# Diver Ecotourism and Disturbance to Reef Fish Spawning Aggregations: It is Better to be Disturbed than to be Dead

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## ABSTRACT

Dive tourism, with proper diver training, has been suggested as an environmentally benign and economically viable alternative to commercial fishing on reef fish spawning aggregations (FSAs). Yet, the disturbance effects of divers on the FSAs must be assessed to ensure that the resource is sustained. We examined over 9 hours of video footage (extracted from over 100 hours of underwater video) filmed at FSA sites in Belize. The footage captured divers interacting with schools of snappers and groupers as they aggregated to spawn. Video also captured diver interactions with whale sharks. Diver behaviors included observations, video recording, flash photography, and tagging of whale sharks. We filmed 746 unique diver–school interactions that included total observations of approximately 200,000 snappers, 4,700 Nassau groupers *Epinephelus striatus* and 200 whale sharks. We recorded 180 spawning events, only 105 of which showed divers disturbing aggregating schools, which affected an estimated 2,100 snappers and 90 groupers. We conclude that small groups of experienced divers, following a code of responsible diving centered upon the precautionary principle and sensitivity to fish breeding behaviors, do not negatively affect schooling or spawning behaviors. Though further research is needed to assess the effects of boat traffic, underwater sound, and larger groups of less experienced divers, dive ecotourism at FSAs represents an economically attractive and less exploitative alternative to commercial fishing.

KEY WORDS: Fish spawning aggregation, dive ecotourism, marine protected areas (MPAs)

# El Efecto del Ecoturismo por Buceo en las Agregaciones de Desove de Peces Arrecifales: Mas Vale Estar Perturbado que Muerto

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# L'Effet de l'Ecotourisme de Plongée sur les Agrégations de Frai de Poissons Récifaux: C'est Mieux Être Perturbé que Mort

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## INTRODUCTION

Coral reef ecosystems in the Gulf and Caribbean provide the cultural, ecological, and economic life support for Caribbean economies through tourism and commercial fishing industries (Carr and Heyman 2008). An integral component for restoring fish stocks and maintaining biodiversity throughout the greater Caribbean has been enacting protection for reef fish spawning aggregations (FSAs) and their spawning habitat through marine reserves that seek to limit or prevent unsustainable or exploitative human behaviors. Many Caribbean FSA sites are utilized by multiple species throughout the year (e.g. Claro and Lindeman 2003, Heyman and Kjerfve 2008, Kobara and Heyman 2010). This insight is valuable from the perspective of fishery management, especially within the Caribbean's highly targeted grouper-snapper complex (Coleman et al. 2000), as spawning fishes demonstrate high site fidelity to temporally and spatially concentrated FSA sites (Heyman and Requena 2003). Designing and implementing reserves focused on protecting one species during spawning can often provide long-lasting benefits for many species.

The predictability of FSA sites both in time and space, however, has made those fish populations that aggregate to spawn more vulnerable to unsustainable fishing pressure. Several Caribbean sites have experienced commercial depletion or collapse (e.g. Sala et al. 2001, Nemeth 2005, Aguilar-Perera 2006, Sadovy de Mitcheson et al. 2008). Many FSA populations are presently several orders of magnitude lower than historical records (Beets and Friedlander 1998, Sala et al. 2001, Burton et al. 2005), although healthy FSAs remain, many of which are located along the Meso-American Barrier Reef System in Belize (Kobara and Heyman 2010). Several of these Belizean FSA sites have been incorporated into a network of reserves and marine protected areas (MPAs) that aim to reduce fishing effort and rebuild stocks (Heyman and Requena 2002, Cho 2005, Heyman 2011).

In spite of their legal protection, FSA sites remain vulnerable to extractive fishing unless there exists a consistent enforcement presence, economic alternatives for fishers who used these resources previously, and optimally, both! It is difficult to anticipate and address the range of possible human disturbances through management plans and their enforcement (Sainsbury et al. 2000, Pollnac et al. 2001, Salas and Gaertner 2004, Jennings 2005, Mora et al.

2009, Smith et al. 2010). Support for management is inexorably linked to its programs being able to demonstrate the ecological and economic benefits they proposed (Davis and Gartside 2001, Agardy 2003, Kaiser 2004, Cook and Heinen 2005).

Ecotourism ventures can often provide real economic and social benefits to displaced fishers while encouraging resource conservation and ecological stewardship (Honey 1999, Carr and Mendelsohn 2003, Krüger 2005). Dive tourism is highly valued at local and larger scales (Davis and Tisdell 1996, Arin and Kramer 2002, Carr and Mendelsohn 2003). It often also meet's Honey's (1999) definition for ecotourism, given that such many dive operations highlight education and support conservation programs while providing low-impact yet viable economic opportunities for local communities. Resource conservation strategies generate measurable ecological benefits that further improve the dive industry or attractiveness of a destination (Dixon et al. 1993, Williams and Polunin 2000, Rudd and Tupper 2002, Sorice et al. 2007).

Yet, dive tourism is not necessarily environmentally benign (Hawkins et al. 1999, Barker and Roberts 2004, Hawkins et al. 2005), and planned economic or ecological benefits may be forfeited if the industry is not properly planned, implemented, or supported. Indeed, research suggests that ecotourism has the capacity to introduce a suite of unique negative effects on both the natural ecosystem and the local community and their resource needs over multiple temporal and spatial scales (Davis and Tisdell 1996, Lindberg et al. 1996, Scheyvens 1999, Stem et al. 2003, Hawkins et al. 2005). The question for any ecotourism industry is how successfully it can provide comparable employment and economic incentives to encourage individuals to enter the industry while, in the case of fisheries, reducing negative human impacts and restoring fish stocks.

Our research specifically examines whether dive tourism negatively affects FSAs, disturbing spawning behaviors in such a manner as to affect reproductive potential and the long-term health of these fish populations, both ecologically and as a resource. And if there are identifiable disturbances to FSAs and fish populations, what level of interaction by divers is required to cause such a disturbance, and most critically, how likely is it that a disturbed aggregation will forgo spawning as a response?

## MATERIALS AND METHODS

### Study Area

This study was conducted largely at Gladden Spit, Belize, a well-documented multispecies spawning aggregation site located at a reef promontory (16º 30'N, 87º 57'W) adjacent to the 1000-m isobath (Heyman and Kjerfve 2008). The multispecies FSA is at the core of the Gladden Spit and Silk Cayes Marine Reserve (GSSCMR). This site is an important for spawning throughout the year for at least 17 species of reef fish (Heyman and Requena 2002, Heyman and Kjerfve 2008). GSSCMR has also become the center for growing marine ecotourism industry in southern Belize. The reserve was established by the Belizean government in 2000 (Ministry of Agriculture and Fisheries 2000) and is currently managed by a partnership between the government and a local non-government organization, the Southern Environmental Association. Gladden Spit provides protection to FSAs through defined conservation zones that prohibit or limit negative human impacts without overly restricting access to the reserve (via a General Use Zone) for stakeholder groups. GSSCMR provides important revenue streams into the local economy through both a managed commercial fishery and recreational tourism ventures. Though the majority of observations were from Gladden Spit, 22% of the total were included from two additional multispecies FSA sites in Belize, Turneffe Elbow and Sandbore, Lighthouse Reef (described in Kobara and Heyman 2010).

**Table 1.** Description of typical behaviors of undisturbed reef fishes at fish spawning aggregation sites (adapted from Domeier and Colin 1997, Heyman et al. 2005)

| School behavior | Behavior description |
|---|---|
| Circling | A densely formed school swimming in a unified circular direction around a central axis at a steady speed. The school, as a whole, shows no vertical movement through the water column. Circling schools are frequently observed near the seafloor and occur prior to rising behaviors. |
| Courtship coloration | Some fishes assume one or more species-specific courtship patterns of coloration that are different from the non-courtship color phase. The percentage of fishes exhibiting courtship coloration increases as spawning approaches. |
| Descending | A densely formed school swimming at a quickened speed while moving vertically down through the water column. Descending schools often form immediately after upward rushes to spawn. |
| Milling | A loosely formed school swimming at a relaxed speed but with no unified direction. Individual fish may be moving at various speeds and directions, but the school as a whole does not noticeably change location. |
| Rising | A densely formed school swimming at a steady speed while moving vertically up through the water column. |
| Rushing | One to several tens of fish use a rapid and chaotic burst of sped to swim toward the surface, often to release eggs and milt. Rushing fish often break from either a rising or circling school. |
| Schooling | A densely formed school swimming at a stead speed in a unified direction for an extended length of time. |
| Slow swim / resting | A loosely formed school swimming in a unified direction but at very slow speeds. Such behaviors are generally restricted to bottom waters. |
| Spawning | A small, chaotic school of several to several tens of fish in near-surface waters (often <10 m) that are actively releasing eggs and milt. |

**Table 2.** Descriptions of observable disturbance behaviors of fishes (adapted from Pitcher 1986, Domeier and Colin 1997, Godin 1997, and Smith 1997).

| Disturbed behavior | Behavior description |
|---|---|
| Color change | The fish reverts to non-courtship coloration. |
| Fin twitch | The fish stops its swimming, tensing its fins. Fin twitches are immediate precursors to flight behaviors. |
| Flight | The fish makes a sudden change in direction followed by a quick burst of speed away from the diver. Flight is considered to be energy-consuming and therefore is a major disturbance. |
| Hiding | The fish seeks the safety of shelter. Hiding behaviors were only observed by members of the Family Serranidae in this study. |
| Maintaining distance | The fish maintains swimming speed but makes adjustments to the direction so that the distance between fish (or school) and diver is maintained. The school maintains shape and structure throughout the diver's pass. |
| Parting | The fish maintains swimming speed but makes adjustments to the direction so that the distance between fish (or school) and diver is maintained. A disturbed school will physically part around a diver, reforming after passing. |
| Slow flight | The fish makes a change in direction and swims for a period of dive away from the diver without gaining speed. |
| Turning away | The fish turns away from the diver but with no additional effort to move away. A fish turning may cause other fish to also respond, leading to an escalating number of disturbed fish. |

### Data Collection and Analysis

Researchers used underwater digital video cameras to record over 100 hours of courtship and spawning behaviors from 1999 through 2008, during peak spawning season for snappers (March through June) and groupers (December through February). Individual interactions between divers and aggregating schools of fish were then extracted and analyzed (described in Heyman et al. 2010). Table 1 describes initial behavior for each fish school while Table 2 categorizes the range of disturbance responses by fish schools to nearby divers.

## RESULTS

From the compiled video, 561 min (9 h 22 min) were extracted, comprising 746 unique events showing fish and diver interactions, as well as courtship and spawning within the FSA (Table 3). For *Lutjanus cyanopterus*, researchers recorded 213 events, with 29 events showing divers disturbing the school, affecting 1,030 fish (1.1% of an estimated 92 870 fish). For *L. jocu*, researchers recorded 184 events, with 12 identified disturbances affecting 1120 fish (1.1% of an estimated 106 000 fish). Finally, 114 events, with 45 observed disturbances of *Epinephelus striatus* FSAs, were recorded, affecting 90 individuals (1.9% of an estimated 4,700 fish). Heyman et al. (2010) fully describes the results that are briefly presented here and in Table 3.

## DISCUSSION AND CONCLUSION

In dive tourism, the excitement of the destination and dive is paramount, and FSA diving offers a tantaliz-

**Table 3**. Summary data for diver interactions with reef fish spawning aggregations. Mean values include ± SD. nd: no data

| Species | Total no. of Interactions | Mean duration of interactions (s) | No. of disturbances | Mean duration of disturbances (s) | Mean no. of Individuals per event | Mean no. of disturbed individuals | No. Mid-water events | No. of bottom events | Mean no. days after full moon |
|---|---|---|---|---|---|---|---|---|---|
| *Lutjanus cyanopertus* | 213 | 56 ± 49 | 29 | 3 ± 1 | 436 ± 611 | 36 ± 48 | 161 | 52 | 2.0 ± 2.6 |
| *Lutjanus jocu* | 184 | 52 ± 51 | 12 | 5 ± 7 | 577 ±636 | 97 ± 137 | 166 | 18 | 1.4 ± 3.2 |
| *Epinephelus striatus* | 114 | 24 ± 17 | 45 | 5 ± 4 | 41 ± 75 | 2 ± 2 | 7 | 106 | 4.6 ± 2.6 |
| *Rhincodon typus* | 175 | 36 ± 40 | 4 | 5 ± 3 | 1.2 ± 0.6 | 1 | 174 | 1 | 3.6 ± 3.0 |
| *Lutjanus analis* | 3 | 19 ± 17 | 1 | 2 | 37 | 1 | 2 | 1 | 2.3 ± 1.2 |
| *Ocyurus chrysurus* | 1 | 9 | 0 | nd | 25 | nd | 1 | 0 | 0 |
| *Epinephelus guttatus* | 1 | 19 | 1 | 2 | 1 | 1 | 0 | 1 | 0 |
| *Mycteroperca bonaci* | 6 | 18 ± 12 | 1 | 4 | 2 ± 1 | 1 | 0 | 1 | 0 |
| *Mycteroperca tigris* | 9 | 90 ± 148 | 2 | 5 | 3 ± 3 | 8 ± 4 | 0 | 9 | 5.3 ± 1.8 |
| *Mycteroperca venenosa* | 1 | 201 | 1 | 7 | 10 | 10 | 0 | 1 | 8 |
| *Caranx spp.* | 39 | 3 ± 2 | 9 | 3 ± 1 | 386 ± 435 | 97 ± 155 | 36 | 3 | 3.0 ± 2.3 |

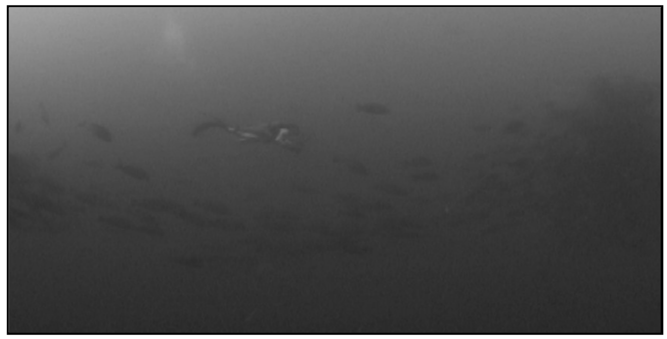
ing, unique experience for divers. Visitors and surface support boat traffic can, however, affect animal behaviors and put habitat at risk (Sorice et al. 2003, Quiros 2007, Sorice et al. 2007, Stensland and Berggren 2007). This creates a paradox for managers who wish to maximize economic potential by increasing tourist, snorkeler, and diver numbers while still focusing on the resource and area stewardship. Our research has shown that, with small groups of properly trained divers, snappers and groupers aggregating to spawn, and the whale sharks that appear to feed on the spawn, exhibit little to no effect by their presence.

Our footage shows that fishes in FSAs avoid divers in a similar manner as they avoid other large animals in the water (Figure 1). Our observations indicate that the likelihood of disturbing a school of fish is greatest when divers are directly above (< 3 m) rising schools of snappers, a response also seen with similarly-positioned whale sharks. School responses were primarily low-energy avoidance behaviors (i.e. parting or maintaining distance), although in a few instances, short duration, potentially high-energy responses (i.e. fin twitches and turning away behaviors that could be preludes to flight) were observed. These high-energy responses have the capacity to be transmitted from one fish to many other fish within the school in a matter of moments, and likely represent the greatest risk to delaying, preventing, or relocating spawning efforts within the water column.

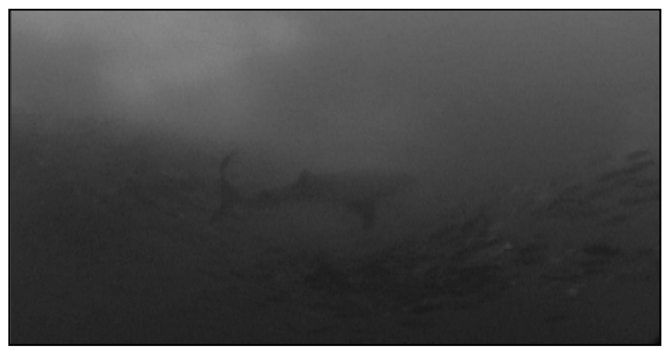
For this reason, divers and dive operators must take care to ensure that high-energy responses are not triggered either deliberately or even accidentally. Our work shows that experienced, cautious divers can successfully conduct themselves underwater without causing fishes to alter their aggregating and spawning behaviors. Indeed, the strongest recommendation that our research can provide is one of cautious, respectful, and responsible diving by educated, experienced divers. As reported by Quiros (2007), whale shark dive tourism in the Philippines has been well served by the adoption of a responsible "Code of Conduct" to ensure that divers and boat traffic do not negatively affect the FSA site or aggregating fishes. Similar 'Codes' are being practiced by divers and dive operations elsewhere (Birtles et al. 2008, de Groot and Bush 2010), and are considered to be a positive draw for visitors, just as MPAs have been in promoting dive tourism (Davis and Tisdell 1996, Carr and Mendelsohn 2003). We encourage that a similar, diver-oriented code be developed and implemented within at Gladden Spit, as well as other FSA sites throughout the Caribbean.

A diver code of conduct highlighting educated diving and outlining responsible interactions with aggregating schools of fish and whale sharks mesh well with existing regulations at Gladden Spit. There, the current situation embraces a precautionary approach, regulating both diving and fishing operations licensed to work within the GSSCMR while maintaining an active research and monitoring program. Dive masters and boats are permitted to operate in the area only after extensive training and appropriate certification. Numbers are restricted to six divers per dive master, 12 divers per boat, and two boats within the aggregation zone at a time (with the daily line-up determined through a lottery system) for 90 minutes each. Recreational divers are limited to a maximum depth of 24 meters (~80 feet) as both a safety measure and

**Figure 1.** Snapper responses to divers and to whale sharks are similar, in that the schools of aggregating fish maintain some distance during .



**A.** *L. cyanopterus* school maintaining distance from a diver



**B.** *L. cyanopterus* school maintaining distance from a feeding *R. typus*

**C.** A parting *Lutjanus cyanopterus* school as a diver and *R. typus* approach precaution against divers creating disturbances to aggregating fishes (Ministry of Agriculture and Fisheries 2000). Regulations are reviewed and adjusted annually through a process of stakeholder meetings and data-sharing from monitoring and research programs. As a hypothetical example, existing regulations that restrict divers approaching whale sharks to a minimum distance of 4.5 m could be readily adapted to FSAs. Most critically, we believe that dive operators must continue to educate and train divers on proper dive etiquette amongst these schools, insist upon buoyancy control, and emphasize the risks of unsafe diving both to divers and FSAs.

The economic incentives for stakeholders to move away from fishery extraction and into dive ecotourism are strong at Gladden Spit, due in no small part to the health of the snapper and grouper FSAs, the uniqueness of the destination and dive experience, and perhaps most critically, from the support of the local community and government agencies in supporting ecotourism ventures. Sala et al. (2001) estimated that limited tourist diving on grouper FSAs in Belize would produce 20 times the income produced from fishing the sites. Hargreaves-Allen (2009) calculated that annual net benefits of US$ 4 million were accrued from tourism at GSSCMR, compared with only US$ 315 000 needed to manage the reserve for the year. Given the unique nature of diving with thousands of large fishes, including endangered species, it is likely that market forces exist that could drive these values higher, thereby providing even higher benefits to fishers exiting the fishery for tourism, the tourism industry itself, and more broadly, the southern Belize region.

Though we show that divers generally do not disturb FSAs, we do not presume this to be impossible, just preventable. In the case of small snorkel and dive tourism operations focusing on interactions with bottlenose dolphins, both Bejder et al. (2006) and Stensland and Berggren (2007) reported that moderate increases in boat numbers and snorkelers in both Zanzibar and Shark Bay, Australia, respectively, led to measurable changes in behavior, particularly of females with calves, as well as decreasing pod sizes. These results suggest that it is possible to disturb a marine community, driving off individuals that are more sensitive to disturbance and that may not return to the site of the interaction.

While we do not want to draw too many parallels between snappers and bottlenose dolphins, it is certainly possible that the accumulation of small, chronic disturbances of boats, fishers, and divers over time, similar to those felt in Zanzibar and Australia with the bottlenose dolphin tourism, may be sufficient to affect and shift fish aggregation timing and site selection. Such shifts would invariably affect ecological fitness and reproductive potential of a fish population, although quantifying the impact may be impossible to quantify or even describe simply as a positive or negative.

In conclusion, dive tourism at Caribbean snapper and grouper FSAs, is potentially an economically valuable industry with net benefits several times larger than fishing. To ensure that the benefits are sustainable, dive tourism should adopt a precautionary approach to FSA diving. A FSA Diving Code of Conduct would serve as an instrument that educates divers to a level necessary for the rigors and risks of FSA diving, outlines appropriate and inappropriate diver behaviors, defines acceptable dive operation and boat traffic protocols, and provides avenues for all stakeholders to be included in the development and review of management programs. As a major purpose of dive tourism is to alleviate fishing pressure at FSA sites while providing economic benefits, The Code of Conduct should be adaptive and responsive to these issues at a range of scales and levels of interactions, so that tourism benefits are not fleeting.

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## LITERATURE CITED

Agardy, T. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **13**:353-367.

Aguilar-Perera, A. 2006. Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast. *Marine Ecology Progress Series* **327**:289-296.

Arin, T. and R.A. Kramer. 2002. Divers' willingness to pay to visit marine sanctuaries: an exploratory study. Ocean & Coastal Management **45**:171-183.

Barker, N.H.L. and C.M. Roberts. 2004. Scuba diver behaviour and the management of diving impacts on coral reefs. *Biological Conservation* **120**:481-489.

Beets, J. and A. Friedlander. 1998. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. *Environmental Biology of Fishes* **55**:91-98.

Bejder, L., A. Samuels, H. Whitehead, and N. Gales. 2006. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Animal Behavior* **72**:1149-1158.

Birtles, A., P. Arnold, M. Curnock, S. Salmon, A. Mangott, S. Sobtzick, P. Valentine, A. Caillaud, and J. Rumney. 2008. Code of practice for dwarf minke whale interactions in the Great Barrier Reef World Heritage Area. Townsville, Australia.

Burton, M.L., K.J. Brennan, R.C. Muñoz, and J. Richard, and O. Parker. 2005. Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley's Hump two years after establishment of the Tortugas South Ecological Reserve. *Fishery Bulletin* **103**:404-410.

Carr, L.M. and R. Mendelsohn. 2003. Valuing coral reefs: a travel cost analysis of the Great Barrier Reef. *Ambio* **32**:353-357.

Cho, L. 2005. Marine protected areas: a tool for integrated coastal management in Belize. *Ocean & Coastal Management* **48**:932-947.

Claro, R. and K.C. Lindeman. 2003. Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. *Gulf and Caribbean Research* **14**:91-106.

Coleman, F.C., C.C. Koenig, G.R. Huntsman, J.A. Musick, A.M. Eklund, J.C. McGovern, R.W. Chapman, G.R. Sedberry, and C.B. Grimes. 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries* **25**:14-19.

Cook, G.S. and J.T. Heinen. 2005. On the uncertain costs and tenuous benefits of marine reserves: a case study of the Tortugas Ecological Reserve, South Florida, USA. *Natural Areas Journal* **25**:390-396.

Coulthard, S., D. Johnson, and J.A. McGregor. [2011]. Poverty, sustainability and human wellbeing: a social wellbeing approach to the global fisheries crisis. *Global Environmental Change*. In Press.

Davis, D. and D.F. Gartside. 2001. Challenges for economic policy in sustainable management of marine natural resources. *Ecological Economics* **36**:223-236.

Davis, D. and C. Tisdell. 1996. Economic management of recreational scuba diving and the environment. Journal of *Environmental Management* **48**:229-248.

de Groot, J. and S.R. Bush. 2010. The potential for dive tourism led entrepreneurial marine protected areas in Curaçao. *Marine Policy* **34**:1051-1059.

Dixon, J.A., L.F. Scura, and T. van't Hof. 1993. Meeting ecological and economic goals: marine parks in the Caribbean. *Ambio* **22**:117-125.

Domeier, M. and P.L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* **60**:698-726.

Ezer, T., D.V. Thattai, B. Kjerfve, and W.D. Heyman. 2005. On the variability of the flow along the Meso-American Barrier Reef system: a numerical model study of the influence of the Caribbean current and eddies. *Ocean Dynamics* **55**:458-475.

Hargreaves-Allen, V. 2009. Is marine conservation a good deal? The value of a protected reef in Belize., Conservation Strategy Fund, Sebastopol, California USA.

Hawkins, J. P., C. M. Roberts, D. Kooistra, K. Buchan, and S. White. 2005. Sustainability of scuba diving tourism on coral reefs of Saba. *Coastal Management* **33**:373-387.

Hawkins, J.P., C.M. Roberts, T. Van't Hof, K. de Meyer, J. Tratalos, and C. Aldam. 1999. Effects of recreational scuba diving on Caribbean coral and fish communities. *Conservation Biology* **13**:888-897.

Heyman, W.D. 2011. Elements for building a participatory ecosystem-based marine reserve network. *The Professional Geographer* **63**(4): 1-14. DOI:10.1080/00330124.2011.585078

Heyman, W.D., L.M. Carr, and P.S. Lobel. 2010. Diver ecotourism and disturbance to reef fish spawning aggregations: it is better to be disturbed than to be dead. *Marine Ecology Progress Ser*ies **419**:201-210.

Heyman, W.D. and B. Kjerfve. 2008. Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bulletin of Marine Science* **83**:531-551.

Heyman, W.D., B. Kjerfve, R.T. Graham, K.L. Rhodes, and L. Garbutt. 2005. Spawning aggregations of *Lutjanus cyanopterus* (Cuvier) on the Belize Barrier Reef over a 6 year period. *Journal of Fish Biology* **67**:83-101.

Heyman, W.D. and N. Requena. 2002. Status of multi-species spawning aggregations in Belize. The Nature Conservancy, Punta Gorda, Belize.

Heyman, W.D. and N. Requena. 2003. Fish Spawning Aggregation Sites in the MBRS Region: Recommendations for Monitoring and Management. The Nature Conservancy, Belize City, Belize.

Honey, M. 1999. *Ecotourism and Sustainable Development: Who Owns Paradise?* Island Press, Washington, D.C. USA.

Jennings, S. 2005. Indicators to support an ecosystem approach to fisheries. *Fish and Fisheries* **6**:212-232.

Kaiser, M. J. 2004. Marine protected areas: the importance of being earnest. *Aquatic Conservation: Marine and Freshwater Ecosystems* **14**:635-638.

Kobara, S. and W.D. Heyman. 2010. Sea bottom geomorphology of multi-species spawning aggregation sites in Belize. *Marine Ecology Progress Series* **405**:243-254.

Krüger, O. 2005. The role of ecotourism in conservation: panacea or Pandora's box? *Biodiversity and Conservation* **14**:579-600.

Lindberg, K., J. Enriquez, and K. Sproule. 1996. Ecotourism questioned: case studies from Belize. *Annals of Tourism Research* **23**:543-562.

Ministry of Agriculture and Fisheries. 2000. Government of Belize, Belmopan, Belize.

Mora, C., R.A. Myers, M. Coll, S. Libralato, T.J. Pitcher, R.U. Sumaila, D. Zeller, R. Watson, K.J. Gaston, and B. Worm. 2009. Management effectiveness of the world's marine fisheries. PLoS Biology **7**:e1000131.

Nemeth, R.S. 2005. Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Marine Ecology Progress Series* **286**:81-97.

Peterson, A.M. and S.M. Stead. [2011]. Rule breaking and livelihood options in marine protected areas. *Environmental Conservation*: In press.

Pollnac, R.B., R.S. Pomeroy, and I.H.T. Harkes. 2001. Fishery policy and job satisfaction in three southeast Asian fisheries. *Ocean & Coastal Management* **44**:531-544.

Quiros, A.L. 2007. Tourist compliance to a Code of Conduct and the resulting effects on whale shark (*Rhincodon typus*) behavior in Donsol, Philippines. *Fisheries Research* **84**:102-108.

Rudd, M.A. and M.H. Tupper. 2002. The impact of Nassau grouper size and abundance on Scuba diver site selection and MPA economics. *Coastal Management* **30**:133-151.

Sadovy de Mitcheson, Y., A. Cornish, M. Domeier, P.L. Colin, M. Russell, and K.C. Lindeman. 2008. A global baseline for spawning aggregations of reef fishes. *Conservation Biology* **22**:1233-1244.

Sainsbury, K.J., A.E. Punt, and A.D.M. Smith. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science* **57**:731-741.

Sala, E., E. Ballesteros, and R.M. Starr. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* **26**:23-30.

Salas, S. and D. Gaertner. 2004. The behavioural dynamics of fishers: management implications. Fish and Fisheries **5**:153-167.

Scheyvens, R. 1999. Ecotourism and the empowerment of local communities. *Tourism Management* **20**:245-249.

Smith, M. D., J. Lynham, J. N. Sanchirico, and J. A. Wilson. 2010. Political economy of marine reserves: understanding the role of opportunity costs. *Proceedings of the National Academy of Sciences of the United States of America* **107**:18300-18305.

Sorice, M.G., C-O. Oh, and R.B. Ditton. 2007. Managing scuba divers to meet ecological goals for coral reef conservation. *Ambio* **36**:316-322.

Sorice, M.G., C.S. Shafer, and D. Scott. 2003. Managing endangered species within the use/preservation paradox: understanding and defining harassment of the West Indian Manatee (*Trichechus manatus*). *Coastal Management* **31**:319-338.

Stem, C.J., J.P. Lassoie, D.R. Lee, and D.J. Deshler. 2003. How 'eco' is ecotourism? A comparative case study of ecotourism in Costa Rica. *Journal of Sustainable Tourism* **11**:322-347.

Stensland, E. and P. Berggren. 2007. Behavioural changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism. *Marine Ecology Progress Series* **332**:225-234.

Williams, I.D. and N.V.C. Polunin. 2000. Differences between protected and unprotected reefs of the western Caribbean in attributes preferred by dive tourists. *Environmental Conservation* **27**:382-291.