Journal of Sea Research 64 (2010) 68–75

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Feeding tactics of a behaviorally plastic predator, summer flounder (*Paralichthys dentatus*)

M.D. Staudinger *, F. Juanes

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

ARTICLE INFO

Article history:
Received 31 December 2008
Received in revised form 23 July 2009
Accepted 2 August 2009
Available online 22 August 2009

Keywords:
Summer flounder (*Paralichthys dentatus*)
Longfin inshore squid (*Loligo pealeii*)
Feeding behavior
Selection
Attack strategy
Swallow orientation

ABSTRACT

In a series of laboratory experiments, the feeding behaviors of summer flounder (*Paralichthys dentatus*) were examined in response to squid and fish prey. Attack and capture tactics were evaluated for their influence on capture success, handling time, and prey-type selectivity. The ambush tactic was the primary behavior (50.6%) used to attack squid. Secondary attack types included active pursuit (42.7%) and stalking (6.7%). Regardless of the prey species targeted or the type of attack employed, summer flounder were equally efficient in capturing prey; capture success rates ranged from 50%–83%. The majority of prey were swallowed in a headfirst orientation (55.3% of squid), however swallow alignment did not significantly affect handling time. Approach times during ambush attacks were greater overall in comparison to active attacks, and relative prey size significantly affected capture times. Despite additional costs in handling time, summer flounder actively selected for mummichogs (*Fundulus* spp.) (attack rate (attacks per minute) = 0.11) over longfin squid (*Loligo pealeii*) (0.08) and Atlantic silversides (*Menidia menidia*) (0.02). Differential attack rates favoring mummichogs suggests a preference towards demersal prey. In the presence of relatively large, fast-moving, and pelagic prey, summer flounder used a greater diversity of attack tactics than have been observed previously under controlled conditions. The behavioral plasticity exhibited by summer flounder is likely mediated by prey behavior and local availability of prey resources in inshore and offshore environments.

1. Introduction

Factors that influence predatory behavior and hence prey selectivity occur on two scales. On a broad scale, encounter rates between predators and prey are controlled by prey abundance, habitat overlap, and foraging tactics (e.g. lie-and-wait, active pursuit). At finer scales, behavior is limited by relative body size, detection abilities, defense mechanisms, activity levels, attack and response behaviors (Mittelbach, 2002). Although the relationship between predator and prey body size has been cited as the most important factor constraining predation (Cohen et al., 1993; Cowan et al., 1996; Dorner and Wagner, 2003; Floeter and Temming, 2003; Juanes et al., 2002; Lundvall et al., 1999; Scharf et al., 2003), prey behavior may be equally influential in mediating capture success, handling times, and attack rates (Juanes et al., 2002; Scharf et al., 2003). Consequently, a comprehensive understanding of prey behavior and predator responses to different prey types may be necessary to effectively model foraging behavior and to predict predator diets (Juanes et al., 2002; Mittelbach, 2002; Scharf et al., 2003).

Flatfish are important predators in benthic habitats. In coastal and offshore environments of the northwest Atlantic, summer flounder (*Paralichthys dentatus*) are regarded as an ecologically and commercially valuable species. Summer flounder have been described as active, day-time feeders (Manderson et al., 2000; Olla et al., 1972; Stickney et al., 1973) and are known to exploit both demersal and pelagic prey types (Latour et al., 2008; Link et al., 2002; Manderson et al., 2000; Staudinger, 2006). Encounter rates with different prey types as well as prey availability vary widely with summer flounder ontogeny and seasonal migration patterns. Estuarine and bay ecosystems are key habitats for juveniles year-round, whereas adults are only present in these areas during the summer and fall (Packer and Hoff, 1999). As adults transition between inshore environments and waters of the continental shelf and slope, their food habits shift dramatically from small crustaceans such as shrimp (Latour et al., 2008; Manderson et al., 2000; Powell and Schwartz, 1979) to fish and longfin squid (*Loligo pealeii*) (Link et al., 2002; Staudinger, 2006).

Previous work has shown that flatfish exhibit a complex array of feeding behaviors that are dependent on both visual and olfactory cues (DeGroot, 1971; Holmes and Gibson, 1983). However, prey offered to predators under controlled conditions have generally been prepared feeds, worms (Bels and Davenport, 1996; Gibb, 1995; Stickney et al., 1973), or mysiids and shrimps (Bergstrom and Palmer, 2007; Holmes and Gibson, 1983; Olla et al., 1972). Although there are exceptions (e.g., Manderson et al., 2000), few studies have reported flatfish predatory responses to fish and large invertebrates as prey. Squid in particular have been neglected from predator–prey

* Corresponding author. Tel.: +1 413 545 0157; fax: +1 413 545 4358.
E-mail addresses: mstaudin@nre.umass.edu (M.D. Staudinger), juanes@nrc.umass.edu (F. Juanes).

1385-1101/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.seares.2009.08.002

behavioral studies despite their importance to the diets of flatfish and a variety of other piscivorous predators (Dawe et al., 1998; Smale, 1996). Squid and other cephalopods possess an array of defense mechanisms and pose unique behavioral challenges to their predators (Hanlon and Messenger, 1996). These behaviors may in turn require or elicit more complex responses by predators to capture and subdue squid in comparison to common fish and crustacean prey.

The purpose of this paper is to describe and quantify attack and capture behaviors used by summer flounder in the presence of large, highly mobile prey. Specifically, we will test summer flounder behavioral responses to longfin squid as prey. In a series of feeding experiments, we evaluate the effects of attack strategy and swallow orientation on handling time and capture success. We also test whether summer flounder exhibit active selection towards squid and two species of prey fish, one demersal and one pelagic.

2. Methods

2.1. Laboratory experiments

Experiments were conducted at the Marine Resources Center of the Marine Biological Laboratory (MBL) (Woods Hole, Massachusetts) between May and September of 2006. Summer flounder ranging in size from 30–48 cm total length (TL) were collected by otter-trawl from Buzzards Bay (Massachusetts), transported to the MBL, and held in flow-through seawater tanks for approximately 1 month prior to use in behavioral trials. Flounder were maintained on a diet of live and frozen fish and squid. Longfin inshore squid to be used as prey in behavioral trials were collected daily by otter-trawl and transported to the MBL in a live-well tank aboard the *RV* Gemma. Atlantic silversides (*Menidia menidia*) and mummichogs (*Fundulus* spp.) were obtained from local bays and estuaries by seining. All prey were acclimated for a minimum of 6 h prior to use in experiments.

Behavioral trials were conducted in a tank that was 3.1 m in diameter, 0.8 m in height, and contained approximately 28,000 l of filtered and circulating seawater. The bottom of the experimental tank was lined with a mixture of gravel and sand approximately 2–4 cm deep, allowing flounder to behave normally and bury beneath the substrate when resting. Water temperatures ranged from 16 to 20 °C and during experiments two 500 W lights were positioned above the tank to aid with filming clarity. All experiments were conducted during the day-time, generally between 09:00 to 13:00 h.

Prior to the start of each trial, three summer flounder of approximately equal size were introduced into the experimental tank and food was restricted for 24 h to standardize hunger levels. An opaque polyvinyl chloride cylinder approximately 1.5 m in diameter and 1 meter in height was lowered into the experimental tank and fifteen prey were added to the interior partitioned area. Prey were allowed to acclimate to the experimental tank for a minimum of 3 h prior to the start of a trial. A trial commenced when the partition was raised out of the tank, exposing prey to predators. Trials lasted approximately 30 min from the time when the partition was initially raised. All predator–prey interactions were recorded by video cameras mounted at two lateral viewing windows and a third camera mounted above the experimental tank.

2.2. Squid–flounder behavioral experiments

In the first set of trials, summer flounder feeding behavior was evaluated exclusively in response to longfin squid as prey. Summer flounder were offered longfin squid ranging in size from 3–21 cm dorsal mantle length (DML). Observed feeding behaviors included attack type, swallow orientation, capture success, and handling time, and were quantified using frame-by-frame analysis of video tape recorded during experimental trials.

Differences in the frequency of total attacks among attack types and swallow orientations were compared using a chi-squared test and executed using the PROC FREQ command in SAS (2003). When an attack was made by a summer flounder it was classified as either successful or unsuccessful. In a successful attack, a prey was captured and ingested by the attacking predator. In an unsuccessful attack, the prey was not consumed. Capture success was defined as the proportion of successful attacks divided by the total number of attacks made over the course of all trials. Proportions of capture successes among attack types were compared using a modified contingency table (Zar, 1984).

Handling times consisted of the following three components: approach, capture, and transport. We defined approach as the time from when a flounder began a lunge sequence and made first contact with a prey. Capture was quantified as the difference in time from the first point of contact with a prey until the time when no part of the prey was visible exterior to the predator's mouth. Transport was measured as the difference in time between the end of the capture sequence and the completion of the last post-manipulation event. All handling time variables were found to be non-normally distributed and were not sufficiently corrected using $\log_{10}$ transformation. A Kruskal Wallis test, the equivalent of a non-parametric ANOVA, was used to contrast differences in handling times among attack types, and swallow orientations with the PROC NPAR1WAY command in SAS (SAS, 2003).

The effects of relative prey size and swallow orientation were evaluated for their influences on handling time using a two-way ANOVA (SAS, 2003). It was expected that capture and transport times would be most affected by these factors since prey manipulation occurs during these two periods; however, due to low sample sizes for transport, only capture times were included in the model. Relative prey size was calculated as the ratio of total squid size (the sum of the lengths of the mantle and arms) (Staudinger et al., 2009) divided by summer flounder total length and grouped into 10% increments (e.g. 0.10–0.19, 0.20–0.29). Capture times were distributed normally within relative size groups therefore a parametric test was appropriate for this analysis.

2.3. Prey-type selectivity

Selective feeding is defined as an observed difference in the distribution of prey types or sizes present in a predator's diet compared to what is in the surrounding environment (Juanes and Conover, 1994). Assuming all prey types are equally available, the prey that a predator attacks most is considered "preferred" and the prey that is attacked least is "avoided".

In prey-type selection trials, summer flounder were given a choice of equal numbers of three prey species: longfin inshore squid, Atlantic silversides, and mummichogs. All squid and fish prey were size-matched as closely as possible. No prey used in a single trial exceeded a 0.15 relative size margin from each other and the mean relative size of all prey was 0.25. To determine if summer flounder were feeding randomly or exhibiting preference for certain prey types, two competing hypotheses were tested. H_0: *attack rates on different prey types do not vary*; H_1: *active choice is evidenced through differential attack rates and summer flounder exhibit preference for one of the prey types.* If the null hypothesis was accepted, selection for different prey types in summer flounder was considered to be passive. Conversely, if the alternative hypothesis was accepted, selection was considered active (Juanes et al., 2002; Juanes and Conover, 1994). In prey-type selection trials, attack rates were measured as the total number of attacks made on each prey species over the total time of all replicate trials, and compared using a chi-squared test. Differences in attack types, capture success rates, and handling times among prey types were assessed using frame-by-frame analyses of video tape recorded during trials and analyzed using a chi-squared test, a modified contingency table, and a Kruskal Wallis test, respectively, as described above.

3. Results

A total of 39 trials were conducted and 121 attacks were observed overall. Predator–prey interactions between summer flounder and longfin squid were assessed in 34 trials. Selectivity and feeding behaviors towards multiple prey types were evaluated in an additional five replicate trials.

3.1. Behavior: attack types

Three attack types were exhibited by summer flounder and described as either ambush, active, or intermediate. Summer flounder also displayed a mock-attack behavior.

Summer flounder initiated ambush attacks from a stationary position either buried beneath or resting on top of the substrate. Prior to making an ambush attack, summer flounder often appeared alert and displayed a raised pectoral fin, pointed vertically, or with its head lifted at an angle from its body above the substrate. When an ambush attack was started from a resting position on top of the sediment, summer flounder were observed to deeply arch their body and brace themselves against the substrate using their anal and dorsal fins. Fin contact with the bottom likely allowed flounder to push off and gain additional momentum when attacking an approaching prey.

Summer flounder were observed to make active attacks after energetically swimming in the water column. Active attacks were also observed after summer flounder glided either laterally, upwards or downwards through the water column. Often when a flounder made an active attack it paused just prior to making a dramatic thrust with its caudal fin and increased its speed as a strike was initiated.

Intermediate attacks were characterized by small movements that advanced a flounder towards a targeted prey while supporting themselves on their anal and dorsal fins. Summer flounder always remained in contact with the substrate prior to completing an intermediate attack. Movements along the bottom could be slow or rapid. Summer flounder were also observed to swivel and change directions during an intermediate approach. A summer flounder executing an intermediate attack might pause for several seconds before completing a strike sequence. The primary difference between an intermediate attack and an active attack was that flounder remained in contact with the substrate and did not swim upwards into the water column.

On multiple occasions, summer flounder demonstrated mock attacks towards prey. This behavior did not qualify as an actual attack because summer flounder did not execute a definitive strike with an open mouth indicating a true attempt to bite and consume prey. Flounder exhibiting mock attacks recognized, oriented, and swam towards prey, but swimming speeds decreased rather than increased when flounder came in close proximity to a prey. Mock attacks were displayed by flounder either actively swimming through the water column or in direct contact with the substrate, approaches similar to active and intermediate attacks, respectively. The majority of mock attacks were observed by summer flounder approaching one or more prey at the water's surface. During these encounters, flounder swam upwards through the water column towards prey and then glided into the cluster of prey. When longfin squid were approached in this manner, they inked and jetted erratically in response, and prey fish darted in at least one random direction before actively swimming away from the approaching flounder. Mock attacks were also made on longfin squid resting on the bottom. Summer flounder initially displayed stalking behaviors, approaching prey while remaining in contact with the substrate with their anal and dorsal fins, and then increased its speed of approach. If an approaching flounder was detected, prey fled upwards into the water column and in the opposite direction of the oncoming predator. Flounder then glided towards where the prey had been and either came to rest on the substrate or continued to swim actively along the bottom or in the water column.

3.2. Behavior: handling times

Approaches on prey were made either from the substrate or while swimming in the water column depending on the attack type employed. The capture portion of the ingestion cycle included biting or chewing of prey or suction of prey into the buccal cavity. All prey were swallowed whole. Relatively large prey were manipulated intact, but forced down the esophagus using repeated buccal and opercular pumping. During transport, prey passed from the buccal cavity through the pharyngeal cavity, the esophagus, and eventually the stomach. Post-manipulation behaviors were characterized by physical movements made by a flounder including jaw protrusions, buccal and opercular pumping, and forced expulsion of debris (e.g. ink) through the opercular cavity. This final portion of the ingestion cycle varied radically in duration with relative prey size and prey alignment as it was swallowed. Summer flounder were observed to clear their pharyngeal and opercular cavities following the successful capture of a prey for up to 4 min after the capture cycle was completed. When the frequency of post-manipulation behaviors exceeded 1 min between events, the primary period of the transport cycle was considered to have ended.

3.3. Behavior: swallow orientation

Summer flounder oriented towards and swallowed prey in three positions; anterior, posterior, and perpendicular. Prey swallowed in the anterior position were ingested headfirst, and tailfirst when swallowed in the posterior position. Capture of prey in the perpendicular orientation was discerned by an initial bite that was oriented somewhere along the length of the body of the prey. The perpendicular orientation was only observed for large prey (>0.30 relative body size) and usually required the flounder to reposition the prey into either an anterior (33%) or posterior (44%) orientation before completion of the capture cycle. Reorientation of a prey was often preceded by violent thrashing of the prey and even striking the prey against the substrate, perhaps to stun the prey while the flounder manipulated it into a more manageable position for ingestion.

3.4. Attack behavior, capture success, and handling times

Out of the 89 attacks observed in behavioral trials using longfin squid as prey, 50.6% of all attacks were classified as ambush attacks (Table 1). The ambush or "lie-and-wait" tactic was therefore the

Table 1
Statistical results from behavioral trials using longfin squid as prey.

Attack type	$N_{Successful}$	$N_{Unsuccessful}$	$Total_{Attacks}$	X^2	*df*	*p*-value
Ambush	31	14	45	30.30	2	<0.0001
Active	20	18	38			
Intermediate	3	3	6			
Total	54	35	89			

Attack type	Capture success (%)	X^2	*df*	*p*-value
Ambush	68.9	0.15	2	>0.05
Active	52.6			
Intermediate	50.0			

$N_{Successful}$, $N_{Unsuccessful}$, and $Total_{Attacks}$ are the frequencies of successful, unsuccessful, and total number of attacks made by summer flounder. Capture success is the percentage of successful attacks made using each of the three attack types. Frequencies of each attack type behavior were compared using a chi-squared test. Differences in the proportions of capture successes among attack types were compared using a modified contingency table.

primary tactic used by summer flounder when feeding on longfin squid ($X^2=30.30$, $df=2$, $p<0.0001$). Active attacks were the second most frequent attack type exhibited by summer flounder and were observed in 42.7% of all attacks. Intermediate attacks were observed least often, comprising only 6.7% of all attacks made.

Although summer flounder were found to alternate between ambush and active attacks, and to a lesser extent intermediate attacks, significant differences were not detected among capture success rates resulting from each attack type ($X^2=0.15$, $df=2$, $p>0.05$) (Table 1). Summer flounder were therefore equally effective in capturing longfin squid regardless of the tactic employed.

The three handling time components, approach, capture, and transport were contrasted among attack types (Fig. 1). Intermediate attacks were excluded from this analysis due to small sample sizes ($n\leq3$). The only handling time component found to differ between ambush and active attack types was approach ($X^2=6.69$, $df=2$, $p=0.04$). Ambush and active approach times ranged from 0.07–0.33 s (median = 0.13 s) and 0.03–0.30 s (median = 0.10 s), respectively. Capture ($X^2=2.11$, $df=2$, $p>0.05$), and transport ($X^2=2.70$, $df=2$, $p>0.05$) handling times were not significantly influenced by attack type.

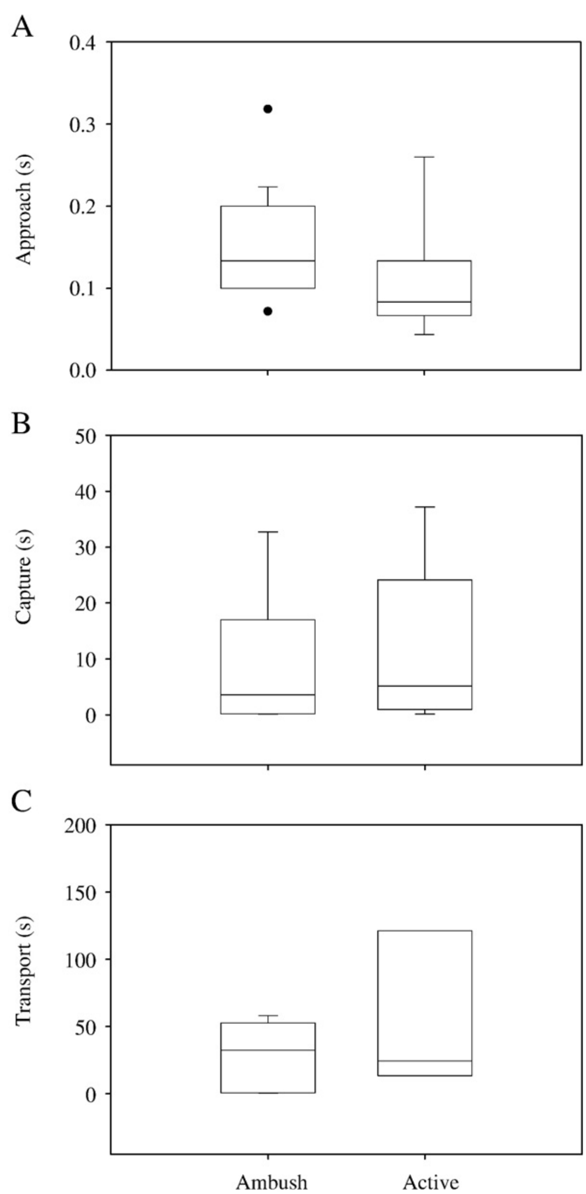

Fig. 1. Handling times of ambush and active attacks made by summer flounder on longfin squid. Intermediate attack types were excluded from analyses due to low sample sizes. Measurements of A) approach B) capture and C) transport are displayed in seconds. Box boundaries represent 25th and 75th percentiles, lines within boxes mark the median. Error bars indicate the 90th and 10th percentiles. Circles show outliers in the 5th and 95th percentiles.

Summer flounder predominantly attacked and swallowed squid in the anterior position ($X^2=8.54$, $df=2$, $p=0.014$) (Table 2). Of the 38 attacks where swallow position was discernible, 55.3% of squid were swallowed headfirst. Longfin squid swallowed in the posterior and perpendicular orientations were observed less often and in nearly equal frequencies, 23.7% and 21.1% respectively. None of the handling time components were found to vary significantly among swallow orientations (Fig. 2).

Relative prey-size predator-size ratios of longfin squid and summer flounder ranged from 0.20–0.50. The effects of swallow orientation and relative prey size were analyzed for 29 attacks. Capture times were significantly impacted by relative prey size but not by swallow orientation (Table 3); the interaction between dependent variables was also not significant ($p=0.57$). Overall, capture times increased with increasing relative squid size ($R^2=0.52$, $p<0.0001$) (Fig. 3). The smallest capture time (0.10 s) was observed for a 0.26 relative sized squid during an anterior swallow orientation. The longest capture period (42.43 s) was observed for a 0.51 relative sized squid during a posterior swallow alignment.

3.5. Prey-type selection

A total of 31 attacks were observed during the 5 replicate prey-type selection trials. Attack rates among prey types varied significantly ($X^2=8.57$, $df=2$, $p=0.01$) indicating summer flounder used active selection when choosing among longfin squid, mummichogs, and Atlantic silversides as prey. Summer flounder exhibited preference for mummichogs, the demersal prey fish, and avoidance towards Atlantic silversides, the pelagic prey fish (Table 4). Attack rates on longfin squid (0.08) were higher than attack rates on Atlantic silversides (0.02) but slightly lower than were observed for mummichogs (0.11) (Fig. 4A). Although differences in attack rates among prey types were detected, capture success rates were found to be comparable across all prey types ($X^2=0.02$, $df=2$, $p>0.05$). Capture success rates ranged from 83% when attacking longfin squid to 67% when foraging on Atlantic silversides (Fig. 4B).

In prey-type selection trials, summer flounder used all three attack types interchangeably when attacking longfin squid ($X^2=0.0018$, $df=2$, $p=1.0$) and mummichogs ($X^2=3.69$, $df=2$, $p=0.16$) (Fig. 5). Only three attacks were observed on Atlantic silversides, an ambush attack which was not successful, an intermediate attack which did result in ingestion, and a third attack where the approach was out of view and could not be classified. Approach and capture times were equivalent among all prey types (all $p\geq0.05$). Alternatively, transport times were an order of magnitude higher for mummichogs (median = 14.9 s) in comparison to longfin squid (median = 0.83 s) ($p=0.037$); no post-manipulation behaviors were observed when Atlantic silversides were consumed (Fig. 6).

Table 2
Frequencies of the positions in which longfin squid were attacked and swallowed by summer flounder during behavioral trials. Differences were tested using a chi-squared test.

Swallow orientation	$N_{Observed}$	% Observed	X^2	df	p-value
Anterior	21	55.3	8.54	2	0.014
Posterior	9	23.7			
Perpendicular	8	21.1			
Total	38				

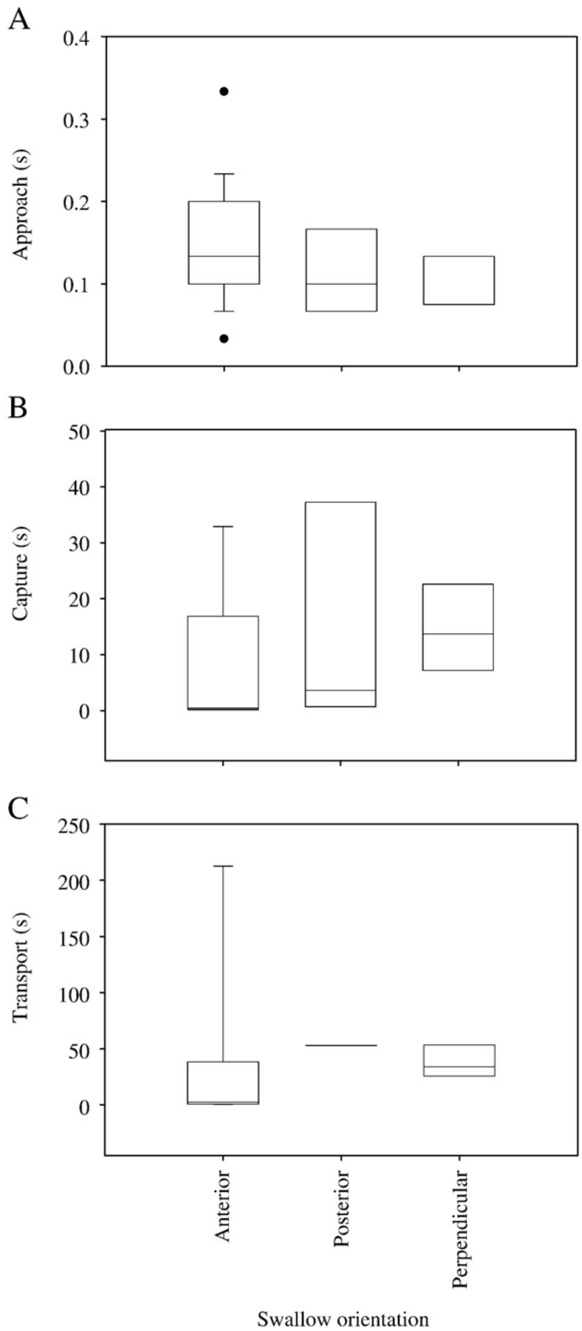

Fig. 2. Handling times of longfin squid swallowed by summer flounder in the anterior, posterior, and perpendicular orientations. Measurements of A) approach B) capture and C) transport are displayed in seconds. Box boundaries represent 25th and 75th percentiles, lines within boxes mark the median. Error bars indicate the 90th and 10th percentiles. Circles show outliers in the 5th and 95th percentiles.

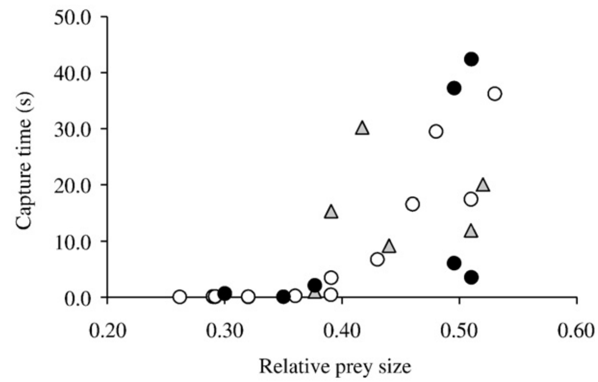

Fig. 3. Scatterplot of capture times (seconds) of relative longfin squid sizes swallowed in anterior (open circles), posterior (closed circles), and perpendicular orientations (triangles) by summer flounder.

4. Discussion

4.1. Attack behavior

Summer flounder exhibited several different types of attacks ranging from lie-and-wait to active pursuit when feeding on longfin squid, mummichogs, and Atlantic silversides. Ambush attacks were the primary tactic used by summer flounder to capture longfin squid and fish prey. Similar to other species of flatfish, summer flounder spend the majority of their lives on or near the bottom and possess morphological characteristics that are well suited for a lie-and-wait predator. Therefore, it should not be surprising that ambush attacks were displayed most frequently; however, lie-and-wait attacks have rarely been observed in summer flounder in the laboratory. Previous studies reported intermediate attacks (e.g. crawling and stalking) as the principal tactic employed to capture demersal prey such as winter flounder (*Pseudopleuronectes americanus*), Atlantic silversides, sand shrimp (*Crangon septemspinosa*), and grass shrimp (*Palaemonetus vulgaris*) (Manderson et al., 2000; Olla et al., 1972). This is in contrast to the present study where we only observed intermediate attacks in 6.7% of attacks made on longfin squid and 25% of attacks made on prey fish. Manderson et al. (2000) hypothesized that the lie-and-wait tactic would be more effective for capturing pelagic prey in certain habitats. We found that capture success rates did not differ among the three attack types suggesting that although summer flounder modify attack behavior in response to prey type and behavior, the tactic chosen does not influence efficiency.

Anti-predator displays exhibited by prey in response to mock attacks indicated summer flounder demonstrated some form of predatory intent and that a threat was apparent. We suggest that mock attacks were used by summer flounder to investigate potential prey (similar to predator inspection by prey; see Krause et al., 2002), or to scatter a group of prey. Another possibility is that if prey detected and reacted to summer flounder at distances too great for a flounder to execute an effective attack sequence, a directed attack was abandoned.

Table 3
Results of a two-way ANOVA testing the effects of the dependent variables swallow orientation and relative prey size on capture time.

Dependent variable	*df*	*SS*	*MS*	*F-value*	*p-value*
Swallow orientation	2	9.6	4.8	0.05	0.95
Relative prey size	3	2069.0	689.7	6.75	0.003
Swallow orientation * relative prey size (interaction)	3	209.2	69.7	0.68	0.57

Relative prey size was calculated as the total length of each longfin squid consumed, divided by the total length of the attacking summer flounder. Capture time was measured in seconds. *df* = degrees of freedom, *SS* = Sum of Squares, *MS* = Mean Square.

Table 4
Attack results of prey-type selection trials.

Prey type	$N_{Successful}$	$N_{Unsuccessful}$	$Total_{Attacks}$	X^2	*df*	*p*-value
Mummichogs	12	4	16	8.57	2	0.01
Longfin squid	10	2	12			
Atlantic silversides	2	1	3			
Total	24	7	31			

$N_{Successful}$, $N_{Unsuccessful}$, and $Total_{Attacks}$ are the frequencies of successful, unsuccessful, and total number of attacks made by summer flounder, respectively. Differences in attack frequencies over the course of all trials were tested using a chi-squared test.

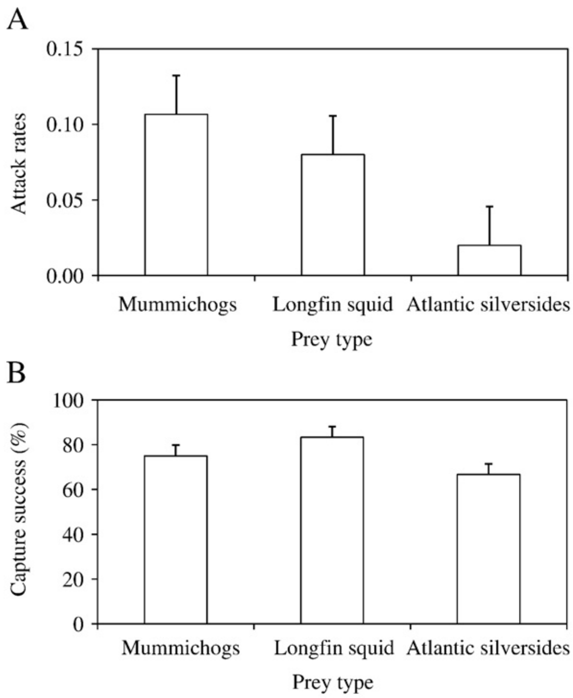

Fig. 4. Prey-type selection trial results. A) Attack rates and B) percent capture successes made by summer flounder on mummichogs, longfin inshore squid, and Atlantic silversides. Vertical bars represent one standard error.

4.2. Handling times

In behavioral trials using longfin squid as prey, approach was the only handling time component found to differ significantly among attack types. When a summer flounder used ambush attacks, the distance covered during the approach sequence was entirely contingent on the height in the water column at which a prey was swimming. Conversely, when summer flounder utilized intermediate and active attacks, the distance at which an attack was initiated was largely controlled by the pursuing flounder. Active attacks made in the water column appeared to enable summer flounder to get closer to longfin squid in comparison to ambush attacks, and likely resulted in shorter approach times.

Stephens and Krebs (1986) define handling time as the pursuit, capture, and consumption of a prey item. Depending on the question addressed, how handling time is quantified may vary substantially among studies and is largely subjective depending on how long an individual fish is observed and the range of species specific post-ingestion behaviors displayed. Of the three components measured in the present study, the capture period was the most reliably measured and the most translatable among studies and species.

Bels and Davenport (1996) suggested extending the handling time cycle to include post buccal cavity manipulation behaviors in plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*) since food not completely cleared from the opercular and orobranchial cavities could potentially impede other activities such as respiration. Because visual confirmation of what was occurring internally was not possible, transport was the handling time component measured with the

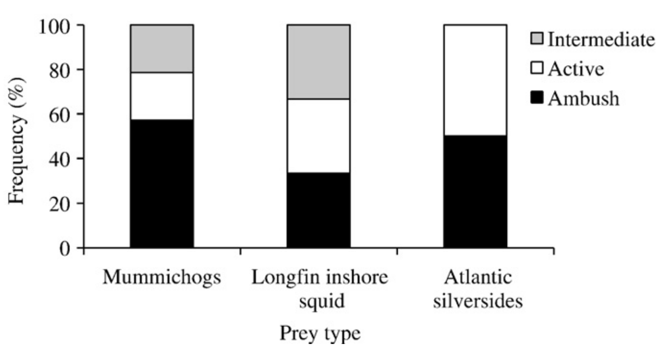

Fig. 5. Frequencies (displayed as percentages) of ambush, active, and intermediate attacks made by summer flounder when attacking mummichogs, longfin inshore squid, and Atlantic silversides during prey-type selection trials.

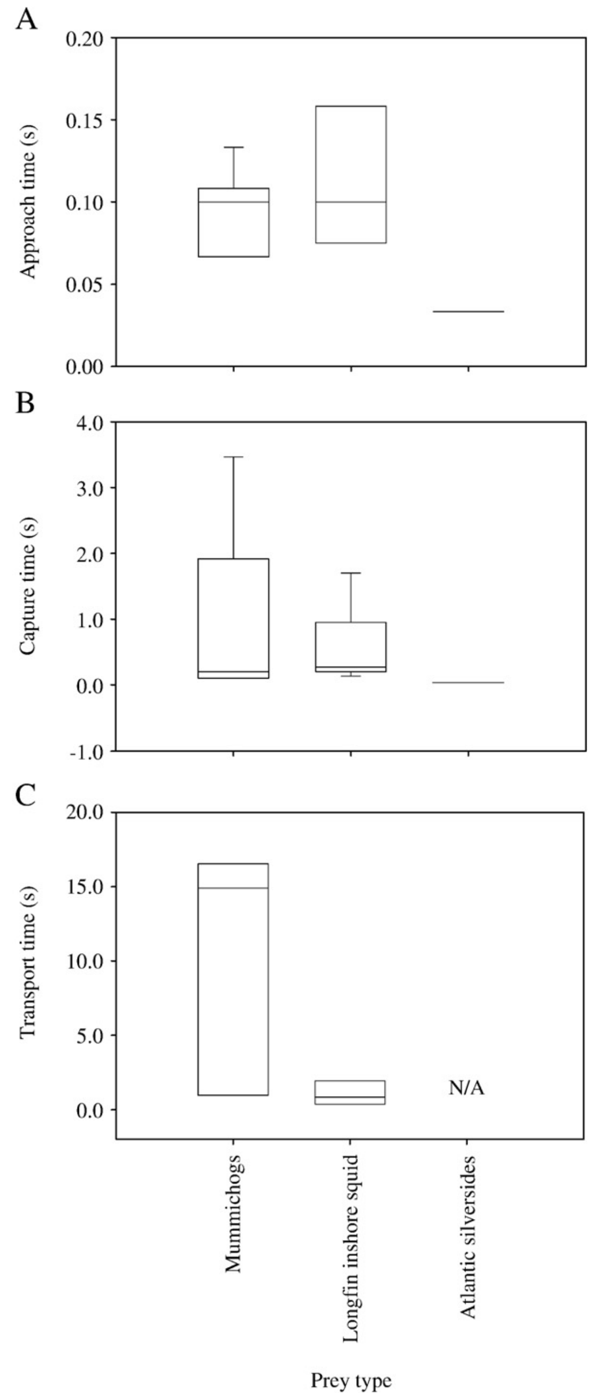

Fig. 6. A) Approach B) capture and C) transport handling times of summer flounder attacks on mummichogs, longfin inshore squid, and Atlantic silversides during prey-type selectivity trials. Transport times were not observed during attacks on Atlantic silversides. All measurements are displayed in seconds. Box boundaries represent 25th and 75th percentiles, lines within boxes mark the median. Error bars indicate the 90th and 10th percentiles.

greatest amount of uncertainty. Although transport was likely underestimated, this component was considered an important aspect of the handling time process since no summer flounder were observed to initiate a new search or attack sequence or transition into a resting position (e.g. burying beneath the substrate) while exhibiting post-manipulation behaviors.

4.3. Swallow orientation

The orientation of prey capture has been found to vary widely among predator–prey species combinations (Ellis and Gibson, 1997; Juanes and Conover, 1994; L'Abee-Lund et al., 1996; Reimchen, 1991; Vehanen et al., 1998). Headfirst swallow orientations have been associated with predators that utilize ambush attack strategies while tailfirst alignments are more characteristic of predators that actively chase their prey (Juanes and Conover, 1994). When making both ambush and active attacks, summer flounder displayed an Ω-shaped body position prior to initiating an approach sequence and rarely made repetitive attempts to capture missed prey. This style of predation is characteristic of a lunger as opposed to a pursuer (Hunter, 1984). Although squid regularly swim backwards (leading tailfirst), ambush attacks yielded capture in the anterior swallow orientation more frequently in comparison to other alignments. During active attacks made on squid swimming at the surface, squid faced towards an attacking flounder and displayed anti-predator arm postures (e.g. upward v-curl) and body patterns (e.g. deep red coloration) (Hanlon and Messenger, 1996). When these anti-predator displays failed to deter an approaching flounder, squid were more often captured by summer flounder in the headfirst orientation. If a fleeing squid was pursued, swimming backwards would orient the squid's anterior end toward its attacker and make it more susceptible to headfirst capture.

Swallowing prey fish in the headfirst orientation is thought to minimize handling times and abrasion caused by morphological traits such as spines, opercula, or fin rays (L'Abee-Lund et al., 1996; Reimchen, 1991). In gape limited predators, swallowing large prey in orientations other than headfirst alignment has the potential to impact normal respiration, or even choke a predator (Bels and Davenport, 1996). Squid possess physical characteristics such as beaks, arms, and suckers which pose an unusual challenge to their attackers (Hanlon and Messenger, 1996). When captured in the posterior or perpendicular orientations, occasionally longfin squid would wrap their arms around the operculum and head (blind and eyed sides) of summer flounder. During these attacks, in an attempt to release a retaliating squid's grasp, summer flounder were observed to thrash and even strike squid against the substrate. We had expected that perpendicular and posterior attacks would result in longer handling times, however the small sample sizes ($n<10$) were likely responsible for the inability to detect significant effects on handling times among the three swallow orientations.

In studies examining feeding behavior in cutthroat trout (*Oncorhynchus clarki*) and brown trout (*Salmo trutta*), headfirst swallow orientation was beneficial in minimizing escape, handling time, and swallowing success (L'Abee-Lund et al., 1996; Reimchen, 1991). These trends were more prominent when prey size increased and approached maximum predator gape sizes. Gape sizes in summer flounder are large relative to squid body depth and width; consequently, summer flounder are not thought to be gape limited when feeding on squid (Staudinger and Juanes, Submitted for publication). Alternatively, squid's behavioral defenses may become limiting to summer flounder regardless of swallow orientation at larger relative sizes (>0.40) as evidenced by sharply increasing handling times. Longfin squid captured in the perpendicular orientation were generally larger (>0.30 relative prey size) than squid captured in anterior and posterior alignments. This difference indicates that larger squid may be more difficult to pursue and orient towards when attacked due to higher swimming speeds and escape velocities (Ellis and Gibson, 1997). There were only two occurrences (4% of all successful attacks) of squid escaping summer flounder once they were captured; once from a perpendicular alignment and once from a posterior alignment. This post capture escape loss is comparatively lower than has been reported (9% escapement) for other piscivorous predators (Reimchen, 1991; Scharf et al., 2003).

4.4. Prey-type selection

In the field, encounter rates with demersal prey are likely to be higher in comparison to pelagic prey, and may explain summer flounder preference for demersal prey types in the present study (mummichogs) and previously (Manderson et al., 2000). Regardless of the prey type chosen, summer flounder were consistently efficient and highly successful (all capture success rates $>65\%$) in obtaining all prey types. Relative prey sizes of squid and fish used in behavioral experiments correspond to the most common sizes found in summer flounder diets in the northwest Atlantic ecosystem (Staudinger and Juanes, Submitted for publication). When feeding on fish and squid, all three attack types were used interchangeably indicating summer flounder could adapt their behavior opportunistically. The only limitation identified when feeding on the different prey types was in the transport component of handling times. However, no post-manipulation behaviors were observed when summer flounder fed on Atlantic silversides. Conversely, transport was an order of magnitude higher for mummichogs in comparison to longfin squid. Summer flounder actively chose mummichogs over other prey types despite the additional cost in handling time. This result suggests that some aspect of prey behavior must have been influential in shaping summer flounder feeding preferences. For example, differential prey reaction distances and activity levels explained a large fraction of the variation in susceptibility to predation of various forage fishes when attacked by bluefish (*Pomatomus saltatrix*) and striped bass (*Morone saxatilis*) (Scharf et al., 2003).

4.5. Summer flounder foraging ecology

Throughout their range in waters along the eastern coast of North America, summer flounder are known to exhibit major shifts in diet with ontogeny (Witting et al., 2004), over regional scales (Latour et al., 2008; Rountree and Able, 1992), and between inshore and offshore habitats (Link et al., 2002; Staudinger, 2006). For example, juvenile and adult summer flounder in the Chesapeake Bay primarily consume mysiid shrimp (*Neomysis* spp.) and bay anchovy (*Anchoa mitchilli*) (Latour et al., 2008), while in the Navesink River in New Jersey, sand shrimp and winter flounder are the dominant prey (Manderson et al., 2000). Alternatively, adult summer flounder found in waters on the continental shelf and slope are primarily piscivorous and teuthopagous; major prey species include clupeiformes, sand lance (*Ammodytes americanus*), butterfish (*Peprilus triacanthus*), and longfin squid (Link et al., 2002; Staudinger, 2006).

The diversity of feeding behaviors observed in the present study suggests that in addition to being opportunistic in what they eat, summer flounder are also flexible in changing how they capture prey. Based on previous studies, summer flounder use intermediate attack behaviors such as crawling, stalking, and shambling when feeding on shrimps, mysiids, and other demersal prey (Manderson et al., 2000; Olla et al., 1972). As shown here, larger, fast-moving, and pelagic prey types may require more complex behaviors including surprise attacks.

Summer flounder appear to alternate between ambush, active, and intermediate attack tactics without compromising efficiency. However in the field, capture success rates will likely differ from observations made under ideal conditions in the laboratory. Factors such as light intensity, turbidity, and the structural complexity of the surrounding environment (e.g., vegetation) can impede visual location of prey

(Lindholm et al., 1999; Manderson et al., 2000). As a consequence, the distance at which a summer flounder can detect an approaching prey will be reduced, pursuit times will be higher, and there will be a higher occurrence of failed attacks (Ellis and Gibson, 1997).

Adult summer flounder may reserve intermediate attack behaviors for predating on demersal prey, and intermediate strategies may only be used during the times of year when their diets are focused on small crustaceans (e.g. in estuarine habitats). Intermediate attack types may be more characteristic of juvenile foraging behavior for two reasons; first, juveniles are confined to inland habitats where shrimps and mysiids comprise the majority of their diets year-round. Secondly, intermediate attacks allow summer flounder to remain camouflaged against the substrate and capture prey using subtle movements, thereby reducing their risk of being detected by predators. Larger, adult flounder are less vulnerable to predation which may enable them to take greater risks and pursue prey in the water column. Longer handling times and higher frequencies of post-manipulation behaviors associated with larger prey may also contribute to increased susceptibility to predation and influence the types and sizes of prey preferred by summer flounder.

5. Conclusions

Flatfish exhibit a wide range of tactics to hunt and capture prey, and feeding behavior is adapted to the behavior of their prey (Holmes and Gibson, 1983). It is likely that because the food habits of summer flounder encompass such a diversity of prey types, the breadth of their behavioral capabilities is also quite varied. Summer flounder have the flexibility to alternate among approaches that are fast and agile to actively pursue mobile prey; patient and surprising, to ambush a passing pelagic prey, or stealth, to creep up on slow-moving or benthic prey. Although the lie-and-wait tactic was the most commonly employed, summer flounder also exhibited active and intermediate attacks to capture longfin squid and fish without compromising efficiency. Since few studies have presented flatfish with large, highly-mobile prey, and to the best of our knowledge this is the first evaluation of predator–prey behavioral interactions using squid as prey, it is uncertain if the behavioral plasticity observed by summer flounder in response to these prey types are characteristic of other piscivorous flatfishes (e.g. Bothiae, Pleuronectidae, and Psettodidae).

Acknowledgements

This study would not have been possible without the help of R. Hanlon, N. Jacobson, the captain and crew of the R/V Gemma and the rest of the staff at the Marine Resources Center/Marine Biological Laboratory. We are also grateful to the Massachusetts Division of Marine Fisheries for their help in collecting specimens and W. Lange at the Woods Hole Oceanographic Institution for allowing us to use his video equipment during experiments. This study was funded by the Woods Hole Oceanographic Institution Sea Grant Program, the Massachusetts Marine Fisheries Institute, and the University of Massachusetts, and the Five College Coastal and Marine Sciences Program.

References

Bels, V.L., Davenport, J., 1996. A comparison of food capture and ingestion in juveniles of two flatfish species, *Pleuronectes platessa* and *Limanda limanda* (Teleostei: Pleuronectiformes). J. Fish Biol. 49, 390–401.

Bergstrom, C.A., Palmer, A.R., 2007. Which way to turn? Effect of direction of body asymmetry on turning and prey strike orientation in starry flounder *Platichthys stellatus* (Pallas) (Pleuronectidae). J. Fish Biol 71, 737–748.

Cohen, J.E., Pimm, S.L., Yodzis, P., Saldana, J., 1993. Body sizes of animal predators and animal prey in food webs. J. Anim. Ecol. 62, 67–78.

Cowan, J.H., Houde, E.D., Rose, K.A., 1996. Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment, ICES. J. Mar. Sci. 53, 23–37.

Dawe, E.G., Bowering, W.R., Joy, J.B., 1998. Predominance of squid (*Gonatus* spp.) in the diet of Greenland halibut (*Reinhardtius hippoglossoides*) on the deep slope of the northeast Newfoundland continental shelf. Fish. Res. 36, 267–273.

DeGroot, S.J., 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. 5, 121–196.

Dorner, H., Wagner, A., 2003. Size-dependent predator–prey relationships between perch and their fish prey. J. Fish Bio. 62, 1021–1032.

Ellis, T., Gibson, R.N., 1997. Predation of 0-group flatfishes by 0-group cod: handling times and size-selection. Mar. Ecol. Progr. Ser. 149, 83–90.

Floeter, J., Temming, A., 2003. Explaining diet composition of North Sea cod (*Gadus morhua*): prey size preference vs. prey availability. Can. J. Fish. Aquat. Sci. 60, 140–150.

Gibb, A.C., 1995. Kinematics of prey capture in a flatfish, *Pleuronichthys verticalis*. J. Exp. Biol. 198, 1173–1183.

Hanlon, R.T., Messenger, J.B., 1996. Cephalopod Behaviour. Cambridge University Press, Cambridge.

Holmes, R.A., Gibson, R.N., 1983. A comparison of predatory behavior in flatfish. Anim. Behav. 31, 1244–1255.

Hunter, J.R., 1984. Inferences regarding predation on the early life stages of cod and other fishes. In: Dahl, E., Danielssen, D., Moksness, E., Solemdal, P. (Eds.), The Propagation of Cod *Gadus morhua* L. Flodevigen Rapp. 1, pp. 533–562.

Juanes, F., Conover, D.O., 1994. Piscivory and prey size selection in young-of-the-year bluefish: predator preference or size-dependent capture success? Mar. Ecol. Prog. Ser. 114, 59–69.

Juanes, F., Buckel, J.A., Scharf, F.S., 2002. Feeding ecology of piscivorous fishes. In: Hart, P.J.B., Reynolds, J.D. (Eds.), Handbook of Fish Biology and Fisheries. Blackwell Science, Malden, MA, pp. 267–283.

Krause, J., Hensor, E.M.A., Ruxton, G.D., 2002. Fish as prey. In: Hart, P.J.B., Reynolds, J.D. (Eds.), Blackwell Science. Malden, MA, pp. 284–297.

Latour, R.J., Gartland, J., Bonzek, C.F., Johnson, R.A., 2008. The trophic dynamics of summer flounder (*Paralichthys dentatus*) in Chesapeake Bay. Fish. Bull. 106, 47–57.

Lindholm, J.B., Auster, P.J., Kaufman, L.S., 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 180, 247–255.

Link, J.S., Bolles, K., Milliken, C.G., 2002. The feeding ecology of flatfish in the Northwest Atlantic. J. Northwest. Atl. Fish. Sci. 30, 1–17.

Lundvall, D., Svanback, R., Persson, L., Bystrom, P., 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Can. J. Fish. Aquat. Sci. 56, 1285–1292.

L'Abee-Lund, J.H., Aass, P., Saegrov, H., 1996. Prey orientation in piscivorous brown trout. J. Fish Biol. 48, 871–877.

Manderson, J.P., Phelan, B.A., Stoner, A.W., Hilbert, J., 2000. Predator–prey relations between age-1+ summer flounder (*Paralichthys dentatus*, Linnaeus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. J. Exp. Mar. Biol. Ecol 251, 17–39.

Mittelbach, G.G., 2002. Fish foraging and habitat choice: a theoretical perspective. In: Hart, P.J.B., Reynolds, J.D. (Eds.), Handbook of Fish Biology and Fisheries. Blackwell Science, Malden, MA, pp. 251–266.

Olla, B.L., Samet, C.E., Studholme, A.L., 1972. Activity and feeding behavior of the summer flounder (*Paralichthys dentatus*) under controlled laboratory conditions. Fish. Bull. 70, 1127–1136.

Packer, D.B., Hoff, T., 1999. Life history habitat parameters and essential habitat of mid-Atlantic summer flounder. Am. Fish. Soc. Symp. 22, 76–92.

Powell, A.B., Schwartz, F.J., 1979. Food of *Paralichthys dentatus* and *Paralichthys lethostigma* (Pisces, Bothidae) in North Carolina estuaries. Estuaries 2, 276–279.

Reimchen, T.E., 1991. Evolutionary attributes of headfirst prey manipulation and swallowing in piscivores. Can. J. Zool. 69, 2912–2916.

Rountree, R.A., Able, K.W., 1992. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-year summer flounder in New Jersey. Trans. Am. Fish. Soc. 121, 765–776.

SAS, S.A.S., 2003. SAS Institute Inc., Carey, NC.

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.

Smale, M.J., 1996. Cephalopods as prey. IV. Fishes. Phil. Trans. R. Soc. Lond. B. 351, 1067–1081.

Staudinger, M.D., 2006. Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf. Fish. Bull. 104, 605–615.

Staudinger, M.D., Juanes, F., submitted for publication. Size-based predation on longfin inshore squid (*Loligo pealeii*) in the Northwest Atlantic. Marine Ecology Progress Series.

Staudinger, M.D., Juanes, F., Carlson, S., 2009. Reconstruction of original body size and estimation of allometric relationships for the longfin inshore squid (*Loligo pealeii*) and northern shortfin squid (*Illex illecebrosus*). Fish. Bull. 107, 101–105.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton, NJ.

Stickney, R.R., White, D.B., Miller, D., 1973. Observations of Fin Use in Relation to Feeding and Resting Behavior in Flatfishes. InPleuronectiformes, Copeia, pp. 154–156.

Vehanen, T., Hyvarinen, P., Huusko, A., 1998. Food consumption and prey orientation of piscivorous brown trout (*Salmo trutta*) and pikeperch (*Stizostedion lucioperca*) in a large regulated lake. J. Appl. Ichthyol. 14, 15–22.

Witting, D.A., Chambers, R.C., Bosley, K.L., Wainright, S.C., 2004. Experimental evaluation of ontogenetic diet transitions in summer flounder (*Paralichthys dentatus*), using stable isotopes as diet tracers. Can. J. Fish. Aquat. Sci. 61, 2069–2084.

Zar, J.H., 1984. Biostatistical Analysis, 4th ed. Prentice Hall, Englewood Cliffs, New Jersey.