Original article

Coordinated hunting behaviors of mixed-species groups of piscivores and associated species at Isla del Coco National Park (Eastern Tropical Pacific)

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Studies of mixed-species groups of animals can reveal emergent complexities of collective behaviors. In this study we collected data on mixed-species hunting groups composed primarily of piscivorous fishes (species composition, abundance, behavioral interactions) and used both multivariate and network analyses to quantify pair-wise and guild level behavioral relationships. Our results indicate that such collective behaviors exhibit consistent patterns of associations (33 species with 282 pair-wise links within the observed network) with 10 dominant species accounting for 60% of pair-wise interactions. Species richness within groups varied (mean = 2.4, range 2-6 species) as did group size (mean = 8.1 individuals, range 2-80). Mixed-species groups, in general, were composed of species representing morphologically diverse forms that appeared to enhance access to shelter sites and implement diverse strategies for prey capture. It is noteworthy that the composition of groups did not reflect the relative abundances of their component species within the overall community of fishes, suggesting that group membership was an elective choice. The identification of these patterns, assuming they are persistent features of these communities, can be used as a foundation for studies to assess dynamics of mixed-species relationships, rates of predator success based on group membership, demographic consequences, and responses to variations in habitat attributes and associated prey resources. Such information could be used to interpret the nature of multispecies interactions within predator communities and potentially aid in conservation and management.

Keywords: Facilitation, Marine protected area, Mutualism, Network, Predation.

Estudios de grupos mixtos de animales puede revelar complejidades y sutilezas del comportamiento colectivo. En este estudio recolectamos datos sobre depredación de grupos mixtos de especies, compuestos principalmente por piscívoros (composición de especies, abundancia, interacciones) y usamos tanto análisis multivariado como de redes para cuantificar relaciones de comportamiento entre pares de especies y a nivel de gremios. Nuestros resultados indican que los comportamientos colectivos exhiben patrones consistentes de asociaciones (33 especies con 382 interacciones entre pares de especies dentro de la red) con 10 especies dominantes que constituyen el 60% de las interacciones entre dos especies. La riqueza de especies dentro de grupos varió (media = 2.4, ámbito 2-6 especies) cómo también el tamaño del grupo (media = 8.1, ámbito 2-80). Los grupos de especies mixtas, en general, estaban compuestos por especies con diversas morfologías que aparentemente aumentan el accesos a lugares estrechos y además, implementa diversas estrategias de captura de presas. Vale la pena resaltar que la composición de los grupos no reflejaba la abundancia relativa de las especies en la comunidad total de peces, sugiriendo que la membresía en el grupo era algo electivo. La identificaín de estos patrones, asumiendo que son características persistentes de la comunidad, se podrán usar en estudios para determinar la dinámica de las relaciones de grupos mixtos, tasa de éxito de depredación basado en la membresía del grupo, consecuencias demográficas y respuestas a varicaciones en las habitat y presas. Esta información servirá para interpretar la naturaleza de las interacciones multiespecíficas dentro de la comunidad de depredadores y potencialmente ayudar en la conservación y manejo de recursos.

Palabras clave: Área marinas protegidas, Depredación, Facilitación, Mutualismo, Red.

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Introduction

Studies of the consequences of mixed-species group behavior (with much work focused on mammals, birds, and insects) have been fundamental to our understanding of the ecological role that such interactions play in terms of enhancement of individual fitness (Dickman, 1992; Sumpter, 2010). Group behaviors are considered a form of facilitation when encounters between organisms benefit at least one in a pair-wise species interaction but cause harm to neither (commensalism), or a mutualism when both species derive a benefit from the interaction (Connor, 1995; Stachowicz, 2001; Bruno et al., 2003). For example, variation in the size and composition of species within foraging groups can enhance efficiency in location of food patches by accessing concealed prey in novel locations and enhance vigilance in identifying predation threats based on variation in sensory abilities (Krause, Ruxton, 2002). From the perspective of higher trophic level predators, cooperation within mixed-species groups can enhance predation success and reduce energetic costs of search (Hebshi et al., 2008). Such interactions among individuals within groups can result in positive population-level effects such as enhanced growth and fecundity (Firth et al., 2015).

In marine fishes, decades of study have been devoted to understanding the ecological consequences of single species group behaviors, primarily those that school or aggregate for feeding, predator refuge, or for reproduction (Pitcher, Parrish, 1993; Kelley et al., 2011). Much less attention has been paid to the behavior of mixed-species groups, especially those that are short term, and the resultant ecological consequences (but see Lukoschek, McCormick, 2002; Sazima et al., 2010). Previous studies have focused on how group foraging enhances the fitness of individuals (Overholtzer, Motta, 2000) and how such interactions are linked to community composition and patterns of diversity (Auster, Lindholm, 2002, 2008). We find that these types of collective behaviors are common attributes of fish communities, most notably those associated with reef features where types and rates of interactions between species are greater (Hobson, 1968; Auster et al., 2013).

Given the role that higher trophic level predators play in structuring marine communities (O'Connor, Bruno, 2007; Heithaus et al., 2008; Sandin et al., 2008; Estes et al., 2011), studies of the collective behaviors of reef piscivores ultimately may provide increased detail on how such interactions within this trophic guild shape the dynamics of both predator and prey populations (Sih et al., 1998; Lima, 2002; Berger-Tal et al., 2011). However, today we remain at a stage where simple but detailed descriptions are needed of the diversity of species interactions, within diverse ecological settings, to provide insight into the range of potential pair-wise responses. Here we describe the web of behaviors exhibited by mixed-species hunting groups of piscivores at Isla del Coco National Park, Costa Rica, in the Eastern Tropical Pacific (ETP), where a recent study concluded that the shallow waters around the island have the highest density of apex predators within the ETP (Friedlander et al., 2012; Alvarado et al., 2016). Such a predator-rich location makes this protected area an ideal natural laboratory to study the interactions of predatory reef fishes in the absence of direct human impacts.

We used approaches from network analysis for quantifying attributes of behavior webs, identified a subset of species that are dominant within the network structure, and discuss the implications of such behavior webs in the ecology of fish communities and for addressing conservation objectives. We suggest that this fish community can serve as a reference for studies of species interactions in the absence of proximate fishing pressure and other chronic human activities in the ETP.

Material and Methods

Isla del Coco is located approximately 550 km south-west of the Costa Rican mainland (Fig. 1). The island and surrounding waters out to 22.2 km, covering an area of 1989 km², constitute a National Park. The isolated 24 km² island is primarily forested with minimal land cover alteration (to support a limited number of park personnel) so there is relatively low sediment load from runoff onto surrounding marine habitats. Limited moorings and areas of allowable anchorage reduce tourism and attendant impacts both on the island and in the water. The marine unit of the park that surrounds the island was designated in 2001 as a no-fishing zone and is well enforced (Cortés, 2016).
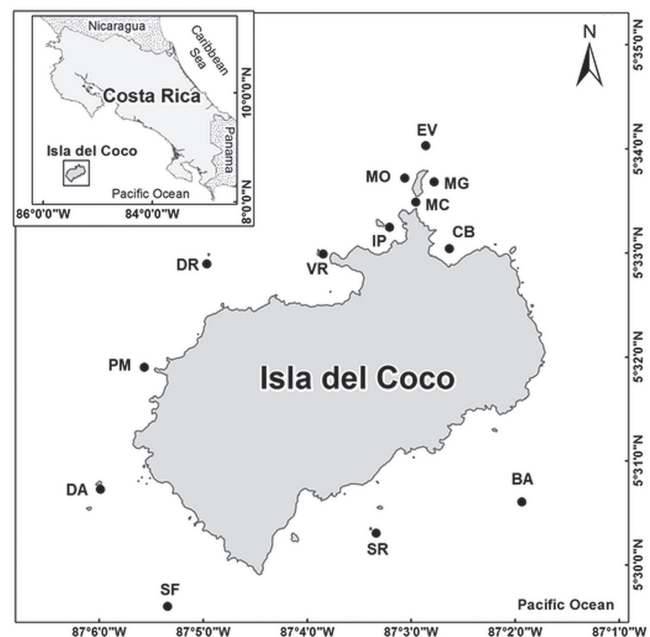

Fig. 1. Location map. BA = Bajo Alcyone, DA = Big Dos Amigos, CB = Chatham Bay, DR = Dirty Rock, EV = Everest, IP = Isla Pájara, MC = Manuelita Channel, MG = Manuelita Coral Garden, MO = Manuelita Outside, PM = Punta María, SF = Shark Fin Rock, SR = Submerge Rock, VR = Viking Rock.

Data were collected using direct underwater observation approaches during two cruises conducted from 1-11 February 2014 (MV Sea Hunter) and 24 February - 6 March 2015 (MV Argo). A modified roving diver transect (*sensu* Schmitt, Sullivan, 1996) was employed to survey behavioral interactions of piscivores and associated species at each station (Fig. 1). SCUBA was employed during 111 person-dives at 39 dive stations between 10 and 35 m depth, for a total dive time of 188 h (inclusive of 2-4 divers on each dive). The submersible vehicle DeepSee (Cortés, Blum, 2008) was used for an additional two dives using the same sampling protocol (Starr *et al.*, 2012; Auster *et al.*, 2016) to extend observations to the 50-80 m depth range for an additional 2.4 h.

During all survey dives data were collected on the interactions between piscivores and potential prey (species identification to lowest possible taxon, number of individuals, and behavioral attributes related to the elements of predation, from search to prey capture), as well as for associated species that modified predator-prey interactions, for each predation event. Divers paused along transects to observe predation related events as they were identified and continued only after a) events ended and predators dispersed or b) groups of fishes involved in each event moved beyond the range of visibility. Primary data were recorded on dive slates, while still photographic and video imagery served to confirm and clarify species and interactions as well as document surrounding habitats. Multiple observers worked different areas and depths during each dive and debriefed post dive to avoid duplicate sets of observations.

Fishes that exhibited predation related behaviors had the following characteristics: (1) two or more fishes exhibited at least one of the sequential components of predatory behaviors, including search, approach, attack, and capture (*sensu* MacNulty *et al.*, 2007); (2) individuals exhibited non-linear swimming and oriented toward potential prey or their shelter sites; and (3) animals moved as a group. Attack and prey capture were not required for an event to be recorded. Each predation related event and associated group composition was treated as a single sample unit.

Cumulative species richness across samples and richness estimator approaches, both Michaelis-Menton and Chao 1 (Clarke, Warwick, 2001), calculated using Primer version 6.1.13 software (Clarke, Gorley, 2006), were used to assess the adequacy of sampling. Descriptive statistics and graphical visualization were used to assess variation in group size and species richness of piscivores across predation events. Network analysis using SOCPROG software v2.6 (Whitehead, 2009) was used to assess the variability in pair-wise species linkages and associations across the network of behavioral interactions. Measures of mixed-species pair-wise links, total occurrences (of mixed-species links) across events, network strength, and eigenvector centrality were calculated to compare and contrast the role of particular species in hunting groups. Mixed-species links were quantified as the total number of pair-wise associations for each species and were independent of the number of such interactions (*e.g.*, species A with species B is one link regardless of the number of times this occurred). Total occurrences across events was the total number of instances across all events that each species was associated with any other species. Indication of presence-absence in single species groups (≥ 3 individuals) was a simple indicator of whether each taxa also hunted in monospecific groups. Network strength was the sum of associations of any species with all other species (Barrat *et al.*, 2004). Eigenvector centrality was a measure not only of how strongly a species was associated to another species, but also the strength of the association of that species to others (*e.g.*, a high eigenvector centrality indicated that a species has strong associations with other species which in turn had strong associations).

Hierarchical cluster analysis also was used to identify patterns of species associations (Minitab 18.1). Survey abundance data were first log (x+1) transformed to minimize variation due to high abundances of some aggregating predators and the large number of zero values in the data set. Hierarchical agglomerative clustering using the Ward linkage and Pearson distance methods was used to minimize within cluster sum-of-squares and produce similar size clusters.

To assess whether the composition of mixed-species groups simply reflected the abundances of component species within the overall fish community, we used a two-sample Z test to compare sample proportions of abundances for the top 12 species observed in mixed-species groups. For this analysis we used species abundance data from this study and results from fish community surveys conducted in July-August 2013 as well as February and November 2014 (sampling approach and sites described in Alvarado *et al.*, 2016; including unpublished community data from Bajo Alcyone, a site that was included in the present work). We used community data from this separate effort (*i.e.*, a total of 345 transects covering 2.0 km^2 area) as fish community surveys were logistically impractical to implement during the cruises reported here.

Foodweb 3D software v1.01 (Yoon *et al.*, 2004) was used to organize the interconnected network of pair-wise species linkages within the behavior web independent of the number of occurrences (simply based on presence of a pair-wise relationship). This network was then used to examine how the structure of the behavior web changed (number of all pair-wise links) with simulated overfishing of five economically-valuable species chosen *a priori* as likely targets for hook fisheries (*i.e.*, *Caranx melampygus*, *Trianodon obesus*, *Dermatolepis dermatolepis*, *Caranx lugubris*, and *Bodianus diplotaenia*). The removal of the entirety of interactions mediated by the target species (*i.e.*, those interactions between target species as well as other species in the community) assumed overfishing to a state of local ecological extinction (*i.e.*, where it can occur in isolated systems and those with low connectivity). The remaining number of pair-wise links was the response to this community level disturbance. This simulation involved a three-stage reduction in fish species

from the current unfished state (*i.e.*, removing the first two species from the list above, then the next, and finally the last two, with the order decided *a priori* based on assumed catchability). A best fit regression through the four points produced a model of the relationship of species richness within the network and complexity based on the number of pair-wise links within the web.

Results

Thirty-three species, or putative species (based on classification at a higher taxonomic level), were observed in 288 mixed-species hunting groups (Tab. 1). Group membership included seven non-piscivorous species that were either followed by, or joined with, piscivores to hunt and ambush prey disturbed by their activities. We concluded our sampling was adequate regarding the diversity of species involved in such group behaviors based on the asymptotic pattern in a species accumulation curve as well as results from Michaelis-Menton and Chao 1 estimators of total species richness (Fig. 2). Species richness and group size varied across observations. The mean species per group was 2.4 (median = 2.0, range 2-6), while there was a mean of 8.1 individuals per group (median = 4.0, range 2-80). Overall, mixed-species groups were primarily composed of species that combined morphologically-diverse forms, including those that could gain access to crevices (flexible and filiform; *e.g.*, *D. dermatolepis*, *T. obesus*, Muraenidae spp.) and those that could rapidly pursue escaping prey (laterally flattened and fusiform; *e.g.*, *C. melampygus*, *C. lugubris*). This pattern was consistent across the depth range of observations (Figs. 3-4).
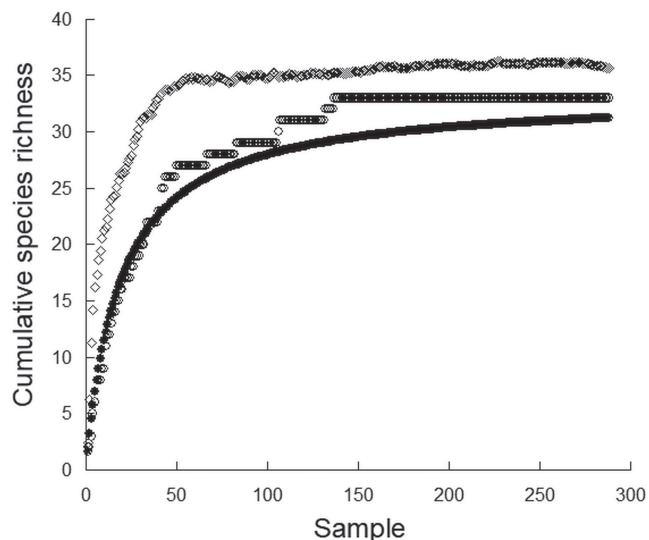

Fig. 3. Examples of mixed-species hunting groups observed to *ca*. 35 m depth. (A) *Caranx melampygus*, *Dermatolepis dermatolepis* and *Bodianus diplotenia* at a crevice. Note *D. dermatolepis* and *B. diplotaenia* are able to maneuver deep into the crevice while *C. melampygus* follow from above and search for escaping prey. (B) Group composed of *C. melampygus*, *Trianodon obesus*, *Cephalopholis panamensis* and unidentified muraenid eel (hidden within crevices) hunt for prey within crevices amongst coral and coral rubble along reef edge. (C) *Lutjanus argentiventris*, *D. dermatolepis*, *C. melampygus* and *B. diplotaenia* hunt for prey as group traverses low relief volcanic pavement along a pinnacle. (D) Group composed of *D. dermatolepis*, *C. melampygus* and *Aulostomus chinensis*. Note position of *A. chinensis* in lead over *C. melampygus*. (E) *C. melampygus* follows above a muraenid eel hunting within narrow crevices. (F) As in previous image, *D. dermatolepis* follows above muraenid eel hunting within narrow crevice. (G) *C. melampygus* follow *B. diplotaenia* hunting over sand and volcanic rubble habitat. (H) *B. diplotaenia* and *A. chinensis* hunt in tandem along edge of pinnacle.

Fig. 2. Cumulative species richness based on consecutive samples (open circles) as well as Chao 1 (open diamonds) and Michaelis-Menton estimates of species richness (solid circles). Values calculated using Primer version 6.1.13 software.
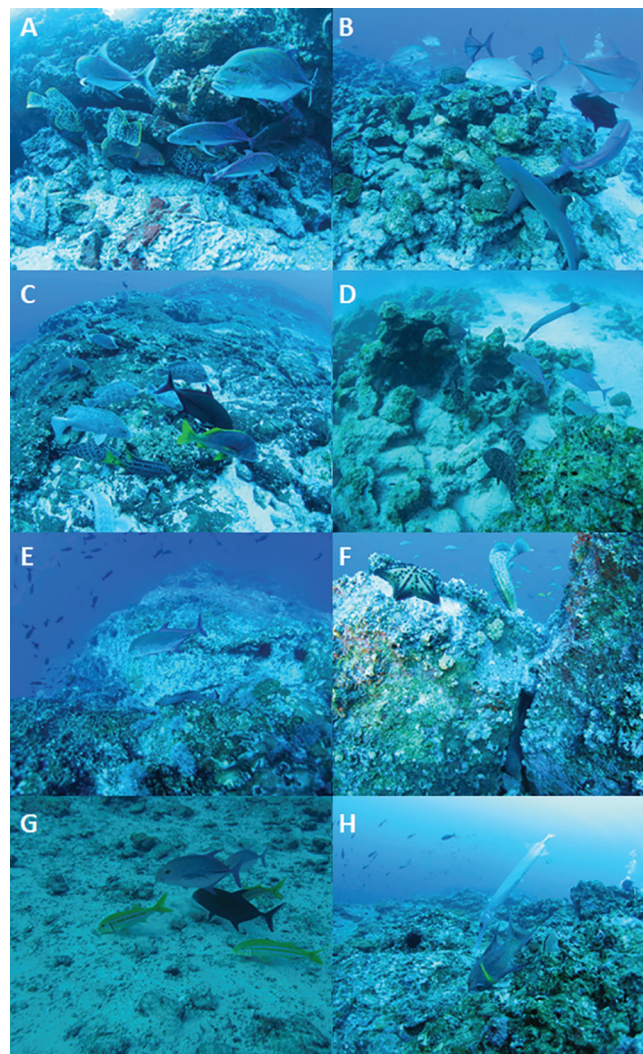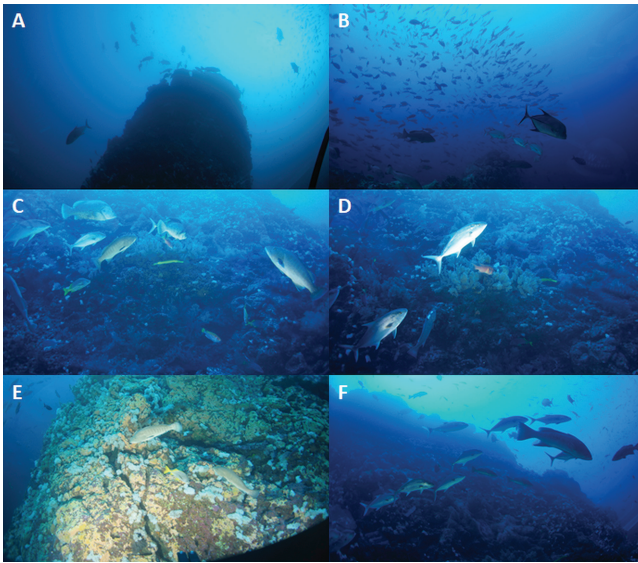
Fig. 4. Examples of mixed-species hunting groups from *ca.* 50-80 m depth at the Everest deep pinnacle site. (A) *Caranx melampygus*, *Caranx lugubris*, *Mycteroperca olfax* hunting in groups around the steep upper slope and peak, where smaller prey fish like *Paranthias colonus* aggregate in the water column. Periodic attacks by single fish and adjacent pairs were observed. (B) *C. melampygus*, *C. lugubris* and *M. olfax* move as a group but widely spaced in this setting. Individual fish attacked proximate prey that reacted to nearby predators. (C) *Seriola rivoliana*, *D. dermatolepis*, *Lutjanus argentiventris*, *Bodianus diplotaenia* and *Aulostomus chinensis* hunt for prey amongst corals and within crevices. (D) Image recorded soon after C (previous image) illustrating *D. dermatolepis* and *B. diplotaenia* entering, and *A. chinensis* emerging from a dense patch of corals to hunt while *S. rivoliana* maneuver above to encounter potential escaping prey. (E) *M. olfax* and *L. argentiventris* follow a moray eel (hidden within narrow crevice). (F) Large group of *S. rivoliana* and *M. olfax* move in tandem around the summit and upper slope, with occasional attacks by individuals on potential prey.

We found it noteworthy that 21.5% (n=62) of events included direct observations of attacks on prey, and that behavioral precursors to attacks were consistent with the elements of predation-related behaviors as described above. Observation of attacks was difficult when predators were hunting along edges of complex seafloor habitats and within crevices, so this value is a minimum estimate of attacks. Confirmation of capture success was not possible from most observations due to angle and distance as well as rapid handling and ingestion of small prey.

Network visualization illustrated the variation between species pairs in the web of associations occurring in hunting groups (Fig. 5). Network metrics (Tab. 1) identified dominant species with highest connectivity across the network. All metrics consistently indicated that 10 species had the greatest degree of interactions within the network based on

the pattern of the negative exponential distributions plotted on species organized by declining values of pair-wise links (Fig. 6). The top 10 species, occurring before the approximate position where values reach an asymptote, were *C. melmpygus*, *D. dermatolepis*, *Aulostomus chinensis*, *Mycteroperca olfax*, *Bodianus diplotaenia*, *C. lugubris*, *Lutjanus viridis*, *Lutjanus argentiventris*, *Anisotremus interruptus* and *T. obesus*. These 10 species accounted for 60% of pair-wise species interactions within the network. *Fistularia commersonii* and muraenidae spp. were just beyond the inflection point for network strength, and exhibited functional roles like similar, higher-ranked species. Specifically, *F. commersonii* was similar to *A. chinensis* as an ambush predator and species of muraenid eel hunted in crevices to an extent greater then *D. dermatolepis* and *T. obesus*. Balistidae spp., fifteenth in rank based on pair-wise links, had a much higher value of total occurrences in samples than species higher or lower on the ranked list. This taxon generally was observed foraging more in the open in a scan-and-pick foraging style (*sensu* Keenleyside, 1979), and served as a focal animal for followers seeking prey flushed by the activity. Fifty-four percent of all species (18 of 33) in this mixed-species behavior web also aggregated in single-species groups with 80% of the ten dominant species exhibiting this same pattern of cooperative behaviors among conspecifics. Such behavior is indicative of a cooperative group hunting (foraging) repertoire within each species.
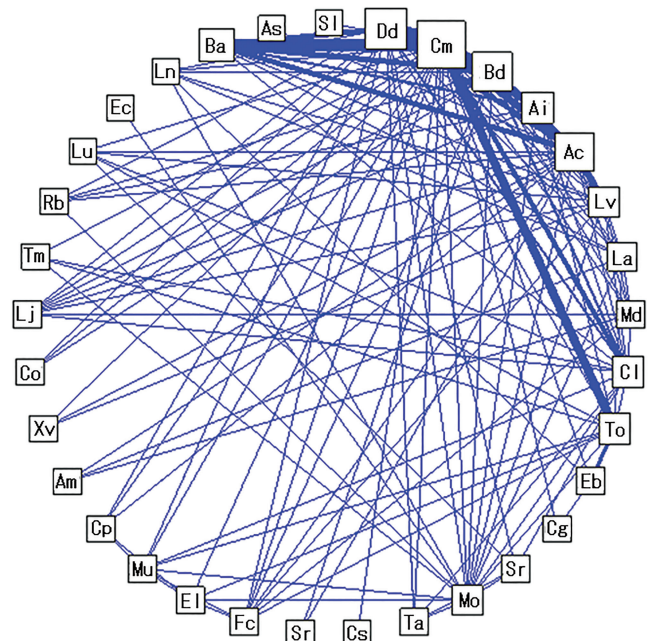

Fig. 5. Network visualization of the web of associations between species (33 species with 288 pair-wise links). The size of each species node is weighted relative to the frequency of each species in any group (abbreviations for each species are defined in Tab. 1). The lines between species nodes are weighted by the relative frequency of associations between each species pair.

Tab. 1. Summary of species observed in mixed-species predation events (by scientific name, two-letter abbreviation and numerical code used in figures) with network measures of mixed-species pair-wise links, total occurrences across events, network strength and eigenvector centrality. Species are listed in descending order of pair-wise links. Presence-absence in single species groups is a simple indicator of whether each taxa also hunts in single species groups (groups ≥3 individuals). Underline of common name indicates a non-piscivorous species involved in mixed-species groups. See text for explanation of measures.

| Scientific name	Common Name	Species Abbrev	Species Numerical Code	Mixed-Species Links	Total Occurrences	Single Species Groups	Network Strength	Eigenvector Centrality
Caranx melampygus Cuvier, 1833	Bluefin trevally	Cm	1	25	150	*	221	0.55
Dermatolepis dermatolepis (Boulenger, 1895)	Leather bass	Dd	2	18	82	*	148	0.46
Aulostomus chinensis (Linnaeus, 1766)	Chinese trumpetfish	Ac	3	17	89	*	128	0.42
Mycteroperca olfax (Jenyns, 1840)	Sailfin grouper	Mo	4	17	15	*	124	0.32
Bodianus diplotaenia (Gill, 1862)	Mexican hogfish	Bd	5	17	67		79	0.31
Caranx lugubris Poey, 1860	Black jack	Cl	6	16	33	*	56	0.19
Lutjanus viridis (Valenciennes, 1846)	Blue-and-gold snapper	Lv	7	16	34	*	51	0.15
Lutjanus argentiventris (Peters, 1869)	Amarillo snapper	La	8	11	14	*	48	0.11
Anisotremus interruptus (Gill, 1862)	Burrito grunt	Ai	9	11	25	*	47	0.13
Triaenodon obesus (Rüppell, 1837)	Whitetip reef shark	To	10	10	36	*	33	0.07
Fistularia commersonii Rüppell, 1838	Cornetfish	Fc	11	9	8		28	0.07
Muraenidae spp.	Moray eel	Mu	12	9	6		18	0.04
Mulloidichthys dentatus (Gill, 1862)	Mexican goatfish	Md	13	9	10	*	14	0.03
Lutjanus jordani (Gilbert, 1898)	Jordan snapper	Lj	14	8	7	*	12	0.03
Balistidae spp.	Triggerfish	Ba	15	8	46	*	12	0.03
Lutjanus novemfasciatus Gill, 1862	Pacific dog snapper	Ln	16	7	3		11	0.03
Epinephelus labriformis (Jenyns, 1840)	Flag cabrilla	El	17	6	4		10	0.02
Lutjanus aratus (Günther, 1864)	Mullet snapper	Lu	18	6	7	*	9	0.02
Cephalopholis panamensis (Steindachner, 1876)	Panama graysby	Cp	19	5	6	*	9	0.02
Thunnus albacares (Bonnaterre, 1788)	Yellowfin tuna	Ta	20	5	6	*	8	0.02
Seriola rivoliana Valenciennes, 1833	Almaco jack	Sr	21	5	5	*	8	0.01
Rypticus bicolor Valenciennes, 1846	Mottled soapfish	Rb	22	5	2		6	0.02
Elagatis bipinnulata (Quoy & Gaimard, 1825)	Rainbow runner	Eb	23	4	13	*	6	0.01
Caranx orthogrammus (Jordan & Gilbert, 1882)	Island jack	Co	24	3	1		5	0.02
Arothron meleagris (Anonymous, 1798)	Guineafowl puffer	Am	25	3	2		5	0.02
Xyrichtys victori Wellington, 1992	Galapagos razorfish	Xv	26	3	3		4	0.01
Carcharhinus galapagensis (Snodgrass & Heller, 1905)	Galapagos shark	Cg	27	2	5		3	0.01
Taeniura meyeni (Müller & Henle, 1841)	Marbled ray	Tm	28	2	3		3	0
Caranx sexfasciatus Quoy & Gaimard, 1825	Bigeye trevally	Cs	29	2	3	*	2	0.01
Scarus rubroviolaceus Bleeker, 1847	Bicolor parrotfish	Sr	30	2	2		1	0.01
Sphyrna lewini (Griffith & Smith, 1834)	Scalloped hammerhead shark	Sl	31	1	1		1	0.01
Epinephelus cifuentesi Lavenberg & Grove, 1993	Olive grouper	Ec	32	1	1	*	1	0
Aluterus scriptus (Osbeck, 1765)	Scrawled filefish	As	33	1	1		1	0
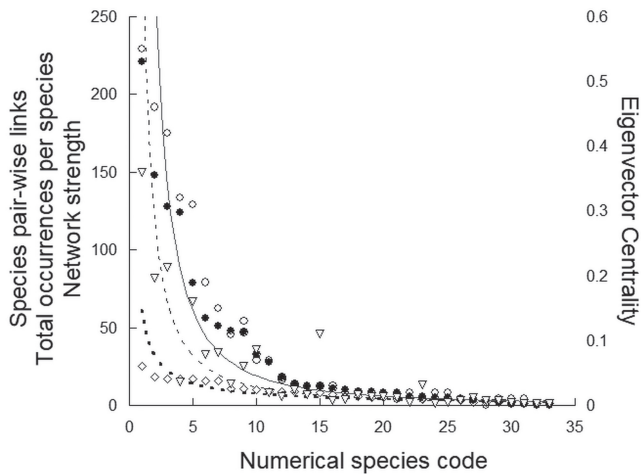
Fig. 6. Relationships between three metrics of network connectivity in order to identify important species within the behavior web (species pair-wise links = open diamond and dotted line, total occurrences per species = open triangle and dashed line, network strength = solid circle and solid line). Species on x-axis in descending order based on value of pair-wise links (as in Tab. 1). Regression lines are based on the power function. Eigenvector centrality values (open circle) plotted for comparison.

Cluster analysis (Fig. 7) identified a cluster of associations for eight of the ten dominant species identified by the network metrics (*i.e.*, in cluster 1). Significantly, there were two distinct clusters linked at larger distances. This pattern is generally consistent with the strength of pair-wise linkages for dominant species in the network diagram (Fig. 6), where piscivores did not form unique groupings, but those dominant species were joined by a diversity of taxa from the pool of local piscivores (*i.e.*, those in cluster 2). The presence of Balistidae spp. and *Elegatis bipinnulata* in cluster 1 is indicative of the strong associations with the dominant interacting species, despite low to moderate numbers of occurrences.
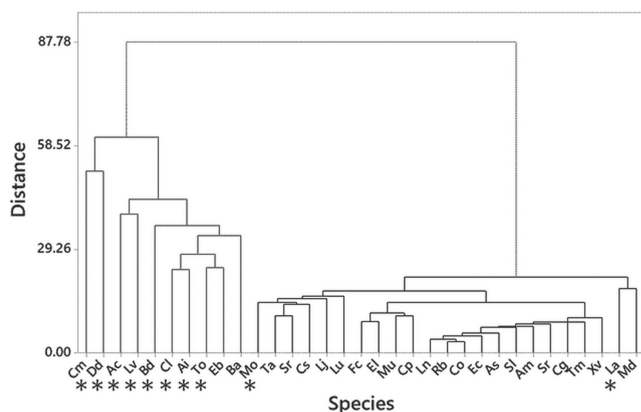

Fig. 7. Cluster analysis of species co-occurrences in groups based on the Ward linkage method and Pearson distance. Abbreviations for each species are defined in Tab. 1. Note two dominant clusters (cluster 1 at left and cluster 2 at right). An asterisk below species codes indicate membership in top 10 species based on mixed-species links.

The composition of mixed-species groups did not reflect the relative abundances of their component species within the overall community of fishes, suggesting that group membership was an elective choice by individuals (Tab. 2). Comparison of the top 12 species in mixed-species hunting groups with their proportional abundance from the overall community resulted in 11 of 12 as significantly different (Z-statistic) at p<0.05 level. While there is a lack of independence based on use of proportional data, this test is unlike a Chi-square test of proportionality as tests for each species yield species-specific results.

Tab. 2. Results of two sample Z test to compare proportions of abundances for the top 12 species observed in mixed-species groups with those from fish community surveys (see text for details).

Species	Proportion Community	Proportion Groups	Z statistic	P<
Caranx melampygus	0.0349	0.2201	34.594	0.01
Dermatolepis dermatolepis	0.0127	0.1959	46.509	0.01
Aulostomus chinensis	0.0159	0.0598	12.794	0.01
Mycteroperca olfax	0.0015	0.0118	8.643	0.01
Bodianus diplotaenia	0.0131	0.0533	12.822	0.01
Caranx lugubris	0.0013	0.0289	19.449	0.01
Lutjanus viridis	0.7988	0.3384	-43.141	0.01
Lutjanus argentiventris	0.0138	0.0118	-0.661	NS
Triaenodon obesus	0.0173	0.0431	7.529	0.01
Fistularia commersonii	0.0018	0.0047	2.606	0.01
Muraenidae spp.	0.0013	0.0035	2.220	0.05
Lutjanus jordani	0.0884	0.0284	-8.572	0.01

The sequential removal of species to simulate fishing effects on the pair-wise behavioral interaction web produced notable results. The unimpacted status quo (33 species with 282 pair-wise links) was followed first by the removal of *C. melampygus* and *T. obesus* (reducing the web to 31 species with 208 pair-wise links), followed by the removal of *D. dermatolepis* (30 species remaining with 174 links), and then *C. lugubris* and *B. diplotaenia* (28 species remaining with 122 pair-wise links). The removal of only five species produced a steep decline in species linkages plotted on richness (Fig. 8), albeit based on dominant species and the strong role they play in interactions across the web.

Discussion

Our results demonstrate that collective behaviors in mixed-species hunting groups of piscivorous fishes exhibited consistent patterns of associations for a set of dominant species and were common to this functional guild within the shallow fish community at Isla del Coco. This work demonstrates the utility of using coupled field observations and network approaches for quantifying the attributes of facilitative behavioral interactions within a particular trophic guild of animals, rather than using food web data alone
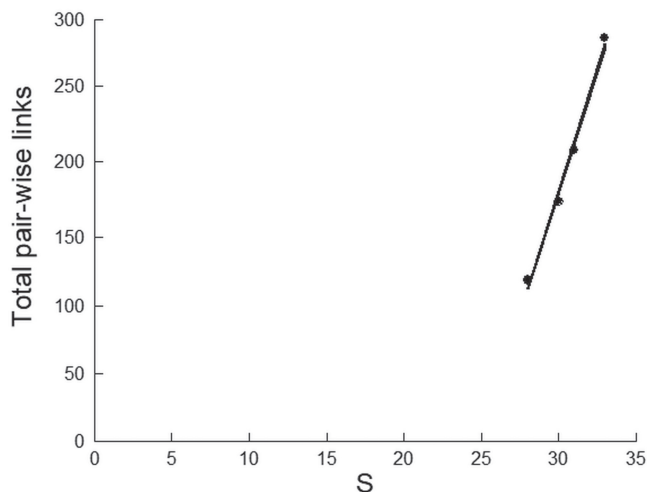
Fig. 8. Linear regression of total pair-wise links in the behavior web on species richness (links = -781.8 + 32.08 S; r2 = 99.1) based on fisheries removal simulation. Noteworthy is the rapid decline in linkages within the behavior web with removal of only several key species. The reduction in species richness is with the sequential removal of first *Caranx melampygus* and *Trianodon obesus*, then *Dermatolepis dermatolepis*, *Caranx lugubris* and *Bodianus diplotaenia* from the data set in this study (see text for detailed explanation).

(*e.g.*, Bascompte *et al*., 2005). Further, while the quantitative aspects of collective behavior between piscivores have been reported from other regions (Bshary *et al*., 2006), this study is one of few addressing such interactions at the guild level (but see Auster *et al*., 2013).

It was noteworthy that the behavioral associations between the diversity of species in the guild were tightly linked to a principal set of 10 dominant species within the network. This pattern indicated that this subset of the diversity within the piscivore guild played an overarching role in mediating the dynamics of these types of facilitative mixed-species interactions. The general pattern of agreement in the relative values of associations between species, revealed across the different quantitative metrics, suggested that multiple measures can be used to assess and verify the functional role each species plays within the guild by engaging in these types of interactions. Such assessments, based on behavioral network metrics, can aid in the identification of ecologically important species that can serve as targets for more detailed study, monitoring, and management attention (Jordán *et al*., 2008). Such quantitative indices also provide a set of measures for this marine protected area that can be used to compare the status of behavioral webs over time, both within and between habitats, and at other protected sites. Contrasts between communities in protected areas and those exploited by fishing, or impacted by other human-caused disturbances, can serve as natural experiments to improve our understanding of these types of species interactions.

The rationale for our fundamental descriptive approach was to provide a foundation for future studies to focus on assemblages or guilds with strong facilitative behaviors, to address and identify the potential for asymmetric responses of impacts to populations and communities. Identifying whether there are limits or rules that govern the scope of these types of interactions will be important for applying what is found in particular settings (*i.e.*, communities, landscapes, habitats) over time and in other places. In this case we find that measures of species richness and group size per event at Isla del Coco were comparable to those observed for mixed-species groups of piscivores at minimally impacted (but not fully protected) sub-tropical reef sites in the western North Atlantic (Auster *et al*., 2013).

Further, results from this study were similar to those from sub-tropical reefs in the western Atlantic and Gulf of Mexico, with an apparent degree of redundancy in the piscivore guild and a subset of species that act as strong interactors within the behavior web (Auster *et al*., 2013). Morphological variation within groups also appeared to be a common element structuring group composition (*e.g.*, Auster *et al*., 2016). However, with such limited sets of observations from other sites for comparison, we could only hypothesize that there were factors that constrained richness, group size, and composition for species in this trophic guild (*e.g.*, Sih *et al*., 1998). There is a clear potential for interference competition between species with similar sizes, morphologies and hunting tactics in regard to finding and capturing prey. Indeed, local density of functionally similar predators may limit the trade-offs in energetic costs and benefits in terms of joining and leaving hunting groups (*e.g.*, Kelley *et al*., 2011; Firth *et al*., 2015). Whether such patterns in richness and group size are conservative ecological properties in unimpacted communities remains to be determined. Yet if these types of ecological limits are widespread, they can serve as reference points to aid in assessments of community state and time-series monitoring. For example, richness in mixed-species hunting groups and patterns of group size were significantly reduced when compared to more heavily fished reef sites in the Gulf of Mexico (Auster *et al*., 2013).

The simulation of overfishing by eliminating five dominant but economically valuable species from the behavior web produced a rapid rate of decline (53%) in pair-wise mixed-species interactions. Despite the coarse approach to addressing this question, we suggest the results can be used as a foundation to develop hypotheses to be tested via observation in fish communities along a gradient of fishing pressure. Indeed, this pattern suggests the potential for a rapid decline in the role behavioral facilitation of hunting can play in a fish community subject to overexploitation and a potential cascade of population and community-level effects (*e.g.*, enhanced survival and expansion of meso-predator and lower trophic level species; Stallings, 2008). Of course, this simulated response assumes that remaining species will not exhibit any form of behavioral compensation (*e.g.*, switching of pair-wise species association, release from behavioral constraints of functionally similar predators; scenarios that are testable in future studies).

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All group hunting observations occurred over the time scale of minutes, with some groups forming and dispersing within the time-frame of observation (< 10 min) while others moved into or out of the field of view within that time. In all cases this facilitation of predation was temporary and not on the same time scale as classic mutualisms that play out over the lifetime of the animals involved (*e.g*., anemone and anemone-fish relationships), although we were not able to develop time budgets for patterns of group membership. Two key aspects of group formation have yet to be resolved. First, the cues used by individuals to initiate the synchronization of behavior remain unknown (Vail *et al*., 2013). Some form of information transfer involved in coalescing groups could involve visual cues related to search behavior, acoustic cues produced by hunting-foraging behavior (*e.g*., jaw and fin movements, bites), chemical cues produced from previous activities (*e.g*., from consumption of prey), or some combination. Overall mixed-species groups at Isla del Coco appeared to fit multiple classes of associations (*sensu* Lukoschek, McCormick, 2002): inter-specific group hunting, following and scavenging, and hunting by riding models of attendant associations. Second, individuals must assess the energetic costs and benefits of group membership as related to timing of joining a group and subsequent departure. This could also involve prior experience of individuals with alternative tactics related to predation success (Matsuda *et al*., 1993) or simply an individual's state of satiation. Issues of change in shelter resources and perceived risk of predation by prey also could play a role in the time investment in group hunting behaviors (Bshary *et al*., 2007). Identifying the behavioral roles of individuals and their predation success rates within groups may shed light on how mixed-species hunting groups are formed and under what conditions.

The primary ecological observations reported here suggest multiple avenues for inquiry. Growth, maturation, and fecundity are fundamentally based on hunting success and energy intake, survivorship based on predator avoidance, and patterns of distribution based on density dependent behavioral interactions, among others. While predator-prey interactions, primarily derived from gut content studies, have been fundamental in quantifying multi-species interactions and the flow of energy derived via prey consumption in marine communities, the bioenergetic trade-offs of collective behavior remain to be evaluated. For example, as prey populations vary in abundance and distribution (*e.g*., based on variation in attributes of habitat), behavioral interactions amongst predators may change (*i.e*., exhibiting context dependency; Bronstein, 1994) either regarding the structure of pair-wise associations or the intensity (frequency) of those associations. Indeed, periodic spawning aggregations of prey fishes can provide a unique trophic subsidy to predators (Mourier *et al*., 2016) and influence the interactions within predator behavior webs. Here we provided an example to establish a fundamental structure for beginning to address such issues. The current literature provides tantalizing examples of the role such interactions might play in the wider context of conservation and sustainable use, but more detailed studies over appropriate space and time scales are needed (Hay *et al*., 2004; Bronstein, 2015). That is, our understanding of the roles such interactions play in regulating populations and communities remain substantially limited. Linking knowledge of variation in behavioral interactions to bioenergetics and ultimately to demographic consequences in fish populations will be the key to linking behavior to conservation and management.

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