, adjusted $R^2 = 0.523$; Fig. 3.2b). The statistical interaction between size difference and mean size was retained in the model, but it was not significant ($P = 0.071$).

After applying the Akaike information criterion, five variables were retained to explain I_d ($F_{5, 114} = 16.13$, $P < 0.001$, adjusted $R^2 = 0.389$; Table 3.1, Fig. 3.2c). I_d became more negative (stronger effect of interference competition) when the focal fish were smaller than their competitors ($P < 0.001$), and when mean length of the focal fish and competitors increased ($P = 0.003$). I_d became more negative when they exhibited more vigilance ($P < 0.001$). The final model retained aggression received and the interaction

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between vigilance and aggression received, but these behavioral parameters were not statistically significant. All other variables were excluded from the model.

Four variables were retained to explain I_r ($F_{4, 115} = 22.66$, $P < 0.001$, adjusted $R^2 = 0.421$; Table 3.1, Fig. 3.2d). I_r became more negative when the focal fish were smaller than competitors ($P < 0.001$). I_r also became more negative when the focal fish exhibited vigilance ($P < 0.001$). Although mean length was retained in the model, it was not statistically significant ($P = 0.249$). However, the statistical interaction between difference in length and mean length was significant ($P = 0.026$).

DISCUSSION

Our results demonstrate the presence of intraspecific interference competition for food in red drum during their early life. The magnitude of interference competition was related to morphological traits of competing individuals and to their behavioral interactions. Size differences between competitors led to asymmetric interference competition (different magnitude of interference competition depending on body size), and the degree of the asymmetry changed with mean body size of competing individuals. Vigilant behavior negatively affected food consumption in addition to the effects of mean size and size difference. Based on changes in I_d, the 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. Based on changes in I_r, the focal fish suffered more from interference competition when

Table 3.1. Analysis of variance for the effect of sizes and behavioral interactions on interference competition. The dependent variable is I_d, or I_r. Model parameters were reduced using the Akaike information criterion.

Source	Coefficient	DF	SS	F	P
I_d					
Difference in length	+0.22	1	496.2	33.34	< 0.001
Mean length	−0.54	1	138.6	9.31	0.003
Vigilance	−3.94	1	516.4	34.69	< 0.001
Aggression received	−1.89	1	16.3	1.10	0.297
Aggression received × Vigilance	+1.22	1	33.2	2.23	0.138
Residuals		114	1696.9		
I_r					
Difference in length	+0.09	1	3.75	50.65	< 0.001
Mean length	−0.02	1	0.10	1.34	0.249
Vigilance	−0.23	1	2.49	33.58	< 0.001
Difference in length × Mean length	−0.004	1	0.37	5.06	0.026
Residuals		115	8.51		

Figure 3.1. Relationship between standard length of fish and (a) search rate, and (b) handling time. (a) Search rate $= -15.565 + 11.486 \times \ln(\text{Length})$, adjusted $R^2 = 0.31$. (b) Handling time $= \exp(0.772 \times 10^{(3.087/\text{Length})})$, adjusted $R^2 = 0.16$.
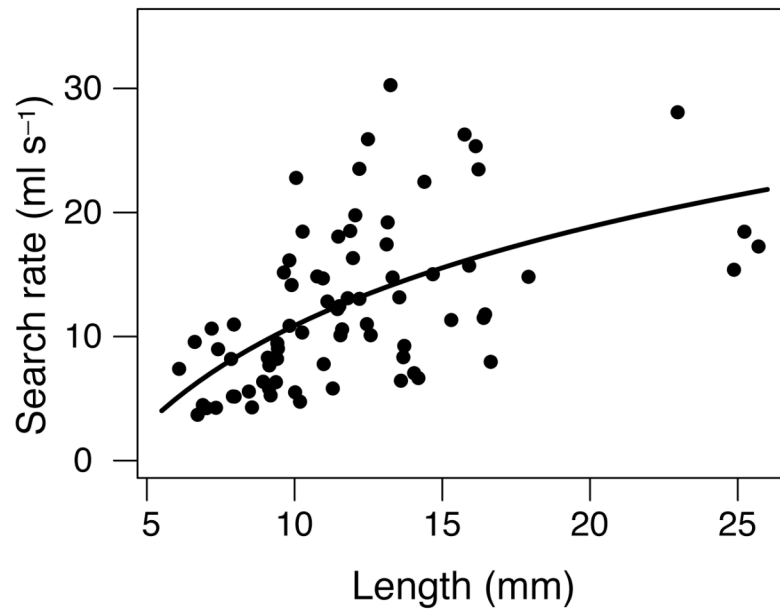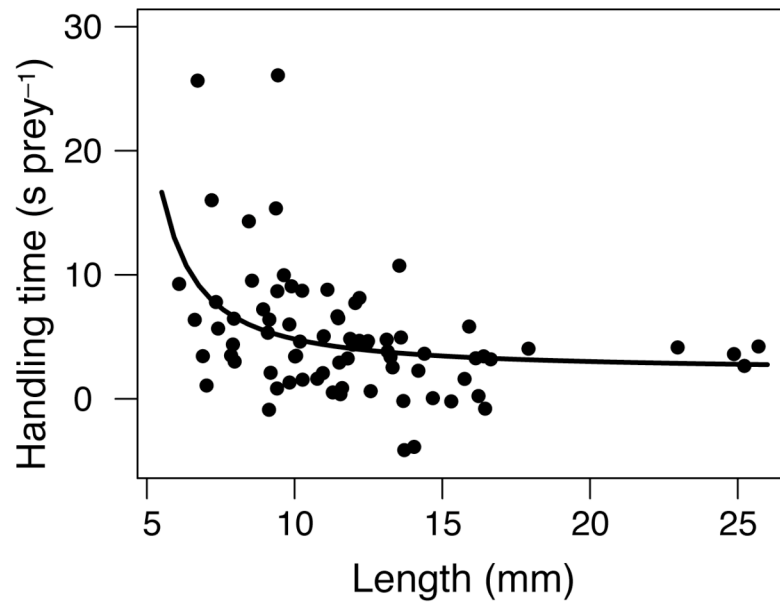
Figure 3.2. Size relationship of competitors and the simulated and observed prey consumed by focal fish. (a) The simulated number of prey consumed by focal fish (exploitative competition only), (b) the observed number of prey consumed by focal fish (exploitative + interference competition), (c) interference competition measured as I_d, the difference between the observed and the simulated number of prey consumed (observed − simulated), and (d) interference competition measured as I_r, the proportion of the observed to the simulated number of prey consumed (observed / simulated). Surfaces were created with penalized regression spline methods (Wood, 2000). Darker surfaces (top) are when the focal fish does not exhibit vigilant behavior (vigilance = 0). Lighter surfaces (bottom) are when focal fish exhibits one vigilant behavior (vigilance = 1).
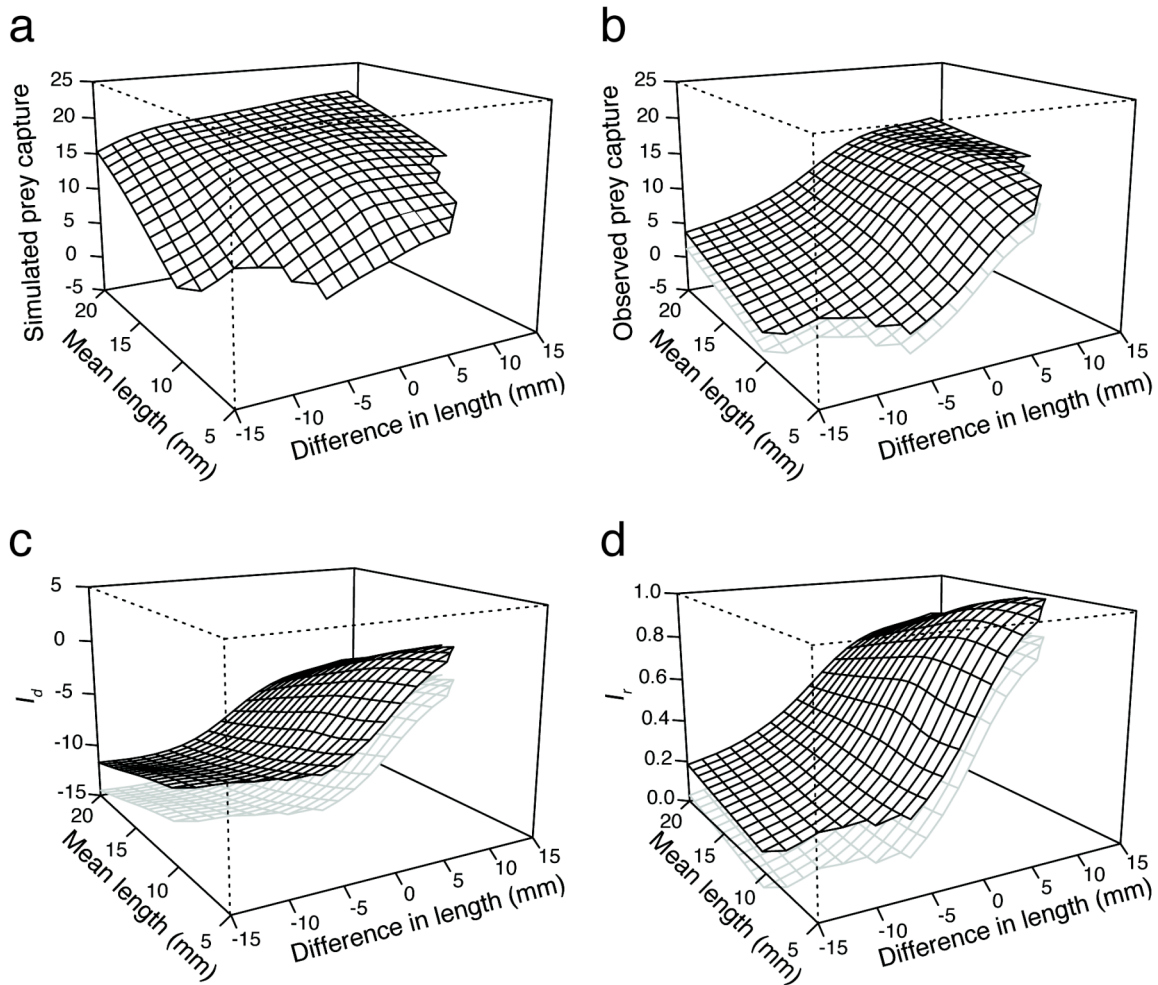
(1) they were smaller than competitors, and (2) they were more vigilant against competitors.

What causes asymmetry in the magnitude of interference competition? If interference competition is caused by agonistic interactions alone, both participants should lose an equal amount of time allocable to feeding during the interactions. As a result, individuals with higher feeding efficiencies (higher search rate, shorter handling time) would forfeit more prey than individuals with lower feeding efficiencies (Beddington 1975) during the same amount of lost time. Under these circumstances, larger individuals should be deprived of more prey than smaller individuals because they have higher feeding efficiencies (Fig. 3.1). Also, if smaller and larger individuals lose an equal amount of time as a consequence of agonistic interactions, both individuals should experience the same proportional reduction in prey consumed (I_r). However, our results showed the opposite trend: smaller individuals were deprived of more prey through interference competition than larger individuals, and they experienced a greater proportional reduction in prey consumed than larger individuals (Fig. 3.2c, d). 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. In terms of the number of prey consumed, interference competition affected a pair of larger fish more strongly than a pair of smaller fish. However, considering that the decrease in proportional interference competition (I_r) was not explained by mean size of a pair, a pair of smaller fish and a pair of larger fish might have spent an equal amount of time for interference regardless of their developmental state (size).

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We think that the cause of asymmetric lost time is due to differences among individuals in the degree of vigilance, since vigilance is a one-way interaction and no kleptoparasitism was observed during the experiment. Vigilance is known to affect feeding rates of waders 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 time lost for feeding (Smallegange *et al*. 2006). Whereas larger individuals may have been less concerned about threats, smaller individuals in our experiments may have spent more time for vigilance to avoid fights rather than foraging. We have demonstrated that smaller individuals show vigilant behavior more often then larger individuals in this species (Nakayama *et al*. 2009). Also, fish may be able to assess a competitor's aggressive status by detecting the subtle hints of a competitor's aggressiveness, such as aggressive display (Ros *et al*. 2006) or chemical signals (Giaquinto and Volpato 1997), which help fish avoid agonistic physical interactions. Our finding that interference competition affects more vigilant individuals more strongly supports the idea that the magnitude of vigilance is the cause of asymmetric interference competition. 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 exhibit high vigilance may increase predation risk because high activity attracts predators (Minderman *et al*. 2006).

Our methods of combining experiments and simulations allow 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 the physical interactions between salamanders. However, this method is difficult to apply when interference competition takes place through non-physical interactions, such as vigilance or chemical substances. Our methods, on the other hand, allow any mechanisms of interference competition because the competing individuals interact freely in any kind of way. In this study, we only tested the effects of size relationships between pairs of fish, but our methods are applicable to investigate other mechanisms of interference competition, such as the effects of competitor density and prey density. Using similar methods of combining the field observations and individual-based models, Scharf *et al.* (2008) reported the effect of competitor density on interference competition when competitors have equal competitive abilities.

Our definition of interference competition was the interactions between individuals that reduce the competitor's access to common resources, which was measured as the decrease in prey consumed by the individuals. However, our methods and definition of interference competition have limitations for understanding effects on population dynamics. 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*), larger fish require a higher density of macroinvertebrates to maintain basal metabolism because

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the increasing prey search rate does not keep up 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). It is necessary to understand not only the direct consequence of interference competition (food intake) but also the after-effects of interference competition (growth and starvation).

Also, the number of prey consumed by individuals can decrease in the absence of interference competition if competing individuals change their prey search rates and handling times. Such changes would alter the magnitude of exploitative competition from those the levels estimated by the simulations. Still, we can conclude that the presence of the competitor negatively affected the feeding rate of an individual as a net effect of interference competition and possibly a change in the magnitude of exploitative competition.

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. Although aggressive interactions (residuals from sizes of competing individuals) did not explain the magnitude of interference competition, it does not mean that aggression is not important. Rather, it implies that the effects of aggressive behaviors on interference competition were already explained by the size relationship between competing individuals. If food resources are routinely limited in the nursery habitats, asymmetric competition of different sizes of young could play an important role in their survival. If larger individuals are favored in growth and survival,

the cohorts spawned early in the spawning season have an advantage when small

individuals from later cohorts arrive in the nursery habitats. Further investigations on

how interference competition affects their growth are required to understand different

survival among cohorts and population dynamics.

Chapter 4: The interplay of competitor size, behavioral interactions and habitat quality in habitat competition

ABSTRACT

We explored the effects of competitor size, behavioral interactions and habitat quality on habitat competition among coastal fish larvae (red drum). In habitat-choice experiments, we tested the hypotheses that (1) newly settled individuals are displaced from the preferred habitat by larger conspecifics, (2) competitor size and behavioral interactions alter the probabilities of habitat shift between the preferred and unpreferred habitats, and (3) individuals increase their time spent in the preferred habitat when the difference in habitat quality between the two habitats is higher (via the addition of food). Continuous-time Markov chain models revealed that the presence of larger conspecifics inhibited a competitor from entering the preferred habitat, whereas the probabilities of a habitat shift for size-matched conspecifics were the same as when individuals were alone. Individuals moved more often to the unpreferred habitat when they received aggressive behavior from conspecifics. When food was present in the preferred habitat (increased difference in quality between habitats) individuals were less likely to leave the preferred habitat, but the presence of food did not attract individuals from the unpreferred habitat to the preferred habitat. The complex interplay between size, behavior and habitat quality has been demonstrated to account for observed changes in habitat use.

INTRODUCTION

Habitat selection is one of the central topics in ecology that links behavior to community and evolutionary ecology (Morris 2003). Most organisms live in spatially heterogeneous environments, and their fitness changes depending on the patches (discrete habitats) in which they live. Organisms distribute themselves among patches so that no individual can increase fitness by moving to other patches (Fretwell and Lucas 1970). This ideal free distribution theory has been expanded by numerous studies (Parker 1978; Morris 1989; Sjerps and Haccou 1994; van der Meer 1997; Railsback and Harvey 2002; Cressman *et al*. 2004; Cressman and Křivan 2006; Houston 2008), however, detailed mechanisms for habitat selection at the level of individual behavior have been rarely incorporated into such models.

Competition for habitat use is often asymmetric. Dominant phenotypes displace subordinate phenotypes from the habitats that are optimal for both phenotypes (Werner and Hall 1976; Maitz and Dickman 2001; Jonsson *et al*. 2008). As a consequence, subordinates are forced to use suboptimal habitats, depending on the densities of dominants and subordinates in optimal habitats (Young 2004), or they become allopatric through adaptive radiation (Connell 1980). In intraspecific competition, the consequences of asymmetric competition are often explained by body size and size-related behavioral interactions. For example, larger conspecifics may have superiority over smaller individuals in interference competition (Persson 1985), whereas size-matched conspecifics sometimes exhibit the most intense competition with escalated fighting (Smallegange *et al*. 2006). It has also been reported in salmonids that individuals can

recognize their dominance rankings based on their body size relative to competitors, which allows them to resolve competition for habitat use in a hierarchical way without actually fighting (Nakano 1995). On the other hand, the habitat use observed in damselfish results from aggressive interactions (Holbrook and Schmitt 2002). Another important factor that can alter competitive environments is the degree of heterogeneity among patches (Hampton 2004; Huss *et al.* 2008). Increased fitness in one patch may attract more individuals that are following the ideal free distribution, but it may also change the competitiveness of co-occurring individuals.

Here, we disentangled the effects of competitor size, behavioral interactions and habitat quality on competition for habitat in red drum (*Sciaenops ocellatus*) larvae. This species settles at about 7 mm standard length in shallow, structured habitats after about 2 weeks in a pelagic period and stay there until they reach about 25 mm (Rooker *et al.* 1998). Because parents are batch spawners (spawning multiple times during a single spawning season), successive waves of cohorts arrive at the settlement habitats, creating different size structures and densities depending on the time of the season. In the wild, both large and small red drum larvae are found in the shallower parts of submerged aquatic vegetation, whereas only small larvae are found in the deeper edges of that habitat (Pérez-Domínguez 2004), inferring that light intensity may play an important role in competition for habitat use in this species. We hypothesized that (1) newly settled individuals spend less time in a lighter (preferred) habitat and more time in a darker (unpreferred) habitat in the presence of larger conspecifics, (2) aggressive behavioral interactions result in the aggressors spending more time in their preferred habitat,

whereas vigilant individuals spend more time in their unpreferred habitat, and (3) individuals increase their time spent in a preferred habitat when the difference in habitat quality between the two habitats is higher (through the addition of food). First, we demonstrated that red drum larvae prefer a lighter habitat to a darker habitat, and then we tested the effects of the size of competitors, behavioral interactions and the presence of food in a multi-factorial way using continuous-time Markov chain models.

MATERIAL AND METHODS

Six batches of red drum eggs were obtained from captive adults at the University of Texas Marine Science Institute (Port Aransas, Texas, USA) on March 11, 15, 22, 23, 26 and April 1, 2009. Spawning was induced by adjusting photoperiod and water temperature. Eggs were spawned at about 2000 h, collected at about 1000 h the next day, sterilized with 5.0×10^{-5} % formalin in sea water for 30 min, and put in 60-l fiberglass rearing tanks, 5,000 eggs per tank. Eggs hatched the next day. Larvae were fed once a day a mixture of rotifers (enriched with Algamac 3000, Aquafauna Bio-Marine, Inc., Hawthorn, California, USA) and artificial diets (Otohime, Reed Mariculture, Inc., Campbell, California, USA) from 1–10 days after hatching, and enriched *Artemia* nauplii and artificial diets from 10 days after hatching and thereafter. Larvae were fed *ad libitum* until they reached target sizes. Water temperature was 27.0 ± 0.3°C (mean $\pm$ SD), and salinity was 26.6 ± 0.8 ppt. No differences in these water conditions were found among the six tanks (ANOVA, temperature: $F_{5, 382} = 0.96$, $P = 0.44$, salinity: $F_{5, 382} = 1.60$, $P = 0.16$). Photoperiod was set at 12 h light and 12 h dark each day.

We created an experimental tank (80 cm wide × 15 cm deep) with two distinct habitats that differed in light intensity (Fig. 4.1). One end of the tank was lit from above with a 150-W incandescent light bulb, and the other side was covered with a black wooden board. We assumed that the light attenuation was negligible through the 15 cm water depth. Three sides of the tank were covered with black paper to minimize visual distractions for the fish, and the front side was left transparent for behavioral observations. A transparent Plexiglas partition was placed in the middle of the tank parallel to the front side of the tank to restrict the perspective depth to 15 cm. An aquarium heater was put behind the partition to maintain a constant temperature during trials.

When fish reached about 8 mm in standard length, 10 focal fish were randomly selected from the rearing tank one day before the experiment. Two to five fish of the same size (size-matched competitors) and two to five larger competitors (about 14 mm) were also selected one day before the experiment. Size-matched competitors were at the same age as the focal fish, and larger competitors were 10–12 days older than the focal fish, which mimics the natural interval of successive cohorts arriving at the nursery habitats (Peters and McMichael 1987). Focal fish and the size-matched competitors were put in 100-ml plastic containers individually with food (50 *Artemia* nauplii), and the larger competitors were put in 1-l plastic containers individually with food (200 *Artemia* nauplii).

On each of the following 3 consecutive days, each focal fish was randomly assigned to one of three treatments: no competitor, with a size-matched competitor, and

with a larger competitor. Each focal fish was tested in all treatments in 3 days. Each trial, regardless of treatment, began by placing a focal fish in a white PVC pipe ($\varnothing 5$ cm, 30 cm long) that stood vertically in the middle of the tank (40 cm from the left end of the tank). Then, the competitor (except for a 'no competitor' treatment) was introduced into the tank. After 10 min of acclimatization, the pipe was gently lifted, releasing the focal fish into the tank. The light side and the dark side of the tank were recorded from the front using two video recorders (Digital Handycam, DCR-TRV350, Sony Corp., Tokyo, Japan). After 20 min of recording, food (50 *Artemia* nauplii) was gently put into the corner of the light side using a pipette, and recording was continued for 10 min. *Artemia* stayed in the light side during this period due to their positive phototaxis and poor locomotor abilities. The order of focal fish tested was randomized each day. The experiment was conducted from 0900 h to 1800 h each day. Water was changed after each experiment. Water temperature was 26.7 ± 0.5 °C, and salinity was 27.1 ± 0.6 ppt (mean $\pm$ SD). In total, three sets of the experiments were conducted (30 focal fish). Sex of the fish was not determined. Animal care and experiments were conducted in compliance with Institutional Animal Care and Use Committee of the University of Texas at Austin (protocol number 07102301).

After the experiments, we euthanized the fish with MS-222 and measured their standard length. We measured the time and the type of behavioral interactions (except 'no competitor' treatment), using an event-recording computer program (JWatcher v1.0, http://www.jwatcher.ucla.edu) by playing back the video at three times the real-time speed. Behavioral interactions were categorized into three types: an aggressive behavior

performed by a focal fish, aggressive behavior performed by a competitor, and a vigilant

behavior performed by a focal fish. An aggressive behavior was recorded when one fish

chased the other fish from behind, or attacked with a rapid swimming speed. A vigilant

behavior was recorded when a fish escaped with a rapid swimming speed without

receiving an aggressive behavior from the other. When two fish faced each other and

swam away in opposite directions rapidly, a vigilant behavior was recorded for both fish.

We also measured the timing of habitat transition between the two habitats (the light side

and the dark side) of focal fish and competitors.

Statistical analysis

The time spent by focal fish in the light side (min per 10-min observation period)

was compared among treatments (no competitor, with a size-matched competitor, with a

larger competitor) and between presence and absence of food using a repeated measures

2-way ANOVA. The number of behavioral interactions observed during the experiment

was log-transformed after adding one and compared between competitor types using a

paired t-test.

The habitat transition of focal fish between the light side and the dark side was

analyzed using a continuous-time Markov chain model (msm v0.8 in R v2.9.0,

http://www.r-project.org). Three factors were included in the models: competitor type (3

levels: no competitor, size-matched competitor, larger competitor), the type of behavioral

interactions between two competing fish (4 levels: no interactions, aggressive behavior

performed, aggressive behavior received, vigilant behavior), and the presence of food (2

levels). We tested the effects of these factors on the transition intensity between two

habitats in a multi-factorial way. We performed a χ^2 test to see whether including factors

improved the model, with a χ^2 statistic equals a deviance between two models, the

degrees of freedom equals the difference in the number of degrees of freedom between

two models (Vanebles and Ripley 2002). Also, the ratios of transition intensities were

computed by bootstrapping 1000 times to estimate statistical significance.

We obtained log-linear effects for each factor (competitor size, behavioral

interactions, food) compared with the model without covariates. When a focal fish was

with a competitor, we also used the Markov chain models with 4-state transitions (both

fish in the light, a focal in the light and a competitor in the dark, a focal in the dark and a

competitor in the light, and both fish in the dark) to test the differences in transition

intensities of focal fish with competitor size (size-matched or larger), taking into account

the competitor's habitat use. We also compared the effects of the presence of a

competitor on the transition intensities of focal individuals before and after the

competitor exhibited an aggressive behavior to determine whether focal individuals

learned the competitors' aggressiveness histories (i.e., an incidence of aggressive

behavior). A significance level (α) was set at 0.05 for all statistical tests.


RESULTS

Standard lengths of the fish we used in the experiments were 8.3 ± 0.1, 8.2 ± 0.1

and 13.9 ± 0.2 mm for focal fish, size-matched conspecifics and larger conspecifics,

respectively (mean $\pm$ SE, n = 30 each). When fish were alone without food, the time

spent in the light side of the tank was significantly greater than 5 min, the expectation for random habitat use ($t = 13.4$, d.f. = 29, P < 0.001). The time spent by focal fish in the light side of the tank was significantly influenced by competitor type ($F_{2,58} = 7.0$, P = 0.002) and the presence of food ($F_{1,29} = 17.3$, P < 0.001; Fig. 4.2). No significant interaction between competitor type and the presence of food was found ($F_{2,58} = 1.4$, P = 0.245). When fish were alone, they spent 8.79 ± 0.22 min in the light side of the tank. When fish were with size-matched competitors, they spent a similar period in the light side (8.73 ± 0.22 min; paired-t test, $t = 0.21$, d.f. = 59, P = 0.836). However, focal fish decreased the time spent in the light habitat when with larger competitors (7.14 ± 0.38 min; paired-t test, $t = 3.7$, d.f. = 59, P = 0.001 after Bonferroni corrections). Focal fish spent more time in the light side after food was added (8.73 ± 0.26 min) than before (7.71 ± 0.22 min).

Focal fish performed 0.10 ± 0.06 (mean $\pm$ SE) aggressive behaviors in 10 min to size-matched conspecifics but none to larger conspecifics. Focal fish received a greater number of aggressive behaviors from larger conspecifics (1.20 ± 0.33) than the size-matched competitors (0.20 ± 0.09, $t = 3.2$, d.f. = 29, P = 0.003). The number of vigilant behaviors was not different between the competitor types (with size-matched conspecifics: 1.97 ± 0.41, with larger conspecifics: 2.30 ± 0.46, $t = 0.52$, d.f. = 29, P = 0.608). No cannibalism was observed.

The two-state Markov chain model without covariates (null model) showed that focal fish were four times more likely to shift from the dark side to the light side than to

Figure 4.1. Light intensity in the experiment tank. Light intensity was measured every 10 cm from the left end of the tank and averaged for three measurements. The dashed line marks the position of a habitat border between the light side and the dark side (the center of the tank).
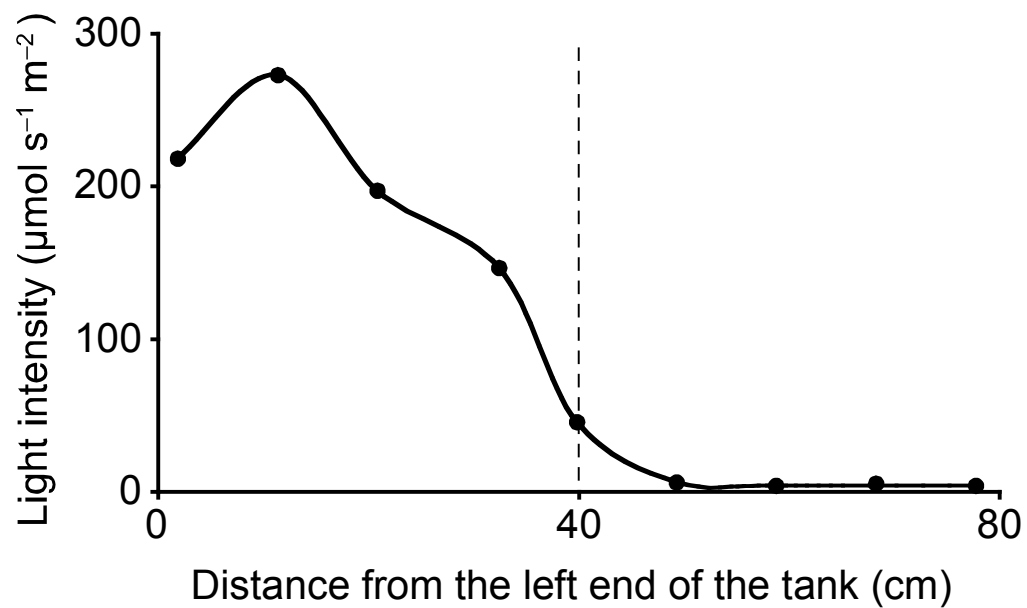
shift in the opposite direction ($q_{21}/q_{12} = 4.12 \pm 0.25$, P < 0.001, Fig. 4.3a). Including the

covariates in the null model significantly improved the model ($\chi^2_{12} = 208.6$, P < 0.001).

Aggressive behavior from conspecifics to focal fish significantly increased the

transition intensity of focal fish from the light side to the dark side, whereas the other

behaviors did not affect the transition intensities (Fig. 4.3b). The presence of size-

matched conspecifics did not affect the transition intensities of focal fish, whereas the

presence of larger conspecifics significantly decreased the transition intensity of focal

individuals from the dark side to the light side (Fig. 4.3c). The presence of food

decreased the transition intensity of focal fish from the light side to the dark side, but it

did not affect the transition intensity from the dark side to the light side (Fig. 4.3d). The

effects of the presence of competitors on the transition intensities of focal individuals did

not change before and after the occurrence of an aggressive behavior performed by either

size-matched conspecifics or larger conspecifics (the log-linear effects after the

occurrence of an aggressive behavior were not significant compared to before an

aggressive behavior, P > 0.05 for both directions and both competitor types).

The 4-state Markov chain model without covariates (Fig. 4.4a) showed that two

fish were approximately two to three times more likely to stay apart than for both to stay

in the dark side of the tank ($q_{32}/q_{23} = 3.44 \pm 0.59$, P < 0.001; $q_{34}/q_{43} = 2.61 \pm 0.38$,

P < 0.001), and that they were four to five times more likely to stay together in the light

side of the tank than to occupy different habitats ($q_{21}/q_{12} = 3.59 \pm 0.32$, P < 0.001,

$q_{41}/q_{14} = 5.76 \pm 0.61$, P < 0.001). Adding covariates (competitor types) significantly

improved the model ($\chi^2_8 = 126.6$, P < 0.001). Presence of larger conspecifics affected

transition intensities of focal individuals: In the presence of larger conspecifics, focal individuals were more likely to use the dark side of the tank alone than in the presence of size-matched conspecifics (Fig. 4.4b).

DISCUSSION

Our results revealed that the presence of competitors, behavioral interactions and the presence of food altered habitat use of individuals in different ways. Red drum larvae stayed longer in the light side of the tank when they were alone; therefore, we will hereafter refer to the light side of the tank as the preferred habitat and the dark side of the tank the unpreferred habitat. Individuals moved to the unpreferred habitat when they received aggressive behavior from conspecifics (Fig. 4.3b), and the aggressive behavior was performed more by larger conspecifics than size-matched conspecifics. The presence of larger conspecifics hindered smaller individuals from entering the preferred habitat, whereas the presence of size-matched conspecifics did not change the likelihood of focal individuals' moving between the preferred and unpreferred habitats compared to when they were alone (Fig. 4.3c). The more detailed 4-state Markov model (Fig. 4.4) showed that larger conspecifics tended to stay in the preferred habitat and that focal individuals stayed in the unpreferred habitat alone to avoid a larger conspecifics. Enhancement of the preferred habitat through the addition of food kept individuals in the preferred habitat if they were already there, but it did not attract individuals from the unpreferred habitat (Fig. 4.3d). The interplay between these factors accounts for changes in the observed habitat use by focal individuals in the presence of a larger competitor or food (Fig. 4.2).

Figure 4.2. Residence time of focal individuals in the light side of the tank when they are alone, with size-matched conspecifics and with larger conspecifics (mean ± SE, min in 10 min). White bars indicate before food was added in the light side, and shaded bars indicate after food was added.
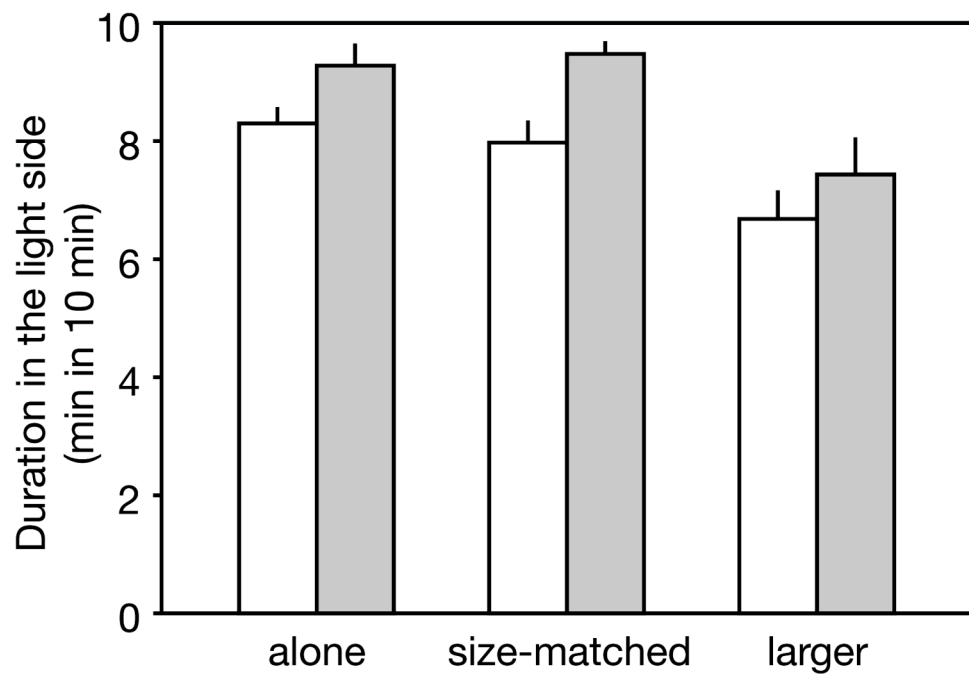
Figure 4.3. Continuous-time Markov chain model with 2-state transitions (light and dark). (a) Transition intensities from the light side to the dark side (q_{12}) and from the dark side to the light side (q_{21}) without covariates. (b) Log-linear effects of behavioral interactions. Top: aggressive behavior performed by focal individual, middle: aggressive behavior received by focal individual, bottom: vigilant behavior. (c) Log-linear effects of the presence of conspecifics. Top: size-matched conspecifics, bottom: larger conspecifics. (d) Log-linear effect of food. Widths of the arrows indicate magnitudes. Filled arrows indicate positive effects and open arrows indicate negative effects. Dashed lines indicate no significant effect.
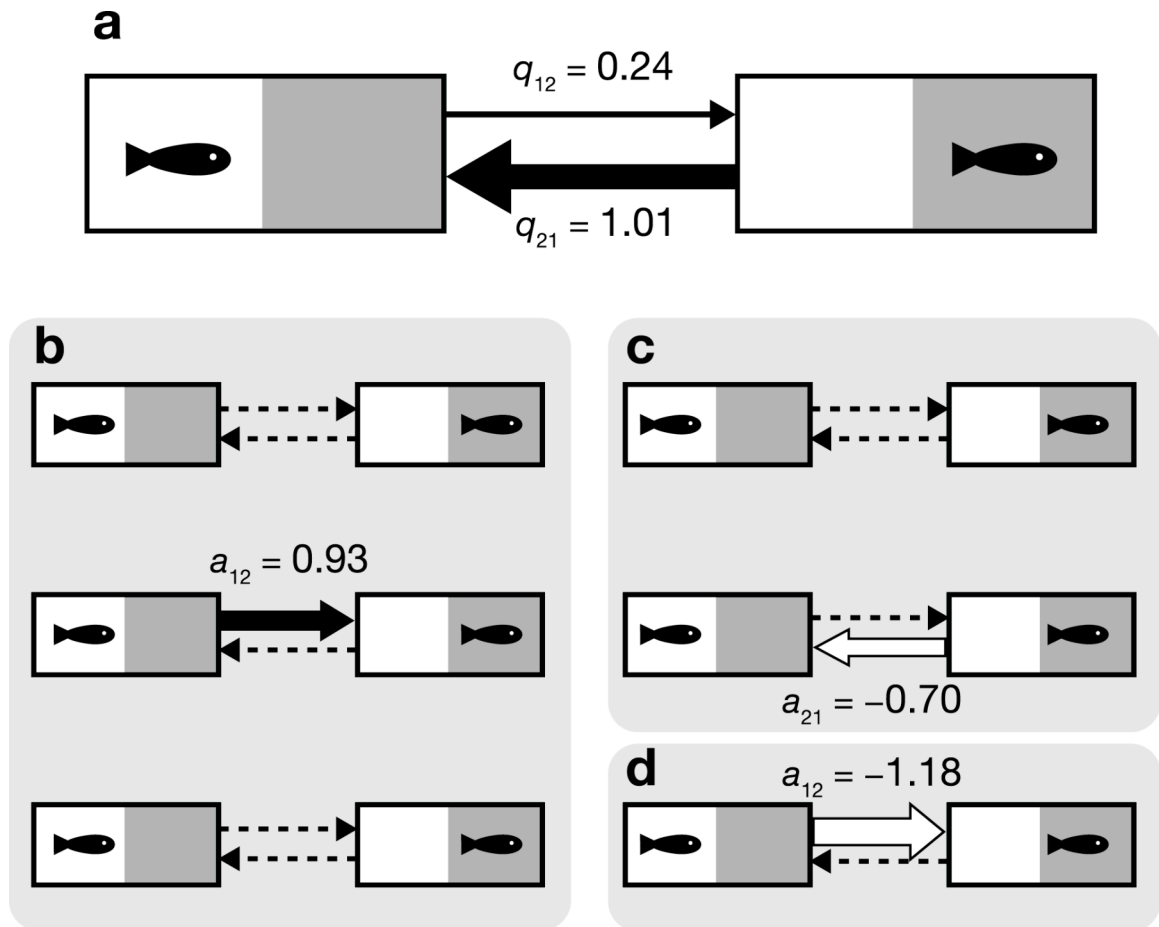
Figure 4.4. Continuous-time Markov chain model with 4-state transitions (both fish in the light side, focal fish in the dark and the competitor in the light, both fish in the dark, focal fish in the light and the competitor in the dark). Black fish represent focal individuals, and white fish represent competitors. (a) Transition intensities without covariates. (b) Log-linear effects of larger conspecifics on transition intensities. Widths of arrows indicate magnitudes. Filled arrows indicate positive effects and open arrows indicate negative effects. Dashed lines indicate no significant effect.
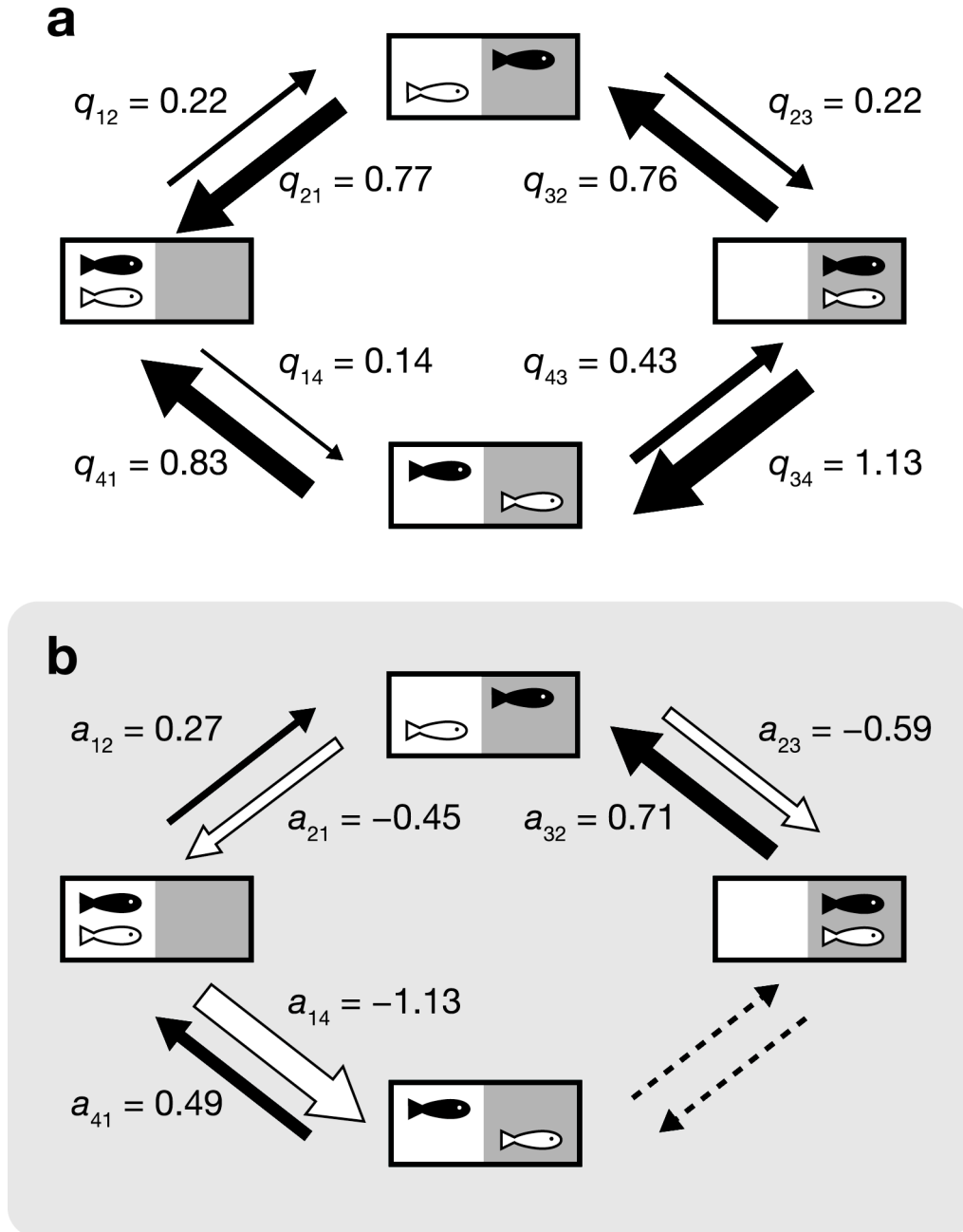
These results may explain the natural patterns of habitat use in red drum larvae. Specifically, smaller red drum larvae occur in the periphery of seagrass beds and both smaller and larger larvae occur in the center (Pérez-Domínguez 2004), consuming partially overlapping prey fields (Soto *et al.* 1998). Size-dependent habitat segregation is often seen as a consequence of intraspecific competition without the developmental change in habitat preference (Bohlin 1977; Cutts *et al.* 1999; Davey *et al.* 2005). Therefore, we can deduce that red drum larvae after settlement experience density- and size-dependent intraspecific competition for habitat use without segregating by size to different niches. It is reasonable to think that competition does not result in niche specialization by size class in the early lives of organisms that breed several times within a single reproductive season, since early cohorts and late cohorts experience different competitive environments. Earliest cohorts settle in nursery areas devoid of older conspecifics, having only members of their own cohort as conspecific competitors. However, late cohorts may experience not only intra-cohort competition but also inter-cohort competition with older conspecifics. Therefore, the strategy for habitat use in early life for such organisms would be to use the preferred habitat if possible, instead of adapting to different habitats at different sizes.

When small red drum larvae are transported inshore for settlement, two scenarios can describe the process. First, the larvae may selectively settle directly from the pelagic stage into the preferred habitat. These newly settled larvae would be able to stay with larger conspecifics in the same habitat unless larger conspecifics exhibit aggressive behavior toward them. Therefore, environmental factors that affect aggressiveness would

be crucial for determining whether newly settled individuals use their preferred habitat. One such factor could be food abundance. As food density increases relative to competitor density, competitors show less aggressive behavior because of the decreased intensity of interference competition (Smallegange *et al.* 2006). The presence of food also increases the quality of the preferred habitat, which would also retain newly settled individuals in the preferred habitat (Fig. 4.3d). Also, if fish density is high and the preferred habitat provides better refuge from predation, high predation pressure may provoke aggressive interactions related to competition for space. Aggressive interactions displace subordinate individuals to unpreferred habitats in damselfish competing for refuge in coral reef habitats (Holbrook and Schmitt 2002).

In the second scenario, red drum larvae may settle randomly among preferred and unpreferred habitats, then those in unpreferred habitat would move to the preferred habitat. In this scenario, in addition to the factors mentioned above, the density of larger conspecifics would be a factor for newly settled larvae to use the preferred habitat. Since our results revealed that the transition intensities of focal individuals did not change before and after an aggressive behavior by conspecifics, the presence of larger conspecifics in the preferred habitats would prevent newly settling individuals from entering the preferred habitats regardless of the aggressiveness of larger conspecifics. Since they had no experience with larger conspecifics prior to the experiments, we can assume that red drum larvae have an innate ability of self-recognition and assessment of competitive abilities of conspecifics without actual competition. This may have evolved through historical competition. Avoiding physical interactions is beneficial as it reduces:

(1) the chance of injury (Leimar *et al.* 1991), (2) energetic expenditures (Briffa and Sneddon 2007), and (3) time spent in competition, making it available for other activities (Smallegange *et al.* 2006). Therefore, competition for habitat use in red drum larvae would result from a combination of current competition (aggressive behavior) and competition past (innate avoidance of larger conspecifics).

It is understandable that focal individuals were more likely to stay longer in the light side of the tank after food was added than before: The preferred habitat became more preferable. Addition of food increased the difference in habitat quality between two sides of the tank. In our experiments, however, the probability of transition from the unpreferred habitat to the preferred habitat did not increase after food was added. One possible reason for this is that focal individuals in the unpreferred habitat could not detect change in quality of the preferred habitat. This violates one of the assumptions in the ideal free distribution theory, in which animals are omniscient. However, theories predict that the ideal free distribution is an evolutionarily stable strategy when animals undergo myopic patch selection without global information on habitat qualities (Cressman and Křivan 2006; Křivan *et al.* 2008). In our experiments, the longer residence time in the preferred habitat with food would be due to a combination of: (1) a higher probability of transition from the unpreferred to the preferred habitat even without food, and (2) a lower probability of leaving the preferred habitat after food was added. In this way, animals can find better habitats without being omniscient.

When fish density is high, the presence of competition with size-matched conspecifics can negatively affect habitat use of individuals (Pimm and Rosenzweig

1981; Reed and Dobson 1993; Young 2004), however, some organisms are attracted to size-matched conspecifics and do not compete with them (Reed and Dobson 1993; Donahue 2006). It is possible that the fish density in our experiments was not high enough to create the negative effect of size-matched conspecifics on habitat use by individuals. However, to force fish to compete for habitat use, we used a much higher density of red drum larvae in the experiments (33.3 m^{-2} when two individuals stayed in the same habitat) than the highest density reported in the wild (11 m^{-2}; Rooker *et al.* 1999). Although we cannot dismiss the effects of density on competition for habitat use from our experiments, we can assert that the effect of size-matched conspecifics on competition for habitat use is weaker than that of larger conspecifics and negligible at densities much lower than in our experiments.

Our results revealed the contrasting effects of different factors (size of competitors, behavioral interactions and the presence of food) on habitat use through changes in transition intensities between habitats. The concurrent presence of aggressive behavior and intrinsic recognition of competitive ability suggest that both current and past competition contributes to patterns of habitat use in red drum larvae. We also suggest that myopic habitat selection can allow larvae to locate and remain in better habitats when animals move frequently between habitats. Recognizing the mechanisms of competition for habitat use at the level of behavioral interactions contributes to a deeper understanding in population dynamics, community ecology and evolution of life-history strategies.

Chapter 5: Multiple breeding as a strategy to avoid interference competition among offspring

ABSTRACT

Multiple breeding (reproducing multiple times in a single reproductive season) has been considered a bet hedging strategy in time to cope with environmental uncertainty of offspring survival, but it can change competitive environments for offspring through its effects on size structure in the nursery habitat. Our goal was to determine the optimal multiple-breeding traits (spawning interval and number of spawning events per season) that maximize total offspring survival, taking into account the effects of size- and density-dependent interference competition among offspring on their growth and habitat use in spatially heterogeneous environments. Using an individual-based model, we simulated the survival of individual red drum larvae (*Sciaenops ocellatus*) over a spawning season under different combinations of spawning interval and number of spawning events. The model took into account the seasonally decreasing water temperature experienced by larvae, which influenced survival through larval growth rate. Our model demonstrated that multiple breeding can be an adaptive strategy to reduce competition among offspring even without considering bet hedging against environmental uncertainty for offspring survival. Increasing number of spawning events and spawning interval were favored as interference competition among offspring intensified. We also found that low-intensity interference competition among offspring increased total offspring survival, suggesting that interference competition is not

necessarily detrimental to parental fitness. This is the first study to demonstrate that the detrimental effects of intraspecific competition on year-class survival can be ameliorated by specific reproductive traits of adults, and that reproductive traits exhibited in nature match expectations for minimizing competition among offspring.

INTRODUCTION

Many organisms reproduce multiple times during their life span, and this is viewed as bet hedging in time to cope with uncertain environmental conditions for offspring survival (Murphy 1968; Charnov and Schaffer 1973; Schaffer 1974; Philippi and Seger 1989; Wilbur and Rudolf 2006; Zeineddine and Jansen 2009). That is, spreading reproductive effort over multiple clutches enables parents to avoid catastrophic failure of recruitment and increase geometric mean offspring survival when the variance in offspring survival is large compared to the post-reproductive survival of parents (but see Orzack and Tuljapurkar 1989; Benton and Grant 1999). Organisms may reproduce once in a reproductive season over several seasons (i.e., iteroparity). Alternatively, they may reproduce multiple times within a single reproductive season (i.e., multiple breeding), which is seen in diverse taxa, including mammals (Fuchs 1982), birds (Slagsvold 1984; Finke *et al.* 1987; Verhulst *et al.* 1997), amphibians (Thumm and Mahony 2002), fishes (Conover 1985; McEvoy and McEvoy 1992) and arthropods (Forsman 2001; Wada *et al.* 2008). However, much less attention has focused on the multiple-breeding strategy compared to iteroparity.

Bell (1976) explored these two strategies (referred to as "seasonal iteroparity" and "continuous iteroparity") by analyzing intrinsic population growth rates without including density dependency and concluded that multiple breeding within a single reproductive season is favored when organisms mature early in life and produce large numbers of eggs. However, the multiple-breeding strategy may, itself, alter offspring survival through its effect on the quality of the nursery habitat, specifically the density and size distribution of conspecifics. Bulmer (1985) analyzed the conditions that favor iteroparity when offspring survival is density-dependent by adopting the model of Charnov and Schaffer (1973), confirming that variability in offspring survival favors iteroparity, whereas variability in parent survival favors semelparity. In the multiple-breeding strategy, however, parents can reduce competition among offspring by adjusting their pattern of multiple breeding, such as the number of reproductive events and the intervals between them. For example, exploitative competition (an indirect negative interaction) among offspring for parental care may exert selection pressure on the reproductive interval to reduce temporal overlap between clutches in multiple-breeding birds (Milinski *et al.* 1995; Verhulst *et al.* 1997; Grüebler and Maef-Daenzer 2008). Similarly, interference competition (a direct negative interaction) within a brood is a selective force that determines optimal brood size in a single reproductive event (Godfray 1995). However, we do not know at all how interference competition among offspring influences the optimal reproductive strategy for multiple breeding, even though interference competition is known from diverse taxa (Schoener 1983). If interactions among offspring change offspring fitness through competition, the behavioral strategies

of offspring that maximize their own fitness could feed back to the reproductive strategies of the parents (Trivers 1974).

Multiple breeding can reduce offspring density within a brood, but it can increase size variability when multiple broods overlap in time as a consequence of short reproductive intervals. One may expect that parents would increase their breeding interval to avoid competition among successive broods, since larger individuals usually have the advantage in interference competition (Persson 1985). Asymmetric interference competition (unequal division of resources among competitors) can result in habitat segregation when environments are heterogeneous in resources that impact growth and mortality, with dominant individuals occupying better habitats and displacing subordinate individuals (Werner and Hall 1976; Maitz and Dickman 2001; Jonsson *et al.* 2008). One may expect a similar situation between early and late broods of conspecifics when they overlap, considering the larger size of early broods when late cohorts appear. However, the situation would be more complex because the dominant status of an individual in competition is dynamic over time, which would affect the multiple-breeding traits of parents. Although several studies have examined asymmetric interference competition for habitat (Sutherland and Parker 1985; Bautista *et al.* 1995; Milinski *et al.* 1995; van der Meer 1997), previous studies have not examined habitat competition among offspring in the context of parental breeding traits.

Multiple breeding is commonly seen in fishes, often referred to as batch spawning. Red drum (*Sciaenops ocellatus*) is a coastal fish that occurs in subtropical and temperate areas and exhibits batch spawning (Wilson and Nieland 1994). Females spawn

synchronously several times during fall (Wilson and Nieland 1994), presumably at about 2-week intervals based on the size distribution of larvae in the settlement habitats (Peters and McMichael 1987). Each spawning event takes place daily for 3–4 consecutive days (S. Nakayama, pers. observation of captive spawners). During 2–3 weeks of pelagic life, larvae are transported into bays by tidal currents (Peters and McMichael 1987; Brown *et al*. 2005) and settle into shallow, structured habitats, such as seagrass beds and oyster beds, at about 7 mm standard length (Rooker and Holt 1997). Larvae feed mainly on copepods and mysids during the settlement period (Soto *et al*. 1998). Fish bigger than 25 mm are rarely caught in these habitats, probably due to a habitat shift to deeper areas (Peters and McMichael 1987). Because a wide range of sizes is observed simultaneously (about 7–25 mm), and the density is locally high (Rooker *et al*. 1999), one can expect interference competition within and among cohorts. At these early life stages, this species exhibits size-dependent aggressive behavior (Nakayama *et al*. 2009), so competition between size classes would be asymmetric.

Using *S. ocellatus* as a model species, we explored the potential for selection pressure imposed by interference competition among larvae to alter spawning traits (spawning interval and number of spawning events) of parents. We hypothesized that interference competition among early life stages affects overall survival of offspring, which, in turn, influences the spawning traits of parents. Our specific hypotheses were that, as the magnitude of interference competition among larvae increases, (1) total recruitment decreases, (2) early cohorts have greater chances of recruiting (faster growth, lower mortality) than later cohorts due to the size-based asymmetric competition, and (3)

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parents increase the spawning interval and increase the number of spawning events to avoid inter- and intra-cohort competition.

MODEL DISCRIPTION

Our goal was to determine the optimal spawning traits (spawning interval and number of spawning events per season) that maximize total offspring survival, taking into account the effects of size- and density-dependent interference competition among larvae on their growth and habitat use in spatially heterogeneous environments. Using an individual-based model, we simulated the survival of individual larvae over a spawning season under different combinations of spawning interval and number of spawning events. The model took into account the seasonally decreasing water temperature experienced by larvae, which influenced survival through larval growth rate. We tracked growth and survival of 15,000 "super-individuals" that represented the whole population of larvae. At the time of spawning, each super-individual represented 10,000 identical larvae (i.e., the worth of one super-individual was 10,000). The worth of a super-individual decreased as it experienced predation and starvation mortality. We eliminated a super-individual from the model when its worth became less than 0.001 because it had virtually no effect on the growth and habitat use of other individuals. The biological information used in the model was mainly based on traits of *S. ocellatus* in the northern Gulf of Mexico.

Environments

We used an area (1 km by 1 km) randomly taken from Redfish Bay, Texas, USA

(27° 54' 29.8" N, 97° 4' 35.6" W) for the settlement habitats for model larvae (Fig. 5.1).

The habitat we modeled was composed of 36.1% seagrass beds and 63.9% open water

(sandy bottom). The map was divided into 200 × 200 grids, with each cell being 5 m

square and assigned to either open water or vegetated habitat. Water depth was set to a

constant 30 cm for all grids, which is a typical height of seagrass beds inhabited by *S.*

ocellatus larvae (Holt *et al.* 1983). Water temperature was homogeneous through all cells

and decreased as the reproductive season progressed (Fig. 5.2). We modeled a 10-year

average water temperature (1998–2007) from records of two observation stations in the

Redfish Bay (Ingleside and Port Aransas; Texas Coastal Ocean Observing Network) with

a trigonometric function. Photoperiod was set at 12 h light and 12 h dark throughout the

reproductive season.

Each cell had two prey types, calanoid copepods (*Acartia* spp.) and mysids

(*Neomysis* spp.). The populations of both prey species increased according to logistic

growth functions, and the rates of increase depended on temperature. Intrinsic population

growth rate (r_0, d^{-1}) was set as $r_0 = 0.0445e^{0.111T}$ for copepods, where T is water

temperature (°C) (Huntley and Lopez 1992). Intrinsic population growth rate for mysid

was set at $0.5r_0$. The carrying capacities (K) for copepods and mysids were estimated as

about 95% of the observed density distributions measured in Aransas Bay, Texas, (27°

57' 23.4" N, 96° 59' 20.5" W) during October 10 and November 19, 2008 (S. Nakayama,

pers. data). The carrying capacity of mysids was higher in seagrass habitat

$(5.0 \times 10^{-4}$ ml$^{-1})$ than open water $(0.8 \times 10^{-4}$ ml$^{-1})$. Although we found a higher density

of copepods in open water than in seagrass, we used the value for open water $(1.2 \times 10^{-2}$

ml$^{-1})$ for the carrying capacity of copepods for both habitat types. Since there was no

information that there were more prey available for copepods in open water than in

seagrass habitats or that planktonic copepods preferred open water to seagrass, we

considered the lower density of copepods in seagrass habitats was due to greater

predation and not a lower carrying capacity. In the model, we assumed that the prey

population in each cell was closed. Prey densities in each cell were monitored hourly by

subtracting the consumption by *S. ocellatus* larvae and by adding the hourly increase

from a logistic population growth model.

We used pinfish (*Lagodon rhomboides*, about 75 mm SL) as predators of

S.ocellatus during settlement periods because they are voracious predators of *S. ocellatus*

(Fuiman 1994) and very abundant in this area (Rooker *et al.* 1998). Predator density was

set at 0.25 m^{-3} in all cells, which produced a survival of 4.0% during the settlement

period when females spawned 4 times at 2-week intervals and when larvae did not

experience interference competition, which was comparable to the reported survival of

3.7% (Rooker *et al.* 1999).

Spawning traits

We assumed that (1) all females had equal annual fecundity of 8 million eggs

each, which is an average value for *S. ocellatus* (Porch 2000), (2) they divided their

annual reproduction evenly over the spawning events, (3) they produced eggs of equal

size, and (4) female mortality or somatic growth during the reproductive season was negligible. Also, we assumed that all females spawned synchronously (Wilson and Nieland 1994), with each spawning event continuing over 4 successive days. In the model, the number of eggs for one spawning event was randomly divided into four, and females spawned each subset of eggs for four consecutive days. The initial spawning date of *S. ocellatus* was set to be August 15, which is typical for *S. ocellatus* in the Gulf of Mexico (Wilson and Nieland 1994).

Pelagic period

Each egg took 21 h to hatch (S. Nakayama, pers. data). An initial length and dry weight at hatching were set at 2.06 mm and 31.27 µg, respectively (S. Nakayama, pers. data). At hatching, each larva was assigned a temperature-dependent daily growth rate (Pérez-Domínguez *et al.* 2006):

$$G = -0.007T^3 + 0.0372T^2 - 0.1953T - 0.2202$$

where *G* is a mean daily increase of length in percent, and *T* is water temperature (°C). Growth rate was randomly assigned hourly to each individual from a normal distribution with a mean of *G* and a standard deviation of 0.4*G* until they reached 7 mm SL. Because growth rate decreases with decreasing temperature, it takes longer to reach settlement size (7 mm) as the season progresses, which increases the variability in settlement timing of the cohort.

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Eggs and pelagic larvae experienced an instantaneous daily mortality rate of 0.27 as a combination of predation, starvation, and advection (Levin and Stunz 2005) regardless of their length. The worth of each super-individual (S) decreased hourly, as $S_{t+1} = S_t \cdot e^{-0.27/24}$. Growth and mortality of each individual was updated hourly until it reached 7 mm, at which time it was located at a random location on the settlement area, including both seagrass beds and sandy bottom (see *Environments*).

Growth and starvation mortality during settlement period

During the settlement period (7–25 mm), hourly growth was calculated using an energy budget approach. Net energy gain was calculated by subtracting metabolic expenditure from total energy acquired in 1 h of foraging. Metabolic energy requirements of larvae increased as they grew and as temperature increased.

The weight and length of a larva were coupled, so that length increased only when weight increased; otherwise, it did not increase the length. The new length was calculated from a weight-length relationship obtained from laboratory-reared *S. ocellatus* (S. Nakayama, pers. data), as $W = 3.590L^{2.995}$. Larvae died from starvation when their weight became 75% of their maximum past weight. The detailed equations used are described in Appendix A.

Feeding with competition

During the settlement period, when red drum larvae are 7–25 mm long, they prey on copepods and/or mysids in each cell. Prey search rate (a, ml s^{-1}) is dependent on fish

length, L (see Chapter 3):

$$a = -15.565 + 11.486 \ln L$$

Interference competition takes place when more than one fish exist in the same cell. Beddington (1975) proposed to include the interference competition term (qp) in Holling's Type II functional response function, such that

$$E = \frac{aN}{1 + ahN + qp}$$

where E is the prey encounter rate in the presence of interference competition (prey s^{-1}), N is prey density (ml^{-1}), h is a handling time (s prey^{-1}), q is the coefficient of interference (s competitor^{-1}, $q \geq 0$), and p is the number of competitors around the focal fish. This equation decreases the prey encounter rate of an individual as the number of competitors increases, and it becomes equivalent to Holling's equation when there is no interference among competitors ($q = 0$). This equation, however, treats all competitors equally competitive, which is not appropriate for red drum of different sizes (see Chapter 3). To solve this problem, van der Meer (1997) proposed "effective competitor units" (v_{jk}), which is the relative competitive weight of competitor k on individual j. From our previous experiments, v_{jk} was calculated as (see Chapter 3):

$$v_{jk} = \frac{3.236 - 0.538\overline{L} + 0.215\Delta L}{3.236 - 0.538\overline{L}}$$

where $\overline{L}$ is the mean length of individuals j and k, ΔL is a difference in length ($j - k$). The numerator represents the decrease in prey capture of individual j by interference with competitor k, and the denominator represents the decrease in prey capture of individual j when competitor k is at the same length as individual j ($\Delta L = 0$). The effective competitor unit becomes greater than 1 when competitor k is bigger than individual j, and less than 1 when competitor is smaller. For example, if individual j is 10 mm and competitor k is 20 mm, v_{jk} becomes 1.4. This means that the magnitude of interference individual j experiences with one 20-mm competitor is equivalent to 1.4, 10-mm competitors. Multiplying the effective competitor unit by the worth of each competitor and summing the effective competitive units of all competitors in the cell, prey encounter rate is calculated as:

$$E' = \frac{aN}{1 + ahN + q\sum_{k=1}^{p} v_{jk}}$$

This equation becomes equivalent to Beddington's equation when all competitors are equal in length (i.e., equal competitive strength) to individual j ($v_{jk} = 1$ for all competitors, sum of $v_{jk} = p$). The sum of v_{jk} was calculated hourly for each individual against all competitors found within a 5-m radius of the individual, assuming that a fish can travel 5 m h^{-1}.

Handling time was obtained using the relationship of the gape width of $S.$ $ocellatus$ (L_{fish}) and prey width (L_i, $i = 1$ for copepods, 2 for mysids) (Kislalioglu and Gibson 1976).

$$h_i = 1 + 0.16^{7.02L_i/L_{fish}}$$

where L_1 is 0.20 mm, L_2 is 1.10 mm for mysids (S. Nakayama, pers. data), and L_{fish} (mm) was obtained as $L_{fish} = 0.10L + 0.12$ (Krebs and Turingan 2003).

Capture rate for each prey (s^{-1}) was calculated as a product of prey encounter rate (E') and prey capture success (P_i). From our experiments, prey capture successes of $S.$ $ocellatus$ for copepods and mysids were calculated as:

$$P_i = a_i W^2 / (b_i + W^2)$$

where W is dry weight (mg) of $S.$ $ocellatus$, which was calculated as $W = 0.00359L^{2.995}$ (S. Nakayama, pers. data). Using a nonlinear regression, we obtained $a_1 = 0.619$ and $b_1 = 2.209$ (copepods), and $a_2 = 0.702$ and $b_2 = 235.829$ (mysids). Details on the experiment are described in Appendix B.

We assigned prey selection based on optimal foraging theory. First, each larva evaluates the energy gain from prey i per unit time required to handle, $C_i P_i / h_i$, where C_i is the energy content of prey. We used $C_1 = 0.0195$ cal (Morris and Hopkins 1983) and $C_2 = 1.3686$ cal (Donnelly et $al.$ 1993). Then a larva evaluates the profitability (f, a ratio

of energy gain to feeding time) by adding the prey item from the one with highest C_iP_i/h_i

until the profitability decreases (Letcher et al. 1996).

$$f = \frac{\sum C_i \cdot E_i' \cdot P_i}{1 + \sum E_i' \cdot h_i}$$

In this way, a larva was assigned to feed on either copepods or mysids, or both. The

densities of prey a larva encountered were randomly drawn from normal distribution with

the mean of actual prey density in the cell and standard deviation of 0.1 of the mean.

Once feeding habits were determined, a larva consumed the assigned prey. Multiplying

capture rate by 3600, we calculated hourly prey consumption. Larvae were allowed to

forage only during light period (12 h d^{-1}), and forced to stop feeding when their

consumption exceeded the daily maximum prey consumption during feeding period.

Maximum consumption (C_{max}, cal d^{-1}) was calculated from the relationship between

temperature and growth in the laboratory (obtained from Pérez-Domínguez et al. 2006):

$$C_{max} = 86842 \cdot W \cdot \exp\left(\frac{-5158.2}{T + 273.15}\right)$$

Predation mortality

During the settlement period, predation mortality of *S. ocellatus* by predators

(pinfish) was dependent on the length of *S. ocellatus* and habitat type. *S. ocellatus* were

less vulnerable to predation as they grow, and predation mortality was higher in open water than seagrass habitats (Rooker *et al.* 1998). Predation mortality rates in open water (Z_{open}, m^{-2} predator^{-1} h^{-1}) and seagrass habitats (Z_{veg}, m^{-2} predator^{-1} h^{-1}) depend on larval length (modified from Rooker *et al.* 1998):

$$Z_{open} = 0.48 \times (-0.1031 \ln L + 0.5081)$$
$$Z_{veg} = 0.48 \times (-0.1461 \ln L + 0.4908)$$

The worth of each super-individual decreased hourly as $S_{t+1} = S_t e^{-z}$. We assumed that there was no predation during dark periods. We also assumed that predation pressure was independent of larval density.

Movements

During the settlement period and at the end of every hour of the feeding period, a larva estimated the realized habitat quality of the current cell and the hypothetical habitat qualities of the adjacent 168 cells (30 m in each direction) if it had stayed there in the previous hour. Habitat quality (Q) was approximated by a ratio of energy gain (ΔC) to mortality rate (Z), which is a commonly used criterion for habitat selection in heterogeneous environments (Gilliam and Fraser 1987; Houston *et al.* 1993):

$$Q = \frac{\Delta C}{Z}$$

Each hour, a larva moved 5 m in the direction of the center of the cell that had the maximum habitat quality out of the 168 nearest cells. The actual habitat quality after movement may become lower than the estimated habitat quality because other competitors would also be moving to the high quality habitats. As a consequence, size distribution and competitor density may change in the cell, which affects prey consumption via interference and exploitative competition. Larvae were not allowed to move beyond the edge of the map.

Simulation experiments

The number of total recruits was simulated with the 24 combinations of spawning traits: number of batches spawned (1, 2, 3, 4, 5, 6) and spawning interval (4, 7, 14, 21 d). For a spawning interval of 4 d, females spawn every day throughout the season, since each spawning event continued for 4 consecutive days. We used these simulations to explore the optimal spawning traits that maximize total recruitment. We also explored how the optimal spawning traits would be influenced by the intensity of interference competition among larvae by changing the intensity ($q = 0$, 0.003, 0.01, 0.03, 0.1, 0.3, 1, 3, 10).

To see the effects of interference competition on each cohort, we calculated weight-specific daily instantaneous growth rates (G), daily instantaneous mortality (Z) and their ratio (G/Z) as an approximation of fitness for each cohort when females divide their total fecundity into 4 and spawn at 2-weeks intervals. G, Z, and G/Z were calculated

for 750 super-individuals randomly taken from the population during the settlement

period, and average values were obtained for each cohort.

RESULTS

Survival rates during the settlement period ranged from 0.64% to 6.06%

depending on the combination of spawning traits (Fig. 5.3). When there was little or no

interference competition ($q \leq 0.003$), spawning the entire annual allotment of eggs at one

time produced maximum survival. Survival decreased monotonically as the number of

spawning events or the spawning interval increased. At intermediate values of q

($0.001 \leq q \leq 0.3$), the survival rate showed a concave relationship with the number of

spawning events and spawning interval in which the maximum survival rates occurred at

spawning twice at a 1-week interval ($q = 0.01$), spawning twice at a 2-week interval

($q = 0.03$), spawning 3 times at 2-week intervals ($q = 0.1$) and spawning 5 times at 2-

week intervals ($q = 0.3$). When q was large ($q \geq 1$), increasing the number of spawning

events or the spawning interval increased survival during the settlement period

monotonically.

Total survival from eggs to recruitment (25 mm) as the product of survival rates

during the pelagic period and settlement period ranged from 0.01% to 0.11% (Fig. 5.4).

Total survival decreased monotonically as the number of spawning events or the

spawning intervals increased when q small ($0 \leq q \leq 0.01$). As the value of q increased,

survival rates showed local maximum values within the ranges we tested for spawning

Table 5.1. Descriptions of variables used in the model.

Variable	Description
W	Dry weight of a fish (μg)
L	Standard length of a fish (mm)
G	Growth rate during pelagic period (%L d^{-1})
D	Calendar day
T	Water temperature (°C)
S	The number of individuals represented by one super-individual
a	Prey search volume (ml s^{-1})
E	Prey encounter rate (prey s^{-1})
N	Prey density (ml^{-1})
h	Prey handling time (s prey^{-1})
q	Coefficient of interference competition (s competitor^{-1})
p	The number of competitor
v_{jk}	Effective competitor unit (competitive weight of competitor k on a fish j in interference competition)
L_{fish}	Gape width of a fish (mm)
L_i	Prey width (mm), i = 1 for copepod, 2 for mysid
$P_{copepod}$, P_{mysid}	Capture success on copepods and mysids
C_i	Caloric value of prey (cal prey^{-1}), i = 1 for copepod, 2 for mysid
C_{max}	Maximum prey consumption (cal d^{-1})
Z	Predation mortality during settlement period (h^{-1}). Z_{open}: open water, Z_{veg}: seagrass habitats
Q	Habitat quality
ΔC	Energy available for growth (cal)
A	Assimilation efficiency
C_{total}	Energy intake (cal h^{-1})
M_{res}	Energy required for resting metabolism (cal h^{-1})
M_{act}	Energy required for active metabolism (cal h^{-1})
E_{SDA}	Energy required for specific dynamic action (cal h^{-1})
E_{Excr}	Energy wasted as excretion (cal h^{-1})
W_{wet}	Wet weight of a fish (g)

Figure 5.1. Habitat map used in the model simulation, randomly taken form Red Fish Bay, Texas, USA (27° 54' 29.8" N, 97° 4' 35.6" W). Light areas represent open-water habitats, and dark areas represent vegetated habitats. Information was taken from Texas Parks and Wildlife Department.
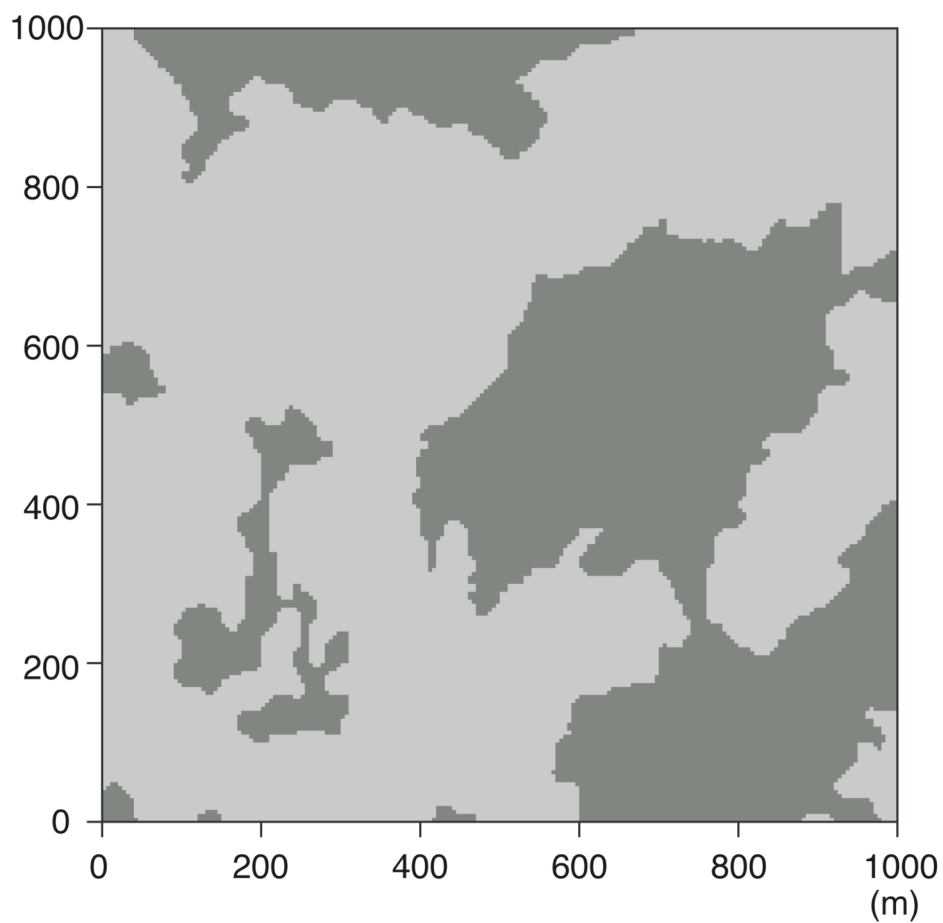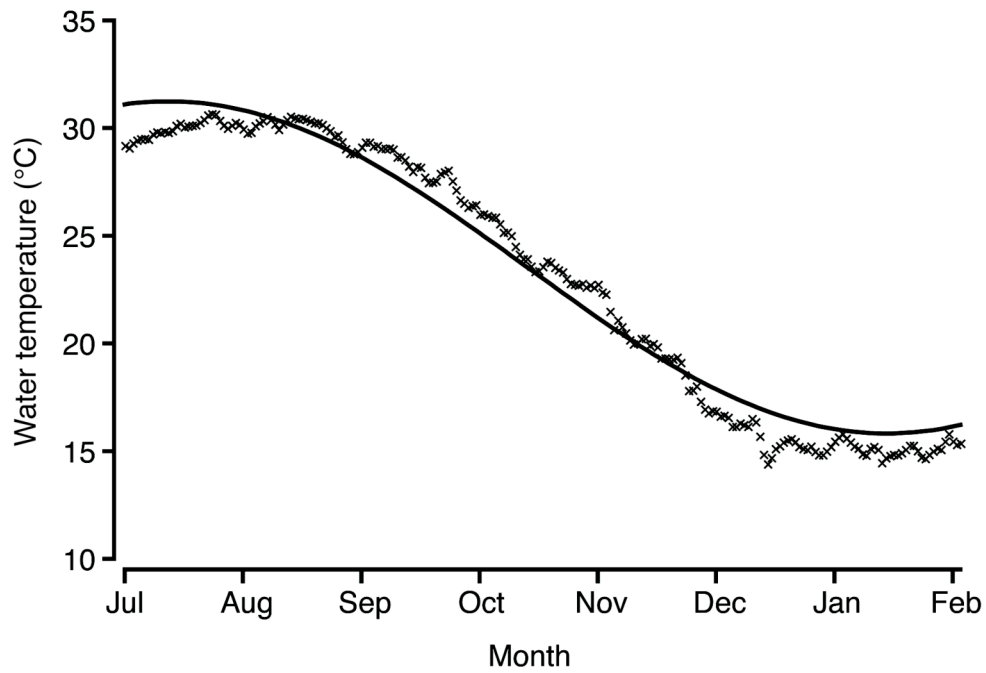
Figure 5.2. Water temperature during the spawning season of *S. ocellatus* in Red Fish Bay, located in the northern Gulf of Mexico. Crosses (×) indicate daily average water temperature for 10 years (1998–2007). A line represents water temperature used in the simulation. $T = 23.530 – 3.266\sin(0.017D) – 6.985\cos(0.017D)$, where T is temperature, D is calendar day.

twice at a 2-week interval ($0.03 \leq q \leq 0.1$), spawning 3 times at 2-week intervals ($q = 0.3$), and spawning 3 times at 3-week intervals ($q \geq 1$).

In general, weight-specific daily instantaneous growth rates (G) decreased as interference competition (q) increased, but the decrease in G became less steep as spawning intervals increased (Fig. 5.5). When there was no interference competition ($q = 0$), the last cohort experienced smaller G, and this trend became more obvious as the spawning interval increased. When q was greater than 0, G was similar among cohorts, but the earliest cohort always had the highest G among cohorts. Daily instantaneous mortality rates (Z) increased as interference competition (q) increased for all cohorts, but these trends became weaker as spawning intervals increased (Fig. 5.6). When interference competition was large ($q \geq 1$), the first cohort experienced smallest Z among all cohorts, but the difference in Z among cohorts decreased as spawning intervals increased. When interference competition was small ($q \leq 0.1$), no consistent trend was observed between the order of cohort and mortality rates.

In general, cohort fitness (G/Z) was higher for the early cohorts than for the late cohorts when parents spawned four times (Fig. 5.7). Cohort fitness decreased as interference competition increased for all cohorts when spawning intervals were short (4 or 7 d), and this decrease became less steep as spawning intervals increased. When spawning intervals were large (14 or 21 days), however, cohort fitness increased under weak interference competition ($q = 0.1$).

For all spawning traits we tested, total survival rates from eggs to recruitment showed a dome-shaped relationship with q (Fig. 5.8). The optimal value of q (for parents)

that resulted in highest survival increased as the number of spawning events increased. Spawning interval did not change these optimal values. Interference competition (q) had less influence on survival rates when the number of spawning events and the spawning intervals were bigger.

DISCUSSION

This is the first study to demonstrate that the adaptation of reproductive traits at the population level could be mediated by competition among young. We do not know the importance of competition among young to the evolution of reproductive traits relative to other selection pressures, such as environmental uncertainty (Schaffer 1974; Bumler 1985; Brommer *et al.* 2000; Wilbur and Rudolf 2006), age structure in a population and age-specific fecundity (Orzack and Tuljapurkar 1989; Benton and Grant 1999) and physiological constraints on reproduction (Partridge and Sibly 1991; Ricklefs and Wikelski 2002; Elkin and Reid 2005), however, our results demonstrate that intraspecific interference competition alone has the potential to alter total offspring survival and therefore influence how females distribute their reproductive effort in time. As interference competition among offspring intensified, maximum recruitment could be achieved by increasing both the number of spawning events per season and the spawning interval, presumably reducing interference competition. As the magnitude of interference competition increased further ($q \geq 1$), the optimal strategy converged on a certain multiple-spawning trait, but total survival from eggs to recruitment decreased. Differences in fitness (G/Z) between early cohorts and late cohorts decreased as parent

Figure 5.3. Survival rates during the settlement period with different numbers of spawning events and spawning intervals. A LOWESS function was applied to obtain the smoothing surface. Top left: $q = 0$, top right: $q = 0.1$, bottom left: $q = 1$, bottom right: $q = 10$. The color key on the right indicates total survival as a percentage of eggs spawned.
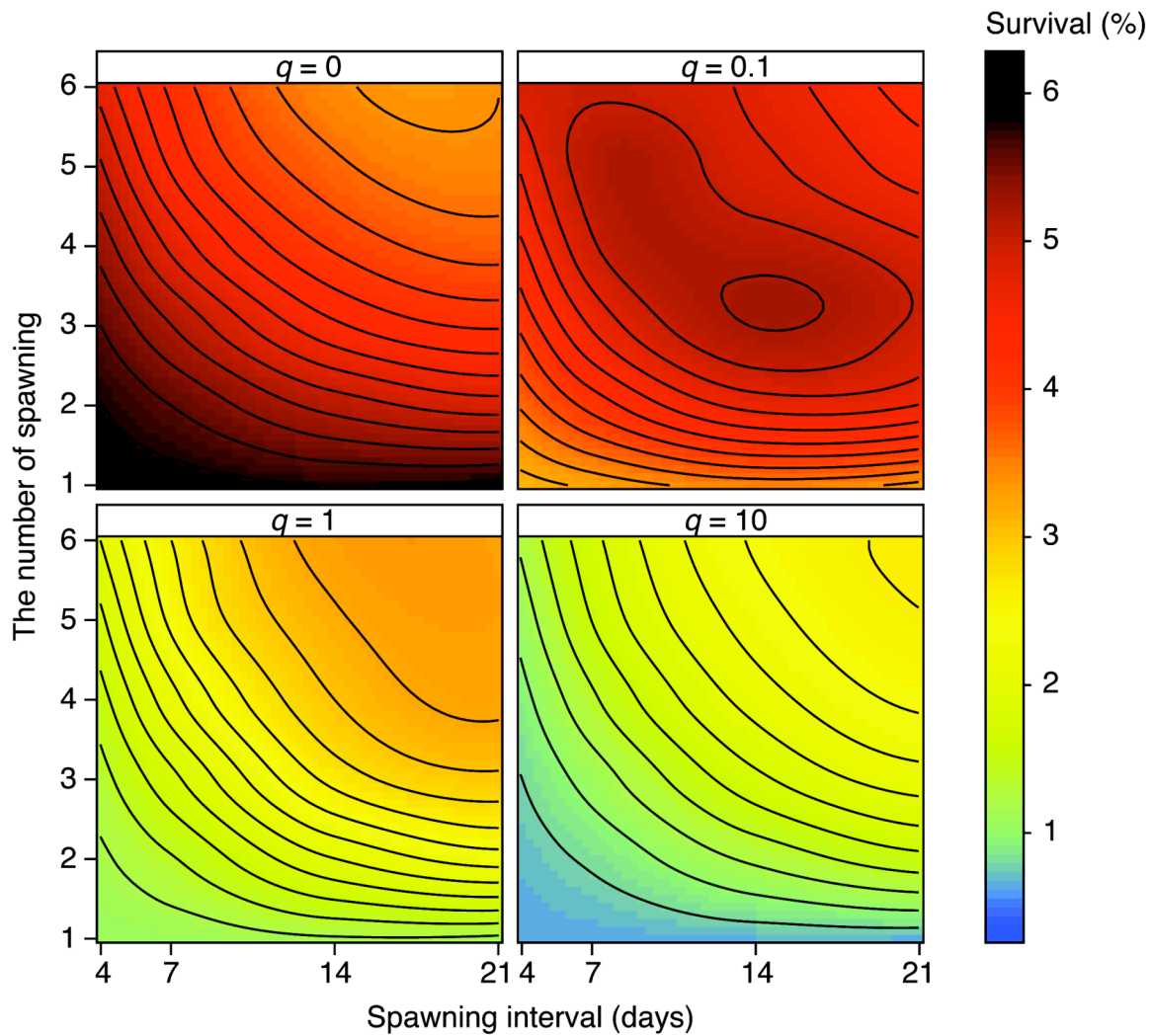
Figure 5.4. Total survival rates from eggs to recruitment with different numbers of spawning events and spawning intervals. A LOWESS function was applied to obtain the smoothing surface. Top left: $q = 0$, top right: $q = 0.1$, bottom left: $q = 1$, bottom right: $q = 10$. The color key on the right indicates total survival as a percentage of eggs spawned.
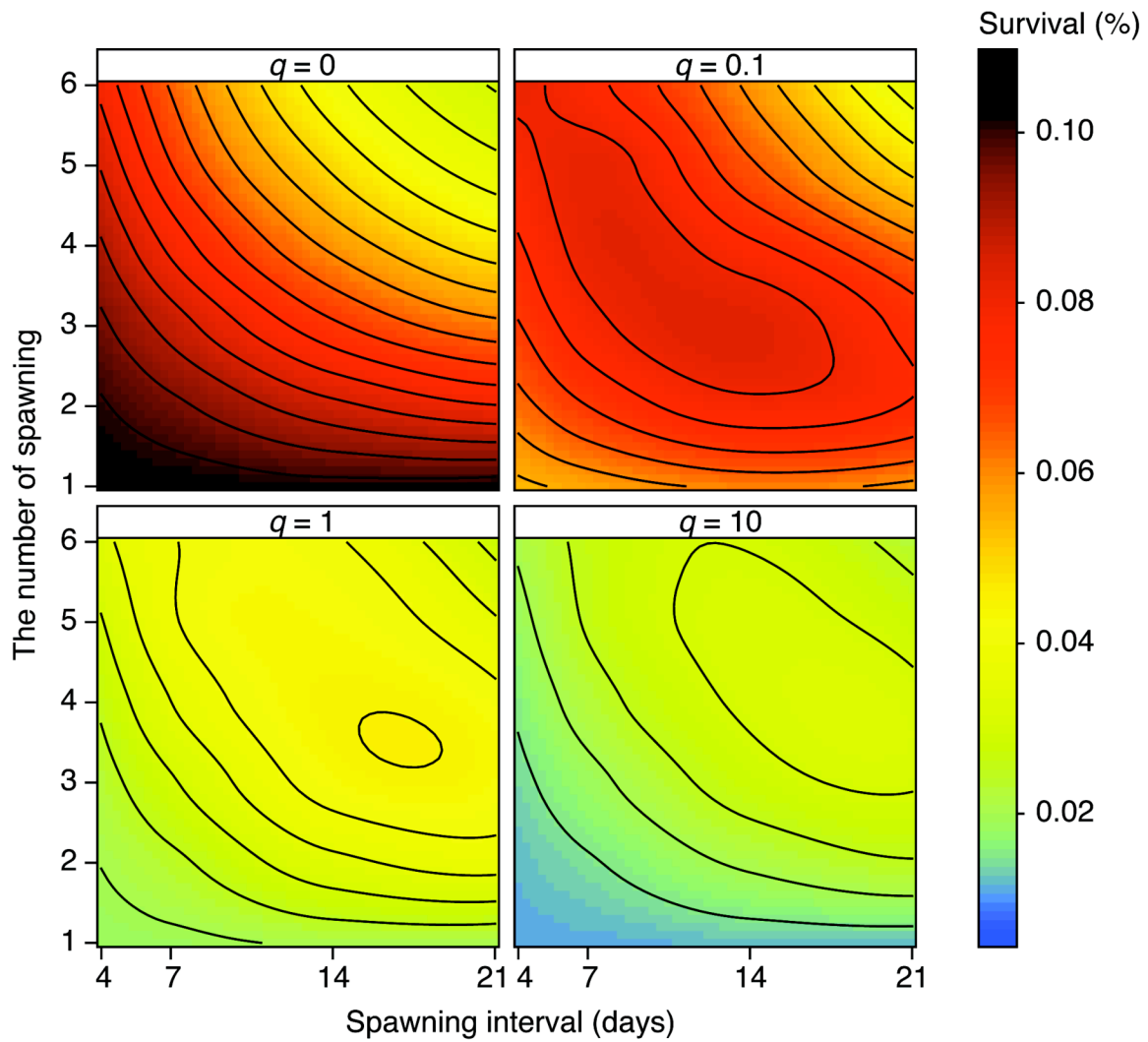
Figure 5.5. Weight-specific daily instantaneous growth rates (G) during the settlement period when females spawn four times. Top left: interval = 4, top right: interval = 14, bottom left: interval = 14, bottom right: interval = 21 (d). The size of square represents the magnitude of G, with larger squares indicating higher G.
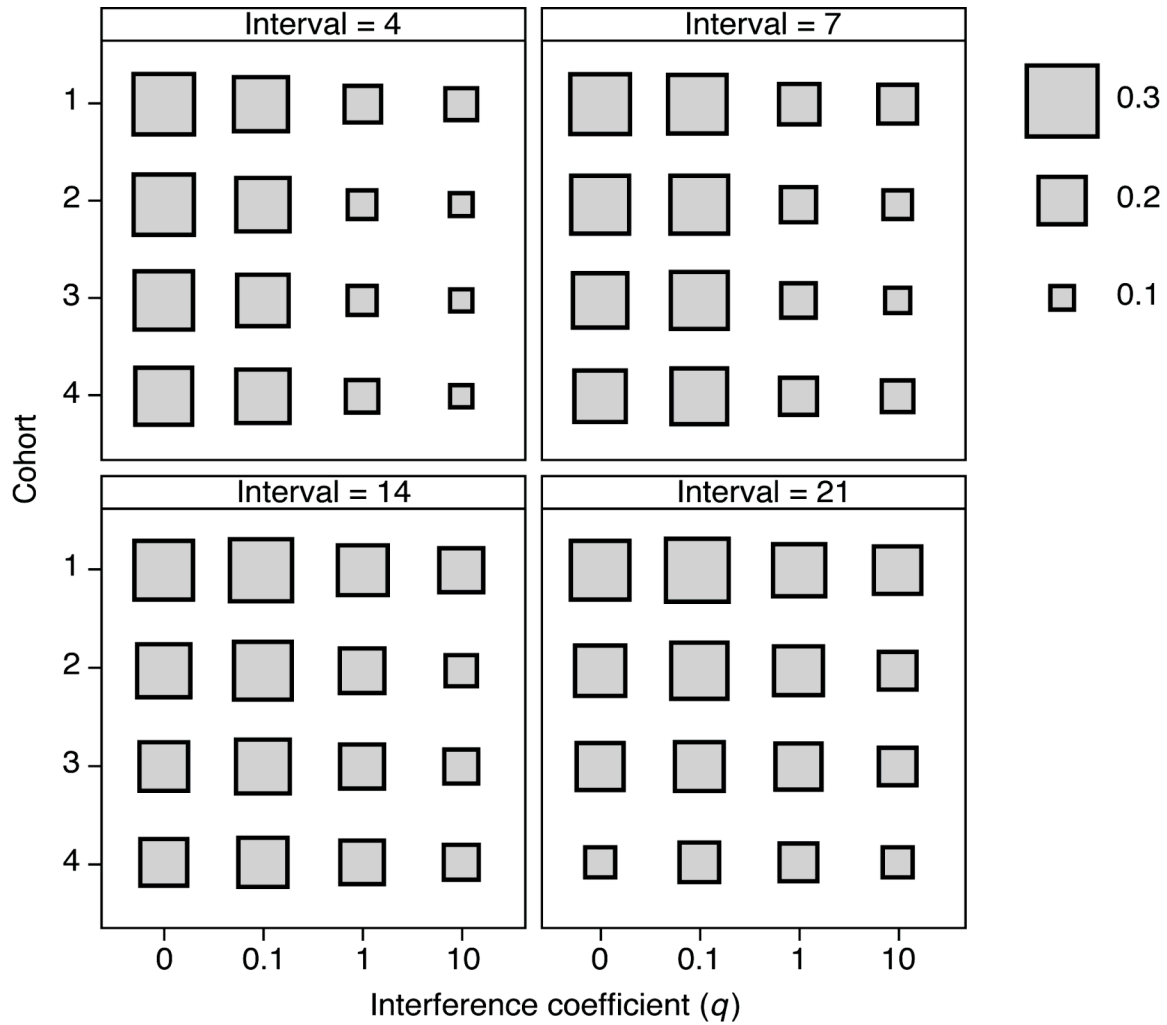
Figure 5.6. Daily mortality rates (*Z*) during the settlement period when females spawn four times. Top left: interval = 4, top right: interval = 14, bottom left: interval = 14, bottom right: interval = 21 (d). The size of each square represents the magnitude of *Z*, with larger squares indicating higher *Z*.
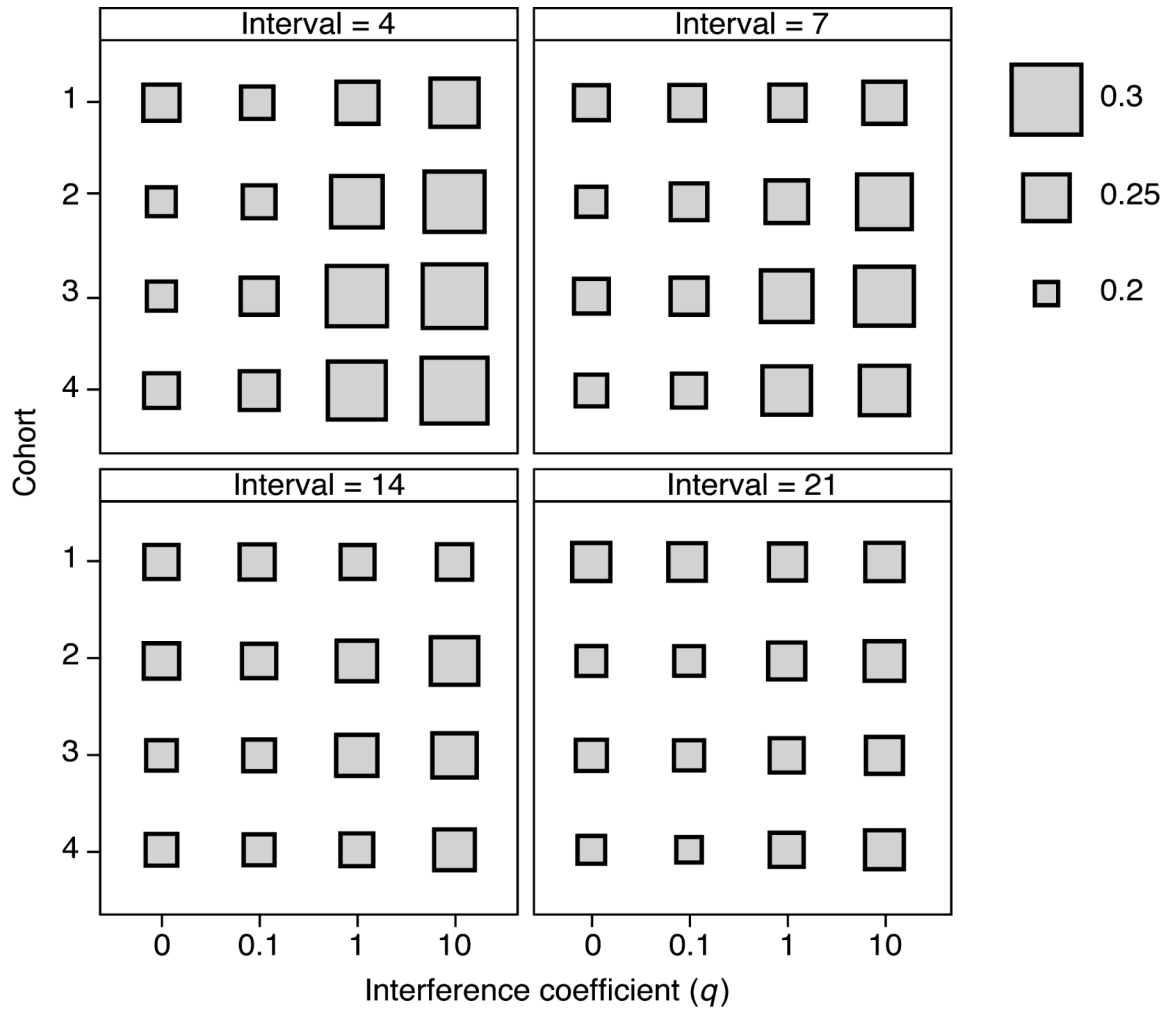
Figure 5.7. Cohort fitness as a ratio of growth to mortality (*G/Z*) during the settlement period when females spawn four times. Top left: interval = 4, top right: interval = 14, bottom left: interval = 14, bottom right: interval = 21 (d). The size of each square represents the magnitude of cohort fitness, with larger squares indicating higher fitness.
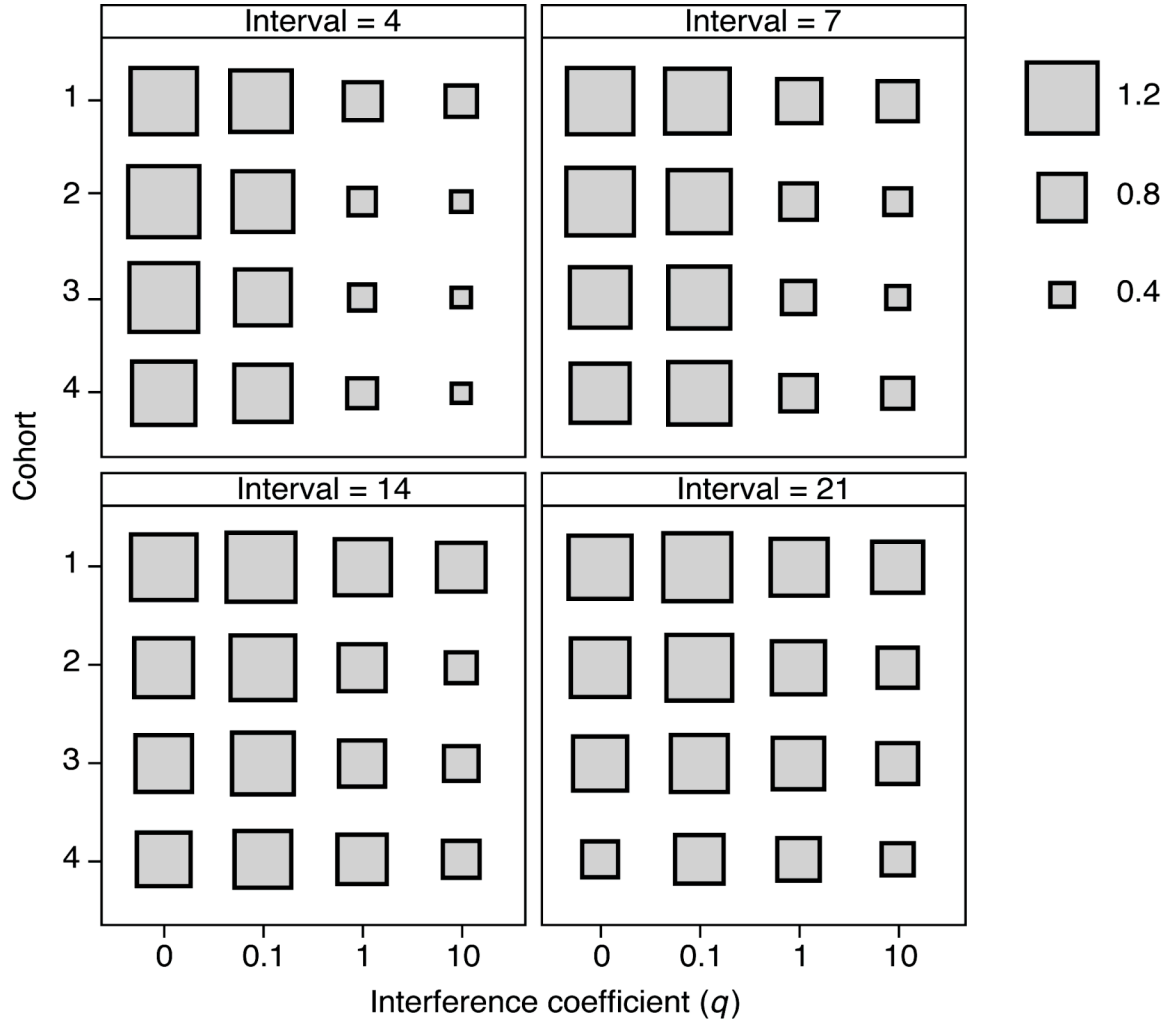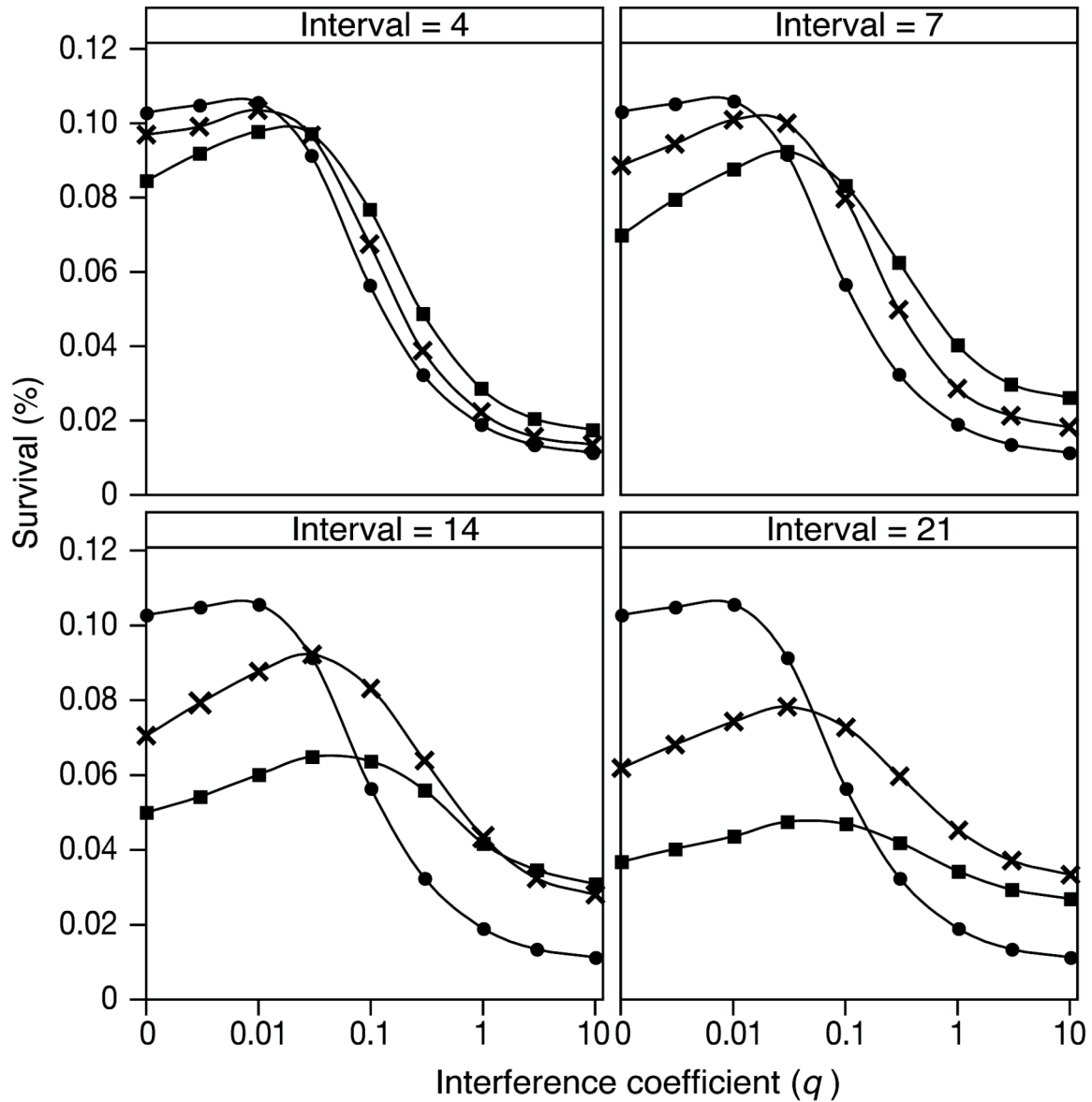
Figure 5.8. Relationship between the magnitude of interference competition (*q*) and total survival rates from eggs to recruitment. Top left: interval = 4, top right: interval = 14, bottom left: interval = 14, bottom right: interval = 21 (d). ●: spawning once, ✕: spawning 3 times, ■: spawning 5 times.

spawned at longer intervals.

Contrary to our hypothesis, we found that interference competition among offspring is not necessarily detrimental. Under all combinations of spawning traits, total offspring survival was higher when there was a low-intensity interference competition ($0.003 \leq q \leq 0.3$, depending on the spawning traits) as compared to when there was no interference competition at all (Fig. 5.8). This is because feeding rates of the smaller individuals decrease to a greater extent than those of the larger individuals through asymmetric interference competition, and as a consequence, the larger individuals experience increased prey availability, enough to offset the decrease in their feeding rates, depending on the magnitude of interference competition. This skews the frequency distribution of individual growth rate, resulting in an increase in mean growth rate of the population. In other words, total survival increases by sacrificing growth of a subset of offspring for the faster growth of the rest. However, as the magnitude of interference competition increases, the reduction in feeding rates of larger individuals through interference competition cannot be counterbalanced by the increase in prey availability, and population growth starts decreasing (Fig. 5.8). An increase in total survival with interference competition may not be observed when prey density is lower than we used in our simulation. In Arctic char (*Salvelinus alpinus*), low prey density reduces size difference within a population because the advantages for the larger individuals through asymmetric exploitative competition cannot keep up with the increasing metabolic demands for growth (Byström and Andersson 2005). Also, interference competition may not increase total survival when prey density is much higher than our simulation, since

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any magnitude of interference competition among offspring will merely decrease the growth rates of all individuals when there are prey enough to satiate all individuals. Therefore, an increase in total survival through asymmetric competition would be a unique phenomenon balanced on prey availability, size-dependent feeding efficiency, asymmetric decrease in feeding efficiency by interference competition and size-dependent energy demands for growth.

In our model, survival rate during the settlement period was maximized by increasing the number of spawning events and spawning interval when interference competition among offspring escalated (Fig. 5.3). This indicates that selection favors multiple breeding with expansion of the reproductive season as the magnitude of interference competition among offspring increases, whereas it favors a single reproductive event as the magnitude of interference competition decreases. The higher number of spawning events is favored because it can reduce instantaneous offspring density in the nursery habitats, and thus decrease both inter- and intra-cohort competition. With a longer spawning interval, females can reduce temporal overlap between cohorts, overcoming the disadvantages to late cohorts through inter-cohort competition as a consequence of size dependency in interference competition (Fig. 5.7). A longer spawning interval is also favored as interference competition increases because each cohort stays longer in the nursery habitats as a consequence of slower growth through intra-cohort competition (Fig. 5.5). The other possible advantage of a longer spawning interval is that it can allow the prey population recover when prey are exploited heavily due to high density of offspring. However, a very long spawning interval may create

temporal pockets of unused niches. This is not only a waste of available niches, but it may also allow other species to intrude. When there is a gradation in environmental conditions for offspring fitness during the spawning season, such as decreasing temperature in our model, it would be beneficial for parents to concentrate production of batches around the optimal time during the reproductive season as long as interference competition among cohorts does not have negative effects on offspring survival.

The optimal spawning trait that maximizes total offspring survival from eggs to recruitment was slightly different from those during the settlement period alone: the same magnitude of interference competition among offspring had a weaker selection pressure for multiple spawning. This is because the optimal spawning trait that maximizes total offspring survival from eggs to recruitment is a compromise between the optimal spawning traits during the pelagic period and those of the settlement period. Since we did not include any density effects on survival during pelagic period, assuming that there would be little exploitative or interference competition among pelagic larvae, the spawning trait that maximizes offspring survival during the pelagic period is to spawn all eggs at once when temperature is optimal (same optimality conditions as during the settlement period when $q = 0$).

The optimal spawning traits for parents are not the same as the optimal spawning traits for their offspring. For parents, the optimal scenario is to spawn once when offspring exhibit weak interference competition ($q = 0.01$), which gives the maximum offspring survival in our model (0.105%). Yet, the behavior of offspring with which they try to increase their own individual fitness favors multiple breeding. Parent-offspring

conflict is often found in organisms with parental care when the young solicit

disproportionate resources among siblings from parents as a result of sibling competition

(Trivers 1974; Godfray and Parker 1992; Neuenschwander *et al.* 2003). However, parent-

offspring conflict can also take place in organisms without parental care. For example in

gregarious insects without parental care (Godfray and Parker 1992), parents reduce clutch

size when exploitative competition takes place among larvae to increase total survival of

offspring. In the same way, we expect that the parent-offspring conflict in *S. ocellatus*

can be resolved through multiple spawning if spawning traits are heritable.

In the northern Gulf of Mexico, *S. ocellatus* is reported to spawn synchronously in

groups at about 2-week intervals for about 2 months (Peters and McMichael 1987). This

spawning trait is remarkably similar to the optimal spawning traits found in our

simulation when offspring experience interference competition ($q \geq 0.1$). Therefore,

interference competition among offspring might occur in nature and it may have exerted

selection pressure to produce the reproductive traits that we see today in *S. ocellatus*. It is

possible, however, that the observed traits may not be a result of selection but rather,

constraints. One of the potential constraints for the multiple-spawning trait in *S. ocellatus*

is a tidal cycle. Tide is a crucial factor for the pelagic larvae of *S. ocellatus* to be

successfully transported into nursery areas where they settle (Brown *et al.* 2005). Thus,

the tidal cycle may have fixed the reproductive trait of *S. ocellatus* first, and the

behavioral and physiological traits of offspring may have evolved to reduce overlap

among cohorts to increase total survival. In other words, tidal cycle may be responsible

for the parameters we used in the simulation model, such as the magnitude of asymmetry

in interference competition with body size and the effects of metabolism and ambient temperature on growth rate.

There are few studies of the multiple-breeding strategy from an evolutionary perspective (for example, Fuchs 1982; Verhulst *et al*. 1997, Forsman 2001) compared to studies on the semelparity-iteroparity continuum, probably due to terminological confusion and ambiguous definitions. We distinguish multiple breeding from iteroparity because it would have evolved through different selection pressures. We have used multiple breeding as a reproductive trait of parents apportioning their reproductive effort per season into multiple batches within a single reproductive season during which their total reproductive effort is unchanged and parental mortality is negligible. In the semelparity-iteroparity continuum, the question is how much effort parents should allocate to the reproduction and how much to their somatic growth. It is, of course, possible that one species can be both iteroparous and a multiple breeder (e.g., *S. ocellatus*). When parents use both iteroparous and multiple-breeding strategies, they would experience trade-offs that pull the reproductive traits in the different directions. Also, the optimal strategy in multiple breeding would become more complex when females experience non-negligible mortalities or increased reproductive effort during a single reproductive season. Further research is required to understand the evolution of life-history strategy in how parents should finance their reproductive efforts to obtain a maximum return.

For simplicity, we assumed that all females have the same multiple-breeding trait in our model. However, it is possible that individual females vary in their multiple-

breeding traits depending on their condition. In migratory birds, for example, inferior parents breed later, waiting for superior competitors to finish using the breeding sites as a consequence of the competition among parents for the optimal time of reproduction for their offspring (Kokko 1999). Also, first-time breeders often experience higher costs for reproduction and less success (Curio 1983; Cam and Monnat 2000). We viewed a female population as one super-organism in our model, but we need a genetic-based model from a game-theory perspective in order to find the optimal reproductive strategies at the individual level; the optimal multiple-breeding strategy we found may not be evolutionarily achievable when each female behaves differently to maximize its own fitness under competition among females.

Chapter 6: Summary and conclusions

This collection of studies was designed to understand the mechanisms and consequences of competition among early life stages of fishes, with a special attention to asymmetric competition and its potential effects on multiple-spawning traits of parents. Multiple-spawning traits seen in many fishes have been thought to be a bet-hedging strategy as an adaptation to environmental predictability for offspring survival, and little attention has been paid to the potential effects of multiple-spawning traits on competitive environments of offspring. Moreover, if competition among offspring is size-dependent, the asymmetry in competitive abilities among individuals would change dynamically with time due to growth, emigration of old cohorts and immigration of new cohorts in the nursery habitat, which would create a complex suite of interactions that affect offspring survival in the near term and, potentially, reproductive traits for optimal parental fitness in the long term. A combination of laboratory experiments and computer simulations was employed to explore the effect on survival of this complex change in relative competitive ability with time and the subsequent effects on the multiple-spawning traits of parents, using red drum as a model organism.

This is the first study that demonstrated the consequences of different factional-spawning traits can be mediated by competition among offspring. Interference competition among offspring alone was shown to be a potential selection pressure on a multiple-spawning trait of parents, even without taking into account effects of environmental predictability on offspring survival. As interference competition among

offspring increased, the number of spawning events and the spawning interval of parents increased to lessen competition among larvae and maximize total survival of offspring. If offspring exhibit social interactions with each other that result in competition for resources to increase their individual survival, the effects of competition among offspring would feed back to the multiple-spawning traits of parents to decrease negative effects of competition among offspring and increase total offspring survival. This study demonstrates the importance of the feedback from offspring behavior to life-history strategy of parents, to which little attention has been paid.

The existence of sociality in red drum larvae was identified for the first time, which laid the foundation for my further studies. This was also the first description of the repertoires of social behavior in this species. We found that the magnitude of aggressive behavior, vigilant behavior and shoaling behavior depends on a combination of absolute and relative phenotypes of competing individuals, such as body lengths and body condition. Little attention has been paid for agonistic and vigilant social behaviors on the early life of fishes, but this study demonstrated competition for food and habitat use among early life stages.

Competition for food and habitat use has been shown to be size-dependent in red drum larvae. Although there have been few studies of competition on early life stages of fishes, the finding that larger size is more advantageous in competition agrees with many previous studies. In this study, however, the detailed relationship between body sizes of competing individuals and the magnitude of interference competition for food was quantified for the first time with a new technique that combined laboratory observations

and foraging theories, which allowed me to apply size-dependent competition for food in projecting recruitment success. Also, detailed analyses using a Markov chain model allowed me to find the mechanisms of competition for habitat use and to discuss the effects of the competition on settlement success in the wild.

This set of studies on size-dependent competition for resources is not only important for the adaptation of reproductive traits of parents, but also applicable to projecting recruitment success under any changes in conditions that affect size-structures and behavioral interactions. We revealed factors that affect competition, such as physical traits of individuals, physical traits relative to the others, behavioral propensities and habitat qualities. Because competition at the individual level can influence population dynamics, monitoring these factors as well as the environmental changes that affect them would help us maintain biodiversity and population health. Also, this study has implications for management aimed at replenishing natural population with hatchery-reared stocks. With the goal of stock enhancement for recreational and commercial fishing, the Marine Development Center of Texas Parks and Wildlife Department have been releasing hatchery-reared red drum into Texas bays. On average, 28.3 million red drums have been released annually from 1991 to 1999, at sizes of 20–30 mm total length (Dr. R. Vega, personal communication). Red drum are released earlier than their natural recruitment season, which has a potential impact on the wild populations survival is size-dependent through competition. Predicting recruitment success from competition could be a guideline for when and how many to introduce hatchery-produced fish without suppressing the natural population.

The importance of intraspecific competition among early life of fishes was focused on this study, but we need to look at the mechanisms and consequences of interspecific competition as well for better understanding in recruitment success. Red drum uses the same nursery habitats as other sciaenids (e.g., spotted seatrout, Atlantic croaker) at different times of the year. Understanding the degree of asymmetry in interspecific competition would allow us to understand the mechanisms of speciation and temporal niche segregation among them. Also, this dissertation demonstrated that competition among offspring is a potential selection pressure on the reproductive traits of parents; however, we don't know its importance relative to other potential selection pressures, such as tidal cycles, interspecific competition, predator dynamics and uncertainty of physical environments. We have to remember that the optimal reproductive trait sought in this simulation model is an evolutionary endpoint that is not necessarily achievable.

Appendices to Chapter 5

APPENDIX A

We calculated the energy available for growth by subtracting resting metabolism (M_{res}, cal h^{-1}), active metabolism (M_{act}, cal h^{-1}), specific dynamic action (E_{SDA}, cal h^{-1}) and excretion (E_{excr}, cal h^{-1}) from a product of total energy consumed (C_{total}) and assimilation efficiency (A):

$$\Delta C = A \cdot C_{total} - (M_{res} + M_{act} + E_{SDA} + E_{excr})$$

Assimilation efficiency was set as a function of dry weight of fish (Peck and Daewel 2007):

$$A = 0.7\left(1 - 0.3e^{-0.003(W-16.864)}\right)$$

We included a temperature effect (Arrhenius effect; Gillooly *et al.* 2001) in a relationship between resting metabolism (M_{res}, cal h^{-1}) and wet weight (W_{wet}, g) in *S. ocellatus* measured at 18˚C (Neill *et al.* 2004):

$$M_{res} = 0.34W_{wet}^{0.8} \exp\left\{\frac{5020(T-18)}{(T+273.15)(18+273.15)}\right\}$$

where $W_{wet} = 1.0 \times 10^{-5} \times (W/3.59)^{1.04}$ (S. Nakayama, pers. data). Resting metabolism was applied for 24 h d^{-1}. Active metabolism was set 2.5 times higher than resting metabolism (Letcher *et al.* 1996), and active metabolism was applied while foraging (12 h d^{-1}, or less if fish achieved maximum prey consumption). E_{SDA} and E_{excr} were set at 0.156 and 0.07 of total consumption (cal h^{-1}), respectively (Houde and Zastrow 1993). ΔC was converted to dry weight (0.004 cal µg^{-1}; Fontaine *et al.* 2007).

APPENDIX B

   We conducted experiments to estimate the capture success of *S. ocellatus* on

copepods and mysids. One *S. ocellatus* larva (4.5–29.5 mm SL) starved for 15–18 h was

put in a plastic chamber (10 × 10 × 10 cm) filled with sea water (about 27ºC, 27 ppt).

After 10-min acclimation, prey were gently introduced in the chamber using a pipette.

We used either 30 adult calanoid copepods (*Acartia* spp., about 0.6 mm in length) or 12

adult mysids (*Neomysis* spp., about 6.1 mm in length) as prey. For copepods, we removed

the fish with a dip net after it exhibited ten feeding bouts, euthanized it with MS-222, and

counted the number of copepods in its gut. For mysids, we directly observed capture

success for ten attacks. When a fish did not make ten attacks in 10 min, we stopped the

observation and calculated the capture success from number of attacks observed during

10 min. In total, 37 and 25 individuals were tested for copepods and mysids, respectively.

The proportion of attacks that were successful ($P_{copepod}$ for copepod, P_{mysid} for mysid) was

regressed on dry weight of the fish (*W*), using the function by Letcher *et al.* (1997) (Fig.

B1):

$$P_{copepod} = \frac{0.619 \cdot (0.001 \cdot W)^2}{2.210 + (0.001 \cdot W)^2}$$

$$P_{mysid} = \frac{0.702 \cdot (0.001 \cdot W)^2}{235.828 + (0.001 \cdot W)^2}$$

Figure B1. Relationship between standard length of *S. ocellatus* and prey capture success rates. O: observed capture success for copepods, ■: observed capture success for mysids.
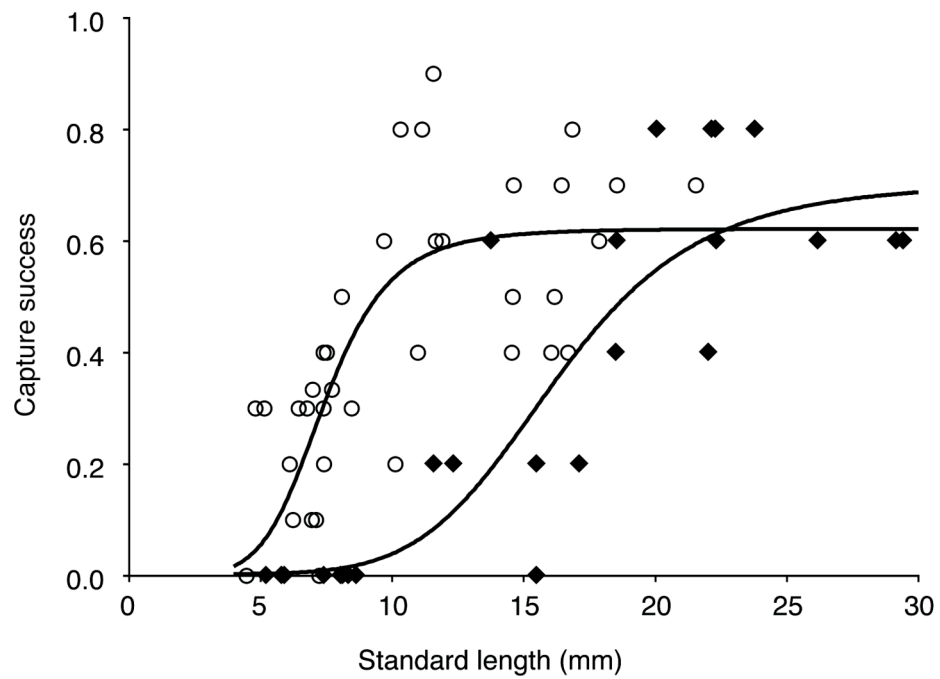
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