



Effects of alternative prey on cannibalism in age-1 bluefish

G. W. BELL*, J. A. BUCKEL† AND A. W. STONER

NOAA National Marine Fisheries Service, James J. Howard Marine Sciences
Laboratory, 74 Magruder Road, Highlands, NJ 07732, U.S.A.

(Received 8 February 1999, Accepted 29 June 1999)

Age-1 bluefish *Pomatomus saltatrix* were offered both age-0 bluefish and age-1 Atlantic silversides *Menidia menidia* in the following proportions: 0 : 1.0, 0.25 : 0.75, 0.5 : 0.5, 0.75 : 0.25, 1.0 : 0. Atlantic silversides were consumed in greater proportion than offered throughout all treatments suggesting strong selection for silversides. There was no evidence of prey-switching. The behavioural processes leading to age-1 bluefish selection of Atlantic silversides was investigated. The proportion of attacks on each prey species was distributed randomly, or slightly higher on age-0 bluefish; however, capture success was greater on silversides than on age-0 bluefish prey. Therefore, age-1 bluefish did not actively select for silversides and the observed selection pattern is a result of passive processes. These findings suggest that prey switching between age-0 bluefish and an alternative prey probably does not act as a stabilizing mechanism in the bluefish population and confirm the importance of capture success in determining piscivore selectivity patterns.

© 1999 The Fisheries Society of the British Isles

Key words: selectivity; switching; cannibalism; alternative prey; density dependent; bluefish; *Pomatomus saltatrix*; Atlantic silverside; *Menidia menidia*.

INTRODUCTION

Bluefish *Pomatomus saltatrix* L., have a world-wide subtropical distribution and are the target of commercial and recreational fisheries wherever they occur (Juanes *et al.*, 1996 and references therein). The life history of bluefish in the western North Atlantic has been described in detail elsewhere (Juanes & Conover, 1995; Hare & Cowen, 1996; Juanes *et al.*, 1996). Adults spawn on the continental shelf of the U.S. east coast, egg and larval stages develop in oceanic waters, and juveniles recruit to nearshore and estuarine waters. Cohorts spawned in the spring and summer recruit to mid-Atlantic Bight estuaries (Nyman & Conover, 1988; McBride & Conover, 1991). Adult landings and juvenile recruitment indices suggest that the U.S. east coast population of bluefish has declined in recent years and historical records indicate dramatic variation in abundance (Baird, 1873; Clark, 1998; Munch & Conover, 1999). Efforts to understand this variation in abundance have centred on survival of early life history stages.

Factors that influence advection of egg and larval stages are believed to affect recruitment success in bluefish (Hare & Cowen, 1993, 1996; Munch & Conover, 1999). However, little is known about how or if year class abundance is affected

*Present address: Department of Marine, Earth and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695-8208, U.S.A.

†Author to whom correspondence should be addressed. Tel.: (732) 872-3132; fax: (732) 872-3088; email: jeffrey.buckel@noaa.gov

during the juvenile phase. McBride *et al.* (1995) found that juvenile bluefish growth rates decreased and losses (emigration+mortality) increased with increasing density. Increased mortality on relatively large cohorts of age-0 bluefish may be due ultimately to predation. Age-0 bluefish are vulnerable to predation from piscivorous fish such as summer flounder *Paralichthys dentatus* L., striped bass *Morone saxatilis* Walbaum, and bluefish.

Bluefish are cannibalistic (Lassiter, 1962; Richards, 1976) but the importance of cannibalism to bluefish population dynamics is unknown. If adult bluefish cannibalize age-0 conspecifics in a density-dependent manner, then cannibalism may influence juvenile bluefish recruitment to the adult stock. The distributions of age-1+ bluefish and age-0 bluefish overlap during summer months in estuarine nurseries and during autumn southward migration; the potential for cannibalism by adult bluefish on smaller conspecifics is probably highest during these periods.

However, alternative prey can be relatively abundant and bluefish feed on a variety of prey types on the U.S. east coast at these times (Buckel *et al.*, 1999a and references therein). The presence of alternative prey has been shown to influence the magnitude of cannibalism in fish (Folkvord, 1997). Bluefish prey selection in a multiple-prey situation will determine the magnitude of cannibalism. When alternative prey are available, the presence of prey-switching behaviour indicates positive density-dependent predation (Murdoch, 1969). Prey switching occurs when the predator preys disproportionately upon the abundant prey type while overlooking the rare prey (Murdoch, 1969).

The hypothesis was tested that age-1 bluefish cannibalize age-0 conspecifics in a density-dependent manner by testing for prey-switching behaviour in the presence of an alternative prey, the Atlantic silverside *Menidia menidia* L. Then it was assessed whether the observed age-1 bluefish selection pattern for Atlantic silversides was a result of active or passive selection processes.

MATERIALS AND METHODS

FISH COLLECTION AND MAINTENANCE

Age-1 bluefish were selected as predators because maximum predatory impact has been estimated to occur in age-1 to age-3 bluefish (Buckel *et al.*, 1999b). Bluefish predators were angled and age-0 bluefish and age-1 Atlantic silverside prey were collected with a 30 m beach seine in Sandy Hook Bay, New Jersey, U.S.A. All fish were maintained for experimentation in the summer 1997 at ambient Sandy Hook Bay temperature and salinity (19–22°C; ~25‰), in circular tanks (1.8 m diameter) at the James J. Howard Marine Sciences Laboratory, Highlands, NJ, U.S.A. Bluefish were fed live and dead fish prey while silversides were fed commercial fish food.

EXPERIMENTAL DESIGN AND CONDUCT

Fifteen trials were conducted to examine for switching behaviour in age-1 bluefish. In each treatment, four age-1 bluefish were offered age-0 conspecifics and age-1 Atlantic silversides for 1 h. Four predators were used because this was a reasonable number of predators for accurate observations by three observers (see below). A total of 24 prey (age-0 bluefish: Atlantic silversides) were provided in one of the following proportion treatments: 0:1, 0.25:0.75, 0.5:0.5, 0.75:0.25, 1:0. Twenty-four prey were used because, for the smallest prey by weight (silversides), this represented a total prey weight equal to the daily consumption rate of the age-1 bluefish ($0.10 \text{ g g}^{-1} \text{ day}^{-1}$; Hartman & Brandt, 1995). Each treatment was replicated three times. However, one 0.5:0.5 replicate was discarded because of low feeding. Experiments were conducted in a 121-kl

aquarium. The oval-shaped tank ($10.6 \times 4.5 \times 3$ m deep) contains eight 1.2×0.7 m observation windows (three on each side and one on each end). Water temperature averaged 20°C (range $19\text{--}21^\circ\text{C}$), and the photoperiod was 12L : 12D throughout all experiment trials.

In addition to these treatments, a predator-absent trial was conducted to quantify prey behaviour at the 0.5 : 0.5 proportion. The location of each prey species was recorded every 5 min for 60 min. The proportion of observations spent at the surface or bottom of the tank was calculated.

Three independent groups of four age-1 bluefish were used in the experimental trials. Five prey treatments were offered to each of these predator groups. The order in which the five trials were conducted was randomized for each series. Each group of bluefish represents a block in a randomized complete blocks design (Sokal & Rohlf 1981); this design was chosen due to the logistical difficulties of moving and acclimating an independent group of bluefish predators for each trial.

Bluefish predators were measured (L_T , mm) and weighed (g) at the beginning and end of the series of five treatments. These initial and final sizes allowed calculation of growth rate from which we could estimate average bluefish size for each trial. There was no significant difference in bluefish size among treatments (mean size was 310 mm in each treatment; one-way ANOVA conducted on mean bluefish size, $F_{4,10}=0.012$, $P=0.999$; Table I).

For at least 2 days prior to the feeding trials, age-1 bluefish were acclimated to a live prey diet using a neutral prey species (the mummichog, *Fundulus heteroclitus* L.). Mummichog are darker in colour, sedentary, and more benthic compared to Atlantic silversides and age-0 bluefish which are lighter in colour, active, and more pelagic. The predators were acclimated to the research aquarium for at least 24 h prior to the start of the trial series. The total weight of prey consumed during each trial was calculated so that an appropriate amount of mummichog could be fed to the predators at the conclusion of the trial to maintain a constant level of hunger throughout the study.

The 24 prey were anaesthetized with MS-222 and then weighed and measured. There were no significant differences between Atlantic silverside (mean overall = 102 mm, $n=108$, s.d. = 1.6) and age-0 bluefish length (mean overall = 104 mm, $n=108$, s.d. = 3.4) in any of the nine paired prey experiments ($P>0.05$) with the exception of one of the 0.5 : 0.5 replicates ($P<0.05$) where mean bluefish L_T (mean = 111, $n=12$, s.d. = 4.2) was slightly larger than mean silverside L_T (mean = 104, $n=12$, s.d. = 3.0) (Table I). Overall, there was no significant difference in prey-predator size ratio (mean = 0.33–0.34) between treatments (one-way ANOVA of tank mean prey-predator size ratio, $F_{4,10}=0.250$, $P=0.903$; Table I).

After measurement, Atlantic silverside and age-0 bluefish were placed in separate, partially submerged cages exactly 2 h prior to the start of a trial to allow prey to acclimate to the presence of predators. Prey cages ($0.9 \times 1.1 \times 1.0$ m deep) were constructed of a polyvinylchloride tubing frame and plastic mesh walls (0.64 cm). The cages were equipped with hinged trap doors at their bottom. All trials began at ~1600 hours. To begin each trial, the trap doors for both prey cages were opened to allow the prey to escape as a cohesive group. The cages were then removed from the tank. During the hour-long trial, three observers recorded the following data on attacks: time, location, type of prey, and capture success. A video record was also taken to validate observer records. At the conclusion of each trial, the surviving prey were removed from the tank and counted.

ANALYSIS

Prey switching was analysed by comparing proportion of total prey consumed to proportion of prey offered (Murdoch, 1969). To determine if the observed selection pattern was a result of an active process, χ^2 tests were used to compare the proportion of prey attacked with the proportion offered for the 25, 50, and 75% age-0 bluefish treatments. These tests were done on the pooled data within each treatment; before pooling these data, replicates were tested for heterogeneity (homogeneity of replicates were found for all three treatments; $P>0.05$). A randomized complete blocks ANOVA

TABLE I. Experimental design and dates for predation trials: mean values of age-1 bluefish total length (L_T), Atlantic silverside L_T , age-0 bluefish L_T , and prey-predator size ratios for both prey species

Treatment (% age-0 bluefish out of $n=24$)	Date	Mean age-1 bluefish L_T (mm) (s.d.)	Mean Atlantic silverside L_T (mm) (s.d.)	Mean age-0 bluefish L_T (mm) (s.d.)	Mean prey-predator size ratio—Atlantic silverside (s.d.)	Mean prey-predator size ratio—age-0 bluefish (s.d.)
0	17 July, 29 July, 1 August	310 (2.5)	102 (1.5)	NA	0.33 (0.006)	NA
25	15 July, 24 July, 6 August	310 (3.5)	101 (1.5)	104 (3.5)	0.33 (0.003)	0.34 (0.009)
50	14 July, 25 July, 8 August	310 (3.3)	102 (0.6)	105 (4.0)	0.33 (0.006)	0.34 (0.008)
75	21 July, 28 July, 31 July	310 (2.5)	103 (2.3)	103 (1.7)	0.33 (0.010)	0.33 (0.007)
100	18 July, 23 July, 4 August	310 (3.4)	NA	103 (3.8)	NA	0.33 (0.009)

NA, Not applicable; s.d., standard deviation.

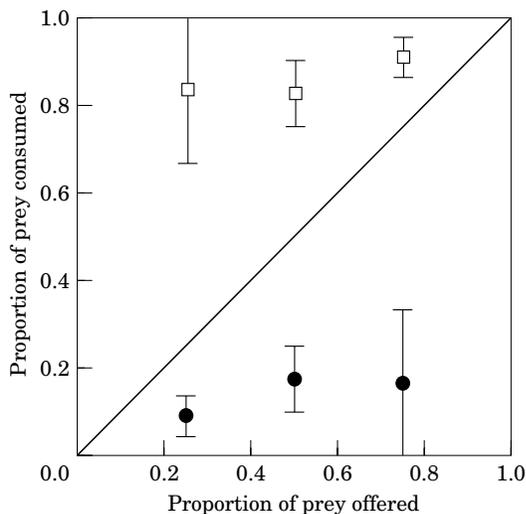


FIG. 1. Test of switching in age-1 bluefish (*Pomatomus saltatrix*) feeding on Atlantic silverside (□; *Menidia menidia*) and age-0 bluefish (●). Mean proportion (\pm S.E.) of the total prey consumed, compared with the proportion of each prey species offered. The diagonal line represents random feeding.

was conducted to determine the effect of prey type and per cent age-0 bluefish on age-1 bluefish capture success for the 25, 50, and 75% age-0 bluefish treatments.

RESULTS

Age-1 bluefish did not exhibit prey-switching behaviour. The mean proportions of silversides and age-0 bluefish consumed out of the total prey consumed did not change with increases in the proportion of prey offered (Fig. 1). However, Atlantic silversides constituted a greater proportion of the total prey eaten than of the total prey offered throughout all treatments.

The proportion of attacks on each prey species was distributed randomly in the 75% bluefish treatment ($\chi^2=2.29$, $P=0.130$) [Fig. 2(c)]. In the 25 and 50% bluefish treatments, the proportion of attacks on both prey species were significantly different from random ($\chi^2=6.370$, $P=0.012$ and $\chi^2=4.260$, $P=0.039$, respectively); age-0 bluefish were attacked significantly more than expected [Fig. 2(a), (b)]. The combined number of attacks on age-0 bluefish and Atlantic silversides was 300. Of these, 149 attacks were made on age-0 bluefish and 151 on Atlantic silverside.

Prey type had a significant effect ($F_{1,10}=29.706$, $P=0.0003$) on capture success of age-1 bluefish while per cent age-0 bluefish ($F_{2,10}=0.718$, $P=0.511$) did not. Capture success by age-1 bluefish was greater when preying on Atlantic silverside than age-0 bluefish across all treatments (Fig. 3). Additionally, there was no interaction between prey type and per cent age-0 bluefish ($F_{2,10}=1.178$, $P=0.347$).

Both species of prey were attacked more frequently at the surface than at the bottom of the tank. Of 198 attacks on bluefish, 153 were made at the surface while only 45 attacks occurred near bottom waters. There were a total of 267 attacks on Atlantic silversides; 153 attacks were made at the surface and 114 near

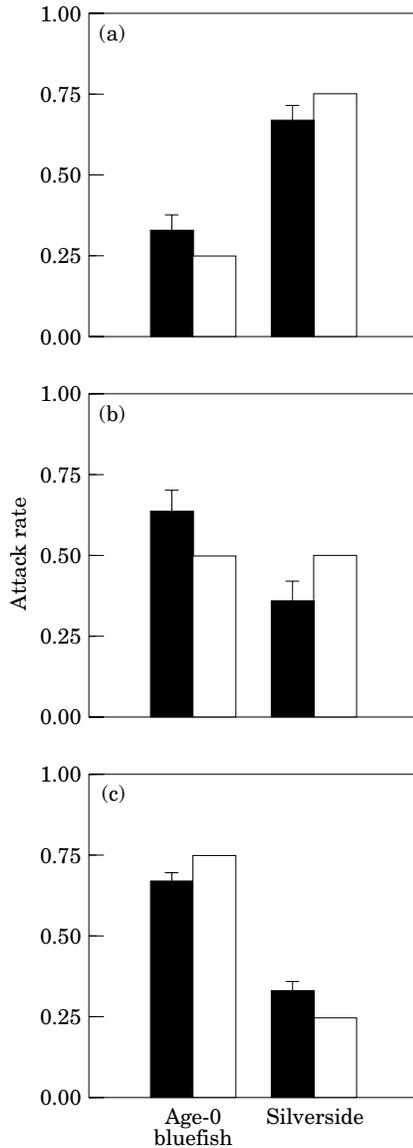


FIG. 2. Mean observed attack rate (■; +S.E.) by age-1 bluefish (*Pomatomus saltatrix*) on Atlantic silverside (*Menidia menidia*) and age-0 bluefish for each treatment compared to a random attack distribution (□). The observed attack rate was compared to that expected from random attacks for the following treatments using a χ^2 test (P values): (a) 25% age-0 bluefish ($P=0.012$); (b) 50% age-0 bluefish ($P=0.039$); (c) 75% age-0 bluefish ($P=0.130$).

the bottom. Predator capture success was significantly lower at the surface than near the bottom for Atlantic silverside ($P<0.001$) and age-0 bluefish ($P=0.035$; Fig. 4). During the predator-absent trial, the group of Atlantic silversides spent about 50% of the observed time at the surface whereas age-0 bluefish spent 100% of the time in surface waters.

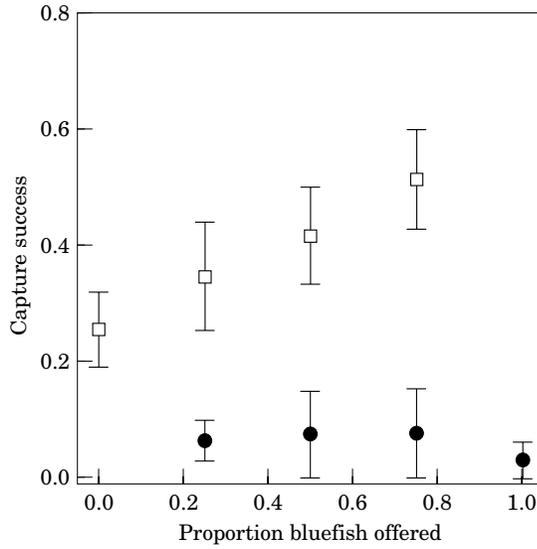


FIG. 3. Mean proportion of successful attacks (\pm s.e.) by age-1 bluefish (*Pomatomus saltatrix*) on Atlantic silverside (\square ; *Menidia menidia*) and age-0 bluefish (\bullet) compared with proportion bluefish offered.

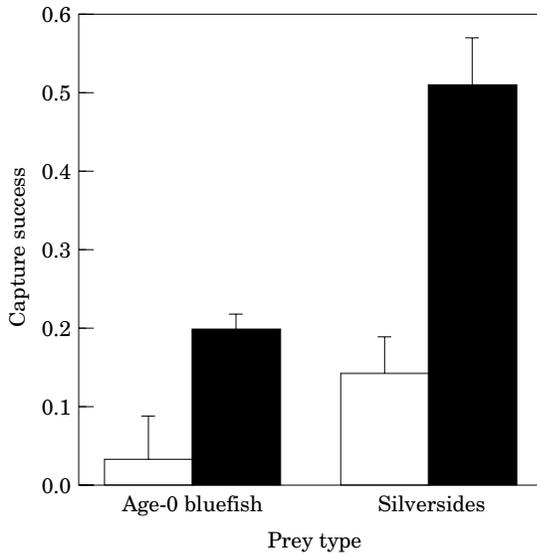


FIG. 4. Mean proportion of successful attacks (\pm s.e.) by age-1 bluefish (*Pomatomus saltatrix*) on Atlantic silverside (*Menidia menidia*) and age-0 bluefish at the surface (\square) and bottom of the tank (\blacksquare) with all data combined. Student's *t*-test was used to compare mean proportion of successful attacks at each location for each prey species (age-0 bluefish $P=0.035$; for Atlantic silverside $P=0.0007$).

DISCUSSION

Cannibalism has been suggested to affect year class success significantly in several fish species (Chevalier, 1973; Dwyer *et al.*, 1987; Livingston, 1993; Henderson & Corps, 1997). Predation can cause compensatory mortality (positive density dependence) which can lead to decreased recruitment variability

or compensatory mortality (negative density dependence) which can lead to increased recruitment variability (Bailey, 1994). Conclusions related to these mechanisms assume that availability of alternative prey is relatively stable; this assumption may not be valid. The present experiments tested for the presence of switching behaviour (Murdoch, 1969) as a potential mechanism which causes density-dependent mortality when alternative prey are present. No evidence of prey switching was found and it was concluded that this mechanism does not lead to density-dependent predation by age-1 bluefish.

Age-1 bluefish did cannibalize age-0 bluefish in the aquarium experiments. This observation confirms the occasional presence of age-0 conspecifics in bluefish diets (Lassiter, 1962; Richards, 1976) and is not surprising given that adult bluefish are known to consume a variety of fish species (Buckel *et al.*, 1999a and references therein). The laboratory data were limited to age-1 bluefish feeding on spring-spawned bluefish; a higher incidence of cannibalism may have occurred at lower prey-predator size ratios (e.g., if older, larger bluefish or smaller age-0 bluefish such as summer-spawned bluefish had been used). However, it is considered that the sizes of age-0 bluefish did not compromise ingestion, especially since bluefish are able to sever their prey (Scharf *et al.*, 1997). Sogard & Olla (1994) found that age-0 walleye pollock *Theragra chalcogramma* (Pallas) were capable of cannibalizing prey of the same cohort that were nearly 60% of the body length of the predator. Age-1 bluefish were provided with prey that were 30% of their body length; this represents a prey-predator size ratio within the range observed in adult bluefish diets (Buckel *et al.*, 1999a).

Age-1 bluefish appear to exhibit strong selection for Atlantic silversides. However, there were equal or slightly higher attack rates on age-0 bluefish compared with Atlantic silversides throughout all treatments. One possible explanation for this observation is that age-0 bluefish tend to be more visible because they are deeper-bodied and shinier than Atlantic silversides. Since bluefish are visual predators (Olla *et al.*, 1970) this may have led to a higher encounter rate on age-0 bluefish and therefore biased the attack rate toward age-0 bluefish. Another potential reason for higher attack rates on age-0 bluefish is that the proportion of prey changes each time a prey is consumed. Because more Atlantic silversides were consumed, there may have been a tendency for the amount of age-0 bluefish offered to be biased upwards compared to the initial proportions offered. However, this is unlikely because the attack data broken down into 15-min intervals showed no increasing trend in attacks on age-0 bluefish. Similar to our results, Juanes & Conover (1994) found that even though juvenile bluefish appeared to select smaller prey, they attacked all sizes equally.

Atlantic silversides were the predominant prey in age-1 bluefish diets across all ratio treatments. Age-1 bluefish have a higher capture success when feeding on Atlantic silversides compared with age-0 bluefish. Consequently, age-1 bluefish did not select actively for Atlantic silversides and the observed selection pattern resulted from a passive process. Capture success is known to influence piscivore selectivity patterns (Wahl & Stein, 1988; Ellis & Gibson, 1997) including size-selectivity in age-0 bluefish (Juanes & Conover, 1994). Age-0 bluefish and Atlantic silversides were matched in length but age-0 bluefish weighed about

twice as much as Atlantic silverside prey. As a result of this difference in weight, age-0 bluefish may have faster swimming and burst speeds or be more difficult to ingest (Wahl & Stein, 1988); these attributes probably explain the observed capture success differences. For example, Scharf *et al.* (1998) found that handling times of juvenile bluefish feeding on striped bass (deep-bodied prey with spines) were higher and capture success lower compared with Atlantic silversides (slender with no spines) at equal prey-predator size ratios.

Prey location may have contributed also to differences in capture success. Age-1 bluefish had a higher capture success on both prey types when attacking near the bottom of the tank compared to the surface. This is likely due to trapping against the two-dimensional bottom *v.* the more three-dimensional surface (i.e., prey can jump out of the water). Silversides were attacked more frequently at the bottom compared with age-0 bluefish. The differences in location of attacks may have resulted from prey behaviour. During the predator-absent trial, Atlantic silversides spent about 50% of the time at the tank surface, whereas age-0 bluefish spent 100% of the time at the surface. Although not quantified, Atlantic silversides appeared to spend more time at the surface in the presence of age-1 bluefish, possibly related to the increased risk of predation at the bottom of the tank. Similarly, Major (1978) found that the jack *Caranx ignobilis* (Forsskål) had higher capture success on Hawaiian anchovy *Stolephorus purpureus* (Fowler) against the sides and bottom of a net pen compared within open water.

There was a low incidence of cannibalism. Field data support the laboratory findings. Cannibalism of age-0 bluefish on the U.S. east coast is generally rare (Morris, 1984; Naughton & Saloman, 1984; Buckel *et al.*, 1999a; but see Lassiter, 1962). Folkvord (1997) reviewed several field studies of cannibalism in cod *Gadus morhua* L. and found that the abundance of age-0 cod relative to other prey items probably influenced the magnitude of cannibalism (but see Macpherson & Gordo, 1994). Similarly, cannibalism will probably be high in bluefish (e.g. Lassiter, 1962) when the abundance of smaller conspecifics is large and alternative forage fish are rare. This may occur during summer in estuarine nurseries and autumn during southward migration. Because age-1 bluefish did not exhibit switching behaviour when feeding on age-0 conspecifics, it is concluded that cannibalism by age-1 bluefish in the presence of alternative prey may not lead to positive density-dependent regulation.

We thank A. Bejda, K. Gilligan, J. Manderson, F. Morello, J. Pape, B. Phelan, J. Rosendale, and L. Stehlik for assistance with fish collection, maintenance and experiments. The manuscript was improved by the comments of J. Cross and two anonymous reviewers. This work was performed while G.W.B. held a NOAA-Cooperative Marine Education and Research undergraduate internship through Rutgers University and J.A.B. held a National Research Council-NOAA Research Associateship.

References

- Bailey, K. M. (1994). Predation on juvenile flatfish and recruitment variability. *Netherlands Journal of Sea Research* **32**, 175–189.
- Baird, S. F. (1873). Natural history of some of the more important food fishes of the south shore of New England. Part II. The bluefish. *Report of the U.S. Commissioner of Fish and Fisheries for 1871 and 1872*, 235–252.

- Buckel, J. A., Fogarty, M. J. & Conover, D. O. (1999a). Foraging habits of bluefish, *Pomatomus saltatrix*, on the U.S. east coast continental shelf. *Fishery Bulletin*, in press.
- Buckel, J. A., Fogarty, M. J. & Conover, D. O. (1999b). Mutual prey of fish and humans: a comparison of biomass consumed by bluefish, *Pomatomus saltatrix*, with that harvested by fisheries. *Fishery Bulletin*, in press.
- Chevalier, J. R. (1973). Cannibalism as a factor in first year survival of walleye in Oneida Lake. *Transactions of the American Fisheries Society* **102**, 739–744.
- Clark, S. H. (Ed.) (1998). Status of the Fishery Resources off the Northeastern United States for 1998. *NOAA Technical Memorandum NMFS-NE-115*.
- Dwyer, D. A., Bailey, K. M. & Livingston, P. A. (1987). Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 1972–1984.
- Ellis, T. & Gibson, R. N. (1997). Predation of 0-group flatfishes by 0-group cod: handling times and size-selection. *Marine Ecology Progress Series* **149**, 83–90.
- Folkvord, A. (1997). Ontogeny of cannibalism in larval and juvenile fishes with special emphasis on Atlantic cod. In *Early Life History and Recruitment in Fish Populations* (Chambers, R. C. & Trippel, E. A., eds), pp. 251–278. London: Chapman & Hall.
- Hare, J. A. & Cowen, R. K. (1993). Ecological and evolutionary implications of the larval transport and reproductive strategy of bluefish *Pomatomus saltatrix*. *Marine Ecology Progress Series* **98**, 1–16.
- Hare, J. A. & Cowen, R. K. (1996). Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. *Limnology and Oceanography* **41**, 1264–1280.
- Hartman, K. J. & Brandt, S. B. (1995). Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1647–1666.
- Henderson, P. & Corps, M. (1997). The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. *Journal of Fish Biology* **50**, 280–295.
- Juanes, F. & Conover, D. O. (1994). Piscivory and prey size selection in young-of-the-year bluefish: predator preference or size-dependent capture success? *Marine Ecology Progress Series* **114**, 59–69.
- Juanes, F. & Conover, D. O. (1995). Size-structured piscivory: advection and the linkage between predator and prey recruitment in young-of-the-year bluefish. *Marine Ecology Progress Series* **128**, 287–304.
- Juanes, F., Hare, J. A. & Miskiewicz, A. G. (1996). Comparing early life history strategies of *Pomatomus saltatrix*: a global approach. *Marine and Freshwater Research* **47**, 365–379.
- Lassiter, R. R. (1962). Life history aspects of the bluefish, *Pomatomus saltatrix* (Linnaeus), from the coast of North Carolina. M.S. Thesis. North Carolina State College, Raleigh.
- Livingston, P. (1993). Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasii* in the eastern Bering Sea. *Marine Ecology Progress Series* **102**, 205–215.
- Macpherson, E. & Gordo, A. (1994). Effect of prey densities on cannibalism in Cape hake (*Merluccius capensis*) off Namibia. *Marine Biology* **119**, 145–149.
- Major, P. F. (1978). Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpurus*. *Animal Behaviour* **26**, 760–777.
- McBride, R. S. & Conover, D. O. (1991). Recruitment of young-of-the-year bluefish *Pomatomus saltatrix* to the New York Bight: Variation in abundance and growth of spring- and summer-spawned cohorts. *Marine Ecology Progress Series* **78**, 205–216.

- McBride, R. S., Scherer, M. D. & Powell, J. C. (1995). Correlated variations in abundance, size, growth, and loss rates of age-0 bluefish in a southern New England estuary. *Transactions of the American Fisheries Society* **124**, 898–910.
- Morris, T. L. (1984). *Food of Bluefish*. NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole Laboratory Reference Document 84–26.
- Munch, S. B. & Conover, D. O. (1999). Recruitment dynamics of bluefish (*Pomatomus saltatrix*) from Cape Hatteras to Cape Cod, 1973–1995. *ICES Journal of Marine Science*, in press.
- Murdoch, W. W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* **39**, 335–354.
- Naughton, S. P. & Saloman, C. H. (1984). Food of bluefish (*Pomatomus saltatrix*) from the U.S. south Atlantic and Gulf of Mexico. *NOAA Technical Memorandum NMFS-SEFC-150*.
- Nyman, R. M. & Conover, D. O. (1988). The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. *Fishery Bulletin* **86**, 237–250.
- Olla, B., Katz, H. & Studholme, A. (1970). Prey capture and feeding motivation in the bluefish, *Pomatomus saltatrix*. *Copeia* **1970**, 360–362.
- Richards, S. W. (1976). Age, growth and food of bluefish from east-central Long Island Sound from July through November 1975. *Transactions of the American Fisheries Society* **105**, 523–525.
- Scharf, F. S., Buckel, J. A., Juanes, F. & Conover, D. O. (1997). Estimating piscine prey sizes from partial remains: testing for shifts in foraging mode by juvenile bluefish. *Environmental Biology of Fishes* **49**, 377–388.
- Scharf, F. S., Buckel, J. A., Juanes, F. & Conover, D. O. (1998). Predation by juvenile piscivorous bluefish (*Pomatomus saltatrix*): the influence of prey to predator size ratio and prey type on predator capture success and prey profitability. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1695–1703.
- Sogard, S. M. & Olla, B. L. (1994). The potential for intracohort cannibalism in age-0 walleye pollock, *Theragra chalcogramma*, as determined under laboratory conditions. *Environmental Biology of Fishes* **39**, 183–190.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. New York: W. H. Freeman and Company.
- Wahl, D. H. & Stein, R. A. (1988). Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* **117**, 142–151.