Food Webs 15 (2018) e00087

Contents lists available at ScienceDirect

Food Webs

journal homepage: www.journals.elsevier.com/food-webs

American alligators are predators of Paddlefish: An undocumented predator-prey linkage affecting Paddlefish population dynamics

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ARTICLE INFO

Article history:
Received 19 February 2018
Received in revised form 15 May 2018
Accepted 15 May 2018
Available online xxxx

Keywords:
Predation
Southeastern U. S.
Top-down control

ABSTRACT

It has been suggested that adult Paddlefish *Polyodon spathula* have no natural predators with the exception of humans and few heterospecific freshwater fishes which tend to target only early life stages (i.e., larvae, age-0 juveniles). However, we photographically documented another natural predator, the American alligator. The predation event took place in a small waterbody (0.8 ha) over a 45-minute period during which the alligator frequently transported the Paddlefish onto land, and retracted back into the water. This is the second event of its kind documented in this small river system. From a capture-recapture study, we have identified over 100 fish in the pool, 50 of which were surgically implanted with an acoustic transmitter for continuous monitoring of emigration. However, two have unexplainably disappeared, presumably from predation. Given the two known alligator mortality events, and two potential additional events suggested by transmitter disappearance, we presume adult Paddlefish predation may be more common than previously thought. Although adult Paddlefish were thought to have no natural predators, this newly documented predator-prey linkage provides support that alligator predation on Paddlefish may occur more frequently in southeastern waterbodies than previously believed, particularly when Paddlefish are in high abundance or in relatively small systems such as ours.

Adult Paddlefish *Polyodon spathula* (Polyodontidae) (Fig. 1) are believed to have no natural predators because their large body size exceeds gape width of most predators. The primary mortality source for adult Paddlefish is harvest for sport and caviar throughout many large rivers that drain to the Gulf of Mexico. Considerations for heterospecific predators have been confined to other freshwater fishes including Sauger *Sander canadensis*, Walleye *S. vitreus* (Mero et al., 1994; Parken and Scarnecchia, 2002), and Channel Catfish *Ictalurus punctatus* (Tidwell and Mims, 1990) which target early life stages (i.e., larvae, age-0 juveniles). However, in freshwater systems of the southeastern United States, the range of the Paddlefish overlaps with a large-bodied predator, the American alligator *Alligator mississippiensis* (Alligatoridae), hereafter alligator. We photographically documented an alligator that captured a free-swimming Paddlefish from a 0.8-hectare waterbody (33.271780, −88.775906) (Fig. 2). The alligator, estimated to be >3.5 m in total length, consumed a Paddlefish estimated to be 1.5 m in total length. Length estimation for the alligator was determined by estimating the distance in inches from the front of the alligator's snout to the eyes which is proportional to the total body length in feet. This also suggests the alligator's sex to be male based on size and morphology. We witnessed the predation event over a 45-minute period, during which the alligator periodically brought the fish onto land and retracted back into the water. This is the second documented Paddlefish predation by an alligator in this small river system. These predation events provide evidence that alligators are a natural predator of Paddlefish.

Alligators are distributed throughout contiguous coastal salt marshes and inland wetland systems (Subalusky et al., 2009) of southeastern states including Arkansas, Oklahoma, Texas, Louisiana, Mississippi, Alabama, Georgia, Florida, North Carolina, and South Carolina (IUCN, 1996) and serve an important role in their ecosystems, as engineers and apex, predators. They manipulate their environment through the creation of seasonal wallows, or burrows (also known as "gator holes") during the breeding season which retain water and serve as a refuge for a diverse range of animal taxa including amphibians, fish, turtles, snails, and fish-eating birds (McIlhenny, 1935; Craighead, 1968; Jones et al., 1994; Mazzotti and Brandt, 1994; Palmer and Mazzotti, 2004). They also help to shape their communities via top-down control, where the predator controls the structure of population dynamics of other species within the ecosystem. Alligators, like some other apex predators (e.g., bears, raptors) have the ability to regulate both aquatic and terrestrial animal populations (Carpenter et al., 1985; Rosenblatt and Heithaus, 2011; Nifong and Silliman, 2013). Alligators have a wide foraging breadth, capable of consuming taxonomic groups ranging from seeds, aquatic and terrestrial insects, crustaceans, mollusks, fishes, amphibians, reptiles, birds, and various mammals (Nifong et al., 2012;

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https://doi.org/10.1016/j.fooweb.2018.e00087
2352-2496/

Fig. 1. Adult American Paddlefish body morphology and size reference. Paddlefish are capable of reaching impressive sizes. This individual was nearly 1.6 m in length, and weighed over 17 kg. The photograph was taken at Sam D. Hamilton Noxubee National Wildlife Refuge, Brooksville, Mississippi (33.271780, −88.775906), during Paddlefish population sampling in February 2017.

Rosenblatt et al., 2015) and even larger-bodied prey including deer (*Odocolieus* spp.) (Shoop and Ruckdeschel, 1990).

Prey selection by alligators is a function of the prey community composition. In ecosystems dominated by easy-capture prey items, such as mollusks, alligators take advantage of these prey. In the absence of such prey, they must pursue more difficult, mobile prey which are often associated with lower attack success rates, and longer handling times (Rosenblatt et al., 2015) proportional to prey size and gape width (Kislalioglu and Gibson, 1976). Given alligators tendencies to feed at or near the water's edge, fish contribute a significant proportion to alligator diets (Delany and Abercrombie, 1986; Grigg and Kirshner, 2015). However, fish taxa may be underrepresented in stomach content analyses due differential digestion rates compared other taxa such as turtles, snails, crayfish, birds, and mammals (Delany and Abercrombie, 1986; Rosenblatt et al., 2015).

Top-down control of Paddlefish populations was previously assumed to be limited, with the exception of angler-harvest. Other reports on mortality have included discard mortality from snagging (Scarnecchia and Stewart, 1997), commercial bycatch (Dieterman et al., 2000; Paukert and Fisher, 2001; Quinn et al., 2009; Bettoli and Scholten, 2006; Kerns et al., 2009; Ridgway, 2016), boat propeller strikes (Purkett, 1963; Scarnecchia and Stewart, 1997; Killgore et al., 2011; Whiffield and Becker, 2014), and passage through dams (Coker, 1929; Rosen and Hales, 1980). In systems where the range of alligators and Paddlefish overlap, alligator predation on Paddlefish may be an alternate source of mortality, perhaps contributing to biased estimates of population parameters such as abundance, mortality and survival.

Fig. 2. American Alligator feeding on an adult Paddlefish. The Alligator periodically transitioned between the turbid water and densely vegetated riparian area during feeding. The photograph was taken at Sam D. Hamilton Noxubee National Wildlife Refuge, Brooksville, Mississippi (33.271780, −88.775906), during Paddlefish population sampling in June 2017.

Paddlefish may serve as a sub-optimal prey target for alligators in the absence of easier-obtained resources. Paddlefish are one of the largest freshwater fishes in the U.S., with sizes exceeding 1.8 m and 45 kg (Ross and Brenneman, 2001). They have a primarily cartilaginous skeletal structure, except for their jaws, a scale-less exterior, and highly-compact muscle tissue, making them easily metabolized by the highly acidic digestive fluids (pH ≤ 2) within the gastric system of alligators (Coulson et al., 1964). Additionally, their swimming pattern and "cruiser" morphology (Hoover et al., 2005) may make Paddlefish a desirable prey target given capture success by alligators. Hoover et al. (2009) cautiously described the biomechanics of swimming by juvenile Paddlefish as "that of pelagic, slow-swimming sharks which also have long rostra (although not as long as those of paddlefish) and heterocercal tails." While potentially easier to capture than other fish taxa, we believe their pelagic tendencies and constant swimming may present some challenges for ambushing predators such as alligators, associated with moderate attack success and a longer handling time. Following prey capture by an alligator, items must be manipulated prior to consumption. This is achieved through "whiplashing", or lifting prey from the water and thrashing (as was also witnessed during our observation), or "death rolling," as another method of prey handling to compensate for the Alligator's lack of rotational flexibility (Grigg and Kirshner, 2015). During our observation, the alligator manipulated the Paddlefish carcass in the shallow transitional zone between the aquatic and terrestrial interface (Fig. 2) before retracting into the water with the Paddlefish.

This observation is part of research to estimate Paddlefish population dynamics and evaluate movement in a small, regulated waterbody in northeast Mississippi. We implanted 50 acoustic transmitters between 2016 and 2017 into a subset of our tagged Paddlefish ($n > 100$ unique individuals) during this effort. We continuously monitor emigration using a multiple-receiver acoustic array downstream of our sampling area. This provides us with known times that transmitters are within the detection distance of our receivers to confirm emigration. Based on our monitoring detections, we have evidence that two acoustically tagged Paddlefish which were not detected by the downstream array, have unexplainably disappeared from the small waterbody, presumably from predation (Fig. 3). Tag failure or illegal angler harvest are potential sources of tag disappearance. However, an acoustic receiver in the waterbody allows us to monitor the duration of time that acoustically tagged Paddlefish remain in the waterbody throughout our study. Faulty tags can be determined immediately by the absence of detections in the waterbody following transmitter implantation or by confirming whether or not the transmitter is operational during subsequent recaptures. We presume that if an alligator consumed an acoustically tagged Paddlefish, the transmitter would likely remain detectable following defecation or regurgitation in the pool. Illegal angler harvest is