

To fight, or not to fight: determinants and consequences of social behaviour in young red drum (*Sciaenops ocellatus*)

Shinnosuke Nakayama¹⁾, Alfredo F. Ojanguren & Lee A. Fuiman

(Department of Marine Science, University of Texas Marine Science Institute, 750 Channel View Drive, Port Aransas, TX 78373, USA)

(Accepted: 22 October 2008)

Summary

Social behaviour 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 behaviours 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 behaviour increased as body size increased, but aggressive behaviour 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 behaviour. Fish that more frequently displayed aggressive behaviours tended to occupy the lower part of the water column. Body size and condition were important determinants of social interactions between red drum larvae. Our results suggest competitive disadvantage for the larvae from late cohorts when they recruit to the nursery habitats where larger larvae from early cohorts have already occupied.

Keywords: aggressive behaviour, grouping behaviour, size, body condition, vertical position.

Introduction

Social behaviour, such as aggression and cooperation, has evolved in many organisms to increase fitness. Organisms try to maximize individual fitness

¹⁾ Corresponding author's e-mail address: shin.nakayama@mail.utexas.edu

by competing for resources, such as food, territories, or mates, or by co-operating with other individuals (Krebs & Davies, 1993). Although social behaviour 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 & Lott, 2000), but engaging in fighting is costly in terms of energy and time (Briffa & Sneddon, 2007). Grouping behaviour can increase fitness as well, by decreasing predation pressure, increasing foraging efficiency, and increasing mating success (Dugatkin, 2002). In migratory animals, grouping behaviour 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 & Godin, 1995), competition for food (Johnsson, 2003), and risk of disease transmission (Côté & Poulin, 1995). Therefore, the balance between the costs and benefits of social behaviour 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 behaviour. 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 behaviour 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 aculeatus*) spend less time in a shoal than satiated individuals (Krause, 1993). Growth rate and age may also affect social behaviour (Jönsson et al., 1998; Côté, 2000; Vøllestad & 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 behaviour. Fighting intensity in male jumping spiders (*Euophrys 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 behaviour in many fishes (Pitcher et al., 1986; Ward & Krause, 2001).

Social behaviour is mutual and cannot be of individual decision because behaviour 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 behaviour. Therefore, it is important to measure the effect of individual phenotypic traits on social behaviour as well as the effect of differences in these traits between interacting individuals in order to understand the mechanism of decision-making in social behaviour. 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 behaviour. Depending on conditions, larval red drum show both aggressive and cooperative (grouping) behaviour with conspecifics. Their synchronous batch-spawning reproductive strategy over a 2–3 month period during Autumn (Peters & 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/m²) and wide range of sizes (8–25 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 behaviour could interfere with growth and survival of larvae depending on their arrival to the nursery habitat.

We experimentally investigated how social behaviour 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 behaviour 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 & Moore, 1998). Males mature in 3 years and females in 5 years, which is about 70 cm and 75 cm fork length, respectively (Hoese & 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 7–25 mm standard length) are found in the centre of seagrass meadows, but only smaller individuals (8–12 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, TX, USA). Spawning was induced by manipulating photoperiod and temperature. Eggs of two batches (27 October and 9 November 2005) were obtained from a single pair of adults and transferred to a laboratory at The University of Texas Marine Science Institute (Port Aransas, TX, USA) within 18 h after spawning. After treating eggs with $1 \times 10^{-5}\%$ formalin for 30 min to prevent fungal infections, approximately 5000 viable eggs from the same spawn were put into each of two 60-l fibreglass 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. The 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 4×10^5 rotifers (*Brachionus* spp.) enriched with nutrients for 45 min (Algamac-2000, Aquafauna Bio-Marine, Hawthorne, CA, USA) in each tank daily until 11 days after hatching. From 12 days after hatching, fish were fed 6×10^4 enriched *Artemia salina* nauplii.

Behavioural 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 days after hatching, one individual was netted randomly from each of two rearing tanks; fish that showed obviously abnormal behaviour were avoided. At 1800 h, each fish was put into one side of a 9-l Plexiglas tank ($40 \times 15 \times 15$ cm), which was divided vertically 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 behaviour of the fish was observed through the fourth wall. The bottom of the tank was covered with sand and a single piece of artificial 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 behavioural interactions (aggression and avoidance) and duration of grouping behaviour between the two individuals was recorded. Aggression was the sum of the number of displacements and attacking behaviours. 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 behaviour was defined as one fish approaching the other with rapid acceleration. In most cases attacking behaviour 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 behaviour from the other fish. Grouping behaviour was defined as two individuals swimming closely (arbitrarily established as within 5 cm of each other, approximately 2–7 body lengths) at approximately the same speed and direction. During grouping behaviour, 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 3–6 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 denotes days after hatching. The initial total length (2.0 mm) was used from our 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 generalised linear model, total number of aggressive events, total number of avoidance events, and total duration of grouping behaviour were analysed 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 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 analysing the number of aggressive events and avoidance. For analysing the duration of grouping behaviour, differences were calculated as the absolute value of the difference between the two fish because grouping behaviour is a mutual behaviour. 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 account 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 behaviour, gamma-Poisson distribution and log link function were specified (McCullagh & 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 behaviour, 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, Chicago, IL, 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 0.2 , 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 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 and total length) did not affect the number of avoidance events and were removed from the model (Table 2). Total duration of grouping behaviour 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 3).

Table 1. Generalised linear model for total number of aggressive events.

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

The overall model is statistically significant ($\chi^2_4 = 190.31$, $p < 0.001$).

Table 2. Generalised linear model for total number of avoidance.

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

The overall model is statistically significant ($\chi^2_2 = 16.13$, $p < 0.001$).

Table 3. Generalised linear model for total duration of grouping behaviour.

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

The overall model is statistically significant ($\chi^2_3 = 152.49$, $p < 0.001$).

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 ($F_{1,98} = 5.04$, $p = 0.027$, Figure 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 behaviour ($p = 0.891$), 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 ($p > 0.05$).

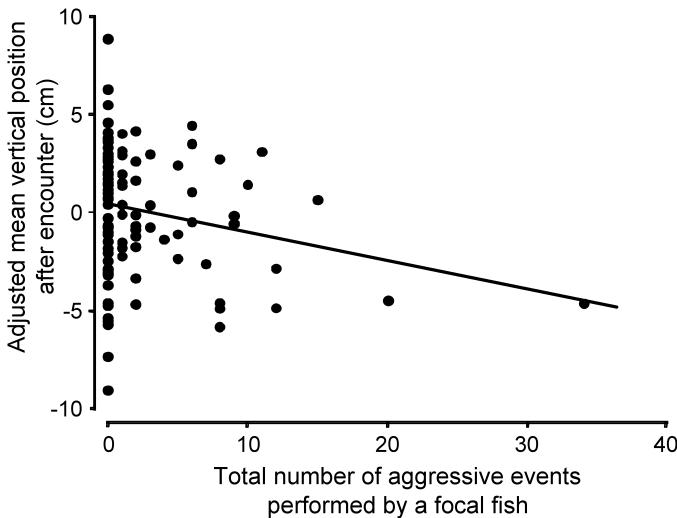


Figure 1. Total number of aggressive events performed by a focal fish during 30 min observation and mean vertical position of a focal fish from the bottom after encounter. Mean vertical position was adjusted with the effect of mean vertical position before encounter ($r^2 = 0.048$, $p = 0.027$).

Discussion

A fish displayed aggressive behaviour more frequently when (1) it was small (earlier developmental state), (2) it was bigger than its opponent, (3) it was in poor condition and (4) the condition of its opponent was even poorer. 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 its opponent and (2) it was in poor condition. Grouping behaviour lasted longer when (1) the two fish were close in size, (2) the fish were large (later developmental state) and (3) they were 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), body condition, and how they differ between two individuals are determinants of social behaviour 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 behaviour 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 behaviour 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 behaviour occurred in the smallest fish examined (7.5 mm total length), suggesting that onset of aggressive behaviour in red drum is before or around the beginning of the settlement stage. Phenotypic differences between individuals seem to be important for aggressive behaviour. Individuals with larger body size or better condition tend to show more frequent aggressive behaviour toward individuals with smaller body size or poorer condition. These individuals of larger body size or better condition are more likely to win the contest and individuals of smaller body size or poorer condition are more likely to pay a cost for fighting (Huntingford & Turner, 1987). As a consequence, the competitively inferior fish may choose to avoid encounters that would expose them to aggressive behaviour and thereby reduce the risks of increased energy expenditure (Wilson et al., 1990), decreased time available for foraging (Ruzzante & 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 periphery of seagrass bed (Pérez-Domínguez, 2004) support this idea.

Aggressive behaviour was displayed more frequently when individuals were in poorer 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 & Houston, 1990; Dugatkin & Ohlsén, 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 behaviour, as well as the absolute physiological conditions of the individuals. Thus, aggressive behaviour 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 behaviour in the wild.

Young red drum are known to be cannibalistic when reared in tanks at elevated densities (Chang & Liao, 2003). The aggressive behaviour observed in our trials were, however, not solely an attempt at cannibalism because aggressive behaviour was also observed when the two fish were at similar sizes, or even from smaller to larger individuals. If this is the case, aggressive behaviour 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 & 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 behaviour sometime during the larval period (Hunter & Coyne, 1982; Gallego & Hearth, 1994; Nakayama et al., 2007). The ontogenetic increase we observed in the duration of grouping behaviour in red drum larvae may reflect an increasing benefit of grouping behaviour. 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 behaviour to increase survival. It seems unlikely that a group of only two individuals could create a confusion effect to increase survival (Landau & Terborgh, 1986; Krause, 1994), but a group of two could increase survival by increasing vigilance against a predator (Brown & Warburton, 1999) or increased time available for other activities by cooperative predator inspection (Dugatkin & Alfieri, 1991). The cost of resource competition within a group (Grand & Dill, 1999) would also affect grouping behaviour. Our results suggest that fish can benefit most from grouping behaviour 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 & 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 when individuals were smaller than their opponents, which is the opposite trend of aggressive behaviour. This indicates that fish change their behaviour from avoidance to grouping to aggression as their size increases relative to their opponent. The decision between aggressive and grouping behaviour would change depending on resource abundance and predation pressure (Huntingford & Turner, 1987; Krause & Ruxton, 2002). Scarce resources would create an agonistic environment, whereas high predation pressure should favour grouping behaviour.

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 behaviour 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 behaviour 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 they inhabit in the seagrass meadows, which height 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 odour and subsequent aggression toward non-kin has been studied intensively in salmonids (e.g., Brown & Brown, 1993, 1996), but kin discrimination would be less likely under field conditions (Griffiths & 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 behavioural 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 behavioural interactions were reared in different tanks and had not met each other before the test.

The behavioural 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 & Minello (2001) found higher survival of newly settled red drum larvae in structurally complex habitats than in non-vegetated habitats. Aggressive behaviour 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 behaviour 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.

Acknowledgements

We thank Dr. Robert Vega and the Coastal Conservation Association/Central Power and Light Marine Development Center for maintaining broodstock of red drum and providing eggs. We also thank the people in our lab (Dr. Kiersten Madden, Mr. Charles Foster and Ms. Somabha Mohanty) and two anonymous referees for constructive suggestions and comments in preparing this manuscript. This research was supported by a grant from the US National Science Foundation (OCE-0425241) to L.A.F. This is the University of Texas at Austin Marine Science Institute Contribution No. 1487.

References

- Akaike, H. (1974). A new look at the statistical model identification. — *IEEE Trans. Autom. Contr.* 19: 716-723.
- Almany, G.R. (2004). Priority effects in coral reef fish communities of the Great Barrier Reef. — *Ecology* 85: 2872-2880.

- Beckman, D.W., Wilson, C.A. & Stanley, A.L. (1988). Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the northern Gulf of Mexico. — Fish. Bull. 87: 17-28.
- Briffa, M. & Sneddon, L.U. (2007). Physiological constraints on contest behaviour. — Funct. Ecol. 21: 627-637.
- Brown, G.E. & Brown, J.A. (1993). Social dynamics in salmonid fishes: do kin make better neighbours? — Anim. Behav. 45: 863-871.
- Brown, G.E. & Brown, J.A. (1996). Kin discrimination in salmonids. — Rev. Fish Biol. Fish. 6: 201-219.
- Brown, C. & Warburton, K. (1999). Social mechanisms enhance escape responses in shoal of rainbowfish, *Melanotaenia duboulayi*. — Environ. Biol. Fish. 56: 455-459.
- Chang, E.Y.Y. & Liao, I.C. (2003). Sibling cannibalism of young red drum, *Sciaenops ocellatus*, in relation to size disparity and metabolic rates. — Environ. Biol. Fish. 68: 407-415.
- Comyns, B.H., Lyczkowski-Shultz, J., Nieland, D.L. & Wilson, C.A. (1991). Reproduction of red drum, *Sciaenops ocellatus*, in the northcentral Gulf of Mexico: seasonality and spawner biomass. — NOAA Tech. Rep. NMFS 95: 17-26.
- Côté, S.D. (2000). Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. — Behaviour 137: 1541-1566.
- Côté, I.M. & Poulin, R. (1995). Parasitism and group size in social animals: a meta-analysis. — Behav. Ecol. 6: 159-165.
- Couzin, I.D., Krause, J., Franks, N.R. & Levin, S.A. (2005). Effective leadership and decision-making in animal groups on the move. — Nature 433: 513-516.
- Cristol, D.A. (1992). Food deprivation influences dominance status in dark-eyed juncos, *Junco hyemalis*. — Behaviour 43: 117-124.
- Dugatkin, L.A. (2002). Cooperation in animals: an evolutionary overview. — Biol. Philos. 17: 459-476.
- Dugatkin, L.A. & Alfieri, M. (1991). Tit-for-tat in guppies (*Poecilia reticulata*): the relative nature of cooperation and defection during predator inspection. — Evol. Ecol. 5: 300-309.
- Dugatkin, L.A. & Ohlsén, S.R. (1990). Contrasting asymmetries in value expectation and resource holding power: effects on attack behaviour and dominance in the pumpkinseed Sunfish, *Lepomis gibbosus*. — Anim. Behav. 39: 802-804.
- Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. — J. Appl. Ichthyol. 22: 241-253.
- Fuiman, L.A. (1994). The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. — J. Fish Biol. 45 (Suppl. A): 55-79.
- Gallego, A. & Hearth, M.R. (1994). The development of schooling behaviour in Atlantic herring *Clupea harengus*. — J. Fish Biol. 45: 569-588.
- Grand, T.C. & Dill, L.M. (1999). The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition? — Anim. Behav. 58: 443-451.
- Griffiths, S.W. (2003). Learned recognition of conspecifics by fishes. — Fish Fish. 4: 256-268.
- Griffiths, S.W. & Armstrong, J.D. (2000). Differential responses of kin and nonkin salmon to patterns of water flow: does recirculation influence aggression? — Anim. Behav. 59: 1019-1023.

- Hoese, H.D. & Moore, R.H. (1998). Natural History Series, No. 22: Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters, 2nd edn (Moody Jr., W.L., series ed.). — Texas A&M University Press, College Station, TX.
- Holt, S.A., Kitting, C.L. & Arnold, C.R. (1983). Distribution of young red drums among different sea-grass meadows. — Trans. Am. Fish. Soc. 112: 267-271.
- Hunter, J.R. & Coyne, K.M. (1982). The onset of schooling in northern anchovy larvae, *Engraulis mordax*. — CalCOFI Rep. 23: 246-251.
- Huntingford, F.A. & Turner, A.K. (1987). Animal conflict. — Chapman & Hall, London.
- Jakobsson, S., Brick, O. & Kullberg, C. (1995). Escalated fighting behavior incurs increased predation risk. — Anim. Behav. 49: 235-239.
- Johnsson, J.I. (2003). Group size influences foraging effort independent of predation risk: an experimental study on rainbow trout. — J. Fish Biol. 63: 863-870.
- Jonart, L.M., Hill, G.E. & Badyaev, A.V. (2007). Fighting ability and motivation: determinants of dominance and contest strategies in females of a passerine bird. — Anim. Behav. 74: 1675-1681.
- Jönsson, E., Johnsson, J.I. & Björnsson, B.T. (1998). Growth hormone increases aggressive behavior in juvenile rainbow trout. — Horm. Behav. 33: 9-15.
- Kokko, H. (1999). Competition for early arrival in migratory birds. — J. Anim. Ecol. 68: 940-950.
- Komdeur, J. (2006). Variation in individual investment strategies among social animals. — Ethology 112: 729-747.
- Krause, J. (1993). The influence of hunger on shoal size choice by three-spined sticklebacks, *Gasterosteus aculeatus*. — J. Fish Biol. 43: 775-780.
- Krause, J. (1994). The influence of food competition and predation risk on size-assortive shoaling in juvenile chub (*Leuciscus cephalus*). — Ethology 96: 105-116.
- Krause, J. & Godin, J.G.J. (1995). Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. — Anim. Behav. 50: 465-473.
- Krause, J. & Ruxton, G.D., eds (2002). Living in groups. Oxford series in ecology and evolution (May, R.M. & Harvey, P.H., eds). — Oxford University Press, Oxford.
- Krebs, J.R. & Davies, N.B., eds (1993). An introduction to behavioural ecology, 3rd edn. — Blackwell, Oxford.
- Krebs, J.M. & Turingan, R.G. (2003). Intraspecific variation in gape-prey size relationships and feeding success during early ontogeny in red drum, *Sciaenops ocellatus*. — Environ. Biol. Fish. 66: 75-84.
- Landeau, L. & Terborgh, J. (1986). Oddity and the 'confusion effect' in predation. — Anim. Behav. 34: 1372-1380.
- Lang, F., Govind, C.K., Costello, W.J. & Greene, S.I. (1977). Developmental neuroethology: changes in escape and defensive behavior during growth of the lobster. — Science 197: 682-684.
- Leimar, O., Austad, S. & Enquist, M. (1991). A test of the sequential assessment game: fighting in the bowl and doily spider *Frontinella pyramitela*. — Evolution 45: 862-874.
- Maher, C.R. & Lott, D.F. (2000). A review of ecological determinants of territoriality within vertebrate species. — Am. Midl. Nat. 143: 1-29.
- Maynard Smith, J. (1982). Evolution and the theory of games. — Cambridge University Press, Cambridge.

- McCullagh, P. & Nelder, J.A. (1989). Generalized linear models, 2nd edn. — Chapman & Hall, London.
- McNamara, J.M. & Houston, A.I. (1990). State-dependent ideal free distributions. — *Evol. Ecol.* 4: 298-311.
- Metcalfe, N.B. & Thomson, B.C. (1995). Fish recognize and prefer to shoal with poor competitors. — *Proc. Roy. Soc. Lond. B: Biol.* 259: 207-210.
- Nakayama, S., Masuda, R. & Tanaka, M. (2007). Onsets of schooling behavior and social transmission in chub mackerel *Scomber japonicus*. — *Behav. Ecol. Sociobiol.* 61: 1383-1390.
- Pérez-Domínguez, R. (2004). Effect of nursery-environment condition on habitat use, growth, survival and endocrine physiology during larval settlement in the red drum (*Sciaenops ocellatus*). Dissertation. — Department of Marine Science, The University of Texas at Austin, Austin, TX.
- Peters, K.M. & McMichael Jr., R.H. (1987). Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae) in Tampa Bay, Florida. — *Estuaries* 10: 92-107.
- Pitcher, T.J., Magurran, A.E. & Allan, J.R. (1986). Size-segregative behaviour in minnow shoals. — *J. Fish Biol.* 29: 83-95.
- Rooker, J.R., Holt, S.A., Holt, G.J. & Fuiman, L.A. (1999). Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. — *Fish. Bull.* 97: 581-590.
- Ruzzante, D.E. & Doyle, R.W. (1991). Rapid behavioral changes in medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. — *Evolution* 45: 1936-1946.
- Stunz, G.W. & Minello, T.J. (2001). Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). — *J. Exp. Mar. Biol. Ecol.* 260: 13-25.
- Vøllestad, L.A. & Quinn, T.P. (2003). Trade-off between growth and aggression in juvenile coho salmon (*Oncorhynchus kisutch*). — *Anim. Behav.* 66: 561-568.
- Ward, A.J.W. & Krause, J. (2001). Body length assortative shoaling in the European minnow, *Phoxinus phoxinus*. — *Anim. Behav.* 62: 617-621.
- Wells, M.S. (1988). Effects of body size and resource value on fighting behaviour in a jumping spider. — *Anim. Behav.* 36: 321-326.
- Wilson, M.A., Gatten, R.E. & Greenberg, N. (1990). Glycolysis in *Anolis carolinensis* during agonistic encounters. — *Physiol. Behav.* 50: 1957-1966.