EFFECTS OF INJURIES ON SPINY LOBSTER, *PANULIRUS ARGUS*, AND IMPLICATIONS FOR FISHERY MANAGEMENT

The spiny lobster, *Panulirus argus*, supports important commercial and recreational fisheries throughout its range from Bermuda to Brazil. Its ecology and physiology are typical of a number of other commercially important palinurid species, which collectively have pantropic distributions (Phillips and Cobb 1977).

A variety of decapod crustacean responses to injuries, primarily limb loss, have been recorded. Aiken (1977) summarized a number of studies conducted in laboratories, some of which found that limb loss greatly accelerated ecdysis. Other observers noted limb loss resulted in reduced growth rates (Chittleborough 1975; Ford 1977; Savage and Sullivan 1978). This paper reports the effects of injuries on growth rates of wild juvenile spiny lobsters, *P. argus*, in Florida and discusses the implications of these effects on *P. argus* biology and its fishery.

Spiny lobsters (Palinuridae) have complex life cycles. Larval, early juvenile, and adult stages of the spiny lobster in Florida, *P. argus*, are ecologically dissimilar and are found separately in relatively discrete habitats. The planktonic phyllosoma larvae spend 5 to 9 mo in the open ocean before metamorphosing into actively swimming postlarvae, called pueruli (Lewis 1951). Pueruli swim into shallow coastal waters where they settle onto the bottom, assuming the benthic existence they will follow the rest of their lives. Postlarval and small juvenile spiny lobsters are found scattered throughout seagrass beds, particularly in shallow inshore areas like Biscayne Bay. Larger juveniles concentrate around rocky outcrops, sponges, and groups of sea urchins for shelter during the day (Khandker 1964; Davis 1971; Berrill 1975). They forage nightly on adjacent grassbeds and open sand areas for small mollusks, echinoids, and crustaceans (Herrnkind et al. 1975). Mature lobsters are generally associated with coral reefs, or other hard bottom, offshore to depths >150 m. The transition from inshore juvenile habitat to habitat offshore is sometimes accomplished by spectacular mass migrations, marked by long queues of lobsters (Herrnkind and Cummings 1964; Kanciruk and Herrnkind 1978).

The fishing season for *P. argus* in Florida extends slightly more than 8 mo from late July through March, with a special 2-d sport fishing season 5 d prior to the beginning of the regular sport and commercial season (Florida Statute 370.14). Recreational diving activity directed at spiny lobster harvest is particularly intense in nearshore areas during the first 6 to 8 wk of each season (Austin 1976). There are also over 1,000 commercial trappers, fishing up to 2,000 traps each, in the fishery (Beardsley et al. 1975).

Methods

At weekly or monthly intervals during 1976 and 1977, spiny lobsters were captured in southern Biscayne Bay, Fla., by hand, bully net, or tail snare and marked with spaghetti tags. The details and efficacy of this tagging procedure were reported by Davis (1978). Data on size (as carapace length, CL), injuries, molt condition, location, and water temperature were recorded. Injuries were recorded as the number of missing legs or antennae, or damage to the abdomen, cephalothorax, or supraorbital horns.

Growth of spiny lobsters takes place as the result of a series of molts, during which discontinuous size changes occur. The rate of growth is dependent on both magnitude of change in size with each molt (molt increment) and the length of the intermolt period. In this study, growth rate was expressed as change in carapace length per week, since nearly all observations of marked lobsters were made at weekly intervals. To reduce the variability inherent in measuring discontinuous changes in carapace length that resulted from random observations of growth during the molting cycle, all changes in size were summed over each class of observations (i.e., winter, summer, injured, or uninjured) and expressed as rates per week.

Results

A total of 7,643 *P. argus* were examined from February 1976 to December 1977. They ranged from 15 to 101 mm CL, with a mean of 60.7 mm CL (Table 1). Mean monthly water temperatures varied from 16° to 32° C.

Observations of growth were made for 844 time intervals, ranging from 1 to 82 wk (mean 20 wk), on 534 individual lobsters in the wild, ranging from 38 to 83 mm CL. Carapace length measurements were replicated by independent observers on the same day for 153 lobsters during the 22-mo tagging period to evaluate the precision of the carapace length measurements by various

TABLE 1.—Monthly summary of size, molting activity, and condition of spiny lobsters, and water temperatures in eastern Biscayne Bay, Fla., 1976-77.

Month	Number of lobsters	Size (mm CL) Min	Max	Mean	Percentage Molting	Injured	Mean water temp (° C)
1976:							
Feb.	1,247	34	84	56.1	8	53	16
Mar.	353	33	83	56.4	9	51	26
Apr.	464	38	86	60.0	12	45	25
May	362	34	79	59.4	12	39	27
June	340	43	87	63.2	14	46	29
July	414	15	85	61.6	8	31	31
Aug.	398	37	83	63.5	7	38	31
Sept.	217	40	96	63.1	6	42	30
Oct.	25	35	89	64.6	12	24	26
Dec.	139	38	85	54.7	13	42	17
1977:							
Jan.	86	33	85	57.7	43	37	16
Feb.	619	30	81	55.5	11	50	18
Mar.	387	31	88	57.3	7	49	23
Apr.	272	39	80	59.2	12	47	25
May	220	39	101	61.8	17	40	26
June	268	27	85	63.6	26	41	28
July	322	35	86	62.1	8	35	32
Aug.	414	30	84	63.6	17	31	32
Sept.	454	30	97	66.9	11	29	30
Oct.	335	32	99	65.3	13	35	27
Nov.	307	32	92	60.1	2	41	24
Total	7,643						
Mean		33.6	87.4	60.7	12.8	40.3	25.7

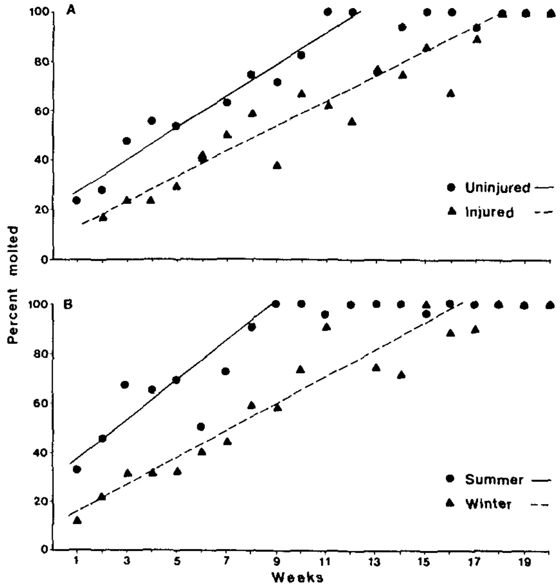

FIGURE 1.—Comparison of molting activity as a function of condition (A) and season (B) for spiny lobsters in Biscayne Bay, Fla.

TABLE 2.—Mean growth variables determined from 1,688 observations on 534 tagged juvenile spiny lobsters in Biscayne Bay, Fla., 1976-1977.

Item	Number of growth intervals observed	Intermolt period (wk)	Observed growth rate (mm CL/wk)	Water temp (° C)
Season:				
Winter	656	15	0.31	21.1
Summer	146	8	0.75	29.1
Condition:				
Injured	465	15	0.31	(1)
Uninjured	379	10	0.51	(1)
All observations	844	12	0.41	25.7

[1]Not available.

technicians. The mean error was 0.3 mm, with a range of −1.8 to +2.1 mm. Consequently, only changes in carapace measurements >2.0 mm were recorded as growth, others were considered measurement errors.

Two factors appeared to affect growth rates: water temperature and lobster condition. Growth rate did not vary with either sex or size within the range observed. Mean intermolt periods were estimated by doubling the time interval over which 50% of the lobsters observed had molted. This assumed that at the time of tagging the lobsters were randomly distributed throughout their molting cycle (Munro 1974). This appeared reasonable since we observed molting activity throughout the year (Table 1), and direct observations of individual lobsters through periodic recaptures confirmed the mean values obtained for the population in this manner (Davis 1978). For example, during winter, the percentage of tagged lobsters that had molted increased weekly from 12% after 1 wk to 22, 31, 32, 40, 44, and 58% after 8 wk, indicating that 50% had molted after about 7.5 wk, resulting in a mean intermolt period of 15 wk (Figure 1). In contrast, the mean intermolt period during summer was only 8 wk (Table 2). The mean intermolt period of injured lobsters was 15 wk, and for uninjured lobsters it was 10 wk (Table 2). The mean growth increments were estimated by examining frequency distributions of observed changes in carapace length. Mean single molt growth increments were significantly larger during the summer and for uninjured lobsters than during the winter and for injured lobsters, respectively (Table 3). Effects of season and lobster condition on growth rate were independent (Table 4).

Predictably, higher summer (May-October) temperatures and longer daylight periods were related to a greater growth rate (0.75 mm CL/wk) than that observed during winter, November through April (0.31 mm CL/wk). This 59% decrease in growth rate between summer and winter was apparently related to the 8.0° C decrease in mean water temperature, from 29.1° to 21.1° C, and the increased frequency of injuries incurred dur-

TABLE 3.—Comparison of mean molt increments (millimeters of change in carapace length) of juvenile spiny lobsters, in Biscayne Bay, Fla.

	Season		Conditions	
Item	Summer	Winter	Injured	Uninjured
$\bar{x}$	6.0	4.7	4.7	5.2
$S\bar{x}$	3.2	3.6	3.8	3.8
t, 306 df	7.75**		2.25*	

$^{**}P \leq 0.01$; $^{*}P \leq 0.05$.

TABLE 4.—Two-way fixed factor ANOVA of effects of season and spiny lobster condition as evidenced by growth rate.

Source of variation	df	SS	MS	F
Subgroups	3	106.50	35.50	
A (columns; condition)	1	34.60	34.60	4.65*
B (rows; season)	1	68.67	68.67	9.23**
A × B (interaction)	1	3.23	3.23	0.43n.s.
Within subgroups (error)	3,784	28,249.73	7.44	
Total	3,787	28,356.23		

$^{*}P \leq 0.05$; $^{**}P \leq 0.01$.

ing the fall and winter fishing season. Growth rates were lowest for injured lobsters during winter and highest for uninjured animals during summer, but injured lobsters grew faster in summer than injured ones in winter. Both of these factors, reduced temperature and injuries, caused increased intermolt periods and reduced molt increments, which resulted in reduced growth rates (Table 2). Change in the length of the intermolt period was the major effect of both factors, but by inspection of the values in Tables 2 and 3, it was apparent that intermolt period was proportionately more important for the injury-caused reduction, whereas decreased molt increment was proportionately more important for the season-related growth reduction.

Discussion

The growth data presented here generally conform both in magnitude and character to that in the published literature for decapod crustaceans, but the precise effect of injuries in the wild and definition of their origin is apparently new information, particularly for *P. argus*. Estimated growth rates for juvenile *P. argus* in the Caribbean, Florida, and Bermuda, range from 0.43 to 0.65 mm CL/wk (Smith 1951; Travis 1954; Sutcliffe 1957; Buesa M. 1965; Witham et al. 1968; Sweat 1968; Little 1972; Eldred et al. 1972; Ting 1973; Munro 1974; Peacock 1974; Olsen and Koblic 1975). The estimates for Biscayne Bay from this study ranged from 0.31 to 0.75 mm CL/wk, but the mean of 0.41 mm CL/wk was the lowest reported. The 1977 winter in Biscayne Bay was the coldest in the previous century (Molinari et al. 1977; McGuirk 1978), and the Bay is already near the northern limit of *P. argus* distribution. That cold winter depressed the mean growth rate somewhat, but another significant factor was that the Biscayne Bay lobster population was the most heavily fished by sport divers of all of those for which growth rates were reported. The injuries resulting from diver activity also depressed the growth rate. It appeared that a combination of cold weather and extremely high fishing activity caused the low growth rate reported in this study.

Variations in growth rates of lobsters have been attributed to several factors, the most common of which is temperature (Crawford and De Smidt 1922; Newman and Pollock 1974; Phillips et al. 1977). Limited food (Sutcliffe 1957; Chittleborough 1970; Newman and Pollock 1974), shelter (Chittleborough 1970), salinity and light (Travis 1954), and injuries (Chittleborough 1974a; Aiken 1977; Ford 1977) have also been cited as factors affecting lobster growth (see Aiken 1977, Dall 1977, and Ford 1977 for a review of lobster growth). The effects of these factors are translated into growth rate variations by changing either intermolt period, molt increment, or both. Most commonly, intermolt is shortened by warm temperatures, darkness, or autotomy of appendages; and lengthened by age, cold, or low salinity. Under some conditions, as in this study, both changes in molt increment and intermolt period occurred (Mauviot and Castell 1976; Aiken 1977; Pollock and Roscoe 1977).

While autotomy may stimulate molting, Chittleborough (1974a) reported that repeated loss of two or three legs or a large number of appendages resulted in decreased molt increment, so the net result was a reduction in growth rate. The results of the current study in Biscayne Bay also clearly demonstrated the adverse impact of injuries on growth rates. However, our observations did not demonstrate any proportional relationship between the degree of injury and the degree of molt increment depression as demonstrated for shore crabs by Kuris and Mager (1975). Most injured lobsters in Biscayne Bay were missing one or both antennae and one or two legs. The growth rate of *P. argus* with these minor injuries, five or fewer missing appendages, was virtually identical to the growth rate of more seriously injured lobsters that survived and which were missing up to nine legs and both antennae. It appeared that even minor losses caused a significant shift in growth pattern.

At the mean growth rate of 0.51 mm CL/wk observed for uninjured lobsters, it took about 51 wk for a juvenile to reach the minimum legal size of 76.2 mm CL from a size of 50 mm CL at age 2 (Lewis 1951; Sweat 1968). At 50 mm CL they began to associate gregariously with the larger juveniles in the eastern bay where they were subjected to fishery pressure. At the injury-depressed growth rate of 0.31 mm CL/wk, it required 84 wk to reach legal harvest size and enter the fishery 33 wk later than uninjured lobsters. During the additional 33 wk required to reach legal harvest size, natural mortality from groupers and other predators undoubtedly eliminated significant numbers of lobsters before they could enter the fishery. Olsen and Koblic (1975) estimated natural mortality of juvenile *P. argus* in Virgin Islands National Park at 34.8%/yr, at that rate, about 22% (33/52 of annual mortality) of the injured lobsters in Biscayne Bay were lost to the fishery as a direct result of their injuries. By the end of the open season, about half of the lobsters in Biscayne Bay were missing several legs and/or antennae. The frequency of injured lobsters dropped through the 4-mo closed season to about 30%, as the population molted at least once without harrassment from fishermen (Table 1). Less than 25% of 963 juvenile lobsters examined from an unfished population at Dry Tortugas, Fla., displayed similar injuries, which were presumably due to encounters with natural predators, difficulties with molting, or other normal stresses (Davis unpubl. data). Fishery induced injuries reduced the yield per postlarval recruit by reducing growth rate and consequently allowing natural mortality to occur over a significantly longer than normal period of time.

Another aspect of injury slowed growth rates is its effect on size of maturity. Maturity in spiny lobsters is apparently more a function of age than size (Chittleborough 1974b). Therefore if growth rate is significantly reduced by fishing activities through injuries, the size of mature lobsters would be reduced in areas of intense fishing activity. In the light to moderately fished Dry Tortugas fishery, the size of first maturity of female *P. argus* was about 90 mm CL for most of the population (78 mm CL smallest ovigerous) (Davis 1975). In the intensely fished lower keys fishery, the size of first maturity was reported at about 80 mm CL (smallest ovigerous 71.4 mm CL) (Warner et al. 1977). However, while age induces onset of maturity, female size is a major limit to fecundity. Creaser (1950) pointed out that a single 130 mm CL female *P. argus* produced as many eggs as four 87 mm CL females. Under the same environmental conditions, a population of injury-stunted lobsters could not produce the number of larvae that a population of normal-sized animals would (Kanciruk and Herrnkind 1976). Spawning fewer larvae may also result in reduced genetic diversity in the *P. argus* population, which would have further detrimental consequences for the management of this valuable resource (Miller 1979).

Intense fishing pressure on commercial concentrations of spiny lobsters inflicts injuries in several ways. Recreational divers inadvertently damage juvenile lobsters in attempting to catch associated larger animals, and by repeatedly catching nearly legal-sized lobsters to measure them. Florida law permits the capture, transportation, and use of sublegal-sized juveniles for attractors (bait) in commercial traps (Florida Statute 370.14), and juveniles are occasionally caught in traps along with adults. These sources of injury to the lobsters are all amenable to standard lobster trap fishery management techniques. Escape vents on traps that would allow small lobsters to leave and a prohibition on handling and transporting juvenile lobsters could eliminate the sources of injury from the trapping segment of the fishery (Bowen 1971). Nursery sanctuaries in which no fishing activity is allowed, and regulations prohibiting the use of hooks and spears by divers could eliminate diver and trap induced injuries.

The response of *P. argus* to injuries is probably representative of most tropical palinurids, and the information developed here could have wide application for fisheries management.

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