

## **The Caribbean spiny lobster, *Panulirus argus*, fisheries.**

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### **Abstract**

The Caribbean spiny lobster is one of the most economically important resources to Caribbean fisheries. High demand and low supply of spiny lobster has driven most fisheries to an excess of fishing capacity and created overfishing conditions in most fisheries. All fisheries are recruitment driven and in the last 10 years recruitment has followed decreasing trends in most fisheries. Along with exploitation, changes in environmental and ecological conditions are likely to be impacting spiny lobster habitat. Population dynamics and fisheries processes that are key to the ecosystem approach to fishery management of the resources are identified and discussed.

### **Introduction**

The Caribbean spiny lobster, *Panulirus argus*, sustains one of the most economically important fisheries in the region with the greatest stock abundances observed in the Western Caribbean and Brazil (Fig. 1). Fisheries developed from circumstantial operations in the early 1960's to fully overcapitalized industries in the 2000's. Landings peaked during 1987-1997 at about 32 to 37 thousand metric tons whole weight with a value exceeding US\$300 million dock side. Regional landings decreased 55% in the 2000's (Fig. 2) mostly due to intensive exploitation but also due to environmental and ecological changes in the spiny lobster habitat. High demand and reduced supply significantly increased prices paid for lobster and have promoted further overcapitalization. Industries and governments are concerned about the existing conditions that may generate missed management opportunities.

Management of the resource is unilaterally attempted in most countries with regulations on minimum size, spawning season closures, and no-take of ripe (berried) females. Control of fishing capacities and landings are rare, and an overriding region-wide lack of enforcement and illegal fishing prevent an orderly utilization of the resource. In this work we briefly describe the main issues concerning the sustainability of Caribbean spiny lobster stocks, including their general biological characteristics that frame fisheries management and the core issues of fishery exploitation.

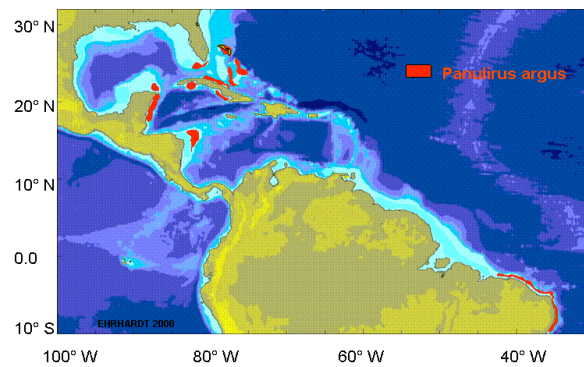


Figure 1. Geographical distribution of the main commercial spiny lobster fisheries in the Western Central Atlantic Ocean.

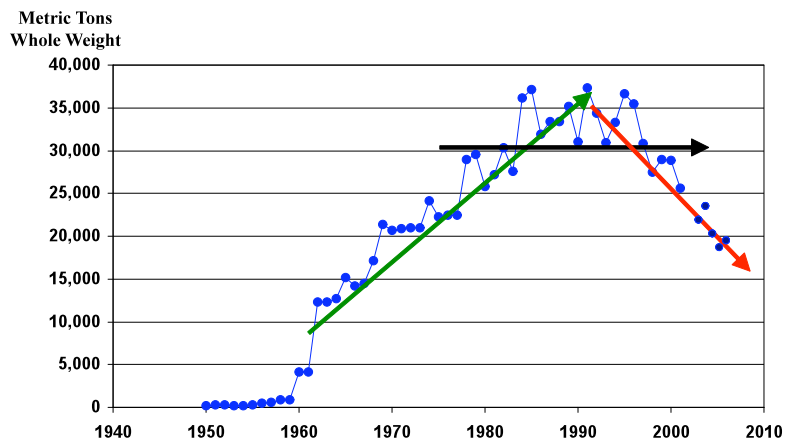


Figure 2. Total Caribbean wide (including Brazil) landings of Caribbean spiny lobster.

### Population dynamic considerations

A significant issue regarding implementation of spiny lobster fishery management policies is the difficulty of defining units of stock due to the protracted planktonic lifespan of the larvae, which disperse in the open ocean before settling in a suitable juvenile habitat. Estimates of pelagic larval duration (PLD) for *P. argus*, extrapolated from modal progressions of phyllosomal stages from plankton samples, range from 6 - 12 months (Lewis, 1951; Sims and Ingle, 1966; Farmer et al., 1989). Only recently has this species been reared in captivity from egg through all its larval stages to the benthic juvenile stage with an observed PLD of 140 - 198 days (mean = 174 days; Matsuda et al. 2007). Given the strong ocean currents dominating the general environment where these larvae are found, it is plausible that they may colonize regions downstream -- thus the Pan-Caribbean theory of spiny lobster population structure (Lyons 1980). This theory is supported by genetic studies showing a lack of geographical differentiation in *P. argus* stocks among Caribbean nations (Silberman, et al. 1994.a), an absence of seasonal variation in the genetic structure of postlarvae arriving at presumed “down stream areas” like the Florida Keys (Silberman, et al. 1994.b), and occasional intrusions of genetically distinct Brazilian *P. argus* postlarvae into Florida (Sarver, et al. 1999). Biophysical modeling of *P. argus* larval dispersal suggest that regional hydrodynamics can have a large impact on the degree to which local populations are self-recruiting or serve as sources of larvae for other regions (Lipcius et al 1997; Stockhausen and Lipcius 2001). A recent set of simulations of *P. argus* dispersal from 13 spawning sites in the Caribbean (Butler et al. 2008a) predicts that the majority of larvae released in the Caribbean may only disperse about 200km because of the strong effects of larval vertical migration on dispersal. However, other larvae in those simulations were advected thousands of

kilometers from their natal source, the difference being that dispersal is also strongly affected by local oceanographic conditions. Although some *P. argus* fisheries located in strongly retentive oceanographic environments probably experience significant self-recruitment, there is likely a high degree of larval connectivity in the Caribbean. As more detailed and reliable estimates of larval dispersal come available, management of *P. argus* stocks should take into account the degree of self-recruitment likely for particular management units, but clearly management actions in one country may have consequences on other regional fisheries. Similarly, significant ecological shifts in some local spiny lobster habitats may be reflected on fisheries in other regions.

The Caribbean spiny lobster larvae are dispersed in the prevailing ocean currents but can be retained in offshore gyres that are persistent enough to constrain their long-lived larvae (Fig. 3). The latter are conspicuous in the Gulf of Honduras off Costa Rica-Panama, off South of Cuba and North of the Bahamas. Gyres and counter currents represent important physical mechanisms for local larval retention and combined with larval behavior (e.g., diel and ontogenetic vertical migration can significantly influence recruitment to local stocks (reviewed in Pineda et al. 2007), contributing to some of the most productive fisheries in the Caribbean (Fig. 3).

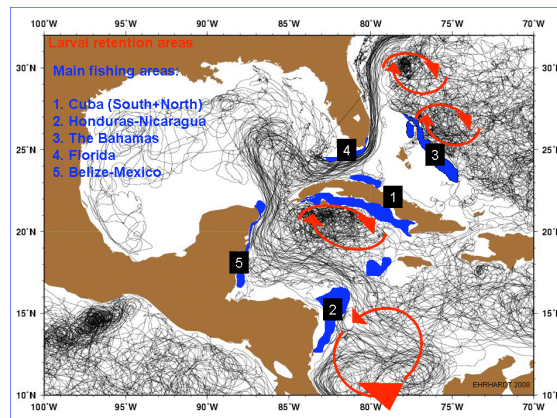


Figure 3. Ocean currents expressed from satellite oceanographic buoys, areas of major larval retention, and main fisheries in the Caribbean region.

Landings mostly correspond to fluctuations in recruitment because they consist primarily of new recruits (Fig. 4) (Cruz et al. 1995; Ehrhardt 2005a and 2007; Puga et al. 2008). Therefore, the dynamics of recruitment mechanisms and the resulting recruitment abundance play an overriding role on the outcome of local spiny lobster fisheries. Recruitment dynamic studies in Cuba (Cruz et al. 2001; Puga and de León 2003; Puga, et al. 2005, 2006, 2008), Florida (Ehrhardt and Fitchett, Submitted) and Nicaragua-Honduras (Ehrhardt 2005a) demonstrate the varying levels of complexity of the processes that control annual production.

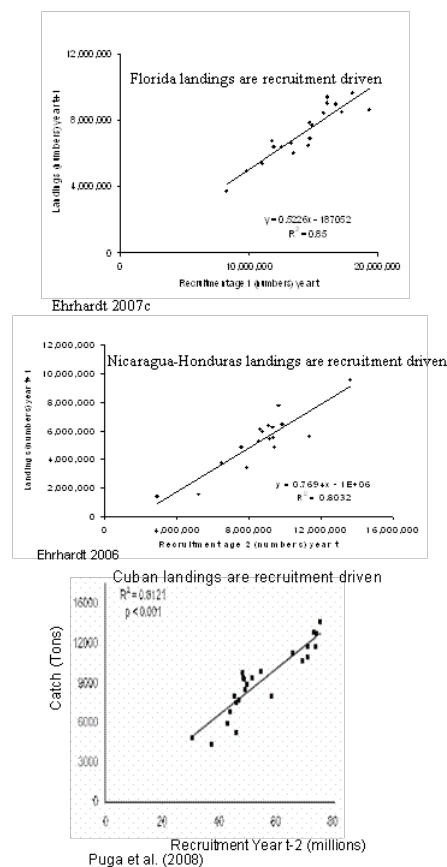


Figure 4. Recruitment driven landings in main Caribbean fisheries.

However, along with postlarval supply sufficient nursery habitat is crucial for successful postlarval settlement and the growth and survival of juveniles that recruit to fisheries (reviewed in Butler et al. 2006). Those regions with the greatest *P. argus* fishery production in the Caribbean are those with the large shallow coastal zones with habitat suitable for nurturing juvenile lobsters. Indeed, local recruitment is not necessarily greatest in areas with the highest concentrations of arriving postlarvae (Herrnkind and Butler 1994; Lipcius et al. 1997), indeed the potential for habitat limitation of *P. argus* recruitment has been experimentally demonstrated in the Bahamas (Lipcius et al. 1997), Florida (Butler and Herrnkind 1992, 1997), and Mexico (Eggleston et al. 1990; Sosa-Cordero et al. 1998; Briones-Fourzan et al. 2001). This is compelling evidence of the importance of nursery habitat for fishery production. The protection of shallow-water nursery habitats for Caribbean spiny lobster should be of major importance to managers seeking to sustain viable fisheries. Settling *P. argus* postlarvae are attracted to the chemical and physical cues produced by red macroalgae and appear to also use pressure cues to select shallow water nursery habitats (Herrnkind and Butler 1986; Butler and Herrnkind 1991; Butler et al. 1997; Goldstein and Butler in review). Macroalgal rich hard-bottom and, secondarily, seagrass are the species preferred settlement habitats but areas with ample crevice shelters are crucial for high survival of later stage benthic juveniles (Marx and Herrnkind 1985; Herrnkind and Butler 1986; Eggleston et al. 1990; Acosta and Butler 1997; Herrnkind et al. 1997; Behringer et al. in press, Bertelsen et al. in press).

Ecological studies carried out on spiny lobster habitat in Cuba recognize several fundamental environmental conditions as negatively impacting juvenile recruitment habitat including: 1) decreased amounts of natural and anthropogenic induced nutrients with the

advent of dam constructions interrupting the natural runoff of nutrient rich fresh water to the spiny lobster habitat (Fig. 5; Puga et al. 2008), 2) increased salinity in juvenile habitats affecting larvae and prey species, 3) incidence of major and more frequent hurricanes impacting habitat structure, and 4) significant coastal zone development including highways that impacted inshore-offshore water exchange. Therefore, the effects of environmental conditions on recruitment are independent of fishery exploitation impacting the adult stock two to three years later (Fig. 6). Experimental studies in Florida confirm the negative effects of siltation (Marx and Herrnkind 1985b; Herrnkind and Butler 1986; Herrnkind et al. 1997), extreme salinity (Field and Butler 1994), and the loss of physical structure (Herrnkind and Butler 1986; Butler and Herrnkind 1997) on postlarval and juvenile lobster survival.

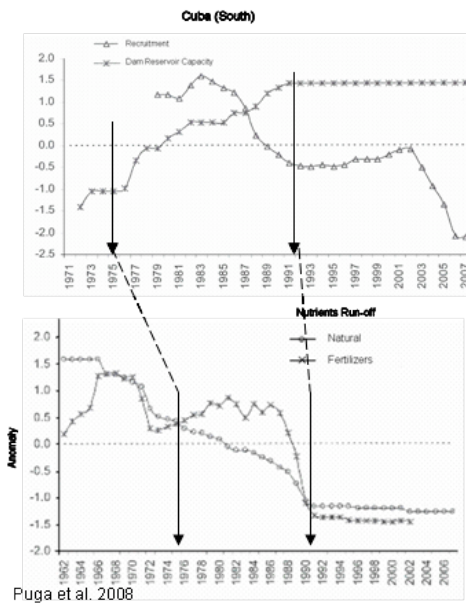


Figure 5. Effects of dam construction and natural nutrient depletion in coastal regions and recruitment trend. Also, significant decrease of fertilizer use impacting anthropogenic induced nutrients to coastal areas (from Puga et al 2008).

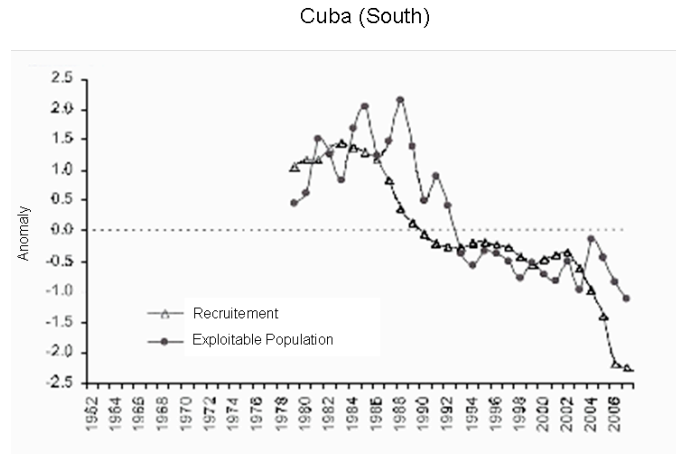
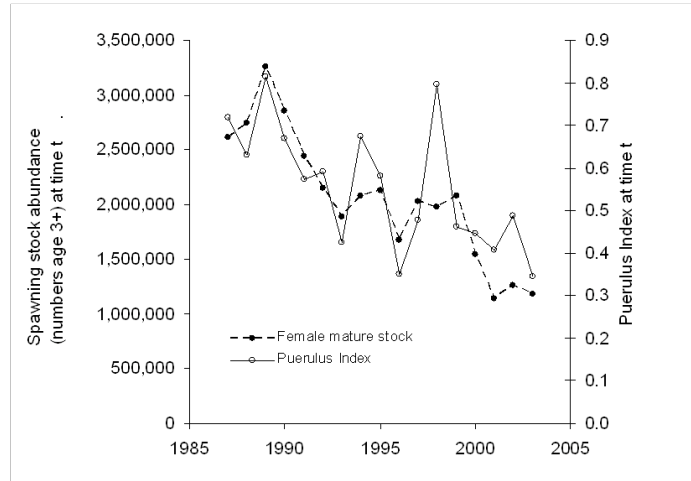


Figure 6. Significant decreasing trend in recruitment antecedes in 3 years the drop in exploitable population (Puga et al. 2008).

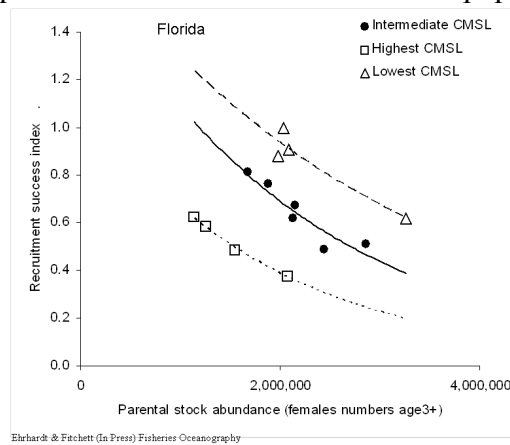
In Florida, the effect of decreasing parent stock on trends in postlarval recruitment is pronounced both in the slopes as well as the variances (Fig. 7), which may imply strongly linked processes (Ehrhardt and Fitchett Submitted). Such decreasing trends are identified with very high exploitation rates exerted on the parent stock as fishing mortality rates are at least twice the magnitude of the natural mortality rate in this fishery (Ehrhardt 2007). However, the most significant feature with this stock is the shift in recruitment success as a function of parent stock density dependent effects (Fig 8), which was found to be correlated with Caribbean mean sea level shifts (Ehrhardt and Fitchett Submitted). A strikingly similar situation was found for the stock in the Nicaragua-Honduras raise (Ehrhardt 2006)(Fig. 9). These conditions are indicative of a shift to lower recruitment success among the most vulnerable early benthic stage postlarvae or juveniles of *P. argus*; therefore, potentially related to physical changes in the suitability of nursery habitat or perhaps disease. It is interesting to note that such effects are more negative during the early 2000's than in the 1990's. These negative trends in Florida are possibly linked to the dramatic loss and slow recovery of sponge shelter for juvenile lobsters over large portions of the nursery (Butler et

al. 1995, Herrnkind et al. 1997, Butler et al. 2005) or perhaps the emergence of a pathogenic disease infecting juvenile lobsters that was first reported in Florida in 1999 (Shields and Behringer 2004).



Ehrhardt & Fitchett (In Press) Fisheries Oceanography

Figure 7. Parent stock-post larval recruitment in the Florida population.



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Figure 8. Density dependence of recruitment success on parental stock abundance for *P. argus* in Florida and the effects of Caribbean Mean Sea Level (CMSL).

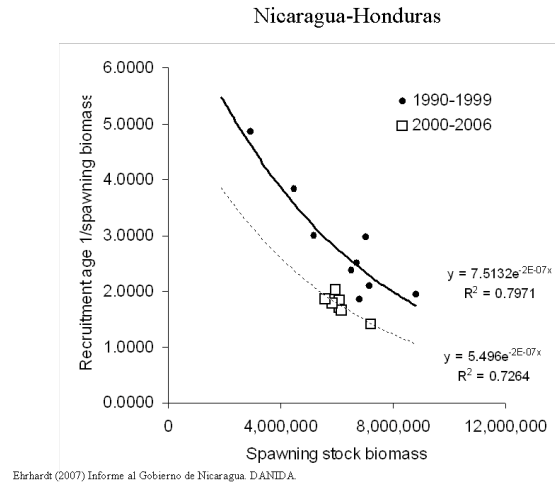


Figure 9. Density dependence of recruitment success on parental stock abundance for *P. argus* in Nicaragua and the effects of Caribbean Mean Sea Level (CMSL).

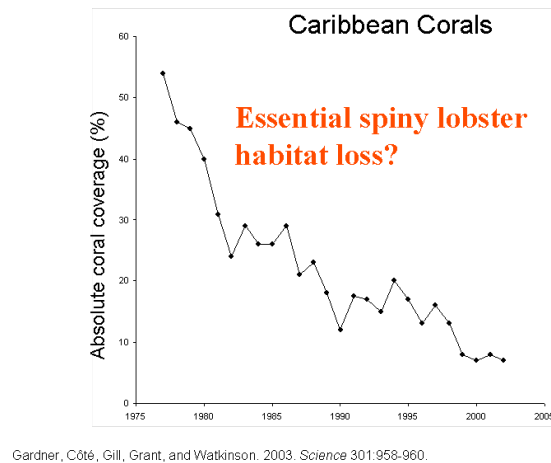


Figure 10. Decreasing trend in the percent of absolute coral coverage in the Caribbean region, observing that the coral bleaching of 1998 had a significant impact on the trend.

Discovery and research on a pathogenic and lethal viral disease (PaV1) that infects primarily juvenile *P. argus* suggests that the disease may be widespread in the Caribbean and at high local prevalence in some areas (Li et al. 2008; Butler et al. 2008b; Behringer et al. 2008, Lozano-Alvarez et al. 2008). These authors estimate that in Florida and Mexico at least 25% of the benthic juveniles die from the disease per annum, which is equivalent to a natural mortality rate of 1.39 – a mortality that is four times

higher than the natural mortality rate assumed for the recruited age classes. Transmission of the virus can be by several mechanisms (contact, ingestion, and to a more limited extent waterborne), but lobster avoidance behavior appears to limit the local spread of the virus in nature (Behringer et al. 1986, Butler et al. 2008). Early benthic juvenile susceptibility to infection may increase at higher temperatures, but not so for larger juveniles or adults whose susceptibility to disease also does not appear to be associated with changes in salinity or individual nutritional condition. There is no obvious management mechanism that might thwart the further spread of this disease but it will be important to link these episodic events to populations and assess their impacts on production.

Another important consideration regarding decreasing trends in postlarval recruitment is the close association of the coral reef habitat to spiny lobster population dynamics. There has been considerable loss of critical coral habitat (Fig. 10) throughout the Caribbean region since the 1980's, particularly after the significant coral bleaching events of 1998 and 2005. It is not known, however, if there are functional links between those events and the health of the lobster spawning stock that depends in part on the coral reef habitat for food and shelter.

### **Fishery considerations**

Landings from each of the main spiny lobster fisheries in the Caribbean decreased consistently from the mid-1990's to the mid-2000's (Fig. 11). Most conspicuous are declines in North Cuba (75%), South Cuba (45%) and Florida (50%), whereas landings from the Nicaragua-Honduras rise are the least affected with only an 18% reduction and

The Bahamas with a decline of 28%. Historically, and in decreasing order, Cuba, The Bahamas, Nicaragua-Honduras and Brazil have been the most important *P. argus* producers (Fig. 12). This order is changing rapidly as Nicaragua-Honduras and The Bahamas followed by Brazil are becoming the principal producers. While natural and anthropogenic effects on spiny lobster habitat, ecology, and population dynamics may be playing a role in this decline so too may be fishing harvests, thus sustainability of the fisheries through reasonable management is still statutory.

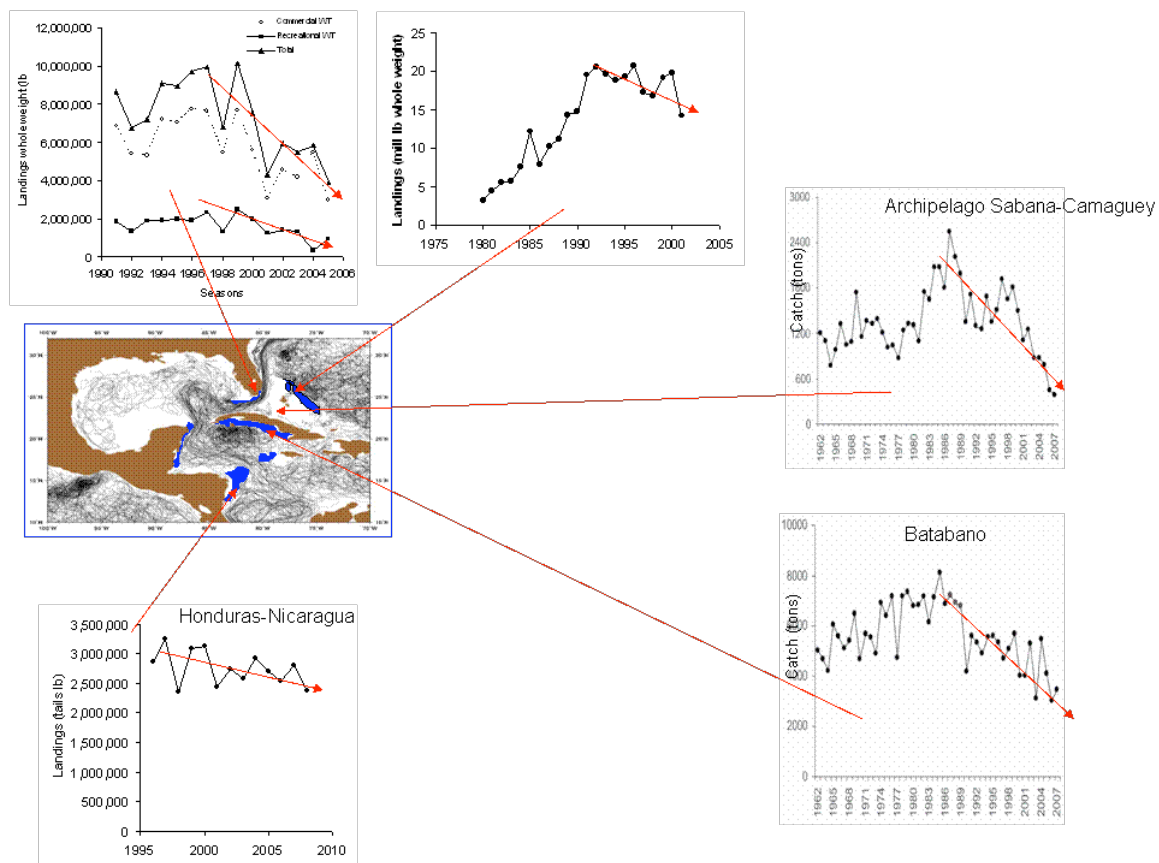


Figure 11. Landing trends according to countries and localities in the Western Caribbean.

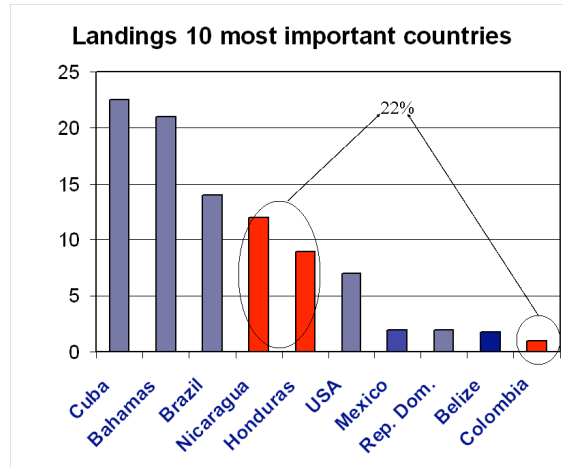


Figure 12. Percentage contribution to total landings by main spiny lobster producing countries until the early 2000's.

One issue facing fisheries management is the open, unregulated character of most fisheries excepting Cuba and Florida. In Cuba, centrally planned fishing operations are based on a projected and sustainable strategic biological catch and effort quota used to control fishing capacity. Florida has a number of well-enforced size and effort regulations in place, including a limit on the number of traps used in the fishery and a trap reduction program that reduced the number of traps in the fishery over the past decade (reviewed in Phillips and Melville-Smith 2006). Until 2007, Nicaragua had a unique biologically acceptable annual catch that was abolished in favor of open access competition. Research on the socio-economic conditions of the spiny lobster fisheries in Nicaragua (Ehrhardt 2006) and ongoing research in Honduras (Ehrhardt per. comm.) show that over 600,000 traps and more than 24,000 compressed air tanks are used in the Nicaragua-Honduras region by 215 trap vessels and 86 dive vessels. In Cuba, the number of vessels was reduced from 310 in 1980-1989 to 198 in 2007 with a reduction from 45,161 to 21,574 days fishing. In the mean time, the closed season was increased

from 90 days to 150 during the same period. In spite of these drastic fishing capacity reductions, landings were not reverted. In Florida, close to 1 million traps were operated until 1992 and these were reduced to about 50% by 1996 through a planned trap reduction that resulted in an attrition of fishers, a significant increase in the efficiency of traps (Fig. 13) and less capital at risk. In spite of this management action, the Florida fishery has not reverted the continued decline in landings. In The Bahamas, there are 700,000 to 800,000 artificial spiny lobster refuges (i.e., condominiums or casitas) in operation that are never retrieved from the fishing grounds and are replaced at the rate of about 20% per year. These are deployed in shallow habitats where they attract many juveniles and where regulations concerning minimum sizes are not respected, controlled, or monitored. The environmental impact of “casita-like” devices has not been assessed in The Bahamas but their effect on nursery habitat and on the survival and growth of juvenile lobsters should be a matter of serious concern in that and other fisheries. Generally, fishing effort in spiny lobster fisheries is negatively correlated to catchability (hence efficiency) because of competing gear factors (Fig. 14); therefore, fishing capacity controls should be an important element in fishery management strategies contributing to less environmental damage and increase economic productivity.

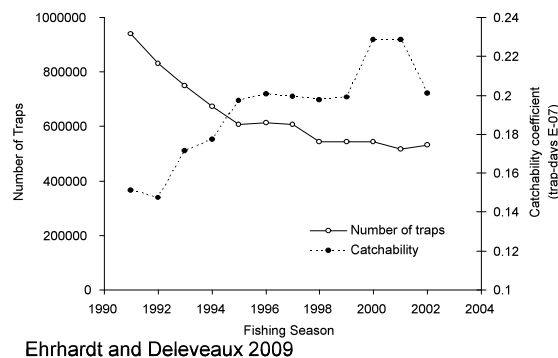


Figure 13. Increased trap efficiency with reduction in number of traps deployed (Florida).

Another significant issue that many trap fisheries face is the cryptic mortality exerted by not retrieving fishing gear (traps) during the closed fishing season. This cryptic mortality by ghost gear may be very large and its effect on stock productivity and impact on reproductive potential of the stocks could be large. Ehrhardt (2006) analyzed the catch rates of trap and diving fleets operating over the same stock but in gear-segregated fishing areas of Nicaragua. Since the implementation of closed season regulations in 2002, catch rates were much higher in the diving operation areas than in the trap operation areas, which is a consequence of the ghost trap mortality (Fig. 15). The situation is more dramatic when comparison of seasonal statistics by fleet are made (Fig. 16). Retrieving the gear at the end of the fishing season has a significant operation cost because of the large number of traps used per vessel (up to 6000 traps/vessel) requires many trips to far away grounds; however, reduced production is an obvious result of not investing in retrieving the gear. Additionally, more studies assessing the ecological impact of trap “debris” left in critical spiny lobster habitat are needed to evaluate this potential threat to the environment and future fishery production.

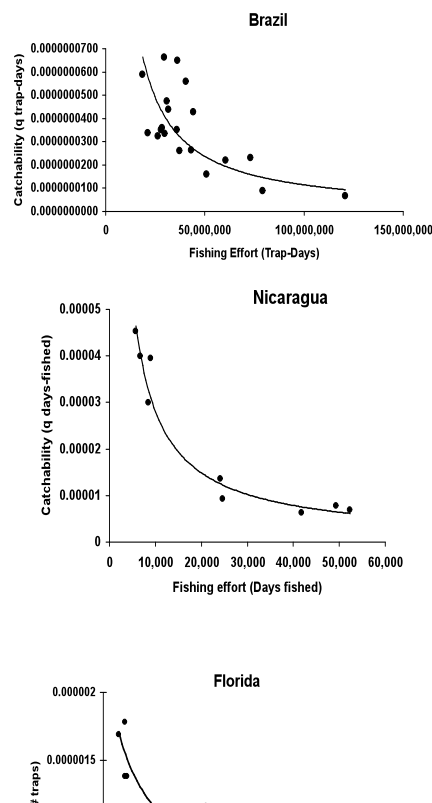


Figure 14. Catchability per trap as a function of total fishing capacity or fishing effort.

The rampant violation of minimum size regulations is undoubtedly one of the most serious issues undermining the sustainable management of *P. argus* stocks in the Caribbean. The countries in the region recognize a 5 ounce tail weight as a minimum size reference; however, landings include all spiny lobsters caught in traps or by divers or even with gillnets (i.e., Brazil). Only in Cuba and Florida do strict regulations and consistent enforcement control such practices. In Florida, however, between 100,000 and 300,000 juvenile spiny lobsters are used seasonally as attractants in traps, and although this practice makes traps significantly more efficient, the biological impact on future spawning potential fecundity and biomass production is estimated to be very large (Lyons and Kennedy 1981; Hunt and Lyons 1986). In the Honduras fishery, about 60% of the landings in weight are illegal size spiny lobsters while in Nicaragua the figure is about 30% (Ehrhardt 2005a). The fishing mortality at age 1 lobsters in the later fishery has increased significantly as a function of fishing effort and the practice of retaining all lobsters that are caught (Fig. 17). The waste in potential reproductive capability by this practice is observed in Figure 18. Successful management needs successful enforcement and illegal size lobsters are trans-shipped to international markets, usually via third party

countries with no fishery regulations regarding the Caribbean spiny lobster. Also, some countries have developed sophisticated markets (e.g., Chinese restaurants) to dispose the very large quantities of illegal size lobsters landed throughout the region. These events are probably responsible for the largest fraction of the depletion observed in spiny lobster stock exploited with no controls, regulations, or enforcement. A positive step forward in this regard is legislation just enacted in 2009 in the United States that bans all importation of spiny lobster that does not meet current minimum size (3 inch carapace length or 5.5 inch tail length) or weight (5 ounces tail weight) regulations in the United States.

A related issue is the preservation or building of lobster spawning stocks via the protection of large individuals. The exponential relationship between female lobster size and egg production is well established for *P. argus*, as it is for all spiny lobsters (reviewed in MacDiarmid and Sainte-Marie 2006). In addition, there is evidence for *P. argus* (MacDiarmid and Butler 1999) among others species of lobster (see MacDiarmid and Sainte-Marie 2006) that male size may also affect reproductive success via sperm limitation. Thus, there is good reason for some degree of protection for large male and female lobsters, which together contribute far greater to egg production than smaller individuals (Bertelsen and Matthews 2001).

The creation of no-take marine protected areas (MPAs) that exclude fishing in areas where lobsters spawn are one management action that leads to demonstrable increases in lobster size and abundance within MPAs (reviewed by Butler et al. 2006), including those inhabited by *P. argus* (Bertelesen and Matthews 2001; Cox and Hunt 2005). As with all management measures, the effectiveness of MPAs in boosting spawning stock potential depends on enforcement and the fraction of the stock that is

ultimately protected by regulation. There is often considerable resistance by the fishing industry to expansion of the size or number of MPAs, so increasing spawning stocks remains a challenge for fishery managers. One approach proposed by Steneck et al. (in press) is to expand the spawning stock “footprint” of small, scattered MPAs by linking the benefits of no-take MPAs with those attained by implementing maximum size limits throughout the rest of the fishery. In this way, lobsters that attain a large size within MPAs but venture beyond the MPA boundaries remain protected. Over time, the abundance of large lobsters would build up not only within MPAs but also within the fishable population, thereby significantly boosting spawning stocks. Such measures may be more acceptable to the fishing community than others, because the fishermen need not relinquish any of their current catch – in today’s fully – to over-exploited *P. argus* fisheries (FAO 2004) they now catch very few large lobsters anyway. However, before implementation more detailed simulations to explore optimal MPA coverage and lobster maximum sizes are needed.

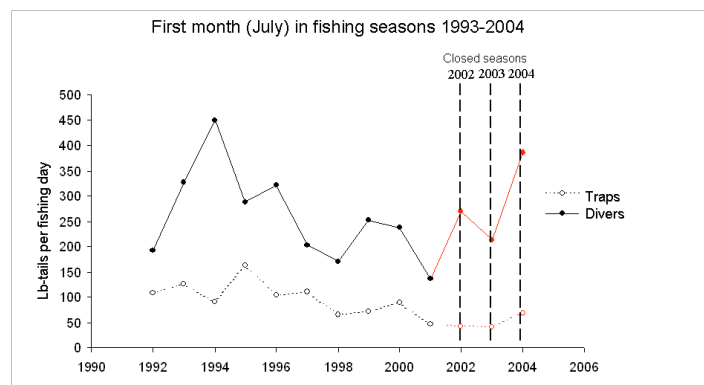


Figure 15. Effects of closed seasons and non-retrieval of traps on the catch rates of trap fisheries relative to diving fisheries in areas not affected by ghost gear.

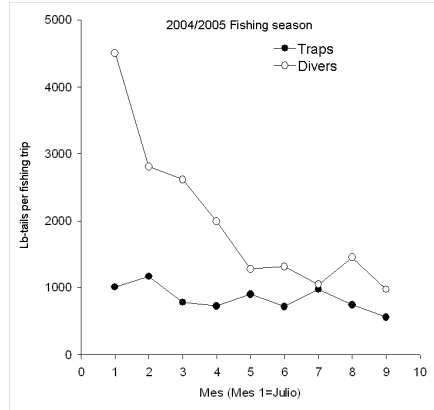


Figure 16. Effects seasonal non-retrieval of traps on the catch rates of trap fisheries relative to diving fisheries in areas not affected by ghost gear.

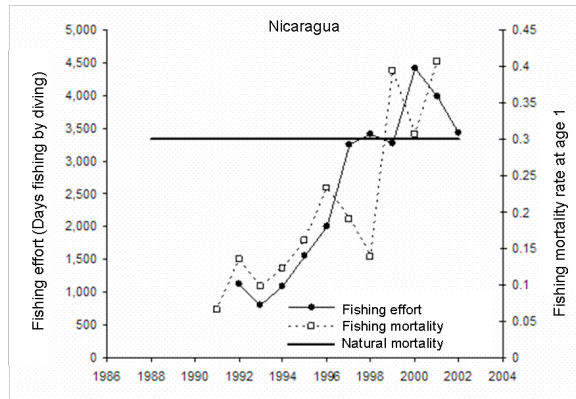


Figure 17. Fishing mortality trend of juvenile lobsters and fishing effort in the Nicaragua fishery.

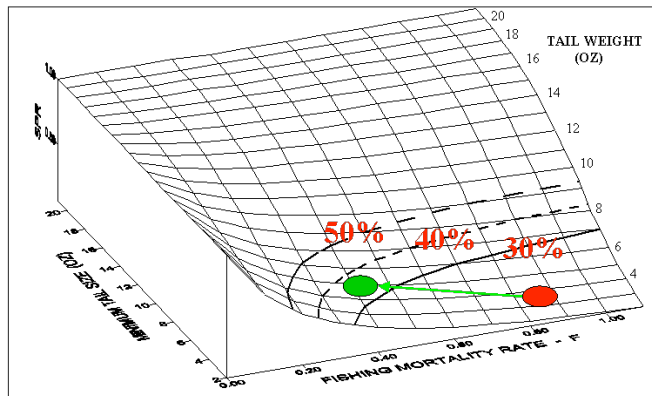


Figure 18. Spawning potential ratio of spiny lobsters under different minimum tail weight size and fishing mortality. Gains in this ratio by increasing minimum size indicated by the dots and their trajectories.

## Conclusions

1. Most fisheries are recruitment driven; therefore, understanding recruitment mechanisms as well as the environmental and ecological effects on recruitment dynamics are paramount to the objectives of ecosystem based fishery management.
2. Environmental and ecological effects on *P. argus* stocks are evident in the Cuba and Florida fisheries. In spite of strict fishery regulations, low production has not been averted. Loss of critical spiny lobster habitat in the region are apparent and perhaps unavoidable, but assessments of long range impacts must be done to correctly dimension sustainability. Without a proper understanding of the environmental and ecological features that affect recruitment and how those conditions are likely to change in the coming years, it will be impossible to implement sustainable spiny lobster fishery management actions.
3. With few exemptions (i.e., Cuba and Florida) enforcement of spiny lobster fishery regulations is absent or not effective. No attempts to manage these valuable fisheries will succeed in the absence of adequate enforcement.
4. Illegal harvest of juvenile spiny lobsters is rampant in most countries and an open market for these products has flourished in the region and in many countries that import *P. argus*. Enforcement of minimum size regulations presents a unique opportunity for successful Caribbean wide management of the resource.
5. Excess of fishing capacity is much larger than is needed in most countries, with the possible exception of Cuba and Florida where regulations maintain effort-controlled fisheries. Fishing capacity reduction should be a fundamental initiative in an ecosystem approach to spiny lobster management in the Caribbean.

6. Related to the over-capitalization of fisheries is the cryptic mortality exerted by lost gear (i.e., “ghost gear”), especially during the off season, which is a problem that remains largely unaddressed in most Caribbean nations.
7. Virus infections of mostly juveniles are a major source of mortality that needs to be assessed relative to stock production and reproductive potential under present exploitation schemes. This represents one of the most challenging scientific issues regarding ecosystem-based management.
8. In the face of so many potentially negative and, at least in the short term, unmanageable impacts on Caribbean lobster stocks (e.g., pollution, habitat loss, climate change, disease), protection and even expansion of spawning stocks is the most beneficial management action available for safeguarding the region’s valuable lobster fisheries. Traditional fishery management actions (e.g., minimum size limits, protection of berried females, seasonal closure of fishing during the breeding season) as well as new ecosystem-based approaches (e.g., no-take MPAs combined with maximum size limits throughout the fishery) are needed to help ensure the long-term sustainability of Caribbean spiny lobster stocks.

## References

- Acosta, C.A. and M. J. Butler IV. 1997. The role of mangrove habitat as nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. *Marine and Freshwater Research* 48:721-728
- Behringer, D.C., M. J. Butler IV, W. F. Herrnkind, J. H. Hunt, C. A. Acosta, and W. C. Sharp. Is seagrass an important nursery habitat for the Caribbean spiny lobster, *Panulirus argus*, in Florida? Submitted to *New Zealand Journal of Marine and Freshwater Research*
- Behringer, D.C. Jr., M.J. Butler IV, and Jeffery Shields. 2006. Avoidance of disease in social lobsters. *Nature* 441: 421
- Behringer, D.B., M.J. Butler IV, and J.D. Shields. 2008. Effect of PaV1 infection on Caribbean spiny lobster (*Panulirus argus*) movement, condition, and survival. *Journal of Experimental Marine Biology and Ecology* 359: 26-33

- Bertelsen, R.D., M. J. Butler IV, W. F. Herrnkind, and J. H. Hunt. In press. Regional Characterization of Hard-bottom Nursery Habitat for Juvenile Caribbean Spiny Lobster Using Rapid Assessment Techniques. *New Zealand Journal of Marine and Freshwater Research*.
- Bertelsen R.D. and T.R. Mathews. 2001. Fecundity dynamics of female spiny lobster (*Panulirus argus*) in a south Florida fishery and Dry Tortugas National Park lobster sanctuary. *Marine Freshwater Research* 52:1559-1565
- Briones-Fourzán, P., Lozano-Alvarez, E. 2001. Effects of artificial shelters (casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. *Marine Ecology Progress Series*, 221, 221–232.
- Butler, M.J., IV and W.F. Herrnkind. 1991. Effect of benthic microhabitat cues on the metamorphosis of postlarvae of the spiny lobster *Panulirus argus*. *Journal of Crustacean Biology* 11:23-28.
- Butler, M.J., IV and W.F. Herrnkind. 1992. Spiny lobster recruitment in south Florida: field experiments and management implications. *Proceedings of the Gulf and Caribbean Fisheries Institute* 41: 508-515.
- Butler, M.J. IV, J.H. Hunt, W.F. Herrnkind, T. Matthews, M. Childress, R. Bertelsen, W. Sharp, J.M. Field, and H. Marshall. 1995. Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobster *Panulirus argus*. *Marine Ecology Progress Series* 129: 119-125
- Butler, M.J. IV, W.F. Herrnkind, and J. H. Hunt. 1997. Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. *Bulletin of Marine Science* 61: 3-19
- Butler, M.J. IV and W.F. Herrnkind. 1997. A test of recruitment limitation and the potential or artificial enhancement of spiny lobster populations in Florida. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 452-463
- Butler, M. J. IV. 2005. Benthic Fisheries Ecology in a Changing Environment: Unraveling Process to Achieve Prediction. *Aquatic Living Resources* 18: 301-311
- Butler, M.J. IV, T. Dolan, J. H. Hunt, W. F. Herrnkind, and K. Rose. 2005. Recruitment in degraded marine habitats: a spatially-explicit, individual-based model for spiny lobster. *Ecological Applications* 15: 902-918
- Butler, M.J. IV, R.S. Steneck, and W.F. Herrnkind. Juvenile and adult ecology, pp. 263-309 in Lobsters: Biology, Management, Aquaculture, and Fisheries, B. Phillips (ed), Blackwell Publishing, Oxford.
- Butler, M.J. IV, R. Cowen, C. Paris, K. Matsuda, and J. Goldstein. 2008a. Long PLDs, Larval Behavior, and Connectivity in Spiny Lobster. International **Coral Reef Symposium**.
- Butler, M.J. IV, D.C. Behringer, J.D. Shields. 2008b. Transmission of *Panulirus argus* virus 1 (PaV1) and its effect on the survival of juvenile Caribbean spiny lobster. *Diseases of Aquatic Organisms* 79: 173-182.
- Cruz, R., M.E. Leon, and R. Puga. 1995. Prediction of commercial catches of the spiny lobster *Panulirus argus* in the Gulf of Batabano, Cuba. *Crustaceana* 68: 238-244.
- Cruz, R., E. Diaz, M Baez, and R. Adriano. 2001. Variability in recruitment of multiple life stages of the Caribbean spiny lobster, *Panulirus argus*, in the Gulf of Batabano, Cuba. *Marine and Freshwater Research* 52: 1263-1271.

- Ehrhardt, N.M. 2005a. Assessment of the economic impact of illegal undersized landings of spiny lobsters, *Panulirus argus*, in the Nicaraguan fishery. Danish Agency for International Development (DANIDA) Final Report to the Ministry of Development, Industry, and Commerce. Government of Nicaragua. 38 p.
- Ehrhardt, N. 2005b. Population dynamic characteristics and sustainability mechanisms in key Western Central Atlantic spiny lobster, *Panulirus argus*, fisheries. *Bull. Mar. Sci.* 76:501–526.
- Ehrhardt, N.M. 2006. Integrated study of the spiny lobster fishery in the Atlantic coast of Nicaragua with special emphasis on the issue of diving. Danish Agency for International Development (DANIDA) Final Report to the Ministry of Development, Industry, and Commerce. Government of Nicaragua. Managua, Nicaragua. April 2006. 94p.
- Ehrhardt, N. 2007. Assessment of seasonal exploitation of the spiny lobster, *Panulirus argus*, in Florida. Final Report. MARFIN/NOAA Project NA05NMF4331081: Meta population stock assessment methods incorporating climatic and ecosystem effects for the Florida spiny lobster fishery. 65p.
- Ehrhardt, N. 2007. Brazil stock assessment. Report of the Third FAO/CFRAMP /WECAFC Regional Workshops on the Assessment of the Caribbean Spiny Lobster (*Panulirus argus*). Merida, Yucatan, Mexico. September 2006.
- Ehrhardt, N., and V. Deleveaux. In Press. Management of Fishing Capacity in a spiny lobster (*Panulirus argus*) Trap Fishery: Analysis of Trap Performance under the Florida Spiny Lobster Trap Certificate Program. *Fishery Bulletin*. March 2009.
- Ehrhardt, N., and M. Fitchett. Submitted. Dependence of recruitment on parent stock of the spiny lobster, *Panulirus argus*, in Florida. *Fisheries Oceanography*.
- Eggleston, D., Lipcius, R., Coba-Centina, L., & Miller, D. (1990) Shelter scaling regulates survival of juvenile spiny lobster, *Panulirus argus*. *Marine Ecology Progress Series*, 62, 79–88.
- FAO 2004. The state of world fisheries and aquaculture. FAO, Rome 153pp
- Goldstein, J.S. and M.J. Butler IV. In review. Behavioral enhancement of onshore transport by postlarval Caribbean spiny lobster (*Panulirus argus*). *Coral Reefs*
- Herrnkind, W.F. and M.J. Butler IV. 1986. Factors regulating settlement and microhabitat use by juvenile spiny lobsters, *Panulirus argus*. *Marine Ecology Progress Series* 34: 23-30.
- Herrnkind, W.F., M.J. Butler IV, and R.A. Tankersley. 1988. The effects of siltation on the recruitment of spiny lobsters (*Panulirus argus*) in south Florida. *Fisheries Bulletin* 86: 331-338.
- Herrnkind, W.F. and M.J. Butler IV. 1994. Settlement of spiny lobsters, *Panulirus argus* in Florida: pattern without predictability. *Crustaceana* 67: 46-64
- Hunt, J.H. and W.G. Lyons. 1986. Factors affecting growth and maturation of spiny lobsters, *Panulirus argus*, in the Florida Keys. *Canadian Journal Fisheries and Aquatic Science*, 43: 2243-2247.
- Li, C., J. D. Shields, R. E. Ratzlaff, and M. J. Butler IV. 2008. Pathology and hematology of the Caribbean spiny lobster experimentally infected with *Panulirus argus* virus 1 (PaV1). *Virus Research* 132: 104-113
- Lipcius, R. N., W. T. Stockhausen, D. B. Eggleston, L. S. Marshall, Jr., and B. Hickey. 1997. Hydrodynamic decoupling of recruitment, habitat quality and adult abundance

- in the Caribbean spiny lobster: source-sink dynamics? *Marine and Freshwater Research* 48: 807–815.
- Lozano-Alvarez, E., P. Briones-Fourzan, A. Ramirez-Estevez, D. Pacencin-Sanchez, J.P. Huchin-Mian, and R. Rodriguez-Canul. 2008. Prevalence of *Panulirus argus* virus 1 (PaV1) and habitation patterns of healthy and diseased Caribbean spiny lobster in a shelter-limited habitat. *Diseases of Aquatic Organisms* 80: 95-104.
- Lyons W. G. 1980. Possible sources of Florida's spiny lobster population. *Proceedings of the Gulf and Caribbean Fisheries Institute* 33: 253–266.
- Lyons, W.G. and F.S. Kennedy, Jr. 1981. Effects of harvest techniques on sublegal spiny lobsters and on subsequent fishery yield. *Proceedings Gulf and Caribbean Fisheries Institute* 33: 290-300.
- MacDiarmid, A.B. and M. J. Butler IV. 1999. Sperm economy and limitation in spiny lobsters. *Behavioral Ecology and Sociobiology*. 46: 14-24
- MacDiarmid, A.B. and B. Sainte-Marie. 2006. Reproduction pp. 45 – 77 in Lobsters: Biology, Management, Aquaculture, and Fisheries, B. Phillips (ed), Blackwell Publishing, Oxford.
- Marx, J.M. & Herrnkind, W.F. (1985a) Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for juvenile spiny lobsters, *Panulirus argus*. *Bulletin of Marine Science*, **36**, 423–431.
- Matsuda, H., J.S. Goldstein, T. Takenouchi, and M.J. Butler IV. 2008. A description of the complete development of larval Caribbean spiny lobster *Panulirus argus* (LATREILLE, 1804) in culture. *Journal of Crustacean Biology* 28: 306-327.
- Phillips. B.F. and R. Melville-Smith. 2006. *Panulirus* species pp. 359 – 384 in pp. 263-309 in Lobsters: Biology, Management, Aquaculture, and Fisheries, B. Phillips (ed), Blackwell Publishing, Oxford.
- Pineda, J., J.A. Hare, and S. Sponaugle. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20: 22-39
- Puga, R. and de León, M.E., 2003. La pesquería de la langosta en Cuba. In: Report of the Second Workshop on the Management of Caribbean Spiny Lobster Fisheries in the WECAF Area. FAO Fish.Rep.715: 85-91.
- Puga, R., Hernández-Vázquez, S., López-Martínez, J., León, M.E. de,. 2005 . Bioeconomic modelling and risk assessment of the Cuban fishery for spiny lobster *Panulirus argus*. *Fish. Res.* 75(1-3), 149-163.
- Puga, R., M. E. de León, N. Capetillo, R. Piñeiro y O. Morales. 2006. Evaluación de la pesquería de langosta en Cuba. Taller Regional sobre la evaluación y la ordenación de la langosta común del Caribe (*Panulirus argus*). Mérida, México, del 19 al 29 de septiembre de 2006:20 pp.
- Puga, R., R. Piñeiro, N. Capetillo, M.E. de León and L.S. Cobas. 2008. Estado de la pesquería de langosta espinosa (*P. argus*) y su relación con factores ambientales y antrópicos en Cuba. Informe de Caso de Estudio del Programa: *PNCT: Los cambios Globales y la Evolución del Medio Ambiente Cubano*. Proyecto: *Bases Oceanográficas para el estudio de las afectaciones del cambio global en la biodiversidad marina y costera de Cuba*. Tarea: *Evaluación de las posibles afectaciones del Cambio Climático a la Biodiversidad Marina y Costera de Cuba*. Centro de Investigaciones Pesqueras. Septiembre de 2008. 29p.

- Sarver, S.J., D.W. Freshwater, and P.J. Walsh. 2000. The occurrence of the Brazilian subspecies of the spiny lobster (*Panulirus argus westonii*) in Florida waters. *Fish. Bull. U.S.* 98:870-873.
- Shields, J.D. and D.C. Behringer. 2004. A new pathogenic virus in the Caribbean spiny lobster *Panulirus argus* from the Florida Keys. *Diseases of Aquatic Organisms* 59: 109-118.
- Silberman, J.D., Sarver, S.K. and Walsh, P.J. 1994.a. Mitochondrial DNA variation and population structure in the spiny lobster, *Panulirus argus*. *Mar. Biol.* 120: 601-608.
- Silberman, J.D., Sarver, S.K. and Walsh, P.J. 1994.b. Mitochondrial DNA variation in seasonal cohorts of spiny lobster (*Panulirus argus*) postlarvae. *Molec. Mar. Biol. Biotechnol.* 3: 165-170.
- Sosa-Cordero, E., Arce, A.M., Aguilar-Davila, W. & Ramierz-Gonzalez, A. 1998. Artificial shelters for spiny lobster *Panulirus argus* (Latreille): an evaluation of occupancy in different benthic habitats. *Journal of Experimental Marine Biology and Ecology*, 229, 1–18.
- Stockhausen, W.T. and R.N. Lipcius. 2001. Single large or several small marine reserves for the Caribbean spiny lobster? *Marine and Freshwater Research* 52: 1605-1614
- Stockhausen, W.T., Lipcius, R.N. & Hickey, B.H. 2000. Joint effects of larval dispersal, population regulation, marine reserve design, and exploitation on production and recruitment in the Caribbean spiny lobster. *Bulletin of Marine Science*, 66, 957–990.