2008-06-23

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Recommended Citation

Ciaccio, Jennifer Louise, "The Effects of Maturation and Experience on the Predatory Efficiency of the Whitespotted Bambooshark, Chiloscyllium plagiosum" (2008). *Open Access Dissertations*. 126.
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THE EFFECTS OF MATURATION AND EXPERIENCE ON THE PREDATORY EFFICIENCY OF THE WHITESPOTTED BAMBOOSHARK, *CHILOSCYLLIUM PLAGIOSUM*

By

Jennifer Louise Ciaccio

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

August 2008

UNIVERSITY OF MIAMI

A thesis submitted in partial fulfillment of
the requirements for the degree of
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THE EFFECTS OF MATURATION AND EXPERIENCE ON THE PREDATORY EFFICIENCY OF THE WHITESPOTTED BAMBOOSHARK, *CHILOSCYLLIUM PLAGIOSUM*

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CIACCIO, JENNIFER LOUISE (Ph.D., Biology)
The Effects of Maturation and Experience on the (August 2008)
Predatory Efficiency of the Whitespotted Bambooshark,
Chiloscyllium plagiosum.

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Steven Green.
No. of pages in text. (126)

Foraging presents a significant challenge for neonatal predators. Both physical maturation and predatory experience may improve predatory abilities. To tease apart which improvements in predatory abilities were due to increased maturation and which to increased experience, several experiments that isolated the effects of maturation and experience were conducted. Individual whitespotted bamboosharks, *Chiloscyllium plagiosum*, improved predatory efficiency with both maturation and experience. Physical maturation, when isolated from experience, improved predatory efficiency of naïve sharks foraging on shrimp, an elusive prey, but not of sharks foraging on worms, a non-elusive prey. Predatory experience, when isolated from maturation, improved predatory efficiency of sharks foraging on worms but not of sharks foraging on shrimp. Both maturation and experience are important in the development of whitespotted bamboosharks' predatory abilities and may influence the type of prey they can exploit.

To determine whether whitespotted bamboosharksare able to retain the ability to capture and eat prey after a period of prey absence, sharks that had 20 days of foraging experience were denied access to live prey for 18 days, after which they were re-exposed to live prey. Predatory efficiency of sharks did not decrease during the 18 day prey-absence period. After sharks were re-exposed to live prey, their predatory efficiency was similar to that of sharks of the same age with equivalent experience but no prey-absence period, but was higher than that of naïve sharks. Whitespotted bambooshark retain the ability to catch and consume prey after a short period of prey absence. This retention may improve their ability to forage on prey that is spatially or temporally patchy.

To determine whether experience with one prey type affects the whitespotted bambooshark's ability to forage on novel prey, sharks that had 20 days of experience foraging on one type of prey (either worms or shrimp) were given foraging trials with the other prey. Experience with one prey improved sharks abilities to forage on novel; sharks foraging on novel prey were as efficient as sharks that had foraged on that prey for 20 days. Whitespotted bambooshark can maintain or easily modify many predatory skills when foraging on novel prey.

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GENERAL INTRODUCTION

Foraging skills are among the most crucial sets of behaviors a young predator can acquire, as the inability to find, catch, and consume prey will lead to increased mortality risk (Blaxter and Ehrlich, 1974; May, 1974; Rice *et al*., 1987). Many factors may influence the acquisition of predatory skills. Physical maturation may cause predatory behaviors to change due to improvement in neuromuscular coordination and increased sensory ability (in cichlid fish, *Cichlasoma managuense* - Meyer, 1986; in black-footed ferrets, *Mustela nigripes* - Vargas and Anderson, 1999) or morphological and scaling changes (in cichlid fish - Meyer, 1987; in swellsharks - Ferry-Graham, 1998a). Experience may allow a predator to hone existing skills and develop new ones through learning (in cats, *Felis silvestris* - Caro, 1980 and Leyhausen, 1973; in garter snakes, *Thamnophis sirtalis* - Krause and Burghardt, 2001 and Burghardt and Krause, 1999; in fifteen-spined sticklebacks, *Spinachia spinachia* - Croy and Hughes, 1991a, b; in black-footed ferrets, *Mustela nigripes* - Vargas and Anderson, 1999). Several factors may cause changes in prey preferences, including changes in prey availability, changes in the relative sizes of predator and prey (in whelks, *Nucella emarginata* - Gosselin and Chia, 1996; in iguanas, *Ctenosaura pectinata* - Cooper and Lemos-Espinal, 2001), ontogenetic changes (Grossman *et al*., 1980; Keely and Grant, 2001; Jackson *et al*., 2004), and experience with prey (in lynx spiders, *Oxyopes salticus* - Punzo, 2002a, b; in barramundi, *Lates calcarifer* (Actinopterygii: Perciformes)- Crossland, 2001). Many of these factors may act in concert to improve predatory behaviors and increase efficiency.

Predators that can forage efficiently on a species after an absence of that prey from their diet or after feeding on another species would have an advantage over those that cannot. Garter snakes retain the ability to feed efficiently on their initial prey after a period of feeding on alternate prey (Krause and Burghardt, 2001). Foraging efficiency of fifteen-spined sticklebacks decreases during periods of prey absence and is quickly reduced to naïve levels (Croy and Hughes, 1991a). In addition, experience with more than one prey species at a time may interfere with the improvement of predatory skills. Garter snakes and sticklebacks that were fed alternately on different prey did not increase foraging efficiency as quickly as those that were fed either one alone (Krause and Burghardt, 2001; Croy and Hughes, 1991a).

Generalist predators may have an increased burden when learning predatory behaviors because, while they have more prey species available to them than a specialist does, the most successful foraging strategy may be different for each type of prey (Morse, 1980). In order to overcome this difficulty, a predator may be able to develop a foraging strategy that is relatively stereotyped and effective for many prey species. This ability would be enhanced if a predator could easily modify the strategy to each prey species.

Experience and learning influence foraging behaviors of many groups of animals, as many foragers rely on experience and memory to find suitable foods and handle them efficiently (Kamil *et al.*, 1987; Kamil and Sargent, 1981). Relatively few studies, however, have examined the role of learning in active hunting of elusive prey (Burghardt and Krause, 1999; Caro, 1980; Croy and Hughes, 1991a, b; Krause and Burghardt, 2001; Leyhausen, 1973; Polsky, 1977; Vargas and Anderson, 1999). In addition, little is known of the development of predatory behaviors, as many of the studies have been performed on adult or sub-adult organisms. Many predatory skills are acquired shortly after birth or hatching, a time when experience may be most important to developing a predator's repertoire.

Some of the most intensive studies on the ontogeny of predation have been performed on domestic cats (Caro, 1980; Leyhausen, 1973). The social behavior of cats, however, introduces many confounding factors when studying predation. Predatory behaviors may be learned from their mother before kittens are weaned, prior to independent foraging. In addition, predatory behaviors can be learned and honed during play with siblings.

To separate the roles of maturation and predatory experience on the development of predatory behavior in a vertebrate, an intensive study of a single species is needed. The effects of experience on predation should be examined using naïve individuals with limited relevant experience. To have truly naïve individuals, a study species should have precocious young that receive no post-natal parental care. The species should also have very low levels of sociality, without social learning or play. In addition, neonates should be morphologically similar to older individuals allowing them to feed on the same types of prey in the same manner. Such a predator species should also feed on prey species that are behaviorally diverse so that it may need to capture and consume them in different ways. Finally, the predator species should have the ability to learn or improve predatory behaviors through experience. The Indo-Pacific whitespotted bambooshark, *Chiloscyllium plagiosum*, meets all of these requirements, making it an ideal species to study the development of predatory behavior.

This dissertation research examines factors affecting the development of predation in whitespotted bamboosharks. In Chapter One, the effects of maturation and experience on the development of predatory behavior of hatchling whitespotted bamboosharks are examined. Experiments were designed to disentangle the degree to which improved predatory efficiency is a product of experience or is a consequence of a general increase in sensory abilities and motor skills. In Chapter Two, foraging skill retention is examined by re-introducing live prey to sharks following a period during which access to live prey was denied. In Chapter Three, the effects of prior predatory experience on the ability of sharks to forage on novel prey are examined. These experiments taken together form a comprehensive study of the development of predation in whitespotted bamboosharks.

Study Species

Whitespotted bamboosharks, *Chiloscyllium plagiosum*, are small benthic reef sharks that inhabit near-shore areas of the Indo-Pacific Ocean between India and Japan (Compagno, 2001). Adults can reach sizes of 83 cm (males) and 95 cm (females). Females are oviparous, laying 2 eggs every 6-7 days. Precocious neonates (16.6 cm mean total length, 14.1g mean mass) hatch after 116-144 days (Tullis and Peterson, 2000). Because neonates hatch from eggs, the exact age of the hatchling sharks can be known.

Although little is know of their natural foraging habits, adult whitespotted bamboosharks feed mainly on benthic invertebrates, especially crustaceans. Kinematic studies have shown that, while hatchlings use a combination of ram-feeding and suction-feeding (Lowry and Motta, 2007a), adults primarily use suction feeding (Wu, 1993).

Care and Housing of Sharks

Filtered fresh seawater was obtained from the University of Miami's Rosenstiel School of Marine and Atmospheric Sciences (RSMAS) hatchery facility. The water was stored in 18-gallon plastic tanks until use. If fresh seawater was unobtainable, salt water was made using Instant Ocean® sea salt.

Eggs at varying stages of development were obtained from SeaWorld, Orlando between April and September 2005 and between May and November 2006. Eggs were housed in a 20-gallon glass aquarium and hatchling sharks were housed in two 22-gallon cylindrical plastic live bait tanks, each with a Cascade® 200 Filter (700 liters/hour), a submersible heater with a thermostat set at 25ºC and a 20 gallon aquarium aerator with an aerator stone attached. Filter cartridges with activated carbon were checked weekly and changed at least monthly or as needed. Salinity and ammonia levels were checked daily and adjusted as needed. Salinity was adjusted to a specific gravity between 1.020 and 1.024 by adding Instant Ocean® sea salt or distilled water that had stood at least 24 hours. Ammonia levels were kept below 0.25 ppm by treating the water with Kordon® Amquel as directed. Fecal material was removed daily by hand-siphoning it out of the tank. There were never more than 30 eggs or 15 sharks per tank. Eggs were checked daily for mortality. Dead eggs were immediately removed. Upon hatching sharks were sexed, assigned a number, systematically placed into experimental groups and moved from the egg housing tank to the shark housing tank. All methods and procedures were approved by University of Miami IACUC (#A-3224-01).

On days when sharks were not participating in experimental foraging trials, they were fed individually in small plastic tanks, eliminating the possibility that competition between sharks for food might later affect the foraging trials. The tanks (33cm x 19cm x 11cm) were filled to approximately 4cm depth with water from the housing tanks. Sharks were fed small cubes of fresh tuna (1-2 mm /side) *ad libitum* for 5 minutes to prevent overfeeding. Up to 3 tuna cubes were manually placed directly in front of the sharks. New pieces were added after the shark ate the previous pieces, after approximately 30 seconds of not eating (sharks would not eat old pieces) or after sharks moved to a different section of the tank. After the shark was removed, all remaining tuna pieces were removed using a fine mesh net. Water was changed after three or four sharks had fed or when the water temperature dropped.

Sharks were moved between the housing tank and feeding or experimental tanks using a small plastic transport container (18cm x 13cm x 6cm) with a lid to prevent the shark from leaping out. In order to remove a shark from a tank, the transport container was lowered into the tank. The shark was then hand-corralled into the container. The container was raised slightly above the water and the lid was placed on. The amount of water in the container varied with the depth of the tank water, but there was always enough so that the shark was completely immersed. The shark was never in the transport container for longer than 2 minutes. In order to release the shark into the new tank, the container was placed on its side as deep as possible in the tank. The lid was then removed, releasing both the shark and any water that was in the container.

Sharks were weighed weekly in a small plastic tank (14cm x 14cm x 10cm) with approximately 2cm of water. Sharks were brought to the scale in the transport container, hand-lifted out the container and placed in the weighing tank, which had been tared with the water in it. This method minimized the time the shark was out of the water. After weighing was complete, the shark was lifted out of the weighing tank and gently placed in the transport tank. If necessary, water was added to the weighing tank.

Live Prey

Two types of live prey, sand worms (*Nereis virens*) and ghost shrimp (*Palaeomonetes* sp.), were used during experiments to simulate non-elusive and elusive prey. These two prey types are found in the whitespotted bambooshark's natural diet and differ a great deal in morphology and behavior. Worms often remain motionless for several minutes at a time. When they do move, they crawl fairly slowly or, occasionally, they swim for short distances before settling on the bottom. Worms do not flee or noticeably change their behavior when approached by a shark. In contrast, shrimp swim or tail-flip until they come in contact with the wall of the tank in which they are placed. Generally, they then swim or walk around the perimeter of the tank, occasionally remaining stationary for short periods. When approached by a shark, shrimp typically either swim up in the water column or tail-flip away from the shark. Shrimp may also walk backwards away from the shark. Occasionally, shrimp do not change behavior when approached by a shark.

Because of these differences in prey elusivity, sharks foraging on worms may behave differently from sharks foraging on shrimp. Generally, predators modulate both their attack and capture behaviors when presented with different types of prey (Burghardt and Krause, 1999; Crompton *et al*., 1977; Croy and Hughes, 1991a, b; Deban, 1997; Elshoud-Oldenhave and Osse, 1976; Ferry-Graham *et al*., 2001; Hiiemae and Crompton, 1985; Krause and Burghardt, 2001; Lauder, 1981; Liem, 1979, 1980; Nemeth, 1997a, b;

Norton, 1991; Porter and Motta, 2004; Sanderson, 1988; Van Wassenbergh *et al*., 2007; Vineyard, 1982; Wainwright, 1989; Wainwright and Lauder, 1986; Wainwright and Turingan, 1993). Additionally, elusive prey test the limits of a predator's abilities. Attacks on elusive prey such as shrimp generally must be faster and initiated from a greater distance than attacks on non-elusive prey such as worms (Ferry-Graham *et al*., 2001; Norton, 1991; Nemeth, 1997a; van Leeuwen and Muller, 1984). Suction-feeding fish may also modulate the amount of suction produced in response to the elusiveness of prey (Elshoud-Oldenhave and Osse, 1979; Liem, 1979; Lauder, 1981; Wainwright, 1986; Wainwright and Lauder, 1986).

Sand worms

Sand worms were obtained from SeaBait Maine, Ltd. The worms were shipped overnight in airtight bags with a density of 2 dozen worms per bag. The worms were placed in a plastic tank (33cm x 19cm x 11cm) filled with approximately 4 cm of sea water and approximately 2 cm of gravel lining the bottom. The worms were fed flake fish food daily. Water was aerated using a 10-gallon aquarium aerator with an aerator stone and was changed weekly.

Shrimp

Small ghost shrimp were obtained as needed from various aquarium stores. They were maintained in a 2-gallon tank with a built-in filtration/aeration system. The bottom of the tank was covered with approximately 2 cm of gravel. Shrimp were fed flake fish food daily and the water was changed as needed.

Experimental Design

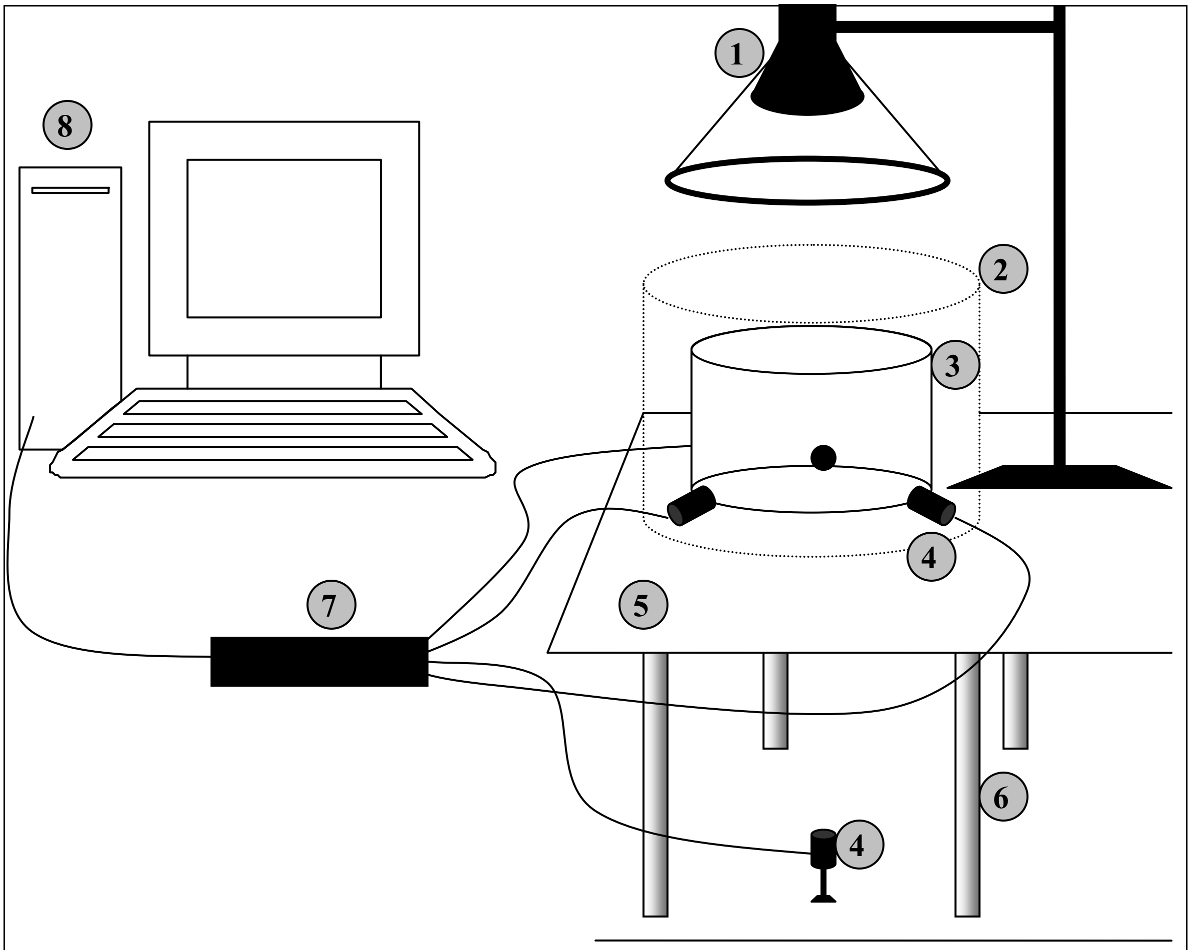
Upon hatching, sharks were systematically assigned into one of six experimental groups so that each group had an equal number of sharks (or as close as possible) at any given time. If a shark was removed from the study, it was replaced by the next shark to hatch. The six experimental groups differed in the age during which they were exposed to live prey and the type of live prey to which they were exposed (Table 1). This arrangement allowed comparisons between groups of sharks of the same experience level but different ages and between groups of sharks of the same age but different experience levels using the same groups of sharks for the comparisons.

Table 1: Experimental groups, age at prey introduction and prey type. * If a shark did not catch prey on day 40, trials continued on subsequent days until the shark caught at least one prey animal.

Group	Age of shark when exposed to live prey (days)	Prey type	Subsequent procedures
A	2-21	Worm	Fed on tuna cubes from days 22-39 and re-exposed to worms on day 40
B	21-40	Worm	Switched to shrimp on day 41
C	40*	Worm	
D	2-21	Shrimp	Fed on tuna cubes from days 22-39 and re-exposed to worms on day 40
E	21-40	Shrimp	Switched to worm on day 41
F	40*	Shrimp	

Foraging Trials

Foraging trials were conducted during the periods of prey exposure indicated in Table 1. Video-recordings of sharks foraging on live prey were obtained using the experimental setup shown in Figure 1. After a shark was placed in the foraging tank, it was allowed to acclimate for at least 20 minutes. During the shark's acclimation period, three prey animals that would be used for the trials were weighed to ensure that it was 1-2% of the shark's last recorded body weight if the prey was a worm or 0.5-1.5% of the shark's body weight if the prey was a shrimp. After being weighed, prey animals were kept in small Petri dishes of water from their housing tank until use. A small holding arena (an inverted plastic 16-ounce cup with the bottom cut out) was then placed inside the foraging tank in order to contain the prey animal until the start of the trial. A single prey animal was placed in the holding arena and allowed to acclimate for at least 2 minutes and no more than 5 minutes. The foraging trial began when the holding arena was removed by hand from the foraging tank, allowing the prey animal to move freely in the tank. The holding arena was removed from the tank without regard to the position of the shark. The trial ended when the shark had eaten the prey animal and began searching again or after 15 minutes had expired. If the prey animal was not eaten, it was removed from the tank and not used again. Each shark was given three consecutive foraging trials per day.



1 – Fluorescent lamp with 25-watt fluorescent bulb. Lamp is clamped to a ring stand.
2 – White nylon filter.
3 – Clear plastic foraging tank (33 cm diameter, 20 cm height) surrounded by a white paper cylinder that shielded the observer from the shark. The foraging tank was filled to a 4 cm depth with water from the shark's housing tank.
4 – Black and white waterproof bullet camera: 3 cameras mounted to the sides of the tank 120^o from each other, one mounted below.
5 – Clear Plexiglas sheet.
6 – Aluminum glass-topped table with glass removed.
7 – Quad processor to merge synchronous video from the four cameras into a single video feed.
8 – Computer to digitize and store the video.

Figure 1: Experimental set-up used to video-record foraging trials.

Behavioral Scoring

Digital video (30 frames/second) of the foraging trials were recorded using Roxio® Easy Media Creator 7.5 and were scored for the frequency and duration of several behaviors (Table 2) using Noldus® Observer v5.0 software. The videos were initially observed at normal speed (30 frames/second). When the shark's behavior changed, the video was again viewed at slower speeds as needed. The final determination of when a behavior began or ended was made as the video was reviewed frame-by-frame.

Table 2: Descriptions of discrete behaviors scored during foraging trial.

Behavior	Description
Not searching	swimming in the water column without mouth or snout in contact with bottom or not moving
Searching	swimming or crawling on its fins, with mouth or snout in contact with bottom
Contacting	shark touches prey with underside of snout or mouth
Attacking	changing direction and/or speed toward prey while opening mouth
Ambush-attack	shark does not swim or crawl prior to attacking prey, moving only its head toward prey
Pin-attack	shark positions its mouth directly above prey and moves its head downward while opening its mouth; shark's pectoral fins and tail are in contact with the bottom at the start of the attack
Lunge-attack	shark's head and body are in line with prey during attack and move toward prey as mouth opens
Capture	shark closes mouth on prey
Transporting	swallowing or repositioning prey in its mouth until the shark begins to search again

Shark behavior

Naïve sharks behave similarly whether foraging on shrimp or worms. Initially, naïve sharks remain stationary with their heads raised off the bottom for several minutes; many do not move during an entire trial. Often, while the shark is immobile, it is approached by the prey. When the prey moves near the shark's mouth, the shark employs an ambush-attack by lowering its head toward the prey and opening its mouth. If the prey does not approach the shark, the shark usually begins to move within a few minutes after prey is released. This movement consists of short bursts of swimming or crawling. The shark changes direction between bursts of movement and generally keeps its mouth or snout in contact with the substrate. This pattern of movement is apparently involved in searching for prey. If the shark encounters a worm, it attacks the worm and always captures it. If the shark encounters a shrimp, it attacks the shrimp, but the attack may not result in capture due to the shrimp's anti-predator behaviors. If the shrimp escapes, the shark typically resumes searching.

Searching sharks generally use two types of attacks, a pin-attack and a lunge-attack. In a pin-attack, the shark positions its mouth directly above the dorsal side of the prey and opens its mouth while moving its head downward. The shark's pectoral fins and tail are in contact with the substrate during this type of attack. Pin-attacks are used when attacking either worms or shrimp. In a lunge-attack, the shark's head and body are in line with the prey. The shark opens its mouth while moving toward the prey, attacking it from the side. Generally, lunge-attacks are used only when attacking shrimp.

Once the shark captures prey, it either repositions the prey in its mouth or transports it using one or more transport bouts that likely involve suction. During a transport bout (Figure 2), the shark raises itself on its pectoral fins, then opens its mouth and either takes in or expels water while raising its pectoral fins off the bottom. It then closes its mouth and settles back into its starting position. The shark may repeat these behaviors several times until the prey is completely swallowed. High-speed video recording would be required for a more detailed analysis of these behaviors.

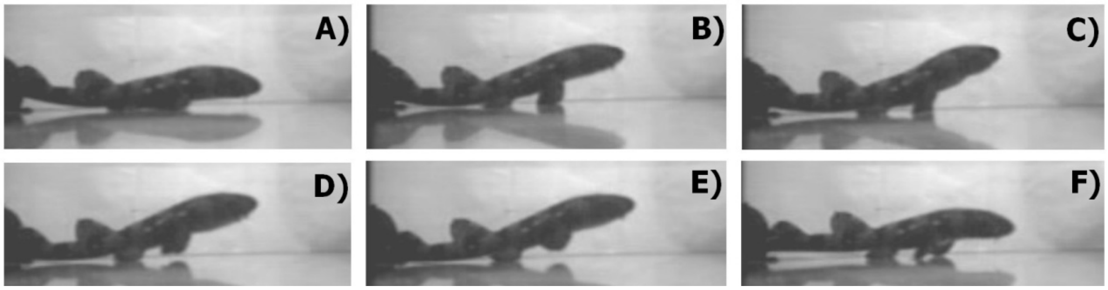


Figure 2. A transport bout. A) starting position, B) raising onto its pectoral fins, C) opening mouth and taking in or expelling water, D) closing mouth and raising fins off bottom, E) settling back, F) starting position. This sequence lasted 0.67 seconds.

After twenty days of foraging only on worms, sharks develop some predatory behaviors that are different from those of sharks that had foraged only on shrimp. The typical shark that has foraged on worms searches for prey by continually crawling on its pectoral and anal fins or slowly swimming with its fins in contact with the bottom, making seemingly random turns in the center of the foraging tank (Figure 3A – central searching). While moving, it keeps its snout in contact with the bottom, sweeping its head back and forth. When the shark encounters a worm, it positions its mouth on the dorsal side of the worm and then captures it, ingesting the worm in a single transport bout.

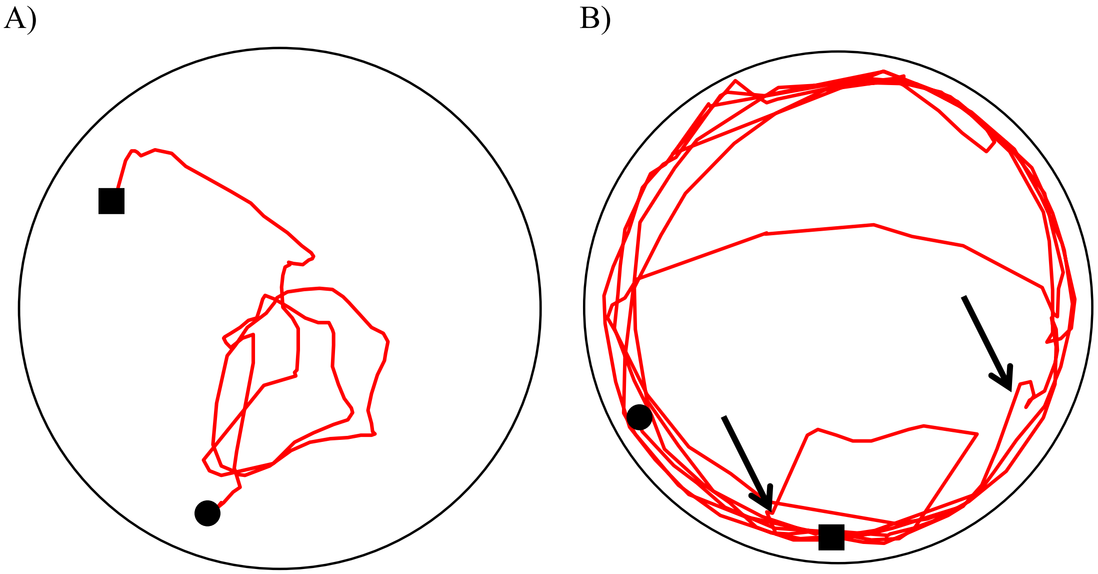


Figure 3. Examples of shark foraging paths from the start of the foraging trial until prey-capture. A) a representative path from a worm-fed shark foraging on a worm with central searching behavior. B) a representative path from a shrimp-fed shark foraging on a shrimp with perimeter searching behavior. Squares represent a shark's starting point and circles represent where a shark captured the prey. Arrows indicate where the shrimp-fed shark encountered but did not capture the shrimp. Paths were created using Noldus ® Ethovision 3.1 from videos of sharks searching for prey in foraging tanks.

In contrast, the behaviors of sharks that have foraged on shrimp for twenty days are much more variable. The typical shark searches for prey by swimming rapidly along the bottom or just above it, following the perimeter of the tank and occasionally making 180° turns or crossing the center of the tank (Figure 3B – perimeter searching). While moving, the shark makes limited lateral movements of its head and either keeps its barbels in contact with the bottom or periodically touches its snout to the bottom. When the shark encounters a shrimp, its behavior becomes very variable in response to the shrimp's escape behavior. The shark may immediately attack the shrimp, either lunging directly at the shrimp while swimming (lunge-attack) or stopping and positioning its mouth above the shrimp (pin-attack) prior to ingestion. Alternatively, the shark may follow the shrimp, matching the shrimp's speed and direction before attacking the shrimp. If the shark does not successfully capture the shrimp, it may continue to follow the shrimp for a few seconds, attacking it again or it may search the immediate area by slowly crawling around with its mouth on the bottom (similar to a shark searching for worms) for a few seconds before swimming around the tank perimeter again. After capturing the shrimp, the shark is typically unable to swallow the shrimp completely in a single transport bout. If the shark must reposition the shrimp in its mouth for transporting, it kills or incapacitates the shrimp before spitting it out and ingesting it again. Even if the shark does not reposition the shrimp, it generally performs several transport bouts.

Statistics

Statistical analysis will be discussed in detail in the appropriate chapters. Because sample sizes are small and the data are not normally distributed, non-parametric statistics are used throughout the study. Wilcoxon matched pairs signed ranks tests are used when comparing two trials of the same sharks. Mann-Whitney U tests are used when comparing two groups of sharks of the same age or experience level. Kruskal-Wallis tests are used when comparing three groups of sharks of the same experience level. Additional methods are described in the chapters that follow.

CHAPTER ONE:

The effects of physical maturation and predatory experience on the predatory efficiency of the whitespotted bambooshark

Background

Foraging presents a considerable challenge for neonatal predators. If they are unable to forage successfully soon after endogenous feeding has ended, they are subject to starvation and increased predation risk. Postnatal feeding requires that neonates be able to perform effectively several tasks (Curio, 1976). First, they must be able to find and recognize edible prey. Second, they must be able to capture prey despite anti-predator behaviors that the prey uses. Finally, they must be able to handle prey so that it can be consumed. Some skills necessary to perform these tasks may be present at birth, at least at a rudimentary level; otherwise, they must be quickly developed. Predatory abilities may be improved by increases in physical maturation of the predator, experience with prey, or a combination of these factors.

Physical maturation may cause predatory abilities to change due to improvement in neuromuscular coordination, to increased sensory ability, or to morphological and scaling changes. Older inexperienced black-footed ferrets, *Mustela nigripes,* are more likely to kill successfully than younger ones, probably due to increased motor skills and sensory abilities (Vargas and Anderson, 1999). Central American cichlid fish, *Cichlasoma managuense*, increase foraging efficiency with increased size, perhaps due to increased eye size and therefore visual acuity (Meyer, 1986). In addition, foraging on only one prey type causes changes in head and jaw morphology, affecting the types of prey that fish can utilize as adults (Meyer, 1987). Simply increasing size can greatly affect predatory abilities. Unlike adults, hatchling swellsharks, *Cephaloscyllium ventriosum*, rely on ram feeding rather than suction feeding. Although hatchlings produce the same kinematic behaviors necessary for suction feeding as larger sharks, they are unable to produce the force necessary to overcome the inertia of the prey (Ferry-Graham, 1998a).

Experience may allow a predator to hone existing skills and develop new ones through learning. The influences of experience and learning on foraging behaviors have been studied for many groups of animals (reviews: Kamil *et al*., 1987; Kamil and Sargent, 1981) and for several predators. Neonatal garter snakes, *Thamnophis sirtalis*, handle and swallow their prey more quickly with increased experience (Krause and Burghardt, 2001; Burghardt and Krause, 1999). Similarly, fifteen-spined sticklebacks, *Spinachia spinachia*, increase overall foraging efficiency after experience with a single prey species, increasing the frequency of some behaviors, such as head-on attacks on prey items, while decreasing the frequency of other behaviors, such as spitting out prey for repositioning (Croy and Hughes, 1991a). Additionally, predators may be born with certain essential predatory skills that are improved or changed with increased experience. While domestic cats, *Felis silvestris catus*, typically kill their prey with a dorsally oriented bite to the neck regardless of prior experience, other predatory behaviors that allow felids to effectively capture and position prey are learned and honed through experience (Leyhausen, 1973). Kittens that have experience with live mice or live birds become more efficient and successful predators than kittens with no prior experience with live prey (Caro, 1980). Similarly, black-footed ferrets, *Mustela nigripes*, without prior experience nape-bite hamsters to kill them; ferrets with experience capturing and handling live hamsters, however, are more likely to kill successfully than ferrets that were fed dead hamsters (Vargas and Anderson, 1999).

Both experience and maturation can increase foraging efficiency in predators but the relative contribution of each has not been adequately examined. Many studies do not control for the effect of age or size on predatory behaviors. A study of the effects of both experience and maturation on predatory behavior of a single species is needed. The effects of experience on predation should be examined using naïve individuals, so a study species should have precocious young that receive no post-natal parental care. The species should have little opportunity outside the experimental conditions to learn or practice skills. In addition, neonates should be morphologically similar to older individuals allowing them to feed on the same types of prey in the same manner. The whitespotted bambooshark, *Chiloscyllium plagiosum*, satisfies all of these requirements and is therefore an excellent study species.

The study reported in this chapter examines the roles that experience and maturation play in the ontogeny of predatory behavior of neonatal whitespotted bamboosharks, *Chiloscyllium plagiosum*. Experiments were designed to disentangle the degree to which improved predatory efficiency is a product of experience or is a consequence of a general increase in sensory abilities and motor skills that occur during maturation. They do so by examining the effects of increases in both maturation and experience together and individually. In addition, these experiments taken together form a comprehensive study of the ontogeny of predation in whitespotted bamboosharks.

Methods

Experimental Design

To determine the effects of physical maturation and experience with live prey on the predatory efficiency of whitespotted bamboosharks, sharks of three different ages were given foraging experience with live prey, either sand worms or ghost shrimp (Figure 1.1). Ten naïve "younger" sharks (A), after being fed small cubes of fresh tuna one day after hatching, were given foraging experience with live worms from 2 days old until 21 days old. Sharks were given three foraging trials each day with one live worm per trial. Each trial lasted until the shark had completely swallowed the worm but was ended after 15 minutes if the shark failed to capture prey within that time. Nine naïve "older" sharks (B) were fed tuna cubes until 21 days old, when they were given their first day of foraging trials with live worms. Older sharks were given foraging experience from 21 days old until 40 days old. Nine naïve "oldest" sharks (C) were fed tuna cubes until 40 days old, when they were given their only day of foraging trials with live worms. One younger shark and one older shark received less than 20 days of foraging trials due to temporary inabilities of the supplier to ship live worms and were therefore not included in some comparisons.

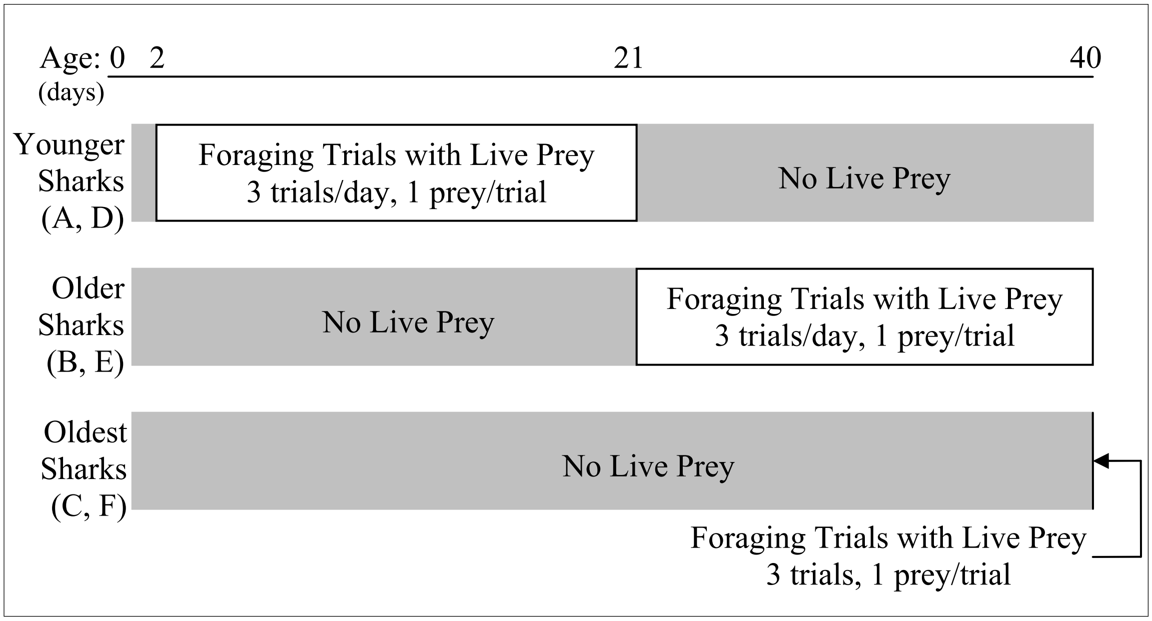


Figure 1.1. Overall experimental design to determine the effects of physical maturation and experience with live prey, both in concert and alone, on predatory efficiency of whitespotted bamboosharks. Gray areas represent days when sharks were fed small cubes of fresh tuna. Letters A through F indicate sets of sharks included in the design.

The same design using live shrimp instead of live worms in all trials was used to compare different sets of younger, older and oldest sharks. Eleven younger sharks (D), eleven older sharks (E) and eight oldest sharks (F) were given foraging trials with live shrimp. One older shark received less than 20 days of foraging trials due to a temporary inability of the supplier to ship live shrimp and one older shark died before it was 40 days old. These sharks were therefore not included in some comparisons.

The same overall design and sets of sharks (labeled A through F) were used for all the following comparisons to determine effects of increases in both maturation and experience, of maturation alone, and of experience alone. All foraging trials were video-recorded and scored using the methods described in the general introduction of this dissertation (pages 9-12).

Maturation and Experience Together

To determine whether predatory efficiency of whitespotted bamboosharks improves with increases in both maturation and experience, predatory efficiencies of nine naïve younger sharks were compared to their predatory efficiencies after 19 days of predatory experience, as were predatory efficiencies of eight naïve older sharks (B) (Figure 1.2).

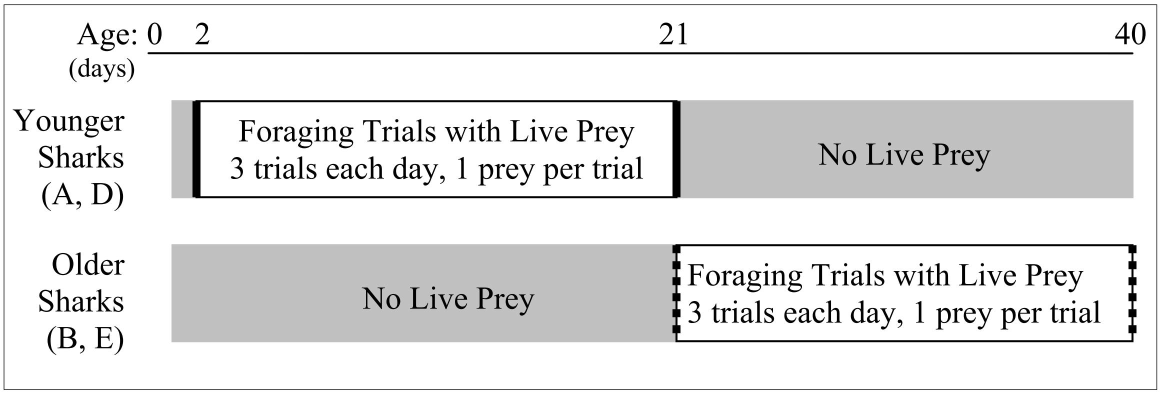


Figure 1.2. Experimental design to determine the effects of increases in both maturation and experience. The first foraging trials of naïve sharks were compared to their last foraging trials after 19 days of experience foraging on live prey. Gray areas represent days when sharks were fed small cubes of fresh tuna. Solid vertical bars represent the foraging trials used for comparisons between naïve and experienced younger sharks. Broken vertical bars represent the foraging trials used for comparisons between naïve and experienced older sharks. Letters A through E indicate sets of sharks included in the design.

The same design using live shrimp instead of live worms in all trials was used to compare different sets of younger and older sharks. Predatory efficiencies of eleven naïve younger sharks (D) and nine naïve older sharks (E) were compared to their predatory efficiencies after 19 days of predatory experience.

Maturation Alone

To determine the effects of physical maturation alone on predatory efficiency of whitespotted bamboosharks, predatory efficiencies of equally experienced sharks of different ages were compared (Figure 1.3). Predatory efficiencies of ten naïve younger sharks (A), nine naïve older sharks (B), and nine naïve oldest sharks (C) were compared. To determine whether maturation alone improves predatory efficiencies of experienced sharks, predatory efficiencies of younger and older sharks were compared after 19 days of foraging trials. One younger shark and one older shark did not receive 20 days of foraging trials due to temporary inabilities of the supplier to ship live worms and were therefore not included as experienced sharks.

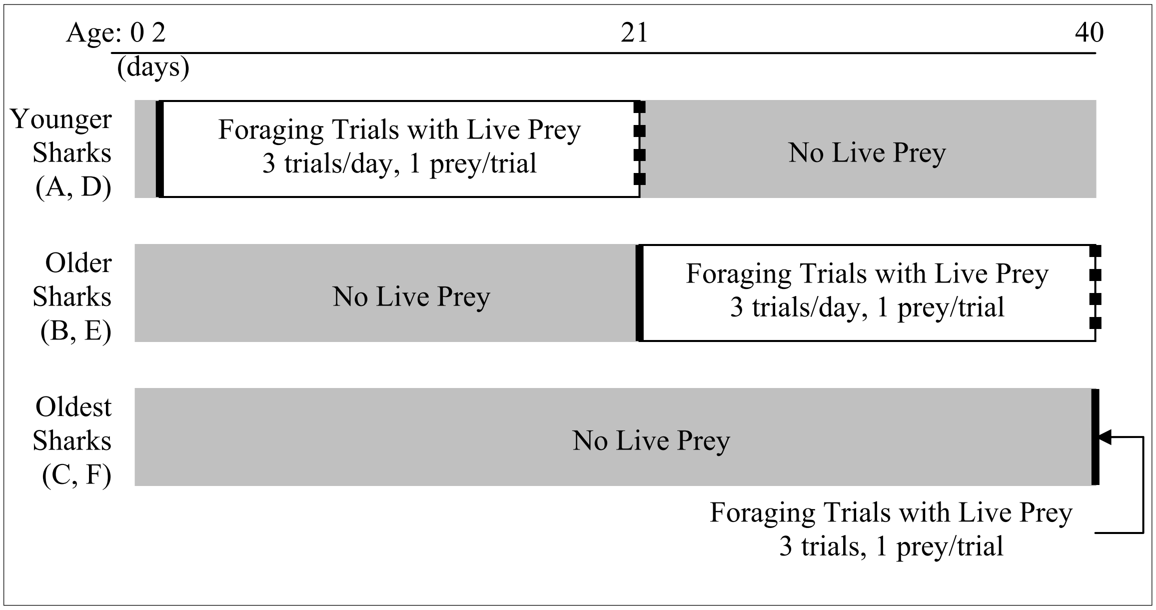


Figure 1.3. Experimental design to determine the effects of maturation alone. Predatory efficiencies of naïve sharks of three different ages were compared, as were predatory efficiencies of equally experienced sharks of two different ages. Gray areas represent days when sharks were fed small cubes of fresh tuna. Solid vertical bars indicate days when naïve sharks of different ages had their first experience with live prey and broken vertical bars indicate days when experienced sharks of different ages had 19 days of foraging trials. Letters A through F indicate sets of sharks included in the design.

The same design using live shrimp instead of live worms in all trials was used to compare different sets of younger, older and oldest sharks. Predatory efficiencies of eleven naïve younger sharks (D), eleven naïve older sharks (E) and eight naïve oldest sharks (F) were compared, as were predatory efficiencies of younger and older experienced sharks after 19 days of foraging trial. One older shark did not have 20 days of foraging trials due to a temporary inability of the supplier to ship live shrimp and one older shark died before it was 40 days old. They were therefore not included with experienced sharks.

Experience Alone

To determine the effects of experience alone on predatory efficiency of whitespotted bamboosharks, sharks with foraging experience were compared to naïve sharks of the same age (Figure 1.4). Predatory efficiencies of nine experienced younger sharks (A) were compared to predatory efficiencies of nine naïve older sharks (B) at 21 days old. The same design using live shrimp instead of live worms in all trials was used to compare different sets of eleven experienced (D) and eleven naïve (E) sharks at 21 days old.

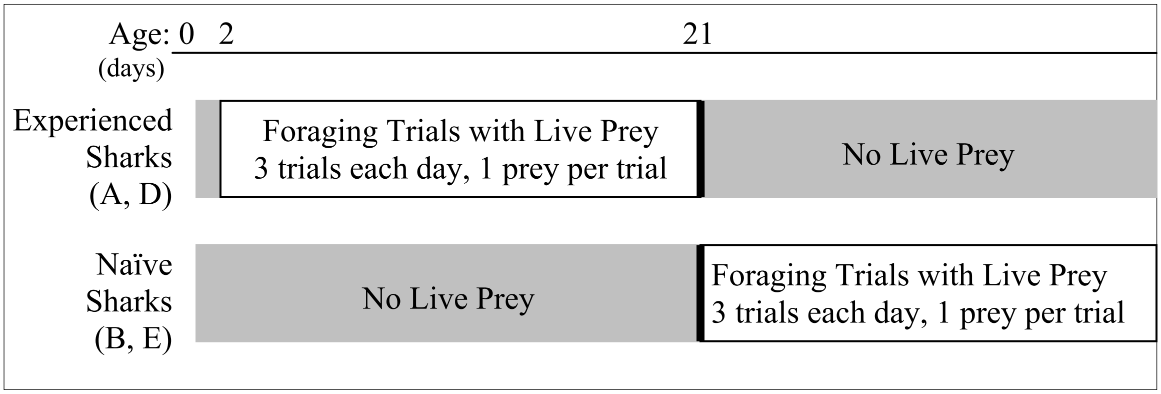


Figure 1.4. Experimental design to determine the effects of experience alone on 21-day-old sharks. Predatory efficiencies of naïve sharks were compared to those of experienced sharks. Gray areas represent days when sharks were fed small cubes of fresh tuna. Dark vertical lines at day 21 represent the foraging trials used for comparisons between experienced and naïve sharks. Letters A through E indicate sets of sharks included in the design.

A similar design was used to compare 40-day-old experienced and naïve sharks (Figure 1.5). Predatory efficiencies of eight experienced older sharks (B) were compared to predatory efficiencies of nine naïve oldest sharks (C) at 40 days old. The same design using live shrimp instead of live worms in all trials was used to compare different sets of nine experienced (E) and eight naïve (F) sharks at 40 days old. Forty-day-old "experienced" sharks in sets B and D were the same animals previously classified as 21-day-old "naïve" sharks. One shark that had been foraging on worms and one shark that had been foraging on shrimp did not continue foraging trials due to temporary inabilities of suppliers to ship live prey and one shark that had been foraging on shrimp died before it reached 40 days old; these three sharks were therefore not included in the "experienced" groups.

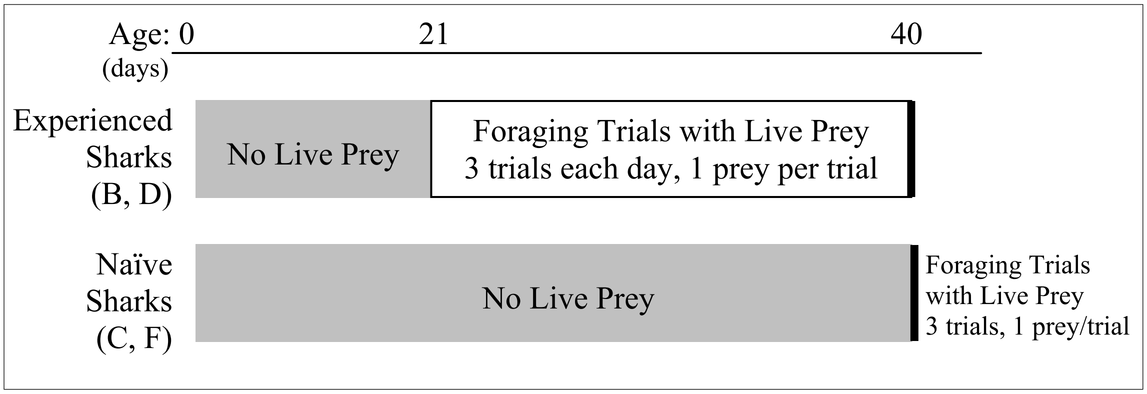


Figure 1.5. Experimental design to determine the effects of experience alone on 40-day-old sharks. Predatory efficiencies of naïve sharks were compared to those of experienced sharks. Gray areas represent days when sharks were fed small cubes of fresh tuna. Dark vertical lines at day 40 represent the foraging trials used for comparisons between experienced and naïve sharks. Letters B through F indicate sets of sharks included in the design.

Predatory Efficiency

Two indices of predatory efficiency were measured, capture rate and latency to consume prey. Capture rate (prey captured/min) was defined as the number of prey (0, 1, 2, or 3) captured during three consecutive trials divided by the sum of the durations (up to 15 minutes each) of those trials. Capture rate was calculated for the first and the last days of foraging trials. Because some sharks did not attempt to capture prey on the first day of trials, later trials from days when sharks attempted to capture prey were also used. If a naïve shark did not capture prey on the first day of trials, then the shark was fed tuna cubes for its meal that day and trials continued on subsequent days (3 trials per day). Adjusted capture rates for these naïve sharks were calculated using the first trial in which each shark attempted to capture prey and the following two trials.

Latency to consume prey was defined as the time for the shark to consume the prey after the barrier separating the shark from the prey was removed. Latency to consume prey was measured on the first day and the last day of trials on which sharks actually captured prey. To minimize the effects of hunger and motivation of the sharks, only the first trial of the day in which each shark captured prey was used for comparisons (Sass and Motta, 2002; Croy and Hughes, 1991b). Because elusiveness of prey varied within prey type (i.e., some shrimp did not move as the shark approached them and were captured on the first attack, while others moved rapidly and required many attacks for the shark to capture them), an adjusted latency to consume prey was calculated by subtracting latency between first and final attacks from latency to consume prey, minimizing the effects of prey's anti-predator behavior. Latency to consume prey was subdivided into smaller components for further analysis (Table 1.1).

Table 1.1. Components of latency to consume prey.

Component	Description
Latency to search	Time from removal of barrier separating shark from prey until shark swims or crawls on its fins with its mouth or barbels in contact with substrate
Latency to first attack	Time from beginning of search until the first instance in which the shark changes speed and/or direction toward prey while opening its mouth
Latency between first and final attacks	Time from first attack until shark touches prey with its mouth or snout immediately prior to closing its mouth on the prey
Latency between contact and capture	Time from shark touching prey with its mouth or snout until closing its mouth on the prey
Duration of transport	Time from shark closing its mouth on prey until shark swallows prey and begins searching

Statistical Analyses

Statistical analyses were performed using SYSTAT®® 11.0. Boxplots were created using SPSS® 11.0. Horizontal bars within boxplots represent median values.

Boxes represent quartiles above and below medians. Whiskers of boxes represent minimum and maximum values within 1.5 boxlengths (boxlengths represent the interquartile range) of box edges.

Maturation and Experience

Wilcoxon matched pairs signed-ranks tests were used to examine differences in capture rates and in latencies to consume prey between sharks' first and last days of foraging trials. If significant differences in latencies to consume prey were found ($p<0.05$), then post-hoc comparisons of the components listed in Table 1.1 were performed.

Maturation Alone

Kruskal-Wallis tests were used to examine differences among naïve sharks of three different ages in capture rates and in latencies to consume prey. If significant differences were found ($p<0.05$), pair-wise comparisons were performed. Mann-Whitney U tests were used to examine differences between equally experienced sharks of two different ages in capture rates and latencies to consume prey. If significant differences in latencies to consume prey were found ($p<0.05$), then post-hoc comparisons of the components listed in Table 1.1 were performed.

Experience Alone

Mann-Whitney U tests were used to examine differences between naïve and experienced sharks of the same age in capture rates and in latencies to consume prey. If significant differences in latencies to consume prey were found ($p<0.05$), then post-hoc comparisons of the components listed in Table 1.1 were performed.

Results

Maturation and Experience Together

To determine whether predatory efficiency improves with increases in both maturation and experience, predatory efficiencies of naïve sharks were compared to their predatory efficiencies after 19 days of foraging trials (Figure 1.2). If predatory efficiency improves with both maturation and increases in experience, then capture rates after 19 days of foraging trials should be higher than capture rates on the first day of foraging trials. Latencies to consume prey after 19 days of foraging trials should also be shorter than latencies to consume the first prey.

Capture Rate

Sharks improved their capture rates with both maturation and increases in experience. Capture rates for both younger and older sharks after 19 days of foraging trials on either worms or shrimp are significantly different from and higher than their capture rates on the first day of foraging trials (Table 1.2, Figure 1.6). Although these findings suggest that maturation and increases in experience improve predatory efficiency, these results may have been influenced by the failure of many naïve sharks to capture any prey on their first day of foraging trials.

Table 1.2. The effects of both maturation and increases in experience on capture rates for sharks when they are naïve and after 19 days of predatory experience. Younger sharks foraged on live prey from 2 days to 21 days old. Older sharks foraged on live prey from 21 days to 40 days old. Capture rates were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes statistically significant results ($p < 0.05$).

Age group	Live prey	Experience level	# of sharks	# of sharks that did not catch prey on first day of trials	Median (captures /min)	Range (captures /min)	T (p)
younger	worm	naïve	9	2	0.055	0-0.79	2.666 (0.008)*
		experienced	9	-	1.90	0.118-16.3	
older	worm	naïve	8	1	0.181	0-2.05	2.240 (0.025)*
		experienced	8	-	1.12	0.127-14.8	
younger	shrimp	naïve	11	7	0	0-0.098	2.192 (0.028)*
		experienced	11	-	0.087	0-1.66	
older	shrimp	naïve	9	5	0	0-0.111	2.547 (0.011)*
		experienced	9	-	0.094	0-1.12	

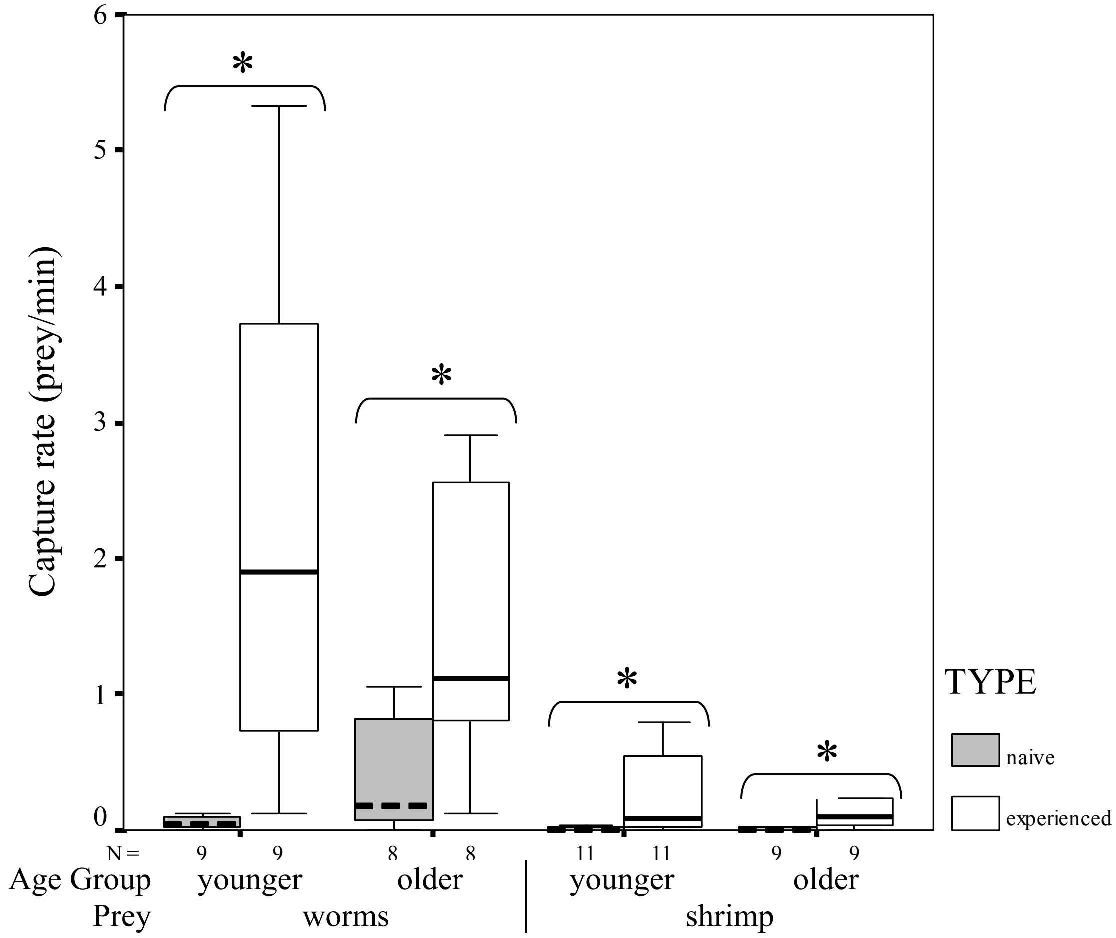


Figure 1.6. The effects of both maturation and increases in experience on capture rates for sharks on the first and last days of foraging trials. Naïve sharks, after being fed small cubes of fresh tuna on all previous days, were foraging on live prey for the first time. After 19 consecutive days of experience foraging on one prey type, sharks were experienced. Capture rate was defined as number of prey captured during the three daily trials divided by the sum of the durations of the three trials. The black solid or dashed bars within each box represent the median value. The boxes represent the quartiles above and below the medians. The whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

The failure of naïve sharks to capture prey may be due to factors other than maturation and experience; some hatchling sharks may be not ready to feed by the time they start trials or some naïve sharks may not immediately identify live prey as food (particularly shrimp, given that more than half of the sharks given shrimp as live prey did not capture prey on the first day of trials). To isolate the effects of maturation and experience, the influences of other factors were minimized by comparing capture rates on the last day of trials with adjusted capture rates calculated from the first trial in which each shark attempted to capture prey and the following two trials (rather than capture rates on the first day of exposure to prey).

Because improvements in capture rates from the first day to the last day of trials (Table 1.2) may be due to a larger proportion of sharks being ready to eat and able to identify prey on the last trial day compared to the first, an examination of adjusted capture rates once sharks have attempted to capture prey, indicating that they are both ready to eat and able to identify prey as food, should be revealing. If maturation and increases in experience do improve predatory efficiency of sharks that are ready to eat and can identify their prey, capture rates should improve from the first trial in which sharks attempt to capture prey to the last day of trials. For sharks foraging on worms and younger sharks foraging on shrimp, capture rates on the last day of trials are significantly different from and higher than these adjusted capture rates (Table 1.3); improvements in these capture rates are therefore not merely due to changes in readiness to eat or identification of prey. For older sharks foraging on shrimp, however, capture rates on the last day of trials are not significantly different from adjusted capture rates; improvements seen in Table 1.2 may therefore be due to naïve older sharks not identifying shrimp as potential food. Because capture rates include trials in which sharks did not capture prey, further analyses are needed to determine whether maturation and increases in experience improve predatory efficiency when sharks actually capture prey.

Table 1.3. Adjusted capture rates and capture rates on the last day of trials. Adjusted capture rates were calculated using the first trial in which sharks attempted to capture prey and the following two trials. Younger sharks foraged on live prey from 2 days to 21 days old. Older sharks foraged on live prey from 21 days to 40 days old. Five younger sharks and two older sharks foraging on shrimp did not capture shrimp within three trials of first attempting to capture shrimp. Capture rates were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes statistically significant results ($p < 0.05$).

Age group	Live prey	Experience level	# of sharks	Median (captures/min)	Range (captures/min)	T (p)
younger	worm	first capture attempt	9	0.088	0.030-0.79	2.666 (0.008)*
		last day	9	1.90	0.118-16.3	
older	worm	first capture attempt	8	0.223	0.058-2.05	2.100 (0.036)*
		last day	8	1.12	0.127-14.8	
younger	shrimp	first capture attempt	11	0.0238	0-0.098	2.090 (0.037)*
		last day	11	0.087	0-1.66	
older	shrimp	first capture attempt	9	0.051	0-0.111	1.718 (0.086)
		last day	9	0.094	0-1.12	

Latency to consume Prey

To determine whether maturation and increases in experience improve predatory abilities when sharks actually capture prey, latencies to consume the first prey that sharks captured were compared to latencies to consume prey on the last day of trials. Two younger sharks and one older shark foraging on shrimp did not capture prey on the last day of trials, so the last day they actually captured prey was used for analysis. When latencies to consume the first prey were compared to latencies to consume prey on the last day of trials, latencies to consume worms improve, but latencies to consume shrimp do not (Table 1.4, Figure 1.7). Latencies to consume worms on the last day of trials are significantly different from and shorter than sharks' latencies to consume their first worms; latencies to consume shrimp on the last day sharks capture prey, however, are not significantly different from latencies to consume their first shrimp. Although the median latency to consume shrimp of younger sharks decreased between the first prey captured and last day of trials, the latencies to consume shrimp of three sharks increased (by 587 sec., 426 sec., and 18 sec.). A shark's ability to capture prey is not only a function of the shark's predatory abilities, but is also due to the prey's ability to elude capture. As sharks increase their predatory skills, they may be able to capture more elusive prey; more elusive prey, however, may still be take longer to capture than less elusive prey. To determine whether sharks foraging on shrimp improve their predatory skill, the influence of prey behavior was minimized by subtracting the latency between first and final attacks from the latency to consume prey.

Table 1.4. The effects of both maturation and increases in experience on latency to consume prey. Younger sharks foraged on live prey from 2 days to 21 days old. Older sharks foraged on live prey from 21 days to 40 days old. Latencies to consume prey were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes statistically significant results ($p < 0.05$).

Age group	Live prey	Experience level	# of sharks	Median (seconds)	Range (seconds)	T (p)
younger	worm	first prey captured	9	165	28.5-1260	-2.666 (0.008)*
		prey captured on last day of trials	9	12.8	1.80-55.6	
older	worm	first prey captured	8	203	11.8-809	-2.380 (0.017)*
		prey captured on last day of trials	8	15.2	3.20-92.3	
younger	shrimp	first prey captured	11	318	61.4-717	-1.245 (0.213)
		prey captured on last day of trials	11	103	15.4-967	
older	shrimp	first prey captured	9	224	23.0-699	-0.770 (0.441)
		prey captured on last day of trials	9	231	42.5-464	

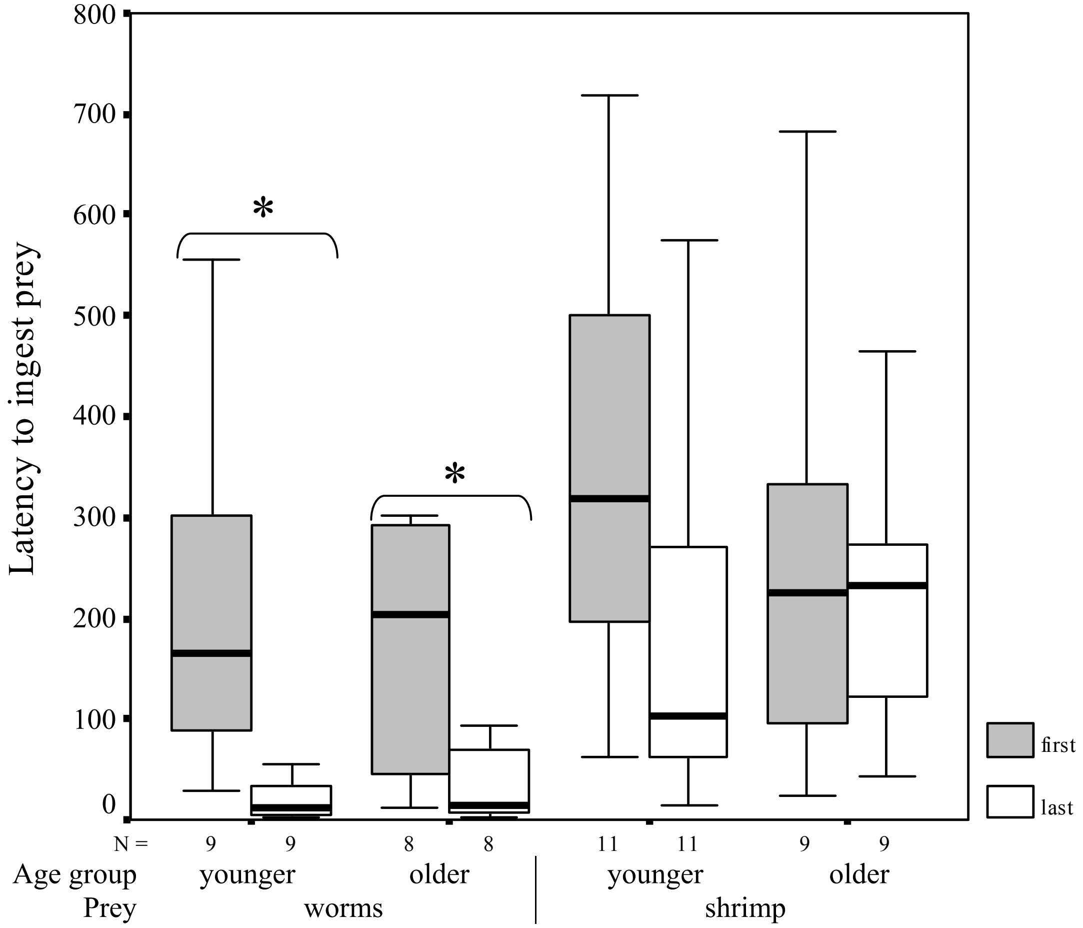


Figure 1.7. The effects of both maturation and increases in experience on latency to consume prey. Latencies to consume the first prey sharks captured were compared to latencies to consume prey on the last day of trials. Younger sharks foraged on live prey from 2 days to 21 days old. Older sharks foraged on live prey from 21 days to 40 days old. Latency to consume prey is defined as the time for the shark to ingest the prey after the barrier between them is removed. Black bars within each box represent median values. Boxes represent quartiles above and below the medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

When latency to consume shrimp is adjusted, sharks' latencies to consume shrimp on the last day they actually capture prey are significantly different from and shorter than sharks' latencies to consume their first shrimp (Table 1.5, Figure 1.8). Because latencies between first and last attacks were removed, trials in which sharks captured shrimp on the first attack (as was the case in many trials in which sharks captured their first shrimp) were unaffected by the adjustment. Because all sharks foraging on worms captured worms on the first attack, latencies to consume worms did not require any adjustment. Because sharks improve in latency to consume worms or adjusted latency to consume shrimp with maturation and increases in experience, each discrete component of latency to consume prey was analyzed to determine where improvements lie.

Table 1.5. Adjusted latencies to consume the first shrimp that sharks capture and shrimp captured on the last day of trials. Younger sharks foraged on live prey from 2 days to 21 days old. Older sharks foraged on live prey from 21 days to 40 days old. Latency to consume prey was adjusted by subtracting the latency between first and final attacks. Adjusted latencies to consume shrimp were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes statistically significant results ($p < 0.05$).

Age group	Experience level	# of sharks	Median (seconds)	Range (seconds)	T (p)
younger	first shrimp captured	11	318	58.8-717	-2.934 (0.003)*
	shrimp captured on last day of trials	11	52.6	15.4-132	
older	first shrimp captured	9	96.5	23.0-699	-2.073 (0.038)*
	shrimp captured on last day of trials	9	55.3	23.2-93.1	

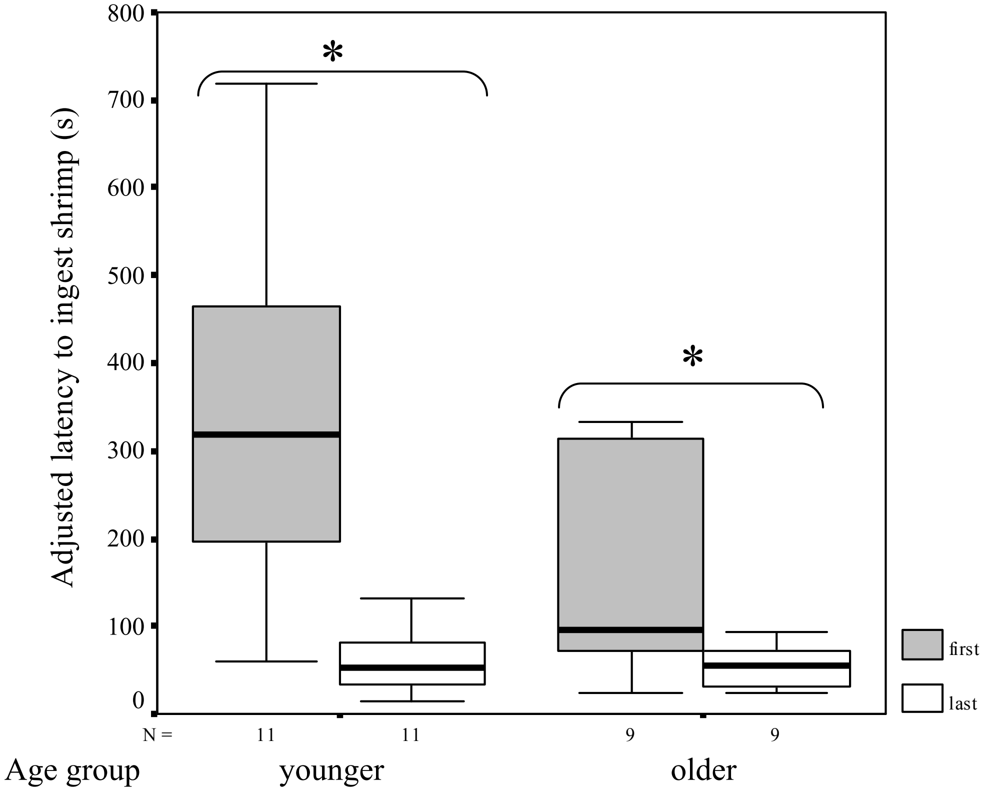


Figure 1.8. Adjusted latencies to consume the first shrimp that sharks capture and shrimp captured on the last day of trials. Younger sharks foraged on live prey from 2 days to 21 days old. Older sharks foraged on live prey from 21 days to 40 days old. Adjusted latency to consume shrimp was calculated by subtracting the latency between first and final attacks. Black bars within each box represent median values. Boxes represent quartiles above and below the medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

Post-hoc comparisons reveal that several components of the latency to consume worms differ significantly with maturation and increases in experience. For younger sharks foraging on worms, the latency to search, the latency between contact and capture, and duration of transport decrease significantly between the first and last days sharks capture worms (Table 1.6). In two trials, younger sharks did not search at all; the shark remained still while the worm moved around the tank until it crawled under the shark's mouth and was eaten. When these sharks are removed from analyses, latency to search and latency to first attack decrease between the first and last days that sharks capture worms (Table 1.7). Because latency between contact and capture and duration of transport would not be affected by whether the shark searched prior to contact with the worm, these variables were not re-analyzed. For older sharks foraging on worms, the latency to search and the duration of transport decrease between the first and last days sharks capture worms (Table 1.6). In one trial, an older shark did not search at all. When this shark is removed from analyses, latency to search decreases between the first and last days that sharks capture worms (Table 1.7).

Table 1.6. Components of latency to consume the first worms that sharks captured and worms captured on the last day of trials. Younger sharks foraged on live worms from 2 days to 21 days old. Older sharks foraged on live worms from 21 days to 40 days old. Because all worms were captured on the first attack, latency between first and final attacks was 0 and therefore omitted from the table. Components of latency to consume worms were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes significant results ($p < 0.05$).

Component	Younger sharks (n = 9)			Older sharks (n=8)		
	First day Median (range) seconds	Last day Median (range) seconds	T (p)	First day Median (range) seconds	Last day Median (range) seconds	T (p)
Latency to search (from removal of barrier until start of search)	12.5 (0-294)	0 (0-9.37)	-2.380 (0.017)*	33.0 (0-283)	0 (0 -2.97)	-2.366 (0.018)*
Latency to first attack (from start of search until first attack)	62.8 (0.03-1004)	8.53 (0.97-54.2)	-1.836 (0.066)	23.8 (0.33-765)	13.4 (2.20-88.6)	-0.420 (0.674)
Latency between contact and capture (from last contact with prey until capture of prey)	3.33 (0.27-11.0)	0.20 (0.10-2.37)	-2.547 (0.011)*	2.34 (0.20-4.04)	0.15 (0.06-0.47)	-2.521 (0.012)*
Duration of transport (from capture of prey until complete ingestion of prey)	12.4 (3.27-240)	2.30 (0.63-11.8)	-2.547 (0.011)*	5.49 (0.94-143)	1.03 (0.83-3.57)	-2.380 (0.017)*

Table 1.7. Latency to search and latency to first attack of sharks that searched prior to ingesting the worm. Components of latency to consume worms were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes significant results ($p < 0.05$).

Component	Younger sharks (n = 7)			Older sharks (n=7)		
	First day Median (range) seconds	Last day Median (range) seconds	T (p)	First day Median (range) seconds	Last day Median (range) seconds	T (p)
Latency to search	9.04 (0-294)	0 (0-9.37)	-1.992 (0.046)*	19.2 (0-283)	0 (0 -2.97)	-2.201 (0.028)*
Latency to first attack	64.8 (18.1-1004)	8.53 (2.23-54.2)	-2.028 (0.043)*	39.8 (5.23-765)	18.1 (2.20-88.6)	-0.676 (0.499)

Post-hoc comparisons reveal that several components of the latency to consume shrimp differ significantly with maturation and increases in experience. For younger sharks foraging on shrimp, the latency to search and duration of transport decrease between the first and last days that sharks capture shrimp (Table 1.8). In three trials, younger sharks did not search at all; the shark remained still while the shrimp moved around the tank until it crawled under the shark's mouth and was eaten. When these sharks are removed from analyses, latency to search and latency to first attack decrease between the first and last days sharks capture shrimp but latency between first and last attack does not (Table 1.9). For older sharks foraging on shrimp, the latency to search decreases between the first and last days sharks capture shrimp (Table 1.8). In three trials, older sharks did not search at all; the shark remained still while the shrimp moved around the tank until it crawled under the shark's mouth and was eaten. When these sharks are removed from analyses, latency to search decreases between the first and last days sharks capture shrimp but latency to first attack and latency between first and last attack do not (Table 1.9). Because duration of transport would not be affected by whether the shark searched prior to ingestion of the shrimp, this variable was not re-analyzed.

Table 1.8. Components of latency to consume the first shrimp that sharks captured and shrimp captured on the last day that sharks actually capture shrimp. Younger sharks foraged on live shrimp from 2 days to 21 days old. Older sharks foraged on live shrimp from 21 days to 40 days old. Because sharks did not come into contact with shrimp before capture, latency between contact and capture was 0 and therefore omitted from the table. Components of latency to consume shrimp were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes significant results (p < 0.05).

	Younger sharks (n=11)			Older sharks (n=9)		
Component	First day Median (range) seconds	Last day Median (range) seconds	T (p)	First day Median (range) seconds	Last day Median (range) seconds	T (p)
Latency to search (from removal of barrier until start of search)	51.1 (0-688)	3.16 (0-42.2)	-2.497 (0.013)*	19.0 (11.9-507)	0 (0-6.94)	-2.666 (0.008)*
Latency to first attack (from start of search until first attack)	92.7 (0-510)	21.2 (1.10-87.0)	-1.956 (0.050)	15.9 (0-294)	15.3 (3.73-57.4)	-0.533 (0.594)
Latency between first and final attack (from first attack until capture of prey)	0.57 (0-72.4)	10.76 (0-937.14)	1.778 (0.075)	1.83 (0-370)	178 (0-389)	1.836 (0.066)
Duration of transport (from capture of prey until complete ingestion of prey)	48.9 (5.30-266)	20.6 (3.23-56.6)	-2.312 (0.021)*	21.2 (3.53-192)	21.6 (7.20-65.7)	-0.178 (0.859)

Table 1.9. Latency to search, latency to first attack and latency between first and final attack of sharks that searched prior to ingesting the shrimp. Components of latency to consume shrimp were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes significant results ($p < 0.05$).

Component	Younger sharks (n=8)			Older sharks (n=6)		
	First day Median (range) seconds	Last day Median (range) seconds	T (p)	First day Median (range) seconds	Last day Median (range) seconds	T (p)
Latency to search	13.3 (0-196)	1.71 (0-42.2)	-2.023 (0.043)*	18.9 (11.9-507)	0 (0-6.94)	-2.201 (0.028)*
Latency to first attack	134 (48.5-510)	12.3 (1.10-80)	-2.201 (0.028)*	47.4 (0-294)	11.4 (3.73-57.4)	-1.183 (0.237)
Latency between first and final attack	0.75 (0-72.4)	7.8 (0-937)	-1.153 (0.249)	29.2 (0-370)	201 (0-389)	-1.521 (0.128)

Increases in both maturation and experience do affect predatory efficiency. For all sets of sharks, capture rates for sharks after 19 days of foraging trials are higher than their capture rates on the first day of foraging trials. For sharks foraging on worms and younger sharks foraging on shrimp, capture rates for sharks after 19 days of foraging trials are higher than adjusted capture rates calculated from the first trial in which sharks attempted to capture prey and the subsequent two trials. For both younger and older sharks foraging on worms, latencies to consume worms on the last day of trials are shorter than latencies to consume their first worms. For both younger and older sharks foraging on shrimp, adjusted latencies to consume shrimp on the last day that sharks capture shrimp are shorter than adjusted latencies to consume their first shrimp. These effects may be due to maturation or to experience or to an interaction between these factors. The following analyses attempt to isolate the contributions of maturation and experience by holding one constant while varying the other.

Maturation Alone

To determine whether maturation alone improves predatory efficiency, the capture rates and latencies to consume prey were compared among sharks of different ages with the same degree of experience (Figure 1.3). If maturation alone improves predatory efficiency, then capture rates for sharks in older age groups should be higher than capture rates for sharks in younger age groups with the same degree of experience. Latencies to consume prey of sharks in older age groups should also be shorter than those of sharks in younger age groups.

Capture Rate

Sharks do not improve capture rates with maturation alone (Table 1.10, Figure 1.9). Capture rates for younger, older and oldest naïve sharks are not significantly different with either type of prey. Capture rates for younger and older experienced sharks are also not significantly different with either type of prey. Although these findings suggest that maturation alone does not improve predatory efficiency, these results may have been influenced by the failure of many naïve sharks to capture any prey on their first day of foraging trials, possibly due to factors other than maturation, such as readiness to eat or ability to identify live prey as food. Because these other factors may be masking the effects of maturation, their influences were minimized by comparing adjusted capture rates calculated from the first trial in which naïve sharks attempt to capture prey and the subsequent two trials (rather than their first days of exposure to prey).

Table 1.10. The effects of maturation alone on capture rates of naïve sharks and experienced sharks of different age groups. Naïve sharks of three different ages (2, 21 or 40 days old) were analyzed using Kruskal-Wallis tests (*H*); experienced sharks of two different ages (21 or 40 days old) were analyzed using Mann-Whitney U tests (U).

Experience level	Live prey	Age group	# of sharks	# of sharks that did not catch prey on first day of trials	Median (captures /min)	Range (captures/min)	Statistics (p)
naïve	worm	younger	10	2	0.055	0-0.79	*H*=1.688 (0.430)
		older	9	1	0.104	0-2.05	
		oldest	9	0	0.108	0.0243-1.74	
experienced	worm	younger	9	-	1.90	0.118-16.3	U=39.0 (0.773)
		older	8	-	1.12	0.127-14.7	
naïve	shrimp	younger	11	7	0	0-0.098	*H*=3.295 (0.193)
		older	11	7	0	0-0.111	
		oldest	8	3	0.032	0-0.58	
experienced	shrimp	younger	11	-	0.087	0-1.66	U=45.0 (0.732)
		older	9	-	0.094	0-1.12	

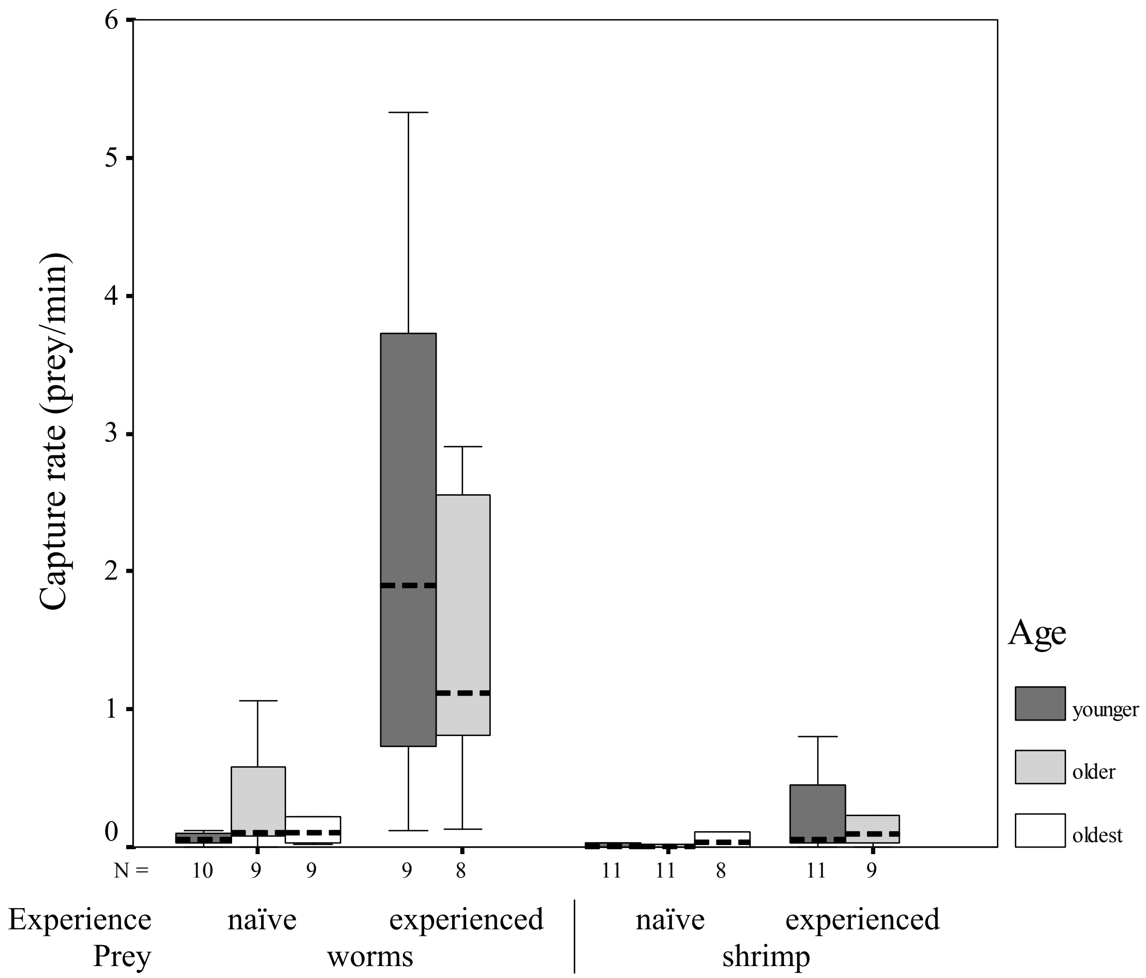


Figure 1.9. The effects of maturation alone on capture rates for naïve sharks of three different ages and by equally experienced sharks of two different ages. Naïve sharks, after being fed small cubes of fresh tuna on all previous days, were foraging on live prey for the first time. Experienced sharks, after 19 consecutive days of experience foraging on one prey type, were foraging on the same live prey. Capture rate was defined as number of prey captured during the three daily trials divided by the sum of the durations of the three trials. Broken black bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. No significant differences were detected.

If the effects of maturation are being masked by naïve sharks not being ready to eat or not identifying live prey as potential food, then an examination of capture rates for sharks that are ready to eat and have identified live prey as potential food should be revealing. If maturation alone does improve predatory efficiency of sharks that are ready to eat and can identify prey, then adjusted capture rates calculated from the first trial in which each shark attempted to capture prey and the following two trials should improve from younger to older age groups. Because foraging trials of oldest sharks were concluded on the first day in which oldest sharks captured prey, three oldest sharks foraging on worms and two oldest sharks foraging on shrimp did not undergo three foraging trials after having attempted to capture prey. These five sharks did not attempt to capture prey until the second or third daily trial during which they captured at least one prey and they were therefore excluded from analyses. Adjusted capture rates were compared among ages (Table 1.11).

Adjusted capture rates for sharks of different age groups foraging on worms are not different; adjusted capture rates for sharks foraging on shrimp, however, are significantly different among age groups. Pair-wise comparisons reveal that adjusted capture rates for younger sharks are significantly different from and lower than adjusted capture rates for both older (Mann-Whitney U = 29.0, p = 0.036) and oldest sharks (Mann-Whitney U = 12.0, p = 0.033), but adjusted capture rates for older sharks are not different from adjusted capture rates for oldest sharks (Mann-Whitney U = 26.0, p = 0.481). Because capture rates include trials in which sharks did not capture prey, further analyses are needed to determine whether maturation alone improves predatory efficiency when sharks actually capture prey.

Table 1.11. Adjusted capture rates calculated from the first trial in which each shark attempted to capture prey and the following two trials of sharks of different age groups. Sharks of different age groups were analyzed using Kruskal-Wallis tests *(H)*. An asterisk (*) denotes statistical differences ($p<0.05$).

Live prey	Age group	# of sharks	Median (captures/min)	Range (captures/min)	*H* (p)
worm	younger	10	0.088	0.030-0.79	3.238 (0.198)
	older	9	0.187	0.058-2.05	
	oldest	6	0.190	0.027-1.74	
shrimp	younger	11	0.0238	0-0.098	6.910 (0.038)*
	older	11	0.051	0-0.111	
	oldest	6	0.072	0.0204-0.73	

Latency to consume Prey

To determine whether sharks' abilities to capture prey improve with maturation alone, latency to consume the first prey captured was compared among sharks of different age groups, as was latency to consume prey on the last day of trials that sharks actually capture prey. Two younger sharks and one older shark foraging on shrimp did not capture shrimp on the last day of trials, so the last day in which they did capture prey was used for analysis. Maturation alone does not improve latency to consume prey (Table 1.12, Figure 1.10). Latencies to consume the first prey of younger, older and oldest sharks are not significantly different regardless of prey. Latencies to consume prey on the last day of trials of younger and older sharks are not significantly different regardless of prey. A shark's ability to capture prey may be influenced by the prey's ability to elude capture. As sharks get older or larger, they may be able to capture more elusive prey, but more elusive prey are still more difficult to capture than less elusive prey. To determine whether sharks foraging on shrimp improve their predatory skill, the influence of prey behavior was minimized by subtracting latency between first and final attacks from latency to consume shrimp.

Table 1.12. The effects of maturation alone on latency to consume prey. Latencies to consume the first prey of sharks of three different ages foraging on the same prey were analyzed using Kruskal-Wallis tests (*H*). Latencies to consume prey on the last day of trials of equally experienced sharks of two different ages were analyzed using Mann-Whitney U tests (U). No significant differences were detected.

Experience Level	Live prey	Age group	# of sharks	Median (seconds)	Range (seconds)	Statistics (p)
first prey	worm	younger	10	179	28.5-1260	*H*=2.12 (0.347)
		older	9	144	11.8-809	
		oldest	9	350	15.2-671	
last day of trials	worm	younger	9	12.8	1.80-55.7	U=30.0 (0.564)
		older	8	15.2	3.20-92.3	
first prey	shrimp	younger	11	318	61.4-718	*H*=3.05 (0.218)
		older	11	139	21.1-700	
		oldest	8	109	58.8-1140	
last day of trials	shrimp	younger	11	104	15.4-968	U=36.0 (0.305)
		older	9	232	42.5-464	

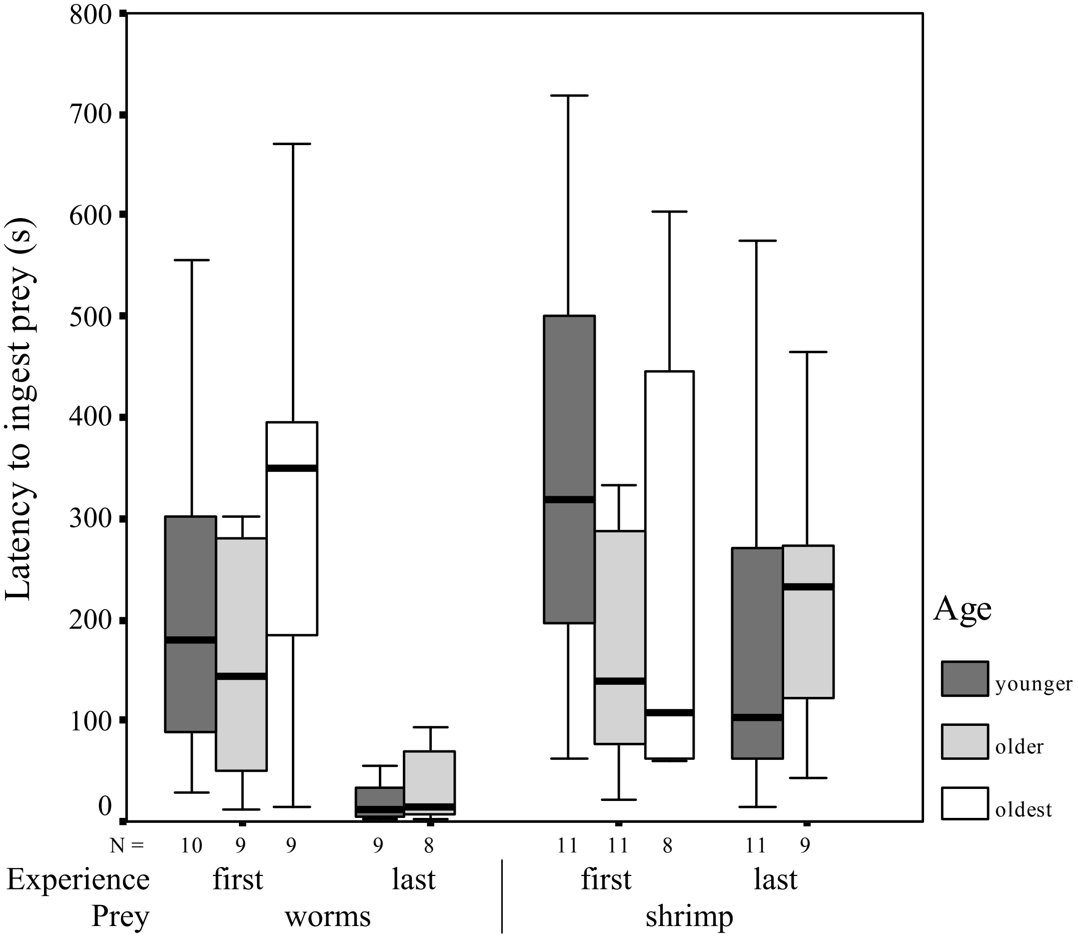


Figure 1.10. The effects of maturation alone on latency to consume the first prey sharks capture and on latencies to consume prey on the last day of trials. Latency to consume prey is defined as the time for the shark to ingest the prey after the barrier between them is removed. Black bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. No significant differences were detected.

When latencies to consume shrimp are adjusted, latencies to consume the first shrimp by sharks of different ages are significantly different (Table 1.13, Figure 1.11); adjusted latencies to consume shrimp on the last day of trials, however, are not significantly different. Pair-wise comparisons reveal that adjusted latencies to consume their first shrimp of younger sharks are significantly different from and longer than those of older sharks (Mann Whitney U = 98.0, p = 0.014) and those of oldest sharks (Mann Whitney U = 71.5, p = 0.023). The adjusted latencies to consume their first shrimp of older sharks are not different from those of oldest sharks (Mann Whitney U = 44.0, p = 1.000). Because all sharks foraging on worms captured worms on the first attack, latencies to consume worms did not require any adjustment. Because adjusted latencies to consume shrimp of naïve sharks improved with maturation alone, each discrete component of latency to consume prey was analyzed to determine where improvements lie.

Table 1.13. Adjusted latencies to consume prey of equally experienced sharks of different ages foraging on shrimp. Latency to consume shrimp was adjusted by subtracting the latency between first and final attacks. Latencies to consume the first prey were analyzed using Kruskal-Wallis tests (*H*); latencies to consume prey on the last day of trials were analyzed using Mann-Whitney U tests (U). An asterisk (*) denotes statistical significance (p<0.05).

Experience level	Age group	# of sharks	Median (seconds)	Range (seconds)	Statistics (p)
first prey	younger	11	318	58.8-718	*H*=7.827 (0.020)*
	older	11	84.7	21.1-333	
	oldest	8	76.0	30.2-340	
last day of trials	younger	11	52.6	15.4-132	U=55.0 (0.676)
	older	9	55.4	23.3-93.1	

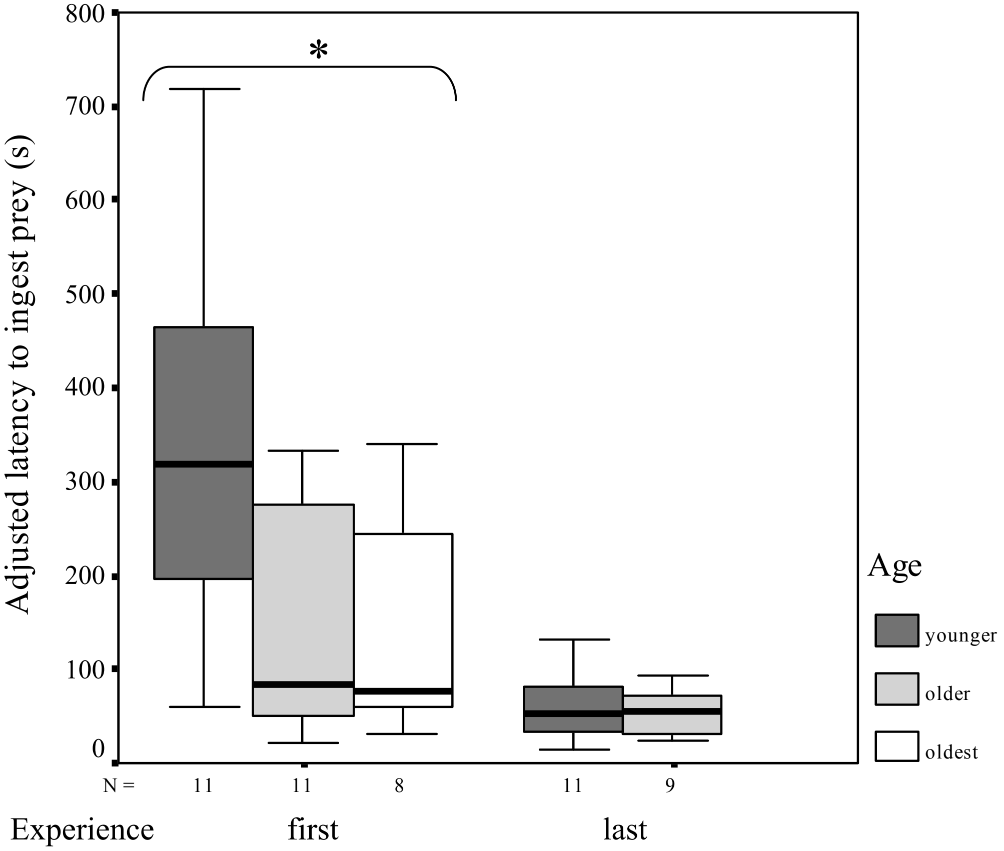


Figure 1.11. Adjusted latencies to consume shrimp of equally experienced sharks of different ages. Latency to consume prey was adjusted by subtracting the latency between first and final attacks. Adjusted latencies were calculated for the first prey ingested and for prey ingested on the last day of trials. Black bars within each box represent median values. Boxes represent quartiles above and below the medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

Post-hoc comparisons reveal that no components of the latency to consume shrimp differ significantly with maturation (Table 1.14). In several trials, sharks did not search; the shark remained still as the shrimp moved around the tank until it crawled under the shark's mouth and was eaten. When these trials (3 younger sharks and 3 older sharks) are removed from analyses, latencies to first attack are significantly different among the three age groups, while latencies to search and latencies between first and last attacks are not different (Table 1.15). Pair-wise comparisons reveal that the latencies to first attack of younger sharks are not significantly different from those of older sharks (Mann-Whitney U = 50, p = 0.059) but are significantly different from and longer than the latencies to first attack of oldest sharks (Mann-Whitney U = 55, p = 0.016). The latencies to first attack of older sharks are not significantly different from those of oldest sharks (Mann-Whitney U = 27, p = 0.600).

Table 1.14. Components of latency to consume the first shrimp of sharks of different age groups. Because sharks did not come into contact with shrimp before capture, latency between contact and capture was 0 and therefore omitted from the table. Components of latency to consume shrimp were analyzed using Kruskal-Wallis tests (*H*).

Components	Younger sharks (n = 11) Median (range) seconds	Older sharks (n = 11) Median (range) seconds	Oldest sharks (n = 8) Median (range) seconds	*H* (p)
Latency to search (from removal of barrier until start of search)	51.1 (0-688)	18.8 (0-507)	0 (0-130)	4.482 (0.106)
Latency to first attack (from start of search until first attack)	93 (0-511)	15.9 (0-294)	51.8 (15.1-84)	2.714 (0.257)
Latency between first and final attack (from first attack until prey capture)	0.57 (0-72.4)	1.83 (0-371)	0.095 (0-795)	0.030 (0.985)
Duration of transport (from capture of prey until complete ingestion of prey)	48.9 (5.30-267)	21.3 (3.53-193)	29.7 (6.00-256)	3.571 (0.168)

Table 1.15. Latency to search, latency to first attack and latency between first and final attack of sharks that searched prior to ingesting shrimp. Components of latency to consume shrimp were analyzed using Kruskal-Wallis tests *(H)*. An asterisk (*) denotes significant results ($p < 0.05$).

Components	Younger (n = 8) Median (range) seconds	Older (n = 8) Median (range) seconds	Oldest (n = 8) Median (range) seconds	*H* (p)
Latency to search	13.3 (0-196)	18.7 (0-56.9)	0 (0-130)	2.152 (0.341)
Latency to first attack	134 (48.5-511)	31.3 (2.56-294)	51.8 (15.1-84)	6.335 (0.042)*
Latency between first and final attack	0.75 (0-72.4)	4.39 (0-371)	0.095 (0-795)	0.689 (0.708)

Maturation alone improves the predatory efficiency of sharks foraging on shrimp, but not of sharks foraging on worms. After sharks first attempt to capture shrimp, capture rates for older and oldest sharks are higher than capture rates for younger sharks. On the last day of trials on which sharks capture shrimp, however, capture rates for older sharks are not different than capture rates for younger sharks. When sharks captured their first shrimp, adjusted latencies to consume shrimp of older sharks and oldest sharks are shorter than those of younger sharks. On the last day of trials, however, adjusted latencies to consume shrimp of older sharks are not different than those of younger sharks. These observations suggest that largest effect of maturation occurs within the first 21 days after sharks hatch.

Although maturation alone improves the predatory efficiencies of sharks foraging on shrimp, experience may still have an effect. Because maturation alone does not improve the predatory efficiencies of sharks foraging on worms, the improvements observed from increases in both maturation and experience are likely due to increases in experience alone. The following analyses attempt to isolate the effects of experience alone by comparing naïve and experienced sharks of the same age.

Experience Alone

To determine whether experience alone improves predatory efficiency, capture rates and latencies to consume prey of naïve sharks were compared to those of experienced sharks of the same age (Figures 4 and 5). If experience alone improves predatory efficiency, then capture rates for experienced sharks should be higher than capture rates for naïve sharks of the same age. Latencies to consume prey of experienced sharks should also be shorter than those of naïve sharks.

Capture Rate

Experience alone improves capture rates for 21-day-old and 40-day-old sharks foraging on worms and 21-day-old sharks foraging on shrimp. Capture rates for experienced sharks are significantly different from and higher than capture rates for naïve sharks for all conditions except 40-day-old sharks preying on shrimp (Table 1.16, Figure 1.12). Although these findings suggest that increases in experience alone improve predatory efficiency, these results may have been influenced by the failure of many naïve sharks to capture any prey on their first day of foraging trials, possibly due to factors other than experience such as readiness to eat or ability to identify live prey as food. To isolate the effects of experience, the influences of other factors were minimized by comparing capture rates of sharks once they have attempted to capture prey with their capture rates on the last day of trials.

Table 1.16. The effects of experience alone on capture rates for naïve and experienced sharks of the same age. An asterisk (*) denotes statistically significant results ($p < 0.05$).

Age (days)	Live prey	Experience level	# of sharks	# of sharks that did not capture prey on the first day of trials	Median (captures/ min)	Range (captures/ min)	Mann-Whitney U (p)
21	worm	naïve	9	1	0.104	0-2.05	69.0 (0.012)*
		experienced	9	-	1.90	0.118-16.3	
40	worm	naïve	9	0	0.108	0.0243-1.74	63.0 (0.009)*
		experienced	8	-	1.12	0.127-14.7	
21	shrimp	naïve	11	7	0	0-0.111	96.0 (0.016)*
		experienced	11	-	0.087	0-1.66	
40	shrimp	naïve	8	3	0.032	0-0.58	46.5 (0.309)
		experienced	9	-	0.094	0-1.12	

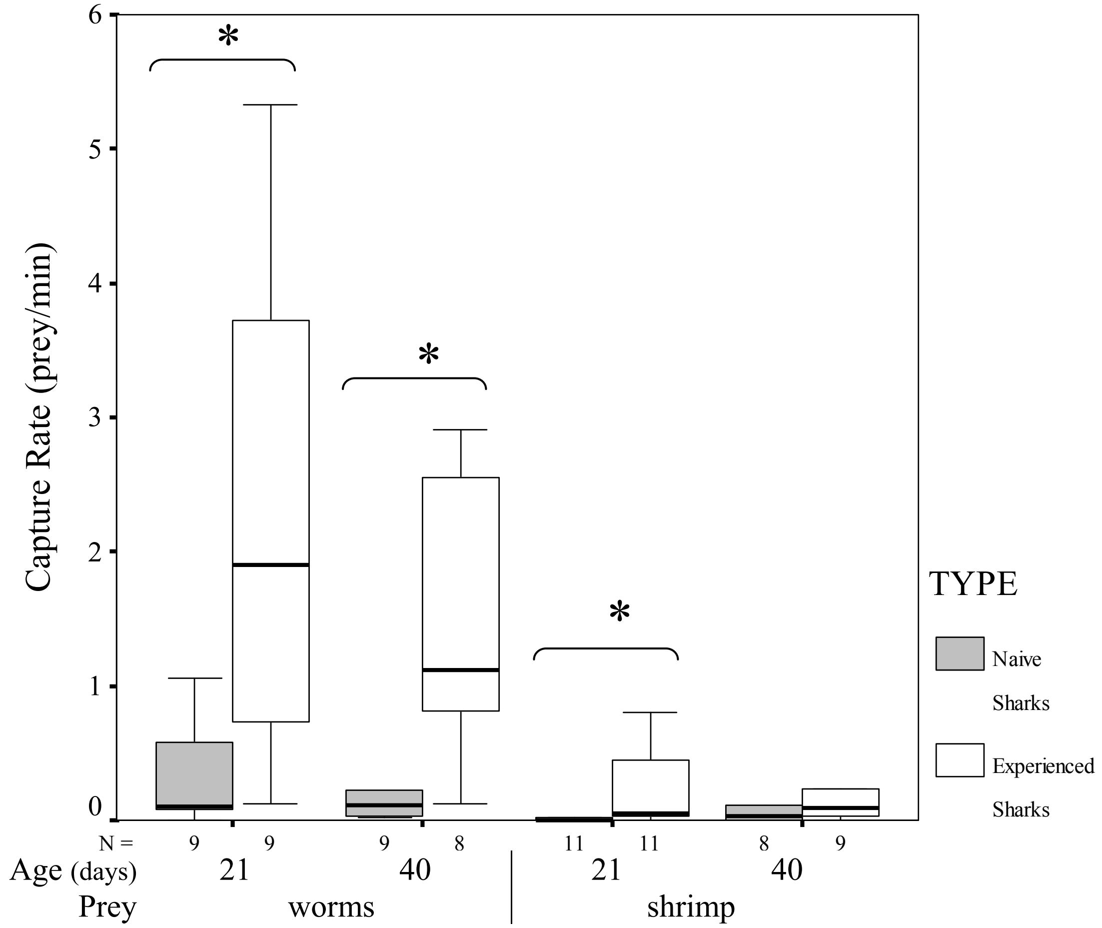


Figure 1.12. The effects of experience alone on capture rates for same-aged naïve and experienced sharks. Capture rate was defined as number of prey captured during the three daily trials divided by the sum of the durations of the three trials. Solid and broken black bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

If capture rates are influenced by more experienced sharks being ready to eat and able to identify prey than naïve sharks, then an examination of capture rates once sharks have attempted to capture prey, indicating that they are both ready to eat and able to identify prey as food, should be revealing. If increases in experience alone improve predatory efficiency of sharks that are ready to eat and can identify their prey, capture rates for experienced sharks should be higher than adjusted capture rates for naïve sharks calculated using the first trial in which each shark attempted to capture prey and the following two trials. Three 40-day-old sharks foraging on worms for the first time and two 40-day-old sharks foraging on shrimp for the first time did not undergo three foraging trials after having attempted to capture prey and were therefore excluded from analyses. Capture rates for experienced 21-day-old sharks foraging on worms are significantly different from and higher than adjusted capture rates for naïve 21-day-old sharks. Capture rates for experienced 40-day-old sharks foraging on worms, however, are not significantly different from adjusted capture rates for naïve 40-day-old sharks, possibly due to the low sample size of naïve sharks (Table 1.17). Capture rates for experienced sharks foraging on shrimp are not significantly different from adjusted capture rates for naïve sharks regardless of age. Because capture rates include trials in which sharks did not capture prey, further analyses are needed to determine whether increases in experience alone improve predatory efficiency when sharks actually capture prey.

Table 1.17. Adjusted capture rates of naïve sharks and capture rates of experienced sharks of the same age. Adjusted capture rates were calculated using the first trial in which each shark attempted to capture prey and the following two trials. An asterisk (*) denotes statistically significant results ($p < 0.05$).

Age (days)	Live prey	Experience level	# of sharks	Median (captures/min)	Range (captures/min)	Mann-Whitney U (p)
21	worm	naïve	9	0.187	0.058-2.05	65.0 (0.015)*
		experienced	9	1.90	0.118-16.3	
40	worm	naïve	6	0.190	0.027-1.74	39.0 (0.052)
		experienced	8	1.12	0.127-14.7	
21	shrimp	naïve	11	0.051	0-0.111	65.0 (0.768)
		experienced	11	0.087	0-1.66	
40	shrimp	naïve	6	0.072	0.0204-0.73	72.0 (0.449)
		experienced	9	0.094	0-1.12	

Latency to consume Prey

To determine whether increases in experience alone improve sharks' predatory abilities when they actually capture prey, naïve sharks' latencies to consume the first prey were compared to same-aged experienced sharks' latencies to consume prey on the last day of trials. Two 21-day-old experienced sharks and one 40-day-old experienced shark foraging on shrimp did not capture shrimp on the last day of trials, so the last day in which they did capture prey was used for analysis. Sharks' latencies to consume worms on the last day of trials are significantly different from and shorter than same-aged sharks' latencies to consume their first worms; sharks' latencies to consume shrimp on the last day of trials, however, are not significantly different from same-aged sharks' latencies to consume their first shrimp (Table 1.18, Figure 1.13). A shark's ability to capture prey may be influenced by the prey's ability to elude capture. As sharks gain experience, they may be able to capture more elusive prey, but more elusive prey may still be more difficult to capture than less elusive prey. To determine whether sharks foraging on shrimp improve their predatory skill, the influence of prey behavior was minimized by subtracting latency between first and final attacks from latency to consume shrimp.

Table 1.18. The effects of experience alone on latencies to consume prey of same-aged sharks on the first day that naïve sharks capture prey or last days that experienced sharks capture prey. Latency to consume prey is defined as the time from the beginning of the trial until the shark has completely consumed the prey. An asterisk (*) denotes statistically significant results (p < 0.05).

Age (days)	Live prey	Trial Day	# of sharks	Median latency (seconds)	Range (seconds)	Mann-Whitney U (p)
21	worm	first	9	144	11.8-809	7.0 (0.003)*
		last	9	12.8	1.80-55.6	
40	worm	first	9	350	15.3-671	4.0 (0.002)*
		last	8	15.2	3.20-92.3	
21	shrimp	first	11	139	21.1- 700	56.0 (0.768)
		last	11	104	15.4- 968	
40	shrimp	first	8	109	58.8- 1140	40.0 (0.700)
		last	9	232	42.5- 465	

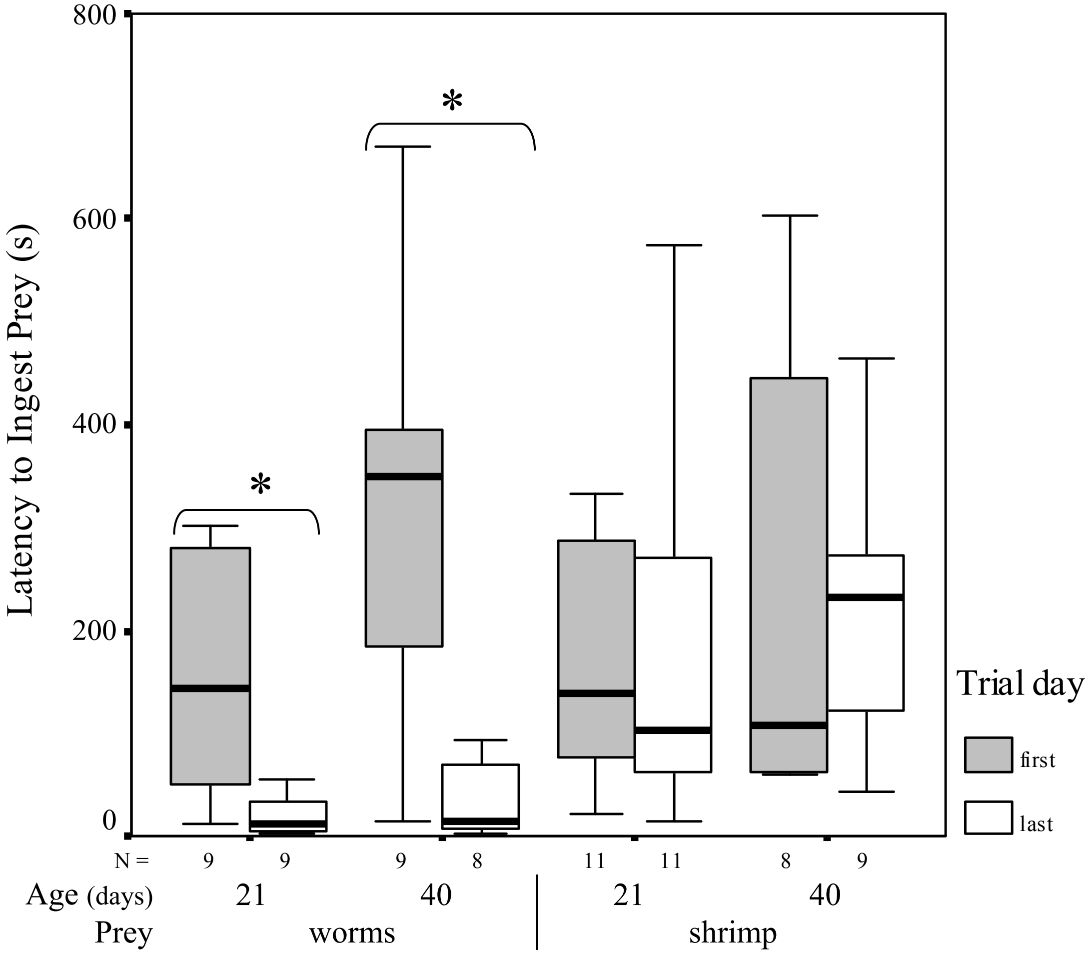


Figure 1.13. The effects of experience alone on latencies to consume prey of same-aged sharks on the first day that naïve sharks capture prey or last days that experienced sharks capture prey. Latency to consume prey is defined as the time for the shark to ingest the prey after the barrier between them is removed. Black bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

When latency to consume shrimp is adjusted, experienced sharks' latencies to consume shrimp on the last day of trials are not significantly different than latencies to consume the first shrimp of naïve sharks of the same age (Table 1.19). Because all sharks foraging on worms captured worms on the first attack, latencies to consume worms did not require any adjustment. Because increases in experience alone improve sharks' latencies to consume worms but not shrimp, each discrete component of latency to consume worms was analyzed to determine where improvements lie.

Table 1.19. Adjusted latencies to consume shrimp on the first day naïve sharks and the last day experienced sharks capture prey. Latency to consume shrimp was adjusted by subtracting the latency between first and final attacks. An asterisk (*) denotes statistical significance ($p < 0.05$).

Age (days)	Live prey	Trial Day	# of sharks	Median latency (seconds)	Range (seconds)	Mann-Whitney U (p)
21	shrimp	first	11	84.74	21.1-333	42.0 (0.224)
		last	11	52.63	15.4-132	
40	shrimp	first	8	76.04	30.2-340	18.0 (0.083)
		last	9	55.36	23.3-93	

Post-hoc comparisons reveal that several components of the latency to consume worms differ significantly between naïve sharks and experienced sharks of the same age (Table 1.20). For 21-day-old sharks, the latency to search and the latency between contact and capture of experienced sharks are shorter than those of naïve sharks. For 40-day-old sharks, the latency to search, the latency to first attack, the latency between contact and capture, and the duration of transport of experienced sharks are all shorter than those of naïve sharks. In one trial, a 21-day-old naïve shark did not search; the shark remained still as the worm moved around the tank until it crawled under the shark's mouth and was eaten. When this trial is removed from analyses, latency to search is shorter for experienced sharks, but latency to first attack is not (Table 1.21), possibly due to the small sample size.

Table 1.20. Components of latency to consume worms for naïve and experienced sharks of the same age. Sharks were either 21 days old or 40 days old. Because all worms were captured on the first attack, latency between first and final attacks was 0 and therefore omitted from the table. An asterisk (*) denotes significant results (p < 0.05).

Component	Age = 21 days			Age = 40 days		
	Naïve (n = 9) Median (range) sec.	Experienced (n=9) Median (range) sec.	Mann-Whitney U (p)	Naïve (n = 9) Median (range) sec.	Experienced (n = 8) Median (range) sec.	Mann-Whitney U (p)
Latency to search (from removal of barrier until start of search)	19.2 (0-283)	0 (0-9.4)	8.5 (0.003)*	56 (0 -111)	0 (0-2.97)	9 (0.005)*
Latency to first attack (from start of search until first attack)	39.8 (0.33-770)	8.53 (0.97-54)	25 (0.171)	183 (3.0-649)	13.4 (2.20-88)	11 (0.016)*
Latency between contact and capture (from last contact with prey until capture of prey)	2.47 (0.20-4.0)	0.20 (0.10-2.37)	10.5 (0.008)*	2.37 (0.07-73)	0.15 (0.06-0.47)	7 (0.005)*
Duration of transport (from capture of prey until complete ingestion of prey)	7.4 (0.94-143)	2.30 (0.63-11.8)	27 (0.233)	3.80 (1.33-130)	1.03 (0.83-3.57)	9 (0.009)*

Table 1.21. Latency to search and latency to first attack of naïve and experienced 21-day-old sharks that searched for prey. An asterisk (*) denotes significant results (p < 0.05).

Component	Naïve (n = 8) Median (range) sec.	Experienced (n=9) Median (range) sec.	Mann-Whitney U (p)
Latency to search	19.2 (0-283)	0 (0-9.4)	8.5 (0.005)*
Latency to first attack	39.8 (5.23-765)	8.53 (0.97-54)	16 (0.054)

Experience alone improves predatory efficiency of sharks foraging on worms, but not of sharks foraging on shrimp. For same-aged sharks foraging on worms, capture rates for experienced sharks were higher than adjusted capture rates for naïve sharks, and latencies to consume worms of experienced sharks were shorter than latencies to worms by naïve sharks. For same-aged sharks foraging on shrimp, however, capture rates for experienced sharks were not different from adjusted capture rates for naïve sharks, and latencies to consume shrimp of experienced sharks were not different from latencies to consume shrimp of naïve sharks.

Experiments isolating the contributions of maturation and experience explain most of the improvements in predatory efficiency observed in the first set of experiments (Figure 1.2). Maturation improves the predatory abilities of sharks foraging on shrimp and experience improves the predatory abilities of sharks foraging on worms. Some improvements, particularly the improvements in adjusted latencies to consume shrimp of older sharks (Table 1.5, Figure 1.8), are not explained. Synergistic effects may exist between maturation and experience.

Discussion

Predatory efficiencies of whitespotted bamboosharks, *Chiloscyllium plagiosum*, improved with increases in both maturation and experience, with maturation alone, and with increases in experience alone (Table 1.22). Maturation and increases in experience, either together or alone, improve all indices of bamboosharks' predatory efficiency except for latency to consume shrimp. This index is greatly influenced by the behavior of the shrimp; some shrimp did not move as the shark approached them and were quickly captured on the first attack, while others moved rapidly and required many attacks over a long period for the shark to capture them. The adjusted latency to consume shrimp, which minimizes the behavior of the shrimp by subtracting the latency between first and final attacks from latency to consume shrimp, is therefore a better index of the shark's predatory ability.

Table 1.22. Summary of results from all experiments. Improvement in predatory efficiency is indicated by "✓" and no improvement is indicated by "0." Because sharks foraging on shrimp did not improve in latency to consume shrimp during any of the experiments, this index is not included in the table.

Prey	Predatory efficiency index	Maturation and experience	Maturation alone	Experience alone
Worms	Capture rate	✓	0	✓
	Adjusted capture rate	✓	0	✓
	Latency to consume worms	✓	0	✓
Shrimp	Capture rate	✓	0	✓
	Adjusted capture rate	✓	✓	0
	Adjusted latency to consume shrimp	✓	✓	0

Increases in both maturation and experience improve capture rates, latencies to consume worms and adjusted latencies to consume shrimp in both younger and older sharks. For sharks foraging on worms and younger sharks foraging on shrimp, capture rates on the last day of foraging trials are higher than adjusted capture rates calculated from the first trial in which sharks attempt to capture prey and the two subsequent trials. For older sharks foraging on shrimp, however, capture rates on the last day of foraging trials are not different from adjusted capture rates, indicating that improvements in their capture rates are due to naïve sharks not identifying shrimp as potential food. Improvements in predatory abilities with increases in both maturation and experience have been observed in several neonatal animals. Whitespotted bamboosharks were found to improve their capture rates of small, bite-sized shrimp during their first year (Lowry and Motta, 2007a). Squid, *Loligo opalescens* (Chen *et al*., 1996), red-backed salamanders, *Plethodon cinereus* (Gibbons *et al*., 2005), and garter snakes, *Thamnophis sirtalis* (Krause and Burghardt, 2001)*,* improved their abilities to capture and consume prey after periods of predatory experience; although these studies acknowledged a possible role of maturation, they attributed improvements in predatory skills mainly to the effects of experience alone. Maturation and experience must be examined individually to determine the contribution of each factor.

Maturation alone improved predatory efficiency of naïve sharks foraging on shrimp but not of experienced sharks foraging on shrimp or sharks foraging on worms. Adjusted capture rates and adjusted latencies to consume shrimp of naïve sharks also improved with maturation. The largest effect of maturation was between newly hatched sharks and sharks 21 days and older, suggesting that important maturational changes occur within the first few weeks of life. These results suggest that maturation may result in neuromuscular, sensory or morphological development that is essential for capturing shrimp, a highly elusive prey, but such development is not necessary for capturing worms, a non-elusive prey. When attempting to capture elusive prey, a fish must attack from a greater distance and with greater velocity than when attempting to capture non-elusive prey (Ferry-Graham *et al*., 2001; Norton, 1991; Nemeth 1997a; van Leeuwen and Muller, 1984). Whitespotted bamboosharks initiated capturing non-elusive worms while in contact with them; in contrast, they initiated capturing elusive shrimp without prior contact. Suction-feeding fish may also modulate the amount of suction produced in response to the elusiveness of prey (Elshoud-Oldenhave and Osse, 1979; Liem, 1979; Lauder, 1981; Wainwright, 1986; Wainwright and Lauder, 1986). Very young bamboosharks may be unable to attain attack speeds or distances necessary to capture shrimp, but even newly hatched sharks can approach and capture non-elusive worms.

Maturation may improve predatory abilities of whitespotted bamboosharks in a number of ways. Maturation may improve bamboosharks' visual acuity. The number of visual receptors in the retina of brown banded bamboosharks, *Chiloscyllium punctatum*, increases during the months after hatching (Harahush, B., pers. com.), potentially affecting sharks' ability to detect shrimp. Maturation may also increase a shark's ability to produce enough suction to overcome an elusive prey's flight response. Kinematic studies of swellsharks, *C. ventriosum*, showed that, while hatchling sharks performed behaviors that should generate suction when feeding, little to no suction is actually produced (Ferry-Graham, 1998a). Kinematic studies of hatchling whitespotted bamboosharks, *C. plagiosum*, showed that sharks' feeding behavior became more suction-dominated throughout their first year, and sharks produced greater suction force (Lowry and Motta, 2007a, b). In a natural environment, neonatal bamboosharks may forage opportunistically on relatively non-elusive prey, capturing elusive prey only when they are older. Many sharks undergo ontogenetic dietary shifts. As lemon sharks (*Negaprion brevirostris* – Cortés and Gruber, 1990), tiger sharks (*Galeocerdo cuvier* – Lowe *et al*., 1996), starspotted-dogfish (*Mustelus manazo* - Yamaguchi and Taniuchi, 2000), Atlantic sharpnose sharks (*Rhizoprionodon terraenovae* – Hoffmayer and Parsons, 2003), and bonnethead sharks (*Sphyrna tiburo* – Bethea *et al*., 2007) grow, they add larger and/or more difficult-to-catch prey to their diets, so it is likely that bamboosharks also exhibit a similar diet shift.

Experience alone improved initial capture rates, adjusted capture rates once sharks identified prey, and latencies to consume prey of sharks foraging on worms. For sharks foraging on shrimp, experience improved only initial capture rates of 21-day-old sharks; once naïve sharks identified shrimp as prey, there was no difference between adjusted capture rates of naïve sharks and capture rates of experienced sharks. Many animals, including many species of fish such as three-spined sticklebacks (*Gasterosteus aculeatus* -Ibrahim and Huntingford, 1992), fifteen-spined sticklebacks (*Spinachia spinachia* - Croy and Hughes, 1991a, b), Atlantic salmon (*Salmo salar* – Reiriz *et al.*, 1998), coho salmon (*Oncorhynchus kisutch* – Paszkowski and Olla, 1985) and Florida largemouth bass (*Micropterus salmoides floridanus* – Wintzer and Motta, 2005), improve feeding efficiency with experience. Experience affects some aspects of predatory abilities of whitespotted bamboosharks that are critical for capturing worms, a non-elusive prey, but are less evident when capturing shrimp, an elusive prey. Experience may enhance sharks' abilities to find their prey or handle prey once it is captured. While the ability to find and handle elusive prey may also be enhanced by experience, the inability to capture elusive prey renders other improvements irrelevant.

To determine which aspects of predatory abilities were affected by maturation and which were affected by experience, latency to consume prey was subdivided into discrete components, each one consisting of a separate predatory task. All components improved with maturation, experience or both except latency between first and final attacks on shrimp (Table 1.23). This component was influenced by the shrimp's degree of elusiveness (some shrimp did not move as the shark approached them and were quickly captured on the first attack, while others moved rapidly and required many attacks over a longer period for the shark to capture them); any improvements in the shark's abilities were therefore not detectable.

Table 1.23. Summary of components of latency to consume prey results from all experiments. improvement in predatory efficiency is indicated by "✓" and no improvement is indicated by "0." No results, due to the fact that the effects of maturation alone were only analyzed in naïve sharks foraging on shrimp and the effects of experience alone were only analyzed in sharks foraging on worms, is indicated by "NR."

Component	Maturation and experience	Maturation alone	Experience alone
Latency to search	✓	0	✓
Latency to first attack	✓	✓	✓
Latency between first and final attacks	0	0	NR
Latency between contact with prey and ingestion	✓	NR	✓
Duration of transport	✓	0	✓

Maturation and experience together and experience alone improved all components leading up to ingestion except latency between first and final attacks. Maturation alone only improved latency to first attack for naïve sharks foraging on shrimp. Experience may therefore be more important than maturation in improving predatory abilities that lead to prey capture. Experience may have caused sharks to associate sensory cues produced by prey with food or to increase sharks' attention to sensory cues. Experienced sharks may have recognized that prey was present sooner than naïve sharks. After fifteen-spined sticklebacks were given experience with a prey type, they oriented to that prey type at further distances than when they were naïve (Croy and Hughes, 1991a). Alternatively, naïve sharks may have been displaying short-term food neophobia, a reluctance to approach and consume novel foods, which would account for experiential decreases in latency to search and latency to first attack. Food neophobia has been found in a variety of organisms, although it has been studied most completely in domestic chicks, *Gallus gallus*, and rats, *Rattus norvegicus* (review – Brigham and Sibley, 1999).

It is also possible that experience unrelated to prey may account for improvements in latency to search. Sharks may have associated their being placed in the foraging tank with food. Alternatively, experienced sharks may have been less disturbed by non-prey stimuli, such as removing the prey-holding arena from the foraging tank, than naïve sharks and were therefore more likely to start searching sooner.

Latency to first attack improved with increases in both maturation and experience of younger sharks regardless of prey type. It also improved with maturation alone for naïve sharks foraging on shrimp and with increases in experience alone for sharks foraging on worms. Maturation may result in increased motor skills allowing the shark to get within striking distance of elusive prey or increasing the shark's speed so that it can cover more ground in a shorter period of time. Experience may allow sharks to orient to prey more quickly. Maturation and experience likely act in concert improve shark's abilities to find prey and move within striking range.

Duration of transport improved with increases in both maturation and experience in younger and older sharks foraging on worms and younger sharks foraging on shrimp. It also improved with experience alone in 40-day-old sharks foraging on worms, but not with maturation alone. Experienced sharks may learn how to attack prey to make it easier to ingest or to position prey for easiest transporting. In fifteen-spined sticklebacks, experienced fish had shorter handling times and fewer prey reorientations than when they were naïve (Croy and Hughes, 1991a).

Overall, maturation and experience are acting in concert to improve the predatory abilities of whitespotted bamboosharks. The maturation level of the shark dictates which potential prey species the shark can effectively utilize, while experience improves the shark's foraging efficiency on that prey. These results have important implications for the release of hatchery-reared fish into the wild. Newly released fish generally have high mortality, due in part to their failure to feed efficiently on natural prey (Ellis *et al*., 2002; Ersbak and Haase, 1983; Nordeide and Salvanes, 1991; Olla *et al*., 1994). Experience with live prey before release into the wild may help overcome this deficit (Brown and Laland, 2001; Furuta *et al*., 1997, 1998; Godin, 1978; Reiriz *et al*., 1998; Steingrund and Fernö, 1997; Ware, 1971; Wintzer and Motta, 2005). Because elusive and non-elusive prey elicit different foraging behaviors, fish may need experience with several types of live prey, particularly prey that is appropriate for their maturation level, in order to survive the transition from the hatchery to the wild.

CHAPTER TWO:

The effects of prey deprivation on the predatory efficiency of the whitespotted bambooshark

Background

Predators that can retain foraging efficiency with a prey species after an absence of that prey from their diet would have an advantage over predators that must relearn foraging skills. Skill retention would be especially important if the particular prey species was initially difficult to catch or required a good deal of experience for the predator to forage on it efficiently. Learning models of optimal foraging theory, however, suggest that forgetting foraging skills which have not been used for some time may be more advantageous than remembering them (Hughes, 1997). According to this view, if predators have a limited amount of memory, they should forget out-of-date skills to make room for skills that are presently needed.

Several studies on the retention of foraging skills by predatory fish have shown that individual species vary in their abilities to retain foraging skills after a particular prey is removed from their diet. The retention of learned predatory skills may be correlated with the predictability of prey abundance; fish in unpredictable habitats such as marine intertidal zones forget quickly while fish in predictable habitats such as freshwater lakes forget more slowly (Mackney and Hughes, 1995). Marine fifteen-spined sticklebacks, *Spinachia spinachia*, begin forgetting foraging skills after two days without live prey and within eight days their skill levels are similar to those of naïve fish (Croy and Hughes, 1991). In threespined sticklebacks, *Gasterosteus aculeatus*, fish from anadromous populations forget foraging skills after 16 days without live prey, but fish from more stable, freshwater habitats do not forget foraging skills after 25 days without live prey (Mackney and Hughes, 1995). Similarly, other freshwater fish show long retention spans. Foraging efficiency of rainbow trout, *Oncorhynchus mykiss,* is retained for 14 days and does not decrease to naïve levels after 3 months (Ware, 1971). Foraging efficiency of silver perch, *Bidyanus bidyanus,* is retained for more than 5 weeks (Warburton and Thomson, 2006).

The whitespotted bambooshark, *Chiloscyllium plagiosum*, is an ideal species to study foraging skill retention. This shark has been shown to increase predatory efficiency with experience (Chapter 1). As a generalist predator, it forages on many types of invertebrate prey that vary in difficulty to capture and in abundance both spatially and temporally (Compagno, 2001). The whitespotted bambooshark is a marine species that forages in “unpredictable” near-shore and reef habitats, so examining its foraging skill retention could add to the knowledge of correlations between skill retention and prey predictability.

The study reported in this chapter tests whether whitespotted bamboosharks with experience foraging on live prey are able to retain efficiency after being denied access to prey for 18 days. If foraging skills are forgotten during this period, then predatory efficiency should decrease. Because sharks grew during this period, decreases in predatory efficiency may be masked by improvements due to maturation. Further experiments compare sharks that have been reintroduced to live prey with same-aged sharks that either have had the same amount of uninterrupted experience with live prey or are naïve. If foraging skills are retained during the no-prey period, re-exposed sharks should be as efficient as experienced sharks and more efficient than naïve sharks. If foraging skills are forgotten, re-exposed sharks should be less efficient than experienced sharks and as efficient as naïve sharks.

Methods

Experimental Design

To determine whether foraging abilities of whitespotted bamboosharks are retained during a period in which sharks are prevented from foraging on live prey, predatory efficiencies of sharks before this period were compared to their predatory efficiencies after they were re-exposed to live prey (Figure 2.1). Seven "re-exposed" sharks, after being fed small cubes of fresh tuna one day after hatching, were given foraging trials with live worms from 2 days until 21 days old. Sharks were given three foraging trials each day with one live worm per trial. Each trial lasted until the shark had completely swallowed the worm but was ended after 15 minutes if the shark failed to capture prey within that time. From 22 days until 39 days old, the sharks were fed only tuna cubes. At 40 days old, sharks were given 3 foraging trials with live worms. Predatory efficiencies on day 21, after 19 days of foraging experience, were compared to predatory efficiencies on day 40, when they were re-exposed to live prey.

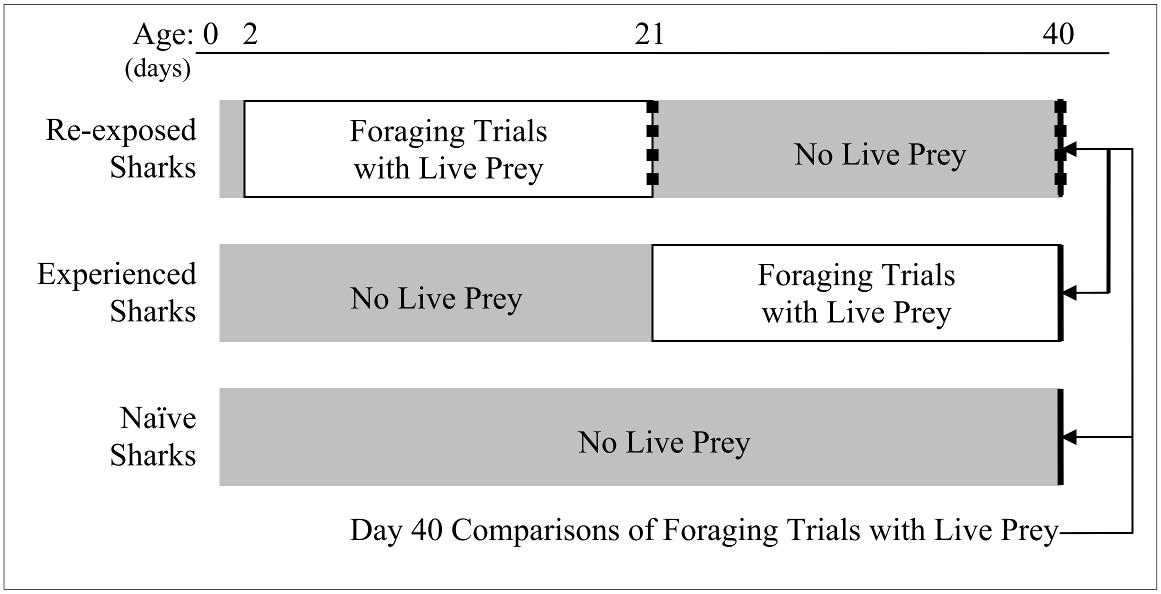


Figure 2.1: Experimental design to determine the effects of a period during which sharks are denied access to live prey on predatory efficiency. Gray areas represent days when sharks were fed small cubes of fresh tuna. Broken vertical bars represent the foraging trials used to compare sharks before they were denied access to live prey and after they were re-exposed to live prey. Solid vertical bars represent the foraging trials used for comparisons between sharks re-exposed to live prey and naïve and experienced sharks of the same age.

Because sharks grew during the no-prey period, decreases in predatory efficiency may be masked by increases due to maturation. To determine whether physical maturation during the no-prey period affected foraging abilities of sharks after they are re-exposed to live prey, predatory efficiencies of 40-day-old "re-exposed" sharks were compared to predatory efficiencies of experienced sharks and of naïve sharks of the same age. Eight "experienced" sharks were fed tuna cubes until day 21 when they were given foraging experience with live worms until day 40. Nine "naïve" sharks were fed tuna cubes until day 40 when they foraged on live worms for the first time.

The same design using live shrimp instead of live worms in all trials was used to compare three other sets of sharks. Predatory efficiencies of eight "re-exposed" sharks were compared before they were denied access to live prey and after they were re-exposed to live prey. To determine whether physical maturation during the no-prey period affected foraging abilities of sharks after they are re-exposed to live prey, predatory efficiencies of “re-exposed” sharks were compared to nine “experienced” sharks and eight “naïve” sharks of the same age. All foraging trials were video-recorded and scored using the methods described in the general introduction of this dissertation (pages 9-12).

Predatory Efficiency

Two indices of predatory efficiency were measured, capture rate and latency to consume prey. Capture rate (prey captured/min) was defined as the number of prey captured on a given day divided by the sum of the durations of the three trials. Capture rates were calculated for re-exposed sharks on the last day of foraging trials before they were denied access to live prey and on the day that they were re-exposed to live prey. Capture rates were calculated for naïve sharks on the first day of foraging trials and for experienced sharks on the last day of foraging trials.

Latency to consume prey was defined as the time for the shark to consume prey after the barrier separating the shark from prey was removed. Latencies to consume prey for re-exposed sharks were measured on the last day of foraging trials before sharks were denied access to live prey and on the day that they were re-exposed to live prey. Latency to consume prey was also measured on the first day of trials on which naïve sharks captured prey and the last day of trials on which experienced sharks captured prey.

Because some sharks did not capture prey on the first or last day of trials, trials from other days were used. If a naïve shark did not capture prey on the first day of trials, then the shark was fed tuna cubes for its meal that day and trials continued on subsequent days until at least one prey was captured. If an experienced shark did not capture prey on the last day of foraging trials, latency to consume prey was measured on the last day of foraging trials in which the shark did capture prey. To minimize the effects of hunger and motivation of the sharks, only the first trial of the day in which each shark captured prey was used for comparisons (Sass and Motta, 2002; Croy and Hughes, 1991b). Latency to consume prey was subdivided into smaller components for further analysis (Table 2.1).

Table 2.1. Components of latency to consume prey.

Component	Description
Latency to search	Time from removal of barrier separating shark from prey until shark swims or crawls on its fins with its mouth or barbels in contact with substrate
Latency to first attack	Time from beginning of search until the first instance in which the shark changes speed and/or direction toward prey while opening its mouth
Latency between first and final attacks	Time from first attack until shark touches prey with its mouth or snout immediately prior to closing its mouth on the prey
Latency between contact and capture	Time from shark touching prey with its mouth or snout until closing its mouth on the prey
Duration of transport	Time from shark closing its mouth on prey until shark swallows prey and begins searching

Statistical Analyses

Wilcoxon matched pairs signed ranks tests were used to examine differences in predatory efficiency of sharks before they were denied access to live prey and after they were re-exposed to live prey. Mann-Whitney U tests were used to examine differences in predatory efficiency between re-exposed sharks and equally experienced sharks of the same age, as well as between re-exposed sharks and naïve sharks of the same age. If significant differences in latencies to consume prey were found ($p<0.05$), post-hoc comparisons of the components listed in Table 2.1 were performed.

Statistical analyses were performed using SYSTAT® 11.0. Boxplots were created using SPSS® 11.0. Horizontal bars within boxplots represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent minimum and maximum values within 1.5 boxlengths (boxlengths represent the interquartile range) of the edges of the box.

Results

Before and after prey absence period

To determine whether foraging skills are retained during a period in which sharks are denied access to live prey, a "no-prey" period, capture rates and latencies to consume prey of sharks before being denied access to live prey were compared to their predatory efficiencies after live prey were reintroduced. The period during which sharks were denied access to live prey did not affect capture rates. Capture rates of sharks after they were re-exposed to live prey are not significantly different from their capture rates before they were denied access to live prey (Table 2.2, Figure 2.2). Although the median capture rates for the 7 sharks foraging on worms increased after sharks were re-exposed to worms, the capture rates for 3 of the 7 sharks decreased. These results suggest that sharks retained predatory abilities during the no-prey period; however, sharks may have decreased in predatory efficiency initially and quickly re-learned the necessary skills. The effect of the no-prey period may therefore only be apparent in the first trial in which re-exposed sharks capture prey. Further analyses are needed comparing the first trial in which re-exposed sharks capture prey with trials on the last day before sharks were denied access to live prey.

Table 2.2. Capture rates for sharks before they were denied access to live prey and after they were re-exposed to live prey. Capture rates were analyzed using Wilcoxon matched pairs signed ranks tests (T).

Live prey	Before or after no-prey period	# of sharks	Median (captures/min)	Range (captures/min)	T (p)
worm	before	7	0.74	0.0290-5.3	0.507 (0.612)
	after	7	1.78	0.231-2.72	
shrimp	before	8	0.0300	0-1.66	1.400 (0.161)
	after	8	0.256	0.046-1.76	

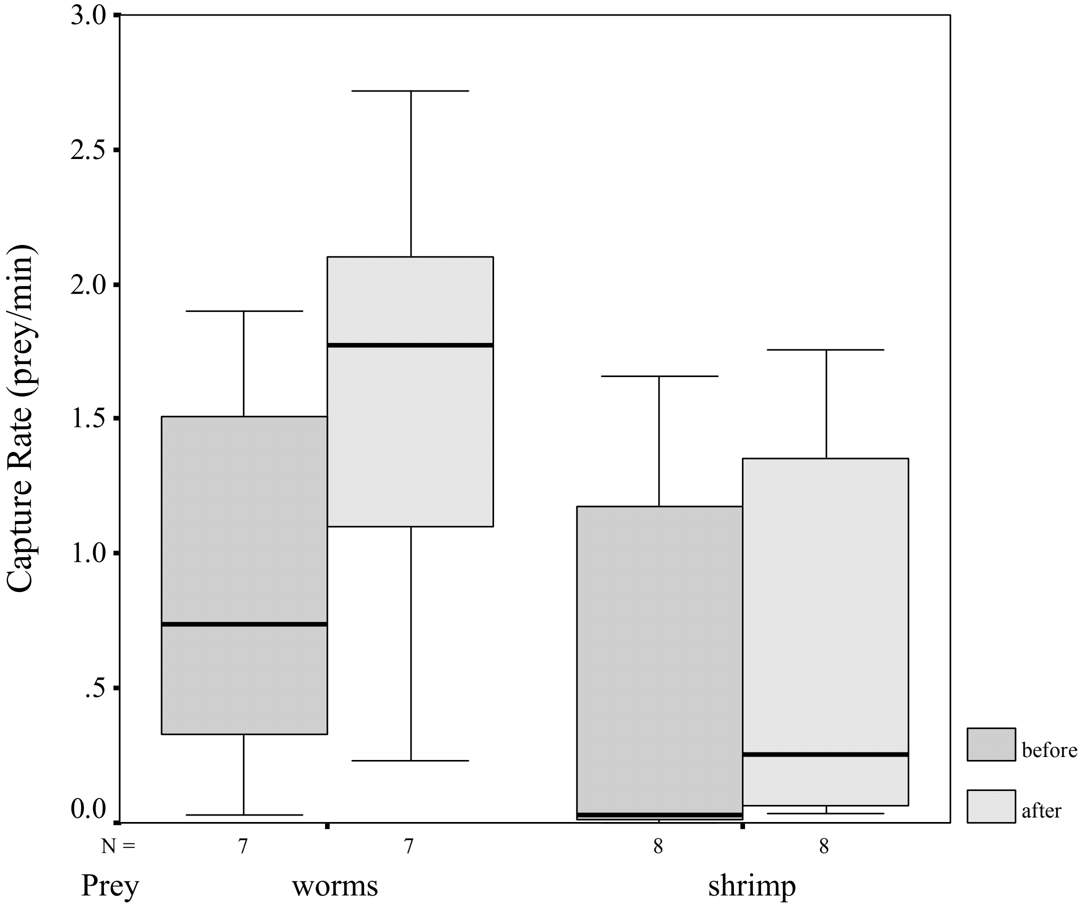


Figure 2.2. Capture rates for sharks before sharks were denied access to live prey and after they were re-exposed to live prey. Capture rate was defined as number of prey captured during the three daily trials divided by the sum of the durations of the three trials. Black bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses.

To determine whether a no-prey period affects sharks' abilities to capture the first prey after re-exposure, latencies to consume prey after they were re-exposed to live prey were compared to latencies to consume prey on the last day before sharks were denied access to prey. A period during which sharks were denied access to live prey did not affect sharks' latencies to consume worms but did improve sharks' latencies to consume shrimp. After the re-exposure to shrimp, sharks' latencies to consume shrimp are significantly different from and shorter than latencies to consume shrimp before being denied access to shrimp (Table 2.3, Figure 2.3), suggesting a maturational effect. Although there is an overall decrease in latency to consume shrimp after the no-prey period, no individual component of latency to consume shrimp accounts for that decrease by itself (Table 2.4).

Table 2.3. Latencies to consume prey of sharks before they were denied access to live prey and after they were re-exposed to live prey. Latencies to consume prey were analyzed using Wilcoxon matched pairs signed ranks tests (T). An asterisk (*) denotes statistically significant results ($p < 0.05$).

Live prey	Before or after no-prey period	# of sharks	Median (seconds)	Range (seconds)	T (p)
worm	before	7	27.6	1.80-56	-0.507 (0.612)
	after	7	26.9	3.23-134	
shrimp	before	8	168	15.4-970	-2.240 (0.025)*
	after	8	80	13.3-820	

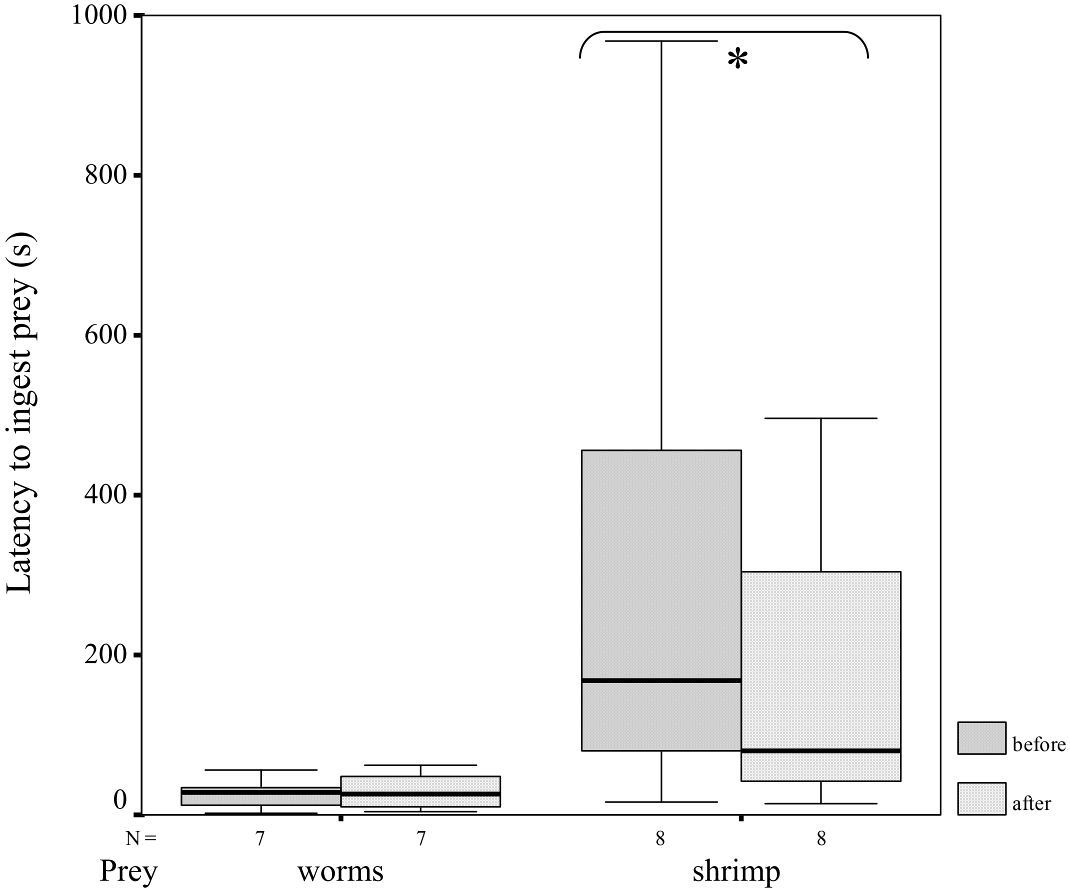


Figure 2.3. Latencies to consume prey of sharks before they were denied access to live prey and after they were re-exposed to live prey. Latency to consume prey is defined as the time for the shark to ingest the prey after the barrier between them is removed. Black bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

Table 2.4: Components of latency to consume shrimp of sharks before they were denied access to live shrimp and after they were re-exposed to live shrimp. Because sharks foraging on live shrimp (n = 8) do not contact the shrimp before they attempt to ingest it, the latency between contact and capture is 0 and is therefore omitted from the table. Components of latency to consume shrimp were analyzed using Wilcoxon matched pairs signed ranks tests (T).

Component	Before Median (range) seconds	After Median (range) seconds	T (p)
Latency to search (from removal of barrier until start of search)	2.58 (0-42)	9.5 (0-60)	1.183 (0.237)
Latency to first attack (from start of search until first attack)	25.0 (6.4-87)	11.1 (0-46)	-1.680 (0.093)
Latency between first and final attack (from first attack until capture of prey)	84 (0-940)	5.20 (0-740)	-1.793 (0.080)
Duration of transport (from capture until complete ingestion of prey)	14.9 (3.23-57)	22.5 (2.40-107)	0.420 (0.674)

While these results suggest that being denied access to live prey does not decrease predatory efficiency, increases in maturation during the no-prey period may have masked a decrease in efficiency. Further analyses comparing sharks re-exposed sharks to experienced sharks and to naïve sharks of the same age are needed to determine the effects of increased maturation.

Same-aged experienced and naïve sharks

To determine whether maturation during a no-prey period affected sharks' foraging abilities, the capture rates and latencies to consume prey of re-exposed sharks were compared to those of experienced and of naïve sharks of the same age. For sharks foraging on worms, capture rates for re-exposed sharks were significantly different from and higher than capture rates for naïve sharks (Table 2.5, Figure 2.4), but not different from capture rates for experienced sharks (which were also higher than those of naïve sharks – Chapter 1, Table 2.16: U = 63.0, p = 0.009). For sharks foraging on shrimp, capture rates for re-exposed sharks were significantly different from and higher than capture rates for naïve sharks (Table 2.5, Figure 2.4), but not different from capture rates for experienced sharks (even though the capture rates for naïve and experienced sharks were not different from each other – Chapter 1, Table 2.16: U = 46.5, p =0.309). These results suggest that sharks retained predatory abilities during the no-prey period; however, sharks may have decreased in predatory efficiency initially and quickly re-learned the necessary skills. The effect of the no-prey period may therefore only be apparent in the first trial in which re-exposed sharks capture prey. Further analyses are needed comparing the first trial in which re-exposed sharks capture prey with the first trial in which naïve sharks capture prey and with trials on the last day that experienced sharks capture prey.

Table 2.5. Capture rates for sharks re-exposed to live prey and for naïve and experienced sharks. Capture rates were analyzed using Mann-Whitney U tests. An asterisk (*) denotes statistically significant results ($p < 0.05$).

Live prey	Experience level	# of sharks	Median (captures/min)	Range (captures /min)	Mann-Whitney U (p)
worm	naïve	9	0.108	0.0243-1.74	58.0 (0.005)*
	re-exposed	7	1.78	0.23-2.72	30.0 (0.817)
	experienced	8	1.12	0.127-14.7	
shrimp	naïve	8	0.032	0-0.58	55.0 (0.015)*
	re-exposed	8	0.256	0.046-1.76	50.0 (0.178)
	experienced	9	0.094	0-1.12	

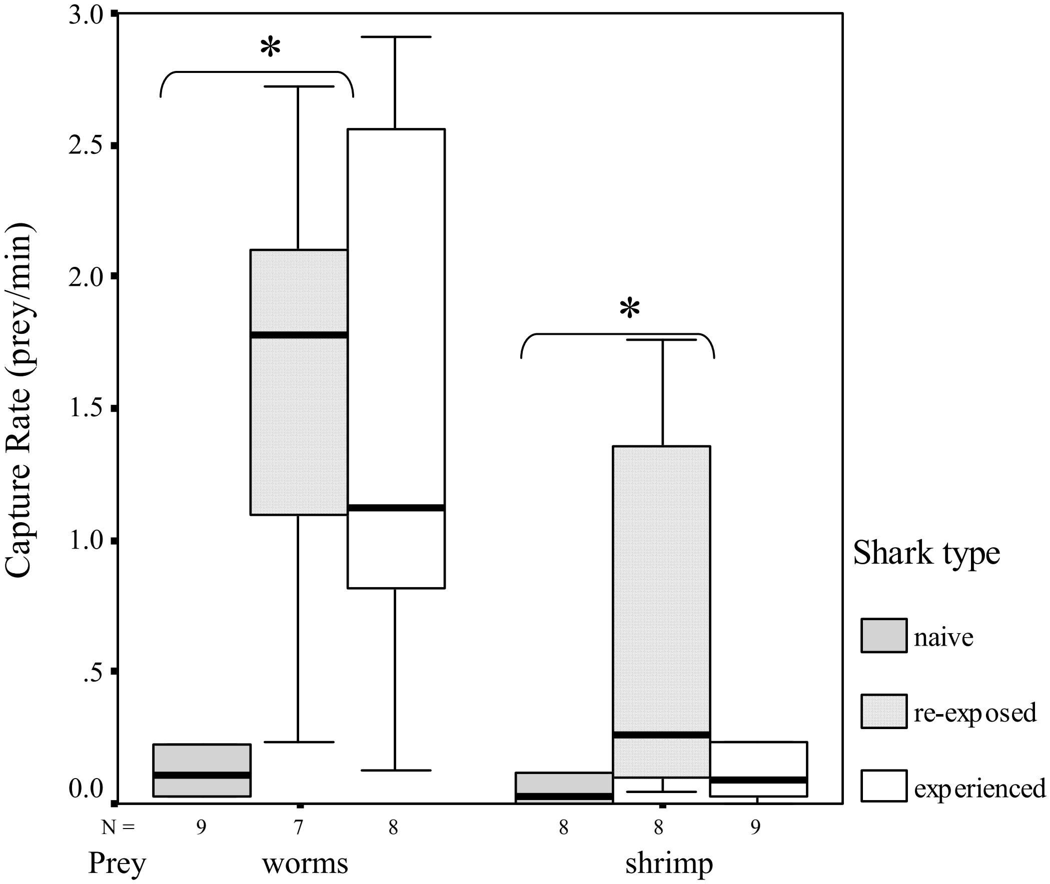


Figure 2.4. Capture rates for sharks re-exposed to live prey and for naïve and experienced sharks. Capture rate was defined as number of prey captured during the three daily trials divided by the sum of the durations of the three trials. Black bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent minimum and maximum values other than outlier values. Outlier values are not shown but are included in analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

To determine whether a no-prey period affects sharks' abilities to capture the first prey after re-exposure, latencies to consume prey of re-exposed sharks were compared to the latencies to consume prey of naïve sharks and of experienced sharks of the same age. Latencies to consume worms of re-exposed sharks were significantly different from and shorter than latencies to consume worms of naïve sharks (Table 2.6, Figure 2.5), but not different from those of experienced sharks (which were also higher than those of naïve sharks - Chapter 1, Table 1.18: U = 4.0, p = 0.002). Latencies to consume shrimp of re-exposed sharks, however, were not significantly different from those of either naïve sharks or experienced sharks (latencies to consume shrimp of naïve and experienced sharks were also not different from each other - Chapter 1, Table 1.18: U = 40.0, p = 0.700). Several components of the latency to consume worms significantly differed between sharks re-exposed to live prey and naïve sharks of the same age (Table 2.7). Latency to search, latency to first attack and latency between contact and capture of sharks re-exposed to live prey were significantly different from and shorter than those of naïve sharks.

Table 2.6. Latencies to consume prey of sharks re-exposed to live prey and naïve and experienced sharks. Latencies to consume prey were analyzed using Mann-Whitney U tests. An asterisk (*) denotes statistically significant results ($p < 0.05$).

Live prey	Experience level	# of sharks	Median (seconds)	Range (seconds)	Mann-Whitney U (p)
worm	naïve	9	350	15.3-671	4.0 (0.004)*
	re-exposed	7	26.9	3.23-134	29.0 (0.908)
	experienced	8	15.2	3.20-92	
shrimp	naïve	8	109	58.8-1135	23.0 (0.345)
	re-exposed	8	80	13.3-820	22.0 (0.178)
	experienced	9	232	42.5-465	

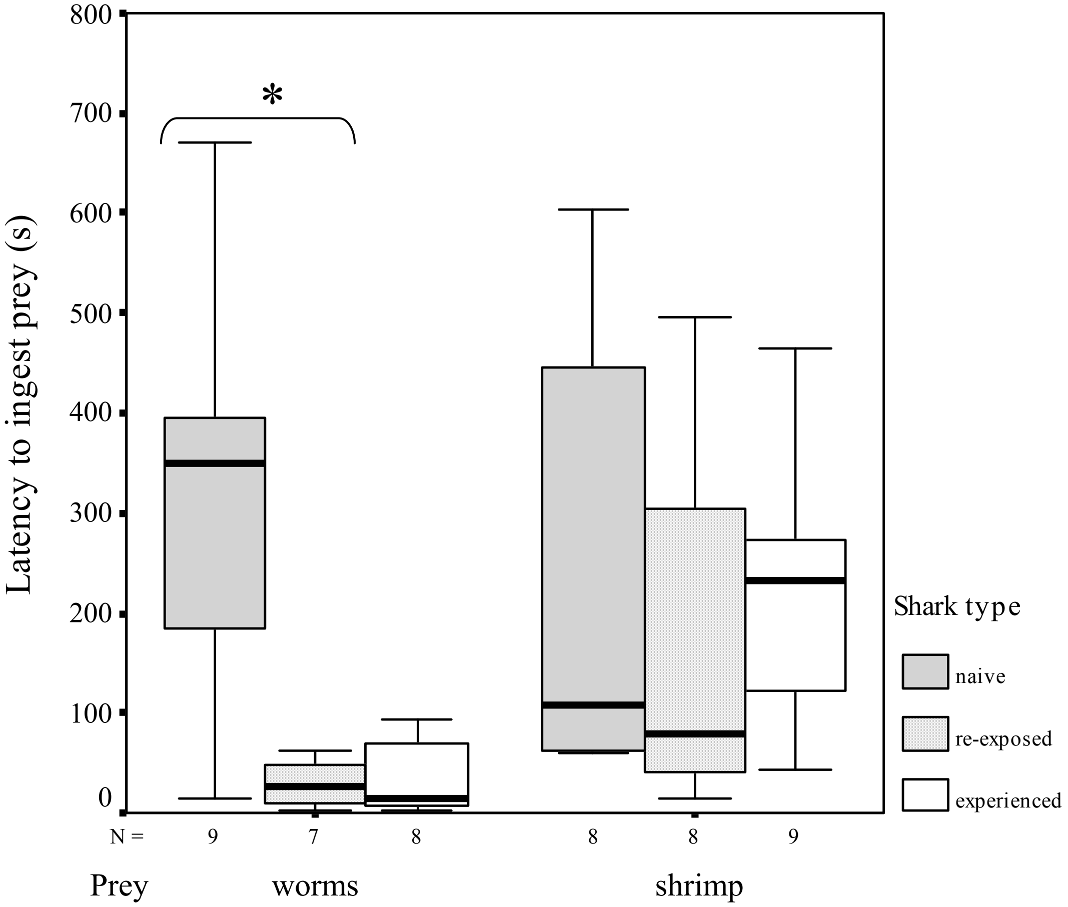


Figure 2.5. Latencies to consume prey of sharks re-exposed to live prey and of naïve and experienced sharks. Latency to consume prey is defined as the time for the shark to ingest the prey after the barrier between them is removed. Black bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

Table 2.7: Components of latency to consume worms of sharks re-exposed to live worms and of naïve sharks. Because all worms were captured on the first attack, latency between first and final attacks was 0 and therefore omitted from the table. Components of latency to consume worm were analyzed using Mann-Whitney U tests. An asterisk (*) denotes significant results ($p < 0.05$).

Component	Re-exposed (n = 7) Median (range) seconds	Naïve (n = 9) Median (range) seconds	Mann-Whitney U (p)
Latency to search (from removal of barrier until start of search)	0 (0-17.8)	56.5 (0-111)	10.0 (0.018)*
Latency to first attack (from start of search until first attack)	11.6 (1.84-54.8)	184 (3.00-649)	9.0 (0.017)*
Latency between contact and capture (from last contact with prey until capture)	0.27 (0.03-0.73)	2.37 (0.07-73)	6.5 (0.008)*
Duration of transport (from capture until complete ingestion of prey)	8.4 (1.20-102)	3.80 (1.33-130)	29.0 (0.791)

Discussion

Neonatal whitespotted bamboosharks retained their abilities to forage on both worms and shrimp when they were re-exposed to live prey after an absence of that prey from their diets. Predatory efficiency of re-exposed sharks did not decrease during an 18 day period with no live prey; latency to consume shrimp actually improved during this period. If improvements in latency to consume shrimp after the no-prey period were due to an increase in motivation for live prey, then latency to search or latency to first attack should have decreased; they did not. Improvements in latency to consume shrimp were therefore probably caused by sharks' physical maturation from 21 days old to 40 days old. Maturation affects the predatory efficiency of sharks foraging on shrimp, but not of sharks foraging on worms (Chapter 1). After 18 days of being denied access to live prey, sharks that had been re-exposed to live prey were as efficient as experienced sharks of the same age and more efficient than naïve sharks, indicating that re-exposed sharks retained learned foraging skills and were not simply older and larger. Skill retention may be very helpful in an unpredictable prey environment as sharks would not have to expend time and energy to relearn foraging skills. Such skill retention would be most beneficial with prey that require a good deal of experience to catch or are difficult to catch, such as shrimp.

Although overall predatory efficiency of re-exposed sharks was retained during the no-prey period, some specific skills may have been forgotten. For 40-day-old sharks foraging on worms, experienced sharks had shorter durations of transport than naïve sharks (Chapter 1, Table 1.20); durations of transport of re-exposed sharks, however, were not different than those of naïve sharks. Skills required to handle prey may be more difficult to retain than skills required to find prey. The skills necessary to ingest the small pieces of tuna that sharks were fed during the absence of live prey may have interfered with the retention of skills necessary to ingest much larger live worms. Leopard sharks, *Triakis semifasciata*, use less suction when ingesting small pieces of food than when ingesting larger pieces (Ferry-Graham, 1998b). Eighteen days of using less suction to capture food may have caused bamboosharks to use less suction than necessary to ingest live worms.

Relatively long term retention of foraging skills in whitespotted bamboosharks does not support Mackney and Hughes' (1995) hypothesis that fish from near-shore marine habitats with unpredictable prey abundances forget foraging skills quickly. Although whitespotted bambooshark habitats in tropical near-shore waters may not be as unpredictable as fifteen-spined stickleback habitats in temperate near-shore waters, temporal variations (monthly, seasonally and in response to environmental conditions) in invertebrate abundances do occur within the whitespotted bambooshark’s range (Nacorda and Yap, 1997).

Several factors may explain why neonatal whitespotted bamboosharks retain learned foraging skills for longer periods than other marine fish. Sharks generally have larger brain-to-body-weight ratios than teleost fish (Northcutt, 1977), and sharks of the same family as the whitespotted bambooshark (Hemiscyllidae) have intermediate brain-to-body-weight ratios among sharks with enlarged telencephalons and cerebellums, (Yopak *et al*., 2007). Because the telencephalon and the cerebellum are associated with procedural memory and skill learning in other vertebrates (Poldrack and Gabrieli, 1997), bamboosharks may have better memories and longer skill retention than some teleosts. In addition, the current study used neonates rather than adults, which may account for the extended retention of foraging skills compared to other studies. Neonates may retain learned skills longer than adults. Increased skill retention may counteract slower learning in neonates; retaining skills may be less costly than relearning them. Neonatal garter snakes, *Thamnophis sirtalis*, are able to retain foraging skills for more than 50 days (Krause and Burghardt, 2001). In the study presented in this chapter, neonates foraged on only one type of prey; their foraging skills may therefore have been retained because no new skills replaced them. Finally, the retention of predatory efficiency in neonatal sharks may be related to food intake patterns of adult sharks. Adults of various shark species may go weeks between meals (Wetherbee and Cortés, 2004) and would benefit by not losing efficiency during this period. Further studies are needed to determine whether sharks in predictable habitats retain foraging skills for longer periods than sharks in unpredictable habitats.

The forgetting of learned responses is a wide-spread phenomenon (Bouton, 1986, 1993, Gleitman, 1971; Spear, 1978). Many learned associations are forgotten after relatively short periods (Pavlov, 1927; Robbins, 1990). Instrumental learning (changes in behavior due to reinforcement) may also be forgotten (Gleitman and Steinman, 1963; Gagne, 1941; Kraemer, 1984; Mote and Finger, 1943). Many forgotten responses, however, can be quickly restored or remembered (Bouton, 1991, Keasar *et al*., 1996; Sanders and Barlow, 1971). Although bamboosharks do not seem to forget foraging skills in eighteen days, certain aspects of experimental design may have diminished forgetting or improved memory recall.

Newly learned skills may interfere with the recall of skills learned in the past (Baddeley, 1986; Underwood, 1957). Retroactive interference, the degraded ability to perform one task due to learning a second task, occurs in many animals including bees (Cheng and Wignall, 2006; Chittka and Thomson, 1997; Dukas, 1995; Koltermann, 1969; Worden *et al*., 2005), pigeons (Kraemer, 1984), rats (Rodriquez *et al*., 1993) and human beings (Barnes and Underwood, 1959; Tell and Schultz, 1972). For bamboosharks, foraging efficiency did not significantly decrease during the period when they were feeding only on tuna cubes; feeding on tuna cubes therefore did not interfere with the ability to forage on worms or shrimp. Interference is greater with increasing stimulus or task similarity (Bouton, 1993; Colborn *et al*., 1999, Gleitman, 1971; Rodriquez *et al*., 1993; Spear, 1971). Feeding on tuna may have therefore been different enough from foraging on live prey that interference did not occur.

Many skills and associations are resistant to forgetting and interference. Odor memories are particularly persistant (Herz and Engen, 1996; Lawless and Engen, 1978; Richardson and Zucco, 1989; Schab, 1991; Staubli *et al*., 1987; Stevenson *et al*. 2007). Recognition of live prey odors may have allowed sharks to quickly recall foraging skills. If prey odor recognition does rapidly restore prey capture behavior, bamboosharks foraging on a variety of prey with different odors would be able to switch among prey types without substantial decrement to their foraging efficiency on any one prey type.

Contextual cues may also cause the retrieval of learned skills and associations (Bouton, 1993; Bouton and Brooks, 1993; Deweer, 1986; Gordon, 1981; Hall and Honey, 1989; Spear, 1971, 1973; Tulving and Pearlstone, 1966; Underwood, 1969). Bamboosharks were fed during the no-prey period in small rectangular tanks rather than the larger, circular foraging tanks. Re-exposure to the foraging tanks may have triggered the memory of predatory skills. If contextual cues do restore predatory skills, sharks that forage on different prey in different habitats would not decrease their predatory abilities on either prey. For example, if one prey type is found only in mud flats and another prey type occurs only in seagrass beds, moving from a seagrass bed to a mud flat would cause sharks to adjust their predatory behaviors to those appropriate for the mud flat prey.

CHAPTER THREE:

The effects of previous experience on the predatory efficiency of the whitespotted bambooshark foraging on novel prey

Background

Many predators learn how to forage for prey, improving efficiency with experience (reviews: Kamil and Sargent, 1981; Kamil *et al*., 1987). Previous experience with prey may enhance a predator's ability to forage on novel prey. A predator may utilize the same skills with novel prey as with previous prey or may modify those skills to fit the new circumstances. Shore crabs (*Carcinus maenas*) with experience crushing dogwhelk shells are able to crush mussel shells in the same manner but must modify skills used to manipulate prey prior to crushing (Hughes and O'Brien, 2001). Similarly, neonatal garter snakes (*Thamnophis sirtalis*) transfer some predatory skills learned from foraging on fish to foraging on worms (Krause and Burghardt, 2001). Additionally, a predator with learning experience may learn faster. Pigeons (Santiago and Wright, 1984), rhesus monkeys (*Macaca mulatta:* Harlow, 1959) and Arabian horses (*Equus caballus:* Sappington and Goldman, 1994) learn to discriminate between two stimuli faster if they had previously been exposed to discrimination tests.

Alternatively, previous experience may impede the predator's ability to forage on novel prey. Skills acquired foraging on previous prey may inhibit the formation of new skills required for foraging on novel prey. Dogwhelks (*Nucella lapillus*) from a population that foraged primarily on barnacles by boring through their shells used the same method to attack mussels, a novel prey, and did not learn the more efficient method of attacking mussels through the gape between the shells (Rovero *et al*., 1999). In addition to behaviors associated with prey capture and ingestion, prey recognition may be affected by prior predatory experience. If a predator has formed a search image of familiar prey, it may not recognize novel prey. Blue jays (*Cyanocitta cristata*) trained to peck at one species of moth (*Catocala relicta*) on a cryptic background were unable to detect a novel moth (*C. retecta*) on a different cryptic background (Pietrewicz and Kamil, 1981).

Previous experience may have no effect on ability to forage on novel prey. A predator may need to learn an entirely new predatory repertoire to forage on a novel kind of prey. Shore crabs that foraged on periwinkles by chipping away their shells were no more or less efficient than naïve crabs at foraging on mussels by crushing their shells (Hughes and O'Brien, 2001).

The whitespotted bambooshark, *Chiloscyllium plagiosum*, is a generalist predator, foraging on many types of invertebrate prey that vary in anti-predator defenses and morphology (Compagno, 2001), and it therefore has the potential to develop specific skills for specific prey. Whitespotted bambooshark increase predatory efficiency with experience (Chapter 1) and will readily feed on non-living food so they can easily be kept from hatching to 40 days old without any opportunity for predation.

The study reported in this chapter tests whether the whitespotted bambooshark's ability to forage on a novel prey type is affected by previous predatory experience. To determine the degree to which previous predatory experience affects sharks' abilities to forage on novel prey, sharks with previous predatory experience were allowed to forage on novel prey. Their predatory efficiencies with novel prey were compared to those of naïve sharks and to those of sharks experienced with that prey. If previous predatory experience impedes sharks' abilities to forage on novel prey, sharks will be less efficient than naïve sharks. If previous predatory experience enhances sharks' abilities to forage on novel prey, sharks foraging on novel prey will be more efficient than naïve sharks and may be as efficient as sharks experienced with that prey.

Methods

To determine whether experience with one prey type affects whitespotted bamboosharks' ability to forage on another prey type, the predatory efficiencies of sharks foraging on novel prey were compared to those of naïve sharks and sharks experienced foraging on that prey (Figure 3.3). Nine "naive" sharks (A) were fed tuna cubes until they were 40 days old, when they were given their only foraging trials with live worms, three foraging trials with one live worm per trial. Each trial lasted until the shark had completely swallowed the worm but was ended after 15 minutes if the shark failed to capture prey within that time. Seven "shrimp-fed" sharks (B) were fed small cubes of fresh tuna until they were 21 days old, when they were given their first foraging trials with live shrimp. Sharks were then given three foraging trials each day with one live shrimp per trial. Shrimp-fed sharks continued to receive daily foraging trials with live shrimp until they were 40 days old. On day 41, shrimp-fed sharks were given 3 foraging trials with novel prey, live worms (1 worm/trial). Eight "worm-fed" sharks (C) were fed tuna cubes until they were 21 days old, when they were given their first foraging trials with live worms (3 trials/day, 1 worm/trial). Worm-fed sharks continued to receive daily foraging trials with live worms until they were 40 days old.

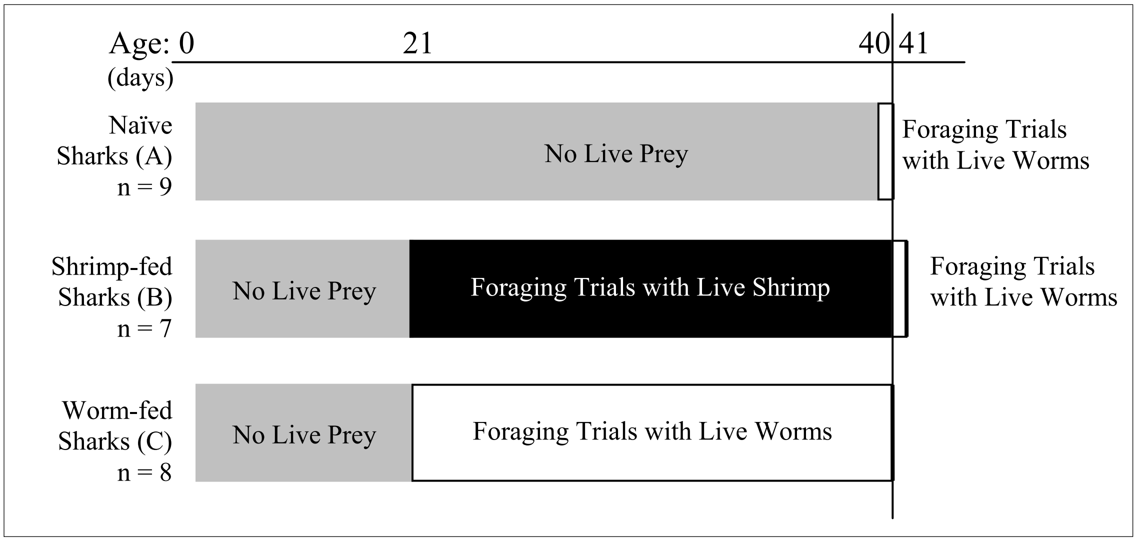


Figure 3.3: Experimental design comparing the predatory efficiencies of shrimp-fed sharks foraging on worms to those of worm-fed sharks and naïve sharks. Gray areas represent days when sharks were fed small cubes of fresh tuna. Black area represents days when sharks had foraging trials with live shrimp (3 trials/day, 1 shrimp/trial). White areas represent days when sharks had foraging trials with live worms (3 trials/day, 1 worm/trial). Letters A through C indicate sets of sharks included in the design.

The same design was used to compare the same set of eight worm-fed sharks (C) foraging on live shrimp for the first time to eight naïve sharks (D) and the same set of nine shrimp-fed sharks foraging on live shrimp (B) (Figure 3.4), although two shrimp-fed sharks did not forage on worms because of temporary inabilities of the supplier to deliver live worms, hence the different sample sizes (7, 9). All foraging trials were video-recorded and scored using the methods described in the general introduction of this dissertation (pp. 9-12).

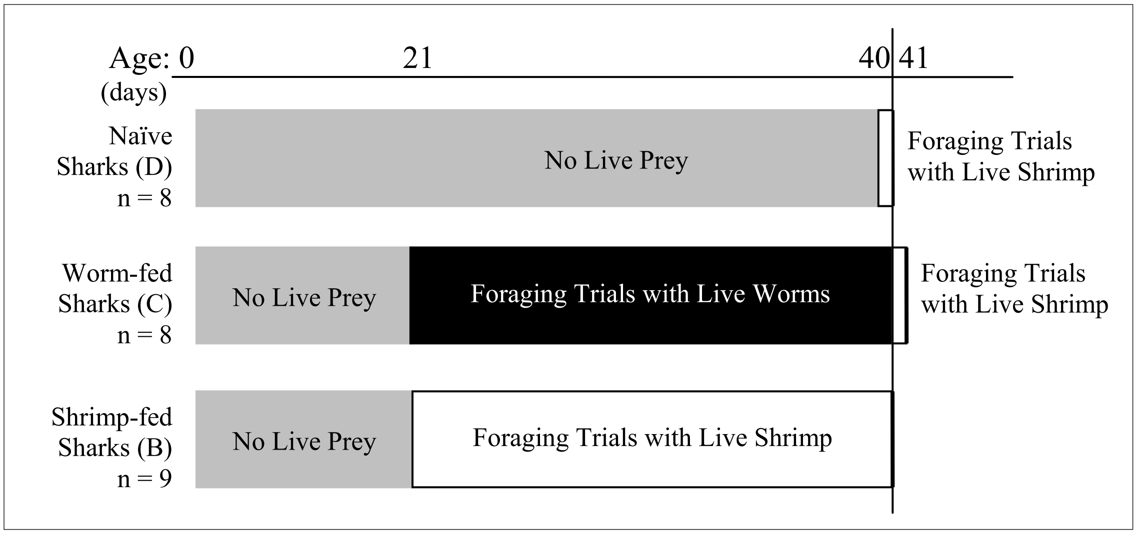


Figure 3.4: Experimental design comparing the predatory efficiencies of worm-fed sharks foraging on shrimp to those of shrimp-fed sharks and naïve sharks. Gray areas represent days when sharks were fed small cubes of fresh tuna. Black area represents days when sharks had foraging trials with live worms (3 trials/day, 1 worm/trial). White areas represent days when sharks had foraging trials with live shrimp (3 trials/day, 1 shrimp/trial). Letters B through D indicate sets of sharks included in the design

Predatory Efficiency

Two indices of predatory efficiency were measured, capture rate and latency to consume prey. Capture rate (prey captured/min) was defined as the number of prey (0, 1, 2, or 3) captured during three consecutive trials divided by the sum of the durations (up to 15 minutes each) of those trials. For shrimp-fed sharks, capture rates were calculated for the last day of foraging trials with shrimp (day 40) and the first day of foraging trials with worms (day 41). For worm-fed sharks, capture rates were calculated for the last day of foraging trials with worms (day 40) and the first day of foraging trials with shrimp (day 41). For naïve sharks, capture rates were calculated on the first day of trials with either worms or shrimp (day 40).

Latency to consume prey was defined as the time for the shark to consume the prey after the barrier separating the shark from the prey was removed. Latency to consume prey was measured on the first day and the last day of trials on which sharks actually captured prey. Because some naïve sharks did not capture prey on the first day of trials, later trials from days when sharks did capture prey were used in analyses. If a naïve shark did not capture prey on the first day of trials, then the shark was fed tuna cubes for its meal that day and trials continued on subsequent days (3 trials per day). To minimize the effects of hunger and motivation of the sharks, only the first trial of the day in which each shark captured prey was used for comparisons (Sass and Motta, 2002; Croy and Hughes, 1991b). Because shrimp-fed and worm-fed sharks foraging on their original prey types differed mainly in their searching and prey-ingesting behaviors, two components of latency to consume prey were analyzed: latency to first attack (from start of search until first attack) and duration of transport (from capture of prey until complete ingestion of prey).

In addition, the frequencies of several behaviors were measured during the same trials as latency to consume prey. The type of each attack that a shark employed was recorded and the proportion of pin-attacks to total number of attacks was calculated for each trial. In addition to attack type, the number of transport bouts that a shark initiated during transport was counted. Finally, the mode of searching (central or perimeter) employed by each shark was recorded for each trial. For a more detailed description of these behaviors, see *Shark behavior* in the General Introduction of this dissertation (pp. 13-15)

Statistical Analyses

Mann-Whitney U tests were used to examine differences in the following measures (capture rate, latency to consume prey, latency to first attack, duration of transport, proportion of pin-attacks to total number of attacks, and number of transport bouts) between shrimp-fed sharks and worm-fed sharks foraging on worms, between shrimp-fed sharks and naïve sharks foraging on worms, between worm-fed sharks and shrimp-fed sharks foraging on shrimp, and between worm-fed sharks and naive sharks foraging on shrimp.

Statistical analyses were performed using SYSTAT® 10.0. Boxplots were created using SPSS® 11.0. Horizontal bars within each boxplot represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent minimum and maximum values within 1.5 boxlengths (representing the interquartile range) of the edges of the box.

Results

Worms as Prey

To determine whether previous experience foraging on shrimp affects predatory efficiency when foraging on worms for the first time, predatory efficiencies of shrimp-fed sharks foraging on worms for the first time were compared to predatory efficiencies of worm-fed sharks and of naïve sharks foraging on worms.

When foraging on worms, capture rates for shrimp-fed sharks are not different from capture rates for worm-fed sharks or from capture rates for naïve sharks (Table 3.1, Figure 3.5), although capture rates for worm-fed sharks are higher than capture rates for naïve sharks (Chapter 1, Table 1.16: U = 63.0, p = 0.009). Because capture rates may be influenced by shrimp-fed sharks learning to capture worms over the course of three daily trials, further analyses are needed to determine whether experience with shrimp affects predatory efficiency of sharks foraging on the first worms they capture.

Table 3.1. The effects of shrimp-foraging experience on capture rates for sharks foraging on worms for the first time. Capture rates for shrimp-fed sharks foraging on worms were compared to capture rates for naïve sharks and worm-fed sharks. Capture rates were analyzed using Mann-Whitney U tests.

Experience level (set of sharks)	# of sharks	Median (worms/min)	Range (worms/min)	Mann-Whitney U (p)
naïve (A)	9	0.108	0.0243-1.74	20.0 (0.223)
shrimp-fed (B)	7	0.154	0.0275-2.74	14.0 (0.105)
worm-fed (C)	8	1.12	0.127-14.7	

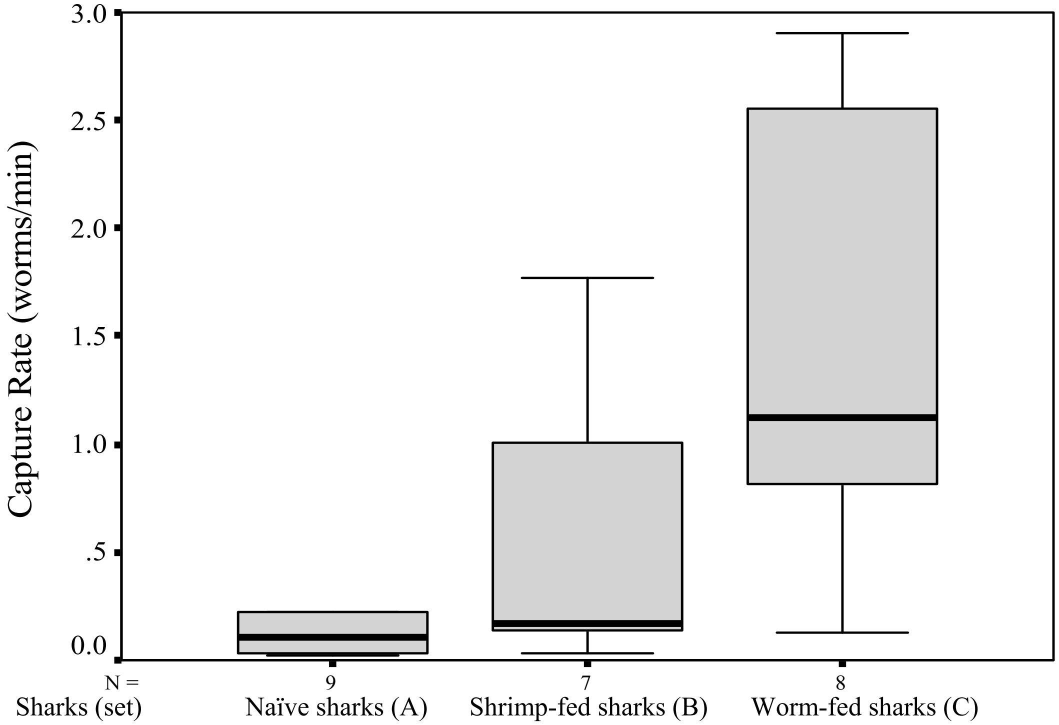


Figure 3.5. The effects of shrimp-foraging experience on capture rates for sharks foraging on worms. Naïve sharks, after being fed small cubes of fresh tuna on all previous days, were foraging on live worms for the first time. Shrimp-fed sharks, after 20 consecutive days of experience foraging on shrimp, were foraging on live worms for the first time. Worm-fed sharks had 19 consecutive days of experience foraging on live worms. Capture rate was defined as number of prey captured during three daily trials divided by the sum of the durations of the three trials. Black solid bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses.

To determine whether experience foraging on shrimp improves sharks' predatory efficiency when they first capture worms, latencies to consume worms of shrimp-fed sharks were compared to latencies to consume worms of worm-fed sharks and of naïve sharks. Latencies to consume worms of shrimp-fed sharks are not different from latencies to consume worms of worm-fed sharks or naïve sharks (Table 3.2, Figure 3.6), although latencies to consume worms of worm-fed sharks are shorter than latencies to consume worms of naïve sharks (Chapter 1, Table 3.3. 18: U = 4.0, p = 0.002).

Table 3.2. The effects of shrimp-foraging experience on latencies to consume worms. Latencies to consume worms of shrimp-fed sharks were compared to those of naïve sharks and of worm-fed sharks. Latencies to consume worms were analyzed using Mann-Whitney U tests.

Experience level (set of sharks)	# of sharks	Median (seconds)	Range (seconds)	Mann-Whitney U (p)
naïve (A)	9	350	15.3-671	16.0 (0.101)
shrimp-fed (B)	7	126	8.8-379	14.5 (0.118)
worm-fed (C)	8	15.2	3.20-92.3	

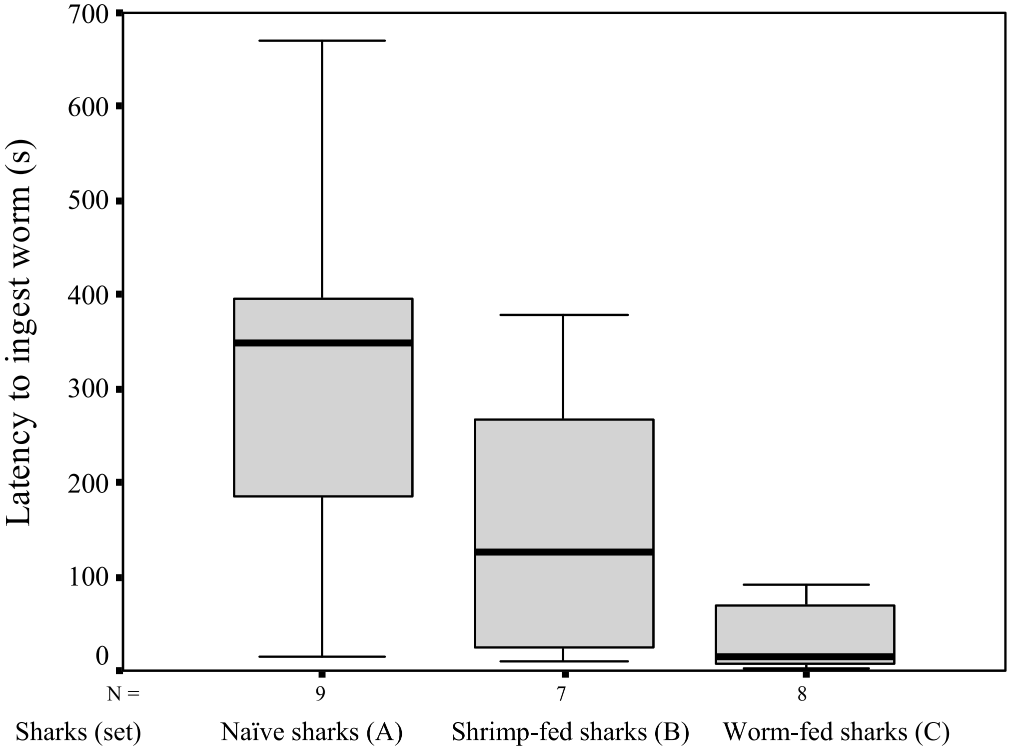


Figure 3.6. The effects of shrimp-foraging experience on latencies to consume worms. Naïve sharks, after being fed small cubes of fresh tuna on all previous days, were foraging on live worms for the first time. Shrimp-fed sharks, after 20 consecutive days of experience foraging on shrimp, were foraging on live worms for the first time. Worm-fed sharks had 19 consecutive days of experience foraging on live worms. Black solid bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses.

When foraging trials are analyzed for discrete behaviors, some differences between shrimp-fed sharks and worm-fed sharks are evident. None of the shrimp-fed sharks adopted the slow, central searching behaviors of worm-fed sharks; rather, they rapidly swam the perimeter of the tank (perimeter searching) and encountered the worm when crossing the center of the tank or when the worm moved to the perimeter. Latencies to first attack worms for shrimp-fed sharks (median = 49 s, range = 2.06-370 s) are not significantly different from those of naïve sharks (median = 183 s, range = 3-650 s, U = 41.0, p = 0.315) or from those of worm-fed sharks (median = 13.4 s, range = 2.20-89 s, U = 21.0, p = 0.418). All sharks captured worms on their first attack using a pin-attack. Durations of transport for shrimp-fed sharks (median = 4.80 s, range = 2.07-71 s) are not significantly different from those of naïve sharks (median = 3.80 s, range = 1.33-130 s, U = 31.0, p = 0.958) but are significantly different from and higher than those of worm-fed sharks (median = 1.03 s, range = 0.83-3.57 s, U = 6.0, p = 0.011). Shrimp-fed sharks use significantly more transport bouts (median = 6, range = 2-27) when consuming worms than worm-fed sharks (median = 1, range = 1-2, U = 54.0, p = 0.002), but not naïve sharks (median = 5, range = 1-23, U = 19.0, p = 0.183).

Shrimp as Prey

To determine whether previous experience foraging on worms affects predatory efficiency when foraging on shrimp for the first time, predatory efficiencies of worm-fed sharks foraging on shrimp were compared to predatory efficiencies of shrimp-fed sharks and naïve sharks foraging on shrimp.

When foraging on shrimp, capture rates for worm-fed sharks are not different from capture rates for shrimp-fed sharks, but are significantly different from and higher than capture rates for naïve sharks (Table 3.3, Figure 3.7) even though the capture rates for naïve and shrimp-fed sharks were not different from each other (Chapter 1, Table 1.16: U = 46.5, p =0.309). Because capture rates may be influenced by worm-fed sharks learning to capture shrimp over the course of three daily trials, further analyses are needed to determine whether experience with worms affects predatory efficiency of sharks foraging on the first shrimp they capture.

Table 3.3. The effects of worms-foraging experience on capture rates for sharks foraging on shrimp. Capture rates for worm-fed sharks were compared to capture rates for naïve sharks and shrimp-fed sharks foraging on shrimp. An asterisk (*) denotes statistically significant differences ($p < 0.05$).

Experience level (set of sharks)	# of sharks	Median (shrimp/min)	Range (shrimp/min)	Mann-Whitney U (p)
naïve (D)	8	0.032	0-0.58	8.0 (0.011)*
worm-fed (C)	8	0.33	0.083-1.01	19.0 (0.102)
shrimp-fed (B)	9	0.094	0-1.12	

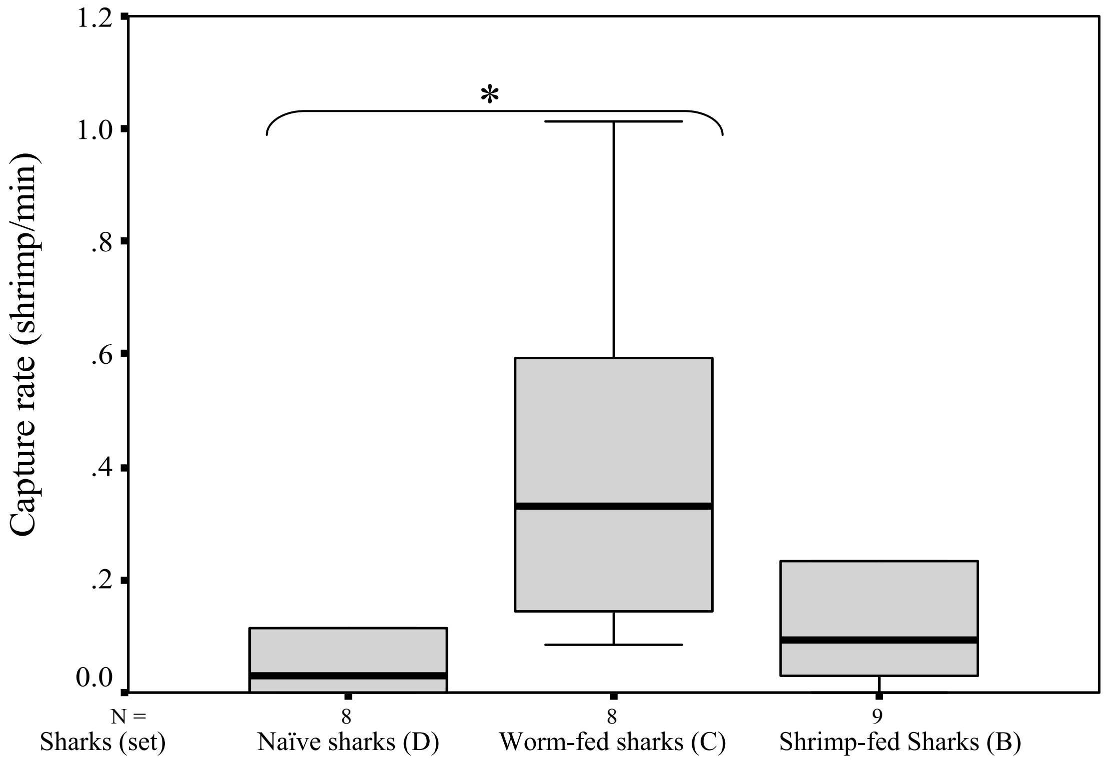


Figure 3.7. The effects of worms-foraging experience on capture rates for sharks foraging on shrimp. Naïve sharks, after being fed small cubes of fresh tuna on all previous days, were foraging on live shrimp for the first time. Worm-fed sharks, after 20 consecutive days of experience foraging on worms, were foraging on live shrimp for the first time. Shrimp-fed sharks had 19 consecutive days of experience foraging on live shrimp. Capture rate was defined as number of prey captured during the three daily trials divided by the sum of the durations of the three trials. Black solid bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses. An asterisk (*) denotes statistically significant differences between bracketed results ($p < 0.05$).

To determine whether experience foraging on worms improves sharks' predatory abilities when they first capture shrimp, latencies to consume shrimp of worm-fed sharks were compared to latencies to consume shrimp of shrimp-fed sharks and of naïve sharks. Latencies to consume shrimp of worm-fed sharks are not different from latencies to consume shrimp of shrimp-fed sharks or of naïve sharks (Table 3.4, Figure 3.8), which were also not different from each other (Chapter 1, Table 3.18: $U = 40.0$, $p = 0.700$).

Table 3.4. The effects of worms-foraging experience on latencies to consume worms. Latencies to consume shrimp of worm-fed sharks were compared to those of naïve sharks and of shrimp-fed sharks. Latencies to consume shrimp were analyzed using Mann-Whitney U tests.

Experience level (set of sharks)	# of sharks	Median (seconds)	Range (seconds)	Mann-Whitney U (p)
naïve (D)	8	109	58.8- 1140	26.0 (0.529)
worm-fed (C)	8	185	68.8-401	
shrimp-fed (B)	9	232	42.5- 465	31.0 (0.630)

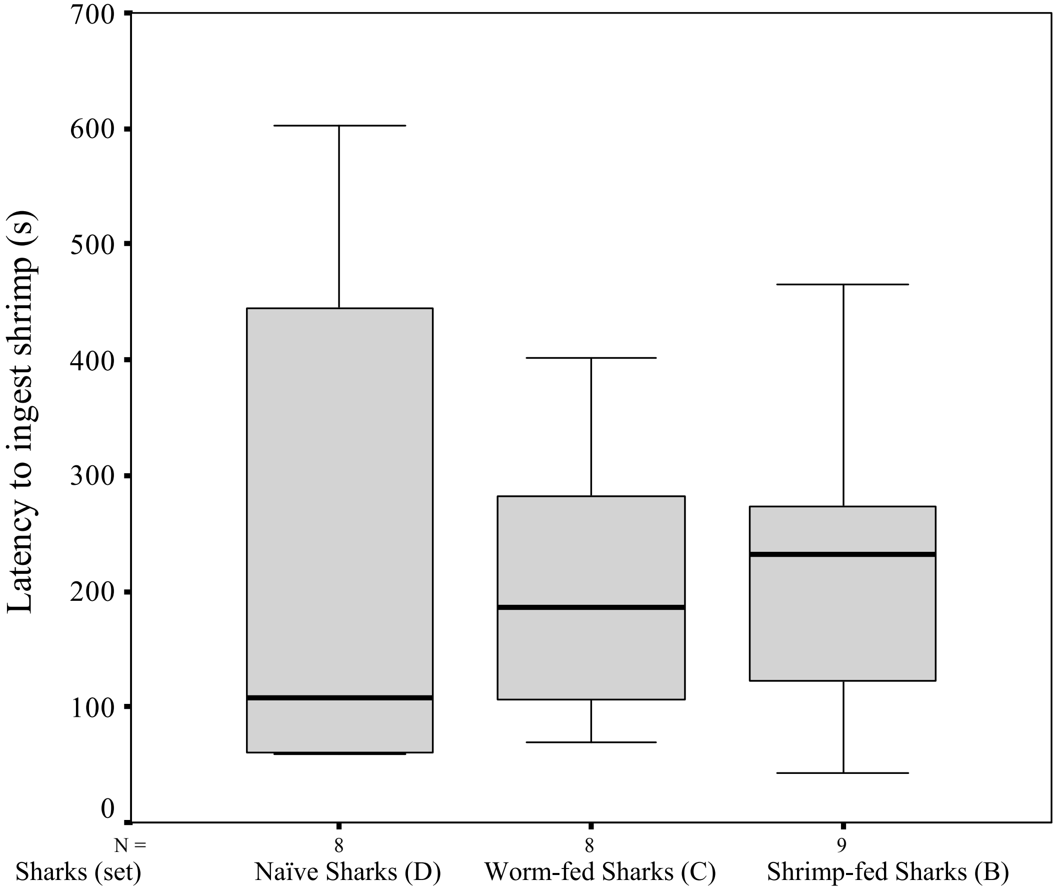


Figure 3.8. The effects of worm-foraging experience on latencies to consume shrimp. Naïve sharks, after being fed small cubes of fresh tuna on all previous days, were foraging on live shrimp for the first time. Worm-fed sharks, after 20 consecutive days of experience foraging on worms, were foraging on live shrimp for the first time. Shrimp-fed sharks had 19 consecutive days of experience foraging on live shrimp. Black solid bars within each box represent median values. Boxes represent quartiles above and below medians. Whiskers of boxes represent the minimum and maximum values other than outlier values. Outlier values are not shown but are included in statistical analyses.

When foraging trials are analyzed for discrete behaviors, some differences between worm-fed sharks and shrimp-fed sharks are evident. Worm-fed sharks did not initially adopt the rapid, perimeter searching behaviors of shrimp-fed sharks; rather, they began searching with the slow, turning method they used when foraging on worms (central searching), although they moved more rapidly. Two worm-fed sharks, however, did start perimeter searching by the end of their trials. Latencies to first attack shrimp for worm-fed sharks (median = 27.7s, range = 0.10-110s) are not significantly different from those of naïve sharks (median = 42.8s, range = 0.10-84s, U = 37.0, p = 0.575) or from those of shrimp-fed sharks (median = 15.3s, range = 3.73-57s, U = 28.0, p = 0.441). Worm-fed sharks attacked shrimp using a significantly greater proportion of pin-attacks (median = 0.58, range = 0-1.00) than did shrimp-fed sharks (median = 0.23, range = 0-0.60, U = 12, p = 0.021), but not naïve sharks (median = 0.57, range = 0-1.00, U = 33, p = 0.915). Durations of transport for worm-fed sharks (median = 16.3 s, range = 2.63-34.2 s) are not significantly different from those of naïve sharks (median = 29.7 s, range = 6.0-256 s, U = 19.0, p = 0.181) or those of shrimp-fed sharks (median = 21.6 s, range = 7.2-66 s, U = 50.0, p = 0.178). Worm-fed sharks do not use significantly more transport bouts (median = 8, range = 1-18) when consuming shrimp than shrimp-fed sharks (median = 9, range = 3-28, U = 52.0, p = 0.121) or naïve sharks (median = 8, range = 2-50, U = 49.5, p = 0.065).

Discussion

While shrimp-fed sharks were not more efficient at foraging on worms for the first time than naïve sharks, they were not less efficient than worm-fed sharks. Shrimp-fed sharks may be able to transfer some but not all predatory skills to foraging on worms. Similarly, shore crabs that had previously fed on dogwhelks were better at foraging on mussels than naïve shore crabs, but were not as efficient as crabs that had previously fed on mussels (Hughes and O'Brien, 2001). Although dogwhelk spires and mussel umbones require similar skills to crack open, other prey-handling skills are specialized to different morphological features of each prey.

When foraging on worms, shrimp-fed sharks maintained the perimeter searching behavior they used when foraging on shrimp, perhaps because they could not localize the odor cues from the worms. Sharks have difficulty finding an odor source in turbulent water (Gardiner and Atema, 2007). Turbulence created by rapid perimeter searching may have dispersed worm odor and confused shrimp-fed sharks. Perimeter searching did not, however, seem to reduce shrimp-fed sharks' abilities to find worms as their latencies to first attack were not different from those of worm-fed sharks.

Shrimp-fed sharks had longer durations of transport than worm-fed sharks and required several transport bouts to consume worms while worm-fed sharks only required one or occasionally two bouts. Shrimp-fed sharks were therefore not using the same method to transport worms as worm-fed sharks. Similarly, dogwhelks that had previously foraged only on barnacles did not adopt specialized mussel-eating skills even after 8 weeks of experience foraging on mussels (Rovero *et al*., 1999). Worms may have been difficult for shrimp-fed sharks to ingest for several reasons. Worms were typically heavier and longer than shrimp; larger food requires more suction to ingest (Nauwerlaerts *et al*., 2007; Wainwright and Day, 2007). Leopard sharks (*Triakis semifasciata*) are able to modulate the amount of suction they produce when feeding on foods of different sizes

(Ferry-Graham, 1998b), and whitespotted bamboosharks may be able to modulate suction as well (Lowry and Motta, 2007a). Shrimp-fed sharks may therefore not have used as much suction when feeding on worms as worm-fed sharks did. Also, shrimp-fed sharks may have tried to kill the worm before complete ingestion. Unlike shrimp, worms can not be easily killed and are therefore moving during ingestion.

Surprisingly, skills used to forage on relatively non-elusive worms can be used to forage efficiently on highly elusive shrimp. Worm-fed sharks' latencies to consume their first shrimp are not different from naïve sharks' latencies to consume their first shrimp but their overall capture rates are higher than those of naïve sharks, suggesting that sharks may be adjusting their predatory behaviors to the novel prey over the course of the three trials. Worm-fed sharks maintained their central searching behaviors but two worm-fed sharks had adopted perimeter searching by the end of their trials, also suggesting that worm-fed sharks adapted their behaviors to foraging on shrimp. Worm-fed sharks used a higher proportion of pin-attacks than shrimp-fed sharks. Because worm-fed sharks were moving slower, they may have been able to approach shrimp without causing rapid escape responses, unlike the rapidly moving shrimp-fed sharks. A close approach may be necessary for pin-attacks to be effective. Worm-fed sharks and shrimp-fed sharks had similar durations of transport, using similar numbers of transport bouts to ingest shrimp. Because worm-fed sharks did not spit shrimp out, it could not be determined whether sharks killed the shrimp before transporting. These results are similar to those found in garter snakes where foraging on worms and foraging on fish require specialized skills (Burghardt and Krause, 1999), but previous experience with one aids in foraging on the other (Krause and Burghardt, 2001). It seems to be easier for the sharks to switch from foraging on worms to foraging on shrimp than the reverse; some foraging techniques, such as perimeter searching, may be easier to learn than others, such as transporting worms.

Worm-fed sharks may, in time, become more efficient than shrimp-fed sharks at foraging on shrimp. When shrimp-fed sharks were younger and smaller, they may have learned predatory skills that are no longer the most efficient skills for older, larger sharks. For example, rapid perimeter searching behavior is not necessary for a 40-day-old shark to find a shrimp (as demonstrated by worm-fed sharks finding shrimp by slowly searching the tank), but it may have been necessary when the shark was younger. When a shark is swimming rapidly, it can not use a pin-attack to capture a shrimp, even though pin-attacks, by limiting the shrimp's escape routes, may be more successful than lunge-attacks. Since latencies to first attack by shrimp-fed sharks and worm-fed sharks were similar, rapid perimeter searching is not less efficient than slow central searching. Sharks may be unable to change one set of efficient behaviors (searching) based on the success of a different set of behaviors (attacking). The efficiency of the learned searching behaviors may limit predatory efficiency of shrimp-fed sharks.

Both shrimp-fed sharks and worm-fed sharks maintained their search behaviors when foraging on novel prey, suggesting that they learned where prey were more likely to be found and concentrated their search on these areas. Area-concentrated searching has also been found in other predators. Sticklebacks (*Gasterosteus aculeatus*) learned to search only those areas of a maze that had previously contained prey and to avoid areas that had never contained prey (Beukema, 1968). Carrion crows (*Corvus corone*) that learned to search for baits under red mussel shells within a given area ignored red mussel shells outside that area (Croze, 1970). Worm-fed sharks may be able to learn fairly quickly that shrimp are more likely to be found along the perimeter of the tank and adjust their search behavior accordingly.

In general, foraging on initial prey did not interfere with the ability to forage on novel prey. Proactive interference, the degraded ability to perform a second response due to learning an initial response, has been shown in a number of situations (review: Bouton, 1993) including spatial and visual discrimination and avoidance learning in rats (Amundson *et al*., 2003; Gleitman and Jung, 1963; Maier and Gleitman, 1967, Spear *et al*., 1980) and operant conditioning tasks in pigeons (Santiago and Wright, 1984; Thomas *et al.*, 1981, 1985). Proactive interference does not seem to affect foraging abilities of bamboosharks because sharks foraging on novel prey are not less efficient than naïve sharks; there may, however, be subtle effects that could not be measured in this study.

Overall, these results presented in this chapter suggest that whitespotted bamboosharks can maintain or easily modify many predatory skills when foraging on novel prey. Generalist predators face a large burden because, while they have more prey species available to them than a specialist does, the most successful foraging strategy may be different for each type of prey (Morse, 1980). In order to overcome this difficulty, a predator may develop a single stereotyped foraging strategy that is effective for many prey species or it may develop an basic foraging strategy that can be easily adapted to each prey species. Alternatively, a generalist may employ completely different predatory behaviors for different prey types. Whitespotted bamboosharks seem be able to utilize behaviors learned foraging on one prey type when foraging on novel prey types. In addition, they may be able to quickly learn new foraging strategies that are specialized for specific prey types.

GENERAL DISCUSSION

This dissertation examines the development of predatory behaviors of whitespotted bamboosharks, *Chiloscyllium plagiosum*. The capture and consumption of prey are among of the first challenges a neonatal predator confronts. If it can not find and capture food soon after endogenous feeding has ended, the neonate has an increased risk of starvation and predation (Blaxter and Ehrlich, 1974; May, 1974; Rice *et al*., 1987). Predatory success may be improved by several factors including post-natal maturation and experience with prey.

Whitespotted bamboosharks improve their predatory abilities with both age and experience. For both younger and older sharks, predatory efficiency improved after twenty days of foraging on either live worms or shrimp. Several neonatal animals improve their predatory abilities with increasing maturation and experience. Over the course of their first year of life, whitespotted bamboosharks improve their capture rates of small, bite-sized shrimp (Lowry and Motta, 2007a). After periods of predatory experience, squid (*Loligo opalescens* - Chen *et al*., 1996), red-backed salamanders (*Plethodon cinereus* - Gibbons *et al*., 2005), and garter snakes (*Thamnophis sirtalis* - Krause and Burghardt, 2001) improve their predatory abilities.

Maturation alone improves the ability of naïve whitespotted bamboosharks to forage on shrimp. Shrimp are highly elusive, translucent, and hard-bodied and, therefore, capturing them efficiently may require sharks to attain a certain level of neuromuscular, sensory or morphological development. The retina of brown banded bamboosharks, *Chiloscyllium punctatum*, continues to develop during the months after hatching (Harahush, B., pers. com.), potentially affecting the ability to visually detect shrimp.

Older sharks may produce more suction when feeding, enough to overcome an elusive prey's flight response. Kinematic studies of hatchling swellsharks (*C. ventriosum*- Ferry-Graham, 1998a) and whitespotted bamboosharks (*C. plagiosum* - Lowry and Motta, 2007a), showed that sharks' feeding behavior became more suction-dominated with maturation.

Experience alone improves the ability of naïve whitespotted bamboosharks to forage on worms. Worms are relatively non-elusive and are therefore easy to capture once they have been detected. Experience improves sharks' abilities to find worms and consume them once they have been captured. Experienced sharks may improve their ability to find worms by associating sensory cues with worms or by increasing their attention to those sensory cues. After fifteen-spined sticklebacks were given experience with a prey type, they oriented to the prey at further distances than when they were naïve (Croy and Hughes, 1991a). Experienced sharks may learn how to handle worms once they are captured. After experience, fifteen-spined sticklebacks had shorter handling times and fewer prey reorientations than when they were naïve (Croy and Hughes, 1991a).

Maturation and experience act in concert to improve the predatory abilities of whitespotted bamboosharks. The maturation level of the shark may determine which potential prey species the shark can effectively utilize; more-elusive or harder-to-eat prey are added as the shark grows. Experience improves the shark's efficiency foraging on that prey; sharks become better able to find and handle prey after previous encounters. In addition, sharks are able to retain predatory skills during an 18-day period when live prey are unavailable. Several fish species vary on the length of time they are able to retain predatory skills, from two days (fifteen-spined sticklebacks, *Spinachia spinachia* - Croy and Hughes, 1991a) to more than five weeks (silver perch, *Bidyanus bidyanus* - Warburton and Thomson, 2006). Skill retention may be very helpful in an unpredictable prey environment as sharks would not have to expend time and energy to relearn foraging skills. Such skill retention would be most beneficial with prey that require a good deal of experience to catch or are difficult to catch, such as shrimp.

Experience with one type of prey improves the ability of sharks to forage on novel prey. Although sharks learn different search, attack and handling behaviors when fed shrimp only or worms only, they are able to adapt those behaviors to foraging on the other prey. Similarly, garter snakes, *Thamnophis sirtalis*, use different skills when foraging on worms or foraging on fish require (Burghardt and Krause, 1999), but previous experience with one aids in foraging on the other (Krause and Burghardt, 2001). Sharks that had experience foraging on worms may be more efficient at foraging on shrimp than shrimp-fed sharks. When shrimp-fed sharks were younger and smaller, they may have learned predatory skills that are not the most efficient skills for older, larger sharks. Because of their past experience, they may be unable to learn more efficient shrimp-foraging skills. These results may explain why experience alone did not improve the abilities of sharks to forage on shrimp.

These results have implications for shark conservation. Shark populations are in global decline due to over-fishing and accidental mortality as by-catch (Castro *et al.*, 1999; Bonfil, 1997; Musick *et al.*, 1993; Compagno, 1987). Recovery of many species may take many years due to sharks' low reproductive potential and slow maturation (Castro *et al.*, 1999; Musick *et al.*, 1993). In addition, the loss of nursery habitats due to anthropogenic factors may hamper recovery efforts (Beck *et al*., 2001; Bonfil, 1997). Because many sharks develop predatory skills while in their nursery habitat, any changes to these habitats may result in changes in behavioral development. Behaviors that are essential for survival when sharks move to deeper water habitats may be affected. If appropriate prey species are not available to neonatal sharks due to anthropogenic effects, experiential improvements in foraging abilities that impact later survival may not occur. Protection of nursery habitats may be essential for the recovery of declining shark populations.

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