

Eating between the lines: functional feeding response of bonnetheads (*Sphyrna tiburo*)

Andrea M. Kroetz · Sean P. Powers

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Abstract Mobile mesopredators can have strong influences in the structuring of marine food webs in shallow coastal ecosystems. Few quantitative estimates of the effects of predation on prey populations by highly mobile mesopredators exist, yet they are necessary to evaluate the impact mesopredators have on prey resources. Quantifying a predator's functional response provides valuable information on how a predator's per capita consumption rate of prey can influence community structure and prey populations. We examined the functional response of bonnetheads (*Sphyrna tiburo*) to one of its few natural prey items brown shrimp (*Farfantepenaeus aztecus*) to determine if per capita feeding rates would increase with increases in prey density. We simulated natural conditions in outdoor mesocosms and offered live prey at varying densities. The functional response of a predator can take one of three forms: linear (type I), rise to an asymptote (type II), and a sigmoid shape (type III). Bonnetheads consumed prey proportional to prey density and demonstrated a response that was in between a type I ($R^2=0.847$, $p<0.01$) and type II ($R^2=0.877$, $p<0.01$) functional response. Bonnetheads showed an increased rate of consumption with initial low prey densities but high

densities of available prey did not consistently result in increased consumption rates. At the maximum prey density offered, bonnetheads consumed less prey than at intermediate densities. Bonnetheads may not have as strong of an influence on prey populations at high prey densities compared to predation impacts at low densities. Bonnethead per capita feeding rates did not conform to a type I, type II, or type III functional response and our results suggest that bonnetheads follow a functional response continuum more closely. This study highlights the importance and difficulty in understanding the feeding ecology of highly mobile mesopredators.

Keywords Small coastal shark · Feeding ecology · Predation · Predator–prey dynamics · Elasmobranch

Introduction

The dynamics between predators and their prey are important in the structuring of communities and prey populations (Lima 1998; Myers et al. 2007; Heithaus et al. 2008). Quantifying predation rates is important both ecologically and economically (Fogarty and Murawski 1998; Myers et al. 2007; Ajemian and Powers 2012), as numerous economically important species are prey for upper level predators. For example, the diets of small coastal elasmobranchs often include commercially important mollusks and some studies have implicated mesopredation in the decline of local fisheries (Peterson et al. 2001; Myers et al. 2007).

A. M. Kroetz · S. P. Powers
Department of Marine Sciences, University of South
Alabama,
Mobile, AL 36688, USA

A. M. Kroetz (✉) · S. P. Powers
Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island,
AL 36528, USA
e-mail: akroetz2@gmail.com

Clearly, understanding the foraging ecology of elasmobranchs is challenging due to their large size and mobile nature; however, smaller sharks found in coastal areas provide a potentially tractable study species. Given the importance of understanding predator–prey dynamics, quantifying a predators functional response is a key starting point for improved management of both predator and prey species.

Predators may respond to changes in local prey density in a numeric or functional manner. The functional response, which describes how predator consumption rate varies with prey density (Solomon 1949), is ecologically important because of its potential influence on prey populations. The number of prey successfully consumed by predators can be measured empirically to characterize the functional response curve. Three main types of functional response have been described for predators (Holling 1959). Type I functional response is a linear function where the number of prey consumed is proportional to the density of prey (i.e. proportional to encounter rate). A type II response occurs when the rate of consumption rises at a decelerating rate to an asymptote as satiation is reached. A type III functional response is sigmoid and reaches an upper asymptote as satiation is reached. This type of response is density dependent as a threshold density is needed for the predator to begin feeding (Real 1977; Hassell 1978).

Many studies have focused on the functional responses of parasitoids and arthropods (e.g. Lipcius and Hines 1986; Rudolf 2008; Rindone and Eggleston 2011) due to their role as consumers of economically important resources and their ease of manipulation. Functional responses of bony fish predators has also been examined but to a lesser extent (Townsend and Risebrow 1982; Buckel and Stoner 2000; Rindorf and Gislason 2005). To our knowledge, only two previous studies have determined the functional responses of elasmobranchs (Reeve et al. 2009; Moustahfid et al. 2010). Reeve et al. (2009) noted that when given a choice, juvenile lemon sharks (*Negaprion brevirostris*) preyed selectively on yellow fin mojarra (*Gerres cinereus*) with increasing prey density, consistent with a type II functional response. More recently, type II and type III responses were described for spiny dogfish (*Squalus acanthias*) and winter skates (*Leucoraja ocellata*), respectively (Moustahfid et al. 2010). The authors noted that teleost and elasmobranch predators responded differently to various prey species, depending on their morphologies and hunting strategies, and that these relationships required further

study before they could be used in multispecies and ecosystem based modeling (Moustahfid et al. 2010).

Bonnetheads (*Sphyrna tiburo*) are a relatively small (80–150 cm) coastal shark common to the Atlantic Ocean and Gulf of Mexico (Compagno 1984). Bonnetheads feed primarily on crustaceans in addition to fish and other invertebrates (Cortés 1999; Bethea et al. 2007). Several studies have examined age and growth (Carlson and Parsons 1997), life history (Parsons 1993), and dietary habits (Cortés et al. 1996; Cortés 1999) of this species in the western North Atlantic Ocean. Despite bonnetheads being one of the more common sharks in the coastal waters of the northern Gulf of Mexico, little is known about the feeding ecology of this species beyond simple diet analyses. The purpose of this investigation was to measure the functional response of bonnetheads to changing densities of a natural prey species, brown shrimp (*Farfantepenaeus aztecus*), an important commercial species in the Gulf of Mexico. Predation rates typically increase with increasing prey density (Holling 1959) and our goal was to determine if predation rates by bonnetheads followed this model.

Materials and methods

We examined the functional response of bonnetheads in outdoor mesocosms between June and October 2011 and June and October 2012. Water temperatures in 2011 ranged from 25.6 to 31.8 °C and in 2012 ranged from 24.7 to 31.9 °C. Bonnetheads were collected with gillnet and hook and line sampling from the coastal waters of Dauphin Island, AL, USA. Bonnetheads collected via gillnets were carefully removed from the nets and care was taken to not damage the gills or cephalofoil of the sharks. Morphometrics (precaudal, fork, natural, and stretch total lengths to the nearest mm) and weight (kg) were recorded for all sharks. Sex was determined using external characteristics and maturity in males was assessed following Clark and von Schmidt (1965). Sharks were transported to the Dauphin Island Sea Lab (DISL) mesocosm facility in tanks measuring 1.0×0.5×0.4-m (length x width x depth) and were supplied with ambient seawater and oxygen. At the DISL, sharks were allowed to acclimate in outdoor flow-through mesocosms measuring 5.0×1.2×1.0-m (diameter x height x depth). Three mesocosms were used as holding tanks and a thin layer of silt lined the bottom of each tank due to the flow-through nature of the mesocosm

system. Bonnetheads were housed in small groups ($n=3$ per tank) and were individually identified by small dorsal punches and by natural markings on individual sharks. Bonnetheads were fed a mixed diet of fish, shrimp, and squid during their acclimation period which ranged from 4 days to 2 weeks. Acclimation was deemed sufficient when sharks were seen actively feeding in their holding tanks.

The experimental mesocosm was designed to mimic natural conditions and was lined with a 2.5-cm layer of clean sand that supported four 1 m² panels of artificial seagrass units consisting of 267 shoots of green ribbon to mimic turtle grass (*Thalassia testudinum*). This density closely resembled that of seagrass beds in the northern Gulf of Mexico (Spitzer et al. 2000). Mesocosms were filled with seawater via a flow-through system and temperatures and salinities were monitored daily using a digital thermometer (Forestry Suppliers model 89103) and refractometer (VEE GEE Instruments model STX-3), respectively. Both male and female bonnetheads sampled from nearby waters were used in the experiments. Bonnetheads were randomly selected from the holding tank for use in experiments and were starved for 24 h prior to trials.

Bonnethead daily ration is estimated to be between 0.51 and 4.38 % body weight day⁻¹ (Tyminski et al. 1999; Bethea et al. 2007) and percentages of live prey that encompassed the high and low ends of daily ration were used (Table 1). Brown shrimp used in the trials were collected from local fishermen. Prey density treatments were randomly selected and bonnetheads were allowed to acclimate in the experimental mesocosm with caged shrimp for 30 min prior to trials. At the end of the acclimation period, prey were released into the mesocosm where trials lasted for 24 h. At the end of each trial, the shark was removed, the mesocosm drained, and remaining prey were collected and counted. Each prey density treatment was replicated three times for a total of 27 trials. After the completion of all trials, sharks were either tagged on the anterior dorsal fin with a plastic swivel tag and released or were donated to the Estuarium at the DISL to be put on public display for educational purposes.

To determine the form of functional response, a generalized equation derived by Real (1977; 1979) was used:

$$N_a = \frac{K \cdot N_t^\beta}{X + N_t^\beta}$$

where N_a = number of prey eaten, K = the maximum rate of consumption (satiation), N_t = initial prey density, X =

density of prey that generates half-maximum feeding ($N_a=0.5 K$), and β = the parameter associated with the form of functional response curve (Real 1979). The form of functional response is linear when $\beta=0$ (type I response), decelerating rising to an asymptote when $\beta=1$ (type II response) and sigmoid when $\beta>1$ (type III response) (Real 1979).

Data measuring the functional response of bonnetheads were analyzed using R Statistical Platform Version 2.15.1 (R Core Team 2012). Mean differences in prey consumed were analyzed using linear and non-linear regressions and were compared to the generalized model of functional response curves. Akaike information criterion (AIC) values were used to select the most parsimonious model.

Results

Abiotic and biotic factors used in the experiments were representative of natural conditions and ranges. Average temperature and salinity during trials in 2011 were 29.6 °C (± 0.5 SE) and 24.6 ppt (± 0.9 SE) and in 2012 were 29.2 °C (± 0.5 SE) and 24.4 ppt (± 0.9 SE), respectively. Bonnethead mean length was 908 mm TL (± 12.1 SE) and mean weight was 2.6 kg (± 0.1 SE) (Table 1). Mean length of shrimp used in trials was 111.2 mm (± 2.0 SE) and mean weight was 9.2 g (± 0.5 SE). Data met the criteria for the assumptions of regression analysis and therefore were not transformed.

Bonnethead feeding rate increased with initial increasing prey density (Fig. 1), and linear regression ($R^2=0.847$, $p<0.01$) and second order polynomial non-linear regression analyses ($R^2=0.877$, $p<0.01$) found the relationships to be significant. AIC values were used to compare the fit of the models and the linear regression (AIC=39.32) and nonlinear regression (AIC=39.33) models were nearly equal (Table 2). Shark body size was non-significant ($R^2=0.07$, $p>0.18$) on consumption rates as was shark sex ($R^2=0.006$, $p>0.71$). Temperature was also non-significant ($R^2=0.003$, $p>0.789$) in overall bonnethead consumption rates.

Bonnetheads displayed a functional response that was between a type I and type II (Fig. 1). When solving for β in the generalized functional response equation, $\beta=0.2$ suggesting that bonnetheads are exhibiting a response that lies between a type I ($\beta=0$) and type II ($\beta=1$). Bonnetheads consumed approximately 50 % of available prey at low prey densities and the percentage

Table 1 Summary table of experimental design used for bonnethead functional response

Number of prey in each treatment	Prey density (m ²)	Percent daily ration	Mean shark TL±SE (mm)	Mean shark weight±SE (kg)	Mean percentage of prey consumed
2	0.1	0.7	887 (±34.8)	2.4 (±0.3)	50
4	0.2	1.4	873 (±26.5)	2.4 (±0.3)	50
6	0.31	2.0	845 (±29.8)	2.0 (±0.2)	50
9	0.46	2.7	960 (±15.8)	3.0 (±0.0)	22
11	0.56	3.4	894 (±48.2)	2.7 (±0.5)	55
13	0.66	4.0	973 (±11.2)	3.2 (±0.2)	23
15	0.77	4.7	926 (±58.0)	2.8 (±0.5)	27
17	0.87	5.4	928 (±17.4)	3.0 (±0.0)	53
22	1.12	6.0	885 (±29.3)	2.2 (±0.1)	23

The number of prey available in each treatment, the corresponding prey density for each treatment, the percentage of daily ration examined, average size and weight of bonnetheads used in each treatment, and mean prey consumed in each treatment are shown

of prey consumed fluctuated between 22 and 55 % with increasing prey densities (Table 1). Linear regression analysis on the proportion of prey consumed showed that consumption of brown shrimp remained relatively constant over all prey densities ($R^2=0.08$, $p<0.235$), suggesting that bonnetheads feed proportionally to prey density (Fig. 2).

Discussion

Previous studies have examined the potential for sharks and other elasmobranchs to impact coastal ecosystem functioning through their consumption of shellfish prey (Ajemian and Powers 2012, 2013). We designed an

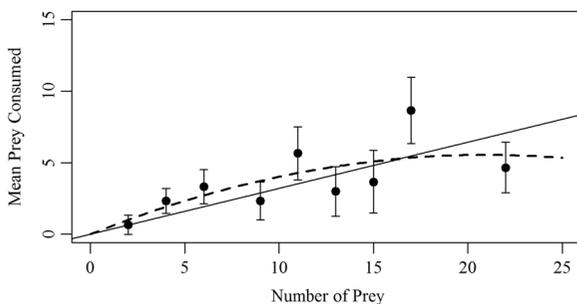


Fig. 1 Average number of prey consumed versus number of prey offered from functional response experiments. Linear (solid) and nonlinear (dashed) regression lines are shown. Error bars represent standard error. Linear ($R^2=0.847$, $p<0.01$) and nonlinear ($R^2=0.877$, $p<0.01$) regressions are both significant suggesting that bonnetheads display a functional response that is between a type I and type II

experiment to assess the functional response of bonnetheads to see how shellfish prey populations are affected. Bonnetheads did not show a distinct form of functional response; instead, this mesopredator exhibited a response that was in between a type I and type II functional response. Both linear and non-linear regression analyses on prey consumption were significant, and AIC values suggest the models fit the data nearly equally. We analyzed our data using the generalized functional response model (Real 1977, 1979) and got similar results to our regression analyses. Our data produced a value of $\beta=0.2$, which lies between a type I and type II functional response. Cumulatively, this body of evidence suggests bonnetheads do not show a distinct form of functional response.

Determining an animal's functional response is predicated on detailed knowledge of their daily ration, yet daily ration can be challenging to estimate as values may change as a function of size, sex, and region (Bethea et al. 2007). For example, daily ration was estimated for young-of-the year, juvenile, and adult bonnethead sharks in the eastern Gulf of Mexico. Daily ration changed significantly depending on sex, life stage, and region in which bonnetheads were captured (Bethea et al. 2007). A combination of field and laboratory experiments have estimated bonnethead daily ration to be between 0.51 and 4.38 % body weight day⁻¹ (Tyminski et al. 1999; Bethea et al. 2007). The type of functional response exhibited by bonnetheads may be affected by each individual shark's daily ration. The sharks that were used in this study were a mix of adult male and female bonnetheads with one sub-adult male and shark sex and

Table 2 Comparison of regression models and results of the generalized functional response model used to determine the functional response of bonnetheads

Model	df	R ²	F	P	AIC	β
Linear regression	8	0.847	44.13	0.000162*	39.32	
Nonlinear regression	7	0.877	24.95	0.0006528*	39.33	
Functional response						0.2

Asterisks indicate statistical significance

body size were not significant factors in consumption rates of bonnetheads. Prey densities that were used in the experiments were based on a range of daily rations (0.7–6.0 % body weight day⁻¹) to encompass the low and high ends of daily ration calculated for this species. Despite the wide range of prey densities used in our experiments, bonnethead functional response was not clear.

The form of a predator’s functional response can vary depending on the prey type. For example, young-of-the-year bluefish (*Pomatomus saltatrix*) exhibit a functional response more characteristic of a type I than type II response when offered striped bass (*Morone saxatilis*) or Atlantic silversides (*Menidia menidia*) as prey and similar to our study the authors were unable to discriminate between the two and identify a distinct form of functional response (Buckel and Stoner 2000). Juvenile lemon sharks feeding on grey snapper (*Lutjanus griseus*) and yellow fin mojarra exhibited switching behavior that is consistent with a type II functional response for yellow fin mojarra but no form of functional response was found for grey snapper (Reeve et al. 2009). Using field data, Moustahfid et al. (2010) showed that a type II functional response model is the best fit for spiny dogfish when

consuming Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), silver hake (*Merluccius bilinearis*), and longfin squid (*Loligo pealei*) prey. However, a type III functional response was equally probable for spiny dogfish feeding on Atlantic herring, Atlantic mackerel, and longfin squid (Moustahfid et al. 2010). Based on AIC values, a type III functional response was the best fit model for winter skates although a type II response was a reasonable fit (Moustahfid et al. 2010).

Feeding duration of elasmobranchs can vary among species and could have an effect on functional response. Juvenile sandbar (*Carcharhinus plumbeus*), lemon, and scalloped hammerhead (*Sphyrna lewini*) sharks have been shown to have varied feeding durations while juvenile lemon and sandbar sharks show asynchrony in their feeding habits (Wetherbee and Cortés 2004). In contrast, several shark species have shown preferred feeding times during the diel cycle. For example, analysis of the feeding chronology of six carcharhinid species showed that feeding occurred throughout the diel cycle with species-specific differences in feeding activity occurring throughout the day (Driggers et al. 2012). Feeding chronology of bonnetheads in the eastern Gulf of Mexico has been examined but with mixed results. Depending on the grouping of stomach content data, bonnetheads either fed more actively during the day or increased their feeding activity during the afternoon and night (Cortés et al. 1996). Further study into the feeding ecology of the bonnethead shark may lead to an increased understanding of its functional response.

The three classic forms of functional response (Holling 1959) were described over half a century ago and may not be applicable to marine systems. The three original forms of functional response were modeled after predator–prey responses of small terrestrial mammals and their prey. Marine and terrestrial predators most likely do not respond in the same manner to changes in prey density and thus may require different approaches to analyzing predator functional response.

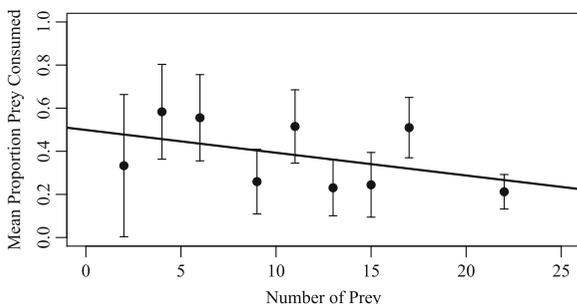


Fig. 2 Mean proportion of brown shrimp consumed versus number of brown shrimp offered from functional response experiments. Error bars represent standard error. Bonnethead consumption of brown shrimp remained relatively constant over all prey densities suggesting that bonnetheads feed proportional to prey density ($R^2=0.08$, $p<0.235$)

For example, the size scaling of a functional response coefficient in an allometric functional response model has been used to determine if terrestrial predator–prey biomass ratios have an effect on functional response (Vucic-Pestic et al. 2010). Based on predator–prey biomass ratios, the scaled coefficient allowed for a varied functional response of arthropod predators, which shifted from a type II to a type III functional response (Vucic-Pestic et al. 2010). This same method of allometric scaling was applied to a marine environment and functional response parameter estimates differed with predator size (Toscano and Griffen 2013). The advantage of allometric scaling of functional response is that it can indicate scaling behavior of a species' foraging ecology and allows for variation in a predator's functional response (Vucic-Pestic et al. 2010). Our findings suggest bonnetheads do not fit into any of the three functional response categories; rather, these small coastal sharks follow more of a functional response continuum. By focusing on the functional response coefficient, shifts in response types can be observed and may be the most appropriate approach in analyzing functional response of marine predators.

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References

Ajemian MJ, Powers SP (2012) Habitat-specific feeding in cownose rays *Rhinoptera bonasus* of the northern Gulf of Mexico. *Environ Biol Fish* 95:79–97

Ajemian MJ, Powers SP (2013) Foraging effects of cownose rays (*Rhinoptera bonasus*) along barrier island habitats of the northern Gulf of Mexico. *J Exp Mar Biol Ecol* 439:119–128

Bethea DM, Hale L, Carlson JK, Cortés E, Manire CA, Gelsleichter J (2007) Geographic and ontogenetic variation in the diet and daily ration of the bonnethead shark, *Sphyrna tiburo*, from the eastern Gulf of Mexico. *Mar Biol* 152:1009–1020

Buckel JA, Stoner AW (2000) Functional response and switching behavior of young-of-the-year piscivorous bluefish. *J Exp Mar Biol Ecol* 245:25–41

Carlson JK, Parsons GR (1997) Age and growth of the bonnethead shark, *Sphyrna tiburo*, from northwest Florida, with comments on clinal variation. *Environ Biol Fish* 50:331–341

Clark E, von Schmidt K (1965) Sharks of the central gulf coast of Florida. *Bull Mar Sci* 15:13–83

Compagno LJV (1984) FAO Species catalogue. Vol. 4. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO Fish Synop 125:251–655

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. *ICES J Mar Sci* 56:707–717

Cortés E, Manire CA, Hueter RE (1996) Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in Southwest Florida. *Bull Mar Sci* 58:353–367

Driggers WB, Campbell MD, Hoffmayer ER, Ingram GW (2012) Feeding chronology of six species of carcharhinid sharks in the western North Atlantic Ocean as inferred from longline capture data. *Mar Ecol Prog Ser* 465:185–192

Fogarty MJ, Murawski SA (1998) Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecol Appl* 8:S6–S22

Hassell MP (1978) Arthropod predator–prey systems. Princeton University Press, Princeton

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol* 23(4):202–210

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. *Can Entomol* 91:293–320

Lima SL (1998) Nonlethal effects in the ecology of predator–prey interactions. *Bioscience* 48:25–34

Lipcius RN, Hines AH (1986) Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67:1361–1371

Moustahfid H, Tyrrell MC, Link JS, Nye JA, Smith BE, Gamble RJ (2010) Functional feeding responses of piscivorous fishes from the northeast US continental shelf. *Oecologia* 163:1059–1067

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–1850

Parsons GR (1993) Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. *Environ Biol Fish* 38:25–35

Peterson CH, Fodrie FJ, Summerson HC, Powers SP (2001) Site-specific and density-dependent extinction of prey by schooling rays: generation of a population sink in top-quality habitat for bay scallops. *Oecologia* 129:349–356

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>

Real LA (1977) The kinetics of functional response. *Am Nat* 111:289–300

Real LA (1979) Ecological determinants of functional response. *Ecology* 60:481–485

- Reeve A, Handy RD, Gruber SH (2009) Prey selection and functional response of juvenile lemon sharks *Negaprion brevirostris*. *J Fish Biol* 75:276–281
- Rindone RR, Eggleston DB (2011) Predator–prey dynamics between recently established stone crabs (*Menippe* spp.) and oyster prey (*Crassostrea virginica*). *J Exp Mar Biol Ecol* 407: 216–225
- Rindorf A, Gislason H (2005) Functional and aggregative response of North Sea whiting. *J Exp Mar Biol Ecol* 324:1–19
- Rudolf VHW (2008) Consequences of size structure in the prey for predator–prey dynamics: the composite functional response. *J Anim Ecol* 77:520–528
- Solomon ME (1949) The natural control of animal populations. *J Anim Ecol* 18:1–35
- Spitzer PM, Mattila J, Heck KL Jr (2000) The effects of vegetation density on the relative growth rates of juvenile pinfish, *Lagodon rhomboides* (Linnaeus), in Big Lagoon, Florida. *J Exp Mar Biol Ecol* 244:67–86
- Toscano BJ, Griffen BD (2013) Predator size interacts with habitat structure to determine the allometric scaling of the functional response. *Oikos* 122:454–462
- Townsend CR, Risebrow AJ (1982) The influence of light level on the functional response of a zooplanktonivorous fish. *Oecologia* 53:293–295
- Tyminski JP, Cortés E, Manire CA, Hueter RE (1999) Gastric evacuation and estimates of daily ration in the bonnethead shark, *Sphyrna tiburo*. American Society of Ichthyologists and Herpetologists. 79th Annual Meeting, Pennsylvania State University, University Park, June 24–30
- Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: body masses constrain interaction strengths. *J Anim Ecol* 79:249–256
- Wetherbee BM, Cortés E (2004) Food consumption and feeding habits. In: Musick JA, Carrier JC, Heithaus M (eds) *Biology of sharks and their relatives*. CRC Press, Boca Raton, pp 223–244