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Scientific Note

Behavior of prey links midwater and demersal piscivorous reef fishes

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Pelagic and demersal guilds of piscivorous fishes are linked by a variety of biological and physical processes that mediate interactions with common prey species. Understanding the behaviors of predators and prey can provide insight into the conditions that make such linkages possible. Here we report on the behaviors of mid-water piscivorous fishes and the responses of prey that produce feeding opportunities for demersal piscivorous fishes associated with "live bottom" ledge habitats off the coast of Georgia (northwest Atlantic Ocean). Prey taxa reduced nearest neighbor distances and retreated towards the seafloor during predatory attacks by mid-water fishes. Demersal fishes subsequently attacked and consumed prey in these ephemeral high density patches. No predation by demersal fishes was observed when prey species were at background densities. If the predator-prey interactions of demersal piscivorous fishes are commonly mediated by the predatory behavior of midwater piscivorous fishes and their prey, such indirect facilitative behaviors may be important in terms of the population processes (*e.g.*, prey consumption and growth rates) of these demersal fishes.

As guildas de peixes piscívoros pelágicos são conectadas às de peixes piscívoros demersais através de diversos processos biológicos e físicos que permeiam as interações com suas presas em comum. O conhecimento do comportamento de predadores e presas pode fornecer idéias a respeito das condições que tornam estes elos possíveis. Relatamos aqui os comportamentos de peixes piscívoros de meia-água e as respostas de suas presas que fornecem, assim, oportunidades alimentares para os peixes piscívoros demersais que vivem associados a fundos rochosos ao largo da costa da Geórgia (Oceano Atlântico). As presas reduziram a distância mínima entre os indivíduos e recolheram-se em direção ao fundo durante os ataques dos peixes de meia-água. Em seguida, peixes demersais atacaram e consumiram as presas destes agrupamentos efêmeros com alta densidade de indivíduos. Não foi observada predação por peixes demersais quando as presas estavam em densidades menores às causadas por ataques de peixes de meia-água. Caso as interações entre presas e peixes piscívoros demersais sejam comumente mediadas pelo comportamento predatório de peixes piscívoros de meia-água e suas presas, estes comportamentos facilitadores indiretos podem ser importantes em termos de processos populacionais (*e.g.*, consumo de presas e taxas de crescimento) para certas espécies de peixes demersais.

Key words: Habitat, Reefs, Live bottom, Prey density.

Hard substratum "live bottom" ledges and reefs are widely distributed in the sub-tropical region off the southeast United States (Wenner *et al*., 1983; Barans & Henry, 1984; Sedberry & Van Dolah, 1984). Live bottom habitats are primarily composed of limestone and sandstone outcrops that rise 1-3 m above the surrounding sandy substratum and are colonized by octocorals, sponges and other diverse epifauna. Outcrops generally are in the form of linear ridges with some as simple topographic rises while others are undercut with deep shaded crevices (Kendall *et al*., 2007). These habitats support a unique fish assemblage compared to surrounding sand habitats (*e.g.*, Sedberry & Van Dolah, 1984) and are focal sites for activities by multiple species of small schooling fishes as well as mid-water and demersal piscivorous fishes (Kracker *et al*., 2008).

Previous studies of reef fishes and those in other topographically complex habitats have documented a diversity of single and multi-species predator-predator interactions that result in novel tactics to enhance opportunities for prey capture (*e.g.*, Hobson, 1968; Strand, 1988; Parrish, 1993; Auster & Lindholm, 2002; Auster, 2008). For example, bluespotted cornetfish (*Fistularia commersonii*) in the Gulf of California follow species such as leopard grouper (*Mycteroperca rosacea*) and graysby (*Cephalopholis panamensis*) to feed on fishes and crustaceans that are flushed from shelters as the later search crevices for prey (Auster, 2005). In these cases such interactions can be classified as direct mutualisms or a form of social facilitation (Bruno *et al*., 2003; Dill *et al*., 2003). However, synergistic but indirect mutualisms between predators can result when one

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species or guild produce conditions that enhance predation opportunities for another without direct behavioral facilitation (Sih *et al*., 1998). Such non-additive effects are expected to affect the assemblage of predators within a community in ways that are different from expected linear responses to changes in predators and prey (Bruno & Cardinale, 2008).

Here we describe the behaviors of mid-water piscivorous fishes and the responses of prey that produced feeding opportunities for demersal piscivorous fishes. These observations are an example of indirect predator-predator facilitation and are based on data collected during a series of six sets of scuba dives at Anchor Reef off the coast of Georgia (31° 37.7' N, 80° 34.6' W; depth 25 m) from 23-25 July 2008.

We observed coordinated predatory behavior among single and mixed species groups of piscivorous fishes (*i.e.*, almaco jack *Seriola rivoliana*, cobia *Rachycentron canadum*, greater amberjack *Seriola dumerili*, Spanish mackerel *Scomberomorus maculatus*, blue runner *Caranx crysos*, and bar jack *Carangoides ruber*) that aggregated and preyed upon highly abundant (schools numbering in the 1000s) juvenile tomtate *Haemulon aurolineatum*, round scad *Decapterus punctatus*, and mackerel scad *Decapterus macarellus* (Fig. 1). Single and mixed species schools of these prey fishes when undisturbed were observed 3-6 m above ledges in resting schools or feeding on zooplankton, primarily in non-polarized aggregations (ca. nearest neighbor distance ≥ 0.75 body length based on visual estimates).

During predation events, prey species rapidly decreased nearest neighbor distances (ca. ≤ 0.25 body length) and shifted vertical distribution downward towards ridges and the surrounding sandy seafloor. In addition to pursuit of prey by the above mentioned mid-water piscivorous fishes at the seafloor, demersal piscivorous fishes (*i.e.*, black sea bass *Centropristis striata*, bank sea bass *Centropristis ocyurus*, scamp *Mycteroperca phenax* and gag grouper *Mycteroperca microlepis*) were observed preying upon these transient high density patches of fishes (Fig. 2). The great barracuda, *Sphyraena barracuda*, was observed attacking prey fishes with coordinated predatory behavior in mid-water and also when station keeping under ledges.

Due to limited visibility it was not possible to define species composition and numbers of mixed and single species groups of piscivorous fishes for all of the predation events observed. However, of 32 predation events by mid-water predators that elicited schooling prey species to increase density and move towards the seafloor, 18 concurrent events of predation by demersal fishes were observed (*i.e.*, nine *C. striata* and *C. ocyurus*, seven *M. phenax*, one *M. microlepis*, one *S. barracuda*). No predation events by these demersal piscivorous fishes were observed during periods when prey were at "non-threat" densities (based on 192 minutes of dive time devoted to observing these types of interactions).

Species composition of piscivorous fishes observed at Anchor Reef as well as patterns of occurrence in single and mixed species groups are summarized in Table 1. Groups of mid-water predators varied in size, ranging from two to >1000 individuals. Tactics for approach and attack varied in detail but commonly groups initiated predation events as a single unit, which caused prey to retreat towards the seafloor. Predator groups then split into smaller numbers or separated as individuals to attack prey aggregations from multiple angles. Attacks generally were initiated from the deeper side of ledges and initially from above schools of prey. Coordinated groups of demersal piscivores did not exceed a maximum of 5 individuals although many more individuals (up to 50 *C. striata* and *C. ocyurus*) moved towards predation events as they unfolded.

We computed Bray-Curtis similarity coefficients for all species pairs from 17 mixed species groups of piscivorous fishes observed during dives. This procedure provided a method of quantifying the similarity of species occurrences within sets of observations (Clarke & Gorley, 2001) with similarity values serving here as indices of the strengths of behavioral relationships between the occurrences of species pairs (Table 2). *Sphyraena barracuda*, *Seriola dumerili* and *Scomberomorus maculatus* all have high pair-wise similarity indices indicating common co-occurrences in foraging groups. *Seriola rivoliana* and *S. dumerili* have a moderate similarity index value but it is lower than the other taxa listed above. The similarity index value between *C. striata* - *C.*

Fig. 1. A school of blue runner *Caranx crysos* (top left) and group of greater amberjack *Seriola dumerili* (right, one visible in photograph) drive prey fishes down to ledge habitat during predation events.

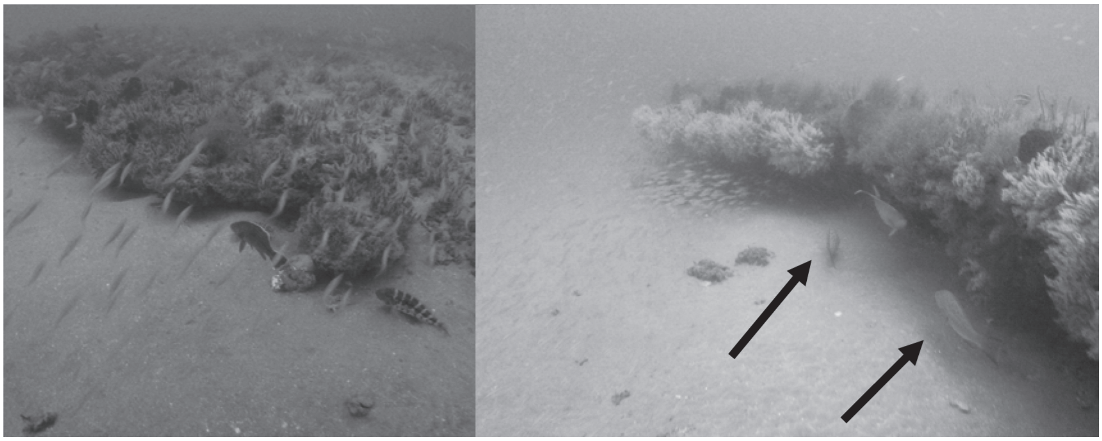

Fig. 2. Black sea bass *Centropristis striata* and bank sea bass *Centropristis ocyurus* (left) in typical orientation at edge of ledge before ambush feeding on prey fish. Two scamp *Mycteroperca phenax* (right, indicated by arrows) along ledge move towards high density aggregation of prey fishes. *Mycteroperca phenax* attacked prey fishes subsequent to this photograph.

ocyurus and *M. phenax* was high, indicating that this mixed species group was common during predation events. *Centropristis striata* and *C. ocyurus* were observed primarily along the deep edge of ledges while *M. phenax* (and *M. microlepis*) occurred adjacent to and under ledges, all proximate to schooling prey when in dense aggregations. Results of a hierarchical clustering procedure based on the Bray-Curtis matrix illustrate the variation in strength of these relationships and yield two primary groups indicative of the consistency of these multi-species associations (Fig. 3).

Here we have described a web of predation behaviors and

Table 1. Piscivorous reef fish species observed at Anchor Reef, total number of individuals observed, rank abundance, number of occurrences in single (S) and mixed species (M) foraging groups, and maximum number of individuals in single species groups. Rank abundance values are the same for species with ties in numerical abundance.

Species	Total observed	Rank abundance	S	M	Maximum number
Almaco jack, *Seriola rivoliana*	3	11	1	1	2
Amberjack, *Seriola dumerili*	38	7	3	9	12
Bank sea bass, *Centropristis ocyurus*	45	5	2	2	8
Bar jack, *Carangoides ruber*	60	3	4	2	27
Barracuda, *Sphyraena barracuda*	41	6	6	10	15
Black sea bass, *Centropristis striata*	285	2	12	7	8
Blue runner, *Caranx crysos*	>1000	1	2	2	>1000
Gag grouper, *Mycteroperca microlepis*	26	9	0	1	-
Scamp, *Mycteroperca phenax*	37	8	3	5	3
Spanish mackerel, *Scomberomorus maculatus*	59	4	7	5	23
Cobia, *Rachycentron canadum*	15	10	1	2	6

the responses of prey that indirectly link mid-water and demersal piscivorous fishes. The linkages between pelagic and demersal fishes are generally considered via a variety of meso-scale physical and biologic processes (Genin, 2004). For example, trophic relationships (*e.g.*, demersal fishes feeding on pelagic prey species and vice versa), ontogenetic shifts in vertical distribution due to life history characteristics (*e.g.*, pelagic juveniles settling to the seafloor to assume a demersal existence), and biologically or physically-mediated processes related to down-welling or advection of prey (*e.g.*, vertical migration of fishes mediated by light intensity, trapping or advection of prey to the peaks and sides of abrupt topographies, and subsequent predation by fishes) all contribute to interactions that transfer mid-water production to seafloor communities (Genin, 2004; Grober-Dunsmore *et al*., 2008).

If the predator-prey interactions of demersal piscivorous fishes are commonly mediated by the predatory behavior of

Table 2. Bray-Curtis similarity matrix based on species co-occurrences in mixed species foraging groups (n=17 mixed species groups of piscivorous fishes). Species codes as follows: AlJ=almaco jack *Seriola rivoliana*, Amb=greater amberjack *Seriola dumerili*, BaJ=bar jack *Carangoides ruber*, Bar=barracuda *Sphyraena barracuda*, Blu=blue runner *Caranx crysos*, Bsb=black sea bass *Centropristis striata* and bank sea bass *Centropristis ocyurus*, Cob=cobia *Rachycentron canadum*, Gag=gag grouper *Mycteroperca microlepis*, Sca=scamp grouper *Mycteroperca phenax*, and SpM=Spanish mackerel *Scomberomorus maculatus*.

	SpM	Bar	Amb	Sca	Bsb	BaJ	Cob	AlJ	Gag
SpM									
Bar	39.39								
Amb	36.32	53.87							
Sca	0.00	0.00	0.00						
Bsb	0.00	0.00	0.00	58.33					
BaJ	7.46	9.09	0.00	0.00	0.00				
Cob	0.00	0.00	3.70	0.00	0.00	0.00			
AlJ	0.00	9.09	29.63	0.00	0.00	0.00	12.50		
Gag	0.00	0.00	0.00	0.00	41.67	0.00	0.00	0.00	
Blu	0.00	30.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00

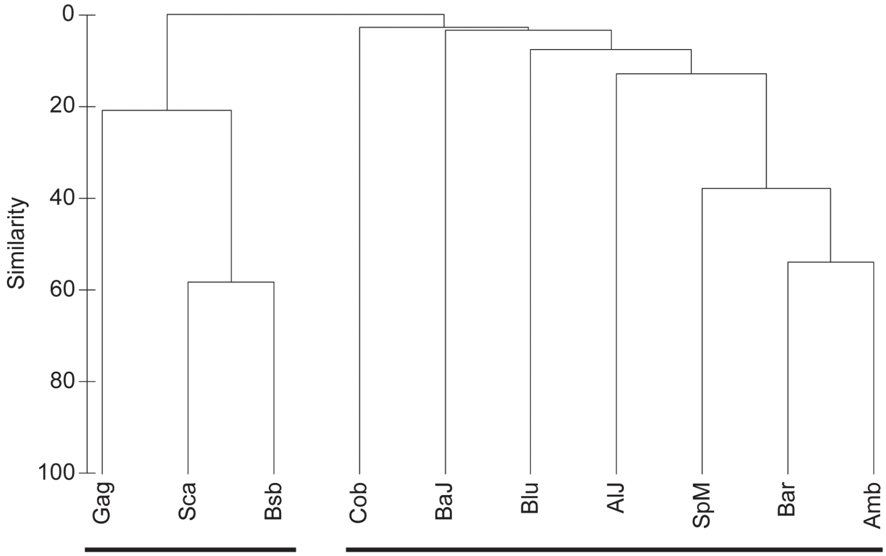

Fig. 3. Results of hierarchical clustering using the group average linkage method. The dendrogram illustrates variable strengths in multi-species relationships and patterns of species groupings (species codes as in Table 2).

midwater piscivorous fishes and their prey, such behavior webs may be important in terms of population processes (*e.g.*, prey consumption and growth rates) of these demersal fishes (*e.g*. Safina, 1990). Evaluating the spatial and temporal extent of such interactions is needed to confirm their importance as well as empirical tests of hypotheses to assess the relative role of direct and indirect facilitative behaviors of co-occurring predators.

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