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TR EL-82-4

Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)

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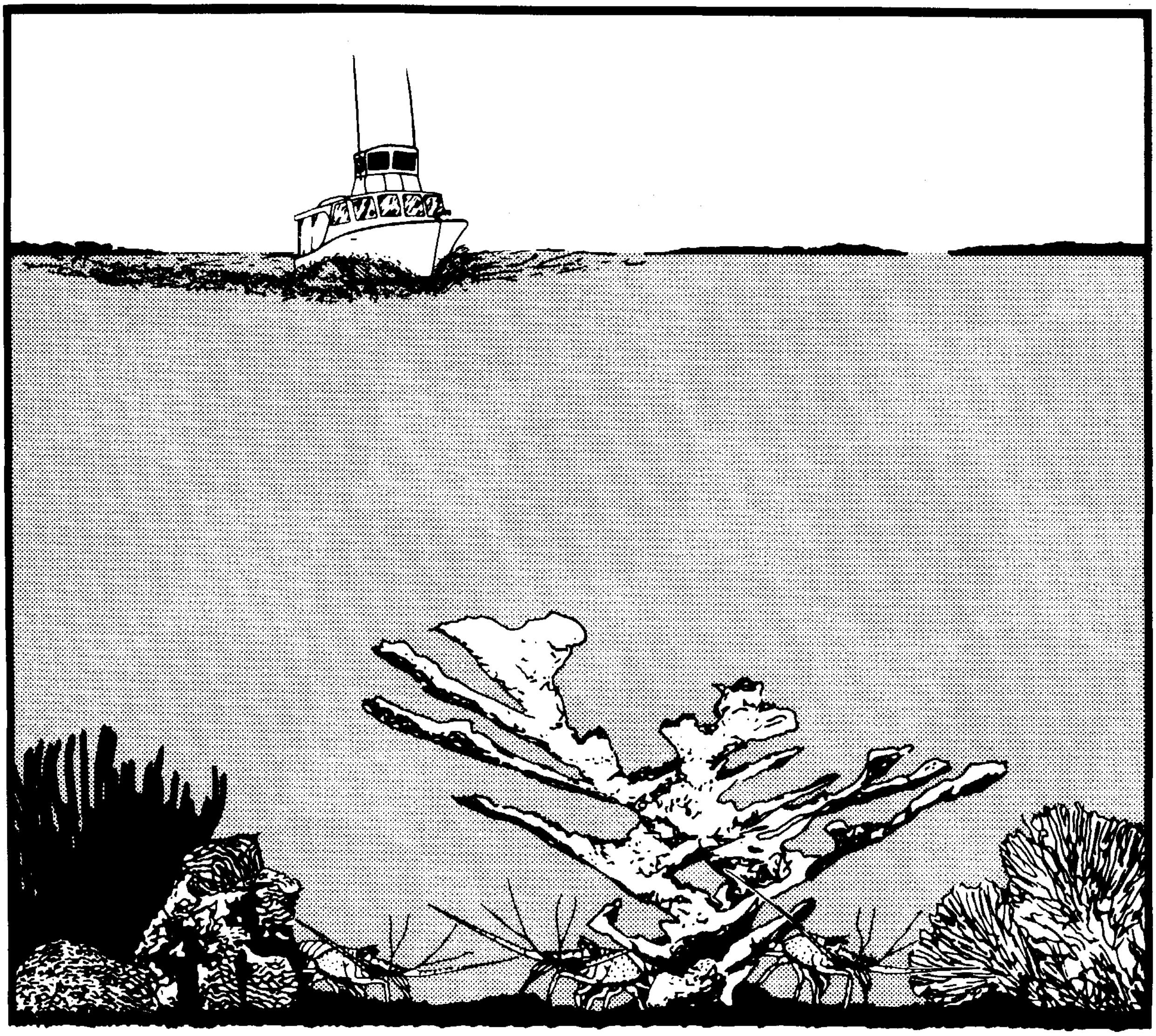

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)

SPINY LOBSTER

by

James M. Marx
and
William F. Herrnkind
Department of Biological Science
Florida State University
Tallahassee, FL 32306

Project Officer
John Parsons

National Wetlands Research Center
U. S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

Information Transfer Specialist
National Wetlands Research Center
U.S. Fish and Wildlife Service
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458

or

U.S. Army Engineer Waterways Experiment Station
Attention: WESER-C
Post Office Box 631
Vicksburg, MS 39180

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(°F - 32)	Celsius degrees

CONTENTS

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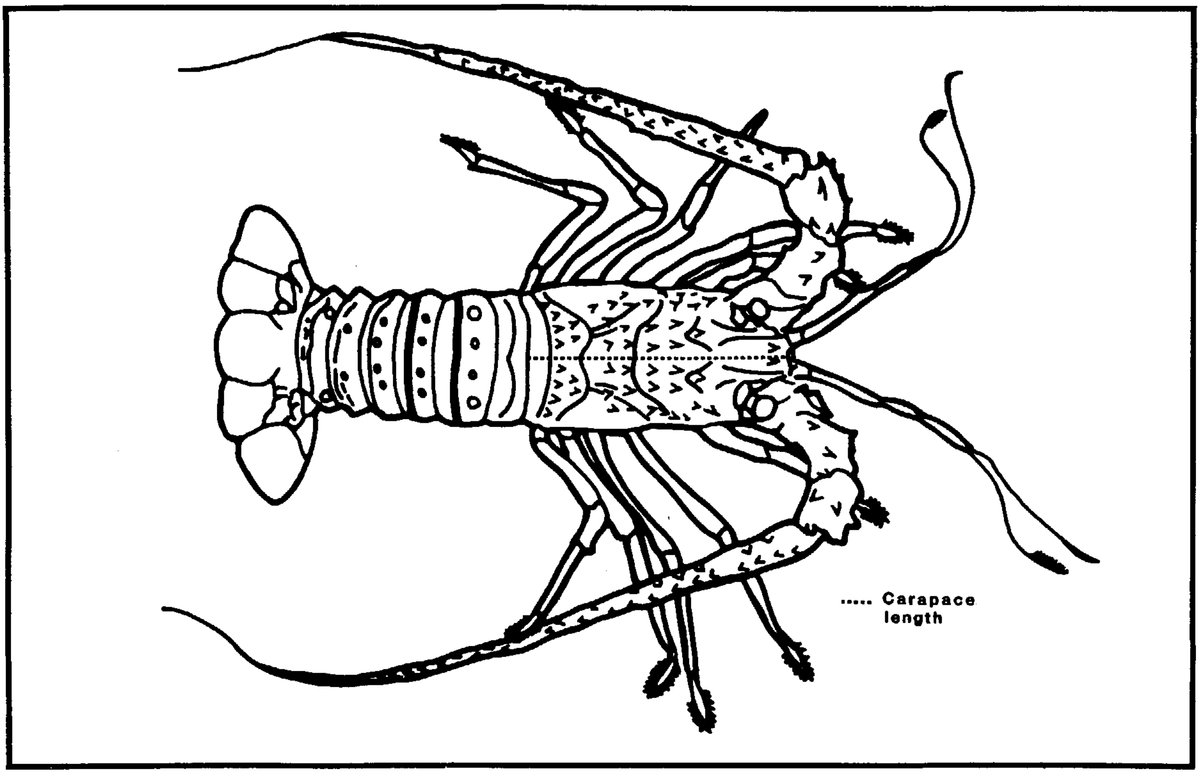

Figure 1. Dorsal view of an adult spiny lobster, Panulirus argus.

SPINY LOBSTER

NOMENCLATURE/TAXONOMY/RANGE

Scientific name. . . . Panulirus argus (Latreille)
Preferred common name. .Spiny lobster, crawfish (Figure 1)
Other common names. .Crayfish, Florida spiny lobster, Western Atlantic spiny lobster, Caribbean spiny lobster, rock lobster, "bug"

Class. . . . . Crustacea
Order. . . . . .Decapoda
Family . . . . Palinuridae

Geographic range: The spiny lobster inhabits the coastal waters and shallow Continental Shelf waters from North Carolina south to Brazil, including Bermuda and the Gulf of Mexico (Williams 1965) (Figure 2). A few specimens have been collected in the Gulf of Guinea, West Africa (Marchal 1968).

MORPHOLOGY/IDENTIFICATION AIDS

General: The subcylindrical carapace is studded with forward-projecting spines, and prominent rostral horns extend over stalked eyes. Long, whip-like antennae are tapered anteriorly and covered with small spines. The slender, elongate walking legs (pereopods) bear setose dactyls. The tail is smooth except where notched along the lateral edges, and the transverse groove on each tail segment is interrupted at the midline. The tail fan is composed of a central telson bordered by a pair of biramous uropods.

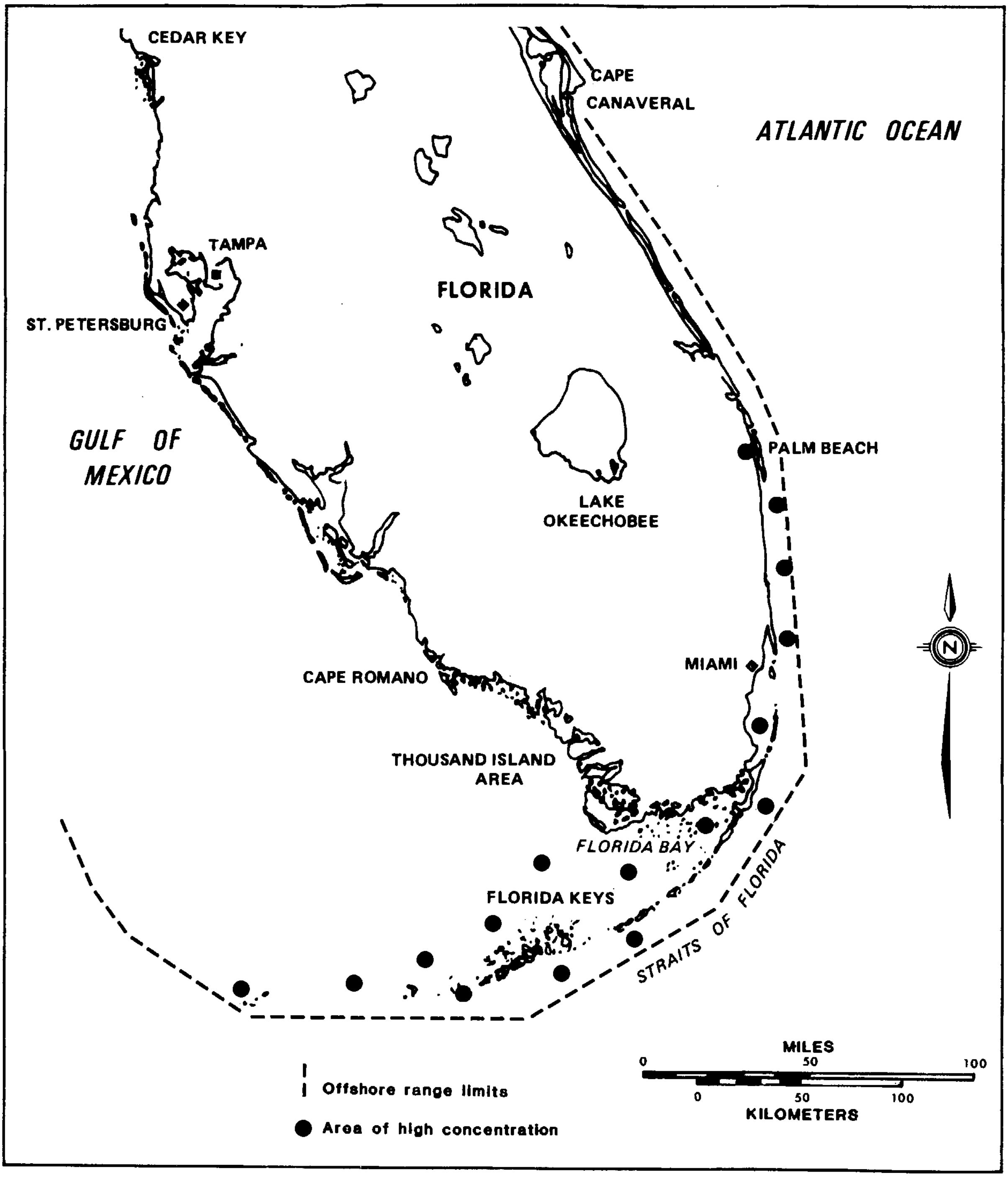

Figure 2. Distribution of the spiny lobster, Panulirus argus, on the south Florida coast.

Color: In young juveniles (7 to 20 mm carapace length; all lengths of lobsters in this profile are carapace lengths unless otherwise stated), the antennae and pereopods are banded with distinct white stripes; a broad white stripe extends along the dorsal midline of the carapace and abdomen. The general body colors are shades of brown, black, and purple. Adult color varies from light gray or tan with green and brown shades to deeper brown with red and black shades. The second and sixth tail segments have large white or yellowish ocelli; small ocelli are dorsolateral on other tail segments. The legs are striped longitudinally with dull blue, and the pleopods are bright orange and black.

Sexual dimorphism: Females are distinguished by the small chela on the dactyls of the fifth pereopods; the adult male is characterized by an elongate second pair of legs bearing extended, curved dactyls. The endopodite of female pleopods is well developed, hooklike, and heavily setose. In males, the raised genital openings lie at the base of the fifth pair of legs; in females they lie at the base of the third pair of legs. The female sternum is striated and narrower at its posterior margin than in the male.

Related species: The sympatric *P. laevicauda* has no dorsal grooves on the tail segments and bears small white spots along the lateral margin of the tail; *P. guttatus* has a single, uninterrupted transverse groove on the second through the fifth tail segments and has many white spots over the body.

REASON FOR INCLUSION IN THE SERIES

Panulirus argus supports major commercial fisheries in south Florida, the Bahamas, Cuba, Brazil, and throughout the Caribbean. Spiny lobsters are mid- to high-level predators and probably are important in structuring marine benthic communities. Throughout their lives, lobsters live among diverse habitats and exhibit behavioral and physiological characteristics that make them excellent test organisms for basic research.

LIFE HISTORY

The life history of the spiny lobster consists of five major phases, having the following distinctive behaviors and habitat use: (1) oceanic planktonic phyllosome larvae, (2) swimming postlarval pueruli (singular = puerulus), (3) early benthic "banded" juveniles, (4) later juveniles (20-65 mm carapace length, CL), and (5) adults. A broad range of marine habitats are used during their life cycle (Figure 3).

Spawning Habits

Most spiny lobster in Florida waters reproduce during late spring and early summer. Crawford and De Smidt (1922) reported peak spawning in April and May; Dawson and Idyll (1951) observed a peak in April (29% of females sampled bore eggs); and Lyons et al. (1981) noted high levels in May (32.8%) and June (30.3%). Davis (1975) reported an April peak (55%) for an unfished population of large lobsters at Dry Tortugas. Yearly variations in peak spawning time depend largely on water temperature. Crawford (1921) reported optimal spawning at 24° C, whereas Lyons et al. (1981) observed that spawning began at 24° C in deep reef areas (30 m). In Florida, there is no direct evidence that lobsters spawn more than once a year, but some repeat spawning by some individuals is suspected in Bermuda waters (Creaser 1950; Sutcliffe 1952).

The spiny lobster spawns in offshore waters along the deeper reef fringes (Kanciruk and Herrnkind 1976; Warner et al. 1977; Lyons et al.

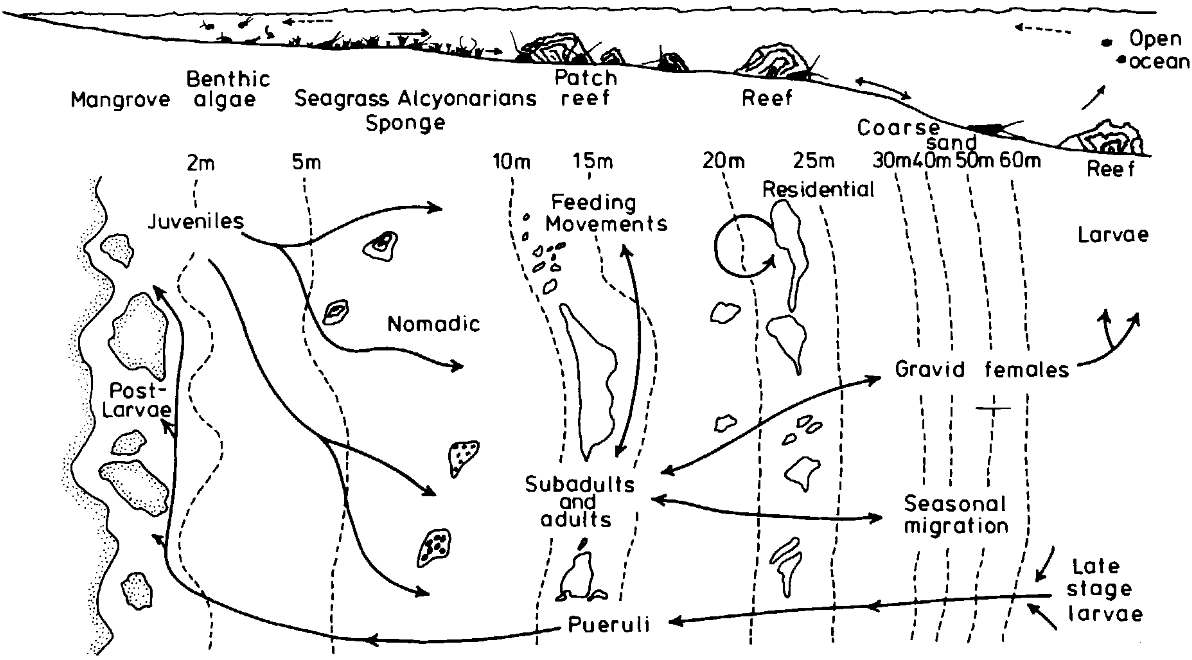

Figure 3. The spatial aspects of the life cycle of the spiny lobster Panulirus argus. The postlarval pueruli move inshore, settling in subtidal algae. Juveniles during the first 2 years of benthic life remain in lagoons and shallow seagrass beds and show both nomadic and residential phases in apparent accord with food and shelter. The subadults gradually emigrate from the nursery and disperse about the extensive shallow (3-10 m depth) banks characteristic of their range. After breeding on the reefs, the females move to waters bordering oceanic currents to release larvae. Adults exhibit seasonal cycles of residency, nomadism, reproductive migration, and inshore-offshore migration (sometimes en masse). The pattern of movement varies considerably over the range of the species (from Herrnkind 1980 reprinted with permission from Academic Press, New York).

1981). Although adult males and females sometimes inhabit bays, lagoons, estuaries, and shallow banks, none are known to spawn there. Requirements of offshore spawning are high shelter quality, suitable water conditions (stable temperature and salinity, low surge and turbidity), and adequate larval transport by oceanic currents (Kanciruk and Herrnkind 1976).

Mating follows a brief courtship involving signals by both male and female. During copulation, the male holds the female sternum to sternum against him and extrudes a spermatophoric mass. The gray tarry spermatophore adheres to the female sternum until spawning. The sperm may remain viable for as long as one month.

Spawning is described in detail by Crawford and De Smidt (1922) and Sutcliffe (1952). The female abdomen is flexed in cuplike fashion beneath the cephalothorax, and the telson and uropods are spread. Eggs (spherical, 0.5 mm diameter) are liberated externally through the gonopores located at the base of the third pair of walking legs. Fertilization begins as a female scratches at the spermatophore packet using the chelate dactyls of the fifth walking legs. The bright orange, yolk-filled eggs adhere to hooklike pleopodal setae on the underside of the abdomen. Fecundity varies directly with size: females 71 to 75 mm long carry 230,000 eggs; females longer than 100 mm may carry over 700,000 eggs (Mota-Alves and Bezerra 1968). Embryonic development lasts about 3 weeks (Crawford 1921). The eggs turn brown a few days before hatching. The phyllosomes emerge from the egg membrane and disperse into the water column assisted by abdominal movements of the female.

The relative (percentage) contribution of each size class in the population to the total number of eggs layed can be estimated using the Index of Reproductive Potential (IRP; Kanciruk and Herrnkind 1976), which states:

$$IRP = (A \times B \times C)/D$$

where
- A = total females within a given size class/total females in the population
- B = % of females bearing eggs in that size class
- C = fecundity of females in that size class
- D = a constant (total eggs laid/100%) derived to set the index of a particular size class at the percentage contribution to the total egg production.

Applying the IRP to the lobster population of the upper Florida Keys, Lyons et al. (1981) estimated that the 76-85 mm CL size class contributed 48% of total egg production. Females longer than 85 mm made up only 20% of all females, but contributed about 41% of eggs. Smaller size classes (< 76 mm CL) constituted 25% of all females, but contributed only 11% of the eggs. Compared to the index values for the unfished population at Dry Tortugas (data provided by Davis 1975), Lyons et al. (1981) estimated that egg production in the Florida Keys was only 12% of that to be expected from an unfished population of similar size.

Intense fishing may have caused a decline in the minimum size of spawning females in Florida waters. The smallest egg-bearing females reported by Crawford and De Smidt in 1922 were 76 mm, but in recent surveys egg-bearing females were as small as 71 mm (Warner et al. 1977) and 65 mm (Lyons et al. 1981). In contrast, the smallest egg bearer observed from an unfished population at Dry Tortugas was 78 mm (Davis 1975). Suggested causes for this apparent decline in size are genetic selection (Warner et al. 1977), modified sexual behavior when large females are rare (Lyons et al. 1981), and reduced growth caused by high injury rates (Davis and Dodrill 1980). The minimum legal size (established in 1965) may not adequately protect spawning stock in Florida (see a related discussion in the section on the Commercial and Sport Fishery).

Larvae

Eggs hatch as transparent, phyllosome (leaf-bodied) larvae. They are morphologically well equipped for planktonic life, bearing long, highly setose appendages extending from a dorsoventrally flattened, bilobed cephalothorax. Phyllosomes swim in a horizontal position by means of the exopodal action of the biramous legs (Provenzano 1968). They undergo a diel pattern of vertical distribution, ascending to surface waters at night and descending during the day (Sims and Ingle 1967). Distribution is otherwise regulated by ocean currents and other factors that influence water circulation patterns (Austin 1972).

Phyllosomes develop through about 11 stages, increasing in size from 2 mm (total length) at hatching to nearly 34 mm before metamorphosis (Lewis 1951). Duration of the phyllosome stage is about 6 to 12 months (Lewis 1951; Lyons et al. 1981).

The uncertainty of the duration of the phyllosome stage renders the question of larval origins problematic. Major factors causing uncertainty are variations in growth rates, delays in metamorphosis, the widespread abundance of larvae, and the inherent complexities of oceanic circulation throughout the western Atlantic region (Lewis 1951; Sims and Ingle 1967; Austin 1972; Richards and Potthoff 1981). The larval source for Florida is unknown, but two different origins are proposed: (1) larvae of Caribbean spawning stocks (Lewis 1951; Sims and Ingle 1967) are transported downcurrent to Florida, and (2) larvae of local stocks are retained by idiosyncratic current patterns off the coast of Florida (Menzies and Kerrigan 1979). Neither proposal is conclusive, and new research approaches are under study, particularly biochemical genetics (Menzies 1981; see Lyons 1981 for a thorough review).

Postlarvae and Early Juveniles

The spiny lobster larva metamorphoses into a puerulus, a brief (several weeks), nonfeeding, oceanic phase (Lyons 1980). The puerulus possesses a number of distinctive features including adaptations for rapid, efficient swimming (e.g., a smooth, lightweight transparent body lacking calcification and spines, and a dorsoventrally flattened carapace).

After metamorphosis offshore (Sweat 1968; Witham et al. 1968), pueruli swim shoreward by night, antennae directed forward, within a few centimeters of the water surface (Lyons 1980). Propulsion is provided by specialized abdominal pleopods. Large numbers of pueruli arrive along the southeast Florida coast and southern shores of the Florida Keys throughout the year, principally during the new and first-quarter lunar phases (Sweat 1968; Witham et al. 1968; Little 1977; Little and Milano 1980). The season of peak recruitment varies considerably from year to year and regionally, but maximum numbers generally arrive inshore in spring; there is a lesser peak in fall (Lyons 1980). Because Florida lobsters spawn almost exclusively in late spring, year-round recruitment of larvae suggests that a substantial number of pueruli originate elsewhere.

Pueruli settle rapidly when they encounter suitable inshore substrate. They acquire reddish-brown pigmentation and within days molt into the first juvenile stage. The distinctive color patterns of early benthic juveniles are a combination of cryptic (different shades) and disruptive (bands or stripes) features that make juveniles in vegetation nearly invisible.

Little is known about factors that stimulate postlarval settlement and specific habitat requirements of early juveniles. Witham et al. (1964) caught postlarvae and young juveniles up to 25 mm long among algal-fouled mangrove roots and algal clumps collected from shallow seagrass beds. Marx (1983) observed postlarvae and juveniles up to 20 mm long in shallow (2-3 m) macroalgal assemblages dominated by several species of the red alga *Laurencia*. Somewhat later stages ($\overline{x}$ = 21 mm CL) inhabited small holes and crevices within a shallow, algal-fouled rubble zone dominated by various red algae, primarily *Laurencia* (Andree 1981). Eldred et al. (1972) and Davis (1979) reported substantial catches of lobsters 11 to 30 mm long in Biscayne Bay by bait shrimp trawlers. Trawling took place over sand/mud bottoms with abundant seagrasses, calcareous green algae, and *Laurencia*.

Early benthic larvae and juveniles apparently concentrate in macroalgae beds along rocky shorelines and may be interspersed among large expanses of seagrass that typify known nursery areas like Florida Bay (Davis and Dodrill 1980; Lyons et al. 1981) and Biscayne Bay (Davis 1979).

Early benthic lobsters tend to live a solitary existence (Andree 1981; Marx 1983). Because they have easy access to their food supply, foraging time for young juveniles and exposure to predators are minimal. Young juveniles are highly aggressive, using the antennae to lash or pry conspecifics, suggesting that dispersed spacing patterns may be maintained by agonistic behavior.

Late Juveniles and Adults

Most lobsters longer than 20 mm aggregate in various sheltering structures in protected bays, including estuaries with high salinity (Olsen et al. 1975; Davis 1979). Shelters include large sponges, coral heads, mangrove roots, grass-bed undercuts, solution holes, rocky outcroppings or ledges, and even clumps of sea urchins (Davis 1971). Most shelters supply partial camouflage, physically deter predators, and provide refuge from physical stress. Adult coloration replaces the cryptic pattern, and late juveniles begin to exhibit active antipredator defense using the antennae as foils.

The ontogenetic transition from "solitary-asocial" to "aggregative-social" is apparently not rigidly fixed, and probably depends in part on the distribution and physical characteristics of lobster shelter (Andree 1981; Marx 1983). Juveniles tend to be nomadic, usually taking shelter after foraging at night. Where juvenile density is high, transient movements are especially apparent in areas of intermittent shelter, e.g., the shallow waters of the Florida Keys (Herrnkind 1980).

Lobsters approaching maturity (70-80 mm) emigrate offshore (Witham et al. 1968; Olsen et al. 1975; Davis 1979). These emigrations are usually gradual and nomadic, but short-term mass movements do occur. These movements widely disperse the lobsters along the reefs that parallel the Florida Keys (Warner et al. 1977; Davis 1979; Herrnkind 1980). Sex ratios inshore indicate that more females than males emigrate offshore (Olsen et al. 1975; Davis and Dodrill 1980; Lyons et al. 1981).

Offshore lobster populations are composed predominantly of adults residing individually or communally in crevices of rock or coral. After foraging at night (up to several hundred meters) most adults return to the same or nearby dens (Herrnkind et al. 1975). Homing apparently involves orientation of the lobster to hydrodynamic (current and wave surge), chemical, topographic, and gravitational (slope) cues (Herrnkind 1980). Adult lobsters are highly selective of dens, residing most frequently in crevices that allow full withdrawal of the body, deny access by large predators, and contain other lobsters (Herrnkind et al. 1975). The preference for an occupied den is generally interpreted as a social response, i.e., being attracted to conspecifics. Both late juveniles and adults are gregarious.

The tendency for adult lobsters to congregate probably is a requirement for adequate defense, mating, and shelter use. Lobsters may resist predators by blocking large den openings or by forming a cohesive group adjacent to less formidable shelters like sponges and sea whips. Males initiate mating by seeking receptive females often found congregated during the day (Lipcius et al. 1983).

Concentrations of spiny lobsters in the waters of the Florida Keys tend to shift in autumn and during the spring reproductive period. Some movements are sex dependent and sometimes cause sharp differences in male-female ratios from place to place

(Herrnkind 1980). Females move to deeper reefs in the spring, presumably to mate and shed larvae (Crawford and De Smidt 1922; Davis 1977; Lyons et al. 1981). At Dry Tortugas, females return to shallow water after releasing their larvae. Normal sex ratios (about 1:1) are restored by fall (Davis 1977). Both sexes emigrate offshore in the fall as water temperatures decline and fall storms arrive (Davis 1977; Kanciruk and Herrnkind 1978; Herrnkind 1982). Sometimes offshore movements are spectacular mass migrations of lobsters forming single-file columns or queues (Herrnkind and Kanciruk 1978; Kanciruk and Herrnkind 1978; Herrnkind 1980).

GROWTH CHARACTERISTICS

The growth of the spiny lobster is largely correlated with the frequency of molting and increment growth while molting (Aiken 1980). Generally, the frequency of the molts and increment growth decline with age, as is borne out by the von Bertalanffy growth model (a decaying exponential curve), which states:

$$L_t = L(1-e^{k(t-t_0)})$$

where L_t = carapace length at time t
L = asymptotic carapace length
e = base of natural logarithms
t_0 = time at which carapace length was 0,
k = the growth coefficient (rate at which L_t approaches L).

Estimates of the growth coefficients (k) in different waters sometimes vary considerably. Coefficients were 0.11 for the lower Florida Keys (Yang and Obert 1978), 0.21 for Florida and Belize combined (Munro 1974), 0.31-0.36 for south Florida (see Gulf of Mexico and South Atlantic Fishery Management Councils [GMSAFMC] 1982), 0.03-0.24 for the Bahamas (Waugh 1981), and 0.43 for St. John, U.S. Virgin Islands (Olsen and Koblick 1975). Variation is caused partly by differences in methodology used to estimate growth, but most differences are caused by changes in environmental conditions. Local variability in food abundance, population density, predatory attacks (inducing injuries), and water temperature greatly affects growth rates of spiny lobsters (Newman and Pollock 1974; Chittleborough 1976; Davis 1979; Aiken 1980; Waugh 1981).

Growth sometimes varies within a relatively small area; consequently, the relations among size, sex, and growth are unpredictable. Furthermore, data from recaptured tagged lobsters are difficult to obtain for all size ranges, prohibiting accurate analysis of molt frequency and increment per molt and the use of von Bertalanffy growth models (Davis 1979; Waugh 1981). Growth data for Florida lobsters are usually shown as mean size increments per unit of time for particular size groups.

The monthly growth rate of spiny lobster (starting with pueruli 6 mm CL) reared for 7 months was 3.8 to 4.2 mm/mo, given an average size of 34 mm (6 mm CL at metamorphosis plus 7 X 4 mm or 28 mm) (Witham et al. 1968); an average growth rate of 5 mm/mo for the first 9-10 months after settlement was estimated from length (CL) frequency data (Eldred et al. 1972) from lobsters sampled in Biscayne Bay. The pattern of length frequency, however, is reliable only up to lengths of 25 mm, after which interpretations of field data are seriously biased by the lack of distinct settling classes. Young juveniles confined in small aquaria with a limited diversity of food grew substantially slower (< 2 mm/mo) than most natural populations (Lewis et al. 1952; Sweat 1968).

Growth rates were estimated during a 2-year tag-and-recapture study in Biscayne Bay and Florida Bay, both of which are major nursery areas (Davis and Dodrill 1980; Davis 1981).

In Biscayne Bay, the mean growth rate of lobsters 40-85 mm long was 1.8 mm/mo. The physical condition of individuals significantly affected growth: uninjured lobsters grew 2.2 mm/mo, but those missing legs and antennae grew only 1.3 mm/mo, a 41% reduction. In Florida Bay, mean growth rate of lobsters of about the same size was 3.3 mm/mo. Injured lobsters grew nearly as fast. Davis and Dodrill (1980) attributed increased growth and the lack of damaging effects from injury to optimal growing conditions and low fishing effort in Florida Bay. In waters near Key West, tagged lobsters 49 to 83 mm long grew an average of 3.1 mm/mo (Little 1972).

The postsettlement time required for juveniles to reach minimum legal size is important to fishery management. Estimates of postsettlement times, and of carapace lengths after 2 years of benthic life, are shown in Table 1. The first 7 months of each growth estimate after the beginning of the puerulus stage (6 mm CL) are based on a mean growth rate of 4.0 mm/mo; thus the lobsters are 34 mm long 7 months after settling (Witham et al. 1968). The remaining 17 months of each estimate are based on growth rates of lobsters over 40 mm long in various areas. For example, the estimated carapace length of injured Florida Bay lobsters after 2 years was 34 mm + (17 mo x 3.2 mm/mo) = 88 mm. The estimated number of months to reach legal size (76 mm) is obtained by dividing 42 mm (76 mm - 34 mm = 42 mm, the growth after 7 mo) by the observed growth rate after 7 months and adding 7 months. From the above data it was calculated that the lobsters reach legal length in about 20 months (42 mm/3.2 mm/mo + 7 mo).

An interaction between sex and growth of spiny lobsters is known (Chittleborough 1976; Aiken 1980). Lobsters of the two sexes show near equal growth in the nurseries of Florida Bay and Biscayne Bay (Davis and Dodrill 1980). However, adult female lobsters grow slower than males. This growth differential has been reported for the lower Florida Keys (Little 1972), Bahamas (Waugh 1981), and U.S. Virgin Islands (Olsen and Koblick 1975).

Table 1. Estimated time[a] for injured and uninjured lobsters at different locations to reach legal size (76 mm carapace length [CL]).

Location and condition	Number of observations	Mean growth (mm/month)	Carapace length (mm) after 2 years	Number of months to reach legal length[a]
Florida Bay[b]	644			
Injured		3.2	88	20.4
Uninjured		3.4	92	19.6
Biscayne Bay[b]	1688			
Injured		1.3	56	40.1
Uninjured		2.2	71	26.5
Key West[c]				
Combined	44	3.1	87	20.9

[a] After puerulus settlement; add 9 months to obtain approximate age.
[b] Based on Davis and Dodrill (1980).
[c] Based on Little (1972).

Length-weight relationships differ significantly by sex. Lyons et al. (1981) derived the following equations:

Males $W = 0.00315\ CL^{2.69934}$

Females $W = 0.00361\ CL^{2.68379}$

where W = wet weight in grams, CL = carapace length in mm.

The derived equation for combined sexes,

$$W = 0.00422\ CL^{2.64091},$$

gives a reasonable approximation.

COMMERCIAL AND SPORT FISHERY

The Florida spiny lobster is a valuable sport and commercial species. The spiny lobster supports Florida's second most valuable shellfishery. In 1980 the commercial catch was 6.7 million lb, with a dockside value exceeding $14 million (National Marine Fisheries Service, Statistical Reporting Service, Miami, Florida). Sport and commercial fishing for this species is concentrated in the Florida Keys (Monroe County). Some spiny lobsters are taken by sportsmen in most coastal waters of Florida.

Fishermen using top-entry wood-slat traps account for 99% of the total commercial catch; commercial divers and shrimpers, who occasionally capture lobsters in trawls (GMSAFMC 1982), account for the remainder. Sport divers use skin- or scuba-diving gear, gloves, and small hand-held nets to catch lobsters. The sport catch is about 10% of the commercial catch and provides a seasonal boost to the tourism-dependent economy of the Florida Keys (GMSAFMC 1982). Regulations in 1984 prohibited lobster fishing from 1 April through 25 July and required that all lobsters must be $\geq$ 76 mm CL or have tail lengths of at least 140 mm. Egg-bearing females must be returned to the sea.

Commercial fishing has intensified greatly since the 1960's. New boats have entered the fishery, the number of traps fished per boat has increased, and Miami-based boats began fishing locally after Bahamian waters were closed to foreign fishing in 1975. Total landings have not risen despite increased fishing intensity. The consequence has been a dramatic decline in catch per trap, e.g., catch per unit effort (CPUE; Table 2). Landings have remained relatively stable since 1970, averaging 4.8 million lb/year. Some fisheries biologists believe that the stable landings indicate stable recruitment and abundance of harvestable stocks. Lowered CPUE is blamed on industrial overcapitalization (Austin 1981; GMSAFMC 1982). Possibly three times the number of traps are fished as are needed to harvest the available yield (GMSAFMC 1982), so total mortality estimates and exploitation ratios increased from 1975-76 to 1978-79 (Table 3). If these increases truly reflect the efficiency of exploitation (resulting from increased effort), total landings should have increased given a constant harvestable stock. In short, stable landings may be a misleading consequence of increased fishing intensity on declining stocks.

Population Size Composition and Reproductive Potential

Lyons et al. (1981) noted a 12-mm decrease (90 mm to 78 mm CL) in the modal length of Florida Keys lobsters since 1945-49 (Dawson and Idyll 1951). The modal carapace length of 78 mm is about 30% smaller than that of the unfished population at Dry Tortugas (100 mm CL; Davis 1977). The decline in the size of the mature female has caused a marked reduction in reproductive potential (egg production). Lyons et al. (1981) estimated the Florida Keys population spawns only

Table 2. The landings (millions of pounds) and ex-vessel values (millions of U.S. dollars) in domestic waters and the landings, number of traps fished, and catch per trap for Monroe County (Florida Keys), 1970-79 (adapted from GMSAFMC 1982).

	Florida landings			Monroe County landings		
Year	Total[a] (lb)	Total ($)	Domestic[b] (lb)	Total (lb)	Number of traps	Catch (lb) per trap
1970	9.9	$ 5.9	6.7	5.2	150,050	35
1971	8.2	7.1	4.7	4.6	147,037	32
1972	11.4	11.8	4.8	4.6	174,490	27
1973	11.2	11.7	5.3	5.0	171,590	29
1974	10.9	13.4	6.6	5.6	227,250	25
1975	7.4	9.9	5.4	4.5	428,250	10
1976	5.3	8.6	4.8	4.1	306,000	14
1977	6.5	10.4	5.1	4.7	408,000	12
1978	5.6	11.9	4.9	4.7	529,200	9
1979	6.0	11.6	5.2	--	--	--

[a] Florida landings include some lobsters caught in foreign waters.
[b] Domestic landings include waters of the entire State of Florida.

Table 3. Size and mortality estimates for the unfished population of spiny lobsters at Dry Tortugas and the fished populations of the lower Florida Keys and the middle to upper Florida Keys (adapted from GMSAFMC 1982).

Location	Lr	Lc	Z	A	F	E	Data source
Dry Tortugas	100	115	1.00	63	--	--	Davis (1977)
Lower Florida Keys (1975-76)	65	78	1.72	82	1.32	0.77	Warner et al. (1977)
Middle to upper Florida Keys (1978-79)	73	81	2.73	94	2.33	0.85	Lyons et al. (1981)

Lr = Size (mm CL) at full recruitment
Lc = Average size of fully recruited population
Z = K (L - Lc)/(Lc - Lr) = Total mortality coefficient
A = 1 - e^{-Z} = Annual mortality rate (%)
F = Z - M = Fishing mortality coefficient
E = F/Z = Exploitation ratio

where L = 190 mm CL, growth coefficient (K) = 0.2, natural mortality (M) = 0.4.

12% of the number of eggs of an unfished population of equal number because the fishery selected and effectively removed the larger, more fecund females. If the decrease in eggs spawned causes a decrease in larvae and recruitment into the fishery, then spawning stocks will have to be better protected. If locally spawned larvae are significant contributors, suggested actions include increasing the minimum legal size and establishing sanctuaries where large, fecund females are protected. If larvae from Florida support lobster fisheries outside of Florida waters and vice versa, cooperative international management agreements may be required (Lyons 1981; Villegas et al. 1982).

Fishery-Induced Juvenile Mortality/ Growth Reduction

Laws enacted in 1976 allow fishermen in Florida to use small, illegal lobsters (locally termed "shorts") as decoys in traps. Fishermen prefer "shorts" over conventional baits such as cowhide or fish heads. Studies confirm that catch rates increase with the number of "shorts" used per trap (Lyons and Kennedy 1981). This practice causes substantial mortality among juvenile stocks. Major stresses are boatside transport and starvation during confinement (Lyons and Kennedy 1981). Loss to the fishery may be substantial because in the 1980's over 500,000 traps are being fished, and fishermen typically use three to five "shorts" per trap (Lyons and Kennedy 1981). Attempts are underway to develop artificial lures as a low-cost alternative (Ache and Hamilton 1982). Another approach would be to require openings of sufficient size among the slats (escape gaps) to allow all undersized lobsters to escape (Lyons and Kennedy 1981).

Injuries to juvenile lobsters (loss of antennae and legs) are commonly caused by attacks from predators and from handling by commercial fishermen and sport divers. In Biscayne Bay, the frequency of injuries increased as much as 50% during the fishing season (Davis and Dodrill 1980). Less frequent injuries were reported for the middle and upper Florida Keys (Lyons et al. 1981). Injured lobsters grow slower (Davis 1981; Waugh 1981) than uninjured lobsters presumably because they are less efficient foragers and because growth is redirected into limb regeneration. Davis (1979) estimated that injuries from commercial handling in Biscayne Bay caused an annual loss of 31,000 lobsters. Lyons et al. (1981) presented evidence that injuries cause high mortality among small (less than legal size) lobsters in the Florida Keys. The Florida State Legislature established a lobster sanctuary in Biscayne Bay in 1979, and the Everglades National Park portion of Florida Bay was closed to recreational lobstering in 1980; both measures were designed to protect juveniles.

Maximum sustainable yield (MSY) for lobster landings in Monroe County is estimated to be 5.9 million lb, on the basis of catch and fishing intensity data obtained from 1952 to 1975 (GMSAFMC 1982). If domestic catches (0.2 million lb), unrecorded landings, and losses due to harvesting practices (estimated at 5.9 million lb) were included, the actual MSY would be nearer to 12 million lb.

ECOLOGICAL ROLE

The diet of spiny lobster phyllosomes has not been sufficiently described. Phyllosomes in culture eat chaetognaths, euphausiids, fish larvae, medusae, and ctenophores (Provenzano 1968; Inoue 1978; Phillips and Sastry 1980). There are no indications that pueruli feed at all (Lyons 1980).

Lobsters are nocturnal foragers throughout the benthic phase, locating food with chemoreceptive setae lining the antennules and dactyls of the walking legs (Ache and Macmillan 1980). They prey upon a wide variety of slow-moving and sedentary animals, including gastropod and bivalve mollusks, crustaceans, and echinoderms (Figure 4). Powerful mandibles crush or chip away at molluscan shells and other types of protective armor. Variations in the diets among recently settled juveniles in concentrations of algae, older juveniles in inshore bays, and adults on coral reefs probably reflect differing prey availability among habitats. Spiny lobsters often are the dominant carnivores (as indicated by total biomass) in their habitat and probably have important ecological effects on marine benthic communities (Berry and Smale 1980).

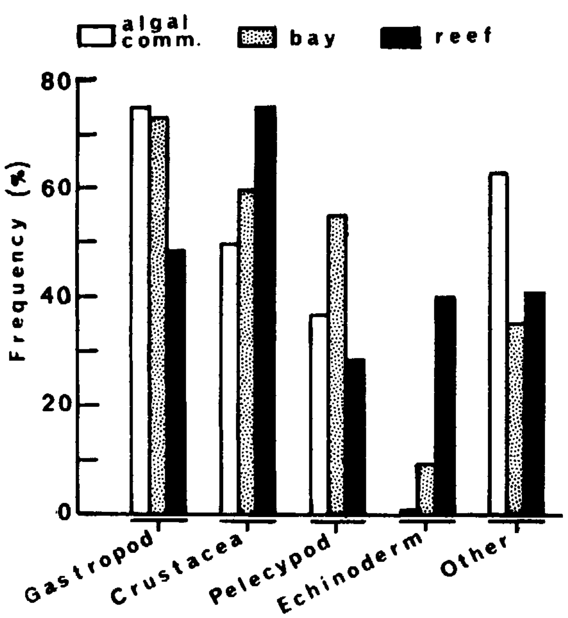

Figure 4. Frequency of occurrence of food items among samples of early benthic lobsters (inshore algal community), later juveniles (bay), and adults (reef) (Herrnkind et al. 1975; Andree 1981).

Substantial numbers of larvae and postlarvae are probably eaten by pelagic fishes (Phillips and Sastry 1980). Pueruli are eaten by benthic (or epibenthic) fauna as well (Gracia and Lozano 1980; Little and Milano 1980). Octopods and portunid crabs prey on recently settled juveniles (Andree 1981). Experiments in aquaria indicate that small fishes (e.g., gray snappers) are probably the most important predators on early benthic stages (Berrill 1976). Because of their relatively large size, spiny exoskeleton, rapid tail-flip escape response, and defense by group formation, late juveniles and adults are well protected from small predators. Large predators, primarily groupers, jewfish, sharks, loggerhead turtles, and octopods, prey on both juvenile and adult lobsters (Kanciruk 1980). Stomachs of large jewfish often contain large lobsters (Crawford and De Smidt 1922).

Competition among lobster species in Florida waters appears to be inconsequential. The other local shallow-dwelling species, Panulirus laevicauda and P. guttatus, are relatively scarce and are restricted mainly to reef habitats.

ENVIRONMENTAL REQUIREMENTS

Habitat

Phyllosoma larvae inhabit the epipelagic zones of the open ocean, which are characterized by relatively constant temperature and salinity, low levels of suspended sediments, and few pollutants. Relatively stable, natural conditions are apparently required for optimum survival. Ingle and Witham (1968) noted that "spiny lobster larvae are extremely delicate, physically, and inordinately fastidious, physiologically." Larvae are particularly sensitive to silt particles, which can, in extreme instances, lodge on their setae, weigh them down, and cause death (Crawford and De

Smidt 1922). Because nutritional requirements change throughout the life of the larvae (Provenzano 1968; Phillips and Sastry 1980), enhanced growth and survival require a diverse, productive oceanic plankton community. Positive correlations between plankton biomass and density of late-stage phyllosomes were reported by Ritz (1972).

Although pueruli settle on isolated oceanic banks where the minimum depth exceeds 10 m (Munro 1974), productive fisheries apparently require well-vegetated shallow habitat for juvenile development. Biscayne Bay and Florida Bay are critical nurseries for Florida lobsters (Davis and Dodrill 1980). These bays are characterized by extensive meadows of benthic vegetation, primarily turtlegrass (Thalassia testudinum), shoalgrass (Halodule wrightii), and various algae (Tabb et al. 1962; Hudson et al. 1970; Eldred et al. 1972). Macroalgal communities interspersed among these areas apparently are important for the earliest benthic stages. Red algae, Laurencia spp., are abundant in waters supporting concentrations of young juveniles (Eldred et al. 1972; Andree 1981; Marx 1983). Intricate algal branching provides young lobsters with cryptic shelter and supports a diverse assemblage of small gastropods, crustaceans, and other prey.

Juveniles larger than 20 mm CL take refuge in both biotic (sponges, small coral heads, sea urchins) and abiotic (ledges, solution holes) structures. The importance of shelter availability on population distribution is magnified because, unlike clawed lobsters, spiny lobsters can modify but not construct dens (Kanciruk 1980). Substantial addition of artificial shelters in Biscayne Bay caused population redistribution but did not increase the numbers of lobsters in the area (Davis 1979). The south Florida juvenile lobster population may be limited by recruitment, emigration, food, and perhaps other factors (Davis 1979).

Adults inhabit coral reef crevices or overhangs, rocky outcroppings, ledges, and other discontinuities in hard substrate. Residential patterns of habitation are apparent in large, permanent dwellings near extensive feeding grounds (Herrnkind et al. 1975). Soft-substrate shelters, like grass-bed ledges, are occupied primarily during nomadic movements. Muddy, turbidity-prone substrates are usually avoided (Herrnkind et al. 1975; Kanciruk 1980).

Throughout benthic life spiny lobsters use other habitats besides those providing shelter. Lobsters concentrated during the day in localized dens disperse at night to forage over adjacent grass beds, sand flats, and algal plains (Herrnkind et al. 1975). Interactions between population density of spiny lobster and food availability have not been studied in south Florida. Extreme variation in growth rates, both among individuals and by habitat, suggests that food abundance is a critical factor, as demonstrated in spiny lobster species elsewhere (Chittleborough 1976).

Temperature

Spiny lobsters generally inhabit waters with annual minimum monthly temperatures that exceed 20° C (George and Main 1967). Along the northern edge of their distribution in Florida, mean monthly water temperatures rarely fall below 16° C (Witham et al. 1968; Hudson et al. 1970; Eldred et al. 1972; Little 1977; Davis 1979). This is just above reported minimum survival temperatures for both larval and benthic life stages. Phyllosomes of the slipper lobster, Scyllarus americanus, which has a geographic range similar to the spiny lobster (Lyons 1970), show retarded development at water temperatures below 16° C (Robertson 1968). Postlarval and young juvenile spiny lobster grow slower and demonstrate higher mortality at temperatures sustained below 16° C (Witham 1974). Postlarval tolerance of short-term, sharp temperature declines to 13° C (Little and Milano 1980) protects them against severe but short-lived cold fronts that sometimes frequent south Florida.

At water temperatures near 13° C, spiny lobsters 65-85 mm CL demonstrate reduced locomotor activity and an inabilty to capture and manipulate prey (Wynne 1979). Direct mortality may occur, especially for lobsters undergoing ecdysis, during rapid water temperature declines to as low as 10° C (Davis 1979). Poor survival at low temperatures, especially if they are sustained for several days, probably limits both the latitudinal and depth distributions of spiny lobsters as well as preventing migration across deep ocean basins like the Florida Straits (Witham 1974; Wynne 1979).

The annual water temperature range in lobster habitats in south Florida is about 18°-31° C. Sharp temperature fluctuations within this range may alter the normal rate of growth of lobsters and their time of settlement. From November to April, the growth of juveniles in Biscayne Bay is reduced by as much as 59%, concurrent with water temperature declines of 8° C (Davis 1979). Growth is rapid but survival is poor at temperatures exceeding 32° C (Witham 1974; Aiken 1980). Growth is optimal between 26° and 28° C. Newly settled postlarvae are particularly vulnerable during temperature extremes and disturbances by hurricanes and winter storms. Fluctuations in juvenile abundance probably are caused by interactions between the rate of settlement and seasonal environmental conditions.

Seasonal temperatures and temperature changes regulate the time of spawning, larval development, and the growth of adults and maturation and growth of juveniles, which vary markedly throughout the geographic range of the spiny lobster (Kanciruk 1980). Year-round spawning occurs in tropical waters (e.g., Venezuela), extended spawning (spring through fall) in the Bahamas, and restricted spawning (March through June) in the Florida Keys. These variations may be caused by a physiological adjustment to differing photoperiods and temperatures (Quackenbush and Herrnkind 1981).

Salinity

Postlarvae do not usually tolerate salinities below 19 parts per thousand (ppt) (Witham et al. 1968). Along the northern Gulf of Mexico, adverse synergistic effects of reduced temperature and variable salinities probably prevent recruitment into nearshore habitats (Austin 1972). Recruitment patterns were disrupted in both 1966 and 1968 in the St. Lucie Estuary when heavy freshwater inflow reduced salinity to below 19 ppt (Witham et al. 1968; Little 1977). Older juveniles are able to use marginal inshore habitats because they are highly mobile and can retreat from unsuitable physical conditions (Herrnkind 1980).

Hydrodynamics

Throughout benthic life, lobsters are influenced by hydrodynamic forces and stimuli (currents, wave surge, turbulence). Puerulus settlement is reduced in areas of strong currents, e.g., channels between the Florida Keys (Little 1977). The post-settlement period may be disrupted by disturbances that alter shelter, interfere with foraging, or cause bodily abrasion. Subadults and adults respond to sharply increased currents and turbulence caused by the first autumnal storms by mass migration (Herrnkind and Kanciruk 1978; Kanciruk and Herrnkind 1978; Herrnkind 1980). Mass movements are particularly striking. The lobsters form single-file lines, or queues, and march in locally precise directions day and night for up to 1 week. The role of sharply increased hydrodynamics in triggering migratory queuing has been experimentally demonstrated (Herrnkind 1982). Mass migration by spiny lobster may redistribute migrants into stable overwintering habitat in deeper reef areas near the Gulf Stream (Herrnkind and Kanciruk 1978). Current flow provides a directional cue both for general orientation and for locating food by chemosenses (Herrnkind 1980).

Oceanic Circulation

Because the movement of phyllosoma larvae is restricted to vertical migration (Phillips and Sastry 1980), ocean circulation patterns are responsible for spreading larvae into distant waters. These patterns consist of (1) initial dispersal of larvae from spawning sites; (2) long-distance transport or retention of larvae; and (3) transport of larvae to nursery grounds. Mechanisms involved in larval transport to south Florida are poorly understood because of complex interactions of major currents of the Gulf of Mexico and Caribbean Sea, seasonal variation in current patterns off the Florida coast, and uncertainty of the extent to which phyllosomes regulate their horizontal distribution by vertical migration into and out of divergent water masses (Sims and Ingle 1967; Little 1977; Menzies and Kerrigan 1979; Lyons 1981). Transport models proposed for other spiny lobster species cannot be strictly applied to spiny lobsters in Florida (Phillips 1981).

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16. Abstract (Limit: 200 words)

The Florida spiny lobster (Panulirus argus) supports major commercial fisheries in south Florida and the Caribbean Sea. Its life history includes several life stages that live in the open ocean, inshore bays, and coastal reefs. The Florida population spawns along deeper offshore reefs in spring and early summer. Fate of locally spawned larvae is uncertain, but significant postlarval recruitment may originate from larvae spawned in foreign waters. After settlement in inshore vegetated habitats, juveniles reach legal harvestable size in about 2 years. The onset of maturity is coincident with a marked emigration offshore. Subsequent seasonal movements cued by reproductive activity and weather disturbances are pronounced. Excessive fishing has caused a decline in the size of the south Florida population and a corresponding reduction in total spawn. The relevance of spawn reduction is uncertain because of questions regarding larval origins and stock-recruitment relations. Water temperatures probably regulate population distribution and the seasonal dynamics of growth and reproduction. Postlarval recruitment is limited to high salinity inshore environments. Hydrodynamic stimuli and water circulation patterns play critical roles throughout the life cycle.

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Lobsters
Feeding habits
Fisheries
Temperature
Life cycles
Growth
Depth
Salinity

b. Identifiers/Open-Ended Terms

Spiny lobster
Panulirus argus
Environmental requirements

c. COSATI Field/Group

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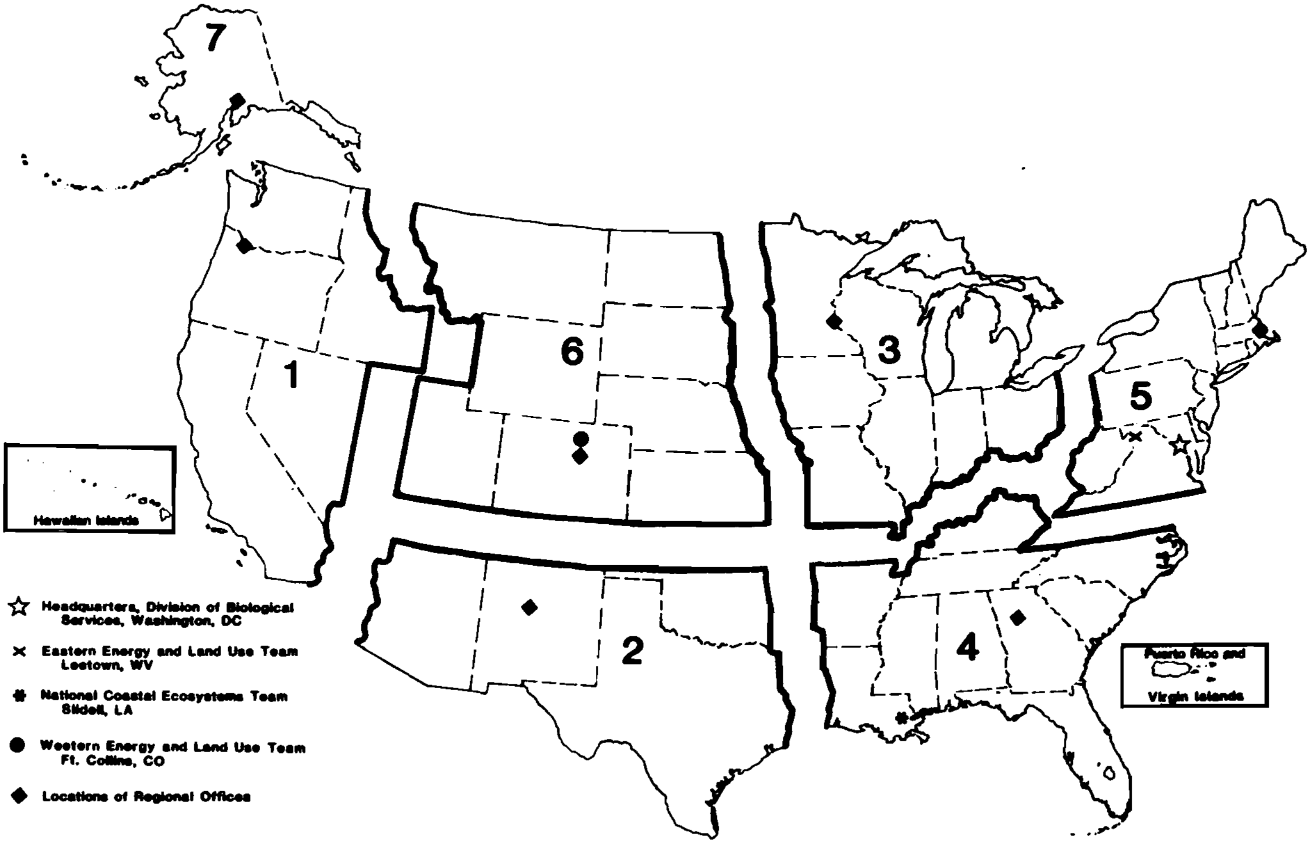

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