



Trophodynamics as a Tool for Understanding Coral Reef Ecosystems

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The increased frequency of publications concerning trophic ecology of coral reefs suggests a degree of interest in the role species and functional groups play in energy flow within these systems. Coral reef ecosystems are particularly complex, however, and assignment of trophic positions requires precise knowledge of mechanisms driving food webs and population dynamics. Competent analytical tools and empirical analysis are integral to defining ecosystem processes and avoiding misinterpretation of results. Here we examine the contribution of trophodynamics to informing ecological roles and understanding of coral reef ecology. Applied trophic studies of coral reefs were used to identify recent trends in methodology and analysis. Although research is increasing, clear definitions and scaling of studies is lacking. Trophodynamic studies will require more precise spatial and temporal data collection and analysis using multiple methods to fully explore the complex interactions within coral reef ecosystems.

Keywords: trophodynamics, coral reefs, ecological roles, trophic ecology, food webs

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INTRODUCTION

Understanding the biological organization and physical nature of an environment has enabled ecological research to play a central role in providing management and conservation advice for important ecosystems. While ecology comprises a wide array of components, food web structure, and trophic links are fundamental aspects of biological organization (Odum and Barrett, 1971; McIntosh, 1986) and encompass a large body of literature. Trophodynamics, “the dynamics of nutrition or metabolism,” was first proposed by Lindeman (1942) and is fundamental in understanding the flow of energy through food webs. Relationships within a community, energy flow, and linkages between biota and the environment are all encompassed in Lindeman’s approach. The idea of energy flow in an ecosystem strengthened earlier studies such as biomass pyramids (Elton, 1927; Turney and Buddle, 2016), opening the way for incorporation of food webs into ecology to understand ecosystem processes (McIntosh, 1986; Sale, 2002). Definition of ecosystem processes is crucial to trophodynamic studies because they encompass biological, physical, and chemical mechanisms that link species and facilitate energy flow. These processes explain the contribution of decomposition, production, and nutrient cycling to ecosystem function (i.e., the way an ecosystem distributes energy) (Libralato et al., 2014). Although trophodynamics was not originally defined for marine ecosystems, researchers have applied this concept to marine food webs including coral reef ecosystems (Paine, 1966; Ryther, 1969). Contemporary trophodynamic analyses integrate ecosystem processes and food webs within a spatially and temporally explicit context to understand energy flow and trophic relationships in coral reefs. In a conservation and management context, trophodynamics can be used to predict the ecological effects of disturbances

or fishing, and trophodynamic patterns are used as indicators for the state of coral reef systems.

Incorporating trophodynamics in marine studies is difficult due to the degree of uncertainty in describing interactions within highly complex marine food webs. Traditionally, marine food webs were thought to be resource-driven systems based on phytoplankton availability to lower-level consumers (Verity and Smetacek, 1996; Frank et al., 2007). For example, Odum and Kuenzler (1955) used trophodynamics to study coral reefs and identified energy pathways through both turf algae and fish to consumers, demonstrating that energy can be derived from both benthic and pelagic sources in a single system. Complex interactions among species also increase challenges in characterizing ecological functions within coral reefs (Huston, 1983; Pinnegar et al., 2000; Hubert et al., 2011). This complexity increases the difficulty in defining the trophic position of an individual or species within a food web (Choat and Bellwood, 1991; Choat et al., 2002; Frisch et al., 2014).

An additional complicating factor is the high level of spatial and temporal variation in coral reef systems, adding to the complexity of mapping ecological functionality on larger scales (Newman et al., 1997). Interpretation of these interactions can be difficult without long-term data (McIntosh, 1986; Sale, 2002) and are challenging to apply in conservation and management (Alva-Basurto and Arias-González, 2014). Physical and biological factors change over space and time in reef ecosystems (Sale, 2002). Therefore, even if trophic interactions have been well-described for a species and reef system in one location, the key processes that regulate ecosystem dynamics can be missed if the system is not observed over appropriate temporal (Scheffer et al., 2008) or spatial scales (Heymans et al., 2016). While quantitative analytical techniques have improved, complexity of trophic variability within populations, tissue turnover rates, and limited understanding of source pools (e.g., benthic vs. pelagic sources) can significantly affect interpretation of results (Layman, 2007; Layman et al., 2012). Furthermore, scaling issues limit the interpretability of trophodynamic data. Due to the complexity and variability of coral reef ecosystems, simplifications are often applied. For example, global databases (e.g., Fishbase; Froese and Pauly, 2000) may be used to source available data in lieu of extensive field collection to obtain site specific data (Bauman et al., 2010; Alva-Basurto and Arias-González, 2014; Ashworth et al., 2014; Ceccarelli et al., 2014; Aguilar-Medrano and Barber, 2016). However, information within these databases is often limited to specific regions. Similarly, reef fish feeding habits and trophic position can differ by population, so modeling over broad areas may not reflect interactions for an entire region unless spatial variation is understood and included (Michener et al., 2007).

Current trends in coral reef management highlight both biodiversity and biomass as indicators of reef health (Huston, 1983; Bellwood et al., 2004; Aguilar-Medrano and Calderon-Aguilera, 2016; Turney and Buddle, 2016). Documented declines in top predators and keystone species from anthropogenic disturbance (Dulvy et al., 2004; Sandin et al., 2008; Estes et al., 2011) have resulted in exploration of trophic cascades and assessment of ecological roles of predators in coral reef reefs

(Heupel et al., 2014; Boaden and Kingsford, 2015; Rizzari et al., 2015; Weijerman et al., 2015; Thillainath et al., 2016). However, identifying trophic cascades is difficult in reef ecosystems. Only recently has there been evidence of a predator driven coral reef trophic cascade, but this was linked to tidal effects reducing predator occurrence rather than fishing effects (Rasher et al., 2017). Given the lack of examples of trophic cascades in coral reef habitats, it is necessary to ensure an appropriate framework is used to interpret data for these ecosystems. While applied research is a necessary step for improved conservation, misinterpretation of ecological roles can lead to poor conservation and management outcomes (Grubbs et al., 2016).

This review explores: (1) the variables most considered in trophodynamics studies, (2) critiques the adequacy of methods used, and (3) contemplates whether recent publications applied methods suitable to support prominent theories in coral reef ecology. We discuss how recent research on drivers of coral reef trophodynamics often do not account for spatial and temporal variation and methodological issues, and provide recommendations for future trophodynamic research.

ARTICLE SELECTION

Searches were performed through different bibliographic platforms to ensure access to the widest range of literature. Web of Science, Scopus, and Google Scholar were used to explore and extract available published material (Falagas et al., 2008). Google Books NGram Viewer (Lin et al., 2012), Scopus (Kähler, 2010), and SciVal (Colledge and Verlinde, 2014) metrics were used to analyze trends in keywords and publications to select articles for review (Table S1). Selection of publications was similar to Libralato et al. (2014) who showed increased frequency of key phrases such as “food chains,” “food webs,” and “trophic level” in publications since 1960 from Scopus and NGram searches. They established an historical timeline for the development of trophodynamics in research, but did not link keyword searches to coral reefs. For this review, 347 abstracts were chosen from 1942 to 2016 and filtered for keywords with highest relevance to trophodynamics in coral reef ecology. To evaluate recent trends in publications, additional searches were performed through Scival for “food web” and “trophic” relative to coral reefs to determine the top 50 keywords based on 291 publications from 2011 to 2016. Herbivores and predators were the two most common trophic groups studied (Table S2). Predators outnumbered herbivores in the literature in the past 5 years with up to 24 publications in 2016 (Table S2). For percent scholarly output, habitat, community structure, trophic level, and stable isotopes were among the top ranking keywords in publication growth.

ECOLOGICAL CONCEPTS, TROPHODYNAMICS, AND CORAL REEFS

The foundation of trophodynamics is the understanding of how food webs contribute to energy flow. In ecology, food web

dynamics are typically based on a hierarchical, pyramid structure where organisms requiring more energy are less abundant than lower level consumers and producers (Libralato et al., 2014). This structure is seen across terrestrial and aquatic environments and is attributed to biomass scaling where resource availability limits the number of large-bodied organisms and higher trophic levels (Trebilco et al., 2013; Hatton et al., 2015). Coral reefs typically follow this classical food pyramid structure, however, due to complex food webs (Choat and Bellwood, 1985) and variability in habitat structure (Cox et al., 2000), it has been difficult to define generalized ecological relationships.

Identification of pathways linking sources of nutrition to consumers is essential for understanding ecological relationships in food webs (Table 1). Low-level organisms in a food web, known as producers (such as phytoplankton), provide energy to higher levels through consumption and assimilation. Large-bodied organisms typically hold higher positions in food pyramids as their energetic requirements require consumption of lower level producers and consumers (Lindeman, 1942). In biochemical ocean cycling, production occurs through: (1) fixing inorganic source pools of dissolved gases from nitrogen (i.e., nitrates, ammonia), carbon (CO₂), and other essential elements (sulfur and hydrogen), or (2) particulate organic food uptake from nitrogen substrate, detritus (marine snow), and carbon into biological cycles (Michener et al., 2007). These sources of primary production are considered food-web baselines in trophic ecology and their availability is largely dependent on environmental and hydrodynamic variables unique to a region (Paulay, 1997). Producers are the origins of bottom-up forcing which influence resource limitation and carrying capacity of higher trophic levels (Terborgh, 2015). Biogeographic differences in reef resource availability are explained by factors such as: latitudinal and longitudinal gradients (Harmelin-Vivien, 2002), distance from human disturbance, position on the continental shelf, degrees of isolation, and oceanographic variables such as sea surface temperature, upwelling, and currents (Paulay, 1997). How each of these components affect food web production and resource availability should be considered in trophodynamic studies.

Within a marine food web, an organism's role in energy transfer is assigned a trophic position (Bowen, 1997; Layman et al., 2012). Interactions among organisms and energy flow are typically defined by resource control or "trophic forcing," where energy flow within a system can be consumer-driven (top-down), resource-driven (bottom-up), or middle-driven (middle-level consumers) (Verity and Smetacek, 1996; Frank et al., 2007; Young et al., 2015). The type of resource control can have major impacts on communities at localized and/or large-scales via cascades or pyramid structures (Sandin et al., 2008; Estes et al., 2011; Sandin and Zgliczynski, 2015). Therefore, it is important to examine how trophodynamics influence a community at a defined scale. Contributions from benthic and pelagic sources limit understanding of bottom-up processes on coral reefs because biogeochemical cycles are not well-described over spatiotemporal scales (Young et al., 2015). Nutrient enrichment and herbivory have been recognized as crucial bottom-up and top-down processes respectively; influencing ecosystem function and community structure and providing competing hypotheses

(Smith et al., 2010). Meanwhile some researchers describe the influence of multiple controlling forces on coral reefs (Lapointe, 1999; Terborgh, 2015), and others report higher importance of specific trophic groups on resource availability (Lewis and Wainwright, 1985; Hughes et al., 1987, 2007). Disruption of trophic levels through loss and mortality of organisms in a community alter the stability of a food pyramid which can lead to trophic cascades.

For example, pressure exerted by higher trophic levels can control abundance of lower trophic groups preventing cascading effects across food webs. This assumes that keystone species and apex predators are the strongest controlling forces on food web dynamics (McClanahan and Branch, 2008). A few cases have described inverse pyramids where the biomass of predators is greater than that of lower level consumers (DeMartini et al., 2008; Sandin et al., 2008; Sandin and Zgliczynski, 2015), which is uncharacteristic of a typical marine environment. These examples have only been documented in near-pristine environments (Sandin and Zgliczynski, 2015; Mourier et al., 2016; Simpfendorfer and Heupel, 2016) and to date have not been reported outside of steep-sided, isolated atolls exposed to upwelling. Whether productivity subsidies supporting inverse pyramids in smaller isolated reefs can be possible for larger, continental environments is unknown. Continental reefs are also exposed to human activity, where high predator abundance is less common (Sandin and Zgliczynski, 2015). Without long-term data, it is unclear whether inverse pyramids are more representative of a natural, balanced state than bottom-up pyramids.

Additionally, functional redundancy and diffuse predation may prevent degradation under disturbance, masking the potential controlling effects of trophic groups or individual species (Bascompte et al., 2005). For example, many reef ecosystems have multiple mesopredators feeding at a similar trophic level. Interactions within and among these species and available prey complicate the ability to define trophic pathways. Aside from the concept of "mesopredator release" caused by removal of apex predators (Stallings, 2008; Ruppert et al., 2013, 2016; Roff et al., 2016a,b), mesopredator influence on communities is largely unknown. Middle-driven systems caused by intermediate consumer influence have only been described for oceanic environments where small pelagic fish control the abundance of both the predator and their prey (Cury et al., 2000; Young et al., 2015). To our knowledge, middle driven systems have not been explored for coral reefs. Beyond defining trophic position, the importance of understanding specific interactions between and among trophic groups is necessary to interpret ecological roles (Figures 1, 2).

The presence of multiple-food webs within coral reefs decreases our ability to understand mechanisms that regulate stability. Based on present knowledge, it is still unclear whether coral reefs behave similar to other marine ecosystems from a trophodynamic perspective. Defining which ecosystem processes contribute to the abundance and biodiversity of coral reefs is controversial (Karlson and Hurd, 1993). While it is generally accepted that coral reef communities are stable, the interactions among communities and connectivity from larval dispersal and

TABLE 1 | Benefits and disadvantages of methods commonly used in trophodynamic study and which ecological concepts they most relate to.

Type	Method	Benefits	Disadvantages	Ecological Concepts
Diet analysis	Stomach contents	<ul style="list-style-type: none"> • Accurate interpretation of diet composition • Offers some taxonomic resolution compared to other methods • Can identify life stage of prey 	<ul style="list-style-type: none"> • Biased toward what has been eaten recently • Empty contents are common in larger animals, can lead to misinterpretation • Biased toward identification of larger prey items • Requires lethal sampling 	Food web dynamics, food web pathways, consumer resource interactions, functional redundancy
	Molecular barcoding	<ul style="list-style-type: none"> • High taxonomic accuracy in degraded or digested samples • Assists resolution of stomach content analysis • Possible to be non-lethal (from fecal samples) 	<ul style="list-style-type: none"> • Can't interpret without sequence database • DNA extraction bias • Does not distinguish size or life stage 	Food web dynamics, food web pathways, consumer resource interactions, functional redundancy
	AA-CSIA	<ul style="list-style-type: none"> • Accounts for diet assimilation (tissues) in addition to recent diet (blood) • Possible to be non-lethal • Does not require ecological baseline for source 	<ul style="list-style-type: none"> • More expensive than traditional SIA 	Trophic position, species biogeographic differences, diffuse predation, functional redundancy
	Stable isotope analysis	<ul style="list-style-type: none"> • Accounts for diet assimilation (tissues) in addition to recent diet (blood) • Possible to be non-lethal 	<ul style="list-style-type: none"> • Need ecological baseline with temporal consideration 	Primary Production, trophic position, biogeographic differences
	Fatty acid analysis	<ul style="list-style-type: none"> • Can be used to compare diet profiles • Does not require ecological baseline for source • Possible to be non-lethal 	<ul style="list-style-type: none"> • Low taxonomic resolution without extensive reference database 	Primary Production, trophic interactions, diffuse predation, functional redundancy
	Total lipid content	<ul style="list-style-type: none"> • Interprets energy allocation and life-history strategy • Community metabolic processes 	<ul style="list-style-type: none"> • Composition can differ between tissues and species • Requires greater understanding of metabolic roles of a species • Best sample type is liver which requires lethal sampling 	Ecosystem health, trophic cascades, functional redundancy, diffuse predation
Ecological modeling	Multi-species Dynamic Models (i.e., Ecopath)/ Aggregate Models	<ul style="list-style-type: none"> • Good for predictions • Accommodate for multi-species • Can account for behavior over a time-series 	<ul style="list-style-type: none"> • Difficult for heterogeneity in data • Increases untestable assumptions • Often includes averaged categorical data 	Trophic cascades, diffuse predation, functional redundancy, ecosystem processes
	Individual-based models	<ul style="list-style-type: none"> • Explores underlying mechanisms • May include predator-prey interactions with a defined spatial scale • Ease in coupling with physical models 	<ul style="list-style-type: none"> • Difficult to incorporate whole ecosystem • Statistical cost to increased coupling 	Trophic cascades, diffuse predation, functional redundancy, ecosystem processes
	Process-based/Mechanistic models	<ul style="list-style-type: none"> • Founded in ecological theory which makes for easy application to known systems • Clearly defined assumptions 	<ul style="list-style-type: none"> • Compromises in scale and resolution in spatial-temporal processes • Experimental design may not match management scales 	Trophic cascades, diffuse predation, functional redundancy, ecosystem processes
Telemetry	Acoustic electronic tagging	<ul style="list-style-type: none"> • Accurate assessment of movement of organisms within the environment, leads to understanding habitat use and predator-prey interactions 	<ul style="list-style-type: none"> • Expensive, which limits sample size • Limited battery life • Increased model performance from more robust analytical tools available 	Consumer resource interactions, nocturnal organisms

recruitment are less well-known (Vance and Steele, 2002). More research is needed to outline consumer-resource interactions and identify knowledge gaps in food webs. While energy availability is an indicator of reef health evidenced by species richness, habitat is also an influential factor (Bellwood et al., 2005). Even at the reef scale, community food web length can differ with habitat (Kolasinski et al., 2016). The importance of understanding spatial dynamics within the study area, whether local or regional, is crucial to assessing ecological roles and energy contribution of a species to a population, community, or ecosystem.

Additionally, more attention should be directed toward the influence of under-studied groups such as non-target, cryptic, nocturnal, and benthic macrofauna (Young et al., 2015). For instance, parasites are rarely included in trophodynamic study despite being the most common consumer type in ecological food webs (Demopoulos and Sikkell, 2015). Recent reef food web models that include parasitism show insignificant changes to overall flow of models, but can dramatically affect specific trophic pathways (Arias-González and Morand, 2006). Parasites are also thought to affect feeding behavior of herbivorous

grazers (Fox et al., 2009). Other cryptic organisms can affect trophic links in consumer species with commonly accepted ecological roles. For example, consumption of copepods (Kramer et al., 2013) and high concentration of autotrophs (Clements et al., 2016) sourced within the epilithic algal matrix (EAM) by parrotfish raises questions about the main components of their nutrition. Exclusion of other trophic links such as connectivity to mangrove or seagrass habitats is also common, where grazers

are known to make nocturnal migrations off coral reefs to avoid micropredation (Sikkel et al., 2017), or exploit foraging opportunities (Nagelkerken et al., 2000). Limited time and resources prevent incorporation of every component of a food web into a study, but the composition of components included, or excluded, requires consideration when interpreting results.

METHODS USED TO STUDY TROPHODYNAMICS IN TROPICAL CORAL REEFS

The main focus of trophodynamic research is determining spatially and temporally appropriate consumption and interactions across trophic groups (Figure 2). Paine (1980) demonstrated the effect of interaction strength of food webs on communities in aquatic systems, and new techniques are constantly being developed to better describe these interactions. Most methods for identifying food web relationships are limited by spatiotemporal scales and variable biological and environmental conditions (Sale, 2002; Chabanet et al., 2010; Layman et al., 2012; Young et al., 2015). Fortunately, new techniques in methodology and analysis are available to enhance ecological study (Table 1). Most of the methods in this section have already been well-reviewed or described by other authors (Layman, 2007; Ilves et al., 2011; Layman et al., 2012; McCauley et al., 2012; Gilby and Stevens, 2014; Young et al., 2015), so this text highlighted publications that used these methods to describe common ecological roles and functions of coral reef ecosystems. Much of the current research focuses on specific groups such as higher trophic levels or herbivores. While this focus helps

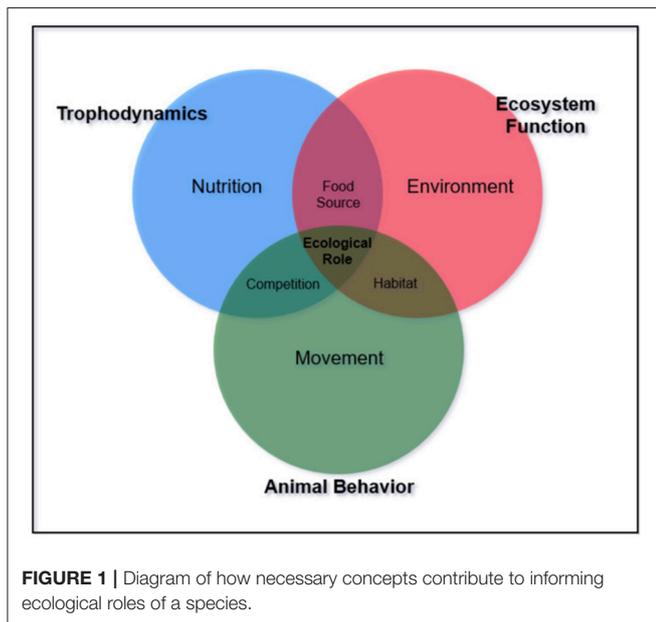


FIGURE 1 | Diagram of how necessary concepts contribute to informing ecological roles of a species.

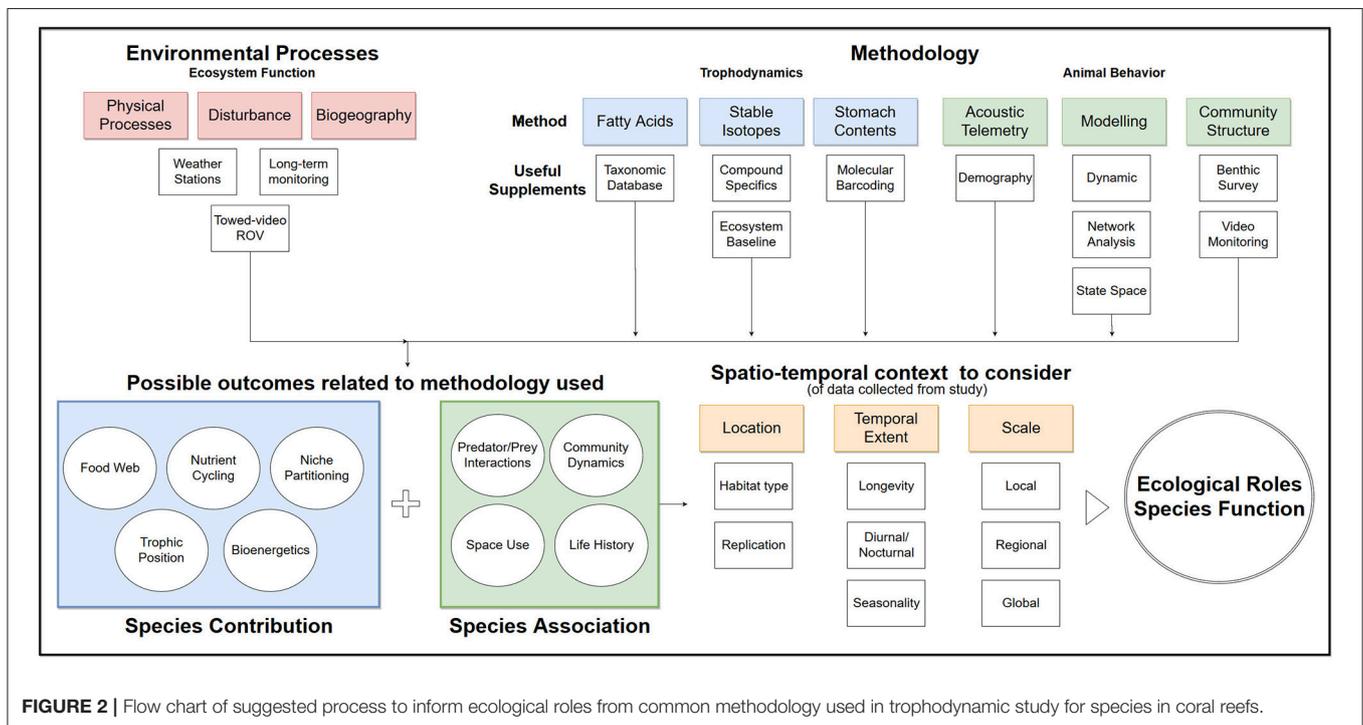


FIGURE 2 | Flow chart of suggested process to inform ecological roles from common methodology used in trophodynamic study for species in coral reefs.

define the roles of certain aspects of the food web, research is still needed to incorporate under-represented components of ecosystems to develop a more comprehensive view of coral reef ecosystems.

Diet Analyses

Diet analysis is one of the most common methods in trophodynamic study along with direct observation of predator-prey-relationships (Choat et al., 2004; Fox et al., 2009; Kramer et al., 2013; Young et al., 2015; Wen et al., 2016). Stomach contents can directly inform what a consumer ingests by examining the frequency of occurrence of species in stomach samples (Cortés, 1999). This method can work well to uncover trophic interactions for commonly occurring and abundant species. However, there is often uncertainty in prey identification and metabolic requirements of a consumer (Young et al., 2015). For species of conservation concern, sample sizes for study can be low as there are limitations to lethal sampling. Non-lethal methods such as gastric lavage show what has been recently consumed (Cortés, 1997; Frisch et al., 2016), but may be unreliable for determining the full scope of the diet of an individual. For larger species such as sharks, angling may also induce gastric emptying before landing (Frisch et al., 2016), which can affect results. In fact, many studies using gastric lavage and baited capture report high proportions of empty stomachs in predators. Due to these limitations, biochemical tracers, and immunological testing through molecular identification of prey (Symondson, 2002) have been used to supplement stomach content studies. Taxonomic molecular barcoding can supplement gut content study and assist in characterization of diet (Paula et al., 2016). Molecular barcodes designed to identify diet specialization on invasive macroalgae by coral reef grazers has uncovered trophic links previously unknown in herbivorous fishes in Hawai'i (Stamoulis et al., 2017). Combination of multiple methods in diet analysis can identify trophic position and food web links for trophodynamics, but care is needed when using these methods to identify ecological roles. Habitat is known to be an important consideration in most ecological studies, and it is mentioned most frequently in studies examining stomach contents (98 percent, Table 2). Yet even recent studies have ignored potential effects of habitat by combining samples across regions without understanding community composition and available prey. Spatial scale and habitat variables are crucial elements to defining diet analysis in trophodynamics research. Seasonal (i.e., temporal) variability in prey abundance or availability must also be considered. While these aspects are present in some studies, they must be more widely applied to help define ecological processes and trophodynamics in coral reefs and other marine habitats.

Biochemical Tracers

Biochemical tracers identify dietary sources in a food web and what individuals directly consume (Post, 2002; Young et al., 2015). Tracers quantitatively measure assimilation through tissues to define the diet of an individual without the uncertainty of species identification of stomach content studies (Post, 2002; Layman et al., 2007). Nitrogen and carbon isotopic enrichment

TABLE 2 | Proportion of reviewed publications that use additional methods for trophodynamic study or mention common keywords in related literature ($N = 398$). EndNote® (Thompson Reuters) was used to annotate documents for searches.

	N	PUBS	Analytical techniques				
			ECOPATH	LM	M	SIA	SC
COMPLEMENTARY METHODS							
Stable isotope analysis	72	0.21	0.39	0.71	0.26	NA	0.50
Ecological baseline	96	0.28	0.54	0.45	0.39	0.42	0.27
Fatty acid analysis	26	0.07	0.14	0.10	0.12	0.21	0.25
Stomach content	44	0.13	0.11	0.19	0.18	0.18	NA
Model	218	0.63	NA	NA	NA	0.78	0.86
Telemetry	33	0.10	0.04	0.17	0.14	0.18	0.11
COMMON KEYWORDS IN REVIEWED LITERATURE							
Abundance	228	0.66	0.79	0.95	0.84	0.65	0.95
Fishbase	70	0.20	0.39	0.43	0.28	0.08	0.25
Ecological role	47	0.14	0.36	0.19	0.18	0.28	0.27
Habitat	238	0.69	0.89	0.90	0.86	0.71	0.98
Community structure	162	0.47	0.61	0.64	0.61	0.42	0.57
Trophic level	131	0.38	0.86	0.50	0.51	0.58	0.57
Trophic cascade	82	0.24	0.39	0.29	0.32	0.22	0.25
Top-Down	59	0.17	0.39	0.21	0.24	0.22	0.23
Bottom-Up	44	0.13	0.39	0.10	0.18	0.15	0.09
Top-Down+Bottom-Up	35	0.10	0.25	0.10	0.14	0.13	0.07
Caribbean	177	0.51	0.68	0.71	0.69	0.53	0.68
Great barrier reef	166	0.48	0.54	0.69	0.61	0.44	0.68
Management	174	0.50	0.93	0.76	0.68	0.50	0.52

PUBS, proportion of total reviewed publications; ECOPATH ($n = 22$); LM, linear model ($n = 42$); M, model ($n = 218$); SIA, stable isotope analysis ($n = 72$); SC = stomach content ($n = 44$).

in bulk tissue are examined through stable isotope analysis to define the relationship between a predator and its prey (Post, 2002; Layman et al., 2007, 2012; McClanahan et al., 2011). For producers, carbon isotope proportions vary due to different methods of energy production through photosynthesis (Michener et al., 2007). Carbon ($\delta^{13}\text{C}$) is used to identify source pools as there is limited variation in values after trophic transfer, while nitrogen ($\delta^{15}\text{N}$) is used to identify trophic position as enrichment is progressive across trophic levels (Kolasinski et al., 2016). Spatiotemporal comparison of diet is also possible with fatty acid analysis. When a predator consumes a species, fatty acids are absorbed with little change in the unique signature, meaning that prey can be identified from adipose tissue and blood samples (Budge et al., 2006). Without a known database of fatty acid profiles, these studies can be limiting. For biochemical tracers, food web limitations mainly come from time and resources available to define an appropriate ecological baseline. Without understanding carbon sources, studies may lack context. For example, carbon flow is challenging to elucidate in coral reefs due to multiple end-members feeding from both benthic and pelagic sources. Application of compound specific amino acid analysis (AA-CSIA) and Bayesian mixing-model techniques can assist in defining these baselines (McMahon et al., 2015). AA-CSIA can provide better baselines by looking at specific amino

acids that fractionate with each trophic step (Bradley et al., 2016). AA-CSIA can also reduce the number of samples for analysis by eliminating the need for an exhaustive baseline. But tissue turnover rates, functional redundancy, and complications in retention of nitrogen in certain organisms can also limit analysis (Post, 2002; Layman et al., 2007, 2012; McClanahan et al., 2011). Without species-specific study, improved techniques, and time-series baselines, it is difficult to get a true estimate of trophic position (Layman et al., 2012). Recently, Matley et al. (2016) showed that diet tissue determination factors and turnover rates measured for temperate species may not apply to tropical species, as $\delta^{15}\text{N}$ enrichment was lower than published values for a slow-growing predatory reef fish. In larger predatory species such as sharks, care in sample preparation is also necessary as urea retention without extraction can severely affect values, which is often not a common method employed for stable isotope analysis (Li et al., 2016). The physical and biogeochemical nature of a habitat can also have large effects on trophic community structure even at a fine scale. For example, Kolasinski et al. (2016) studied macro-invertebrate communities of coral reefs and found significant temporal and spatial differences in food web lengths indicating a variety of energy pathways which complicate trophic level definition. Therefore, consideration should be given to understanding the data sources that may limit research to specific habitats or time periods. Recent studies use large-scale spatial and temporal differences in sample collection as caveats in the discussion (Frisch et al., 2016), as opposed to incorporation into the study design. From reviewed publications, only 42 percent of stable isotope analyses included a reference to carbon sources, and 21 percent for fatty acid analyses; 50 percent of studies used a combination of stable isotopes and stomach contents, while 25 percent used a combination of fatty acid and stomach contents (Table 2). Stable isotopes contributed to 58 percent of studies that assessed trophic levels of organisms and have been used in 39 percent of Ecopath studies. Refined analysis of trophic levels through biochemical tracers is likely to strengthen and improve trophodynamics research as applications of these methods expand.

Ecological Modeling

Statistical models are widely used in ecological studies to understand energy flow and provide a whole of system interpretation. Due to the complexities of marine food webs, trophic relationships are often used to categorize interactions between trophic levels and among individuals within models (Bozec et al., 2005). While linear models often show patterns in specific relationships from quantitative study, they are not robust enough to handle complex food webs such as those on coral reefs (Evans et al., 2013). Dynamic models are required to describe ecosystem organization through networks of species that interact (Liu et al., 2009). In trophodynamic studies, species abundance and diversity are typically categorized by functional groups where diet and habitat similarities are shared by multiple species. This allows simplification of models to a tractable level where input parameters are determined by functional group and often include known values of productivity, biomass, and metabolic efficiency.

While there are multiple dynamic food web models available, Ecopath (Polovina, 1984) is the most commonly used for marine and aquatic study (Heymans et al., 2016) and has been applied to coral reefs. Under the assumption of energy equilibrium, Ecopath uses mass balance equations to determine trophic relationships of biomass and productivity (Polovina, 1984). Ecopath can be fitted for time series with Ecosim (EwE) (Gotelli and Entsminger, 2004) and also account for spatial differentiation of habitat with Ecospace (Opschoor, 1995). While Ecopath is a popular method, few studies using this model in marine research include time series and spatial data, and even fewer are applied to coral reef ecosystems (Heymans et al., 2016).

For Ecopath to be effective, thermodynamics and ecological knowledge behind fitting a model are required to prevent misuse (Evans et al., 2013; Young et al., 2015). Thirty-nine percent of reviewed Ecopath studies (Table 2) for coral reefs used Fishbase (Froese and Pauly, 2000) as a source of data for the model. While this resource is a reputable data repository with relevant diet and productivity information, there is considerable uncertainty in empirical data and regional species variation. Without understanding ontogenetic diet change, temporal and biological shifts in behavior and foraging of a species, responses to disturbance may be poorly interpreted (Young et al., 2015). Even if an organism has a highly specialized diet and small home range, external stressors and biogeography vary (Sale, 2002). Ecopath relies upon the strength of interactions between predators and prey, and requires extensive knowledge of each species fitted into the model. While these models take diet into account, predator avoidance is less well-described and parameters such as refuge availability and niche occupation are difficult to fit into a model. For mobile, large predators, effects on lower trophic groups are poorly understood as top-down forces often result in diffuse predation that is difficult to characterize with Ecopath parameters. Predator-prey structure in ecological models was recently examined and researchers found that more complex models do not necessarily invalidate predicted behaviors in simpler models, but care must be used when employing the latter (Walters et al., 2016). The authors showed how assumptions of feeding rates of predators, prey availability and other factors drastically change isocline patterns in predator-prey models. They note that uniform spatial assumptions should be avoided when using trophic models. Of the reviewed studies, habitat was referenced in 89 percent of Ecopath studies focused on coral reefs (Table 2), but many were not specific to a single area and assumed homogenous habitat across regional scales. Testing underlying assumptions is critical when employing predator-prey models (Heymans et al., 2016), and understanding interactions at an appropriate spatial scale will assist in increasing the efficacy of these models.

While some scientists have urged that more process-based ecological models be developed to identify the underlying mechanistic behavior of an ecosystem (Evans et al., 2013; Turney and Buddle, 2016), recent articles still often ignore dynamics of spatial and temporal variability as well as historical baselines (Lamy et al., 2016). Some authors have moved past dynamic models such as Ecopath and explored individual-based predator-prey population models to account

for spatiotemporal heterogeneity (Thierry et al., 2015). Others have tested vulnerability of reef ecosystems by measuring overall entropy from bioenergetics (Arreguín-Sánchez and Ruiz-Barreiro, 2014), interaction strength between trophic levels (Bascompte et al., 2005) and applied network analysis (Navia et al., 2016). Integration of unified models may also be beneficial. While unified models often are used to explain theories of biodiversity, recent developments of metacommunity analysis between labrid fishes and corals have identified patterns of species associations (Connolly et al., 2017). Species associations are critical in integration of trophodynamics into management. Critics of food web models for coral reefs highlight that any model will be a simplified version of real-time processes and caution should be taken when using them to inform management. Although management is mentioned in 98 percent of reviewed publications (Table 2), few articles using Ecopath in marine environments have been used for management purposes (Heymans et al., 2016). To better inform management, research is needed on spatiotemporal variability to better fit models. As Ecopath provides an informed snapshot of behavior of a system, including variability over space and time may assist in reducing uncertainty.

Telemetry

Acoustic telemetry is widely used in aquatic ecology, but rarely incorporated into trophodynamic studies. Telemetry can be used to better understand the distribution, residency, and behavioral patterns of species and applied to understanding how predators interact with prey (McCauley et al., 2012; Young et al., 2015; Matley et al., 2016). Matley et al. (2016) determined that although two species of co-occurring reef fish had overlapping diets, space use differed between the two species suggesting niche separation. Studying movement can also show how behavior may be affected by environmental stressors and conditions. Telemetry can also be used to supplement other methods to identify behavioral adaptations to resources such as targeting invasive species (Bierwagen et al., 2017). Improved analytical methods for ecology such as network analysis (Espinoza et al., 2015), Bayesian statistics (Johnson et al., 2010) and state-space models (Jonsen et al., 2005) are assisting predictive capability of movement relative to environmental variability. For example, telemetry has helped define population dynamics through focused mark-recapture models (Dudgeon et al., 2015). Other applications such as identifying feeding patterns from movement and prey associations that may influence food web dynamics may play a role in future trophodynamic analyses. Despite the advantages of telemetry, the time and financial investment required may limit sample sizes and application to trophodynamics (Young et al., 2015). Telemetry was used in less than 10 percent of reviewed studies and less than 20 percent in combination with other empirical methods (Table 2).

CHALLENGES AND DISCUSSION

The key challenges in trophodynamic study in coral reefs come from logistical difficulties, methodology limitations, and context

of study design. Whether a study intends to identify an energy pathway, or consider management decisions relating to a species, the conclusions should not go beyond the limitations derived from the study. Sufficient information of reef ecology such as spatiotemporal abundance, distribution, habitat associations, environmental inputs, diet, and life history of a species is necessary to inform ecological roles and function (Figure 2). While recent examples of poor management decisions have created a need for standardizing approaches in the field of trophodynamics (Grubbs et al., 2016), studies are still omitting key concepts before implementing applied research. We have highlighted such studies in relation to popular methods, but also identified recent research that is incorporating and combining new methods to account for some of the challenges faced within the field. In addition to using combined methodology, researchers should consider concepts that better explain the organizational structure of coral reefs and how multiple food webs or communities interact.

Accounting for Variation in Studies

Habitat and community structure are well-documented to be important variables in ecosystem processes, particularly when examining trophodynamics. Yet, scientists often take a “one size fits all approach” to food-web studies. Dornelas et al. (2006) demonstrated that coral reefs cannot be explained by widely-accepted theories of biodiversity, which suggests that spatiotemporal stochasticity observed in coral reefs is not well-understood. This validates the need to understand process based interactions. Most trophodynamic studies of coral reefs come from the Caribbean and Great Barrier Reef, which cover large spatial scales and latitudinal gradients. While biogeographic variability is constantly acknowledged, publications link conservation concern to broad topics such as management zones irrespective of reef variability or geographic position (Frisch et al., 2014; Rizzari et al., 2014; Boaden and Kingsford, 2015), and perform large scale analyses based on databases that do not account for fine-scale variation (Campbell and Pardede, 2006; Graham et al., 2008; Campbell et al., 2011; Barneche et al., 2014; Alonso et al., 2015; Aguilar-Medrano and Barber, 2016). While management zones are important to understanding human disturbance, many studies exploring fishing effects lack historical baselines, movement data, and diet relative to changing diversity and community structure (Greenwood et al., 2010; Edgar et al., 2011). Additionally, the influence of natural cycles is rarely considered (Kruse et al., 2016) although they can play an important role in ecosystem function. A review by Bijoux et al. (2013) discussed the effect of natural cycles (diurnal, tidal, lunar, and seasonal variation) on fish movement where the authors found that studies ignoring natural cycles increased unexplained variation in the data thereby reducing their effectiveness in defining ecosystem processes.

Controlling Forces in Trophodynamics

In addition to lacking spatiotemporal context, researchers may be misinterpreting controlling forces in coral reefs. Across all ecosystems, biomass pyramids and the role of trophic

subsidies are not well-understood (Trebilco et al., 2013). Top-down vs. bottom-up organization of coral reefs is debated in the field, particularly in regard to the focus of conservation efforts (herbivore focused or predator focused). Pyramids are the primary structure used to argue resource control, but may oversimplify the unique and fine-scale interactions that occur at the reef level. Marine food webs have been described as “ecological road maps” and the varying networks that link different trophic levels in coral reefs could explain their resilience to cascading effects (Turney and Buddle, 2016). In coral reefs, the semi-open nature of communities increases the difficulty in mapping food webs from source to consumer and the influence mesopredators may have on lower trophic levels. Trophic cascades were mentioned in 24 percent of reviewed publications, yet there is little empirical evidence documenting cascading effects in coral reefs. Even in the few cases documenting trophic cascades, the results are inconclusive. Estes et al. (2011) used the Northern Line Islands as an example of trophic cascade, but the original research by Sandin et al. (2008) showed no evidence of trophic cascade through use of principle component analysis. The work by Sandin et al. (2008) reflects conclusions made by Bascompte et al. (2005) who showed strength of trophic interactions on coral reefs buffer cascading effects but become weaker under pressure of external perturbations such as overfishing. This does not mean that cascading effects do not exist, but evidence is limited and little is known outside of correlative associations regarding herbivore biomass increases due to predator removal or other effects of disturbance.

In trophic cascades, if a trophic level is added or removed, coral-algal phase shifts and changes in ecosystem stability can occur (Terborgh, 2015). The strongest evidence of cascades found in coral reef systems come from herbivory, where depletion of grazers such as echinoderms from overfishing or pathogens allowed for explosive population growth of macroalgae in the Caribbean (Hughes et al., 1987; Mumby et al., 2005). Rasher et al. (2017) also described a trophic cascade via reduced exposure of herbivores to predators which resulted in variation in feeding patterns based on fear effects. Though the expected negative effects of cascades in reefs aren’t always clear. In cases where conservation efforts have maintained predator populations via reduced fishing, the expected cascading effect of macroalgal increase from a depletion of grazers as prey doesn’t always occur (Mumby et al., 2007). Keystone species and functional redundancy are not always present in reefs with high biodiversity (Hoey and Bellwood, 2009), which makes comparison across spatial scales all the more difficult. Even if assumed cascading events are observed such as phase shifts, finding the cause of such patterns at large spatial scales is challenging (Dulvy et al., 2004). Attention should also be paid to temporal gradients over which cascades occur, considering life-history and growth capabilities of populations as well as lagged effects from perturbations that can occur over extended time periods (Dulvy et al., 2004; Grubbs et al., 2016). The difficulty in linking trophic levels to the same event that categorizes a trophic cascade is difficult to support empirically, particularly when most reefs are already in a degraded state from external stressors. The fact that cascades have not yet been effectively documented for

coral reefs undermines the assumed organization of coral reef food webs. High biodiversity complicates ecosystem models and trophodynamics, but may be key to the functionality of reef ecosystems in a changing environment.

Although pyramid structure is evident in coral reefs, there are high numbers of mesopredators representing intermediate trophic levels that are thought to exhibit functional redundancy. Mesopredators are considered to have less of an effect on the trophic structure of a system (Paine, 1980; Estes et al., 2011), but there is little empirical evidence to support this due to difficulty in defining predator-prey relationships. A recent meta-analysis of food web studies found that aquatic models produced a strong pyramid pattern, suggesting scale variance in predator-prey ratios according to biomass power laws consistent with Hatton et al. (2015) (Turney and Buddle, 2016). The analysis also showed that on average aquatic communities have a higher diversity of mesopredator species than herbivores, with low abundance of top predators. Intermediate effects of mesopredators on aquatic systems are largely unknown and often grouped within many ecosystem types such as intertidal, pelagic, and reef (Hatton et al., 2015). Elasmobranchs and other fishes are known to feed at different trophic levels based on stage of maturity, where they exhibit high functional redundancy as mesopredators and limited redundancy as apex (Navia et al., 2017). Thus, assigning a single ecological role to a species is limiting and can affect the predictive nature of model capability. The role and effects of mesopredators requires further exploration and definition to refine where greatest predation and productivity sources occur in reef systems. Many researchers believe that coral reefs are influenced by both top-down and bottom-up processes, and it should not be a question of one vs. the other (Terborgh, 2015). Further exploration of middle-driven systems and consideration of the driving interactions between trophic groups should be considered.

The Contributions of Trophodynamics to Coral Reef Ecology

There are many components of trophodynamics that we are beginning to understand which can be used to inform ecosystem function and changes over time. Many of these components are shared among marine systems, but discretion should be used when assuming similar trophodynamics processes that are not fully described for coral systems. Current research validates that coral reefs fundamentally have:

- (1) Highly complex, semi-open systems (Sale, 2002).
- (2) Resident species and mobile visitors that utilize reef habitats (Dudgeon et al., 2015).
- (3) Influence from both benthic and pelagic productivity sources (Michener et al., 2007).
- (4) High abundance and diversity which play a large role in ecosystem function (Choat et al., 2004).
- (5) Spatiotemporal variability which is essential to assessing trophic position (Heymans et al., 2016).
- (6) Small areas with high diversity exhibiting functional redundancy between producers and consumers (Aguilar-Medrano and Calderon-Aguilera, 2016).

- (7) Food web omnivory that can weaken chance of trophic cascades, even in the presence of exploitation of predators (Bascompte et al., 2005).
- (8) Predators that are known to exhibit diffuse predation, although their effect on lower trophic levels is still poorly understood (Heupel et al., 2014).
- (9) Cryptic, invertebrate, and nocturnal organisms which are often ignored in food webs (Marnane and Bellwood, 2002; Kolasinski et al., 2016).
- (10) Pyramids of species richness that are not generated by chance. (Turney and Buddle, 2016).

These concepts need to be explicitly considered in study designs of trophodynamic research and uncertainty should be acknowledged before drawing conclusions regarding the ecological role of any species. Additionally, the underlying trophodynamic processes describing these observations should incorporate long-term datasets that accurately reflect the scope of data used. Before describing ecological roles of reef organisms, it is necessary to determine which interactions may have the highest influence on the trophic structure of these complex systems. For researchers, this space is still largely understudied, and collaborative efforts are likely needed to elucidate the mechanisms that contribute to the stability of these ecosystems.

There are still many ecological unknowns in coral reef systems and there will likely never be a perfect approach to fully describe coral reef trophodynamics, but we can strive for better empirical data collection and analysis of patterns. Standardizing the approach to applied questions may help create a more cohesive space for collaboration in future studies. There is a need to apply multiple methods and clear definitions of spatial and temporal scale to meet the needs of trophodynamic research (Figure 2). How a species contributes energetically and how they interact with other species within a community take different methodological approaches and clear synthesis between the two to identify ecological roles. Arguably, coral reef systems do not appear to energetically behave the same as other marine food webs, such as intertidal or pelagic systems, and trophodynamic study should consider different scenarios and models. Based on

concepts in this paper, we suggest recent literature may not adequately acknowledge the unique differences in coral reef food webs against the broader literature in marine trophodynamics, particularly over varying spatiotemporal scales. While theories for coral reefs are constantly being modified, conclusions of many articles still resort to generic descriptions of standard pyramid structure to explain biodiversity. Predation and competition within predator-prey interactions should be further considered in addition to exploring the effects of both bottom-up and top-down approaches. Without a better understanding of essential reef processes that affect ecological roles of species over both space and time, caution should be used in applying results to management and conservation efforts.

AUTHOR CONTRIBUTIONS

All persons who qualify under authorship criteria to this review are listed as authors and all of which take responsibility for the content of the article. All authors SB, MH, AC, and CS contributed to the concept and design of the article. The corresponding author, SB, is responsible for research, acquisition of data, and drafting of the manuscript. MH, AC, and CS contributed equally to critical revisions of content and subject matter within the body of the manuscript. All authors agree that this version of the manuscript is acceptable for submission.

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SUPPLEMENTARY MATERIAL

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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