



Negative effects of increasing group size on foraging in two estuarine piscivores

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Abstract

The effect of predator density on per capita ingestion rates in two estuarine predators, age-0 bluefish (*Pomatomus saltatrix* L.) and age-1 striped bass (*Morone saxatilis* W.), was examined in a 121,000-l research aquarium. Group size treatments were 3, 6, 12, and 24 predators; each treatment was provided with 100 prey (mummichog killifish, *Fundulus heteroclitus* L.) during a 22-h feeding trial. The behaviors of predator and prey were recorded. Predator type and group size had a significant effect on per capita ingestion rates. Bluefish had significantly higher per capita ingestion rates compared to striped bass. For bluefish, per capita ingestion rate was highest in the three predator group, while for striped bass, individuals in the six predator treatment had the highest ingestion rates. From these maxima, per capita ingestion rate values declined to their lowest values in the 24 predator treatment for both species. Several factors that may be responsible for lowered per capita ingestion rates at higher group sizes include predator interference, prey depletion, and anti-predator behaviors of prey. For juvenile bluefish and striped bass being a member of a relatively large group may lead to decreased individual ingestion rates. Given that large group sizes of these species occur in nature, we conclude that these foraging costs must be outweighed by benefits of group membership.

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1. Introduction

Costs and benefits of group membership have been examined from the perspective of both predator and prey. For example, group benefits to prey include early predator detection, predator confusion, and dilution of a predator's effect (Bertram, 1978). Increased probabilities of locating and capturing prey and deterring potential competitors have been observed with increases in group size for predators (Bertram, 1978). For all animals, a cost of group membership can be competition for resources.

In general, group membership in fishes has been shown to have positive effects on foraging on both immobile and mobile prey (Pitcher and Parrish, 1993). Increased feeding rates in larger groups have been observed in goldfish *Carassius auratus* (L.) feeding on benthic flake food (Pitcher and Magurran, 1983), sticklebacks *Gasterosteus aculeatus* (L.) feeding on an immobile 'benthic' prey (Ranta and Kaitala, 1991), and juvenile walleye pollock feeding on sinking food pellets (Baird et al., 1991). Major (1978) found that individuals in groups of three and five jacks *Caranx ignobilis* (Forsskål) had higher capture success and increased per capita ingestion when compared to solitary jacks feeding on schooled anchovy *Stolephorus purpureus* (Fowler). Per capita consumption was significantly higher within a group of five piscivorous perch *Perca fluviatilis* (L.) compared to a solitary perch feeding on piscine prey as a result of facilitation (multiple perch able to confuse prey) (Eklöv, 1992); however, pike (*Esox lucius* (L.); solitary stalking predator) had highest ingestion rates when held alone and suffered interference when in groups of five.

Piscivorous fishes are often observed in larger groups than those described above. Costs of group membership, such as the agonistic interactions observed in pike (Eklöv, 1992), may balance or outweigh the benefits of increased group size at some higher group size even in schooling piscivores. The effect of larger group sizes of piscivores (>5) on per capita ingestion rates is unknown.

The addition of a large number of predators into an experimental arena does not necessarily lead to foraging as a cohesive group. Major (1978) found that jacks, initially in group sizes of three and five fish, broke up into smaller groups during the course of experiments. The influence of increasing predator number on subsequent group size has not been examined with relatively large groups of predators. Enclosure and tank size limitations have constrained our ability to effectively examine these questions and ultimately to determine where the balance between costs and benefits of group membership for relatively large predators feeding on mobile prey occurs.

Bluefish *Pomatomus saltatrix* (L.) and striped bass *Morone saxatilis* (Walbaum) juveniles both feed on fish prey in US east coast estuaries (Manooch, 1973; Hartman and Brandt, 1995; Buckel and McKown, 2002). Bluefish are significantly more successful at capturing fish prey than striped bass (Scharf et al., 2003), and it is predicted that striped bass will gain more from group benefits (e.g., facilitation) than will bluefish. We hypothesize that peak per capita ingestion rates will occur at a larger group size for striped bass when compared to bluefish. For both predators, per capita ingestion rates at relatively large group sizes may be reduced if costs outweigh group benefits. To test these hypotheses, the effects of group size and predator type on per capita ingestion rate in juvenile striped bass and bluefish fed mummichog killifish *Fundulus heteroclitus* (L.), an

aggregating prey, are determined. The influence of increasing predator density on subsequent group size over the course of the experiment is examined to determine if there is an upper limit on group size. Video recordings of fish behavior were used to identify potential mechanisms driving the patterns observed in ingestion rates.

2. Methods

2.1. Experimental fish

Bluefish and striped bass were collected during summer 1998 in the Haverstraw Bay region of the lower Hudson River estuary, NY (41°10' N, 73°10' W), using beach seines. Mummichog were captured using fish traps in Sandy Hook Bay marsh creeks and by beach seining; mummichog are prey of both striped bass and bluefish (Tupper and Able, 2000; Buckel and McKown, 2002). All fish were acclimated in round tanks (1.8 m diameter, 0.6 m deep) with flow-through seawater from Sandy Hook Bay, NJ, USA. All fish were maintained at controlled temperature and Sandy Hook Bay ambient salinities (~ 20 °C; ~ 23 ppt). Laboratory held groups of ~ 100 each of striped bass and bluefish were sampled from with replacement. Individual fish were never used in contiguous trials. During holding, striped bass and bluefish were fed live and thawed fish prey while mummichog were provided with commercial fish food.

2.2. Experimental aquarium

Trials to examine the effects of group size were conducted in a large research aquarium housed in the James J. Howard Marine Sciences Laboratory at Sandy Hook, NJ, USA. A detailed description of the aquarium is provided in Stoner et al. (1999). Briefly, the aquarium is an oval-shaped tank (10.6 × 4.5 × 3 m deep) containing eight 1.2 m high × 0.7 m wide observation windows (three on each side and one on each end; acrylic sheets were used to cover each window recess to eliminate this potential prey refuge) with a volume of 121,000 l and a coarse sand bottom. Water temperature (mean = 20 °C; range = 19–21) and salinity (mean = 23 ppt; range = 21–25) were kept constant throughout all experimental trials. The photoperiod was 14 h light/10 h dark (sunrise = 0600 and sunset = 2000). Sunrise and sunset periods lasted for one half-hour and consisted of a computer controlled series of lights going on (sunrise) or off (sunset) mimicking natural light levels.

2.3. Per capita ingestion rates

The effect of group size on striped bass and bluefish per capita ingestion rate was examined using initial group sizes of 3, 6, 12, and 24 predators. In this design, group sizes with >5 piscivores were represented (a limitation of prior studies; see Introduction); we chose not to use group sizes over 24 predators to avoid logistical difficulties with predator observations and prey supply. These group sizes are referred to as “initial” (see Major, 1978) for the remainder of the manuscript; initial groups broke down into subgroups

which are referred to as “resultant” group sizes. Predators were provided with a fixed number ($n = 100$) of live mummichog killifish. There were three replicates for bluefish and four replicates for striped bass treatments (results from striped bass were more variable). Striped bass and bluefish trials were conducted in early (13 June to 16 July) and late summer (11 August to 10 September; see Table 1), respectively. By conducting bluefish trials in late summer, bluefish were similar in size to striped bass used in early-summer trials.

Each feeding trial lasted 22 h beginning at 1000 and ending at 0800 the following day. On the day prior to a trial, predators and prey were counted, measured (total length, L_t , ± 1.0 mm), and weighed (± 0.01 g). Prey were counted a second time just prior to being introduced into the experimental tank. Predators and prey were fed to satiation the evening (1600–1700) and immediately (~ 0900) before the trial; predators were not hungry at the onset of each trial which allowed prey time to acclimate to their surroundings before predators became aggressive. The ration consumed by the predators before the trial was determined. At the end of each trial, predators and remaining prey were removed from the aquarium and prey were counted. Attention was given to insure that all uneaten prey fish were accounted for after each trial; observations were made through the windows while a net was pressed into the sediment in small increments around the perimeter of the tank where single fish sometimes hid.

To insure predator size differences did not confound results, ANOVAs were used to compare predator size and prey–predator size ratios between treatments. Within each predator type, there were no significant differences in predator size (bluefish TL: $F = 0.023$, $df = 3,8$, $p = 0.995$; striped bass TL: $F = 1.945$, $df = 3,12$, $p = 0.176$; see Table 1) or prey–predator size ratios among group size treatments (bluefish: $F = 1.364$, $df = 3,8$, $p = 0.321$; striped bass: $F = 2.81$, $df = 3,12$, $p = 0.085$; see Table 1).

Similarly, we did not want experimental differences in prey and predator sizes to confound results for the between predator comparisons. Transformations of the dependent variable did not lead to homogeneity of variances so non-parametric comparisons (Mann–Whitney U test) of predator size and prey–predator size ratios were used. Bluefish and striped bass were significantly different in size (Table 1: TL: Mann–Whitney U test, $U = 0.0$, $p < 0.001$). Prey–predator size ratios were not significantly different between the bluefish and striped bass groups (Table 1; Mann–Whitney U test, $U = 56$, $p = 0.063$) although the p value was marginal. These prey–predator size ratios (Table 1) are within the range observed from stomach contents of wild bluefish and striped bass (Scharf, 2001). Although statistically significant (or nearly so), the differences in body size and prey–predator size ratios were minor ($< 5\%$).

2.4. Behavior

Striped bass and bluefish swam continuously in a circular manner generally within close proximity to the tank walls. Video observations from a single camera set at a side window were used to record predator behavior on the far tank wall; recordings were made for 5 min at the beginning of each hour throughout the trial. Dependent variables obtained from the video record for each 5-min period included mean number of predators in passing groups (resultant group size), proportion of groups observed that were at initial group size,

Table 1
Experimental design and start dates for group size trials

Predator	Group size	Date	Mean predator L_t (mm) (S.D.)	Mean predator W (g) (S.D.)	Mean killifish L_t (mm) (S.D.)	Mean killifish W (g) (S.D.)	Mean prey–predator size ratio (S.D.)	Per capita prey available
Striped bass	3	16 June, 23 June, 1 July, 14 July	191 (1.2)	69.14 (2.45)	56 (0.5)	2.26 (0.07)	0.291 (0.001)	33.33
	6	22 June, 25 June, 7 July, 9 July	189 (1.3)	68.34 (1.45)	56 (0.4)	2.18 (0.11)	0.294 (0.003)	16.67
	12	17 June, 24 June, 8 July, 16 July	190 (0)	69.60 (3.77)	56 (0.2)	2.24 (0.16)	0.295 (0.001)	8.33
	24	13 June, 29 June, 30 June, 15 July	191 (1.3)	69.99 (3.26)	56 (0.7)	2.20 (0.13)	0.292 (0.003)	4.17
Bluefish	3	11 August, 1 Sept, and 3 Sept	176 (7.0)	54.41 (6.93)	52 (1.4)	1.71 (0.2)	0.293 (0.005)	33.33
	6	20 August, 27 August, and 9 Sept	175 (5.0)	53.14 (6.34)	51 (0.6)	1.78 (0.2)	0.294 (0.005)	16.67
	12	18 August, 25 August, and 10 Sept	176 (5.0)	54.83 (5.96)	53 (1.7)	1.80 (0.3)	0.301 (0.010)	8.33
	24	19 August, 26 August, and 2 Sept	175 (5.6)	53.55 (6.01)	53 (1.6)	1.91 (0.3)	0.303 (0.007)	4.17

Mean sizes (total length (L_t) and weight (W)) of age-1 striped bass, age-0 bluefish, and mummichog and mean prey–predator size ratios. S.D. = standard deviation.

and an activity index. The activity index was calculated as the number of crossings for the whole group during a 5-min interval (sum of fish that crossed/number of predators in initial group treatment). A single value by replicate for the activity index, proportion of observations at initial size, and group size (predators) was determined by taking the mean of all time point estimates for each trial. Because of an undetected power outage after the third bluefish trial which reset the computerized night-time light levels, video recordings at night (2100–0600) for 9 out of 12 bluefish trials were too dim for observations to be made.

Prey were too small to be seen with video observation given the large size of the research aquarium. Therefore, prey behavior was quantified from direct observations. For the first replicate in the four striped bass group size treatments, we made direct observations every hour and examined the video tapes to determine when striped bass attacks were occurring (see further use of this data below). This information was used to determine when direct observation should be made for striped bass and bluefish trials. Predators had not begun to attack prey during the first several hours of the experiment but aggressive behaviors towards prey were often observed during afternoon, night, and early morning. Therefore, direct observations were made on prey during the afternoon (~ 1600) and early morning (~ 0700) of three replicate trials for each predator type and group size combination; each of these observations lasted around 10 min.

Height in the water column and dispersion were used to quantify prey response to predator groups. Killifish prey stayed in a single group or broke into several groups but behaviors for all prey groups were usually the same. For prey height, the 3 m of the water column were divided into three categories: 1 = bottom meter, 2 = mid meter, and 3 = top meter (the aquarium windows were 1.2 m high, which aided in classification into these categories). Killifish were classified as tightly grouped (1, nearest neighbor distance ~ 1 body length) or dispersed (2, nearest neighbor distance > ~ 1 body length). Occasionally, one group of killifish would be tightly aggregated while another would be dispersed; these were scored as a 1.5 on the dispersal scale. For each 10-min prey observation period (1600 and 0700), a single value was recorded for prey height and dispersion since these did not change during the observation period.

The hourly attack rate data that was collected during the first replicate trial for each striped bass treatment allowed us to examine the influence of foraging activity on predator behavior. Specifically, we compared the hourly estimates of attacks to the mean group size for that hour.

2.5. Analysis

The effects of initial group size and predator type were examined using two-way analysis of variance (ANOVA) on the following dependent variables: per capita ingestion rate, predator activity, proportion of observations at the initial group size, and resultant predator group size. Per capita ingestion rate ($\log_e(y)$), resultant group size ($\log_e(y)$), and proportion of observations ($\arcsin(\sqrt{y})$) data were transformed to stabilize variances. The Tukey HSD test was used for a posteriori comparisons. To insure that ration (g prey/g predator) fed prior to the trial had no influence on per capita ingestion rates, we examined if ration was correlated with per capita ingestion rate. Mann–Whitney U tests and

Spearman rank correlations were used to examine the effects of predator type and initial group size on prey behaviors, respectively.

3. Results

3.1. Per capita ingestion rates

A total of 28 feeding trials were conducted. Both predator type and group size had a significant effect on per capita ingestion rates (Table 2). Striped bass had significantly lower per capita ingestion rates compared to bluefish (Fig. 1 and Table 2). There was no significant statistical interaction between predator type and group size (Table 2). However, bluefish ingestion rates were highest for three bluefish and declined continuously thereafter while per capita ingestion of striped bass initially increased from three to six predators and then decreased (Fig. 1). Post hoc comparisons of ingestion rate data were examined on data pooled across predator species; the group size of 24 predators had significantly lower ingestion rates compared with group sizes of three (Tukey HSD: $p=0.005$) and six predators ($p=0.002$). No other group size level comparisons were significant.

Differences in the amount of prey consumed before an experiment did not influence per capita ingestion rates during the trials. The ration fed prior to a trial was not significantly

Table 2
Predator behavior

Source	<i>df</i>	SS	<i>F</i>	<i>p</i> Value
<i>Per capita ingestion rate</i>				
Predator type	1	0.669	12.752	0.002
Initial group size	3	1.210	7.682	0.001
Interaction	3	0.334	2.118	0.130
<i>Activity</i>				
Predator type	1	120.293	36.437	<0.0001
Initial group size	3	1.429	0.144	0.932
Interaction	3	3.867	0.390	0.762
<i>Proportion at initial group size</i>				
Predator type	1	0.0001	0.002	0.968
Initial group size	3	0.993	7.748	0.002
Interaction	3	0.222	1.721	0.203
<i>Resultant group size</i>				
Predator type	1	0.004	0.227	0.640
Initial group size	3	3.581	215.126	<0.0001
Interaction	3	0.005	0.271	0.846

Two-way ANOVAs with predator type (bluefish and striped bass) and initial group size (3, 6, 12, and 24) as factors. Dependent variables include per capita ingestion rate (log-transformed), predator activity, proportion of observations at initial group size (arcsin-transformed), and resultant experimental group size (log-transformed).

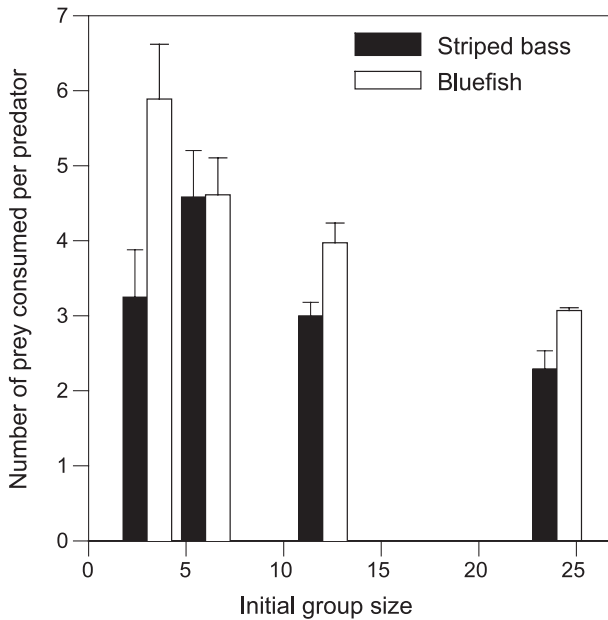


Fig. 1. Mean per capita ingestion rates (\pm S.E.) as a function of initial predator group size for striped bass (*M. saxatilis*; closed bars) and bluefish (*P. saltatrix*; open bars). Striped bass: $n=4$ replicates. Bluefish: $n=3$ replicates.

related to per capita ingestion rates for bluefish ($r = -0.015$, $p = 0.964$) or striped bass ($r = -0.396$, $p = 0.128$).

3.2. Behavior

Striped bass were significantly more active than bluefish but initial group size did not influence predator activity levels (Tables 2 and 3). Striped bass and bluefish from larger

Table 3

Mean activity index (see text for calculations) for age-1 striped bass and age-0 bluefish from group size treatment trials ($n=3$ replicates)

Group size	Activity index	S.E.
<i>Striped bass</i>		
3	10.33	0.72
6	11.88	0.43
12	10.90	1.09
24	10.38	1.83
<i>Bluefish</i>		
3	6.69	0.72
6	6.23	0.84
12	6.13	0.89
24	6.53	1.24

initial group sizes were often observed broken up into smaller groups. Initial group sizes of 3, 6, and 12 striped bass were maintained in ~ 80–95% of observations while the 24 striped bass treatment was observed at its initial group size in ~ 60% of the observations (Fig. 2A). Bluefish that were initially in groups of three or six maintained that group size in ~ 95–100% of observations; however, initial groups of 12 and 24 bluefish were often observed broken into smaller groups (Fig. 2B). Initial group size had a significant effect on the proportion of observations at initial group sizes but predator type did not (Table 2; Fig. 2). The initial group size of 24 predators was maintained significantly less than the three and six predator treatments (Tukey HSD, $p < 0.05$) while the significance of the 12 and

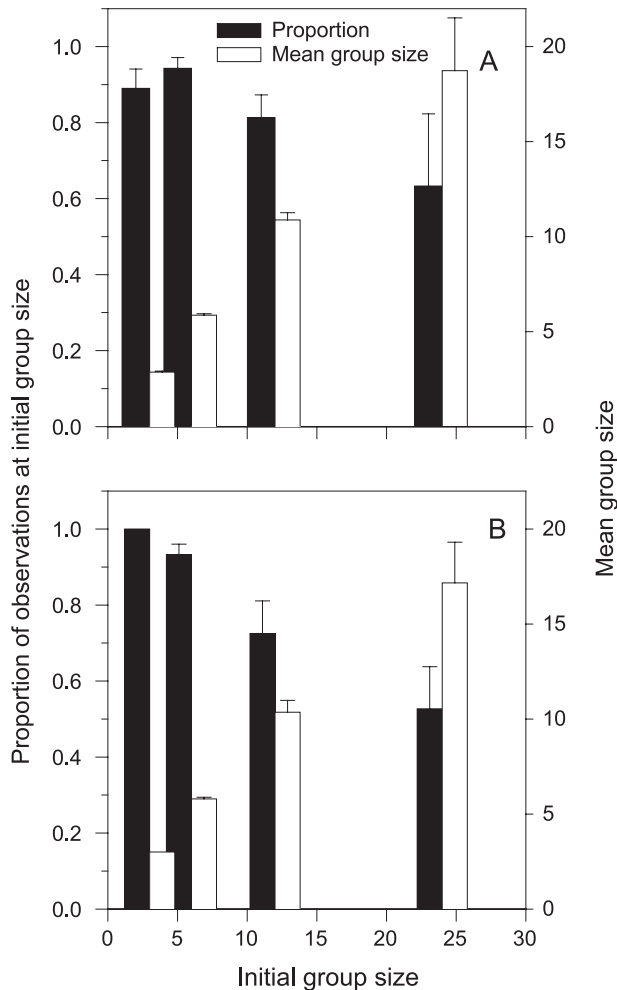


Fig. 2. Mean proportion of observations (\pm S.E.; closed bars) and mean group size (\pm S.E.; open bars) as a function of initial predator group size for (A) striped bass (*M. saxatilis*) and (B) bluefish (*P. saltatrix*). Striped bass and bluefish: $n = 3$ replicates.

three predator treatment comparison was marginal (Tukey HSD, $p=0.064$). Although larger initial groups broke up more often, large differences in mean group sizes between initial group size treatments remained during the experiment for both striped bass and bluefish (Fig. 2A and B). Initial group size had a significant effect on resultant group sizes but predator type did not (Table 2; all multiple comparison for initial group size effect $p<0.001$, Tukey HSD).

For striped bass, group break down was related to foraging activity. In the 12 and 24 striped bass groups, estimates of attack number were negatively correlated with corresponding estimates of resultant group size (12SB, $r=-0.512$, $p=0.012$; 24SB, $r=-0.481$, $p=0.020$) but not for 3 and 6 striped bass (3SB, $r=-0.311$, $p=0.139$; 6SB, $r=-0.373$, $p=0.073$).

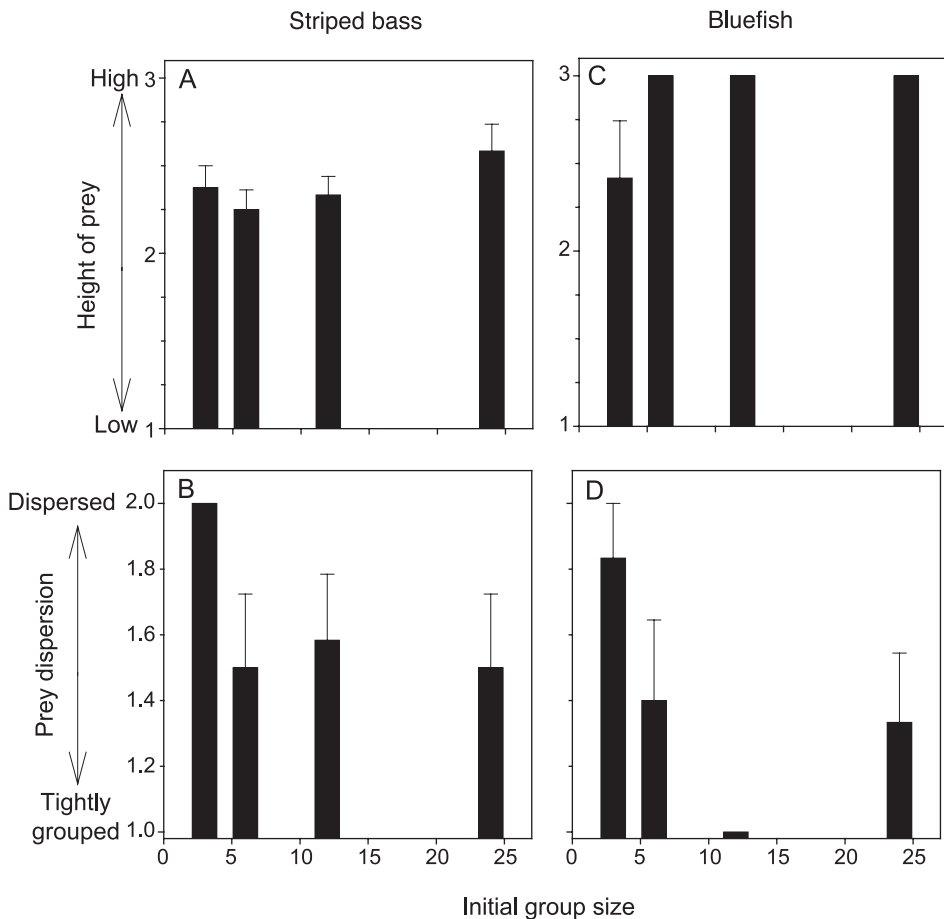


Fig. 3. Mean (\pm S.E.) height (A and C) and dispersion (B and D) of mummichog killifish (*F. heteroclitus*) as a function of initial group size for striped bass (A and B) and bluefish (C and D). Striped bass and bluefish: $n=6$ replicates.

Mummichog prey were at the side of the tank in all observations; occasionally, a small percentage of the prey would move into open water for brief periods. We found no difference in prey behaviors between the ~ 1600 and ~ 0700 observations (Mann–Whitney U tests, $p > 0.05$) so data from these time points were pooled. Prey responded differently to bluefish and striped bass. Prey occupied higher levels of the water column in bluefish trials compared to those trials with striped bass (Mann–Whitney test: $U = 105$, $p < 0.001$). Height of prey in the water column was influenced significantly by initial group size in striped bass (Fig. 3A; Spearman rank correlation: $r = 0.496$, $p = 0.007$) and bluefish (Fig. 3C; $r = 0.511$, $p = 0.013$); the response was an abrupt jump in prey height between the three and six bluefish treatments when compared to the more continuous increase in prey height with increasing initial group size observed for striped bass (Fig. 3A and C). Predator type did not have an influence on prey dispersion (Mann–Whitney test: $U = 195.5$, $p = 0.136$). Initial group size of bluefish had a significant influence on prey dispersion (Fig. 3D; Spearman rank correlation: $r = -0.437$, $p = 0.037$) but initial group size of striped bass did not (Fig. 3B; $r = -0.268$, $p = 0.229$).

4. Discussion

Per capita ingestion rates declined with increasing group size for both striped bass (from 6 to 24 predators) and bluefish (from 3 to 24 predators). It is generally believed that piscivores feeding on mobile prey benefit from group membership (Pitcher and Parrish, 1993); these conclusions are based on studies where per capita ingestion rates of solitary individuals have been compared to small groups (Major, 1978; Eklöv, 1992). For example, individual jack *C. ignobilis* had higher attack success on schooling anchovy *S. purpureus* prey (initial prey group sizes of 25, 100, and 200) when in groups (schools) compared to attacking alone (Major, 1978). Eklöv (1992) examined the effects of group size in adult perch *P. fluviatilis* feeding on groups of juvenile perch; per capita ingestion rates were lower for the one perch treatment than for five perch.

Per capita ingestion rates may only be depressed in groups that are relatively large in size. In Major's (1978) study, there was no significant gain in per capita ingestion between the three and five predator treatments in any of the prey treatments. Compared to the three predator trial, ingestion rates were slightly lower in the five predator trial (200 prey) suggesting that negative effects may occur in jacks at larger group sizes (>5). Although not a piscivore example, Morgan and Colgan (1987) found that ingestion rate leveled off in bluntnose minnows *Pimephales notatus* (Rafinesque) at an initial group size of ~ 10 . Striped bass and bluefish are often observed in large schools in the wild; why travel in relatively large schools if it is costly in terms of prey intake? Benefits of group membership, such as a refuge from predation (i.e., vigilance sharing) or prey detection (i.e., local enhancement; Ryer and Olla, 1992), must outweigh these foraging costs.

Bluefish had higher per capita ingestion rates compared to striped bass even though striped bass were larger. Additionally, prey response differed between the two predators with increased anti-predator behaviors observed in bluefish trials. Scharf et al. (2003) found that bluefish capture success was at least twice as high as that of striped bass when feeding on two piscine prey types, bay anchovy *Anchoa mitchilli* (Valenciennes) and

Atlantic silverside *Menidia menidia* (L.), across a range of prey to predator size ratios. Predators that have high individual capture success are expected to benefit less from group foraging when compared to predators with low individual capture success (Eklöv, 1992). Although not statistically significant, the trend in our data support this prediction. Bluefish achieved the highest per capita ingestion rate when predator number was lowest. However, the small group sizes for striped bass (three and six) gave variable results (possibly due to individual differences in foraging ability) with mean per capita ingestion rate being highest for the six predator group.

Striped bass were more active than bluefish over all group sizes; however, activity levels remained constant with increasing initial group size. There are at least two explanations for the activity difference between the two predators. First, striped bass were on average about 1.5 cm larger than bluefish. Second, striped bass require more attacks to capture a fish prey (Scharf et al., 2003) than do bluefish; more time spent attacking likely translates into higher swimming speeds. The differences in growth rate between age-1 striped bass and the much faster growing age-0 bluefish observed in field and laboratory settings (Buckel and McKown, 2002) may be partially explained by differences in activity level.

Predators altered their behavior as group size increased. The percentage of observations at the initial group size dropped with increasing initial group size but large differences in resultant group size were sustained. Bluefish and striped bass attacked as individuals and in groups (i.e., simultaneous strikes). We did not count the number of predators in an attacking group and assumed that an increasing number of predators were making simultaneous attacks as initial group size was increased. For striped bass, group break up was related to feeding. This could result from smaller groups having more success feeding on aggregated prey. Green jack *Caranx caballus* (Günther) and black skipjack *Euthynnus lineatus* (Kishinouye) attacked prey in groups of ~ 2 predators; individuals or subsets from larger predator groups “splintered off” to attack prey schools (Parrish, 1993). The lack of field data on relatively large groups (>20) of piscivores making attacks or hunting together (see Schmitt and Strand, 1982; Potts, 1980, 1981; Parrish, 1993) and our laboratory results suggests that foraging in relatively large groups may be costly.

Prey depletion could partially explain the decline in per capita ingestion rates with increasing group size in our trials. The number of prey was fixed at 100 and there was no replacement; therefore, the number available per individual predator declined from 33.3 to 4 prey from the 3 to the 24 predator groups, respectively. However, prey were never completely depleted in any of the trials. For example, in the most depleted striped bass and bluefish trials (both 24 predators), there were averages of 45 and 26 remaining prey, respectively. In the 24 striped bass treatment, individuals obtained only half as much prey ($\bar{x}=2.3$) as the 6 striped bass treatment ($\bar{x}=4.6$) during a 22-h feeding trial (Table 1). If individual bluefish in the 24 predator treatment had fed at a rate approaching the three and six bluefish treatment ingestion rates, no prey would have remained after 22 h. Individual predators fed below their maximum ingestion rates in larger predator groups even when relatively large numbers of prey remained.

Given that prey depletion is not the sole reason for declines in per capita ingestion, what are other possible explanations for the reduction in per capita ingestion rates in the

larger predator groups? Possibilities include competitive interactions such as interference and increased anti-predator behaviors of prey at larger predator group sizes. Our predator observations were not designed to quantify intraspecific competition but behaviors such as chasing, nipping, or biting were never observed. The group break down that we observed in larger predator groups may have been an attempt at reducing interference. Eklöv (1992) concluded that intraspecific competition negatively influenced the feeding and growth of pike from five pike treatments compared to single pike treatments.

The increased use of surface waters by prey and tighter prey aggregations when larger predator groups were present could have led to lowered predator attacks and/or capture success. Potts (1981) found that anti-predator responses of prey occurred more often when exposed to relatively large groups of jacks (*Caranx* spp.) (>4) compared with small groups (≤ 4). Neill and Cullen (1974) found that fish prey became more difficult to capture the longer an attack period lasted because of increased anti-predator responses. Charnov et al. (1976) distinguished between ‘exploitation depression’ and ‘behavioral depression’ of prey resources when determining if a patch of prey is less than optimal to a predator. Exploitation depression occurs when prey numbers are depleted as a result of predator consumption while behavioral depression results from prey being more difficult to capture because of anti-predator responses. The anti-predator behaviors observed for prey exposed to relatively large numbers of piscivores in this study as well as exploitation and interference competition were all likely important contributors to the lowered per capita ingestion rates.

4.1. Conclusions

We found a significant negative effect of group size on feeding rate when food per fish decreases in both striped bass and bluefish in a relatively large experimental arena. Larger groups of predators broke down into smaller groups possibly to alleviate interference competition. Besides absolute declines in resource abundance (exploitative competition) and interference competition, “behavioral depression” of prey resources faced with relatively high densities of predators may also have been important in causing resource limitation. The relative importance of these three mechanisms for population level phenomena such as density dependence in fishes is an area for future study.

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References

- Baird, T.A., Ryer, C.H., Olla, B.L., 1991. Social enhancement of foraging on an ephemeral food source in juvenile walleye pollock, *Theragra chalcogramma*. Environ. Biol. Fishes 31, 307–311.
- Bertram, B.C.R., 1978. Living in groups: predators and prey. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioural Ecology: An Evolutionary Approach. Blackwell, London, pp. 64–96.
- Buckel, J.A., McKown, K.A., 2002. Competition between juvenile striped bass and bluefish: resource partitioning and growth rate. Mar. Ecol. Prog. Ser. 234, 191–204.
- Charnov, E.L., Orians, G.H., Hyatt, K., 1976. Ecological implications of resource depression. Am. Nat. 110, 247–259.
- Eklöv, P., 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. Anim. Behav. 44, 313–326.
- Hartman, K.J., Brandt, S.B., 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Trans. Am. Fish. Soc. 124, 520–537.
- Major, P.F., 1978. Predator–prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpurus*. Anim. Behav. 26, 760–777.
- Manooch III, C.S., 1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle Sound, North Carolina. Chesap. Sci. 14, 73–86.
- Morgan, M.J., Colgan, P.W., 1987. The effects of predator presence and shoal size on foraging in bluntnose minnows, *Pimephales notatus*. Environ. Biol. Fishes 20, 105–111.
- Neill, S.R.S.J., Cullen, J.M., 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. J. Zool. 172, 549–569.
- Parrish, J.K., 1993. Comparison of the hunting behavior of four piscine predators attacking schooling prey. Ethology 95, 233–246.
- Pitcher, T.J., Magurran, A.E., 1983. Shoal size, patch profitability and information exchange in foraging goldfish. Anim. Behav. 31, 546–555.
- Pitcher, T.J., Parrish, J.K., 1993. Functions of shoaling behaviour in teleosts. In: Pitcher, T.J. (Ed.), Behaviour of Teleost Fishes. Chapman & Hall, London, pp. 363–439.
- Potts, G.W., 1980. The predatory behaviour of *Caranx melampygus* (Pisces) in the channel environment of Aldabra Atoll (Indian Ocean). J. Zool. 192, 323–350.
- Potts, G.W., 1981. Behavioural interactions between the Carangidae (Pisces) and their prey on the fore-reef slope of Aldabra, with notes on other predators. J. Zool. 195, 385–404.
- Ranta, E., Kaitala, V., 1991. School size affects individual feeding success in three-spined sticklebacks (*Gasterosteus aculeatus* L.). J. Fish Biol. 39, 733–737.
- Ryer, C.H., Olla, B.L., 1992. Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. Anim. Behav. 44, 69–74.
- Scharf, F.S., 2001. The influence of behavior on size-structured predator–prey interactions: prey susceptibility, predation selection, and population-level consequences for juvenile estuarine fishes. Doctoral dissertation, University of Massachusetts, Amherst. 219 pp.
- Scharf, F.S., Buckel, J.A., McGinn, P.A., Juanes, F., 2003. Vulnerability of marine forage fishes to piscivory: effects of prey behavior on susceptibility to attack and capture. J. Exp. Mar. Biol. Ecol. 294, 41–59.
- Schmitt, R.J., Strand, S.W., 1982. Cooperative foraging by yellowtail, *Seriola lalandei* (Carangidae), on two species of fish prey. Copeia 1982, 714–717.
- Stoner, A.W., Bejda, A.J., Manderson, J.P., Phelan, B.A., Stehlik, L.L., Pessutti, J.P., 1999. Behavior of winter flounder, *Pseudopleuronectes americanus*, during the reproductive season: laboratory and field observations on spawning, feeding, and locomotion. Fish Bull. 97, 999–1016.
- Tupper, M., Able, K.W., 2000. Movements and food habits of striped bass (*Morone saxatilis*) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh. Mar. Biol. 137, 1049–1058.