Information Gaps in the Trophic Roles of Caribbean Reef Fishes

Vacíos de Información en los Roles Tróficos de Peces Arrecifales del Caribe

Manque D'information sur les Rôles Trophiques des Poissons Récifaux dans les Caraïbes

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ABSTRACT

Determining the ecological roles that fishes play in the complex trophic relationships of coral reef systems depends on our ability to detect changes in the fish community composition and function. The functional redundancy of fishes in different habitats is highly influenced by species composition and ontogenetic shifts in diets and feeding behavior across species, as evidenced by different patterns of habitat use and migrations during different life stages. To better understand trophic structure in these communities, we conducted an extensive literature review of trophic functional traits of 274 marine fish species in the U.S. Caribbean. The data were applied to fish community data collected by NOAA's Coral Reef Ecosystem Monitoring and Assessment project (2001 and 2012). Fish traits were extracted for juvenile and adult fish stages separately and selected based on: ontogenetic diet shifts, habitat use for feeding, vertical habitat association, feeding behavior, diet plasticity, and trophic location in the food web. Presence and absence of functional traits were recorded because differences in trait measurements among studies were expected. Traits of adult stages were better documented than traits of juveniles. Trophic level was the most frequently recorded trait for adults (95%) and feeding ground was best documented for juveniles (17%). Feeding ground was the poorest trait recorded for adult stages (61%), as was vertical habitat association for juvenile stages (1%). Significant gaps in knowledge of trophic roles of juvenile fishes represent a need to increase research efforts to understand juvenile trophic ecology. We provide recommendations for research to address these gaps and to use this dataset for functional diversity analysis.

KEY WORDS: Fish trophic roles, ontogenetic changes, functional traits

INTRODUCTION

Understanding the ecological roles that fishes play in the complex trophic relationships of coral reef systems depends on our knowledge of fish trophic ecology and our ability to detect changes in community composition and function. A new approach to evaluate changes in ecosystem function of fish communities includes functional diversity, which accounts for similarities and differences among species based of their functional roles related to ecosystem functions (Cadotte *et al*. 2011, Diaz and Cabido 2001). Models of functional diversity describe the relationship between species richness and species functions as a positive and asymptotic curve called "functional redundancy" (Elmqvist et al. 2003, Peterson et al. 1998). The redundancy in species functions suggests that more than one species providing a specific ecosystem function is present at a single spatial and temporal scale (Elmqvist et al. 2003, Peterson et al. 1998). Functional redundancy increases the resilience of a system or its degree of self-organization to resist departures from equilibrium states following disturbances (Folke et al. 2004, Holling 1973, 1996) such as intensive fishing. In the case of reef fishes, functional redundancy should be highly influenced by species composition and ontogenetic shifts in diets, as evidenced by different patterns of habitat use and migrations during different life stages of a species (Helfman et al. 1997, Werner and Gilliam 1984). This fact suggests that juvenile fish can play a different ecological role than adult fish in marine systems, but the identification of changes in functional roles of fish species depends on the available information for both juvenile and adult stages, separately. The main goals of this study were to identify gaps in information about the functional roles related to the trophic function of juvenile and adult stages for 274 fish species of the U.S. Caribbean, and to conduct a quality analysis on compiled information based on location, time, and sample size of reviewed studies.

METHODS

Study Sites

We focused on eleven databases of fish community surveys that covered MPAs and non-protected areas located off southwest and southeast Puerto Rico, and off the U.S. Virgin Islands (USVI) archipelago (Table 1). Habitat composition of the studied sites included primarily coral reef and colonized hard bottoms, with secondary cover including seagrasses, emergent vegetation (mangroves), macroalgae, and unconsolidated bottoms. The presence of a variety of habitat types in studied sites assured broad representation of local coastal fish communities and important benthic habitats used during fish ontogenetic shifts.

Characterization of Fish Communities

Communities were characterized by the Fish Assessment and Monitoring Program and the Biogeography Branch of the National Oceanic and Atmospheric Administration (NOAA) in Puerto Rico, and the U.S. Virgin Islands from 2001 to 2012 (NOAA et al. 2007a,b,c; for more details visit: http://www8.nos.noaa.gov/biogeo_public/query_main.aspx). Location of

Table 1. Fish surveys sites conducted by NOAA in studied areas

Island	MPA	Years of survey	Total number of recorded fish species
Puerto Rico	Guanica NR^	2010-2012	141
	La Parguera NR^	2000-2012	259
	Jobos Bay NR	2009	112
	Bahias Bioluminiscentes de Vieques NR	2007	110
USVI – St. Croix	Buck Island CRNM	2003-2012	215
	St. Croix East End Marine Park^	2003-2012	213
USVI – St. John	Coral Bay APC^	2003-2011	180
	U.S. Virgin Islands NP^	2001-2011	244
	U.S. Virgin Islands CRNM^	2001-2011	244
USVI – St. Thomas	St. James MRWS^	2012	148
	Cas Cay–Mangrove Lagoon MRWS	2012	148

Abbreviations of MPAs: NR (Natural Reserve); CRNM (Coral Reef National Monument); APC (Area of Particular Concern); NP (National Park); MRWS (Marine Reserves and Wildlife Sanctuaries). (*) Surveys shared by more than one MPA. Coral Bay, U.S. Virgin Islands National Park, and U.S. Virgin Islands CRNM shared 212 surveys around St. John. Guanica and La Parguera Natural Reserves shared 287 surveys located between MPAs' boundaries. Benthic cover classes were established according to Kendall et al. (2001) classification.

surveys were established in a random stratified sample design by habitat type, and conducted by following a standardized technique of 100 m^2 belt transect visual census. Information gathered during each census included identification of fish species, an estimation of the fork length at 5 cm classes up to 35 cm, and number of individuals to calculate fish biomass by life stages (NOAA et al. 2007a,b,c).

Compilation of Fish Functional Traits for the U.S. Caribbean

Fish traits related to the trophic function of marine fish species in the U.S. Caribbean were populated in a database of 274 fish species that recorded by NOAA in all MPAs. Traits were selected based on ontogenetic diet shifts that fish species exhibit by migrating between different habitats, diet plasticity, trophic location in the food web, and habitat use (Micheli et al. 2014, Oliveira et al. 2012, Stuart-Smith et al. 2013). Traits included in this compilation were vertical habitat association (Stuart-Smith et al. 2013) and feeding ground, which is a previously unexamined trait for functional diversity analysis of marine fish communities. These traits describe the habitat type and location in the water column used as feeding ground. Feeding social behavior is another new behavioral trait included in this study, which describes species social strategies that avoid predation and minimize energetic costs during feeding. Trophic level was included because it describes the trophic position of a species within a community (Micheli et al. 2014, Oliveira et al. 2012, Stuart -Smith et al. 2013). Trophic level of each fish species was calculated by using the TropLab software (Pauly et al. 2000) based on information from diet content analysis. Prey items, another new trait included in this study, describes the trophic niche amplitude of a fish species by considering the taxonomic groups consumed by the species (Oliveira et al. 2012). Feeding category, a common used trait to classify trophic groups, was included in this study because it describes the trophic role of a species in a community (Oliveira et al. 2012, Stuart-Smith et al. 2013).

Traits were extracted for juvenile and adult fish stages separately from a literature review of information from Puerto Rico and the U.S. Virgin Islands as primary sources of information, and information from other Caribbean islands and mainland Caribbean Region as secondary sources of information. Literature review included information in both English and Spanish. Juvenile stages of fish species were identified following the criteria of Dorenbosh et al. (2004, 2007) and Nagelkerken and van der Velde (2002). Presence (1) and absence (0) of functional traits were recorded for this study because differences in trait measurements among studies was expected.

Quality Analysis for Trait Information

Quality of compiled information was analyzed by using three qualitative criteria based on location of study sites, time of publication, and sample size (Table 2). The last criterion was applied only to traits derived from diet content analysis of fish species. All criteria were used to identify species with good, intermediate, and poor quality of information, or no information. Species with good quality had scores greater than or equal to 30, representing species for which there was updated information about traits for habitats of Puerto Rico and the U.S. Virgin Islands, and had a high sample size for diet content analysis (>10 samples). Species with intermediate quality of information had scores between 15 and 29, and species with poor quality had scores below 15. Species with intermediate and poor quality represent fishes with variable information among general locations, decades of publication, and sample sizes for diet content analysis.

Table 2. Criteria used for quality analysis of functional traits

Criteria	Score			Criteria used in each functional trait					Maximum score by species
	3	2	1	VHA	SFB	TF	FG	TL, PI, FC	
Location	Puerto Rico and U.S. Virgin Islands	Other Caribbean Islands	Mainland Caribbean Region	x	x	x	x	x	
Time of publication	2000 - 2015	1980 - 1999	1950 -1979	x	x	x	x	x	
Sample size (# samples)	> 10	3 – 10	< 3 or observations					x	
Maximum score by trait				6	6	6	6	9	33

Abbreviations: (VHA) Vertical habitat association, (SFB) Social feeding behavior, (TF) Time of feeding, (FG) Feeding ground, (TL) Trophic level, (PI) Prey items, (FC) Feeding categories.

RESULTS

Literature Review

A total of 335 references, published from 1956 to 2015, were reviewed to extract functional traits for juveniles and adults stages of 274 fish species that inhabit marine habitats in the U.S. Caribbean. Reviewed publications included 263 peer-reviewed journal articles, 21 conference proceedings, 25 books, 12 PhD and MS theses, 11 governmental reports, one class project report, one encyclopedia article, and one poster presentation. A relatively high number of publications with information about functional traits for studied species were found between 2000 and 2010, with more than 15 publications per annum in some years. Information for juveniles was found in 15% of publications, for adults in 10%, and for collapsed information for juvenile, sub adult, and adult stages fish stages in 29% of publications. The majority of publications (46%) did not specify life stages of fish species, and instead the information was referred as individuals of a fish species inhabiting coral reef areas. For these specific publications the compiled information was assigned to adult stages.

Study sites of publications that contained fish functional traits varied within the Caribbean region. A good quantity of literature about diet contents of fishes was found for Puerto Rico and the U.S. Virgin Islands (54% of publications). Information about social feeding behavior and vertical habitat association was extracted mainly from publications of the mainland Caribbean region (48% and 70%, respectivelly). Feeding grounds were identified mainly from studies of other Caribbean islands (40%). Few publications containing information about time of feeding were found for all three locations (8 publications).

Much more information on functional traits was found for adult stages than for juveniles (Table 3). More than 60% of the total species sampled had functional trait information for adult stages, with the trophic level being the most frequent trait (96% of species). The most frequent trait for juvenile stages was feeding ground, with information for 17% of species. The quality analysis was conducted only for adult stages because little information was found for juvenile stages.

Quality Analysis for Trait Information of Adult Stage

For our database, the majority of fish species in adult stages had intermediate quality information (66% of all species sampled), followed by species with poor (15%) and good (14%) quality (Table 4). Few species had no information (5% of total species). Fish families having species with good quality information ($\geq$ 50% of total species) included Acanthuridae, Abulidae, Aulostomidae, Balistidae, Bothidae, Carcharhinidae, Centropomidae, Chaetodontidae, Congridae, Dactylopteridae, Monacanthidae, Scombridae, Scorpaenidae, Sphyraenidae, and Tetraodontidae (Figure 1). Fish families with intermediate quality information ($\geq$ 50% of total species) included Apogonidae, Belonidae, Blenniidae, Bothidae, Carangidae, Carcharhinidae, Chaenospidae, Cirrhitidae, Dasyatidae, Diodontidae, Ephippidae, Gerreidae, Gingly-

Table 3. Number of fish species within functional trait categories

Trait	Juveniles	Adults
Vertical habitat association	3	252
Social feeding behavior	6	189
Feeding time	2	242
Feeding ground	47	167
Trophic level	34	263
Prey items	34	214
Feeding category	34	246

mostomatidae, Grammatidae, Haemulidae, Holocentridae, Inermiidae, Kyphosidae, Labridae, Lutjanidae, Malacanthidae, Megalopidae, Mullidae, Muraenidae, Myliobatidae, Ophichthidae, Opistognathidae, Ostraciidae, Pempheridae, Pomacanthidae, Pomacentridae, Priacanthidae, Scaridae, Sciaenidae, Serranidae, Sparidae, Sphyraenidae, Syngnathidae, and Synodontidae. Fish families with poor quality information (≥ 50% of total species) included Callionymidae, Chaenospidae, Mugilidae, and Ogcocephalidae. Congridae and Microdesmidae were characterized for having high percentage of species with no information. Other species with no information included Echeneidae, Gobiidae, Labridae, Labrisomidae, Lutjanidae, and Syngnathidae families.

DISCUSSION

This study is the first to compile functional trait information related to the trophic function of both juvenile and adult stages for 274 fish species recorded in marine habitats of the U.S. Caribbean. A high number of publications with information about functional traits for adult stages were found (published since 1956), which revealed that more than 60% of fish species in the database had information about vertical habitat association, diet content, and time of feeding.

Quality of trait information compiled for adult stages had intermediate (66% of species) and low quality levels (14% of species). The low percentage of fish species with good standards of information included those with trait information compiled for Puerto Rico and the U.S. Virgin Islands (published since 2000) and with high sample sizes for diet content analysis. Fish families with good and intermediate quality of information included species of commercial importance, common species, and those commonly included in characterization of trophic functional groups in reef fish communities. The large tendency of only intermediate quality in trait information suggests that there is a lack of studies describing behavioral functional traits, such as social feeding behavior and identification of feeding grounds, for adult fish stages in the U.S. Caribbean.

Trait information for juvenile stages was scarce, and only 17% of fish species had information about location of feeding grounds and diet content. This finding indicates that there is a lack of knowledge on the trophic ecology of juvenile stages not only in Puerto Rico and the U.S. Virgin Island, but also throughout the Caribbean region. The lack of information for juvenile stages represents a large gap in

Table 4. Quality analysis of information about functional traits for fish species in adult stages

Quality of information	Max score by species	Number of species within the score
No information	0	15
Poor	1-11	41
Intermediate	12-22	180
Good	23-33	38
Total species		274

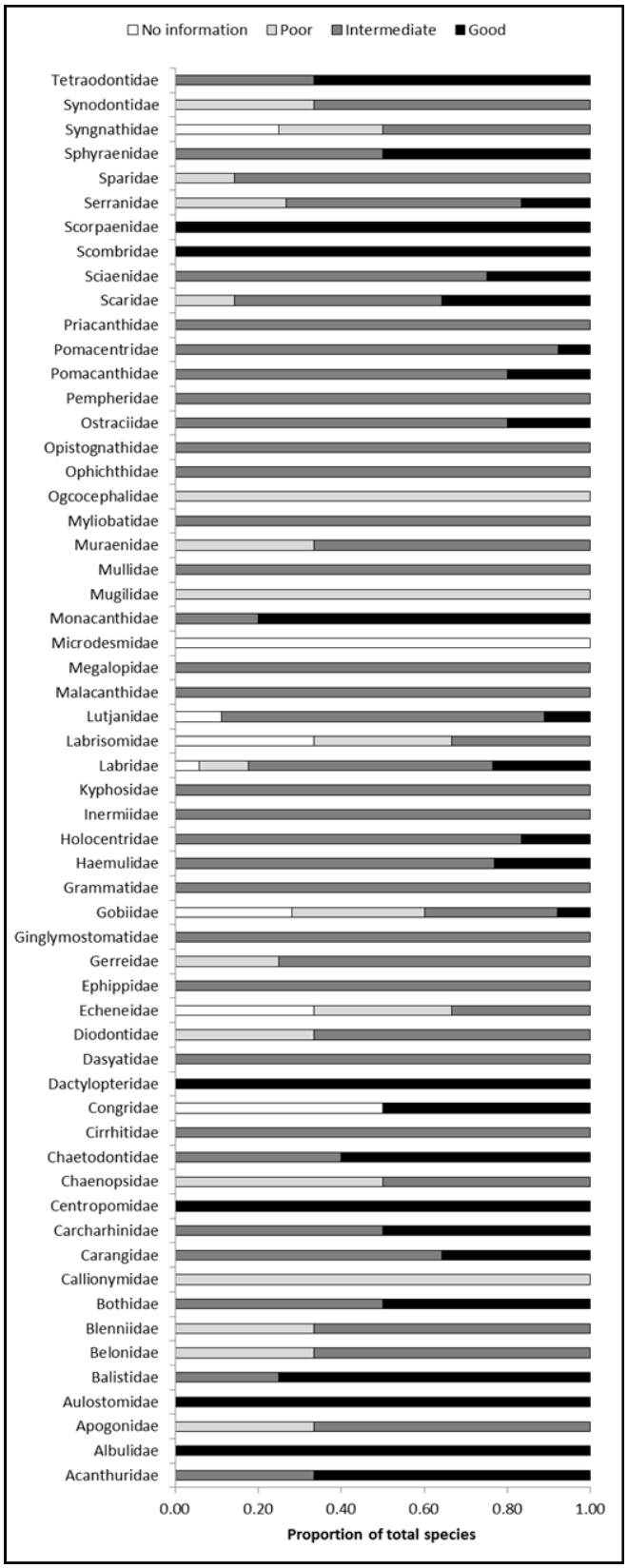

Figure 1. Quality analysis of functional trait information for adult stages of fish families.

knowledge to understand the basic trophic ecology of fish species, and also represents a gap in information that supports ecosystem-based management and conservation efforts for juvenile stages.

Because ecosystem-based management is needed for marine and coastal resources the Caribbean region, it is important to concentrate efforts in non-commercial species, as well as on cryptic and rare species to understand changes in the functional redundancy and diversity of Caribbean marine ecosystems. Methodologies different from diet content analyses have evidenced the trophic role of fish species in other areas of the Caribbean, and can be applied to species with no data or poor information quality. Stable isotope analysis conducted on fish tissues during juvenile and adult stages have provided evidence of ontogenetic changes in the trophic structure of fish communities, as well as on the identification of feeding grounds and potential food sources in other Caribbean islands and the Gulf of Mexico (Carreón-Palau et al. 2013, de la Morinière et al. 2003, Layman et al. 2007, Nagelkerken et al. 2006, Vaslet et al. 2012). Stable isotope analysis of fish tissues is not necessarily a lethal technique, and it can be used as a proxy to fill-in gaps in knowledge about the trophic ecology of species lacking other information. The collaboration among research groups working in the U.S. Caribbean will be important tool to identify the trophic roles of juvenile fish stages, as well as of species with no data or poor information. These collaborations can include lab work to analyze diet contents, conduct stable isotope analysis in fish tissue, and by populating existing trait databases, such as this one or fishbase.org. We encourage researchers to discuss the associated uncertainty and quality of compiled trait information, as well as the geographic variation found in trait values throughout the Caribbean region because different emerging functional properties of marine fish species can be used to identify and analyze functional diversity at local or regional scales.

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