



Size-dependent susceptibility of longfin inshore squid (*Loligo pealeii*) to attack and capture by two predators

Michelle D. Staudinger^{*}, Francis Juanes

Department of Natural Resources Conservation, University of Massachusetts, Amherst, 160 Holdsworth Way, Amherst, MA 01003-9285, United States

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ABSTRACT

Cephalopods are primary prey to a wide range of predators in marine food-webs, yet a basic understanding of the mechanisms controlling predation risk and demand on their populations is lacking. Feeding experiments were conducted to evaluate how relative prey size and behavior mediate the susceptibility of squid to predation. Attack and capture of longfin inshore squid (*Loligo pealeii*) were quantified using two predators: bluefish (*Pomatomus saltatrix*) a pelagic, cruising predator, and summer flounder (*Paralichthys dentatus*) a benthic, ambush forager. Predator selectivity, prey susceptibility, and prey profitability were estimated as a function of relative prey size from predator–prey interactions during behavioral trials. Patterns in attack rates suggested that size-selection on squid was constrained by passive processes rather than active choice for both predators. The susceptibility of squid to predation by bluefish was strongly dependent on relative prey size; however, flounder were equally efficient at capturing all sizes of squid offered. Handling times increased exponentially with relative prey size and were the primary constraint on selectivity and profitability in flounder. Prey profitability was a dome-shaped function of relative squid size in both predators. Overall, the relative size and values at which profitability was maximized were higher in bluefish indicating they were the more efficient predator of squid. Squid succumbed to greater time-dependent mortality rates than Atlantic silversides (*Menidia menidia*) and mummichogs (*Fundulus sp.*) suggesting that when equal amounts of squid and fish are available in the environment, squid will be selectively ingested by bluefish and flounder. In addition to the influence of relative prey size, predator foraging behaviors and size-dependent encounter rates were thought to be important factors affecting selection on squid in the northwest Atlantic ecosystem.

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1. Introduction

Age and size structure of prey populations are strongly impacted by the selective feeding behaviors of their predators (Brooks and Dodson, 1965; Rice et al., 1993; Christensen, 1996; Claessen et al., 2002). Selection is evidenced when the distribution of prey sizes or types found in a predator's diet differs from what is available in the nearby environment (Ivlev, 1961; Juanes and Conover, 1994). When selectivity is observed, differences between diet and the environment may reflect active choice by the predator, or passive selection due to morphological and behavioral limitations of predators and prey (Werner, 1974; Christensen, 1996; Ellis and Gibson, 1997). Attack rates differentiate between active and passive modes of selection and are generally measured in the laboratory due to difficulties of obtaining data in the field. Active choice implies that a predator is responding to inherent differences in prey and chooses to pursue some more frequently than others (Greene, 1986). When attack rates are found to differ among

prey, active choice is demonstrated, and the prey that is attacked most is deemed “preferred”. Alternatively, if all prey encountered by a predator are attacked equally but the diet is skewed towards a range of prey sizes or types, then selection must be passive (Juanes et al., 2002).

Selective foraging behaviors have been well explored in piscivorous fishes and are strongly dependent on the relative sizes of predators and their prey (Rice et al., 1993; Juanes and Conover, 1995; Mittelbach and Persson, 1998; Scharf et al., 1998; Dorner and Wagner, 2003). Behavioral components of predator–prey interactions such as handling time and capture success rates provide quantitative measures of the costs associated with acquiring progressively larger prey (Werner, 1977; Rice et al., 1993; Scharf et al., 2003) and explain why certain prey are selectively ingested over others (Greene, 1986; Juanes et al., 2001). Predators should select prey that minimize costs of capture and maximize net energetic rewards, thus maximizing foraging efficiency and overall profitability (Schoener, 1971; Greene, 1986; Stephens and Krebs, 1986; Sih and Christensen, 2001). Interspecific differences in predator foraging tactics and prey response behaviors are also important in shaping predator selectivity and prey vulnerability (Sih and Moore, 1990; Manderson et al., 2000; Juanes et al., 2002; Scharf et al., 2002).

^{*} Corresponding author. Tel.: +910 962 2093; fax: +910 962 4066.
E-mail address: staudinger@uncw.edu (M.D. Staudinger).

Prey vulnerability to a given predator is contingent on the probabilities of being encountered, attacked, captured, and ingested (Greene, 1986; Bailey and Houde, 1989; Scharf et al., 2003; Taylor, 2003). Predation risk, or susceptibility, is primarily influenced by the detection and evasion abilities of the prey species (Greene, 1986; Bailey and Houde, 1989). Attack and capture probabilities have been quantified for many forage fish including Atlantic silverside (*Menidia menidia*), bay anchovy (*Anchoa mitchilli*), Atlantic menhaden (*Brevoortia tyrannus*), winter flounder (*Pseudopleuronectes americanus*) and shiners (*Notropis spp.*) (Manderson et al., 1999; Hartman, 2000; Manderson et al., 2000; Scharf et al., 2003; Taylor, 2003); however, comparable studies do not exist for cephalopods. Squid are important constituents of marine food-webs (Smale, 1996; Bax, 1998; Bowman et al., 2000), and many predators that consume fish also eat squid. These two prey types can alternate in predator diets over seasonal and ontogenetic time scales (Smale, 1996; Staudinger, 2006), and predators typically consume a narrower range of relative squid sizes in comparison to prey fish (Staudinger and Juanes, 2010a).

Squid are functionally similar to fish in terms of their habitat distributions, range of body sizes, and schooling behavior, yet unlike fish squid lack bones and spines (Packard, 1972). These morphological characteristics should heighten squid susceptibility by increasing capture probabilities and decreasing the costs associated with handling times (Werner, 1977; Rice et al., 1993). Squid are thought to reduce predation risk by using highly advanced visual capabilities and anti-predator defenses including jet propulsion, ink, and camouflage (Hanlon and Messenger, 1996). Few studies have quantified components of predator–prey interactions using squid as prey (Staudinger and Juanes, 2010b), hence our ability to predict predator feeding patterns and assess the relative vulnerabilities of squid and forage fish is limited (Rice et al., 1993; Mittelbach and Persson, 1998; Scharf et al., 2003).

The purpose of this study was to determine the role that size and behavior play in mediating predation risk in squid. To accomplish these objectives, a series of laboratory experiments were conducted to quantify attack and capture behaviors on longfin inshore squid (*Loligo pealeii*) by two predators representing contrasting foraging tactics. Bluefish (*Pomatomus saltatrix*) was selected as a pelagic, cruising predator and summer flounder (*Paralichthys dentatus*) was chosen as a benthic, ambush predator. Both predators commonly forage on squid in coastal waters of the northwest Atlantic (Bowman et al., 2000; Staudinger, 2006). Attack rates established whether predators use active or passive selection when foraging on squid and if preference is exhibited towards a specific size range. Size-dependent capture success rates and handling times quantified the costs associated with obtaining progressively larger squid and were combined with information on relative prey mass to estimate size-dependent profitability functions (foraging efficiencies) respective to each predator. Lastly, time-dependent survival rates were used to evaluate if predation risk by bluefish and flounder varied as a function of relative squid size and if squid were more susceptible to predation in comparison to two species of forage fish.

2. Methods

2.1. Collection and maintenance of experimental animals

Summer flounder ranging in size from 36 to 47 cm Total Length (TL) were collected from Buzzards Bay, MA as part of the Massachusetts Division of Marine Fisheries spring 2006 trawl survey. Bluefish ranging in size from 31 to 63 cm TL were caught by hook and line from local bays and estuaries surrounding Woods Hole, MA during summer 2007. After capture, fish were transported to the Marine Resources Center at the Marine Biological Laboratory (MBL) in Woods Hole, MA, maintained in tanks with recirculating, biofiltered seawater, and fed a diet of live and frozen fish and squid. Bluefish and

flounder were acclimated to captivity for approximately 1 month and were considered ready for use in feeding trials when live food was accepted on a daily basis.

Longfin inshore squid ranging in size from 2 to 21 cm Mantle Length (ML) were collected daily from Vineyard and Nantucket Sounds using a modified trawl net and transported back to the MBL facility. Squid were either transferred into the experimental tank, or if it was necessary to hold squid overnight prior to use in trials, they were housed in a 1 m diameter (d) holding tank and fed live fish and small squid. No squid used in trials were held for more than 48 hours (h). Squid that had visible abrasions to their epithelium or showed signs of lethargy were not used in trials. Atlantic silversides and mummichogs (*Fundulus sp.*) ranging in size from 6 to 11 cm TL were collected by beach seine approximately 24 to 48 h prior to use in feeding trials and maintained on pellet feed. Prey fish were held in partitioned screen boxes in the same holding tanks as squid.

Water temperatures (16°–20 °C) and photoperiods for specimen holding tanks and the experimental arena mimicked late spring–early summer conditions. In addition to natural light from adjacent windows, fluorescent lighting was maintained on a 10:14 h, light:dark schedule. Tanks were lined with a mixed gravel and sand substrate approximately 2–4 cm deep which allowed squid to camouflage and flounder to bury.

2.2. Experimental set-up

Feeding trials using summer flounder as predators were conducted between June and August of 2006, and bluefish trials were conducted between June and August of 2007. All trials took place in a 28 × 10³ l, 3.1 × 0.8 m (d, height) tank lined with the same sand and gravel substrate as specimen holding tanks. The area surrounding the experimental tank was lined with black plastic sheeting to prevent disturbance to acclimating animals and during filming.

Three predators of approximately equal size were chosen for each trial and allowed to acclimate to the experimental tank for at least 24 h. When predators were used on successive days a minimum of 24 h elapsed between trials. Food was withheld 24 h prior to the start of all trials to standardize predator hunger levels. Approximately 3 h prior to the start of each trial, an opaque PVC cylinder 1.5 × 1 m (d, height) was lowered into the center of the experimental tank using a pulley system and 15 prey were placed inside the partition. The partition allowed predators and prey to acclimate simultaneously; although visual contact was restricted, water movement between the compartments likely resulted in some exchange of olfactory information. A trial commenced when the partition was raised above the tank and predators and prey began to interact. Trials were recorded using Panasonic miniDV PV GS500 video cameras that were manually operated at two lateral viewing windows located on opposite sides of the experimental tank, and from a third camera mounted above the tank. Two 500 W lights were positioned above the tank to aid with filming clarity. Predator–prey behavioral components were assessed using frame-by-frame analysis (30 frames/s) of video recorded during each trial.

Three sets of experiments were conducted to evaluate size-selection, survival probabilities, and prey type susceptibility. In the first experiment, patterns in attack rates assessed size-selection on squid. Three predators of approximately equal size were offered 5 squid from 3 different relative size-classes, for a total of 15 prey. Squid size-classes were grouped in 10% increments ranging from 0.10 to 0.79. Each trial lasted 30 min and all predator–prey interactions were recorded. When a trial was complete, all remaining squid were removed from the experimental tank and measured to determine which individuals from each size-class had been consumed.

In the second experiment, susceptibility to predation was compared among relative squid size-classes by measuring time-dependent survival probabilities. Three size-matched predators were

offered 15 squid that were all within the same relative size-class (e.g., 0.20–0.29). Predator–prey interactions were recorded for the first 30 min of each trial, after which visual counts were made of the number of squid surviving at 1, 2, and 3 h from the start of the trial.

In the third experiment, prey-type susceptibility was evaluated by offering 3 size-matched predators 5 squid, 5 Atlantic silversides, and 5 mummichogs. Relative prey sizes were matched as close as possible and ranged from 0.15 to 0.35. Attacks on all prey were recorded for the first 30 min, after which visual counts of the number of individuals remaining in each prey group were made at 1, 2, 3, 6, 9, 12, and 24 h.

2.3. Repeated measures

To determine whether repeated use of individual predators affected feeding behaviors over the course of all trials, we assessed 1) whether predators reached feeding saturation with successive use in trials and 2) if predator feeding efficiency increased with repeated use over time. Feeding saturation was measured by comparing the total number of attacks (successful + unsuccessful) made by each group of three predators over successive days of use. Predator efficiency examined whether capture success rates varied for each group of fish (identified by TL) over all trials. Capture success was determined by dividing the number of successful attacks by the total number of attacks made during each trial. Unsuccessful attacks did not result in ingestion but included attempts where a prey was obtained by the predator and escaped or was rejected during the manipulation period.

Distributions of total attacks and capture success rates were found to be highly skewed; therefore, a Friedman's nonparametric two-way ANOVA was used to test treatment differences using a randomized complete block design (Zar, 1984). Fish groups were treated as subject variables and the number of days used in trials was assigned as the treatment variable. All tests yielded nonsignificant *p*-values (all *p*-values ≥ 0.18), suggesting that repeated use of bluefish and flounder did not influence feeding behaviors.

2.4. Size selection, capture success, and handling times

To determine if size-selection on squid was active or passive, attack rates from size-selection trials were calculated by dividing the total number of attacks made on each relative size class (e.g., 0.20–0.29) by the total time in minutes in all trials where that size-class was offered. A Kruskal Wallis test was used to compare attack rates among relative squid size-classes and was approximated by a chi-square distribution. Results are reported as a chi-square statistic. Based on previous studies using piscivores, attack rates were expected to decrease with increasing prey size (Juanes and Conover, 1994). Capture success was determined by dividing the number of successful attacks by the total number of attacks made on each relative squid size-class. Capture success rates from size-selection and time-dependent survival trials were pooled when significant differences were not detected between the two trials types using an ANOVA (all *p*-values ≥ 0.49). Least squares regression analysis was then used to assess the strength of the relationship between relative prey size (independent variable) and capture success.

Handling times were quantified as the time in seconds from when a predator made first contact with a prey until the time when the prey was no longer visible outside the predator's mouth and rapid opercular movement ceased (Christensen, 1996; Scharf et al., 2003). Because some attacks were obscured, handling time information was not available for every attack made. Handling times from size-selection and time-dependent survival trials were combined and analyzed as a function of relative prey size (independent variable) using least squares regression. Handling times typically increase at an exponential rate with increasing prey size in piscivorous fishes (Hartman, 2000; Scharf et al., 1998, 2002, 2003, 2009). Bluefish and

flounder data appeared to be nonlinear thus, both linear and exponential functions ($y = ae^{bx}$) were fit to the data. The model with the strongest coefficient of determination (R^2) was selected to explain trends for each predator.

2.5. Profitability

Prey profitability was estimated by relative prey mass \times handling time⁻¹ \times capture success (Scharf et al., 1998; Hartman, 2000; Scharf et al., 2003). Handling times and capture success represented the energetic costs of obtaining squid and were estimated using the equations and mean values, respectively, derived from size-selection and time-dependent survival trials. Relative prey mass (prey mass/predator mass) was assumed to be roughly equivalent to energetic intake and represented the benefit received by each predator for ingesting a squid (Steimle and Terranova, 1985; Scharf et al., 2003). Lengths of each prey and predator were measured directly and converted to mass (wet weight) using published length–weight relationships (Lange and Johnson, 1981; Wigley et al., 2003). Profitability curves were generated by inserting relative prey mass, handling time, and capture success values respective to each 0.01 relative predator–prey length increment for all possible combinations between 0.05 and 1.0. Prey profitability was expected to be a dome-shaped function of relative squid size (Scharf et al., 1998; Hartman, 2000; Scharf et al., 2003). To determine whether profitability data were best fit by a quadratic polynomial, linear, logistic, or power function, coefficients of variation (R^2) and residual sum of squares were examined to select the most appropriate model. Because capture success can play a significant role in shaping foraging efficiencies of some (e.g., piscivores) but not all predators (e.g., planktivores) (Stephens and Krebs, 1986; Scharf et al., 1998; Sih and Christensen, 2001), profitability curves were estimated with and without the capture success variable to determine its overall influence on the model.

2.6. Survival analysis

Survival rates from time-dependent survival and prey-type susceptibility trials were evaluated using survival or time-to event analysis (Cox and Oates, 1984; Allison, 1995). To test whether survival rates differed among relative squid size-class in time-dependent survival trials and prey species in prey-type susceptibility trials, Cox's proportional hazards regression was executed using the PROC PHREG command in SAS (SAS, 2003). The Hazard (or risk) ratio estimated the percent increase per unit time in predation risk experienced by each relative size-class and prey type respective to each predator. Additionally, the hazard function determined if predation risk for each squid size class and prey type increased, decreased, or remained constant over the course of trials. The Cox regression technique was chosen because it does not require knowledge of the underlying probability distribution of the hazard function, thus it is less restrictive than other models. Because time is ranked, the model is not sensitive to multiple time intervals. The model also allows for stratification of variables and tied events and was the most appropriate model for the datasets analyzed in this study (Castro-Santos and Haro, 2003).

3. Results

Over the course of 40 trials, bluefish made 61 attacks on prey; 34 trials were completed using flounder during which, 118 attacks were observed (Table 1). On average flounder attacked and consumed more prey per trial than bluefish. A wider range of relative squid size-classes were tested using flounder (0.10–0.79) compared to bluefish (0.10–0.59) (Table 2). The smallest (≤ 0.19) and largest relative squid size-classes (≥ 0.50) had the fewest number of replicates due to

Table 1

Number of feeding trials (# Trials), total number of attacks (# Attacks), and hours of observation conducted using bluefish and summer flounder as predators and longfin squid as prey.

Trial Type	# Trials	# Attacks	Hours of observation
<i>Bluefish</i>			
Size-selection	19	30	9.5
Survival	16	26	48
Preference	5	5	2.5
Total	40	61	60
<i>Summer flounder</i>			
Size-selection	13	30	6.5
Survival	16	57	48
Preference	5	31	2.5
Total	34	118	57

limited availability of squid in local waters and because of the difficulties of keeping small squid alive in captivity.

3.1. Size selection, capture success, and handling times

Attack rates did not differ ($p > 0.05$) among squid size-classes and size-selection was inferred to be passive in both bluefish ($X^2 = 6.69$, $df = 4$, $p = 0.15$) and flounder ($X^2 = 5.49$, $df = 6$, $p = 0.50$) (Fig. 1). Capture success rates decreased linearly with increasing relative squid size in bluefish ($R^2 = 0.844$, $F = 16.25$, $p = 0.03$), but a significant trend was not detected in flounder ($R^2 = 0.002$, $F = 0.01$, $p = 0.94$) (Fig. 2). Capture success rates were greatest for the smallest (0.10) and largest squid size-classes (0.60) tested using flounder. Nonetheless, few attacks were made on these two size-classes ($n \leq 2$), and overall trends were not affected when they were excluded from analyses. Handling times increased exponentially with increasing relative squid size in bluefish ($y = 1.58e^{3.33x}$, $R^2 = 0.46$, $n = 27$, $p = 0.0005$) and flounder ($y = 0.23e^{10.94x}$, $R^2 = 0.68$, $n = 27$, $p < 0.0001$) (Fig. 3). Handling times ranged from 0.03 to 16.1 seconds (s) in bluefish, and 0.10–95.9 s in flounder. On average, handling times were 4–5 times greater in magnitude (16.37 s) in flounder compared to bluefish (3.64 s).

3.2. Profitability

Profitability data were best fit by the quadratic polynomial model as a dome-shaped function of relative prey size in bluefish ($R^2 = 0.76$, $n = 1253$, $p < 0.0001$) and flounder ($R^2 = 0.50$, $n = 1702$, $p < 0.0001$). Peak profitability values were greater for bluefish (0.004) in comparison to flounder (0.002) and corresponded to relative squid sizes between 0.40 and 0.50 in bluefish and 0.20–0.30 in flounder (Fig. 4). When capture success was removed from profitability estimations, bluefish data were best fit by a quadratic polynomial model ($R^2 = 0.50$, $n = 1253$, $p < 0.0001$), and flounder data by a logistic model ($R^2 = 0.04$, $n = 1702$, $p < 0.0001$). Removal of capture success from the bluefish model increased maximum values by an order of

Table 2

Number of bluefish and summer flounder feeding trials conducted using each relative size-ratio class.

Relative prey size	Bluefish		Summer flounder	
	Size-selection	Survival	Size-selection	Survival
0.10–0.19	7	5	2	0
0.20–0.29	15	6	4	4
0.30–0.39	19	5	9	5
0.40–0.49	12	0	12	4
0.50–0.59	4	0	7	3
0.60–0.69	0	0	3	0
0.70–0.79	0	0	2	0
Total trials	19	16	13	16

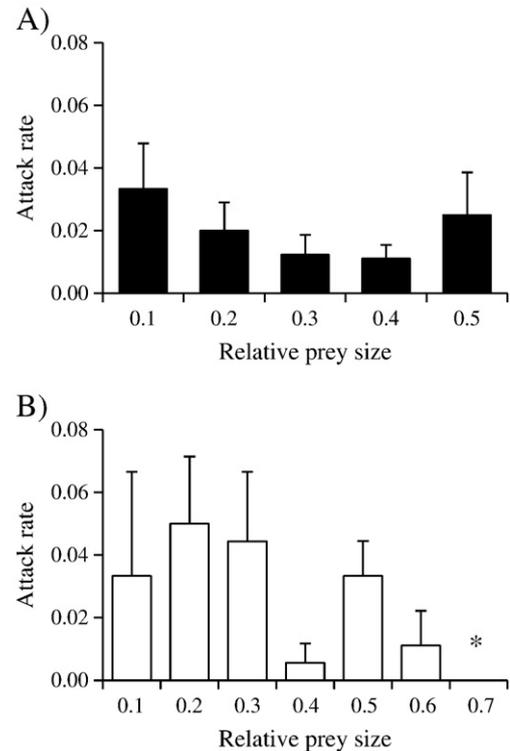


Fig. 1. Attack rates on relative size ratios of longfin inshore squid by A) bluefish and B) summer flounder during size-selection trials. Bars show calculated standard errors (1 SE); * indicates no attacks were observed although the size group was offered.

magnitude and shifted the peak of the curve to relative squid sizes between 0.70 and 0.80. When capture success was removed from the flounder model, profitability steeply rose between relative squid sizes of 0.05 and 0.30 and then reached a plateau for all values ≥ 0.30 . Overall, peak profitability values did not vary considerably between flounder models that included and excluded capture success.

3.3. Time-dependent survival

In bluefish trials, significant differences in squid survival rates were observed among relative size groups ($X^2 = 6.90$, $df = 2$, $p = 0.009$). The 0.10–0.19 relative squid size group was found to be most susceptible to bluefish predators and predation risk (Hazard ratio = 0.96) decreased by 4.3% (per minute) in progressively larger size groups (Fig. 5). Significant differences in survival rates among relative squid size-classes were not detected in the presence of flounder ($X^2 = 2.02$, $df = 3$, $p = 0.16$) (Fig. 6); however, when data from all size-classes were pooled, squid survivorship declined exponentially (Log likelihood = -166.2 , $X^2 = 4.85$, $p = 0.03$). Hazard functions increased with time for bluefish and flounder. This suggests that predators did not reach feeding saturation and squid were at risk at all times during trials.

3.4. Prey-type susceptibility

Predation risk differed significantly among squid and fish prey in the presence of both bluefish ($X^2 = 21.63$, $df = 2$, $p < 0.0001$) and flounder ($X^2 = 13.11$, $df = 2$, $p < 0.0003$). Differences in predation risk among prey types were more pronounced in flounder (Hazard ratio = 0.50) compared to bluefish (Hazard ratio = 0.35) (Fig. 6). Of the three prey types, squid experienced the highest mortality rates, silversides had the lowest mortality rates, and mummichogs were intermediate. As was seen in time-dependent survival trials, mortality rates were higher overall in the presence of bluefish for all prey types compared to flounder.

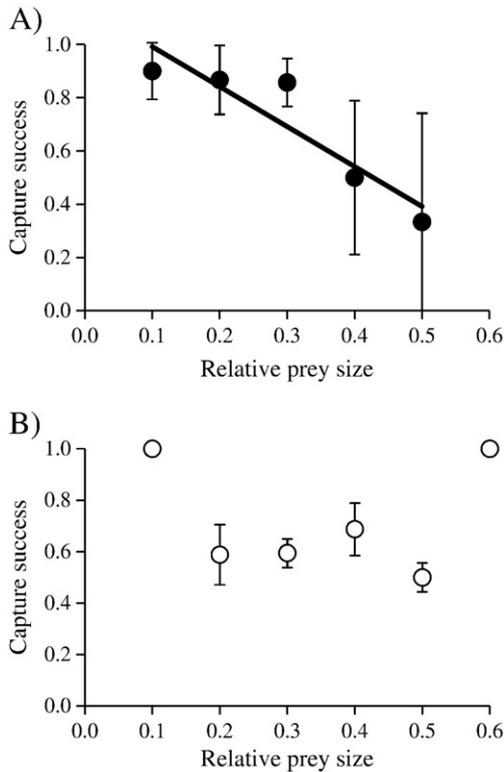


Fig. 2. Capture success rates for A) bluefish and B) summer flounder on longfin inshore squid. Regression equations were estimated by the equations $y = -1.5x + 1.14$, $r^2 = 0.844$, $p = 0.03$ for bluefish and $y = -0.05x + 0.75$, $r^2 = 0.002$, $p = 0.94$ for summer flounder. Standard error bars (1 SE) and significant regression lines are shown.

4. Discussion

4.1. Size selection, capture success, and handling times

Patterns in bluefish and summer flounder attack rates suggest that size-selection on longfin squid was the result of passive processes rather than active choice. In the absence of active choice, size-selection can often be explained by encounter and capture probabilities, the product of which shapes prey vulnerability (Greene, 1983, 1986; Sih and Moore, 1990; Juanes, 1994). A strong negative relationship was demonstrated between bluefish capture success rates and relative squid size; additionally, relatively smaller squid succumbed to higher mortality rates in time-dependent survival trials. Trends observed in the lab were similar to the distribution of squid sizes typically found in bluefish diets in coastal waters of the northwest Atlantic (Staudinger and Juanes, 2010a) indicating that small squid are selectively ingested by bluefish because they are easier to catch.

Various authors have proposed that predator and prey behaviors are as important as size in shaping predation risk (Greene, 1986; Sih and Moore, 1990; Manderson et al., 2000; Scharf et al., 2003). Regardless of the combination of relative squid size-classes offered to bluefish in size-selection trials, the smallest squid available (relative sizes ranging from 0.12 to 0.25) were successfully attacked and captured most often. Squid appeared to school with the smallest individuals on the periphery and squid < 5 cm ML (≤ 0.10 relative size) often separated themselves from the rest of the school in loose aggregations or swam near the surface by themselves. These behaviors appeared to predispose the smallest squid to predation by bluefish. Step-wise attack patterns on small, medium, and large Atlantic silversides have been reported previously by Juanes and Conover (1994). Additionally, Scharf et al. (2002) found bluefish to target solitary bay anchovy however, it was the largest individuals

that separated from schools and were selectively consumed. These observations provide further evidence that size-dependent vulnerabilities of different prey are highly species-specific and mediated in part by the attack tactic used by the predator and the schooling behavior of prey.

Flounder were equally efficient at capturing all squid sizes and squid survival did not vary as a function of relative prey size. Previous studies have also shown that flounder capture success rates do not vary among prey types or when flounder pursue and attack prey at different depths in the water column (Olla et al., 1972; Staudinger and Juanes, 2010b). Flounder diets typically include high proportions of large squid (≥ 0.30) (Staudinger and Juanes, 2010a), yet predation risk was not found to vary among squid sizes classes. In comparison to cruising predators, ambush predators often consume larger and older prey (Greene, 1986; Juanes, 1994). Greene (1986) argued that when selection was passive, this discrepancy could be explained by an increase in the importance of encounter probabilities. Both summer flounder and longfin squid are associated with benthic habitats during the day-time (Olla et al., 1972; Macy, 1982) and their spatial and temporal overlap in regional shelf waters should be high. Furthermore, large prey are assumed to have higher encounter rates with predators because they are more active and easier to detect than smaller prey (Juanes, 1994; Sih and Christensen, 2001; Taylor, 2003).

Morphological traits such as prey body depth and predator gape size are known to affect selection, handling times, and prey escapement in piscivores (Wahl and Stein, 1988; Hambright, 1991; Scharf et al., 2003). The sizes of squid used in our experiments were well below the gape limits of bluefish and flounder (Staudinger and Juanes, 2010a) yet handling times increased rapidly when flounder ingested squid ≥ 0.35 and were the primary cost measured in flounder profitability estimates. Bluefish mouth gapes are slightly larger than summer flounder (Staudinger and Juanes, 2010a), and their tooth structure allows them to sever prey into small pieces (Bemis et al.,

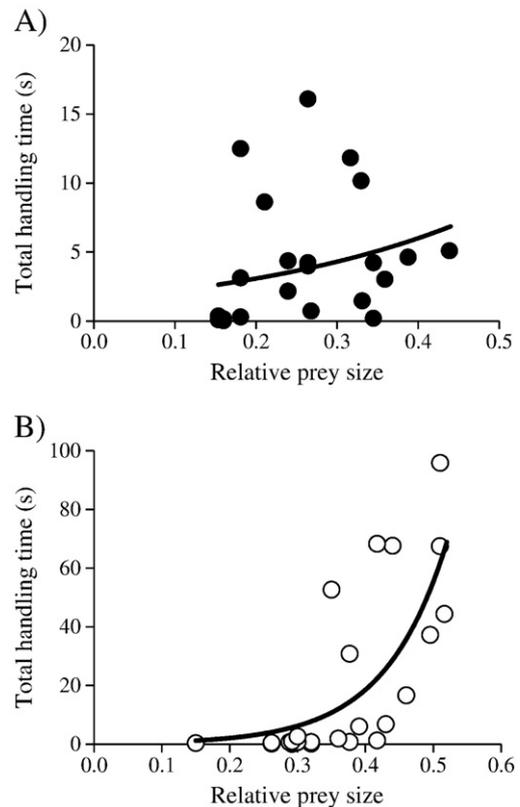


Fig. 3. Handling times for A) bluefish and B) summer flounder. Regressions were estimated using the equations $y = 1.58e^{3.33x}$ for bluefish and $y = 0.2333e^{10.94x}$ for summer flounder. Note differences in scale in the y-axis.

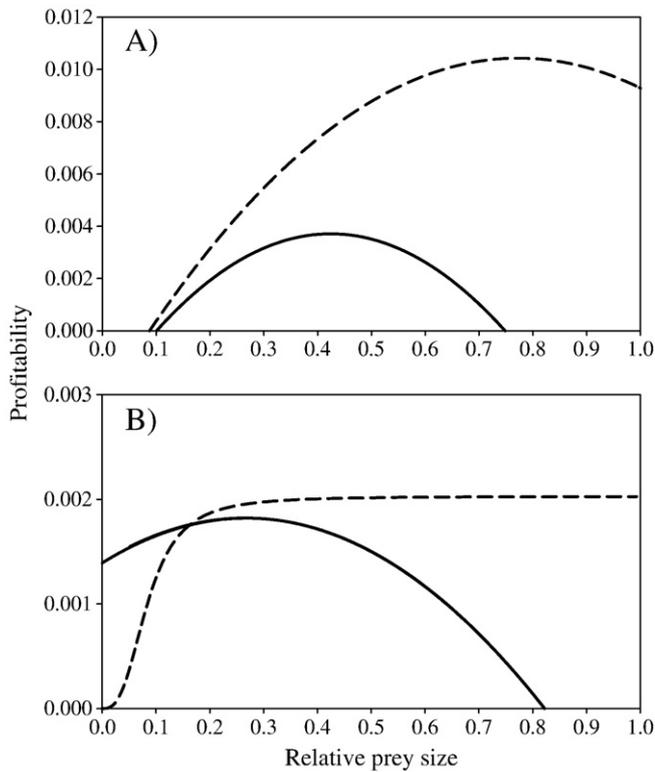


Fig. 4. Size-dependent profitability functions for A) bluefish and B) summer flounder predating on squid. The full profitability model (solid line) was estimated using (relative prey mass \times handling time $^{-1}$ \times capture success) and fit by a quadratic polynomial function for all relative predator–prey size ratios between 0.05 and 1.00. Profitability estimates excluding capture success (dashed line) were fit by a quadratic polynomial function for bluefish and a logistic function for flounder. Note differences in scale in the y-axis.

2005). Shearing dentition is thought to reduce handling times and give bluefish an advantage in foraging efficiency compared to other piscivorous predators (Scharf et al., 1997; Hartman, 2000; Scharf et al., 2009). This capability was evident in our study as squid were bitten into chunks during several attacks, and pieces were occasionally regurgitated and scavenged by other bluefish. Bluefish clearly have an advantage over flounder in their abilities to manipulate squid as prey; furthermore, our results suggest that squid are easier for bluefish to handle compared to other prey types. Previous studies using fish as prey reported bluefish handling times to increase at stronger exponential rates and climax at values higher than were found here (Scharf et al., 1998, 2002, 2003, 2009).

Similar to striped bass (*Morone saxatilis*) (Scharf et al., 2009), summer flounder swallow their prey whole and took considerably longer than bluefish to ingest large (≥ 0.30) prey. Flounder frequently rested on the bottom with their heads raised at an angle above the substrate and exhibited jaw protrusions and opercular expansions (Bels and Davenport, 1996). These behaviors demonstrated that consumption of large squid was highly strenuous to flounder yet this did not preclude them from attacking large squid in feeding trials. Under natural conditions flounder consume squid up to 0.60 relative to their own body size, whereas squid ≥ 0.40 are rare in bluefish diets (Staudinger and Juanes, 2010a). Since flounder and other ambush predators are more dependent on prey-initiated encounters than cruising predators, they must be opportunistic and attack large prey even if they are energetically more costly to manipulate.

4.2. Profitability

Optimal diet theory was developed primarily for predators that employ active choice, and forage on non-mobile prey (Mittelbach,

1981; Stephens and Krebs, 1986). Consequently, capture success and encounter probabilities are often excluded from estimates of prey profitability and predator foraging efficiency (Juanes, 1994; Sih and Christensen, 2001). Recent studies have demonstrated that capture success strongly impacts size-dependent profitability functions in piscivores (Fuiman, 1989; Scharf et al., 1998; Juanes and Conover, 1994; Sih and Christensen, 2001). Similar to the results of Scharf et al. (1998, 2003, 2009), the removal of capture success significantly changed profitability values for bluefish. Peak profitability values were less sensitive to the removal of capture success in flounder; however, the shape of the curve and the amount of variation explained by the reduced model was considerable. These findings provide further evidence that capture success does not influence foraging efficiencies equally in all predators and should be considered in future studies (Juanes, 1994; Sih and Christensen, 2001).

The present study reports one of the few estimates of prey profitability for a flatfish predator (but see Rice et al., 1993) and the only known quantifications using squid as prey. Squid profitability peaked in summer flounder at lower relative prey sizes than have been reported previously for all other predator–prey combinations except between striped bass and shiners (Scharf et al., 1998; Hartman, 2000; Juanes et al., 2001; Scharf et al., 2002, 2003, 2009). The steep rise in handling times associated with ingesting squid ≥ 0.30 yielded considerably lower profitability estimates for flounder than were determined here for bluefish, and in previous studies with striped bass (Hartman, 2000; Scharf et al., 2003). These findings suggest that handling time is the primary constraint on flounder foraging efficiency. Since profitability estimates are scarce for other flatfish and benthic predators, it is uncertain whether the costs associated with obtaining squid are a species-specific constraint, or a general disadvantage of the ambush predation strategy.

Relative squid sizes that maximized profitability in bluefish were greater than previous estimates for Atlantic menhaden and striped

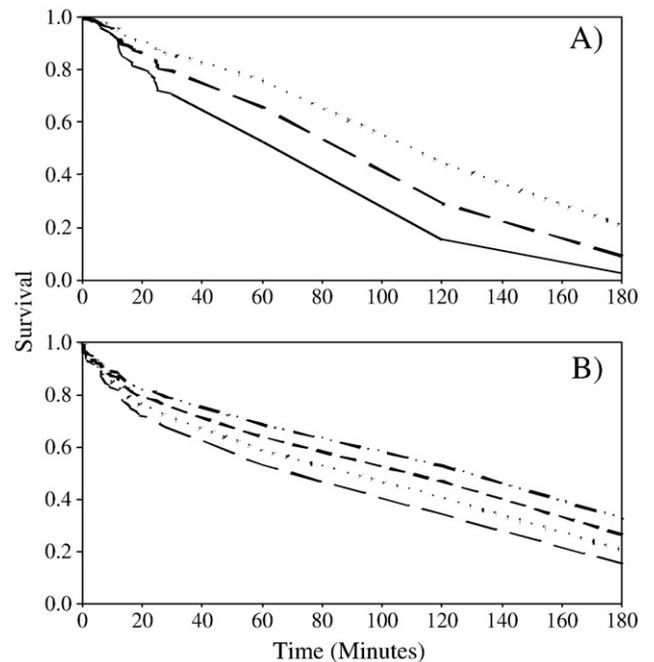


Fig. 5. Size-dependent survival rates of longfin inshore squid in the presence of A) bluefish and B) summer flounder. Survival curves were estimated using Cox regression analysis. Significant differences were detected among survival rates of relative size groups in the presence of bluefish ($X^2 = 6.90$, $df = 2$, $p = 0.009$) but not flounder ($X^2 = 2.02$, $df = 3$, $p = 0.16$). Relative size groups tested for bluefish ranged from 0.10 to 0.39 and 0.20 to 0.59 for summer flounder and are denoted as 0.10–0.19 (solid line), 0.20–0.29 (long dash), 0.30–0.39 (dotted), 0.40–0.49 (short dash), and 0.50–0.59 (dash-dot-dot).

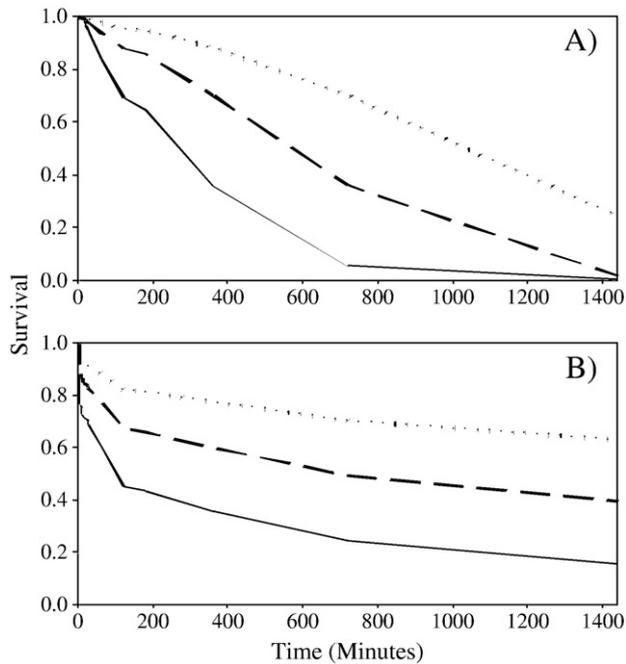


Fig. 6. Time-dependent survival rates of longfin inshore squid (solid line), mummichogs (long dash), and Atlantic silversides (dotted line) in the presence of A) bluefish and B) summer flounder predators.

bass but lower than bay anchovy (Scharf et al., 1998, 2002, 2003, 2009). Prey that possess deep bodies and dorsal spines have lower susceptibilities to predators and are less profitable compared to prey with soft and shallow bodies (Hambright, 1991; Scharf et al., 2003); consequently, squid profitability should be higher than menhaden and striped bass at similar relative sizes. Differences in swimming speeds and anti-predator behaviors are potential explanations for why squid were less profitable than bay anchovy (Schoener, 1971; Scharf et al., 2003).

4.3. Prey type susceptibility

Time-dependent mortality rates were higher for squid in comparison to Atlantic silversides and mummichogs in the presence of bluefish and flounder. This was an unexpected result since squid were thought to have a more complex array of anti-predator behaviors than forage fish (Hanlon and Messenger, 1996). Squid susceptibility (capture success) was similar to or higher than most forage fish species including bay anchovy and menhaden (Scharf et al., 2002, 2003), yet food-habit studies indicate that squid rarely dominate the total diets of summer flounder and bluefish (Bowman et al., 2000; Buckel et al., 1999a; Staudinger, 2006). We conclude that aspects of prey behavior not represented in our analyses and encounter rates must be playing a major role in shaping overall vulnerabilities to predators in coastal waters of the northwest Atlantic (Greene, 1986).

It should be noted that the high capture success rates achieved by bluefish and flounder may have been an artifact of conducting experiments in the confines of captivity. Tanks sizes were large enough that squid were able to elicit a range of defensive behaviors and substrate was provided for camouflage. Nonetheless, high light intensities may have increased predator detection of squid and increased their susceptibility to attack and capture especially by flounder which are typically associated with benthic, low-light environments. Risk to predation may also have been heightened due to a lack of structural complexity which provides refuge from predators in the field (Michel and Adams, 2009).

5. Conclusions

Our results provide some of the first quantifications of size-dependent attack and capture behaviors on squid. This information is necessary for predicting size-based predator–prey interactions and should be particularly relevant to modeling bluefish and summer flounder foraging habits given their potential to impact squid and other forage populations in the northwest Atlantic (Buckel et al., 1999b; Overholtz et al., 2000). Capture success was the primary behavior limiting selection in bluefish and should be useful to predict size-dependent mortality rates on squid regionally; however because capture success rates may be higher in the laboratory than in the wild, overall trends may be more reliable than the magnitude of the values reported here. Attack probabilities and capture success rates did not explain differences in squid sizes typically observed in flounder diets (Staudinger and Juanes, 2010a); therefore encounter rates must be important in controlling size-selective feeding patterns in flounder (Greene, 1986). Future research should collect empirical data on size-dependent encounter rates between flounder and squid to determine the strength of this relationship. Prey behavior was not accounted for in the variables measured in this study however, anti-predator defenses used by squid such as flight and ink should also play a decisive role in shaping squid's vulnerability to predation and deserve further investigation (Hanlon and Messenger, 1996).

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