BEHAVIOR WEBS OF PISCIVORES AT SUBTROPICAL LIVE-BOTTOM REEFS

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ABSTRACT

Direct visual and acoustic observations at subtropical reefs off the southeast United States and northeast Gulf of Mexico revealed a complex web of behavioral interactions within and between mid-water and demersal guilds of piscivorous fishes. While mixed-species groups of mid-water and demersal piscivores stalked and attacked common prey species independently, facilitative behaviors between mid-water and demersal piscivores were common in each region. In the latter case, prey reduced nearest neighbor distances and retreated toward the seafloor during predatory attacks by mid-water fishes. Demersal fishes subsequently attacked and consumed prey in these ephemeral high density patches. Aggregations of fishes in other trophic guilds, unassociated with predation events, modified movements of prey fishes and provided camouflage for piscivores that occurred within and along the periphery of those aggregations. Demersal piscivores often assumed the role of mid-water piscivores when the abundance of mid-water piscivores was low and when demersal piscivores were larger than mid-water species. Young-of-the-year great barracuda, *Sphyraena barracuda* (Edwards, 1771), also assumed this role, generally when other piscivores were absent. Such behavioral interactions appear to be common in these communities. If predator-prey relationships are regularly facilitated by these types of mixed-species interactions, such facilitative behaviors may be important in terms of population processes (e.g., yielding increases in prey consumption with resultant increases in growth rate, and fecundity). A framework for testing such predictions provides a pathway for assessing the population consequences of such interactions.

Hard substratum reef features, composed of sandstone and other consolidated biogenic and sedimentary materials, are widely distributed across the shallow sloping continental shelf off the southern United States and in the Gulf of Mexico (Wenner et al. 1983, Barans and Henry 1984, Sedberry and Van Dolah 1984, Thompson et al. 1999). Such reefs are generally linear features emerging from surrounding fine-grain sediments and are colonized by a diverse community of structure-forming suspension-feeding invertebrates (e.g., octocorals, sponges) and macroalgae (Thompson et al. 1999, Kendall et al. 2007). The topography of these "live-bottom" reefs ranges from only centimeters in height with a sediment veneer and sparse epifaunal invertebrate community to several meters in height with deep undercut ledges and a dense fauna along the elevated edges (Kendall et al. 2007). Accelerated flows produced as tidal currents interact with reef structures (Hamner et al. 1988, Wolanski and Hamner 1988), produce focal habitats that support aggregations of fishes, including dense aggregations of planktivorous fishes and associated resident and transient piscivores (Sedberry and Van Dolah 1984, Kracker et al. 2008). Reefs are sparsely distributed (spatially rare) so these habitats have the potential to exhibit strong but localized interactions among prey and predator species (Auster et al. 2009, 2011).

Facilitative behavioral interactions between vagile predator species in ocean settings are often difficult to describe and more difficult to quantify. The role that pelagic predators play in facilitating the feeding of seabirds by driving prey to the surface is relatively well documented (Au and Pitman 1986, Safina 1990, Ribic et al. 1997, Clua and Grosvalet 2001, Robinson and Tetley 2007), in part due to the ease of making extended observations at the air-sea interface. Such interactions are a common component of pelagic food webs, suggesting that shifts in the abundance of species may have cascading effects (Hebshi et al. 2008).

Our understanding of behavioral interactions among predators in deeper regions is limited, due in part to constraints on time underwater for direct observations and visibility that often is lower than the spatial scale at which such interactions unfold. Limited sets of observations demonstrate that piscivorous fishes operate singly, in mono-specific groups, and in mixed-species groups (Hobson 1968, Parrish 1993, Sancho 2000, Auster 2005), with individuals changing strategies and associations based on local conditions (Auster 2008). Intra- and inter-specific groups can directly facilitate prey capture by herding and confusing prey for other group members to attack or ambush (Hobson 1968, Strand 1988, Parrish 1993, Auster et al. 2009). Further, the predatory actions of one or more groups can indirectly facilitate attack and consumption of prey by other fishes outside such groups (i.e., positive behaviorally mediated indirect interactions or BMII, sensu Dill et al. 2003, also see Auster et al. 2009, 2011). Given these previous observations, it appears the full suite of interaction types (monospecific and mixed species groups as well as direct and indirect interactions to facilitate prey capture) can play out in multiple habitats with high density predators and prey.

Here we describe the behavioral interactions of piscivorous mid-water and demersal fishes at subtropical live-bottom reefs off the coast of Georgia (USA) in the western North Atlantic and off the coast of Florida in the northeast Gulf of Mexico. These observations are used to construct a topological behavior web of the interactions of mid-water and demersal piscivores, their prey, and those associated species that modify predator-prey interactions. We show that inter-specific behavioral interactions are common attributes of piscivores in these reef fish communities and propose a framework for assessing the demographic consequences of such interactions.

Methods

A modified roving diver transect (sensu Schmitt and Sullivan 1996) was employed at undercut medium and high relief "live-bottom" reefs off the southeast United States (hereinafter SEUS), primarily in Gray's Reef National Marine Sanctuary (see Kendall et al. 2005, 2007 for a full description of reef classifications), during June 2009, 2010, and late May 2011, as well as in the northeast Gulf of Mexico (hereinafter GOM) in late August–September 2010 and late June–early July 2011 (Fig. 1). Study reefs occurred between approximately 15 and 27 m depth in both regions. During survey dives, one diver collected data on the interactions between piscivores and prey (species, number, and behavioral attributes related to capture of prey), as well as for associated species that modified predator-prey interactions, for each predation event. Divers paused along transects to observe predation events as they were identified and continued only after predation events ended and predators dispersed. A second diver collected data on community composition, video, and still imagery to document habitats and species interactions, and served as a safety diver. Dive time of the second diver was not included in total time calculated for survey effort.
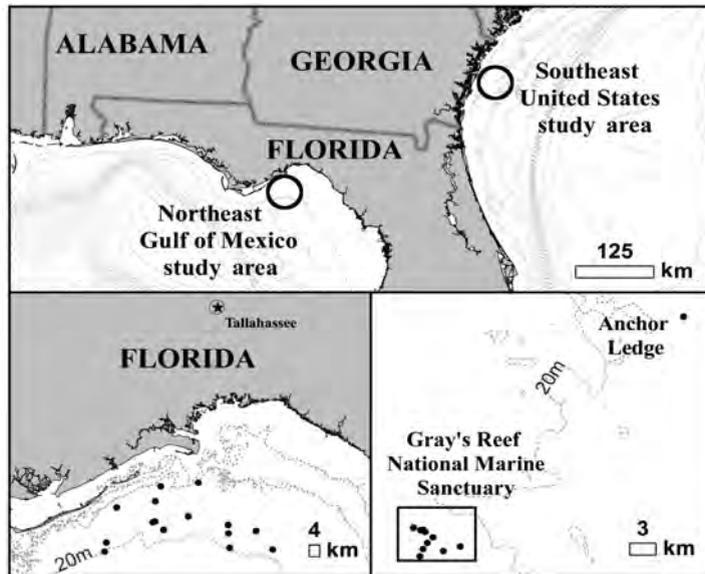
Figure 1. Location of study reefs off southeast US coast (bottom right) and in northeastern Gulf of Mexico (bottom left).

The "predation event" was the sample unit for the present study and included any component of a detection (based on visually identified changes in predator behavior with regard to orientation toward potential prey), stalk, attack, and capture sequence (sensu Lima and Dill 1990). Some events were identified from the attack phase of the sequence while others began with predators orienting toward or stalking prey and the sequence ended before an attack if prey avoided or reacted in a manner that caused the predator to end the predation sequence. Prey capture was not required for an event to be included as a sample. In all cases, a predation event required a predator or group of predators to alter prior behavior and direct movement toward potential prey and for prey to react. Multiple events could occur at the same transect location and were identified as separate events based on a break in time and new groupings of predators. Multiple attacks, by multiple individuals and species, also occurred within single events.

The roving diver technique was used because of our a priori decision to focus on the undercut ledge habitats of offshore reefs and the highly variable direction and length of ledges over the seafloor (see fig. 1c in Auster et al. 2011). Further, in an earlier 2008 study (Auster et al. 2009, unpubl data), we found that encounter rates of predation events were higher by swimming along ledges rather than making observations from stationary positions. Divers collected data on fishes observed along the tops of ledges as well as those found in the undercut crevices. Distance between divers and interacting fishes varied based on visibility but generally exceeded 2 m. Data were discarded (or not recorded) if there were obvious reactions of predators and prey to the presence of divers during events. Such reactions included flight behaviors away from divers swimming along reefs or from particular actions and movements by divers (e.g., rapid hand motions, exhalant bubbles).

Predator-prey interactions were described by enumerating the number of individuals and species of mid-water and demersal piscivores per event, abundance of prey taxa, sequence of behaviors related to predation events, interactions with associated species and habitat, and additional elements of behavioral interactions. Observations were summarized across regions in a topological behavior web that takes a functional group approach, with interaction strengths quantified for each link between functional groups for each region. Interaction

strength values are the percent occurrence of each link based on the total number of events in each region. Species level interactions were identified using FoodWeb 3D software (version 1.01) and based on the total number of links to co-occurring piscivores summed across all events for each region. Hierarchical-clustering (PRIMER software version 5.2.8) was implemented to identify patterns in species associations among events within each region using standardized log (x+1)-transformed abundance data for each species and single linkage clustering with ranked similarities. Ranked similarities, rather than actual similarity values, were used to facilitate comparisons of dendrograms for each region.

A high-resolution Dual Frequency Identification Sonar (DIDSON; Sound Metrics, Lake Forest Park, Washington, USA) was deployed during daytime (1551–1836 UTC) via electromechanical cable from shipboard on 17 July, 2009, at Anchor Ledge off the SEUS to test approaches for assessing variation in the spatial extent of predator-prey interactions in the absence of divers (see Moursund et al. 2003 for a description of the system). The system was configured to operate at 1.8 mHz to ensonify a region from approximately 2 to 11 m distance from the sensor with a 28.8° × 12° volume centered on the axis of the transducer producing 96 beams. The sensor was oriented to observe along the reef edge approximately parallel to the reef axis. Data were recorded at approximately 8 frames s^{-1} and individual data files were 12 min in duration. Predation events were extracted from each file and assessed for predator group size (i.e., based on the greatest number of predators over the areal extent of the ensonified region) and the spatial extent of prey response (i.e., based on the difference between the areal extent of prey immediately prior to predator approach and then during approach or attack). The mean rate of predation events (events min^{-1}) was calculated as the average of the mean number of predation events min^{-1} for each 12-min sonar file. Split-beam hydroacoustics surveys were conducted in 2009 using a Biosonics DTX echosounder system operating at 120 kHz to describe the structure of fish aggregations in the water column around SEUS reefs during daytime.

Results

We observed 274 predation events off the SEUS and 105 events in the GOM based on 64.6 and 16.6 hrs of bottom time devoted directly to predation surveys, respectively. Piscivores in both regions were observed initiating predation events as individual predators as well as in monospecific and mixed-species groups that included both mid-water and demersal species (Fig. 2A–E; also see video clips in online supplementary material). There were clear differences between regions in the classes of predatory interactions that occurred at reefs (Table 1). At SEUS reefs, 72% of events involved mixed-species groups of piscivores. A majority of those events at SEUS reefs involved facilitation between mid-water and demersal piscivores (67% of events), where stalking and attacks by mid-water piscivores caused prey to escape toward the reef where demersal piscivores then stalked and attacked the resultant and ephemeral high density prey patches. In total, mid-water fishes made 192 attacks prey during predation events that resulted in 130 attacks (68%) by demersal predators. Demersal predators attacking prey alone occurred only 47 times. In contrast, 40% of events at GOM reefs involved mixed-species groups of piscivores , with the different types of events occurring with approximate equal frequency (Table 1). Of 47 actual attacks by mid-water predators, 18 (38%) resulted in a subsequent attack by demersal predators. Demersal predators alone attacked prey only 19 times.

The number of mid-water and demersal piscivore species involved in each event as well as the total number of individuals in each event varied considerably within and between regions (Figs. 3, 4; all count data were non-normal, Anderson-Darling

tests: all $P < 0.005$). Group size for events was larger (Mann-Whitney test: $P = 0.027$) and contained more species (Mann-Whitney test: $P < 0.001$) at SEUS reefs (median group size = 8.0, median number of species = 2.0) than in the GOM (median group size = 5.0, median number of species = 1.0). Events with only a single individual (and by definition a single species) were rare (12% of events in SEUS, 9% in GOM). Species of both mid-water and demersal piscivores observed at SEUS and GOM reefs were similar, although the percent occurrence for each species based on the total number of events in each region varied (the full list of species, functional role, and number of events in which each was observed in each region are summarized in Appendix 1).

Aggregating prey, regardless of species, behaved in a similar manner with regard to distribution over reefs and response to predators regardless of size (i.e., the range of prey taxa size was approximately 10–80 mm total length based on visual estimates). Prey taxa reduced nearest neighbor distances from 0.75–2 body lengths to <0.25 body lengths during attacks (i.e., from approximately 160 mm when undisturbed to <10 mm shortest distance between individuals during attacks), producing ephemeral high density prey patches for demersal piscivores (spatial relationships were based on diver-based visual estimates of length and distance gauged against objects of known length such as a scale on dive slate). The diversity of prey in each region (Appendix 2) varied with species richness of prey taxa and was lower at individual GOM reefs as well as in aggregate (i.e., species richness SEUS = 10, GOM = 4). Tomtate (see Appendices 1 and 2 for species and authorities) was the most common prey taxa. Off the SEUS, multiple prey taxa (scads, scup, and tomtate were most common) were often present at individual reefs and species were generally spatially segregated (Fig. 5A–D). For example, young-of-the-year (YOY) tomtate and YOY scup occurred separately and adjacent to one another in spatially extensive (i.e., meters to tens of meters) aggregations along the reef edge (from just above the seafloor to 2 m out and above the undercut edge). Schools of juvenile and adult round and mackerel scad and YOY silverside occurred high in the water column, also as single species schools or stratified by height above the bottom. The only inter-specific groupings of prey taxa we observed were mixed species schools of scads, with both species of the same size class. Split-beam sonar records illustrate the spatial variation in abundance and distribution of fish over reefs (primarily prey taxa due to their extreme abundance) and the relative paucity of prey resources away from reefs (Fig. 6).

Species from surveys were parsed into functional groups based on the spatial position and functional role in predation events (Fig. 7). Interaction strengths varied by region. The lower frequency of interactions between mid-water and demersal predators for the GOM region is due to the lower frequency of facilitative interactions between the two functional groups. Individual opportunists took advantage of ephemeral patches of high density prey but did not move far (ca. <5 m) from proximate shelter sites (Fig. 2F). Associated species that served as camouflage for mid-water and demersal piscivores attacks, as well as to constrain movements of prey schools, were of limited importance (in approximately 20% of events; Fig. 2G–J). Absent from the behavior web are transient piscivores that were observed outside of surveys, and include sandbar shark, *Carcharhinus plumbeus* (Nardo, 1827), great hammerhead, *Sphyrna mokarran* (Rüppell, 1837), tiger shark, *Galeocerdo cuvier* (Péron and Lesueur, 1822), and bottlenose dolphin, *Tursiops truncates* (Montagu, 1821).
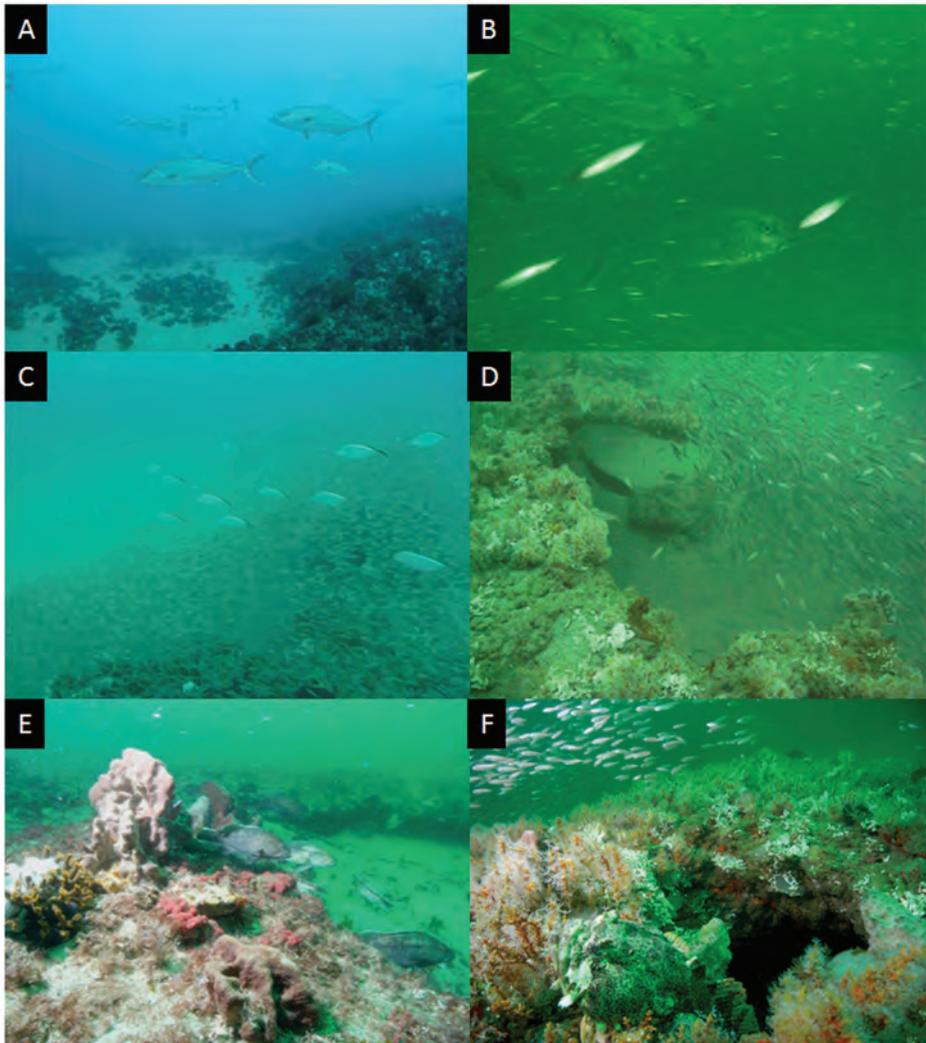
Figure 2. Images illustrating a range of piscivore-prey interactions. (A) Greater amberjack and great barracuda in mixed species aggregation in search of prey. (B) Group of greater amberjack attacking scad in water column above reef. (C) School of bar jack swimming over scad species above reef. Note that prey school is in discrete layer above reef. (D) Dense aggregation of prey species retreating to reef and then attacked by scamp grouper. (E) Seven black sea bass moving to edge of reef in response to predatory behavior of mid-water piscivores above reef. (F) Oyster toadfish, an individual opportunistic piscivore (see text for detailed explanation), emerging from reef shelter and attacking ephemeral prey school that retreated to reef during attack by mid-water piscivores. *(Opposite page)* (G) A large great barracuda (circle) rejoining a school of Atlantic spadefish after leaving school to stalk potential prey. (H) Scamp grouper moving along seafloor under and in synchrony with school of Atlantic spadefish. (I) Black sea bass moving along reef amongst aggregation of cubbyu. (J) Scamp grouper in water column above reef functionally acting as mid-water piscivores, driving prey towards the reef during attacks.
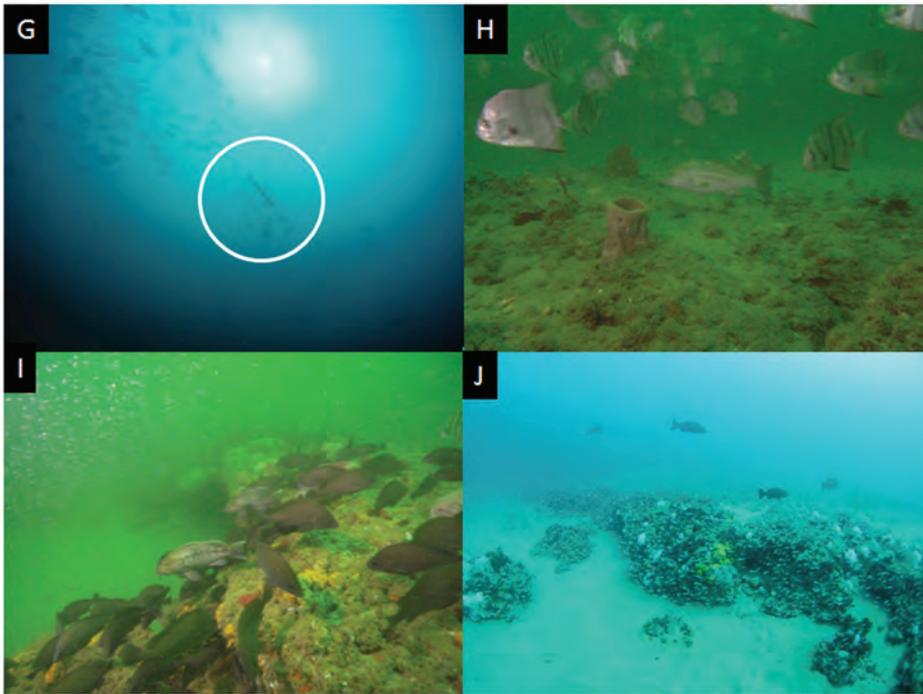
Figure 2. Continued.

Noteworthy is the flexibility in the role that primarily demersal piscivores can play as mid-water predators in both study regions. Red snapper, scamp, and gag grouper assumed this role in the SEUS region in 10, 15, and 3 events, respectively (Fig. 2K–L). In the GOM, red snapper, scamp, gag grouper, and gray snapper assumed this role in 11, 1, 4, and 5 events, respectively. Such interactions were not dominant in terms of the total number of interactions. In general, these were large individuals (primarily >40 cm TL) that ventured above the reef (more than about 2 m height) only when other mid-water piscivores were small or in low local abundance.

YOY great barracuda also varied in spatial use of reef habitat by stalking and attacking prey from positions just above the seafloor as well as from mid-water (Fig. 5F). These small piscivores (25–100 mm TL) took up a mid-water position primarily in the local absence of large predators above the seafloor and within cover of larger aggregations of prey (see Auster et al. 2011 regarding YOY barracuda at reefs). YOY barracuda occurred in 103 predation events in the SEUS region. Of these, YOY barracuda were the sole initiators of facilitative interactions, chasing prey toward demersal

Table 1. Summary of predation events on subtropical reefs in each of two geographic regions based on functional classification (as defined in text).

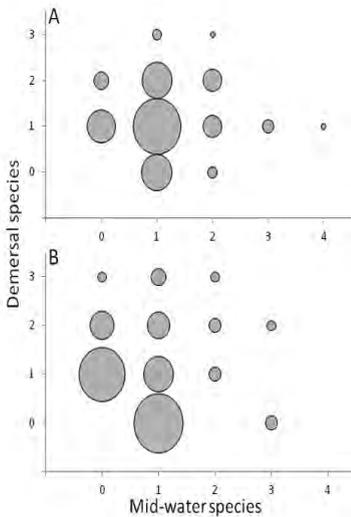|	Southeast US	Gulf of Mexico
Number predation events observed	274	105
Percent events with facilitation between mid-water and demersal predators	67%	28%
Percent events with mid-water predators only	16%	36%
Percent events with demersal predators only	17%	36%
Percent events with mixed-species (regardless of functional type)	72%	40%

Figure 3. Distribution of mid-water and demersal species per event for (A) southeast US (SEUS) and (B) Gulf of Mexico (GOM). Size of circles is relative and based on percent of total number of events. Note the dominance of multispecies interactions including both mid-water and demersal piscivores in the SEUS region while a greater percent of single species events occurred in the GOM.
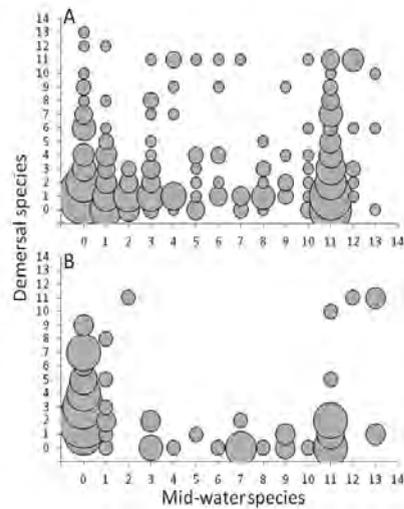
Figure 4. Distribution of number of individuals per event, parsed by mid-water and demersal piscivores, for (A) southeast US (SEUS) and (B) Gulf of Mexico (GOM). Size of circles is relative and based on percent of total number of events. Events in the SEUS region exhibit a gradient of predator abundance while events in the GOM primarily are composed of groups of either demersal or mid-water species.

piscivores in 74 events. Twenty other events involved YOY barracuda as well as adult mid-water piscivores initiating such facilitative interactions. Some events involved up to 60 YOY barracuda, aggregated in different areas in and around schools of prey. For example, one event had approximately 20 individuals along the outer edge of an aggregation of thousands of YOY tomate and scup, with 40 interspersed within the school. Individuals and groups initiated separate attacks that were sometimes nearly instantaneous with others occurring after a period of quiescence. Within the prey school, individuals did not always react simultaneously, with reactions from some single attacks limited to approximately 1 m radius from the predator, while after single attacks, and larger attacks by groups, sent the entire school toward the reef over linear distances of meters to tens of meters. Only a single event involving YOY barracuda was observed in the GOM region, with 27 individuals within an aggregation of thousands of YOY tomtate. Fourteen attacks were observed with no interactions involving demersal piscivores.

Viewed in aggregate, this pattern of variability in species assuming the role of mid-water piscivore suggests three community states (Fig. 8), based on the sequential loss or absence of potential predators or competitors (i.e., primary: mid-water piscivores, secondary: demersal piscivores, tertiary: YOY piscivores). Here we view community state as a local attribute (i.e., at the scale of individual reefs) without linking local abundance to population status.

Species-level behavior webs indicate that both the SEUS and GOM regions have similarly complex behavior webs based on patterns of connectivity among species
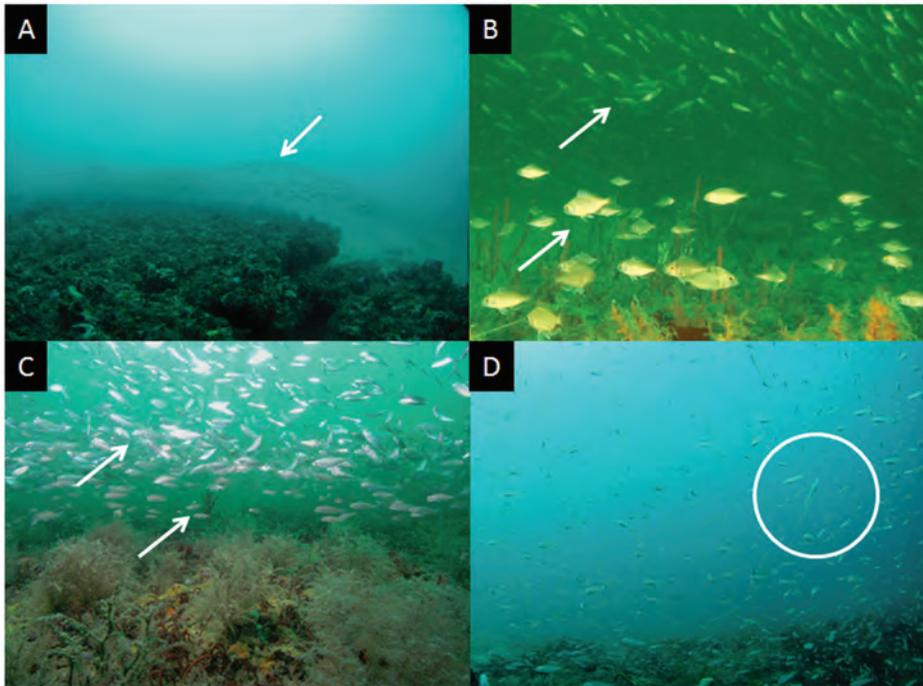
Figure 5. Images illustrating the distribution of fishes at reefs that were targeted by piscivores. (A) Distinct band of zooplanktivores at reef edge. (B) Prey species immediately above reef segregated by species with young-of-the-year (YOY) scup beneath scad. (C) YOY tomtate segregated below scad immediately above reef. (D) YOY great barracuda (in circle) within aggregation of YOY tomate.
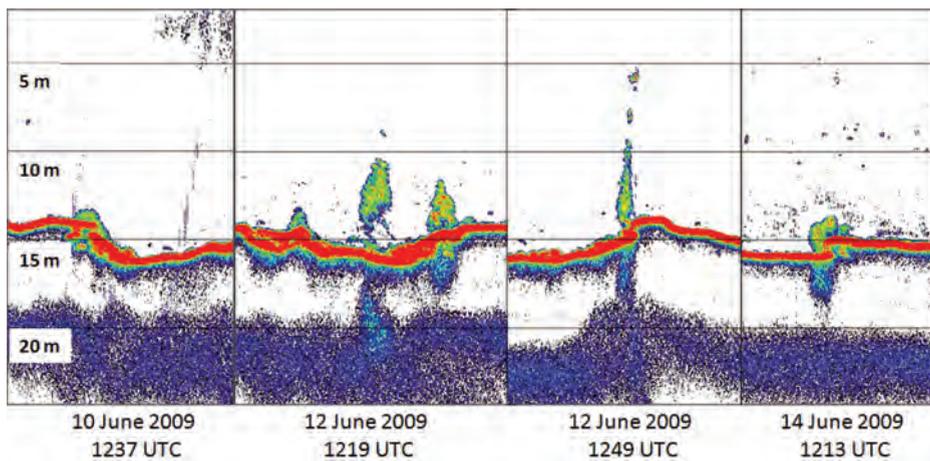

Figure 6. Examples of variable distributions of prey at undercut reefs from split-beam hydroacoustic records (depth m along left). Warmer colors indicate stronger acoustic return. Linear red lines depict seafloor topography and disjunct red lines indicate undercut ledges ensonified along the track line. Yellow-green "clouds" around and over the seafloor are dense aggregations of fishes.

Midwater Piscivores

Almaco jack
Bar jack
Blue runner
Gag grouper
Gray snapper
Great barracuda
Greater amberjack
Red snapper
Scamp
Spanish mackerel

Single and multi-species groups,
Cooperative predation,
Camouflage in resting schools

N total = 274/105

Serve as camouflage to attack
from in and proximate to school

11/3

Atlantic spadefish
Lookdown

Single and
multi-species
schools

79/65

Prey Taxa

Mackerel scad
Round scad
Scup
Tomtate
Redear herring
Atherinid sp.

Single and multi-species groups

Constrains
movement
and position of
schooling prey

6/0

Demersal Piscivores

Oyster/leopard toadfish
Reticulated moray
Sand diver
Spotted moray
White-spotted soapfish
Gulf flounder
Belted sandfish
Carolina hake

Tactics as
individual
opportunists

2/3

Serve as camouflage to attack
from in and under school

81/60

Bank sea bass
Black sea bass
Gag grouper
Gray snapper
Red snapper
Scamp
Sand diver

Single and multi-species groups,
Cooperative predation

Serve as camouflage to
attack from aggregations

6/17

Cubbyu
Spottail pinfish
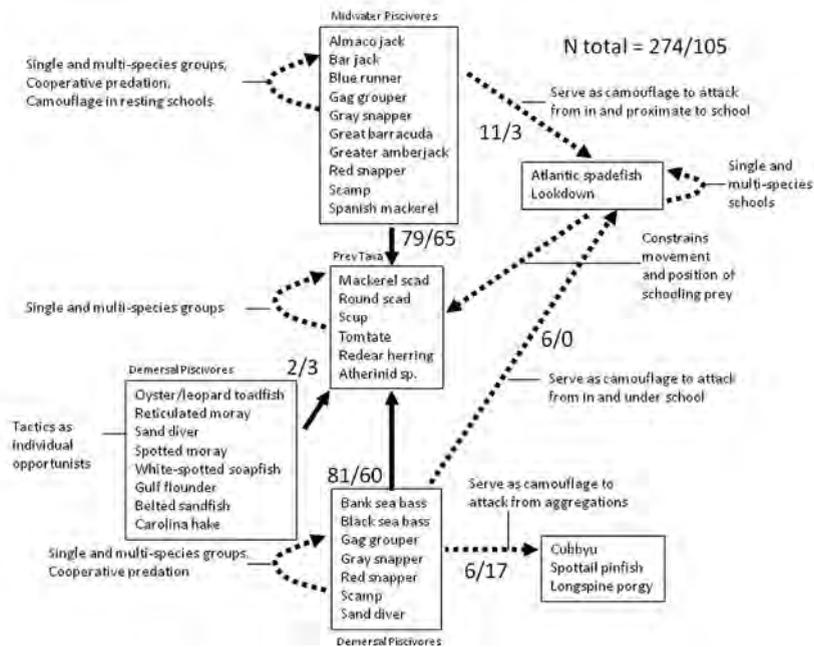Longspine porgy

Demersal Piscivores

Figure 7. Generalized behavior web illustrating interactions of predominant reef piscivores, associated taxa influencing predator-prey interactions, and reef associated prey. Boxed nodes include species observed across all events in the functional role as labeled. Solid lines indicate predator-prey interactions and direction of arrows indicate focus of predators on prey taxa. Dotted lines indicate facilitative interactions. Loops back to each node represent single and mixed species groups within the functional role. Numbers at each link indicate relative interaction strengths as a percent of total events in each region (southeast US/Gulf of Mexico).

(i.e., the total number of co-occurring piscivores across all events for each focal species). Here key taxa are those that have the largest numbers of associations (i.e., linkages in behavior webs) based on mixed species groupings. For demersal piscivores, black and bank sea bass off the SEUS have the greatest number of links (i.e., with 13 co-occurring species), while scamp grouper is ranked second with links to 10 species and gag grouper is third with eight links. In the GOM region, gag grouper has the greatest number of links (i.e., 11), with gray snapper having eight and red snapper having seven links to co-occurring species. Blue runner, Spanish mackerel, and greater amberjack are the highest ranked mid-water piscivores off the SEUS with 11, 8, and 8 links, respectively. Spanish mackerel, blue runner, and greater amberjack are the highest ranked in the GOM region with 8, 7, and 6 links, respectively.

Dendrograms from hierarchical clustering of piscivore composition in each event revealed consistent patterns in the relationships among species from each region (Fig. 9). Piscivores did not form multiple groupings with unique species in either region. Instead, species were aggregated in a single primary grouping with a gradient of ranked similarity of occurrence in multi-species groups. This pattern was consistent with the variation observed in species groups among events. That is, species groupings for both pelagic and demersal components were not unique but were composed of species from a pool of local piscivores.
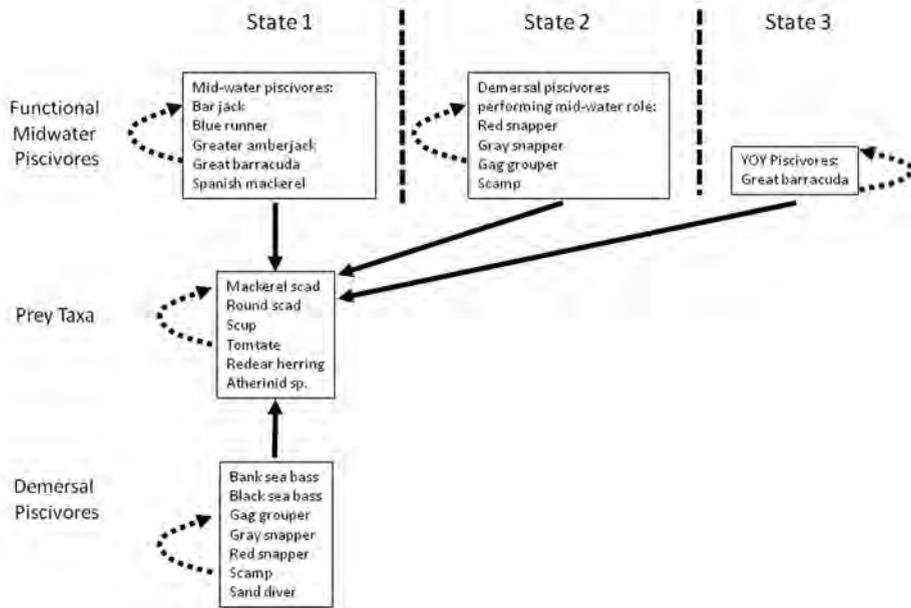
Figure 8. Behavior web parsed by the distinct groupings of species in the functional role of mid-water piscivore. State of the mid-water piscivore guild varied amongst reefs in each region. Dotted lines back to each node represent single and mixed species groups within the functional role.
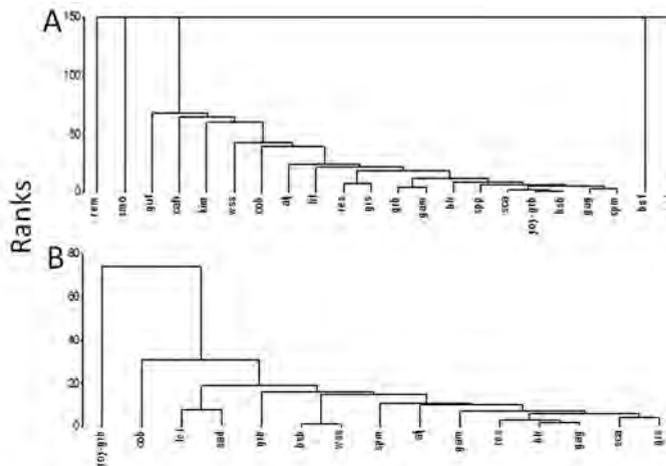

Figure 9. Dendrograms based on hierarchical clustering of species occurring in predation events at (A) southeast US (SEUS) and (B) Gulf of Mexico (GOM). Species codes as follows: alj=Almaco jack, blr=blue runner, bsb=black-bank sea bass, bsf=belted sandfish, cah=Carolina hake, cob=cobia, gag=gag grouper, gam=greater amberjack, grb=great barracuda, grs=gray snapper, guf=gulf flounder, km=king mackerel, let=leopard toadfish, lit=little tunny, oyt=oyster toadfish, rem=reticulated moray, res=red snapper, sad=sand diver, sca=scamp, smo=spotted moray, spm=Spanish mackerel, spp=spottail pinfish, wss=whitespotted soapfish, yoy-grb= young-of-the-year barracuda.
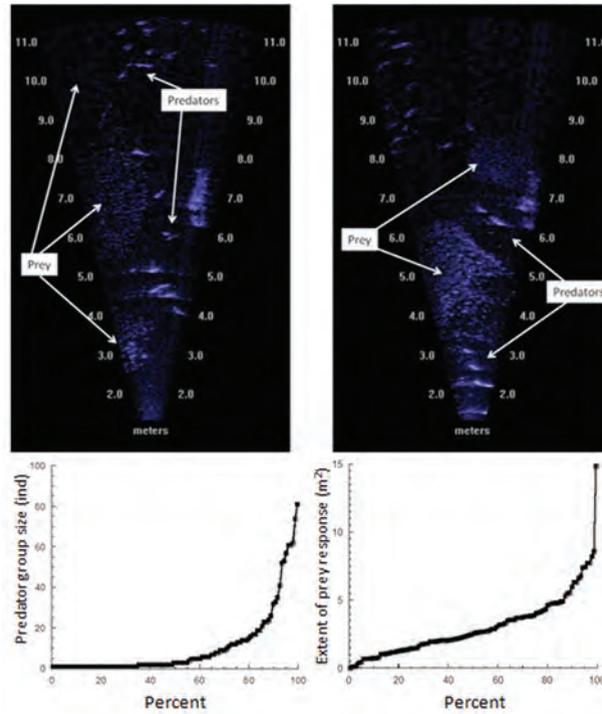
Figure 10. (Top) Frame-grabs of a predation event as examples of piscivore-prey interactions observed via DIDSON on 17 June, 2009, at the 26 m Anchor Ledge site off the southeast US. Numbers along the display indicate distance (m) from transducer. Note shifts in distribution of prey (in this case primarily young-of-the-year tomtate and round scad) and predators (primarily greater amberjack), formation of vacuoles in prey aggregations, and variation in prey density during attacks (time difference between left and right panel is 4 s). (Bottom) Cumulative distribution (percent) of observations of predator group size (number of individuals) and spatial extent of prey response (m^2) based on the area prey schools contracted from nominal background distribution prior to predation events. Both plots illustrate the large variation in the data derived from DIDSON for each metric. See text for analysis of the relationship between predator abundance and extent of prey response.

While limited in terms of sample time, acoustic records from a single deployment of the DIDSON at Anchor Ledge (n = 16 12-min data files; n = 111 predation events) confirmed general patterns of predator and prey interactions observed by divers throughout the study. First is the variation in the extent and patchiness of prey. Divers observed distinct patches of prey that were highly variable over space and time and occurred on the linear scale of meters to tens of meters along the edge of reefs, sometimes exceeding the range of visibility. During the DIDSON deployment the mean areal extent of prey, undisturbed by predators, was 7.26 m^2 (SD 4.50) in the ensonified region, with a range of 0.90–24.29 m^2 over the 192-min observation period. Predator group size and the extent of prey response varied across a wide range of values (Fig. 10). Mean group size per event was 10.4 individuals (SD 16.8) and mean extent of prey response was 2.99 m^2 (SD 2.16). Although the number of predators is expected to be linearly related to the area of prey reacting to attacks, there was no significant correlation between predator abundance and the spatial extent of prey response (r^2 = 1.7, P < 0.10). Using each of the 16 acoustic files as sample units,

we calculated a mean predation event rate of 0.485 events min^{-1} (SD 0.305, min = 0.0, max = 1.25).

Discussion

Our underwater observations enabled the identification and description of a general pattern of facilitative interactions of piscivores at subtropical reefs in the SEUS and GOM. While such interactions vary by group size and composition as well as the extent of intra- and inter-specific species interactions, they are nonetheless a common element in these reef communities. Further, we infer that group facilitation, because of its common occurrence in predation events, plays an important role in predator success and potentially has important demographic consequences for those predator species.

Variation in the overall percentage of events involving facilitative interactions within and between mid-water and demersal piscivores at reefs off the SEUS vs GOM could be due to variation in species composition, variation in predator strategies, or geographic variation in the extent of fishing mortality. Due to differences in assessment strategies and scale of observations, it is unclear if the population status of piscivores varied significantly between the two regions (i.e., more depressed piscivore populations at northeastern GOM reefs) or the pattern simply masks variation between reefs within regions. The study reefs off the SEUS were located primarily within Gray's Reef National Marine Sanctuary. Anchoring (that allows targeted hook-and-line effort) and spearfishing are prohibited in the Sanctuary, thereby reducing fishing pressure at particular reefs. Further, fishing effort generally is expended closer to shore in this region so distance from shore is also a control on effort. At GOM sites many recreational fishing boats anchor at popular reef sites that were included in our list of stations and spearfishing is widespread. While acknowledging study sites in both regions were primarily in federal waters, the proximate source of angler effort was the state of Florida for GOM and Georgia for the SEUS. Based on data from 2006, there was approximately an order of magnitude more recreational fishing effort expended off Florida than Georgia (USFWS 2006), suggesting that fishing mortality could be greater at the GOM reefs.

Redundancies in the functional role of species, with regard to predatory behavior (i.e., behavioral compensation), maintains interactions despite changes in species composition (i.e., variations in abundance at local scales). We have observed that demersal piscivores, as well as YOY piscivores, can fill the behavioral role of mid-water initiators for positive indirect interactions. In addition, Stallings and Dingeldein (2012) suggest that changes in functional roles could be due to learned behaviors. Furthermore, the role of YOY piscivores depends upon patterns of recruitment. For great barracuda (Auster et al. 2011 and herein) that are seasonal spawners (Kadison et al. 2010), there may be a seasonal component to the role that this life history stage can play. It remains unclear if larger YOY disperse when size disparities between predators and prey become too large for camouflage within aggregations of prey to be effective.

Distribution of predators and prey, as well as distribution of risk, varies at the spatial scale of meters over reefs (Table 2). From the perspective of shelter resources, the area of undercut ledge has both crevice and shade (sensu Helfman 1981, McCartt et al. 1997), the highest density of habitat-forming fauna, and complex accelerated flows

Table 2. General patterns of small-scale spatial variation in prey and piscivore abundance, as well as attributes of habitat over adjacent segments of reefs (relative value as L = low, M = medium, H = high).
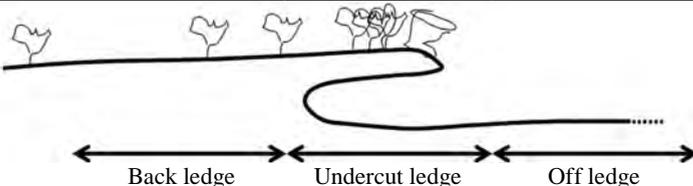
	Back ledge	Undercut ledge	Off ledge
Prey spp. abundance	M	H	L
Mid-water piscivore abundance	M	H	M
Demersal piscivore abundance	M	H	L
Biotic habitat-cover	M	H	L
Geologic habitat-cover	L	H	L
Per capita prey risk	M	L	H

that deliver planktonic prey. The result here is the highest abundances of prey and predators. The back ledge area supports a lower density of emergent fauna, dependent in part on the depth of sand cover over hard substratum. Such habitat configuration is typical of low relief reef habitat (Kendall et al. 2007). While no deep crevice habitat or shade is available, the habitat-forming fauna provide cover (shelter and flow refuge) for fishes. The fine-grained sedimentary habitat in front and away from the ledge generally grades into a relatively flat landscape (sand ripples, depressions, patchy emergent fauna attached to isolated pieces of hard substratum). However, we have observed some reefs with collapsed and exposed sections of ledge in front of the current ledge margin, which extends the influence of the reef structure by meters to tens of meters. In addition, the effects of the reef structure on tidal flow patterns, as it influences the distribution of planktivores and species that seek refugia from flow, is unclear. However, some aggregations of prey species have been observed feeding up to 5 m in front of reefs and seek refuge at the reef only when approached by potential predators.

Based on the hydroacoustic data, the distribution of prey aggregations and the spatial scale of some predation events (up to and beyond 11 m linear distance along a ledge) can be larger than the range of visibility for visual surveys (although sufficient sampling from visual census can identify the variation in species interactions). The non-linear variation in response of prey across the range of predator abundance observed using the DIDSON suggests prey taxa did not always view predators as a significant threat (Brown et al. 2006, Wirsing et al. 2010). High variation in this relationship could also be the result of some predators moving above or below rather than through aggregations of prey in some events. In addition, some predators might be present outside the volume sampled by the beam, resulting in undercounting predators. Nonetheless, predation activity did influence the spatial extent of prey availability to demersal piscivores.

Based on the high rate of predation events observed during the limited deployment of the DIDSON during this study, more extensive use of this or similar technology in the future could quantify the role that facilitative interactions play in sustaining high trophic level predators at reef systems. Field studies to obtain systematic quantitative data on predation rates in relation to the abundance of mid-water predators,
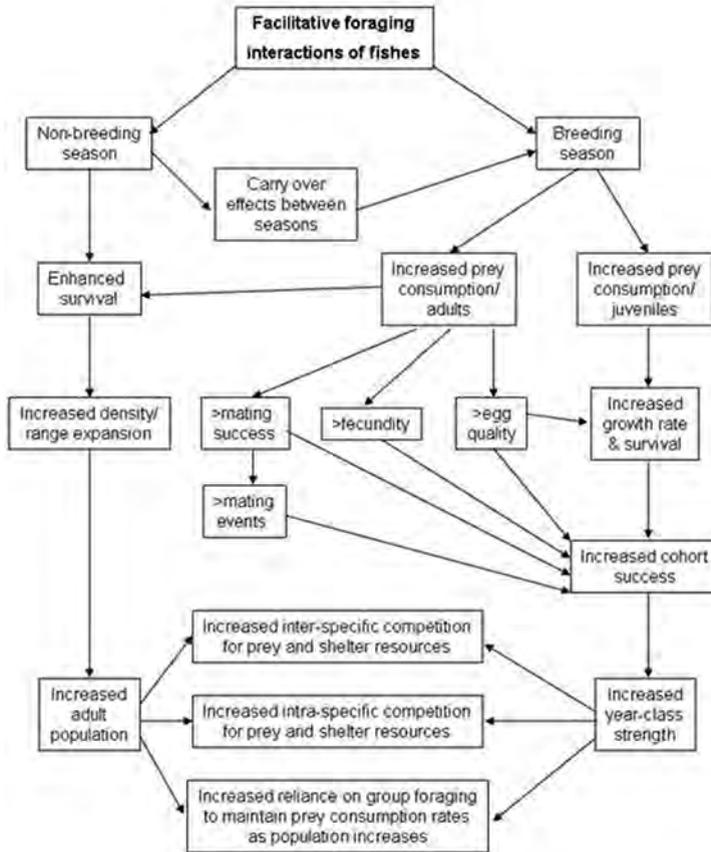
Figure 11. Potential effects of facilitation of piscivory during reproductive and non-reproductive periods (based on and modified from Robb et al. 2008). Each node identifies an element in the life history of a species that can be tested for response to variations in behavior.

potential prey, and the spatial extent of enhanced opportunities for predation by demersal piscivores will be critical for understanding spatial variation of interactions across reefs and regions. While the DIDSON can be deployed for extended periods, visual reconnaissance by divers or remote camera will be required to identify acoustic targets. Perhaps equally important is the need to link the abundance and behavior of mid-water piscivores and prey to demersal piscivores that are often on and under ledges and poorly resolved in the acoustic records.

While we have shown that direct and indirect behavioral interactions of mixed-species groups are common attributes of the piscivore guild in these sub-tropical reef fish communities, the role such interactions play in the demographics of species remains to be quantified. Such interactions, while interesting at a fundamental science level, take on much greater importance with regard to conservation and management if they result in population level consequences (e.g., increased growth and fecundity based on greater rates of prey capture due to facilitative interactions). There are multiple segments of the life history of the species of interest that could respond to variation in such interactions (Fig. 11) as they relate to growth and fecundity. Using a

conceptual model that links direct and indirect facilitative interactions to population processes forms the foundation for developing approaches to test hypotheses under field conditions for defining the role of these interactions in the population dynamics of species of both economic and ecological importance. Demersal reef piscivores appear to be good targets for such studies as they have low movement rates, at least seasonally, and prey capture rates can then be linked to localized prey resources and co-occurring piscivores. Based on the extent of interaction links across the species-level behavior webs, black and bank sea bass, gag grouper, red snapper, gray snapper, and scamp appear to be logical focal species to test such predictions.

Certainly, continued study of these types of behavior webs will lead to a more nuanced understanding of the functional roles that fishes play in these localized reef systems. Our results, if such patterns prove to be consistent and widespread, suggest a blurring of the strict compartmentalization and pathways of species interactions (i.e., variation in classically defined roles of mid-water and demersal piscivores). Such understanding will be important for spatial management of marine ecosystems. For example, the efficacy of fishing for mid-water fishes, nominally assumed to be transient and having minor local effects on reefs could be evaluated in regard to the presence and strength of these types of behavior webs (Grober-Dunsmore et al. 2008). If there are demographic consequences, and our observations suggest this seems likely given the extent to which they occur, then developing a mechanistic understanding of interactions, monitoring status and trends, and incorporating such interactions into multispecies population models could be important to improve predictions of population and community level responses.

Acknowledgments

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Appendix 1. Scientific and common names of all species observed in each functional role. The total number of predation events, by region, for each species is indicated at right [based on 274 predation events in the southeast US (SEUS) region and 105 events in the Gulf of Mexico (GOM); 64.6 and 16.6 hrs of bottom time devoted directly to predation surveys, respectively]. Black and bank sea bass are listed together as identification to species level was not possible for all events due to visibility. Class is based on functional role as a mid-water piscivore and indicates if each species is primarily a mid-water (M) or demersal (D) piscivore (see text for explanation).

Scientific name	Common name	SEUS	GOM	Class
Functional mid-water piscivores				
Seriola rivoliana Valenciennes, 1833	Almaco jack	7	14	M
Caranx ruber (Bloch, 1793)	Bar jack	1	0	M
Caranx crysos (Mitchill, 1815)	Blue runner	22	11	M
Rachycentron canadum (Linnaeus, 1766)	Cobia	2	1	M
Mycteroperca microlepis (Goode and Bean, 1879)	Gag grouper	3	4	D
Lutjanus griseus (Linnaeus, 1758)	Gray snapper	0	5	D
Sphyraena barracuda (Edwards, 1771)	Great barracuda	115	28	M
Seriola dumerili (Risso, 1810)	Greater amberjack	31	11	M
Scomberomorus cavalla (Cuvier, 1829)	King mackerel	1	0	M
Euthynnus alletteratus (Rafinesque, 1810)	Little tunny	2	0	M
Lutjanus campechanus (Poey, 1860)	Red snapper	10	11	D
Decapterus punctatus (Cuvier, 1829)	Round scad	0	2	M
Mycteroperca phenax Jordan and Swain, 1884	Scamp	15	1	D
Scomberomorus maculatus (Mitchill, 1815)	Spanish mackerel	41	10	M
Diplodus holbrookii (Bean, 1878)	Spottail pinfish	6	0	D
	Unidentified	1	0	M
Demersal piscivores				
Serranus subligarius (Cope, 1870)	Belted sandfish	1	0	
Centropristis striata (Linnaeus, 1758)	Black seabass	149	3	
Centropristis ocyurus (Jordan and Evermann, 1887)	Bank seabass			
Rachycentron canadum (Linnaeus, 1766)	Cobia	1	0	
Mycteroperca microlepis (Goode and Bean, 1879)	Gag grouper	34	36	
Lutjanus griseus (Linnaeus, 1758)	Gray snapper	7	16	
Sphyraena barracuda (Edwards, 1771)	Great barracuda	1	0	
Paralichthys albigutta Jordan and Gilbert, 1882	Gulf flounder	2	0	
Opsanus pardus (Goode and Bean, 1880)	Leopard toadfish	0	2	
Lutjanus campechanus (Poey, 1860)	Red snapper	3	11	
Synodus intermedius (Spix and Agassiz, 1829)	Sand diver	0	8	
Mycteroperca phenax Jordan and Swain, 1884	Scamp	96	17	
Diplodus holbrookii (Bean, 1878)	Spottail pinfish	2	0	
Rypticus maculatus Holbrook, 1855	Whitespotted soapfish	8	2	
Individual opportunists				
Serranus subligarius (Cope, 1870)	Belted sandfish	0	3	
Urophycis earllii (Bean, 1880)	Carolina hake	1	0	
Paralichthys albigutta Jordan and Gilbert, 1882	Gulf flounder	0	1	
Opsanus pardus (Goode and Bean, 1880)	Leopard toadfish	0	2	
Opsanus tau (Linnaeus, 1766)	Oyster toadfish	1	0	
Muraena retifera Goode and Bean, 1882	Reticulate moray	1	0	
Synodus intermedius (Spix and Agassiz, 1829)	Sand diver	4	5	
Gymnothorax moringa (Cuvier, 1829)	Spotted moray	1	0	
Rypticus maculatus Holbrook, 1855	Whitespotted soapfish	2	1	

Appendix 1. Continued.

Scientific name	Common name	SEUS	GOM	Class
Associated species used by piscivores as camouflage				
Chaetodipterus faber (Broussonet, 1782)	Atlantic spadefish	21	2	
Holacanthus bermudensis Goode, 1876	Blue angelfish	0	3	
Pareques umbrosus (Jordan and Eigenmann, 1889)	Cubbyu	5	2	
Lachnolaimus maximus (Walbaum, 1792)	Hogfish	0	8	
Stenotomus caprinus Jordan and Gilbert, 1882	Longspine porgy	1	0	
Selene vomer (Linnaeus, 1758)	Lookdown	6	0	
Epinephelus morio (Valenciennes, 1828)	Red grouper	0	3	
Diplodus holbrookii (Bean, 1878)	Spottail pinfish	14	0	
Haemulon plumierii (Lacépède, 1801)	White grunt	0	8	

Appendix 2. Scientific and common names of prey species observed during predation events. Round and mackerel scad are listed together as identification to species level was not possible for all events due to visibility. The total number of events in which each species occurred, by region, is indicated at right [based on 274 predation events in the southeast US (SEUS) region and 105 events in the Gulf of Mexico (GOM); 64.6 and 16.6 hrs of bottom time devoted directly to predation surveys, respectively].

Scientific name	Common name	SEUS	GOM
Family Atherinidae	Anchovy, Atheriniid sp.	5	1
Chloroscombrus chrysurus (Linnaeus, 1766)	Atlantic bumper	1	0
Pareques umbrosus (Jordan and Eigenmann, 1889)	Cubbyu	2	0
Harengula humeralis (Cuvier, 1829)	Redear herring	6	0
Decapterus punctatus (Cuvier, 1829)	Round scad	115	16
Decapterus macarellus (Cuvier, 1833)	Mackerel scad		
Stenotomus chrysops (Linnaeus, 1766)	Scup	130	0
Diplodus holbrookii (Bean, 1878)	Spottail pinfish	9	0
Haemulon aurolineatum Cuvier, 1830	Tomtate	120	75
Rypticus maculatus Holbrook, 1855	Whitespotted soapfish	2	0
	Unidentified	1	16