

Within Habitat Variability in Productivity, Not All Grassbeds Are Created Equal: Implications for Marine Reserves

GEORGE D. DENNIS
Caribbean Marine Research Center
805 East 46th Place
Vero Beach, FL 32962

ABSTRACT

Whether a reserve's objective is biodiversity or production the food base is a critical consideration. At this time no amount of effort by scientists can make a productive reserve from an unproductive site. While encompassing a variety of habitats in a reserve improves the prospects for productivity within a habitat, such as grassbeds or mangroves, variation in productivity may result in selection of a low production area. Sampling of grassbeds and mangroves suggest that selection of a habitat on a general basis is not adequate and productive areas (critical habitat?) must be identified and incorporated into reserve designs. The challenge for scientist is to develop methods to rapidly assess the quality of an area to decide whether to include or exclude it in a reserve plan. Recommendations are given as to what factors might be examined.

KEY WORDS: Marine habitats, grassbeds, productivity

INTRODUCTION

For marine reserves to be successful the habitat to be incorporated in them must be carefully evaluated. The success or failure of a reserve may depend on the proper balance of habitat types. Presence of some habitats is critical due to their role as foraging or nursery areas. Inclusion of a particular habitat type such as grassbeds is not enough as there is considerable variability in quality within habitats. Previously coral reefs were thought to be an oligotrophic closed system in which productivity was based on efficient recycling of nutrients. We now know that the classic model of production based on algae · herbivores · carnivores may not be appropriate where planktivores are common (Russ, 1991). It is now evident that there is significant input to reef systems from plankton cycled through planktivorous reef fishes. While it is still unclear as to the magnitude of the impact of this energy source it must be substantial based on the abundance of these fishes. The relationship between fish abundance and habitat complexity is well established but it is still unclear what are the relative roles of food and structure.

A broad production base would be advantageous to maximize production in a fishery reserve. This may favor a lower diversity system with higher productivity. Habitat diversity is not necessary nor likely to enhance production.

While all habitats required by various life history phases need to be included in a reserve so as not to bottleneck population size there needs to be a adequate food base which may be habitat or site specific. This requires knowledge of the energy pathways for the target species. Standing crop and productivity of reef fishes have been correlated with topographical relief though there is considerable variability in abundance under seemingly similar topographic conditions (Carpenter *et al.*, 1981; Marshall, 1985). This may be attributed to differences in productivity from outside sources such as plankton. Smith and Tyler (1973) suggest that planktivores food source would never be a limiting factor but this does not take into account the considerable variability in distribution of plankton on reefs.

A habitat may look lush and productive but certain intangibles may still be missing that result in low use of the habitat by fishery species. For example Stoner *et al.* (1996) found that only very specific relatively small areas of the grassbeds were used as nursery grounds by queen conch (*Strombus gigas*) while nearby grassbeds of seemingly similar quality were not used. The determination of these intangible factors is particularly difficult if a species has been fished down to a very low abundance and can take considerable research resources to determine.

Piscivorous fishes, such as grouper and snapper, are the most sought-after reef fishes. Their abundance may be governed by the adequacy of the production base available. If this was the case there should be a positive correlation between piscivore abundance and prey species. In New Caledonia Kulbicki (1988) found no general relationship between potential prey and number of predators but for specific grouper species there was a strong positive relationship between known prey and predator abundance.

On the Great Barrier Reef planktivores were abundant at all sites across the shelf but reached their greatest abundance where zooplankton was most abundant (William and Hatcher, 1983). In contrast only about 11% of the northwest Hawaiian island fish assemblage are planktivorous (Parrish *et al.*, 1985). Parrish suggests that the influence of land mass might account for this difference. In this region there was considerable local variation in piscivore abundance that was attributed to food availability (Parrish *et al.*, 1986). Habitat selection may be based on prey availability (or quality) rather than structural complexity. This suggests that difference between high and low productivity reefs is due to differences in the food base. Transient plankton (those that come from outside the system) may make a significant contribution to energy availability. Here I will focus on the potential impact of plankton and planktivores on enhancing productivity of fishery reserves.

METHODS

To examine the role of planktivores in affecting reef productivity three habitats, mangroves, seagrass beds, and reefs, were compared as to planktivore composition. Eighteen mangrove sites were sampled by visual census in the La Parguera area of southwestern Puerto Rico. Nine grassbed sites were sampled by trawl around Lee Stocking Island, Bahamas. At four grassbed stations seasonal samples were taken and data from two periods (December 1991 and August 1992) representing the greatest variation in environmental conditions were used to make comparisons here. Diver visual censuses on reefs off Lee Stocking Island and at Molasses Reef in the Florida Keys were used for reef comparisons.

I assigned species to five categories: benthivores (B), herbivores (H), macrocarnivores (MC), omnivores (O), and planktivores (P) based on reported feeding habits (Randall, 1967) to make trophic comparisons among sites.

RESULTS AND DISCUSSION

Assessing the role of planktivores

Potential productivity should be a criterion for area selection in marine reserves but how can this be easily assessed? If an area is historically known to be productive then it is likely to be productive as a reserve. If historically good but now poor it could possibly be rehabilitated. An unproductive area can not easily be made productive. Selection of historically productive areas is built into the selection process but what about areas where there is little information? If planktivores might be indicators of above average productivity then two areas, nearshore and offshore, should be examined.

Seagrass beds

While it is hard to compare directly due to different sampling methods it is evident that there is a wide range of standing crops of fishes on grassbeds throughout the Caribbean (Weinstein and Heck, 1979; Baelde, 1990; Sedberry and Carter, 1993). The use of seagrass beds as nursery areas has been questioned (Sogard *et al.*, 1987). I repeatedly sampled by trawl grassbeds in a shallow water tidal flow field north of Lee Stocking Island over a year's period. In this area only 8% of the fish taken were juveniles of reef based species while the remainder were part the resident grassbed assemblage. One trawl station fell within an area identified as a nursery area for conch. The fish assemblage found there was not remarkable. Overall there was a decline in abundance of fishes with distance from oceanic influence with most of this difference occurring in the diurnal fish assemblage. Trends differed between day and night with significantly more fish taken during the day. There were significant differences among sites and diurnal collections in total number of individuals though number of taxa did

not differ. When compared with five other nearby grassbeds this area was the most productive by a factor of two. Based on these findings I do not believe this area can not be considered a nursery area.

While the habitat characteristics have not been analyzed in detail there are no obvious differences among flow field sites. For such a relatively low dimensional habitat (when compared with reefs) the large variability that is not grass-density dependent is perplexing unless there is substantial variability in productivity among the sites. As the decline in fish abundance parallels the distance from the oceanic plankton source this might be due to declining planktonic input though the number of planktivores is very low (Figure 1). Nocturnal planktivores, such as apogonids, dominated the grassbeds suggesting that resident plankton may be more important than transient plankton. Stoner (pers. comm.) noted variation in plankton abundance among grassbed sites on the bank based on settlement tube collections. This suggests to me that plankton might enter the grassbed system directly through settling out of the water column by-passing planktivores. This mechanism might explain variation among sites but needs further examination. Whether the availability of external energy sources is a prerequisite for a productive grassbeds is yet to be resolved.

Mangroves

Large schools of anchovies, clupeids, and atherinids can be found in nearshore areas of the tropics. These "bait fish" provide an important food base yet are hard to enumerate. A survey of mangrove prop-root habitats in Puerto Rico revealed a highly variable composition of fishes especially commercially important species. Piscivores such as, *Sphyrna barracuda*, *Lutjanus apodus*, and *Lutjanus griseus* are common in mangroves (Dennis, 1992). The presence of large schools of *Jenkinsia* spp., *Anchoa* spp., and *Harengula* spp. form a substantial food resource for these piscivores. Excluding bait fish, piscivores make up the next most important trophic group (36.9%) in the mangroves of southwestern Puerto Rico (Figure 1). There was a positive correlation ($r = 0.478$) between bait fish and piscivore abundance though there is considerable scatter in the data. Where bait fish are absent the fish assemblage was clearly quite reduced. The origin of plankton that feeds these bait-fish is not clear to me but their schools typically occur in nutrient rich nearshore water thus might be locally generated. At Lee Stocking Island oceanic waters are very oligotrophic and there are no nearshore nutrient sources. Not surprisingly bait fishes are not common.

The number of bait fish schools and their location could be quickly and easily mapped out from the surface in clear tropical waters. Sampling for composition could be done by typical fishery gear such as cast net. This information would be useful in assessing the quality of a particular area for use as a

reserve.

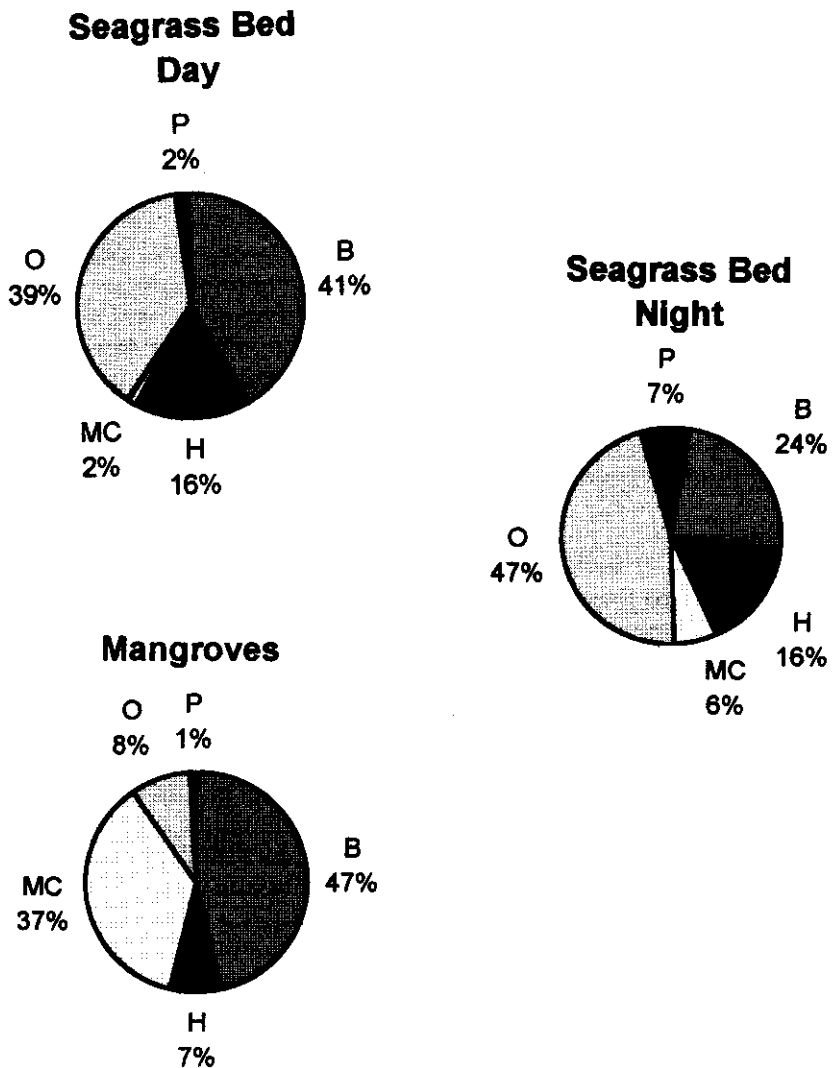


Figure 1. Trophic composition of fishes in seagrass beds (day and night) and mangroves.

Reefs

Diurnal reef planktivores are typically found along the shelf edge where they have access to the transient open-ocean zooplankters (Hobson, 1991). Hamner *et al.* (1988) concluded that these fishes formed a "wall of mouths" that do not allow any zooplankton to reach the reef substrate until processed through the digestive tract. The presence of planktivores provides a conversion of an external energy (plankton) into a more useable benthic form (fecal pellets) (Robertson, 1982). Planktivorous fishes other than bait fishes provide a secondary level of food to piscivores. Their abundance may indicate the presence of a substantial and important food source. A low abundance of planktivores may result in low production of piscivores. The most common and widespread reef planktivores are creole (*Clepticus parrae*) and blue head (*Thalassoma bifasciatum*) wrasses both form highly mobile aggregations that are very contagiously distributed leading to high variability in visual assessment. The area where they are most abundant is usually a relatively narrow zone along the shelf edge that could more easily be surveyed hydroacoustically with taxonomic composition validated by drop camera or diver.

If plankton abundance varies seasonally its impact on reef fishes might be hard to measure. Seasonal variability in planktivore biomass was not observed at Molasses reef where all other trophic components varied significantly (Figure 2) thus suggests that the planktonic food source may be somewhat regular (Dennis and Bright, 1988).

When fish assemblages at two shelf sites (Perry reef and Shelf edge) were compared to two bank sites (Rainbow Garden and Norman's Pond Patch Reef) at Lee Stocking Island there were significantly fewer planktivores on the bank more isolated from the oceanic planktonic source (Figure 3). Between the two bank sites there was significantly fewer planktivores at Rainbow Garden farthest from the tidal pass. This difference in abundance also corresponds to lower plankton levels on the bank (Al Stoner, pers. comm.). As described by Hobson (1991) the shelf edge reefs were dominated by larger planktivores, such as, creole wrasse while bank reefs predominately have smaller species such as bicolor damselfish.

Many shelf-edge planktivore aggregations that I have observed are stable through time though they may move laterally up or down the shelf. Again this suggests a reliable source of plankton in the area. Due to the high variability in abundance of these species substantial sampling may require to get accurate estimates of their abundance. A less variable measure of planktonic input might be obtained from more site-faithful species, such as *Chromis* spp. or *Stegastes partitus*, to assess the contribution of plankton to the local food base. These pomacentrid species are smaller planktivores that have a wide distribution among habitats and make use of smaller zooplankton that may be resident on reefs but

adults feed high in the water column thus must make considerable use of transient plankton (Hobson 1991).

The bicolor damselfish (*Stegastes partitus*) is the most abundant pomacentrid at many Caribbean locations (Emery, 1973; Clarke, 1977; Waldner and Robertson, 1980) and is primarily planktivorous as adults (Randall, 1967; Emery, 1968). Its restricted movement after settlement makes it susceptible to the vagaries in planktonic food supply, which might directly control abundance (Stevenson, 1972). Adult abundance of bicolor damselfish was fairly consistent through time whereas another common planktivore the bluehead wrasse was highly variable at Molasses reef (Figure 2). Whether this is due to a fluctuating food source or greater mobility in the bluehead is unclear.

The *Chromis* species form dense aggregates on the seaward edge of many reefs. De Boer (1978) found that density of blue chromis (*C. cyanea*) was correlated with planktonic food supply. Also the uneven distribution of blue chromis on reefs was suggested to be the result of food supply. Brown chromis (*C. multilineata*) are also planktivorous and form large aggregations most often along the reef edge (6 - 20 m depth) (Myrberg *et al.*, 1967). The brown chromis is more abundant than the blue chromis at shallower reef front sites (Emery, 1973; Clarke, 1977). Enumerating these species as an aggregate group may provide a useful index as there is great similarity in feeding behavior and food habits would be less affected by differences in reef habitat. The juveniles of both species are more substrate attached thus may use resident plankton and would be much more variable in numbers due to recruitment variability. The abundance of adult *Chromis* spp. might be a reasonable index of plankton contribution to a given reef area.

CONCLUSION AND RECOMMENDATIONS

A quantitative assessment of bait fishes and reef planktivores would provide an estimate of the contribution of plankton to the food base. This could be an important criterion in selecting areas for inclusion in marine reserves. We still have little knowledge of the importance of plankton to the reef system. We need to determine more exactly the relationship between predator (piscivores) and prey (planktivores). Whether the energy pathway is direct or through secondary production of the benthos also needs to be determined. Through a comparison of high and low productivity areas the relative contribution of benthic and planktonic food sources could be determined. The system might be complex requiring both external planktonic sources and benthic secondary production. If so the proper selection of habitats would be critical to maximize productivity. If not already explicitly done an evaluation of the habitat quality based on potential productivity should be part of every reserve assessment.

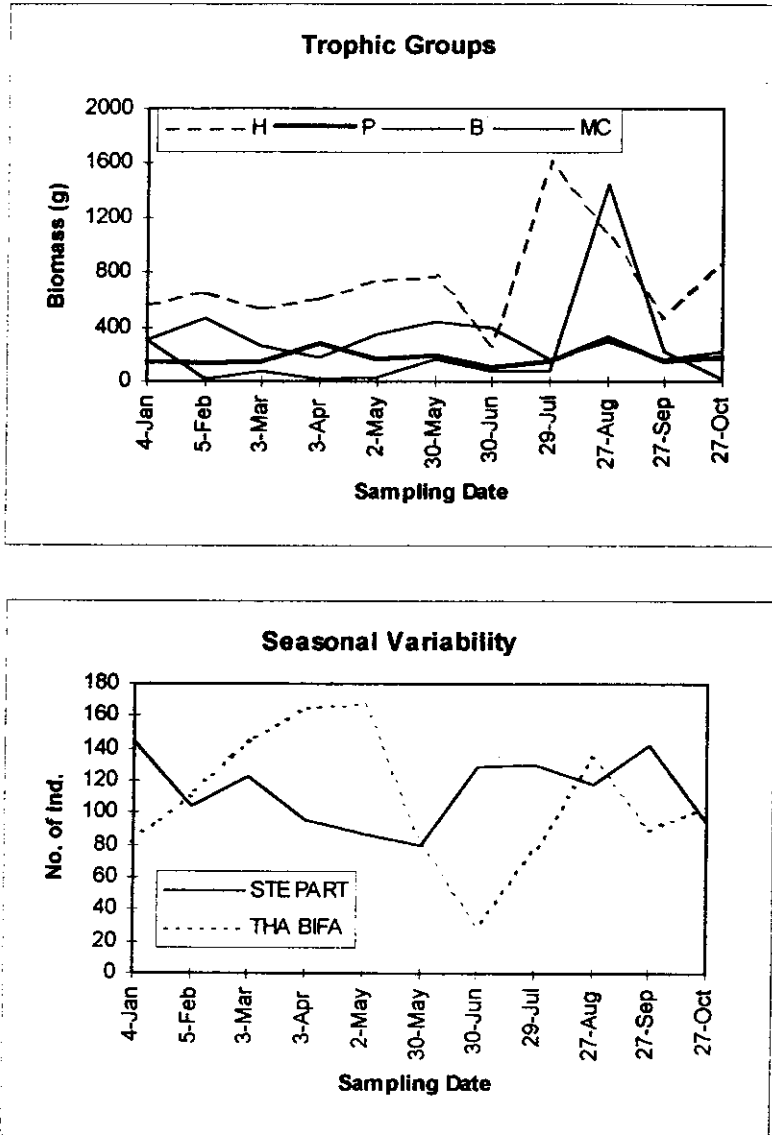


Figure 2. Seasonal variability in trophic components and individual abundance of two planktivores (*Stegastes partitus* and *Thalassoma bifasciatum*) on the forereef of Molasses Reef, Florida Keys.

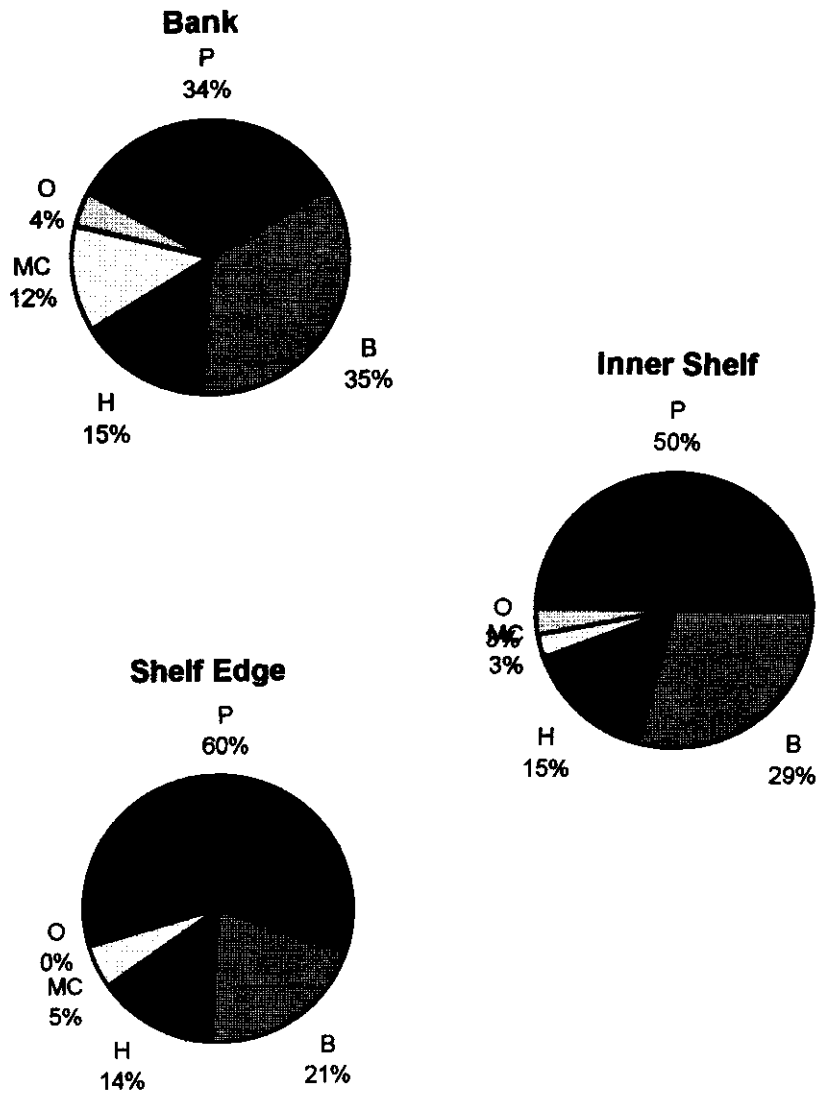


Figure 3. Trophic composition of reef fish assemblages on the bank, inner fringing reef, and shelf edge at Lee Stocking Island, Bahamas.

LITERATURE CITED

- Baelde, P. 1990. Differences in the structure of fish assemblages in *Thalassia testudinum* beds in Guadeloupe, French West Indies, and their ecological significance. *Mar. Biol.* **105**: 163 - 173.
- Carpenter, K.E., R.I. Mclat, V.D. Albaladejo, and V.T. Corpuz. 1981. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proc. 4th Inter. Coral Reef Symp. Manila*, **2**: 497 - 502.
- Clarke, R.D. 1977. Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Mar. Biol.* **40**: 277-289.
- De Boer, B.A. 1978. Factors influencing the distribution of the damselfish *Chromis cyanea* (Poey), Pomacentridae, on a reef at Curaçao, Netherlands Antilles. *Bull. Mar. Sci.* **28**(3): 550 - 565.
- Dennis, G.D. 1992. Island mangrove habitats as spawning and nursery areas for commercially important fishes in the Caribbean. *Proc. Gulf Carib. Fish. Inst.* **41**: 205 - 225.
- Dennis, G.D. and T.J. Bright. 1988. The impact of a ship grounding on the reef fish assemblage at Molasses Reef, Key Largo National Marine Sanctuary, Florida. *Proc. 6th Inter. Coral Reef Symp., Townsville*, **2**: 213 - 218.
- Emery, A.R. 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bull. Mar. Sci.* **23**: 649 - 770.
- Hamner, W.M., M.S. Jones, J.H. Carlton, I.R. Hauri, and D. McB. Williams. 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bull. Mar. Sci.* **42**(3): 459 - 479.
- Hobson, E.S. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. Pages 69 - 95. Chap. 4. in: P.F. Sale (ed.), *The ecology of fishes on coral reefs*. Academic Press, New York, NY. 754 p.
- Kulbicki, M. 1988. Patterns in the trophic structure of fish populations across the SW lagoon of New Caledonia. *Proc. 6th Inter. Coral Reef Symp. Townsville*, **2**: 89 - 94.
- Marshall, N. 1985. Ecological sustainable yield (fisheries potential) of coral reefs, as related to physiographic features of coral reef environments. *Proc. 5th Inter. Coral Reef Congr. Tahiti*, **5**: 525 - 530.
- Myrberg, A.A., B.D. Brahy, and A.R. Emery. 1967. Field observations on reproduction of the *Chromis multilineata* (Pomacentridae), with additional notes on general behavior. *Copeia* **1967**(4): 819 - 827.

- Parrish, J.D., M.W. Callahan, and J.E. Norris. 1985. Fish trophic relationships that structure reef communities. *Proc. 5th Inter. Coral Reef Congr. Tahiti*, 4:73 - 78.
- Parrish, J.D., J.E. Norris, M.W. Callahan, J.K. Callahan, E.J. Magarifuji and R.E. Schroeder. 1986. Piscivory in a coral reef fish community. *Develop. Environ. Biol. Fishes* 7:285 - 297.
- Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5:665 - 847.
- Robertson, D.R. 1982. Fish faces a fish food on a Pacific coral reef. *Mar. Ecol. Prog. Ser.* 7:253 - 265.
- Russ, G.R. 1991. Coral reef fisheries: effects and yields. Pages 601 - 635. Chap. 20. in: P.F. Sale (ed.) *The ecology of fishes on coral reefs*. Academic Press, New York, NY, 754 p.
- Sedberry, G.R. and J. Carter. 1993. The fish community of a shallow tropical lagoon in Belize, Central America. *Estuaries* 16(2):198 - 215.
- Smith, C.L. and J.C. Tyler. 1973. Direct observations of resource sharing in coral reef fish. *Helgol. wiss. Meeresunters* 24: 264 - 275.
- Sogard, S.M., G.V.N. Powell, and J.G. Holmquist. 1987. Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover. *Mar. Ecol. Prog. Ser.* 40:25 - 39.
- Stevenson, R.A. 1972. Regulation of feeding behavior of the bicolor damselfish (*Eupomacentrus partitus* Poey) by environmental factors. Pages 278 - 302. Chap. 7. In: H.E. Winn and B.L. Olla (eds.) *Behavior of Marine Animals. Vol. 2: Vertebrates*. Plenum Press, New York, NY.
- Stoner, A.W., P.A. Pitts and R.A. Armstrong. 1996. The interaction of physical and biological factors in the large-scale distribution of juvenile queen conch populations in seagrass meadows. *Bull. Mar. Sci.* 58:217 - 233.
- Waldner, R.E and D.R. Robertson. 1980. Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae). *Bull. Mar. Sci.* 30:171 - 186.
- Weinstein, M.P. and K.L. Heck. 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and in the Gulf of Mexico: Composition, structure and community ecology. *Mar. Biol.* 50:97 - 107.
- Williams, D. McB. and A.I. Hatcher. 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 10:239 - 250.