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

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A B S T R A C T

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.

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).

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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 handing 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 28×10^3 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