

The Caribbean Spiny Lobster, *Panulirus argus*,  
Enhancement of the Fishery With Oceanographic Tools and  
Spatial Division of Fishing Grounds Between  
Cooperatives and Sanctuaries

by

Harry W. Branch

An essay of distinction  
submitted in partial fulfillment  
of the requirements for the degree of  
Masters of Environmental Studies  
The Evergreen State College

June 1994

This Essay of Distinction  
for the  
Master of Environmental Studies Degree by

Harry W. Branch

Has been approved for  
The Evergreen State College

by

David J. Milne

David Milne

July 5 '94  
Date

### Abstract

The spiny lobster's life history is a good example of the utilization of geographic space for life cycle closure, a process common among many species of fish. The nature of their planktonic migration holds answers to questions which are critical to *P. argus* management. Other questions concern what can be done to overcome severe limitations in protective juvenile habitat. Cuba has a greater harvest than all the rest of the Caribbean combined because Cuba has constructed an extensive system of artificial structures called "pesqueros" in the juvenile habitat which offer protection from predation for juvenile lobsters. Habitat enhancement programs, such as the development of *pesqueros*, when incorporated into market systems usually involve the division of space. Shared or appropriated management is a recognized option in facilitating the division of space. Japan, Mexico, Belize and the northeastern U.S. have all successfully incorporated cooperatives into systems of co-management.

Despite heavy fishing throughout the Caribbean, the species continues to flourish. *P. argus* may have established *de facto* sanctuaries in hard-to-reach places. If *P. argus* have established successful breeding sanctuaries, they are an unique example of the fruitfulness of the concept.

Determining a species' use of physical space is critical to understanding its population dynamics. Geographic space should be a consideration in all management schemes. In the case of *P. argus*, it would be possible to appropriate the management of certain fishing grounds to cooperatives while encouraging the construction of *pesqueros*. Other areas should be declared breeding population sanctuaries. The two concepts coincide because both involve the division of geographic space.

## Table of Contents

	Page
1. Introduction .....	1
2. The Spiny Lobster and its Environment .....	4
3. The Nature of the Species .....	13
One or Many Populations? .....	13
Absolute Abundance and Variation .....	19
4. Management: Numbers and Space .....	25
The Maximum Sustained Yield Concept .....	25
Predicting the Harvest .....	28
5. Balancing Harvest and Conservation Needs .....	31
Some Basic Tools .....	31
Cooperatives .....	35
Sanctuaries .....	40
6. Conclusion .....	44
Table 1. ....	47
Literature Cited .....	48
Appendix .....	56

1      **The Caribbean Spiny Lobster *Panulirus argus*:  
Enhancement of the Fishery with Oceanographic Tools  
and Spatial Division of Fishing Grounds  
Between Cooperatives and Sanctuaries**

**1. Introduction**

Caribbean spiny lobsters lead eclectic lives in a variety of environments. They begin life as minute planktonic larvae, drifting on undiscerned oceanic currents. After a dramatic metamorphosis from passively drifting plankton to actively swimming nekton, and another metamorphosis to the benthic stage, young spiny lobsters settle and move to the edge of shore. As they mature, they move offshore in several stages and ultimately take up residence in the crannies of coral or rock formations that make up outer reefs.

Spiny lobsters have an extended planktonic larval stage, as long as 22 months. Understanding the reasons for this extended period of planktonic migration is essential to understanding important questions pertinent to their management. What factors determine absolute (potential) abundance? What factors regulate variation in abundance from year to year? Do Caribbean spiny lobsters comprise one large population, or are there numerous local populations? What management tools will guarantee the survival of *P. argus* while supplying

a large, regular harvest?

Management programs aimed at harvesting a maximum sustained yield of lobsters have been implemented throughout the Caribbean. Size limits, bioeconomic recruitment models, and other tools of management, currently aimed at increasing yield, can now be evaluated in light of data on lobster life cycles and indigenous conservation practices for their real effectiveness and their effects on sustainability of the resource.

Spiny lobsters, living in tropical coastal waters world-wide, are under the management of many different national governments, each with its own local considerations and solutions. Events deriving from political, legal, and economic decisions have had detrimental impacts in some jurisdictions. Other countries have developed management schemes that have improved local fisheries and might serve as models for coastal fisheries of other species as well as *P. argus*. Some of the most successful management schemes involve cooperatives directly in development, management, and marketing processes.

There are reasons to suspect that substantial numbers of *P. argus* individuals may be escaping capture by taking up permanent residence in places that are difficult to fish. If such groups exist, they have

established their own sanctuaries. Fish sanctuaries, spaces free of fishing pressure, may be an effective way of protecting populations of fish. Despite heavy fishing throughout the Caribbean, *P. argus* numbers are not depleted. If lobsters have established their own sanctuaries, they are a unique example of the potential success of this concept.

Blending tradition, science, and co-management in the structuring of localized small scale artisanal fisheries such as that of the Caribbean spiny lobster, will update existing management techniques. Support of the division of fishing space among harvesters as a traditional management scheme, and the establishment of additional sanctuaries (which is compatible with the concept of dividing fishing grounds because both involve the division of geographic space) can strengthen the sustainability of lobster fisheries.

## 2. The Spiny Lobster and its Environment

There are numerous species of lobsters, divided between the families Nephropidae (clawed lobsters) and Palinuridae (spiny lobsters). There are similarities and differences between the two families. Clawed lobsters such as the American lobster (*Homarus americanus*) have claws where spiny lobsters have long, pointed spines. Clawed lobsters have a brief, 3 week larval stage while spiny lobsters have an extended larval stage of up to 22 months.

Spiny lobsters hatch as tiny planktonic forms, 1.5 mm long, barely visible to the human eye. During this stage in life (termed the phyllosoma) the lobster is flattened dorso-ventrally, and has long legs and large eyes on the ends of protuberant peduncles. The phyllosoma propels itself amid the marine zooplankton with feather-like setae on the ends of the two anterior limbs. The phyllosoma's movements are primarily vertical, down in the water column during daylight and up in the water column during darkness. Its rate of ascent and descent ranges between 15 and 20 meters per hour. The larvae undergo ten or so distinct morphological changes and many molts, growing to about 35mm (Phillips and Sastry, 1980).

*P. argus* larvae undergo a profound transformation during a single molt to enter the puerulus stage which



physically resembles a juvenile lobster. With the advent of its puerulus stage, the spiny lobster no longer moves as plankton, up and down in the water column to capture favorable currents, but joins the world of nekton -- actively swimming fish. Puerulus stage spiny lobsters are about 35mm long. While swimming, a streamlined profile is maintained by holding the antennae together in front of the body, extending the abdomen, holding the tail straight and retracting the legs. They swim at a rate of about half a meter per second, actively seeking coastal waters.

Spiny lobsters appear to be able to control the timing of their metamorphosis to the puerulus stage, which may occur well off-shore. The metamorphosis from puerulus to juvenile stage may also occur offshore, followed by onshore juvenile migration and habitat selection (Kanciruk, 1980). The ability to regulate the timing of metamorphosis often follows a wide ranging larval stage, a trait which will become important in chapter two (Sinclair, 1988). As a result of this transformation, lobsters move from post-larval puerulus to post-puerulus benthic existence (Herrnkind *et al*, 1994). The earliest benthic, juvenile stage, prefers a depth of less than 3 meters on mangrove roots, pilings, grass beds and grassy undercuts.

Juveniles between one and two years of age usually

live alone, secreted in dense cover. Juveniles older than two years move a short distance offshore to patches of algae (especially *Laurencia*) and other protective habitats where they often live tightly packed in clusters (Herrnkind *et al*, 1994). Nearing maturity they move to slightly deeper seagrass and patch reef habitats and to the fringes of deeper reefs. They move further offshore with the onset of the molt that brings about sexual maturity (Herrnkind and Lipcius, 1989).

Carapace length (CL), a universally accepted way of gauging lobsters, is measured between the rostral horns (supra-orbital spines) and the posterior edge of the cephalothorax (Herrnkind *et al*, 1989). The maximum CL length of *P. argus* is about 190 mm CL, corresponding to an age of 20 years. Fished and unfished populations average 70-90 mm and 100-145 mm CL respectively. In different parts of the Caribbean, the size at which females reach sexual maturity has been reported to be as small as 45 mm CL and as large as 80-90 mm CL. These size differences may reflect genetic variation, or differences in fishing pressure, diet, population density, or water temperature (Kanciruk, 1980).

Habitat for mature *P. argus* is typically rock or coral outcrops, under-cuts and sponge and coral reef structures. Dens are chosen in naturally occurring

crannies. Spiny lobsters prefer a den with a narrow opening that can be easily defended. Dens in inshore environments tend to contain equal numbers of males and females. Dens in oceanic environments sometimes contain single large males and numerous egg bearing females (Herrnkind and Lipcius, 1989). Large, dominant males will normally occupy the most favorable dens. Dominant males have been observed prying females from other dens and forcing them back to their own harems (Kanciruk, 1980).

Spiny lobsters forage at night using chemoreception. The antennules convey distant features, and the tips of the pereopods (dactyls) confer contact details or movements. They forage with a dancing gait, antennae stretched forward and antennules twitching (Kanciruk, 1980).

Palinurid defenses include their spiny exoskeletons and long pointed antennae. Quick tail flapping facilitates a rapid, rearward retreat over 10-50 meters, amid a turbid cloud of sediment if retreating over loose substrata. A lone spiny lobster caught in an open area is, however, easy prey for a variety of species including sharks, skates, snappers, groupers, octopuses, dolphins, and loggerhead turtles. In open areas, a group of threatened lobsters will form a defensive pod formation with all members facing

outward, antennae pointing toward an attack from any direction. The resulting pincushion is an effective defense (Kanciruk, 1980).

Lobsters make sounds characterized as popping, fluttering, and rasping. These sounds, occurring mainly in dens, may be ways of claiming territory, and they may be sonic beacons which lobsters can home in on when, for example, returning to the den after a night of foraging (Gray, 1992; Kanciruk, 1980). Spiny lobsters have been observed co-inhabiting dens with moray eels. The eel, rather than devouring the lobster as it might normally, appears to use the lobster as an attractant for octopi, the eel's preferred meal. The lobster gains protection in return for serving as bait (Kanciruk, 1980).

Each year, large numbers of young Caribbean spiny lobsters embark on an impressive mass exodus to deeper water. Squalls and cool temperatures during fall induce migratory behavior. Lobsters begin by massing near open areas. In response to a particular squall or some other stimulus, they simultaneously move out. Up to 70 individuals form long, compact lines called queues (Herrnkind *et al*, 1973). By forming queues, lobsters substantially reduce their hydrodynamic drag (Kanciruk and Herrnkind, 1978). The line of lobsters travels rapidly, day and night, into deep offshore waters.

Lobsters leading queues in the field can be of any size, age or sex. Leadership of queues frequently changes underway (Kanciruk and Herrnkind, 1978). Lobsters later returning to near-shore waters probably do so in smaller groups.

The reason for this seasonal mass migration is unknown. There are no logical explanations based on feeding or reproductive needs. The lobsters are compelled by their instincts; the sight of a lobster walking past will induce other lobsters to fall in line (Kanciruk and Herrnkind, 1978). One theory is that offshore migration may be an adaptive holdover from the last ice age, when lobsters needed to escape chilling seasonal inversion layers near shore. It may also be that the migration is an evolved mechanism by which the population ritualistically moves to the increased safety of deeper waters.

Male spiny lobsters have been seen apparently tracking the scent of females and courting the females by stroking and caressing them with the forelimbs. *P. cygnus* (Australian Western Rock Lobster) males have been observed confronting females in their shelters, and persistently attempting to withdraw them with their forelimbs. If the male's attempts are persistent enough, the female's resistance will often wane. The male then pulls the female into an upright stance and

mating occurs, a "tangle of legs in a head to head and belly to belly affair (Gray, 1992)."

Sperm is deposited on the female's belly in a protective gel termed the tar spot. Sperm is stored in this manner until eggs emerge from the oviduct through small pores at the base of the third pair of legs. The eggs flow in a steady stream for about an hour while the female sits upright spreading the tail-fan and swimmerets to form a basket that catches and holds the eggs. During this process the female, using the claws on her walking legs, scratches and breaks the protective gel covering the sperm, and (using her swimmerets) fans sperm over the eggs. Almost all eggs are successfully fertilized. The "berried" female carries the fertilized eggs semi-exposed in a brood-chamber on the ventral area of her tail, carefully ventilating and grooming them. The eggs hatch after incubating for a period of from less than a month to more than two months, depending on water temperature. All eggs hatch within a period of several hours. The emerging larvae take about an hour to straighten their legs and eye stalks and then immediately swim toward the surface where they are carried away in currents and begin their extended larval existence (Gray, 1992).

In the deep tropical oceans that *P. argus* larvae inhabit, nutrient levels are often below the level of

detection. Most areas of the world's tropical oceans are oligotrophic; nutrients rather than solar radiation are the limiting factors. Solar radiation typically penetrates to several times the depth it reaches in temperate oceans. The compensation level for tropical phytoplankton is deep. There is a permanent thermocline. Most nutrient salts in tropical oceans lie below 600 to 1000 feet depth. In the Atlantic Ocean nitrate concentrations within 20 degrees latitude of the equator are usually about 1/100th the levels of the least fertile temperate regions. Phosphate levels are even lower, below the limit of detection in many cases (Russell-Hunter, 1970). In the central Atlantic, the euphotic layer is up to 120 meters deep. Herbivores live below this layer during the day and migrate at night to the surface to feed on what algae manage to grow in the clear nutrient-free water. As an example of their low productivity, deep sea fisheries world-wide, comprised primarily of tuna fisheries, supply about 5 million tons of fish annually, whereas the world's upwelling areas could easily yield 100 million tons.

The tropical habitat of the adult spiny lobster is typically also low in phytoplankton and primary production (Herrnkind and Lipcius, 1989). Phytoplankton production in tropical seas remains low rather than cycling through the seasonal succession of blooms and

die-offs characteristic of seas in higher latitudes. There are, as a result, no clearly defined seasonal cycles of zooplankton. In offshore, deep tropical oceans, the lack of seasonal changes creates stable systems in which nitrogen, silicon, and phosphorus are continually re-cycled by planktonic plants and animals. Little is lost to the deep sea floor which largely consists of barren red clay (Cushing, 1975). Areas of nutrient-rich upwelling in the California, Peru, Canary and Benguela currents, do not support major spiny lobster fisheries. Thus nutrient abundance does not appear to be a requirement for spiny lobsters to flourish. However, in some cases such as those noted by Polovina in Hawaii (1989, 1994), spiny lobsters appear to increase in abundance with the introduction of nutrients to their ecosystem.



### 3. The Nature of the Species

Management of *P. argus* hinges upon two crucial questions: Are there local populations within the species, each with its own geographic range? And what factors control their numbers, their maximum potential abundance in the absence of human harvest, and their variations in abundance from season to season?

#### One or Many Populations?

Does the species *P. argus* comprise one large population or numerous local populations? The importance of considering the possible existence of local populations of species is now recognized as critical in fisheries management. Heincke first identified local populations of Atlantic Herring in 1898 (Sinclair, 1988: 10). Management of Herrings as though they consisted of a single population has seriously degraded certain vulnerable local populations. We have persistently managed as though species were single populations, yet among whom local populations sharing a common environment for much of the year have been at the high or low limits of their abundance (Sinclair, 1988: 51).

If, on the other hand, *P. argus* is panmictic, if the species is one large population living throughout the Caribbean and whose larvae migrate through the

North Atlantic gyre, then concerns about the abundance of eggs take on a larger, i.e. Caribbean-wide, scale.

Much of what we know about lobster distribution, abundance, mortality, reproduction, and movements comes from sampling of fisheries, a process that leaves many ecological and behavioral characteristics unknown, particularly those of the spiny lobster's extended larval stage (Ford, 1980). The answer to the question of whether the Caribbean spiny lobster comprises one large or many local populations might come from a detailed investigation of their larval stage.

Spiny lobsters occupy a world wide belt centered in the tropics, between latitudes 45 degrees north and 45 degrees south (Kanciruk, 1980). Migration patterns during the long larval life of spiny lobsters are basically unknown. Larvae of *Panulirus cygnus* have been found 1500 km offshore from their point of origin in Western Australia. Three other species of spiny lobster larvae have been found in the Pacific 1800 to 2000 nautical miles from their probable points of origin (Phillips and Sastry, 1980). Larvae found far from their point of origin aren't necessarily going to find a place to settle and mature, and yet they may.

The question of larval migration is explored in depth by Michael Sinclair in his "member/vagrant" hypothesis (Sinclair, 1988: 71). Sinclair states that

life cycle closure over a geographic space is the reason for most larval migrations. Spatial constraints are important in sexual reproduction in the oceans. Speciation is the result of life cycle selection that enables finding and selecting a sex partner. At the time of breeding, those individuals that find each other, the "members" of the population, are selected for, those "vagrants" that don't are selected against. Geographic opportunities permitting life cycle closure are the key to the evolution and isolation of sexually reproducing local populations and ultimately species. The species' location in space makes it persistent, not its number of individuals. The existence of a *P. argus* population depends on the ability of larvae to remain aggregated during their first few months of life and to return as adults to their point of origin to breed with others of their population (Sinclair, 1988: 28, 147).

Many sexually reproducing marine populations spawn at the edge of a system of circulation that remains the same from year to year. The effect is circular migration in water columns, estuarine circuits, persistent gyres, or bounded areas. It is critical that each population maintain its genetic integrity; each must possess isolating mechanisms that safeguard reproductive isolation.

Considering *P. argus*' fecundity and population

replacement needs, each larva has about one chance in a million of surviving to adulthood. During their extended larval stage, spiny lobsters endure a high rate of mortality, yet the extended larval stage must have evolved to utilize some environmental opportunity. (The clawed lobster, *Homarus americanus*, has by contrast evolved a larval stage of about three weeks duration (Phillips and Sastry, 1980)). Extended larval stages may reflect the extent of a physical system to which a species is adapted. Some larvae must travel farther than others to return to their natal region. The lengths of larval stages for different species of spiny lobsters (9-11 months for the Caribbean *P. argus*, less than that for *P. interruptus* in California, and 15 or more months for *P. cygnus* in Australia) may be defined and required by the spatial scale of their larval drift. The spatial scale of the oceanic system, the size of the persistent gyre or whatever system a population uses to entrain its larvae, delineates its absolute abundance. Since the absolute abundance of the Caribbean spiny lobster is considerable, we would expect them to be utilizing a substantial range (Sinclair, 1988).

Part of the Gulf Stream current flows in a gyre whose circuit by drift takes nine months to complete. The Gulf Stream is a great river, fifty miles wide and

fifteen hundred feet deep, part of which circles the entire central Atlantic Ocean (Rudloe, 1988). The largest breeding lobsters in the Bahamas (95-110 mm CL) occupy offshore fringes of reefs along the Gulf Stream edge (Kanciruk and Herrnkind, 1978). These spiny lobsters cast their offspring adrift on the outer edge of their adult habitat where the larvae will be carried away in the Gulf Stream. Maturing larvae return after nine months at sea, in reciprocating oceanic currents.

The Bahamas and Bermuda are located in the Atlantic Ocean along the edge of the Gulf Stream. Large numbers of larvae pass through in continually, wildly fluctuating numbers. Eddies bringing Gulf Stream currents to both the Bahamas and Bermuda can generate extraordinary population increases (Ward 1986; Farmer *et al*, 1989). Mean annual post-*puerulus* settlement in south Florida exhibits random variations of as much as twenty fold (Marx 1986). The year-round presence of late stage larvae in the area suggests that recruits are probably from multiple points of origin, and that changes in facilitative currents are the cause of abrupt changes in recruitment (Marx, 1986; Ward, 1989). Larvae leave and arrive in great numbers on the Gulf Stream. They may circumnavigate the Atlantic, or ride an assortment of Gulf Stream "rings" and "outbreaks" back to the Caribbean via the Sargasso Sea (Farmer *et*

al, 1989).

There is a random distribution of exceptionally good seasons among the annual harvests of Caribbean nations' (e.g. Venezuela's harvest goes from 951 metric tons (mt) in 1981, to between 200 and 300 mt each year until 1986, when the number goes up again to 964 mt, see table 1). There is a similar distribution of exceptionally poor seasons (e.g. Costa Rica in 1981 and 1982). Some changes may be the result of political decisions. There is, nonetheless, significant variation among annual harvest levels. Annual harvests are better or worse in general terms as well. Recruits are like handfuls of seeds blowing in on a wind of distant origins.

There are arguments in favor of the theory that there are numerous local populations of lobsters. Interactions between the currents of the Caribbean and the Gulf of Mexico are complex. Currents around Florida vary seasonally with periodic eddies and counter-currents (Marx, 1986). A few comprehensive analyses of the movements of phyllosoma larvae have shown that by migrating vertically and riding hydrologic currents at different depths or swimming among the plankton in rotating eddies, lobster larvae may avoid drifting too far, and return to their approximate place of origin upon settling (Phillips and Sastry, 1980). If, however,

there were numerous local populations, each occupying different hydrologic systems, one might expect to find corresponding differences in the lengths of their larval stages or other differences in life history or biology, none of which have been documented.

Drift around the North Atlantic gyre and the spiny lobster's larval stage both take nine months to complete. The location of the current, its size, local explosions of larval abundance associated with invasion of Gulf Stream waters, and indications that the larvae can prolong their metamorphosis from nektonic to benthic existence (Kanciruk, 1980), all confirm that the Caribbean spiny lobster's larval migration carries it around one complete cycle of the North Atlantic gyre. It seems unlikely that numerous local populations would use this vast system of migration and return to specific points of origin within the Caribbean. Rather it is likely that one large population entraining its larvae in the North Atlantic gyre would experience erratic local fluctuations in the influx of post larva *P. argus*. It seems likely that the species constitutes one large panmictic population.

#### **Absolute Abundance and Variation**

In some cases, the abundance of juvenile spiny lobsters is not limited by food or space (Marx, 1986).

In other cases, however, survival and growth appear to be density dependent (Polovina, 1989). Where such is the case, we may duplicate the effects of natural mortality in densely populated areas by harvesting a portion of the population before the individuals reach sexual maturity. This might also be productive biologically and economically because the "vulnerable surplus" of a population is being harvested at points where limiting factors are naturally operating (Errington, 1946). This is practiced in some areas. Australia's spiny lobster fishery harvests are comprised of 40% whites, pre-mature albeit legal sized lobsters (Phillips, 1986).

Florida's *P. argus* fishery may be losing productivity by not considering some oceanographic factors. Florida lobster fishermen bait their traps with live decoys, immature lobsters which draw mature cohorts into the traps by acoustic or chemical attraction. The undersized lobsters are ultimately returned to the water. Setting unbaited traps near baited traps is futile so the practice of baiting traps is universal. Handling, exposure, and confinement of the sub-legal sized lobster slows its growth. Exposed lobsters have been shown to experience a sharp increase in lactic acid concentration and a drop in blood pH accompanied by impaired locomotory activity (Hunt and



Lyons, 1986). They are stressed, damaged, exposed to the air and displaced in habitat (Brown and Caputi, 1986). Lobsters having been trapped and returned are confused and easy prey. Finding safe habitat requires open movement which increases the spiny lobster's chance of being attacked by an octopus or other predator (Brown and Caputi, 1986). Loss to the Florida industry is difficult to calculate. It is at least \$1.5 million and possibly as much as \$9 million per year (Heatwole et al, 1988). Simply harvesting the immature lobsters after harassing them might make the system more productive, particularly if their growth is density dependent.

The causes of variation, of differences in abundance between years, are the subject of considerable debate. The question is whether abiotic factors such as temperature, salinity, dissolved oxygen, and currents, or biotic interactions such as predation or competition for limited food or space, primarily regulate population abundance.

D.H. Cushing (1975: 180) hypothesizes in the "match/mismatch" theory that interannual differences in abundance are due to differences in the timing of phytoplankton blooms. Young fish larvae rely on a diet of young herbivores such as copepods, which in turn rely on phytoplankton and algae. Stratification and

destratification of water columns during spring and autumn cause phytoplankton blooms in temperate areas. The depths and intensities of thermoclines vary from year to year, as do winds, rainfall and currents, all affecting the timing of blooms. Species born after a bloom can expect to benefit from a transfer of energy through the trophic web.

Michael Sinclair's "member/vagrant" hypothesis proposes that geographic space and the same mechanisms of sexual reproduction that create local populations, are the regulators of abundance. Geographic opportunities permitting life cycle closure are necessary if individuals are to locate other members of their populations with which to mate. A common way for fish to accomplish this is by an annual migration which begins when the population spawns at the edge of an oceanographic system that is consistent from year to year. The geographic opportunities provided by these systems - water columns, estuarine circulation, persistent gyres, and bounded areas - are limited in space and subject to physical oceanographic processes. Their variability creates interannual differences in abundance (Sinclair, 1988).

Zooplankton abundance in the more eutrophic waters lying over continental shelves appears to be constrained by available light and physical factors

other than food. Zooplankton display behavior such as migrating vertically in water columns to pursue food and persist geographically. Ichthyoplankton (fish larvae) tend to reside near the surface drifting on currents, although in the case of spiny lobster larvae this is not the case (Gray, 1992). Zooplankton abundance in the clear waters of the open ocean, where spiny lobster larvae range, is more likely to be food limited (Sinclair, 1988: 20, 137).

For example, there was a sudden decline in the Hawaiian lobster fishery in 1989. Overfishing did not seem to be a likely cause; there were plenty of breeding lobsters in the area. There was a corresponding decline in seabirds and monk seals. Using a satellite mounted color scanner designed to pick up light reflected from chlorophyll, researchers measured phytoplankton abundance. This combined with oceanographic and weather data seems to indicate that winds caused unusually active mixing of oceanic layers between 1977 and 1988. The thermocline was much deeper than it was previously or has been since, which brought deep nutrient rich waters to the nutrient poor surface. Phytoplankton populations soared in the tropical sunlight. Herbivorous zooplankton populations, being dependent on the success of phytoplankton, also fared well in the nutrient enriched waters, and the abundance

of lobster and other larvae feeding on copepods and other herbivores increased. The commercial lobster fishery grew during the 1980's in response to unusually high numbers of lobsters. When weather patterns changed, the levels of phytoplankton decreased and lobster populations declined (Polovina, 1994).

#### 4. Management: Numbers and Space

There are two basic concepts of management at work in the *P. argus* fishery. The first concerns maximizing the sustainable biological output of a fishery. The second concerns the use of oceanographic tools to determine seasonal abundances of lobsters and to manage the harvest.

##### The Maximum Sustained Yield Concept

The Maximum Sustained Yield (MSY) concept is an expansive, complicated system of models which has evolved throughout the last century. In recent years, with declines in some fish populations, the models have come under some scrutiny (McGoodwin, 1990). Sociologists, anthropologists, and economists have produced parallel concepts of maximum and optimum social and economic yields. The MSY concept is nonetheless the prevailing philosophy of Caribbean spiny lobster management. MSY modelling seeks to predict the maximum allowable catch, beyond which greater fishing effort decreases in efficiency, and a lesser effort decreases the total catch unnecessarily. To fish more than the effort needed for the MSY is said to be "wasteful of effort." To fish less is "wasteful of food (Larkin 1977)."

One management tool designed to extract a maximum

yield from a population of fish is the setting of a minimum size limit. Fish grow fastest prior to the onset of sexual maturity. Lobsters change their focus of energy use from growth to production of gametes and to associated behaviors at the onset of maturity. Establishing a minimum allowable size limit at about the size of sexual maturity allows each female the theoretical possibility of spawning once, thereby guaranteeing a seed stock, and makes her eligible for harvest when her growth slows perceptibly (Hunt and Lyons, 1986).

Estimating size at the onset of maturation is critical for MSY modelling (Hunt and Lyons, 1986). A marked change in growth rate occurs when the Caribbean spiny lobster reaches about 75 mm CL, and this is often estimated to be the size at maturity. The minimum legal harvest size in south Florida is 76 mm CL, or three inches, even though few spiny lobsters are reproductively functional below 85 mm CL in the south Florida population (Hunt and Lyons, 1986). Venezuela sets the minimum size at 100 mm CL (Posada, 1992).

Although increasing a population's biological output, continually harvesting a population's "teenagers" can produce an evolutionary side effect. The continual harvesting of first time spawners favors individuals that mature early and selects out those

that mature later. The offspring of young, first-time spawners evolve over generations into a population that matures earlier. Since growth slows at maturity, maturity comes to smaller adults. Applying the concept of the MSY is likely to lead to instability because of the progressive tendency toward less quantitatively and qualitatively successful spawners (Larkin, 1977; Hancock, 1980). A reduction in age classes caused by harvesting first time spawners can reduce evolutionary fitness, and can create greater vulnerability to catastrophic events (Larkin, 1977).

Spawner/recruit models are a commonly employed tool of MSY management. These models are based on the assumptions that the abundance of fish is density dependent and that there is a correlation between spawners and recruits that can be graphically illustrated. In reality, it has been difficult to demonstrate that the abundance (not to be confused with survival and growth) of populations of fish is density dependent. It is easier to demonstrate that the abundance of sexually reproducing fish is not regulated by density dependent factors (Sinclair, 1988: 100). Year classes fluctuate "widely without obvious relationship to adult population size (Sinclair, 1988: 22)." If fish abundance is not density dependent, and annual fluctuations in parent and recruited populations

are not correlated, then spawner/recruit models would have to be viewed with some skepticism. Margalef (in Sinclair, 1988, pg.74) states that "Volterra-Lotka models have various disadvantages: they ignore the discontinuity of individuals (quantification) and space, and operate in a sort of 'ether' of very unreal properties."

### Predicting the Harvest

Throughout the Caribbean, post-*puerulus* settlement is measured on artificial collectors placed throughout the juvenile habitat. Prediction methods vary from complicated quadratic regressions to simple linear regressions and the use of stock-recruitment models (Phillips, 1986; Marx, 1986). Since the settling larvae make up the population entering the commercial fishery in four years, their relative abundance becomes a valuable predictive tool. Populations of three year old juveniles predict the catch two years in advance, and four year old juveniles predict what the following year's catch will be. Sampling these age groups has not been as widely used as have post-*puerulus* collectors (Caputi and Brown, 1986).

Periods of heavy phytoplankton production appear to be beneficial to larval survival and growth (Polovina, 1994). Measuring phytoplankton, or even



larval abundance itself, might serve as a precursor to the currently widespread practice of estimating post-larval puerulus settlement. Between 1966 and 1968, plankton net tows around Florida revealed increased numbers of planktonic lobster larvae. These increases were reflected in the abundances of later generations of settling larvae, juveniles and adults (Marx, 1986). In Belize, fishermen have noted a positive correlation between the populations of phytoplankton and lobster larvae, but attribute this phenomenon to a "red tide" killing fish that normally prey on lobster larvae (Sutherland, 1986).

Planktonic organisms, including lobster larvae, are dependent on the relative success of the next trophic level and ultimately on primary production by phytoplankton. Photosynthesis by phytoplankton is how energy is brought into the system (Russell-Hunter, 1970). There is a temptation to use this knowledge to manipulate the habitat of *P. argus*. The application of fertilizer to certain areas of the sea, via a diffuse pathway of entry, has been considered as a way of increasing primary production. The nitrates and phosphates that are lacking in tropical off-shore oceans are overabundant nearshore where agricultural run-offs and sewage discharges overload local systems with nutrients (Russell-Hunter, 1970). Extreme care

would have to be taken that no substances are applied to marine systems which cannot be assimilated and that ecological systems are not disrupted (Portmann and Lloyd, 1986). The missing ingredients for life further offshore are poisonous to an area like Florida Bay (Russell-Hunter, 1970).

There might be some possibility of enhancing local populations by "manipulation of critical habitats whose scarcity may contribute to population bottlenecks" (Herrnkind et al, 1994). By examining the life histories of lobsters and enhancing or harvesting at the time and place of their limiting factors, we might improve yield and sustainability. Our efforts would ideally duplicate the actions of nature, while improving the productivity of lobster fisheries. The use of casitas described in the next chapter, is an example of enhancing a habitat by bypassing a critical shortage of shelter for juvenile lobsters.

## 5. Balancing Harvest and Conservation Needs

Because of *P. argus's* great market value, the pressure to harvest is tremendous. Policy regarding the species varies greatly between countries. In general, *P. argus* is fished relentlessly yet its abundance continues. There is no apparent limit to the harvest, and yet common sense demands some level of restraint.

Certain basic tools are commonly used in Caribbean management schemes. Some of the most successful tools may be "pesqueros" or "casitas," artificial habitats constructed in protected waters. Some countries have established systems of co-management with fishermen's cooperatives as a means of effective management.

Larger, older individuals of the species may occupy sanctuaries among off-shore reefs. The ability of these individuals to produce enormous numbers of offspring may denote the efficacy of breeding sanctuaries for the maintenance of breeding stocks.

### Some Basic Tools

Conservation measures at the fisheries manager's disposal include closing areas, closing seasons, restricting gear, setting a total allowable catch, imposing subsidies or taxes, limiting entry, encouraging shared or appropriated management, and knowing when to do nothing (McGoodwin, 1990).

The United Nations Law of the Sea (UNILOS 82, UNILOS II and UNILOS III) declares that each coastal nation has exclusive rights to the marine resources lying in an Exclusive Economic Zone (EEZ) within 200 miles of its shores. UNILOS 82 created important resource bases for a number of formerly colonized, now developing nations. The Caribbean spiny lobster is one of the best examples of these resources (McGoodwin, 1990). The Palinurid spiny lobsters support some of the most valuable fisheries in the world (Ford, 1980). Dockside price in Belize for spiny lobster in 1987 was \$9.25 U.S./lb. (Bert and Hochberg, 1992).

In the words of James McGoodwin (1990), "Management should facilitate the flow of productive resources, including labor, into the most valuable and productive areas." Article 62(1) of the Law of the Sea Convention (LOS convention) declares that the governments of coastal countries shall promote optimum utilization of the marine resources within their EEZ (Hinds, 1992).

About 95% of the world's 8 million fishermen, are small scale fishermen. They catch half of the fish that people consume. The fish caught by these small operators represent an important source of protein. Their catch is often locally distributed among people who need it most.

On any given year, Cuba's harvest is equal to or greater than all other countries' combined. (e.g. 12,644 mt vs. 10,084 mt for 1984, see Table 1). This may be the result of Cuba's location and other environmental factors or it may be the result of habitat enhancement or increased fishing effort. The Cuban *P. argus* fishery is highly developed in three phases.

First, Cuban fishermen maintain a system of pesqueros in shallow sea-grass beds. These artificial shelters, similar to the Mexican casitas, are harvested by divers using gaffs and nets. The second system of harvest is the setting of haul traps at deeper fringing reefs and the shelf break. The third system is the setting of net traps in the paths of *P. argus* during their off-shore migrations (Chubb and Brown, 1991).

Although net trapping of migrating lobsters may run the risk of over-harvesting a massing population, *P. argus* migrations are comprised primarily of young adults. Larger, older individuals generally do not partake in the ritual (Herrnkind et al, 1973). Harvesting young, migrating lobsters leaves larger, older lobsters to continue breeding. Harvesting lobsters during their migration may harvest the "vulnerable surplus" thereby having no impact on population dynamics (Errington 1946).

"Bully-netters" trap *P. argus* during their offshore migration in Bimini. Harvesting in this manner, each boat catches 500-1000 lobsters per day. Thirteen boats fishing a migratory route near Bimini can harvest 20,000 lobsters during the animals' four days of migration. Considering that the nets missed large areas of the bottom and that the nets weren't placed during the night while lobsters continued to migrate, the population of migrating lobsters is estimated to be many times the number caught (Herrnkind et al, 1973).

It is possible that the reason for the large Cuban harvest lies in the extensive construction of pesqueros or casitas. Casitas can substantially improve survival rates of *P. argus* juveniles, for whom suitable protective shelter is often a severely limiting factor (Eggleston et al, 1989; Smith and Herrnkind, 1992). Juveniles older than two years reside in sea grass beds and other open space in near-shore waters where there is little cover from predators. *Panulirus argus* juveniles crowd in tightly packed clusters under patches of algae and other protective cover where they can find it (Herrnkind et al, 1994).

### Cooperatives

Casitas have not found common use outside of Cuba,

partly because of the difficulty of incorporating their management into a market system. There is little incentive for an individual to build and maintain casitas because they are so easily robbed. In some cases cooperatives have demonstrated an ability to bridge this kind of problem. Cooperatives foster a community sense for the resource. They allow for the division of space into widely recognized, easily enforced, cooperatively held fishing grounds, while encouraging independence and entrepreneurship among individuals.

Co-management arrangements between cooperatives and governments have been successful in many cases (McGoodwin, 1990). Since 1949, Japanese coastal fishermen have been guaranteed access to and "ownership" of living aquatic resources through a combination of traditional tenured customary procedures and modern legislation. The Fisheries Cooperative Association, which is managed entirely by local communities of commercial fishermen, is the economic hub of fishing communities. Commercial fishermen cannot work without joining an FCA. Fishing territories (iriais) are divided among fishing villages along lines that extend back to feudal times. In some cases villages share a space, one village fishing one species while a neighboring village fishes another, using

different gear (Ruddle, 1989).

Cooperatives have played a vital role in the development and assessment of the spiny lobster and stone crab fisheries in Belize (Bert and Hochberg, 1992). The Northern Fishermen's Cooperative in Caye Caulker and Belize City has been particularly effective (Sutherland, 1986).

Cooperatives in Belize play an active role in managing and monitoring their turfs (designated fishing grounds). Co-ops provide handling facilities, credit, and fishing supplies, immediate cash payment for lobsters, and a share of the co-op's profits at the end of each season. The co-ops market lobsters directly to buyers in the international market without losses to middlemen and monopolistic export companies that have historically plagued Belize's fisheries. High prices, often obtained by auctioning to the highest bidder, have brought economic success to most fishermen. Reported individual incomes from lobster fishing run as high as \$63,000 U.S. The most minimal effort in a good year will bring \$20,000 U.S. (Sutherland, 1986).

Small scale fishermen often have astute, empirical knowledge of local ecosystems. Because of their close association with a localized area they often can detect when they have approached the lower-bound limits of a fishery, the point of bioeconomic equilibrium. Many



small scale fishermen have the advantage of economic and occupational pluralism; people turn to farming or other activities when fish populations decline or are not in season. Customs and traditions, such as taboos against fishing in particular areas or at particular times, often play important roles in the restraint of fishing effort in coastal aboriginal societies (McGoodwin, 1990).

It is traditionally the case in most small scale, near-shore, artisanal fisheries that fishing space is divided. Groups or individuals assert formal or informal rights to fishing grounds. Management has in some cases attempted to integrate and formalize traditional methods which are working (McGoodwin, 1990). A number of spiny lobster management systems are based on the division of space.

Division of fishing grounds into zones was established in the 1930's in Mexico. Fishing cooperatives, structured like agrarian collectives called ejidos, were given title to fish particular species in specified areas (Miller, 1989).

Members of the Cozumel and Vigia Chico co-ops divide their zones among members. These parcelas or campos, ranging in size from .5 km<sup>2</sup> to more than 3 km<sup>2</sup>, are established through informal means such as expanding to another fisherman's boundary marker. In an

effort of combined habitat enhancement and harvesting, fishermen build artificial shelters called "casitas" that simulate crevices in reefs and position these 20-30 meters apart. Fishermen free-dive in the shallow waters (2-7 meters) and gather lobsters from the casitas using a gaff and net. Typically seven to ten lobsters are harvested from each casita, although sometimes several dozen may be caught. Thirty to fifty casitas are checked daily and not revisited for a week or more. As of 1989, 107 members of the Vigia Chico co-op utilized more than 10,000 casitas over a 160 km<sup>2</sup> area of Ascension Bay. The Cozumel cooperative fishes in Espiritu Santo Bay to the south in much the same way and with the same productive results. Use rights and limited access in areas controlled by the Cozumel and Vigia Chico cooperatives make the spiny lobster fishery successful and manageable there (Miller, 1989).

In 1980, there were six cooperatives operating in Quintana Roo, Mexico, each with clearly defined boundaries. Access to fish all lobsters was reserved by federal law to cooperatives. Established cooperatives north of the Cozumel and Vigia Chico regions unsuccessfully resisted the incursion of additional co-ops and the resulting division of existing campos. Newcomers initially formed cooperatives to take finfish, and then (through legal maneuvering) to take

lobsters. Virtual open-access has led to near abandonment of the system of casitas in the north. There is reduced incentive to maintain casitas in an atmosphere of free-ridership (Miller, 1989).

### Sanctuaries

The commercial lobster fishing season ends in Florida with the opening of a recreational lobster diving season. "Lobstermania" brings tens of thousands of people to the Florida Keys. The season is a boon to local restaurant, motel, and charter businesses, but it is devastating to lobsters. After Lobstermania, it would seem that there is not a mature, living lobster left in Florida (Rudloe, 1988).

After being fished as heavily as they have been throughout the Caribbean, why is *P. argus* still so abundant? Annual catches throughout the Caribbean between 1979 and 1989 don't appear to be declining. If the member/vagrant theory is correct, *P. argus* has a large absolute or potential abundance because of the size of the system which retains larvae, the North Atlantic gyre (Sinclair, 1988: 35). But where do the eggs continue to come from?

It has been proposed that there are substantial numbers of larger, older *P. argus* avoiding capture by occupying naturally inaccessible havens (Farmer et al,

1989). The largest adult *P. argus* live offshore in the steep, rocky outer fringes of reefs (Herrnkind and Lipcius, 1989; Herrnkind et al, 1994). Areas where currents flow and surf pounds are off limits to all but the most diligent fishing efforts. Small sections of habitat far from shore may be unknown or not lucrative enough for harvest. Mature spiny lobsters tend to reside and forage in localized areas (Gray, 1992). If a lobster should find an un-fished area and remain there, it could avoid capture indefinitely.

The idea of a protected breeding population would explain why lobsters have not declined in numbers despite a massive fishing effort, and have not evolved into smaller, earlier maturing individuals, despite size limit management.

Larger, older, more fertile lobsters of the kind found in deeper water, produce a disproportionately large number of eggs. Fecundity varies widely, from 50,000 to 800,000 eggs per female (Morgan, 1980). At Bimini, *P. argus* females 96-100 mm CL representing 3.6% of the population provided 13.9% of total egg production. Newly mature females in the same study, though much more numerous, provided only 2.3% of total egg production (Kanciruk, 1980). The correlation between size and fecundity among *P. cygnus* in Australia has also been shown to be a curvi linear one, wherein

the largest females may produce up to a million eggs in one spawning (Gray, 1992).

If large breeding lobsters are living in safe havens, they have established *de facto* breeding sanctuaries, geographic areas that are never fished. These sanctuaries may be the key to the species' ability to withstand heavy harvests. They should not be confused with sanctuaries such as the 2500 square nautical mile Olympic Coast National Marine Sanctuary, which is not a fish sanctuary. For this region... "No sanctuary fishing or aquaculture regulations are proposed nor are in the scope of regulations. Fish resources in the Sanctuary are already extensively managed by existing authorities (NOAA, 1993)."

Deliberately established breeding fish sanctuaries might be on the scale of the Hol Chan Reserve in Belize which is 5 square miles of inland mangroves, midwater grass and algae patches, and outer coral reef. The Hol Chan Reserve is a true fish sanctuary. Sedentary species such as grouper, conch, and spiny lobsters follow natural life spans. The reserve has been attracting large numbers of tourists who come to swim among the big tame fish. One of very few fish reserves world-wide, Hol Chan Reserve in Belize has been showing biological and economic promise (Sutherland, 1986).

Setting space aside for fish is compatible with

the idea of dividing fishing space among cooperatives; both concepts are spatial. Dividing coastal waters spatially between competing cooperatives and fish sanctuaries would be an effective, easy-to-enforce management system.

Breeding sanctuaries as a management tool have great potential. Unfortunately, a literature search reveals no real data on their effectiveness. Sanctuaries have been difficult to protect from both illegal and legal fishing for a long enough period to study. The economic incentives to fish have proven stronger than all but the most "scientific" arguments.

The effectiveness of sanctuaries as breeding grounds would be difficult to quantify. We at present must virtually accept the concept on reason without proof, as much for what they don't do as for what they do. Sanctuary populations achieve normal age demographics. Larger, older fish with greater fecundity produce offspring that don't genetically drift over generations toward smaller individuals.

If *P. argus*' success at resisting depletion despite heavy fishing is due to its protection in *de facto* sanctuaries, then we have concrete evidence of the value of breeding havens.

## 5. Conclusion

The Caribbean spiny lobster is a venerable animal. The distances that an adult has covered, the changes it has undergone in the course of maturing, the physical attributes and social behaviors it has evolved, are amazing.

The issues pertaining to the commercial harvest of the Caribbean spiny lobster epitomize the most important questions of commercial fisheries management. Are they one or many populations? How is their absolute abundance determined? What causes variation in abundance from year to year? How can fisheries best be structured to protect both fish and fishermen?

The weight of evidence is that *P. argus* is one population. The Caribbean spiny lobster has a large absolute abundance coinciding with a large geographic opportunity, the North Atlantic gyre. There are numerous accounts of larvae leaving and arriving on Caribbean Shores via the Gulf Stream, and of resultant fluctuations in abundance.

We should re-examine recruitment models and biological or bioeconomic models to determine if they are "more precise than accurate (Larkin, 1977)," or a set of "unchallengeable assumptions," examples of the "'fallacy of misplaced correctness' long prominent in the history of human error (Errington, 1946)."

Oceanographic management tools work well. A total allowable catch can be established based on post-*puerulus* settlement. The oceanographic tools for estimating the abundance of phytoplankton, lobster larvae, or post larvae settlement are inexpensive and easy to use. They are well suited to the management of small scale fisheries, such as Caribbean spiny lobster fisheries.

Since the establishment of 200 mile EEZs, management of spiny lobsters has come under the control of countries throughout the Caribbean, each with its own politicians, managers, and courts, and each with its own opportunities to maximize the benefits of the *P. argus* harvest. Enhancing protection in the juvenile habitat may be a way of greatly increasing productivity. To accomplish these improvements, geographic space may best be divided, and cooperatives may be the best way of facilitating this division. In addition to dividing coastal waters between sanctuaries and fishing grounds, governments need to protect sanctuaries from poachers and fishing cooperatives from free-ridership which allows newcomers and interlopers to turn management into chaos. Systems incorporating co-management between governments and cooperatives of independent fishermen have shown great promise. Systems combining traditional and modern methods of fishing



effort restraint can implement the best of both worlds.

Economic pressures to increase the harvest are great because of the spiny lobster's high market value. The only way of maintaining the Caribbean spiny lobster's abundance, and improving the chances of economic survival of those who make their living harvesting the species, is to ensure that commercial and sport fisheries are not operating in an atmosphere of anarchy.

Some portion of *P. argus*' breeding population has remained protected by occupying hard-to-reach places. As market pressures continue, enterprising individuals will find ways of harvesting these largest and most valuable lobsters. It will be easiest to create sanctuaries before fishing ventures of this type become established.

**Table 1.** The catches in metric tons over an eleven year period among major harvestors of *P. argus*

	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	Total
Antigua	132	101	51	44	50	140	117	120	120	150	150	1,175
Bahamas	2,755	2,894	2,051	2,463	2,808	3,456	5,513	3,573	4,591	5,071	6,194	41,369
Belize	663	555	760	660	680	650	730	520	530	581	537	6,866
Costa Rica	41	25	5	4	120	376	207	60	60	60	60	1,018
Cuba	11,000	10,567	10,663	11,674	10,929	12,644	13,578	11,795	12,795	11,710	11,170	128,525
Dominican Republic	339	166	229	270	546	165	784	429	823	274	814	4,839
Haiti	150	200	200	200	250	250	250	250	250	250	250	2,500
Honduras	3,429	2,198	1,989	1,689	3,932	3,068	4,065	5,320	1,490	1,629	1,483	30,292
Martinique	97	104	98	114	106	107	95	83	64	93	100	1,061
Mexico	696	689	825	979	926	939	702	973	1,019	1,062	771	9,581
Nicaragua	2,230	1,849	1,129	638	1,549	1,429	1,159	798	1,124	650	1,067	13,622
Turks Caicos	400	400	308	372	301	369	279	175	194	192	208	3,198
U.S.A.	2,699	2,959	2,463	2,649	2,053	2,369	1,667	2,362	2,169	2,438	2,438	26,266
Venezuela	165	209	951	302	241	203	202	964	184	201	805	4,427

From: FAO (Food and Agriculture Organization of the United Nations). 1984 and 1991 Yearbooks of Fishery Statistics

## Literature Cited

Bert, T.M., and R.J. Hochberg. 1992. "Stone Crabbing in Belize". Proc. Gulf and Caribb. Fish. Inst. Vol. 41 pp. 363-382.

Brown, R.S., and N. Caputi. 1986. "Conservation of Recruitment of the Western Rock Lobster (*Panulirus cygnus*) by Improving Survival and Growth of Undersize Rock Lobsters Captured and Returned by Fishermen to the Sea." Can. J. Fish. Aquat. Sci., Vol. 43: 2236-2242

Caputi, N. and R.S. Brown. 1986 "Relationship Between Indices of Juvenile Abundance and Recruitment in the Western Rock Lobster (*Panulirus cygnus*) Fishery." Can.J. Fish. Aquat. Sci., Vol. 43: 2131-2139.

Chubb, C., and R. Brown. 1991. "Fisheries at Ascension Bay in Mexico and in Batabano Gulf in Cuba." SPC (South Pacific Commission) Fisheries Newsletter. no. 59. pp 24-26. Noumea, New Caledonia.

Cushing, D.H. 1975. Marine Ecology and Fisheries. Cambridge University Press.

Eggleston, David B., Romauld N. Lipcius, and David Miller. 1989. "Enhancement of Spiny Lobster Survival by Artificial Shelters: Habitat, Scaling, and Spatial Effects upon Predation Intensity." Proc. Gulf and Caribb. Fish. Inst. Vol. 42. pp. 127-136.

Errington, Paul L. 1946 "Predation and Vertebrate Populations." Quarterly Review of Biology. Vol. 21. pp. 144-177.

FAO (Food and Agriculture Organization of the United Nations). 1984. Yearbook of Fishery Statistics. Vol. 58. Rome, Italy.

Farmer, Mary W., Jack Ward, and Brian E. Luckhurst. 1989 "Development of Spiny Lobster (*Panulirus argus*) Phyllosoma Larvae in the Plankton near Bermuda". Proc. Gulf and Caribb. Fish. Inst. Vol 39. pp. 289-302

Ford, Richard F. 1980. "Introduction to Ecology." In: Cobb, J. and B. Phillips, Ed. The Biology and Management of Lobsters. p. 189 Academic Press. New York.

Gray, H. 1992. The Western Rock Lobster. Westralian Books. Geraldton, West Australia.

Hancock, D.A. 1980. "Introduction to Management." In: Cobb, J. and B. Phillips, Ed. The Biology and Management of Lobsters. p. 181 Academic Press. New York.

Heatwole, Douglas W., John H. Hunt, and Frank S Kennedy. 1988. "Catch Efficiencies of Live Lobster Decoys and Other Attractants in the Florida Spiny Lobster Fishery." Florida Marine Research Publications, Florida Department of Natural Resources. No.44

Herrnkind, W.F., P. Jernakoff, and M.J. Butler IV. 1994. "Puerulus and Post-Puerulus Ecology". Spiny Lobster Management: current situation and perspectives. Blackwell Sci Publ. London

Herrnkind, William F., Paul Kanciruk, Joseph Halusky and Richard McLean. 1973. "Descriptive Characterization of Mass Autumnal Migrations of Spiny Lobster, *Panulirus argus*." Proc. Gulf and Caribb. Fish. Inst. Vol. 25.

Herrnkind, W.F. and R. N. Lipcius. 1989. "Habitat Use and Population Biology of Bahamian Spiny Lobster." Proc. Gulf and Caribb. Fish. Inst. Vol. 39.

Hinds, Lennox. 1992. "World Marine Fisheries: Management and Development Problems." Marine Policy. September.

Hunt, John H., and William G. Lyons. 1986. "Factors Affecting Growth and Maturation of Spiny Lobsters, *Panulirus argus*, in the Florida Keys." Can. J. Fish. Aquat. Sci., Vol. 43: 2243-2247.

Kanciruk P. 1980. "Ecology of Juvenile and Adult Palinuridae (Spiny Lobsters)." In: Cobb J. and B. Phillips, Ed. The Biology and Management of Lobsters. p. 59. Academic Press. New York.

Kanciruk, Paul, and W. Herrnkind, 1978. "Mass Migration of Spiny Lobster, *Panulirus argus* (Crustacea: Palinuridae): Behavior and Environmental Correlates." Bulletin of Marine Science. Vol 28, No. 4: 601-623.

Kimmel, J.J., and R.S. Appeldoorn. 1992. "A Critical Review of Fisheries and Fisheries Management Policy in Puerto Rico." Proc. Gulf and Caribb. Fish. Inst. Vol. 41. pp. 349-363.

Larkin, P.A. 1977 "An Epitaph for the Concept of Maximum Sustainable Yield." Trans. Am. Fish. Soc. no. 106.

Marx, J.M., 1986. "Settlement of Spiny Lobster, *Panulirus argus*, Pueruli in South Florida: An Evaluation from Two Perspectives." Can. J. Fish. Aquatic. Sci., Vol. 43: 2221-2227.

McGoodwin, James R. 1990. Crisis in the World's Fisheries: People, Problems, and Policies. Stanford University Press.

Miller, David L. 1989. "The Evolution of Mexico's Caribbean Spiny Lobster Fishery". In: Berkes, F., Ed. Common Property Resources. Belhaven Press. London. p. 185

Morgan, G.R. 1980. "Population Dynamics of Spiny Lobsters." In: Cobb, J. and B. Phillips, Ed. The Biology and Management of Lobsters. Academic Press. New York. p. 189.

NOAA, National Oceanographic and Atmospheric Administration. 1993. Olympic Coast National Marine Sanctuary EIS/MP. Sanctuaries and Reserves Division. Washington D.C.

Phillips, B.F. 1986. "Prediction of Commercial Catches of the Western Rock Lobster *Panulirus cygnus*." Can. J. Fish. Aquat. Sci. Vol. 43. pp.2126-2130

Phillips, B.F. and A.N. Sastry, 1980. "Larval Ecology." In: Cobb, J. and B. Phillips, Ed. The Biology and Management of Lobsters. Academic Press. New York. p. 11.

Polovina, Jeffrey. 1994. "The Case of the Missing Lobsters". Natural History. February.

Polovina, Jeffrey J. 1989. "Density Dependence in Spiny Lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands." Can. J. Fish. Aquat. Sci., Vol 46: 660-665.

Portmann, J.E., and R. Lloyd. 1986. "Safe Use of the Assimilative Capacity of the Marine Environment for Waste Disposal - Is it Feasible?" Water Science and Technology. V.18. p.233.



Posada L. 1992. "Los Recursos Pesqueros del Parque Nacional Archipiélago de los Roques, Venezuela" Proc. Gulf and Caribb. Fish. Inst. Vol 41 pp. 79-95.

Ruddle, Kenneth. 1989. "Solving the Common-Property Dilemma: Village Fisheries Rights in Japanese Coastal Waters". In: Berkes, Fikret Ed. Common Property Resources. Belhaven Press. London. p. 168.

Rudloe, Jack. 1988. The Wilderness Coast: Adventures of a Gulf Coast Naturalist. E.P. Dutton. New York.

Russell-Hunter, W. D. 1970. Aquatic Productivity: An Introduction to Some Basic Aspects of Biological Oceanography and Limnology. Macmillan Company. London

Sinclair, Michael. 1988. Marine Populations: An Essay on Population Regulation and Speciation. The University of Washington Press. Seattle.

Smith, Kenneth N. and William F. Herrnkind. 1992. "Predation On Early Juvenile Spiny Lobsters *Panulirus argus* (Latreille): Influence of Size and Shelter." J. Exp. Mar. Biol. Ecol., vol.157, pp.3-18.

Sutherland, Anne. 1986. Caye Caulker, Economic Success in a Belizean Fishing Village. Westview Press. Boulder, Colorado.

Ward, Jack. 1986. "Patterns of Settlement of Spiny Lobster (*Panulirus argus*) Post Larvae at Bermuda." Proceedings of the Gulf and Caribb. Fish. Inst. Vol.39.

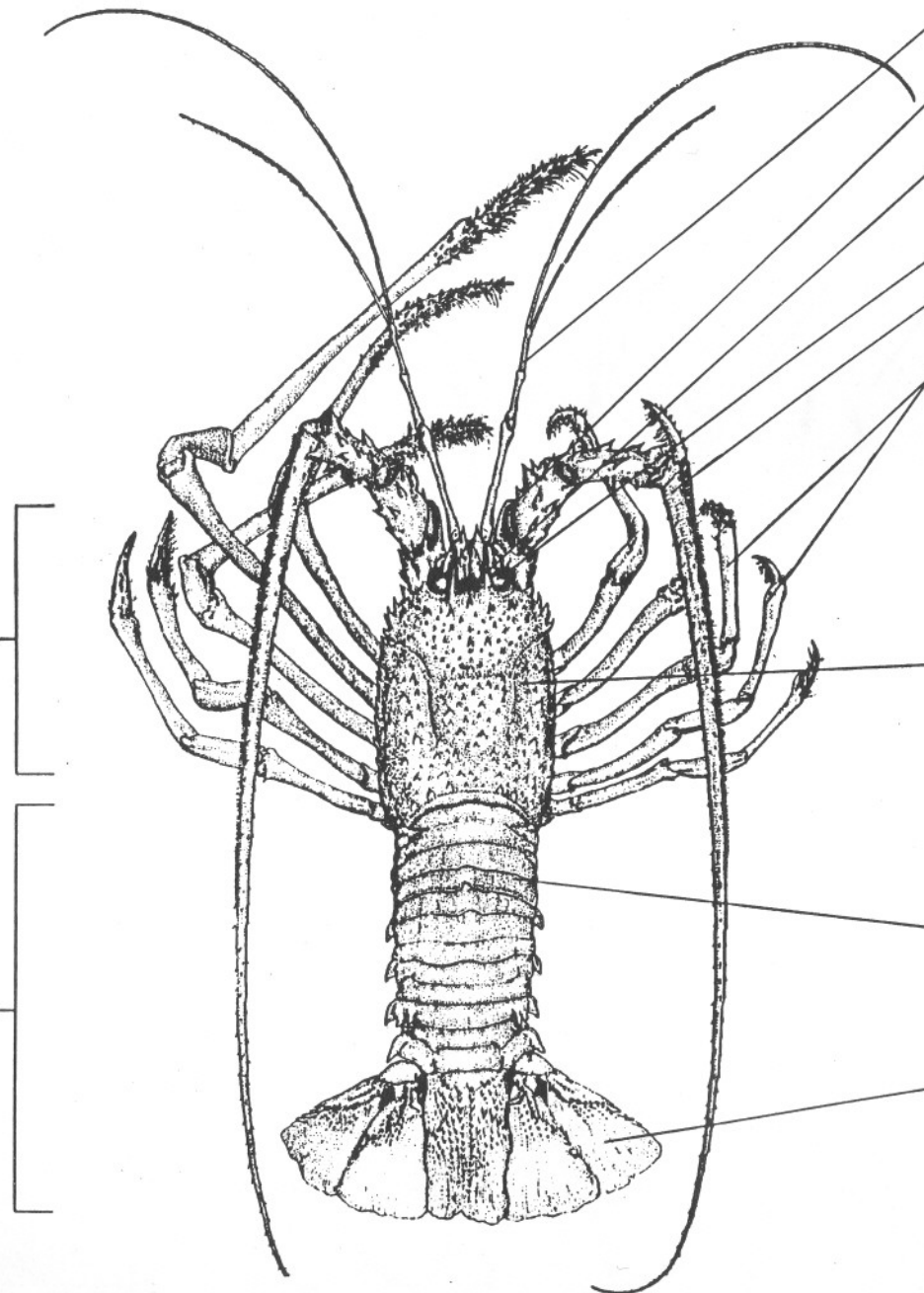
**Figure 3: External features of the western rock lobster:**

(Dorsal view, left side shown as a male, right side as female).

The exoskeleton serves for protection and support of internal organs and for muscle attachment, the joints give flexibility. An examination of the appendages tells much of the way of life, for each is a specialised tool adapted for a particular function in a specific habitat.

- Cephalothorax, the 'head-chest' part of the body, made of about fourteen segments fused together. Attached to it are highly specialised jointed appendages for sensing, feeding, movement, and reproduction. Internally are the major organs, and the gills.

- Abdomen, the 'tail' of six segments, mostly muscular tissue internally. Four segments have swimmerettes, the last is adapted to form a 'tail-fan'.

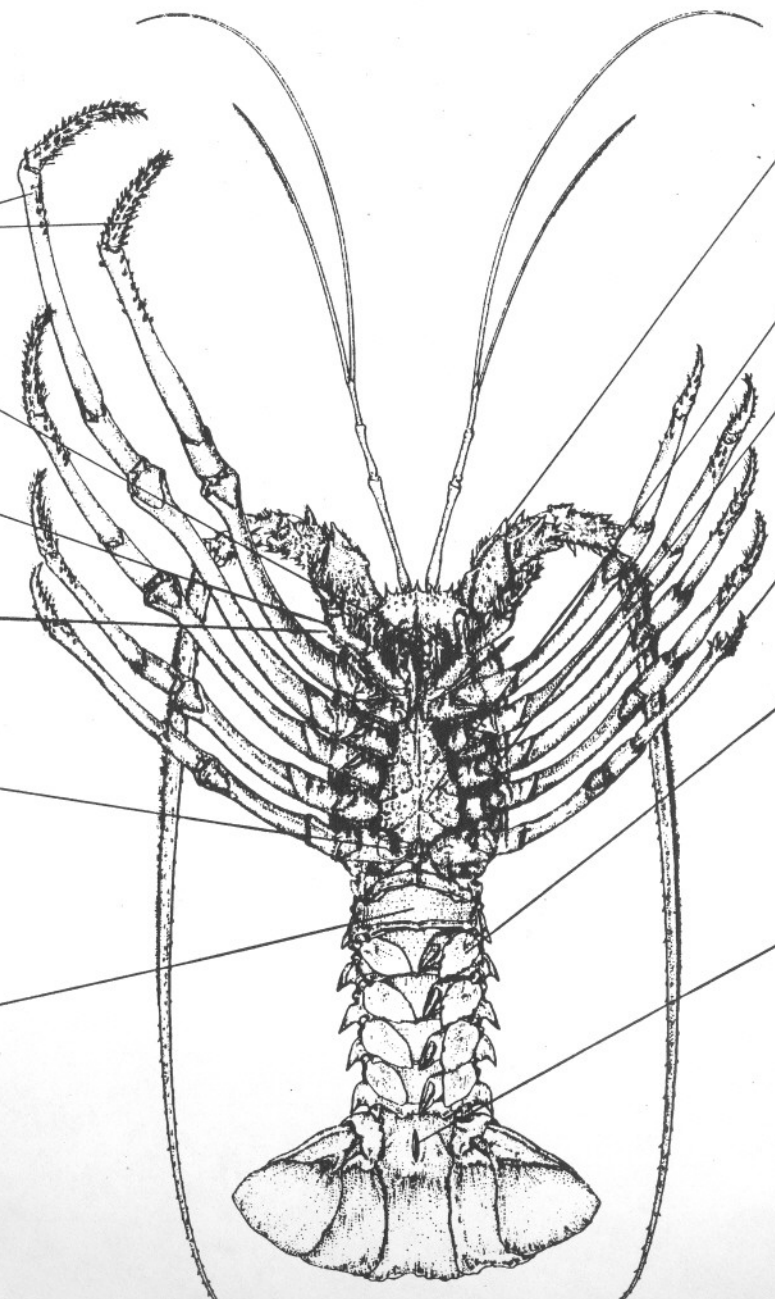


- Antennule, ending in two sensory flagellae.
- Stridulating apparatus which produces sound.
- Two strong, smooth and sharp horns project forward over the eyes.
- Compound eyes.
- Antenna, ending in long sensory flagellum.
- Legs (pereopods) – five pairs, usually called 'walking' legs although most have other specialised functions as well. Internal branches of these appendages (and some mouthparts) end in gills held in the gill chamber beneath the carapace. Unlike 'true' lobsters, claws are lacking.
- Carapace, thick rigid, shield-like, covered with forward-facing sharp stout spines and an almost continuous stubble of short bristles and hairs sensitive to touch. 'Clips' to the underside (sternum) by a 'press-stud' arrangement, which separates at moulting to allow escape from the old shell.
- Overlapping abdominal plates each with two bands of bristles, cover each segment. They are hinged firmly at the sides and joined by membranes, giving flexibility.
- Tail-fan, consisting of central telson and outer uropods, covered with rows of backward facing spines and bristles. It spreads wide, so rapid flexing of the abdomen provides rapid escape from predators – backwards! In females it cups under to support and protect the egg-mass.

Figure 4: External features of the western rock lobster:

(Ventral view, left side male, right side female).

- Elongated forelimbs of male used in mating.
- Jaws (mandibles) surround the mouth.
- Third maxilliped used to hold food and bring it to the mouth.
- 'Exhalent aperture' through which water passes out of the gill chamber.
- Genital pore at base of fifth leg of male, through which sperm and putty-like secretions pass, to be pressed on to the female's abdomen between the fifth pair of legs forming the 'tar-spot'.
- Smooth tough membranes of chitin, flexible due to the lack of calcium, cover the underside of the abdomen.



- Excretory pore through which 'urine' from the 'green gland' is excreted.
- 'Chest' (sternal plate).
- Genital pore at base of third pair of legs of females, through which eggs are released.
- Female fifth leg has a small nipper-like structure at the last joint, used in grooming and cleaning the egg-mass held under the abdomen.
- Swimmerettes (pleopods). In females these leaf-like structures also bear a clasping structure (endopodite) which in the breeding season bear fine hairs (setae) to which the eggs attach.
- Anus, through which indigestible material is excreted.