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Shark scavenging behavior in the presence of competition

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Abstract   The distribution of organisms within a community can often be determined by the degree of plasticity or degree of specialization of resource acquisition. Resource acquisition is often based on the morphology of an organism, behavior, or a combination of both. Performance tests of feeding can identify the possible interactions that allow one species to better exploit a prey item. Scavenging behaviors in the presence or absence of a competitor were investigated by quantifying prey selection in a trophic generalist, spiny dogfish *Squalus acanthias*, and a trophic specialist, smooth-hounds *Mustelus canis*, in order to determine if each shark scavenged according to its jaw morphology. The diet of dogfish consists of small fishes, squid, ctenophores, and bivalves; they are expected to be nonselective predators. Smooth-hounds primarily feed on crustaceans; therefore, they are predicted to select crabs over other prey types. Prey selection was quantified by ranking each prey item according to the order it was consumed. Dietary shifts were analyzed by comparing the percentage of each prey item selected during solitary versus competitive scavenging. When scavenging alone, dogfish prefer herring and squid, which are easily handled by the cutting dentition of dogfish. Dogfish shift their diet to include a greater number of prey types when scavenging with a competitor. Smooth-hounds scavenge on squid, herring, and shrimp when alone, but increase the number of crabs in the diet when scavenging competitively. Competition causes smooth-hounds to scavenge according to their jaw morphology and locomotor abilities, which enables them to feed on a specialized resource [*Current Zoology* 56 (1): 100–108 2010].

Key words   Optimal foraging theory, Prey selection, *Squalus acanthias*, *Mustelus canis*

Performance tests can provide a link between morphological structures or behaviors and environment because they measure an individual on an ecologically relevant task (Lauder, 1995). Optimal foraging theory predicts that predators will make decisions while foraging that will maximize net energy gain, and ultimately fitness, by choosing prey that has a high energy return and low cost (Krebs, 1978). Therefore, performance tests of foraging or feeding strategy can detect the possible interactions (such as jaw morphology and feeding behavior) that allow one species to better exploit a resource that another cannot by identifying under what conditions behavioral response may be adjusted (Wainwright, 1994; Norton, 1995). Broadly defined, a species or population can be characterized as a generalist if it displays a wide pattern of utilization relative to others, or a specialist if it shows a narrow pattern of utilization (Fox and Morrow, 1981; Futuyma and Moreno, 1988). Performance tests that expose an organism to prey types that are available in the habitat, yet are normally not consumed, may examine the range of function of a specialist or a generalist (Sanderson, 1991).

Spiny dogfish *Squalus acanthias* and smooth-hounds *Mustelus canis* are two size-matched sharks that inhabit a similar geographic range in the northwest Atlantic Ocean, including Narragansett Bay, Rhode Island (Compagno, 1984). Spiny dogfish feed on a variety of prey items, including fishes, squid, crustaceans, and ctenophores, often selecting the most abundant prey resource in the area (Compagno, 1984; Alonso et al., 2002). Dogfish modulate capture and processing behaviors as well as jaw muscle function by prey type (Wilga and Motta, 1998; Gerry et al., 2008). These sharks are able to feed on a range and variety of prey types using a suite of feeding behaviors, indicative of a trophic generalist (Schoener, 1971). Smooth-hounds have several morphological and functional modifications that enable them to feed on durophagous prey, including low-cusped crushing teeth (Compagno, 1984), a force-amplifying jaw-lever system (Gerry and Dean, 2005[1]), and synchronous activation of the jaw muscles (Gerry et al., 2008). Smooth-hounds primarily feed on

[1] Gerry SP, Dean MN, 2005. Symphyseal force transmission in the jaws of *Squalus acanthias* and *Mustelus canis*. Society for Integrative and Comparative Biology, poster.

benthic prey, including several types of crustaceans (rock crabs or portunid crabs), mollusks, and flatfish (Gelsleichter et al., 1999; Bowman et al., 2000). Based on cranial morphology and stomach contents, one can presume that smooth-hounds are trophic specialists: they prefer the prey type that matches their morphology.

Studies of interspecific competition may show the feeding behaviors and resource use of a generalist and a specialist. A specialist should handle its preferred prey with greater efficiency, thereby excluding the generalist from the resource (Fox and Morrow, 1981; Futuyma and Moreno, 1988; Egan and Funk, 2006). Competition may cause behaviors to shift in order to acquire the resource, thus increasing or decreasing specializations (Futuyma and Moreno, 1988). For a specialist to compete successfully against a generalist, it should not increase the range of prey items taken; for a generalist to compete successfully against a specialist, it should not alter its diet when faced with competition (MacArthur and Pianka, 1966).

The goal of this study is to investigate scavenging behaviors by observing and analyzing prey selection by spiny dogfish and smooth-hounds. Solitary and competitive scavenging will determine if each species selects the prey items best suited to its morphology and behavior and if competition causes a dietary shift. It is predicted that spiny dogfish will not show a preference for any one prey item and will scavenge on all prey using a variety of behaviors. Smooth-hounds are stereotyped for crushing (Gerry, 2008); therefore, they should select crabs preferentially. Neither species should shift its diet in the presence of competition. An increased diet breadth should be advantageous for dogfish, whereas smooth-hounds should be successful by not shifting their diet from their specialized prey.

1 Materials and Methods

1.1 Species

Ten spiny dogfish *Squalus acanthias* (73 – 83 cm in total length, TL) and ten smooth-hound sharks *Mustelus canis* (90 – 95 cm TL) were collected by otter trawl in Narragansett Bay, Rhode Island, USA and off the coast of Woods Hole, Massachusetts, USA. Sharks were housed by species in two circular tanks (each 3 m in diameter) with a flow-through seawater system at a temperature of 15℃. Dogfish were fed to satiation twice weekly on a diet of herring *Clupea harengus* cut to one-half mouth width or squid (*Loligo* sp.) cut in half. Smooth-hounds were fed a diet of green crabs *Carcinus maenas* sized to mouth width twice weekly and pieces

of herring *C. harengus* or squid (*Loligo* sp.) cut in half once per week.

1.2 Scavenging behavior

Prey selection was quantified by observing a single predator scavenging on prey items in a second circular tank (6653 L). Each shark was acclimated individually in the experimental tank for a minimum of 24 hours prior to the trial, and food was withheld for 48 hours. Trials used for analysis were those in which the shark indicated its willingness to feed by exhibiting increased search behavior after the introduction of prey.

At the beginning of each four-minute trial, all prey items were simultaneously released from the edge of the tank, at the farthest distance from the shark; therefore, position of prey entry shifted among trials. Items were dropped simultaneously so that the shark would not consistently encounter the same prey item first among the trials. Preliminary trials showed that the sharks did not always eat the first prey item in their search path; often other prey items were pushed out of the way in favor of select prey. For each trial, two of each of the following prey were given: herring *C. harengus* cut to one-half mouth width, whole Atlantic silverside *Menidia menidia*, squid (*Loligo* sp.) cut to one-half mouth width, whole green crab *C. maenas* sized to mouth width and with the shell cracked, and whole shrimp (*Penaeus* sp.) sized to one-half mouth width. All prey items were dead because sharks refused live prey in captivity; therefore, prey escape behavior did not affect foraging ability. Prey items were chosen because they represented prey that are naturally found in the diet of dogfish and are a minor part of the smooth-hound diet. In preliminary trials, both species ate all prey items individually. Prey items were kept to a similar size whenever possible to eliminate any confounding effect of prey size, which is known to affect the choice of an organism (Hoyle and Keast, 1987). Additionally, although prey varied in shape and/or complexity of parts, these factors should not affect handling and selection, since dogfish modulate capture and processing behaviors based on prey type (Wilga and Motta, 1998), and smooth-hounds are stereotyped (Gerry, 2008). Three replicate trials were conducted for each shark (*n* = 6) for a total of 18 trials per species.

The number of strikes at the prey (unsuccessful), consumed prey, unconsumed prey, and the order of selection were quantified concurrently with qualitative behavioral observations. Percentages describing prey status were calculated to examine the relative efficiency of each predator because a specialist should have an

increased capture rate when feeding on preferred prey (and thus be more efficient) as compared to a generalist (Sanderson, 1990). Percentage consumed is equal to the number of prey items consumed divided by the total number of items, irrespective of prey type. Percentage rejected is equal to the number of prey strikes (items that were taken but not eaten) divided by the total number of items. Percentage unconsumed is equal to the number of prey items that were ignored divided by the total number of items.

1.3　Scavenging behavior in the presence of competition

For these trials, the experimental setup was similar to that outlined above. Prey selection was quantified by observing a single size-matched predator of each species (two sharks total, chosen at random) scavenging on prey items. The two sharks were acclimated together in the experimental tank for a minimum of 24 hours prior to the trial, and food was withheld for 48 hours. At the beginning of each four-minute trial, four of each of the following prey were dropped into the tank simultaneously: herring cut to one-half mouth width, whole Atlantic silverside, squid cut to one-half mouth width, whole green crab sized to mouth width and with the shell cracked, and whole shrimp sized to one-half mouth width. As above, prey items were released from the edge of the tank at the farthest distance from both sharks (i.e., prey were not released until both sharks were swimming at a similar distance from the prey). The number of strikes at the prey (unsuccessful), consumed prey, unconsumed prey, and the order of selection were quantified. Qualitative behavioral observations were recorded, including which species consumed prey first. Three replicate trials were run for each pair for a total of 12 trials per species.

1.4　Prey preference analysis

Prey preference for all trials was analyzed according to Taplin (2007) by ranking each prey item according to the order in which it was consumed. Although other indices of analysis may be used more frequently (e.g. Manly's α), these indices often assume numbers of prey are in high abundance and that prey items will not be depleted (Krebs, 1999). These terms are not met in the present study; therefore, the rank-order method is more suitable. Taplin's analysis assumes that several prey items are offered simultaneously and that prey items which are eaten last are not distinguished from prey that are not consumed. Each prey item is ranked according to the order that it is consumed, and preference is defined as those prey items that are chosen first, based on social choice theory (Taplin, 2007). Unconsumed prey is given a preference score equal to the average rank of all possible remaining prey items (Table 1). A ranking closer to one indicates preference, whereas values closer to ten indicate no preference or rejection. Preference scores for each individual of each species for each prey type were averaged for replicate trials.

1.5　Statistical analysis

For individuals and prey type, preference scores were tested for normality and equality of variances using the Kolmogorov-Smirnov test ($P < 0.05$) and Levene's equality of error variances test ($P < 0.05$), respectively. All preference data were square-root transformed to achieve normality. A two-way analysis of variance (ANOVA; SPSS, version 15.0) was used to test for differences in prey preference (in the absence and presence of competition) among individuals of each species (dogfish, smooth-hounds), with individual and prey (crab, herring, shrimp, silverside, squid) as fixed effects. A Tukey post-hoc test of prey item was then used to identify differences detected by the ANOVAs ($P < 0.05$). For individuals and prey status, selection rates were tested for normality and equality of variances using the Kolmogorov-Smirnov test ($P < 0.05$) and Levene's test ($P < 0.05$), respectively. A two-way ANOVA was used to test for differences in behavioral selection rates among individuals of each species (dogfish, smooth-hounds), with individual and prey status percentages (consumed, rejected, unconsumed) as fixed effects. A Tukey post-hoc test of prey status was used to identify differences detected by the ANOVAs ($P < 0.05$). A t-test of unequal variances (Microsoft Excel, 2003) of each prey item within a species was used to test for a shift in diet between solitary or competitive

Table 1　Example of prey preference analysis rankings

Prey type	Crab	Crab	Herring	Herring	Shrimp	Shrimp	Squid	Squid	Silverside	Silverside
Order consumed	nc	nc	1	5	2	6	3	4	7	nc
Preference	9	9	1	5	2	6	3	4	7	9

Numbers in the top row indicate the order prey in which were consumed. Nc denotes prey not consumed. The bottom row gives the preference scores corresponding to the order in which prey were consumed.

scavenging. A difference, as indicated by a Bonferroni corrected P-value ($P < 0.01$), shows evidence of a shift in diet.

2 Results

Spiny dogfish and smooth-hounds consumed all prey items. There were no differences among individuals within a species for any of the variables investigated ($P > 0.05$); therefore, the mean values for prey preference for each species are discussed. Furthermore, it should be noted that this indicates there were no differences among individuals that were tested immediately following capture from the wild and those individuals that were held in captivity for six weeks. It is therefore likely that conditioning to prey items did not affect prey selection results.

2.1 Solitary scavenging

When scavenging alone, spiny dogfish prefer squid (2.9) more than herring (4.2), shrimp (5.1), or the remaining prey items ($F_{4, 84} = 29.086$, $P < 0.001$, Fig. 1A). Squid was selected first or second in almost half of the trials. Silversides (6.6) are rarely consumed and are often selected last (Fig. 1A). Crab (7.9) was eaten by only one dogfish; most individuals ignored this prey item. Spiny dogfish consumed (41.3%), rejected (30.3%) or chose not to consume (28.4%) prey equally, as predicted for a generalist feeder ($F_{2,50} = 3.085$, $P = 0.059$, Fig. 2A).
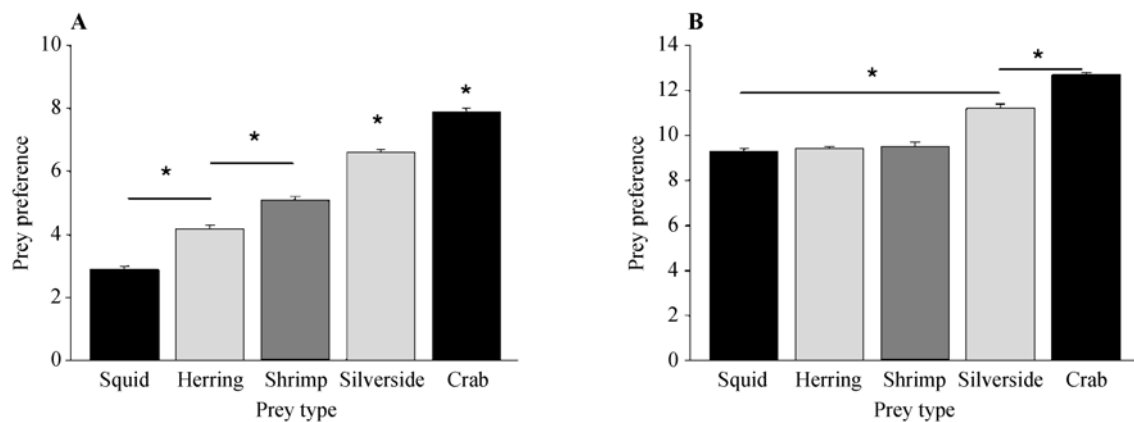
Fig. 1 Mean prey selection scores for spiny dogfish *Squalus acanthias*
A. Scavenging alone. B. In the presence of competition. Values closer to 1.0 indicate preference. Black bars represent similar preference values. An asterisk indicates differences between groups ($P < 0.05$). Results of Tukey test for solitary scavenging: squid < herring, shrimp < silversides, crab; for competitive scavenging: squid, herring, shrimp, silversides < silversides, crab.
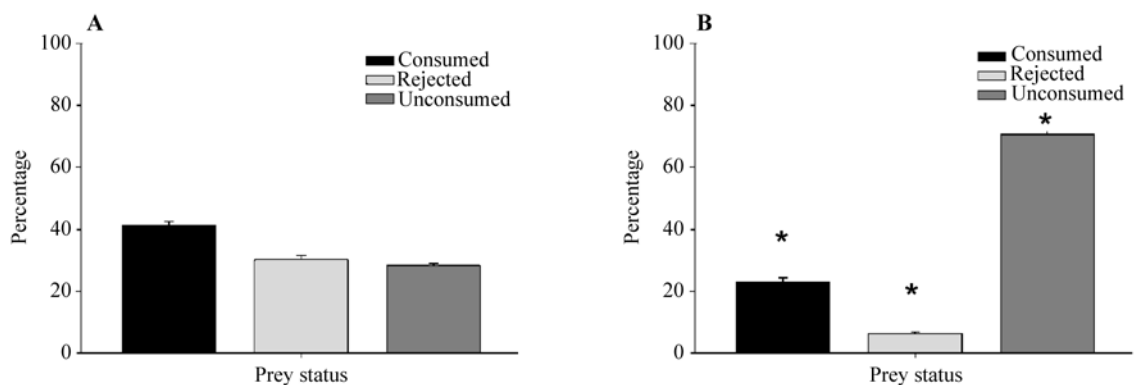
Fig. 2 Mean prey status percentages by behavioral selection for spiny dogfish *Squalus acanthias*
A. Scavenging alone. B. In the presence of competition. Percentage consumed equals the number of prey items consumed divided by the total number of items, irrespective of prey type. Percentage rejected equals the number of prey items taken but not eaten divided by the total number of items. Percentage unconsumed equals the number of prey items ignored divided by the total number of items. Black bars represent similar values. An asterisk indicates differences between groups ($P < 0.05$).

Smooth-hounds preferred herring (3.9) and squid (4.0) more than shrimp (5.2), silversides (6.6), or crabs (7.9) ($F_{4, 89}$ = 23.208, P < 0.001, Fig. 3A) when feeding alone. Herring was consumed as one of the first prey items in two-thirds of the trials. All individuals sampled crab, but this prey was frequently dropped in favor of another prey item. Half of the individuals in this part of the study consumed crab, but in 18 trials, it was selected first or second only twice. Those that did choose crab usually selected it as the fourth or fifth prey item and later in the trial would repeatedly pick up and then drop the second crab. Smooth-hounds consumed prey (43.4%) more than they rejected (26%) or did not consume prey (30%) ($F_{2,53}$ = 6.154, P = 0.005, Fig. 4A).

2.2 Competitive scavenging

When the two species were housed in the same tank, dogfish and smooth-hounds either maintained separate positions within the water column or circled separate areas at the bottom of the tank. The positions changed dependent on each individual (i.e., a dogfish may have swum at the bottom of the tank in one set of trials and a second dogfish may have always swum in the water column) and appeared irrespective of size (which was kept constant) or sex.

Spiny dogfish switched to a non-selective scavenging behavior when feeding in the presence of smooth-hounds. Squid (9.3), herring (9.4), shrimp (9.5), and silversides (11.2) were selected preferentially as compared to silversides and crab (12.7) ($F_{4,64}$ = 5.512, P = 0.001, Fig. 1B). The presence of smooth-hounds caused dogfish to select squid less than when scavenging alone and to include more crabs in the diet (*t*-test, *df* = 25, P < 0.01). The amount of herring, shrimp, or silversides did not shift (*t*-test, *df* = 25, P > 0.01).
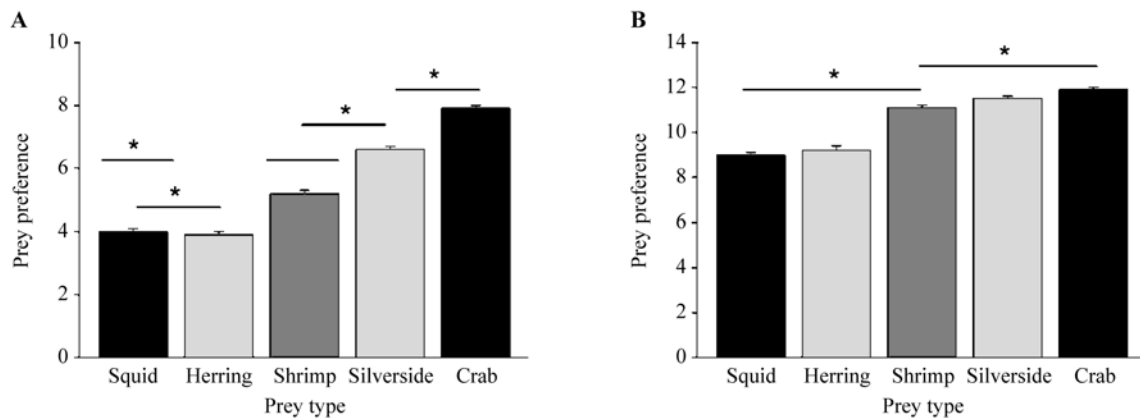
Fig. 3 Mean prey selection scores for smooth-hounds *Mustelus canis*
A. Scavenging alone. B. In the presence of competition. Values closer to 1.0 indicate preference. Black bars represent similar preference values. An asterisk indicates differences between groups based on square-root transformed data (P < 0.05). Results of Tukey test for solitary scavenging: herring, squid < squid, shrimp < shrimp, silversides < silversides, crab; for competitive scavenging: squid, herring, shrimp < shrimp, silversides, crab.
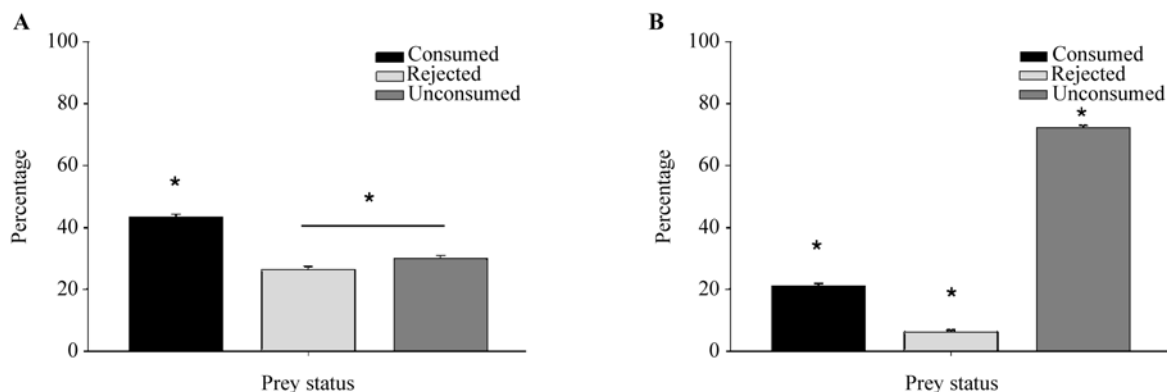
Fig. 4 Mean prey status percentages by behavioral selection for smooth-hounds *Mustelus canis*
A. Scavenging alone. B. In the presence of competition. Percentage consumed equals the number of prey items consumed divided by the total number of items, irrespective of prey type. Percentage rejected equals the number of prey items taken (but not eaten) divided by the total number of items. Percentage unconsumed equals the number of prey items ignored divided by the total number of items. Black bars represent similar values. An asterisk indicates differences between groups (P < 0.05).

Smooth-hounds chose a greater variety of prey items by selecting squid (9.0), herring (9.2), and shrimp (11.1) more than silversides (11.5) or crab (11.9) ($F_{4,64} = 4.395$, $P = 0.004$, Fig. 3B) when a competitor is present. The amount of herring, squid, shrimp, and silversides did not shift from solitary scavenging (t-test, $df = 25$, $P > 0.01$); however, smooth-hounds did include a greater number of crabs in the diet (t-test, $df = 25$, $P < 0.01$).

Both species consumed less prey (dogfish, 23.0%; smooth-hounds, 21.3%) when scavenging together than when scavenging alone. Also, when a competitor was present, neither species rejected many prey items (dogfish, 6.4%; smooth-hounds, 6.4%), signifying that if a prey item was chosen, it was usually consumed. The majority of prey was not consumed by either species (dogfish, 70.6%; smooth-hounds, 72.2%), possibly indicating a trade-off between foraging and defense against competitors (Figs. 2B, 4B).

3   Discussion

Performance tests can predict how an organism is able to utilize resources by relating studies of behavior and morphology with ecology (Wainwright, 1994; Reilly and Wainwright, 1994). These tests may provide a link between laboratory and field-based studies by measuring the ability of a predator to perform an ecological task (Lauder, 1995). For example, stomach contents have been used as a biased measure of predator capture success (Scharf et al., 1998), but coupled with laboratory studies, they may provide knowledge of how often a prey item is selected in the wild (Baremore et al., 2008). Optimal foraging theory is described as a measure of performance by which the predator maximizes the net energy yield per unit of feeding time, including the cost of pursuit, handling, and feeding (Schoener, 1971). Furthermore, predictions based on optimal foraging theory have been supported under semi-natural conditions using immobile prey (Sih and Christensen, 2001). The present study uses dead prey, thereby eliminating pursuit costs and minimizing handling time, two measures of performance that effect how a predator feeds. Therefore, in this study, it is likely that the sharks were scavenging to maximize energy gain.

Data from diet studies show that spiny dogfish are non-selective predators that feed on a variety of taxonomic prey items (Table 2). This strategy is beneficial because it enables these sharks to have a diverse diet and to select the most abundant prey item available within the surrounding area, which is advantageous when resources decline (Jensen, 1965; Holden, 1966;

Alonso et al., 2002). For example, in Argentinian waters, hake and shortfin squid are the two main fisheries; these two prey items frequently occur in the dogfish diet (Table 2) and are considered to be the most important items (index of relative importance; Alonso et al., 2002). In New Zealand, small crustaceans dominate the diet, and teleosts are less important (Table 2) due to the high availability of crustacean prey (Hanchet, 1991). Furthermore, a main fishery in British Columbia is herring (Jones and Geen, 1977), and these prey items appear most frequently in dogfish stomachs in this area (Table 2). In the present study, prey items were available in equal numbers so that chosen prey could be considered preferred prey. Spiny dogfish selected squid, herring, and shrimp more often than silversides or crab, similar to what is chosen in the wild (Table 2). Squid (21 KJ/g), herring (24 KJ/g), and shrimp (21 KJ/g) have greater energy content than green crabs (< 19 KJ/g) (Sidwell et al., 1974). Although the energy content of silversides (22 KJ/g)   (Sidwell et al., 1974) is high, silversides are smaller than the other prey items, making them less profitable. In addition to the low energy content of green crabs, the cost of extracting meat from the carapace of crab may be too high for spiny dogfish. Dogfish have a cutting type of dentition with pointed cusps that are directed laterally (Cappetta, 1987), which do not provide an appropriate tool for cracking a crab shell. Coupled with a head-shaking behavior, this type of dentition is ideal for shredding pieces of softer prey, like fish or squid (Moss, 1972; Wilga and Motta, 1998). The prey is held between the jaws, and the pointed cusps of the teeth slice through the prey with each lateral head-shake. Therefore, by choosing squid, herring, or shrimp as their preferential prey items, spiny dogfish are feeding on the prey that best matches their jaw morphology.

Dogfish showed a dietary shift in prey selection by scavenging on a greater variety of prey items while in the presence of smooth-hounds. When faced with competition, an optimal predator should not reduce its diet (MacArthur and Pianka, 1966). Although dogfish scavenge less on squid when competing with smooth-hounds, by including crabs in the diet, dogfish broadened their range of dietary items and fed optimally. Furthermore, during competition, dogfish scavenged whatever prey was within their search path and rejected few items (6.4%), as opposed to their method of pushing poor-quality prey out of the way when scavenging alone. The increased dietary breadth indicates that dogfish were no longer scavenging in a manner best suited to

their jaw morphology; however, because dogfish can modulate feeding behaviors (Wilga and Motta, 1998; Gerry et al., 2008), they were able to feed on a variety of items in this study.

In contrast to the range of dietary items of dogfish, smooth-hounds feed primarily on crustaceans in every geographic location (Table 2). Rock crabs (*Cancer* sp.) occur most frequently in smooth-hound stomachs, and in the northwest Atlantic they are considered the most important dietary item (72.45%, index of relative importance, Gelsleichter et al., 1999). Furthermore, rock crabs are the most abundant crustacean in Narragansett Bay in the summer months when smooth-hounds are present (GSO Fish Trawl, 2009[*]). Other species of *Mustelus* also have a diet dominated by crustaceans, but shore crabs (*Hemigrapsis* sp.) occur in the stomachs of

other species more often than do rock crabs (Table 2). Unlike this specialized diet, in the present study, smooth-hounds scavenged on herring and squid more than on shrimp, crab, or silversides. Smooth-hounds appear to be adept at turning and braking maneuvers (Gerry, personal observation), and this locomotor ability may aid these sharks when foraging for crabs in a benthic environment. Herring and squid are pelagic prey items that are capable of cruising and burst swimming. Therefore, it is probable that smooth-hounds scavenge on immobile pieces of herring and squid because they provide a greater energetic content than crabs. However, in the wild, smooth-hounds are better suited to maneuver in a benthic environment containing an abundance of crabs than to expend energy swimming after a fast-moving prey item.

Table 2   Summary of diet studies for spiny dogfish and smooth-hounds for several geographic locations

Spiny dogfish	Geographic location				
Stomach contents	Southern New England[1]	British Columbia[2]	New Zealand[3]	Argentina[4]	Britain[5]
Mollusks	36.7	2.9–5.4	5.4–15.5		
Cephalopods	22.4				
Squid	13.9	0.7–2.0	3.1–9.7	40.0*	9.3
Crustaceans	1.3	22.4–27.3	49.9–61.0*		
Cancer sp.	1.1		0.2–1.8		0.6
Shrimp		5.3–11.1			
Teleosts	55.8	51.2–57.3	13.9–15.5		
Hake (Merluccius sp.)	1.2	0.9–7.3		23.33	0.6
Herring (Clupea sp.)	1.9	15.6–23.0*			13.0
Sand eels (Ammodytes sp.)		0.7–2.3			42.2*
Unidentified	23.1*	18.0–18.2	7.1–9.9	15.83	6.2
Ctenophores		2.2–2.8	1.7–4.5	28.33	
Polychaetes		1.0–1.1	1.4–6.9	0.83	0.6
Smooth-hounds	Geographic location				
Stomach contents	Southern New England[1]	Northwest Atlantic[6]	Lower Hudson[7]	California[8]	California[9]	California[10]
Mollusks	0.7	39.06				
Cephalopods	0.7					
Squid				2.0		9.1
Clam pieces			41.2			
Crustaceans	89.6	90.63			91.7	90.9–100
Cancer sp.	68.8*	59.38*	5.9–81.3	35.0	54.2	50.0*
Callinectes		26.56				
Ovalipes sp.	9.5	26.56	66.6–81.3*			
Hemigrapsis				72.0*	87.5*	50.0*
Xanthid crab			17.6–31.2			
Shrimp		6.25	11.1–47.1	33.0		33.3–45.5
Teleosts	7.8	28.13		15.0	4.2	36.4
Polychaetes	0.8	7.81		26.0		

[1]Bowman et al., 2000. [2]Jones and Geen, 1997. [3]Hanchet, 1991. [4]Alonso et al., 2002. [5]Holden, 1966. [6]Gelsleichter et al., 1999. [7]Steimle et al., 2000. [8]Haeseker and Cech, 1993; *Mustelus henlei.* [9]Talent, 1982; *Mustelus californicus.* [10]Talent, 1982; *Mustelus henlei.*

All numbers are given as percentages of frequency of occurrence. An asterisk indicates most frequently occurring prey (of lowest taxonomic grouping) by region.

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[*] Graduate School of Oceanography (GSO) Fish Trawl Survey, 2009. University of Rhode Island.

When scavenging while competing with spiny dogfish, smooth-hounds increased their dietary breadth by feeding on squid, herring, and shrimp. More important, these sharks showed a dietary shift by including a greater number of crabs in their diet while competing than during solitary scavenging. Competition may cause a predator to shift behaviors, causing an increase or decrease in specialization (Futuyma and Moreno, 1988). In this study, competition caused smooth-hounds to scavenge their preferred natural prey of crabs, for which they have morphological and swimming specializations. Dietary specialists often have morphological structures that are adapted to the utilization of a particular resource, which should increase the handling efficiency of the predator, thus increasing fitness (Sanderson, 1990; Ferry-Graham et al., 2002). Smooth-hounds have low-cusped molariform teeth, which, coupled with a force-amplifying lever system, are characteristics indicative of a hard-prey specialist (Frazzetta, 1994; Summers, 2000; Gerry and Dean, 2005). This jaw morphology combined with swimming maneuverability provides smooth-hounds with the tools necessary to feed on a high number of low-energy crustaceans, instead of expending energy to feed on more profitable items at the expense of pursuit and handling costs.

Although the sharks in this study scavenge differently than what is indicated by their feeding behavior in the wild, this study provides an important link between jaw morphology and prey selection and reveals how prey resources may be distributed within a community. Spiny dogfish are pelagic predators that are well-suited to feeding on fishes and squid. However, their behavioral flexibility allows them to include a greater variety of prey items when preferred prey declines, which explains why they feed on the most abundant prey in an area. Smooth-hounds are capable of feeding on crustaceans, an item that other predators often take in only small quantities. This is especially important during competition because it enables smooth-hounds to maintain a level of fitness without decreasing their diet.

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