Complexity in a facilitative behavior web of piscivores and associated species at Isla del Coco National Park (Eastern Tropical Pacific)

Suggested Running head: Behavior web of piscivores

Authors: Peter J. Auster¹,² and Jorge Cortés³,⁴

¹University of Connecticut, Department of Marine Sciences and Northeast Undersea Research, Technology & Education Center, 1080 Shennecossett Rd., Groton, Connecticut 06340 USA; peter.auster@uconn.edu
²Mystic Aquarium – Sea Research Foundation, 33 Coogan Blvd., Mystic, Connecticut 06355 USA.
³Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Ciudad de la Investigación, Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica; jorge.cortes@ucr.ac.cr
⁴Escuela de Biología, Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica.

Corresponding author: Telephone: +1-860-405-9121; email:peter.auster@uconn.edu
Abstract

Discerning the role that facilitative behavioral interactions in mixed species groups of hunting piscivores play in growth and survivorship is important both in our fundamental understanding of fish community dynamics and for developing conservation strategies. In this study we collected data on mixed-species hunting groups (species composition, numbers, behavioral interactions) and used both multivariate and network analyses to quantify pair-wise and guild level behavioral relationships. Our results demonstrate that collective behaviors in mixed species hunting groups exhibit consistent patterns of associations within a set of dominant species (10 of 32 species within the network) and are a common attribute of this functional guild within the shallow fish community at Isla del Coco (to 80 m depth), Pacific Costa Rica. Indeed the removal of only a few dominant species from the behavior web model, to simulate overfishing, reduced the number of pair-wise linkages by 57% (32 species with 282 pair-wise links to 28 species with 122 links). The identification of these patterns, assuming they are persistent features of these communities, can be used as a foundation for time-series monitoring to assess status and change in ecological interactions within the higher trophic level guild of fishes. That said, more work is needed to understand the temporal dynamics of network linkages and intensity of interactions as prey resources vary in distribution and abundance. Such information could be used to interpret the nature of multispecies interactions within predator communities and serve as an aid in conservation and management.

Keywords: facilitation, mutualism, network, predation, fishing, model, scuba, submersible

Introduction

Studies of the ecological consequences of mixed species group behavior in a diversity of major taxa (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, or a mutualism when both species derive a benefit from
the interaction (Stachowicz 2001, Bruno et al. 2003). For example, variation in the size and composition of foraging groups (i.e., mixed species with individuals within feeding guilds) can enhance efficiency in location of food patches and enhance vigilance to identify threats of predation (Krause and Ruxton 2002). From the perspective of higher trophic level predators, cooperation between mixed species groups can enhance predation success and reduce energetic costs of search (Hebshi et al. 2008). Such interactions between 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 and 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 in nature, and the resultant ecological consequences (but see Lukoschek and McCormick 2002). Previous studies have focused on how group foraging enhances the fitness of individuals (Overholtzer and Motta 2000) and how such interactions are linked to community composition and patterns of diversity (Auster and Lindholm 2002, 2008). We find 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 enhanced (Hobson 1968, Auster et al. 2013).

Understanding the structure and variability of such behavioral interactions within populations and communities can provide important insights for their conservation and sustainable use. Given the role that higher trophic level predators play in structuring marine communities (O'Connor and Bruno 2007, Heithaus et al. 2008, Sandin et al. 2008, Estes et al. 2011), studying the collective behavior of reef piscivores ultimately may provide increased detail on the variability of interactions with this trophic guild beyond the scope provided by census data of component species alone (Sih 1998, Lima 2002, Berger-Tal et al. 2011). Here we describe the structure of a behavior web of 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 Eastern Tropical Pacific (Friedlander et al. 2012), making this protected area an ideal natural laboratory to study the interactions of predatory reef fishes in the absence of direct human impacts.

We use approaches from network analysis to quantify attributes of behavior webs, identify a subset of species that are important for maintaining network structure, and discuss the implications of such behavior webs for conservation objectives. Further, 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.

MATERIALS AND METHODS

Isla del Coco is located approximately 550 km south-west of the Costa Rican mainland. Surrounding waters out to 22.2 km, covering an area of 1989 km², is 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 limit tourism and attendant impacts both on the island and in the water. The marine park area surrounding the island was designated in 2001 as a no-fishing zone and is well enforced (Cortés 2016). The entire area is a shallow component of the Coco Volcanic Cordillera (Cortés 2016) with shallow seafloor habitats broadly composed of coral reefs, basaltic rock, and surrounding sand in topographic low points, occurring along the coast and sides of offshore islets and pinnacles (Friedlander et al. 2012, Lizano 2012).

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 and 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 hrs (inclusive of 2-4 divers on each dive). The submersible vehicle DeepSee (Cortés and 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 hrs. During all survey dives data were collected on the interactions between piscivores and potential prey (species identification, 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, Michaelis-Menton and Chao 1 (Clarke and Warwick 2001), calculated using Primer version 6.1.13 software (Clarke and 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 (Primer 6.1.13). A Bray–Curtis matrix of similarity coefficients, for all species pairs, was computed using standardized survey data. The Bray–Curtis similarity procedure provides a method of quantifying the similarity of species occurrences within sets of samples and compare the relative strengths of relationships between the occurrences of species pairs. We used hierarchical agglomerative clustering of the Bray–Curtis matrix using the single linkage method of joining species on scale based on Euclidean distance to compare relationships.

Foodweb 3D software v1.01 (Yoon et al. 2004) was used to organize and visualize 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 pair-wise links) with simulated overfishing of five economically valuable species chosen a priori as likely targets for hook fisheries (i.e., bluefin trevally, white-tip reef shark, leather bass, black jack, Mexican hogfish). The removal of the entirety of interactions mediated by the target species assumed overfishing to a state of ecological extinction. 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 (e.g., first removing one group of species, then another, and so on) to regress a line through four points and produce a linear 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-four species, or putative species (based on classification at a higher taxonomic level), were observed in 288 mixed species hunting groups (scientific and common names in Table 1). Group membership included seven non-piscivorous species that were either followed by, or joined with, piscivores to ambush prey disturbed by foraging and related activities. We concluded our sampling was adequate in regards to 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 considerably across observations (Fig. 3). 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 primarily were composed of species that combined morphologically diverse forms, including those that can gain access to crevices (flexible and filiform; e.g., leather bass, whitetip reef shark, moray) and those that can rapidly pursue escaping prey (laterally flattened and fusiform; e.g., bluefin trevally, black jack). This pattern was consistent across the depth range of observations (Figs. 4 and 5).

The network visualization illustrated the variation between species pairs in the web of associations occurring in hunting groups (Fig. 6). Network metrics (Table 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. 7). The top 10 species, occurring before the approximate position where values reach an asymptote, were bluefin trevally, leather bass, Chinese trumpetfish, sailfin grouper, Mexican hogfish, black jack, blue-and-gold snapper, Amarillo snapper, burrito grunt and whitetip reef shark. Coronetfish and moray eel were just beyond the inflection point for network strength and exhibited functional roles, that for coronetfish were similar to trumpetfish as an ambush predator and for species of moray eel were able to hunt in crevices to an extent greater then
leather bass and white tip reef shark. Triggerfish, fifteenth in rank based on pair-wise links, had a much higher value of total occurrences in samples then species before or after on the ranked list. This is likely due to its tendency to forage more in the open, using strong jaws, teeth and spines for defense, to allow a scan-and-pick foraging style (sensu Keenleyside 1979) and then serve 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 cooperative behavior and a group hunting repertoire within each species.

Cluster analysis (Fig 8) confirmed the strongest associations were found within a dominant group of species identified by the network metrics. There was a notable absence of distinct clusters linked at larger distances, which was consistent with the integrated pattern of pair-wise linkages in the network diagram (Fig. 6). Piscivores did not form unique groupings but those with the highest level of association were joined from the pool of local piscivores. For example, the presence of triggerfish (TR) and rainbow runner (RR) in the region of highest similarity is indicative of the low numbers of occurrences in samples and strong associations with the dominant interacting species.

The sequential removal of species to simulate fishing effects on the pair-wise behavioral interaction web produced noteworthy results. The unimpacted status quo (33 species with 282 pair-wise links) was followed first by the removal of bluefin trevally and white-tip reef shark (reducing the web to 31 species with 208 pair-wise links), followed by the removal of leather bass (30 species remaining with 174 links), and then black jack and Mexican hogfish (28 species remaining with 122 pair-wise links). Note the steep slope in species linkages on richness with the removal of only five species, albeit dominant species within the web (Fig. 10) 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 was a novel demonstration of the utility of using coupled field observations and network approaches for quantifying the attributes of facilitative behavioral interactions within a particular guild of animals, rather than using food web data alone (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 was 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 hunting groups. 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 population monitoring and more detailed management attention (Jordan 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 and to contrast with other areas either protected or subject to exploitation by fishing and other human caused disturbances.

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 in order 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 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 of cluster analyses in this study were similar to 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 of species within groups, that we infer aids in searching for prey within complex habitats, 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 regards 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 northeastern 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 mixed species interactions. Despite the coarse simulation approach used 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 subject to 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 adequate form of behavioral compensation (e.g., release from behavioral constraints of functionally similar predators).
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 lifetimes of the animals involved (e.g., anemone-anemone-fish relationships). While we were not able to develop time budgets for patterns of group membership or assess the behavioral roles of individuals within groups, two key issues emerge. First is there must be cues used by individuals to initiate the synchronization of behavior (Vail et al. 2013). That is, a form of information transfer involved in coalescing groups and 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 group associations (sensu Lukoschek and 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 or simply an individual’s state of satiation. Issues of change in shelter resources and perceived risk of predation also could play a role in the time investment in group behaviors (Bshary et al 2007).

The primary ecological observations reported here suggest several avenues for inquiry. Growth rate, time to maturation and fecundity are all fundamentally based on foraging 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, behavioral interactions amongst predators may change either in regards to the structure of pair-wise associations or
the intensity (frequency) of those associations, as a way to maximize feeding success. Indeed periodic spawning aggregations of prey fishes have been found to provide a unique trophic subsidy to higher trophic level predators (Mourier et al. 2016) and influence the interactions within predator behavior webs. Here we provided 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 the detailed studies over appropriate space and time scales are mostly absent. 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 within marine ecosystems.

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Figures

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

Figure 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).

Figure 3. Distribution of species richness across 288 predation related events (A) and number of individuals per event (B).

Figure 4. Examples of mixed species hunting groups observed to ca. 35 m depth. (A) Bluefin trevally, leather bass and Mexican hogfish at a crevice. Note leather bass and Mexican hogfish are able to maneuver deep into the crevice while bluefin trevally follow from above and search for escaping prey. (B) Group composed of bluefin trevally, white tip reef shark, Panama graysby and unidentified moray eel (hidden within crevices) searching for prey within crevices amongst coral and coral rubble along reef edge. (C) Amarillo snapper, leather bass, bluefin trevally and Mexican hogfish scan for prey as group traverses low relief volcanic pavement along a pinnacle. (D) Group composed of leather bass, bluefin trevally and Chinese trumpetfish. Note position of trumpetfish in lead over trevally. (E) Bluefin trevally follows above a moray eel hunting within narrow crevices. (F) As in previous image, leather bass follows above moray eel hunting within narrow crevice. (G) Bluefin trevally follows Mexican goatfish over sand volcanic rubble habitat. (H) Mexican hogfish and Chinese trumpetfish hunt in tandem along edge of pinnacle.

Figure 5. Examples of mixed species hunting groups from ca. 50 - 80 m depth at the Everest deep pinnacle site. (A) Bluefin trevally, black jack, sailfin grouper hunting in groups around the
steep upper slope and peak, where smaller prey fish like Pacific creolefish aggregate in the water column. Periodic attacks by single fish and adjacent pairs were observed. (B) Bluefin trevally, black jack and sailfin grouper move as a group but widely spaced in this setting. Individual fish attacked proximate prey that reacted to nearby predators. (C) Almaco jack, leather bass, Amarillo snapper, Mexican hogfish and Chinese trumpetfish hunt for prey amongst corals and within crevices. (D) Image subsequent to the previous one illustrating leather bass and Mexican hogfish entering, and Chinese trumpetfish emerging from, a dense patch of corals to search while Almaco jack maneuver above to encounter potential escaping prey. (E) Sailfin grouper and Amarillo snapper follow a moray eel (hidden within narrow crevice). (F) Large group of Almaco jack and sailfin grouper move in tandem around the summit and upper slope, with occasional attacks by individuals on potential prey.

Figure 6. Circular 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 Table 1). The lines between species nodes are weighted by the relative frequency of associations between each species pair.

Figure 7. Contrasts of relationships between four 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, eigenvector centrality = open circle and no regression line due to zeros in data set). Species on x-axis in descending order based on value of pair-wise links (see Table 1). Regression lines are based on the power function.

Figure 8. Dendrogram from hierarchical cluster analysis illustrating patterns of association between species across all samples. Stars indicate the location of the ten dominant species identified by network analysis.
Figure 9. Variations in behavior web trellis structure, using FoodWeb 3D software, simulating overfishing and removal of target species selected a priori. Yellow nodes are species. All pair-wise species interactions (33 species with 282 links) from observations are represented in (A), with Chinese trumpetfish (CT), a dominant but unfished piscivore, indicated for orientation. The trellis was rotated to identify a side view with minimal height. Bluefin trevally and whitetip reef shark were removed from the web as in a heavily overfished state (B), leaving 31 species and 208 total links. Noteworthy is the flattening of the trellis structure in a side view with minimal height. In (C) leather bass, black jack and Mexican hogfish also are removed, leaving 28 species and 122 links.

Figure 10. 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 bluefin trevally and whitetip reef shark, then leather bass, black jack and Mexican hogfish from the data set in this study (see text for detailed explanation).
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<th>Notes</th>
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*Presence* (X) presence in mixed species groups indicates whether each taxa also hunts in single species groups (groups ≥3 individuals). *Absence* (X) 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.
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<td><em>Triaenodon obesus</em></td>
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<td>36</td>
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<td><em>Mullloidichthys dentatus</em></td>
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<td>9</td>
<td>10</td>
<td>*</td>
<td>14</td>
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<tr>
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<td><em>Lutjanus jordani</em></td>
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<td>7</td>
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<tr>
<td>Triggerfish</td>
<td><em>Balistes sp.</em></td>
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<td>*</td>
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<td>Common Name</td>
<td>Scientific name</td>
<td>Species Abbr</td>
<td>Species Numerical Code</td>
<td>Mixed Species Links</td>
<td>Total Occurrences Per Species</td>
<td>Single Species Groups</td>
<td>Network Strength</td>
<td>Eigenvector Centrality</td>
</tr>
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<td>Panama graysby</td>
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<td>6 *</td>
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<tr>
<td>Yellowfin tuna</td>
<td><em>Thunnus albacares</em></td>
<td>YT</td>
<td>20</td>
<td>5</td>
<td>6 *</td>
<td>8</td>
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<td>Almaco jack</td>
<td><em>Seriola rivoliana</em></td>
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<td>5</td>
<td>5 *</td>
<td>8</td>
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<tr>
<td>Mottled soapfish</td>
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<td>2 *</td>
<td>6</td>
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<tr>
<td>Rainbow runner</td>
<td><em>Elagatis bipinnulata</em></td>
<td>RR</td>
<td>23</td>
<td>4</td>
<td>13 *</td>
<td>6</td>
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<tr>
<td>Island jack</td>
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<td>24</td>
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<td>1 *</td>
<td>5</td>
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<td>Guineafowl puffer</td>
<td><em>Arothron meleagris</em></td>
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<td>5 *</td>
<td>3</td>
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<td>3 *</td>
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<td>Bigeye trevally</td>
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<td>32</td>
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<td>Scrawled filefish</td>
<td><em>Aluterus scriptus</em></td>
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<td>33</td>
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<td>1 *</td>
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Figure 1. Location map of survey sites: Bajo Alcyone = BA, Big Dos Amigos = DA, Chatham Bay = CB, Dirty Rock = DR, Everest = EV, Isla Pájara = IP, Manuelita Channel = MC, Manuelita Coral Garden = MG, Manuelita Outside = MO, Punta María = PM, Shark Fin Rock = SF, Submerge Rock = SR, Viking Rock = VR.
Figure 2. Cumulative species richness based on consecutive samples (open circles) as well as Chao 1 (open diamonds) and Michaelis-Menten estimates of species richness (solid circles).
Figure 3. Distribution of species richness across 288 predation related events (A) and number of individuals per event (B).
Figure 4. (Next page) Examples of mixed species hunting groups observed to ca. 35 m depth. (A) Bluefin trevally, leather bass and Mexican hogfish at a crevice. Note leather bass and Mexican hogfish are able to maneuver deep into the crevice while bluefin trevally follow from above and search for escaping prey. (B) Group composed of bluefin trevally, white tip reef shark, Panama graysby and unidentified moray eel (hidden within crevices) searching for prey within crevices amongst coral and coral rubble along reef edge. (C) Amarillo snapper, leather bass, bluefin trevally and Mexican hogfish scan for prey as group traverses low relief volcanic pavement along a pinnacle. (D) Group composed of leather bass, bluefin trevally and Chinese trumpetfish. Note position of trumpetfish in lead over trevally. (E) Bluefin trevally follows above a moray eel hunting within narrow crevices (F) As in previous image, leather bass follows above moray eel hunting within narrow crevice. (G) Bluefin trevally follow Mexican goatfish over sand volcanic rubble habitat. (H) Mexican hogfish and Chinese trumpetfish hunt in tandem along edge of pinnacle.
Figure 5. Examples of mixed species hunting groups from ca. 50 - 80 m depth at the Everest deep pinnacle site. (A) Bluefin trevally, black jack, sailfin grouper hunting in groups around the steep upper slope and peak, where smaller prey fish like Pacific creolefish aggregate in the water column. Periodic attacks by single fish and adjacent pairs were observed. (B) Bluefin trevally, black jack and sailfin grouper move as a group but widely spaced in this setting. Individual fish attacked proximate prey that reacted to nearby predators. (C) Almaco jack, leather bass, Amarillo snapper, Mexican hogfish and Chinese trumpetfish hunt for prey amongst corals and within crevices. (D) Image subsequent to the previous one illustrating leather bass and Mexican hogfish entering, and Chinese trumpetfish emerging from, a dense patch of corals to search while Almaco jack maneuver above to encounter potential escaping prey. (E) Sailfin grouper and Amarillo snapper follow a moray eel (hidden within narrow crevice). (F) Large group of Almaco jack and sailfin grouper move in tandem around the summit and upper slope, with occasional attacks by individuals on potential prey.
Figure 6. Circular 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 Table 1). The lines between species nodes are weighted by the relative frequency of associations between each species pair.
Figure 7. Contrasts of relationships between four 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, eigenvector centrality = open circle and no regression line due to zeros in data set). Species on x-axis in descending order based on value of pair-wise links (see Table 1). Regression lines are based on the power function.
Figure 8. Dendrogram from hierarchical cluster analysis illustrating patterns of association between species across all samples. Stars indicate the location of the ten dominant species identified by network analysis.
Figure 9. Variations in behavior web trellis structure, using FoodWeb 3D software, simulating overfishing and removal of target species selected a priori. Yellow nodes are species. All pair-wise species interactions (33 species with 282 links) from observations are represented in (A), with Chinese trumpetfish (CT), a dominant but unfished piscivore, indicated for orientation. The trellis was rotated to identify a side view with minimal height. Bluefin trevally and whitetip reef shark were removed from the web as in a heavily overfished state (B), leaving 31 species and 208 total links. Noteworthy is the flattening of the trellis structure in a side view with minimal height. In (C) leather bass, black jack and Mexican hogfish also are removed, leaving 28 species and 122 links.
Figure 10. Linear regression of total pair-wise links in the behavior web on species richness (links = -781.8 + 32.08 S; \( r^2 = 99.1 \)) 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 bluefin trevally and whitetip reef shark, then leather bass, then black jack and Mexican hogfish from the data set in this study (see text for detailed explanation).