

ECOLOGY AND GROWTH OF JUVENILE CALIFORNIA
SPINY LOBSTER, *PANULIRUS INTERRUPTUS* (RANDALL)

by

John Marlin Engle CIRCULATING COPY
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Institute for Marine and Coastal Studies
University of Southern California
Los Angeles, California 90007

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ECOLOGY AND GROWTH OF JUVENILE CALIFORNIA SPINY
LOBSTER, PANULIRUS INTERRUPTUS (RANDALL)

by

John Marlin Engle

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UNIVERSITY OF SOUTHERN CALIFORNIA

In Partial Fulfillment of the
Requirements for the Degree
DOCTOR OF PHILOSOPHY
(Biology)

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UNIVERSITY OF SOUTHERN CALIFORNIA
THE GRADUATE SCHOOL
UNIVERSITY PARK
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This dissertation, written by

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under the direction of his Dissertation Committee, and approved by all its members, has been presented to and accepted by The Graduate School, in partial fulfillment of requirements of the degree of

DOCTOR OF PHILOSOPHY

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DEDICATION

This dissertation is dedicated to a good person--a person who lived unselfishly for his family and friends, and who died because his work was his life-- my father.

Morris M. Engle, Jr.

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INTRODUCTION

All the ingenious men,
All the scientific men,
And all the fanciful men in the world
Could not invent anything
So curious and so ridiculous
As a lobster

-- Charles Kingsley (1819-1875)

The exact date and circumstances of this quote are unknown, yet despite a century of scientific investigations on the biology of this "curious" armored creature, culminating in an international conference devoted solely to lobster biology (Phillips and Cobb, 1977), the lobster and its life history remain an enigma.

The life cycle of spiny lobsters, family Palinuridae (Crustacea: Decapoda), can be divided conveniently into three major phases: larval life, juvenile life, and adult life. Each phase is distinguished by differences in morphology, habitat, behavior patterns, and ecological strategies. Larval life, beginning with egg hatching, consists of a succession of planktonic phyllosoma stages followed by metamorphosis into a presettling puerulus larva. Benthic settlement and another metamorphic molt end larval life. The juvenile phase is characterized by rapid growth and development (often in nursery

habitats) which continue until the onset of sexual maturity. Adult life is dominated by the production of several broods of new larvae in a periodic fashion. Finally, there follows a period of senescence, leading eventually to death.

Because of the economic and ecological importance of spiny lobsters in shallow marine systems, the literature is extensive (see bibliographies by Sims, 1966; Kanciruk and Herrnkind, 1976). Despite this worldwide interest, remarkably little is known about lobster ecology and life history tactics. Most research efforts have been concentrated on the adult stage--a reflection of its conspicuousness and accessibility. Ecological studies of the larval stages are impractical at the present time since lobster larvae are poorly accessible in the open sea and extremely difficult to raise in laboratory culture.

The fishery for the spiny lobster Panulirus interruptus (Randall, 1839) in California has declined steadily since peak landings in the 1950s to the point where the 1974 harvest was the second smallest since 1888 (Odemar et al., 1975). Intense fishing efforts can result in a commercial catch consisting primarily of the few year classes of lobsters above legal size (Lewis, 1978). The consequence of long-term fishing pressure is a direct critical dependence of each future commercial catch on current settlement,

survival, and growth. In fringe populations of spiny lobsters, such as the California portion of the range of P. interruptus (see below), the limiting factors on population growth (recovery) might not be density dependent (e.g., adult competition for food or shelter) (Chittleborough, 1970). Instead, density independent conditions affecting recruitment and juvenile survival (e.g., current patterns or temperature extremes) could control population size.

Notwithstanding the above logic, until the past 20 years the only information about the late puerulus and early juvenile stages of most palinurids consisted of morphological descriptions and anecdotal observations of a few specimens. Recently the ecology of juvenile lobsters has received more attention, especially as it concerns the following three topics:

1. puerulus recruitment to inshore areas (Serfling and Ford, 1975a, for P. interruptus; Phillips, 1975a,b, and Phillips and Hall, 1978, for P. longipes cygnus.* Little, 1977, for P. argus*)
2. juvenile habitat (Kensler, 1967, for Jasus edwardsii.* Sweat, 1968; Eldred et al., 1972, for P. argus; Heydorn, 1969b, for J. lalandii.* Lewis, 1978, for J. novaehollandiae*)

*See Appendix I for complete scientific names and geographic locations of these and all other spiny lobster species mentioned in this study.

3. juvenile growth (Sweat, 1968, for P. argus; Pollock, 1973, for J. lalandii; Chittleborough, 1974a, 1975, Phillips et al., 1977, for P. longipes cygnus)

A team of investigators from San Diego State University recently found juvenile P. interruptus in shallow surf grass (Phyllospadix torreyi) beds (see Dexter et al., 1970). Consequently, they were able to obtain specimens for preliminary studies on recruitment, habitat preference, abundance, growth, and behavior (Blecha, 1972; Parker, 1972; Serfling, 1972).

The California spiny lobster is now a prime subject for juvenile lobster ecological investigations for several reasons:

1. juveniles are readily available from discrete sea grass habitats
2. some preliminary information already has been accumulated
3. there is a need for basic research to manage properly the declining stocks in southern California

Objectives of the present study are threefold:

1. to demonstrate which habitats are occupied by juvenile P. interruptus, with special emphasis on the possible role of surf grass (Phyllospadix torreyi) as a nursery
2. to determine the natural growth rate of juvenile P. interruptus and to examine the component processes of growth with respect to their adaptive significance

3. to evaluate the major ecological and behavioral phenomena associated with juvenile P. interruptus survival and growth including population, density, activity patterns, food habits, and mortality

Results from the three areas of investigation will be integrated with ecological information on the larval and adult phases into a tentative strategy for juvenile P. interruptus survival and growth.

Juvenile Habitat

Although it currently is accepted that palinurid pueruli are primarily pelagic forms, the means by which these larvae reach inshore areas is poorly understood (Witham et al., 1968; Serfling and Ford, 1975a; Phillips et al., 1978). The appearance of pueruli in coastal waters usually is seasonal and may be associated with seasonal water temperatures (Serfling and Ford, 1975a) or lunar cycles (Phillips et al., 1978) or both. Once in shallow nearshore areas, some type of habitat selection by the larvae is assumed to occur since experiments with natural and artificial puerulus collectors resulted in differential larval settlement depending on the substrate provided (Witham et al., 1968; Phillips, 1972; Serfling and Ford, 1975a; Lewis, 1978).

The majority of newly settled juvenile palinurids have been found in the shallowest subtidal habitats (0-4 m in depth*). The young of Panulirus argus characteristically are found on soft sediments within sea grass beds in protected estuaries (Witham et al., 1968; Little, 1977), dock pilings (Lewis et al., 1952), or in coral reef embayments (Sutcliffe, 1957). Juveniles of rock lobster species, such as Jasus edwardsii, J. lalandii, and J. novaehollandiae typically inhabit exposed shores with heavily encrusted bedrock reefs, boulders, or caves (Kensler, 1967; Heydorn, 1969b; Pollock, 1973; Lewis, 1978). Panulirus longipes cygnus and P. interruptus juveniles are abundant on exposed or semiprotected rock reefs which are densely covered with sea grasses and bushy algae (Sheard, 1949; Serfling, 1972).

Parker (1972) and Serfling (1972) have proposed that surf grass (Phyllospadix torreyi S. Watson, 1879) provides a nursery habitat for juvenile Panulirus interruptus. Surf grass is a vascular plant that produces dense beds by rhizomatous growth on surf-swept rocks just below the 0.0 tide level in California and Baja California. The nature of the relationship between Phyllospadix and Panulirus interruptus warrants close examination not only because of the

*All depth values reported in this study have been corrected to the mean lower low water (MLLW) datum level (U. S. Dept. of Commerce, NOAA Tide Tables).

ecological significance of surf grass as a unique open coast ecosystem, but also because coastal zone modifications could impact surf grass habitats adversely, resulting in further declines in lobster stocks.

Ideally, a nursery habitat should provide an optimum environment for fostering the growth and development of immature animals. Some of the common characteristics of nurseries include the following (see Williams, 1955):

1. warm, shallow water (0-3 m in depth)
2. calm water, protected from strong waves and currents
3. high productivity, resulting in an abundance of food
4. shelter from physical and biological stresses, often provided by microhabitats.

If Phyllospadix is a lobster nursery habitat (either obligate or facultative), then larvae settling in surf grass beds should have a higher probability of attaining reproductive maturity (either through decreased mortality or through enhanced growth) than larvae settling in other habitats. Consequently, P. interruptus may have evolved mechanisms for preferential settlement and development in surf grass beds. Absolute proof that Phyllospadix is the sole nursery for young P. interruptus is nearly impossible to obtain but strong inferences are possible by investigating the abundances, growth

rates, food habits, mortality, and ecological adaptations of individuals living in the surf grass habitat.

Lobster Growth

T. H. Huxley defined growth simply as "increase in size" (see Davenport, 1899). More recently, growth has been used as a loose term covering a variety of processes occurring at all levels of organization ranging from organismal imbibition of water to the molecular biochemistry of nutrition. Growth not only allows organisms to increase in size, but also serves to maintain, repair, and replace body materials through metabolic and regenerative processes during all stages of the life cycle (Needham, 1964).

The comprehensive nature of growth was recognized by Young (1950) who described it as the addition of material to that which already is organized within a living system. This general definition best recognizes the conceptual peculiarities of growth processes, yet retains the intuitive appeal of Huxley's definition. Ecological studies on live animals preclude the measurement of true biomass production (increase in protein or dry weight); instead, growth is estimated indirectly by measuring the increase in linear size (e.g., carapace length) and the increase in total biomass (e.g., wet weight).

The Molt Cycle

Ever since ecdysis first was reported for the crayfish Astacus in 1712 (see Drach, 1939), scientists have realized that growth in decapod crustaceans depends on periodic shedding of the hard exoskeleton followed by enlargement of the new integument in a coordinated sequence of events known as the molt cycle (see Carlisle and Knowles, 1959; Passano, 1960). The word "molt" will be used here synonymously with ecdysis (as in premolt, postmolt), while recognizing its broader meaning (as in molt cycle) which includes all processes involved in preparation for, and recovery from, ecdysis (Aiken, 1977).

Ecdysis is the most critical phase of the lobster molt cycle. The animal not only is more sensitive to environmental perturbations (e. g., changes in salinity, temperature, oxygen concentration) but it also is more subject to attacks by predators, leading to injury or death and to damage from physical conditions such as wave surge (Chittleborough, 1975). During ecdysis, water is taken up (by drinking) and passed into the hemocoelic spaces via the digestive gland (Dall, 1977). The result is tissue edema that rapidly increases the size of the animal by stretching the soft, newly exposed exoskeleton. The exoskeleton then hardens by mineralization with calcareous materials, thus fixing the size of the lobster until the next

ecdysis. During the intermolt period, water in the hemocoelic spaces is replaced with newly synthesized body tissue. Thus, true growth is out of phase with the physical size increase which occurs at ecdysis. In practice, lobster growth is determined by the increase in size at ecdysis and the frequency with which molts occur.

Growth and Ecology

The study of growth processes fundamentally is important to understanding lobster ecology. Molting cycles are not brief interruptions in an otherwise normal existence. Throughout the life of an individual, they affect metabolic rates, sensory capabilities, behavioral patterns, feeding habits, reproductive activity, and ecological interactions either directly or indirectly (Travis, 1954; Passano, 1960). On the other hand, environmental factors such as temperature, photoperiod, food supply, oxygen concentration, and habitat act (via central nervous system neurohumors) to control the molting cycle (Chittleborough, 1975).

Patterns of individual growth also provide insight into certain aspects of population ecology and life history tactics. For example, the rate of growth determines the time during which the young are exposed to predation and when they become mature reproductively. Ricklefs (1969, p. 1031) states:

Because growth rate sets an underlying pace for other developmental processes, and influences time and energy

budgets of reproduction, it represents a complex of factors which have a major bearing on evolutionary fitness. . . . Phenomena which occur at the organism level, as the growth of individuals may be said to, bridge a gap between the selective forces acting upon individuals and the molecular structures and events which constitute the individual.

Later (p. 1032), he adds:

The growth pattern having the greatest selective advantage is that which results in the most efficient conversion into progeny of time, energy and nutrients available to the species.

Fishery Management and Mariculture Perspectives

Since lobsters represent a valuable food resource, the understanding of lobster growth is not inconsequential. Fisheries biologists must understand lobster growth rates to manage properly this resource. However, the estimation of lobster growth rates not only is complicated by peculiarities of the molting cycle but also by the fact that, since all hard parts are shed periodically, no effective means of aging individuals has been developed. As a consequence, estimates by different investigators of the period of time required for a particular spiny lobster species to reach sexual maturity or legal size have varied by several years (Mitchell et al., 1969; Chittleborough, 1974a; Warner et al., 1977). The solution to this problem is given by Ford (1977, p. 86):

. . . accurate determinations of age-size relationships and growth rates in juveniles, obtained by following individuals

in the laboratory or in the field, provide a useful and reasonably accurate baseline to establish estimates of age-size relationships in larger individuals for which size increase per unit time is known.

Increasing market demand and limited natural populations of lobsters have created large-scale interest in the field of lobster mariculture. Knowledge of growth rates is a paramount consideration in this emerging industry since economic viability is dependent on reducing the costs of production, such as the time required to carry the product through to market size. Special emphasis has been placed on the effects of temperature, nutrition, and space on growth (Hughes et al., 1972; Rauch et al., 1974; Shleser and Gallagher, 1974). Although spiny lobsters are not the primary candidates for lobster mariculture programs at present, the information gained from natural growth studies on them would provide insight into lobster (and other crustacean) growth processes in general.

Juvenile Growth

Recent reviews of lobster growth are provided by Aiken (1977) for the family Homaridae and by Ford (1977) for the family Palinuridae. Hedgecock et al. (1976, p. 348) remarked on the surprising paucity of documentation of growth rates for larval or juvenile lobsters. Early growth studies of juvenile lobsters typically reported observations on only a few animals; consequently, the

significance of their conclusions is doubtful. Later, more sophisticated juvenile growth studies can be divided into three types characterized by the methods employed (see Burkenroad, 1951):

1. analysis of shifts in size-frequency groupings within a field population through time (Nakamura, 1940; Heydorn, 1969b; Eldred et al., 1972; Lewis, 1978)
2. direct measurement of recently captured juveniles before and after ecdysis (Nakamura, 1940)
3. direct observation and measurement of individuals held in laboratory culture systems (Lewis et al., 1952; Kensler, 1967; Sweat, 1968; Witham et al., 1968; McGinnis, 1973; Chittleborough, 1974a, 1975; Phillips et al., 1977)

A combination of all three techniques sometimes was used (Sutcliffe, 1957; Serfling, 1972; Pollack, 1973). The mark-recapture method, commonly used for adult palinurid growth studies, has not been employed to date for juvenile growth determination because small animals are difficult to mark in a noninjurious, yet relatively long-lasting way. Advances in lobster handling and marking techniques should now permit the incorporation of a mark-recapture scheme into a program that includes the above three methods, thereby permitting synthesis of the best information from each method into a comprehensive picture of lobster growth.

Juvenile Abundance

The number of juvenile lobsters within an area at a particular time is a function of larval recruitment, mortality, and movement patterns (relating to activity cycles, resource availability, sociobiological interactions, and migratory phenomena). Common techniques for field abundance determination include catch per unit effort, catch per unit area, and mark-recapture schemes. In practice, all of these methods have limitations, not only because of the poor catchability of juveniles, but also due to the difficulty of accounting for variability introduced by sampling bias and variability caused by the dynamic factors mentioned above. Despite the technical problems, long-term abundance estimates in specific localities, coupled with pertinent field observations, can provide at least order of magnitude information about lobster population dynamics. Lobster abundance then can be evaluated with reference to the holding capacity of the local environment.

Only two field abundance studies have been reported for juvenile palinurids. Heydorn (1959b) determined the relative abundance of juvenile Jasus lalandii in a shallow breakwater by calculating the number of lobsters caught per diver-hour. Chittleborough (1970) trapped 2-6 year old Panulirus longipes cygnus for mark-recapture density determination on shallow coastal reefs in western Australia.

Juvenile Activity Patterns and Gregariousness

Like many other marine animals, spiny lobsters exhibit temporally organized and spatially oriented activity patterns that are influenced by external and internal factors (Allen, 1966). The current state of knowledge about palinurid movement patterns (including research methods, diel rhythms, annual rhythms, foraging patterns, and migratory patterns) and their controlling factors has been reviewed extensively by Herrnkind (1977). In general, adult lobsters alternate diurnal periods of inactivity spent aggregated in shelters with nocturnal activity periods spent solitarily foraging within a particular home range. Juveniles are thought to be active nocturnally and probably have a size-specific home range, but information is available only for large juvenile Panulirus argus (Herrnkind, 1977) and P. longipes cygnus (Chittleborough, 1974b).

Various types of migrations occur in spiny lobsters, often at specific periods within the life cycle (Herrnkind, 1977). Ontogenetic migrations from nursery to adult habitats have been reported for 2-3 year old P. argus (Witham et al., 1968; Olsen et al., 1975; Davis, 1976) and for 2-5 year old P. longipes cygnus (George, 1957; Chittleborough, 1970).

Large aggregations of lobsters are formed prior to mass migrations (Herrnkind, 1977) yet gregariousness also is apparent in

resident populations. The diurnal sharing of cover is thought to have anti-predator value, especially to smaller individuals in mixed size-class aggregations (Berrill, 1975). This may explain the observations that juveniles generally are more gregarious than larger animals (Fielder, 1965; Heydorn, 1969b; Berrill, 1975). Within juvenile aggregations of P. argus and P. longipes cygnus, dominance relationships may be established through aggressive interactions (Berrill, 1975, 1976).

Until recently, the behavioral ecology of lobsters has been inferred from commercial catch data, research trapping programs, or laboratory observations. Surface sampling techniques have numerous drawbacks, especially for studying young animals since lobsters less than two years old rarely are captured (even in traps with small mesh) (Chittleborough, 1970, 1974b; Serfling, 1972). Expanding underwater research programs and the increasing practicality of scuba diving methods have proved valuable in overcoming the above deficiencies. Scuba studies now offer the potential for direct in situ observations of juvenile activity patterns and social behavior with less trauma to the animals than trapping or laboratory impoundment methods (Herrnkind, 1974).

Juvenile Food Habits

Optimum growth for young palinurids requires an abundant supply of readily available food (Chittleborough, 1975). Due to the difficulty in finding juvenile lobsters, their feeding habits and their competitors for food resources remain unidentified. Adults consume a wide variety of food items, ranging from algae and sea grasses to annelids, arthropods, mollusks, echinoderms, and bryozoans (Hindley, 1977). Despite their reputation as scavengers, established because of their attraction to baited traps, the food items most commonly eaten by palinurids are live mollusks (Lindberg, 1955, and Winget, 1968, for Panulirus interruptus; Heydorn, 1969b, for Jasus lalandii; Berry, 1971, for P. homarus). These slow-moving or sessile animals are located primarily by contact chemoreception, grasped by the anteriormost pereopods and maxillipeds, and crushed by the powerful mandibles. Laboratory food preference and growth studies indicate that juveniles feed in a similar manner (Kensler, 1967, for J. edwardsii; Serfling, 1972, for P. interruptus; Phillips et al., 1977, for P. longipes cygnus). However, since large food items used in laboratory studies were broken open or cut up for the lobsters, these items are not likely to be available to young animals in the field.

Juvenile Mortality

Lobster mortality may result from a variety of environmental factors operating independently or in combination, including temperature extremes, low oxygen concentrations, storm-related water turbulence, lack of shelter, insufficient food, disease, molting complications, competition, and predation. Ultimately, most juvenile lobster mortality probably is due to predation (Munro, 1974). The prolific production of larvae by palinurids is a good indication that mortality is high in these animals before sexual maturity is reached. Although the greatest mortality is thought to occur during larval life (Lazarus, 1967), juvenile mortality probably is not insignificant. If, as with most animals, lobster vulnerability to predation is a function of body size, then a highly vulnerable juvenile eventually would outgrow the capacity of potential predators to consume it, thus achieving what Paine (1976) has termed "a refuge in size." Winget (1968), investigating trophic relationships in adult Panulirus interruptus, concluded that predation on large individuals probably has only a minor effect on the population size.

Other than a few reports of suspected predators, no information is available on juvenile lobster predation. Natural predation can be documented directly by field observations of predator-prey interactions and indirectly by examination of gut contents of suspected predators. In a discrete juvenile lobster population, if other forms

of mortality are low and potential predators are present, then decreases in juvenile abundance will reflect the importance of predation. Morphological and behavioral anti-predator adaptations may provide supportive evidence for the significance of predation to the juvenile life phase.

The Biology of *Panulirus interruptus*
(Randall, 1839)

Distribution

The California spiny lobster, *Panulirus interruptus* (Randall, 1839), is a decapod crustacean of the suborder Reptantia and the family Palinuridae; in this family there are eight genera and about 42 species distributed in tropical and warm temperate seas throughout the world (George and Main, 1967). Its geographical range extends from Monterey Bay, California to Magdalena Bay, Baja California, plus a restricted area at the northern end of the Gulf of California (Duffy, 1973); the area of greatest abundance is located in central Baja California (Lindberg, 1955; Johnson, 1960). South of Cedros Island, Baja California, the southern extent of *P. interruptus* overlaps with the northern extent of *P. inflatus*.

Adult lobsters characteristically inhabit rocky areas extending from the low intertidal zone to depths of 70 m or more (Allen, 1916; Lindberg, 1955). All types of rocky or rock-sand

substrata, including bedrock, rubble rock, and boulder rock, are suitable habitats so long as they possess crevices or discontinuities of sufficient size to shelter individuals or aggregations. Typical plant cover in lobster habitats includes surf grass (Phyllospadix torreyi), southern sea palms (Eisenia arborea), and low bushy brown algae in shallow water (0-7 m); kelp forests (Macrocystis pyrifera) and low coralline algae in moderate depths (8-20 m); and large-bladed brown algae, such as Laminaria farlowii and Agarum fimbriatum, in deeper water (>20 m).

Behavioral Ecology

During the day, one or more (up to several hundred) P. interruptus may reside in a particular crevice or "den," while nearby crevices remain vacant. Activity is minimal; most time is spent facing the den entrance with the paired antennae projected outward. Some intraspecific interactions believed to represent territoriality or dominance behavior have been observed in lobster aggregations in the field (Lindberg, 1955) and in laboratory pools (Roth, 1972).

Shortly after sunset, especially on dark nights, lobsters leave the shelter to forage singly on rock reefs or nearby sand plains. Subadults and adults can be seen combing through clumps of bushy algae, digging into soft sediments, or appressed to hard

substrates feeding on attached organisms. A large variety of food items may be consumed, including algae, sponges, hydroids, polychaetes, mollusks, crustaceans, and sea urchins (Lindberg, 1955), but mollusks and crustaceans make up the bulk of the diet (Winget, 1968). On the other hand, P. interruptus may be preyed upon by octopus (Octopus spp.), sheephead (Pimelometopon pulchrum), cabezon (Scorpaenichthys marmoratus), kelp bass (Paralabrax clathratus), and moray eels (Gymnothorax mordax). However, Winget (1968) concluded from studies on these and other suspected predators that predation on adult lobsters is negligible.

Although the population stability at specific localities may vary depending on the nature of the habitat, degree of environmental and human disturbance, and season of the year (Ford and Serfling, 1970), adult P. interruptus generally are residential (Lindberg, 1955; Odemar et al., 1975). For most individuals, nocturnal activity is confined to a particular range, the size of which probably is dependent on food availability. Movements within this range appear to be directed; specific feeding areas may be visited each night followed by homing to the same reef or den before dawn. M. Olsson, V. Paul, and R. Arkin (personal communication) have observed individually-tagged lobsters occupying the same dens for periods of 200 to 300 days.

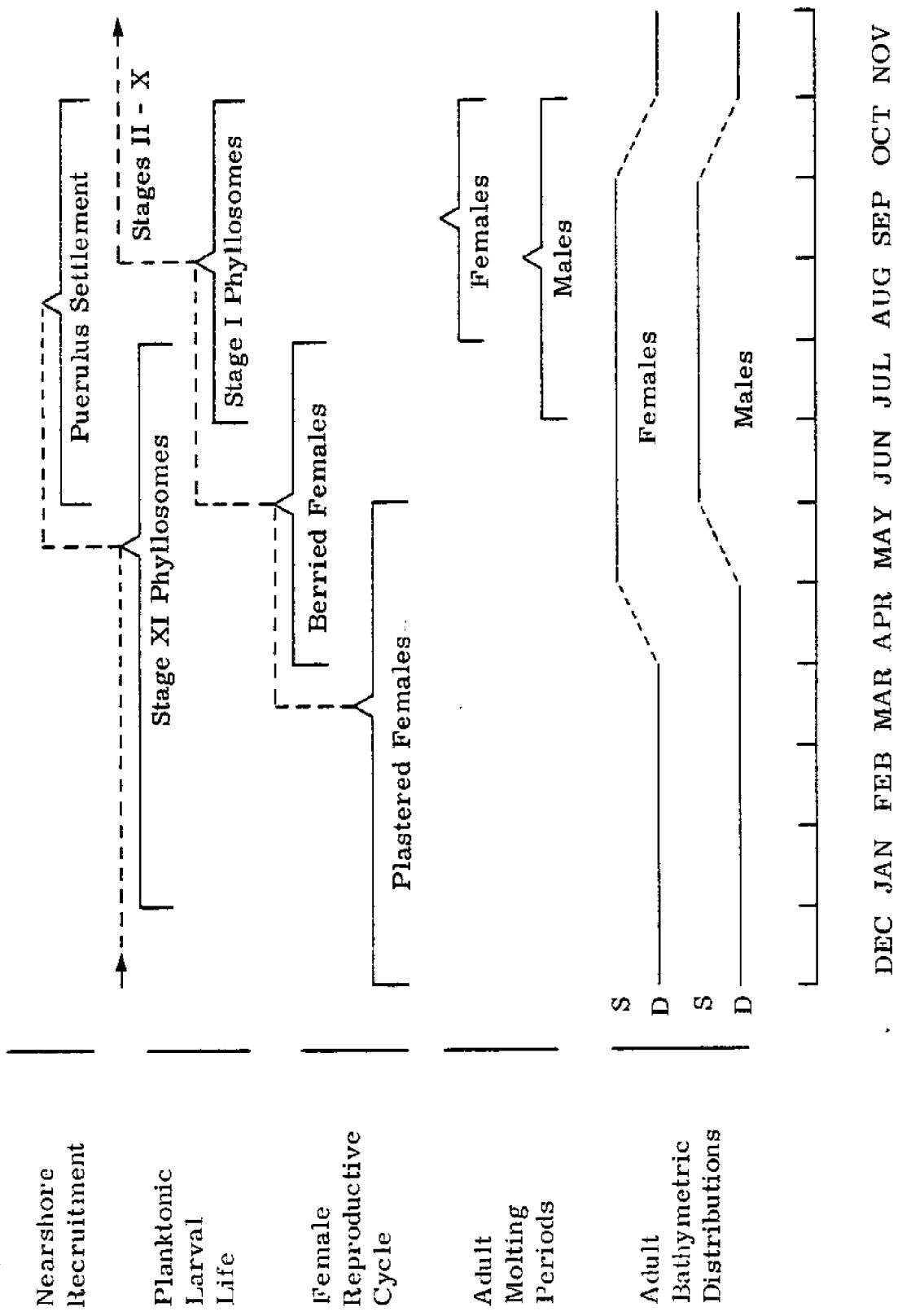
Despite the residential nature and the infrequency of long-shore movements ("nomadism") in P. interruptus, seasonal inshore-offshore migrations (see Fig. 1) are undertaken by a considerable portion of the population (Lindberg, 1955; Mitchell et al., 1969). In a two-year study at San Clemente Island, California, Mitchell et al. (1969) found large numbers of lobsters of both sexes in shallow water (<9 m) from June through September, the period when the summer thermocline was best established. As thermal stratification decayed in October, the animals gradually moved into deeper water (at least 15-30 m). During the winter most of the observed population was offshore. By early April, as surface temperatures were rising, plastered females (i.e., females bearing spermatoophores) began reappearing in shallow water. Shoreward movement of males began in May and by mid-summer the annual migratory cycle was completed.

Life History

Seasonal migratory patterns in P. interruptus may be associated with reproductive behavior and growth phenomena (Mitchell et al., 1969) (Fig. 1). Mating takes place in deep water from December through March, as evidenced by the presence of tar-like spermatoophores on the sterna of the females. Shortly after these plastered females move inshore 50,000 to 800,000 eggs are extruded,

Figure 1. Temporal sequences of life history phenomena in Panulirus interruptus based on data from Johnson (1960), Mitchell et al. (1969), and Serfling and Ford (1975a).

\wedge = peak abundance period
D = deep
S = shallow



fertilized, and attached to the pleopods (Allen, 1916; Lindberg, 1955; S. Nelson and D. Farris, personal communication). Warm summer sea surface temperatures expedite embryonic development, which is completed in nine to ten weeks (Allen, 1916). Peak hatching of larvae from the eggs takes place in July, after which the females begin production of a new exoskeleton in preparation for the annual molt--a process that may be associated with movement into deeper water in the fall (Mitchell et al., 1969).

Subsequent to hatching from the egg, young P. interruptus pass through a series of eleven planktonic "phyllosoma" stages which are characterized by their transparent dorso-ventrally flattened bodies with long fragile legs (Johnson, 1956). The larvae apparently drift passively with prevailing water currents, feeding on soft-bodied zooplankters such as chaetognaths, fish larvae, and hydromedusae (Mitchell, 1971). Dexter (1972) was able to raise phyllosomes through six stages (eight molts) in a laboratory culture system, but apparently nutritional inadequacies caused roughly 50% mortality between each molt. Analysis of collections of 3,358 phyllosomes from 1949 to 1955 by Johnson (1960) showed that these larvae spend roughly seven to nine months in the open sea, growing from 1.4 mm in Stage I to 29 mm in Stage XI, and that later larval stages occur in diminishing numbers and at greater distances from

the coast. Dispersion and mortality may explain the fact that the number of Stage XI larvae was only 2.7% of the number of Stage I larvae. In southern California, especially the Channel Islands area, seasonal development of countercurrents, gyres, and eddies may be critical for successful inshore recruitment to offset the southward and seaward drift caused by the California current (Johnson, 1960).

Late stage phyllosomes, present in the water column from January to July (Fig. 1), eventually metamorphose into the "puerulus" stage which is similar in appearance to the adult lobster except that the second antennae are three times the body length and the animal is completely transparent (Johnson, 1956; Parker, 1972). The fact that relatively few pueruli have been collected despite extensive oceanic sampling programs caused speculation that these larvae were primarily benthic (Johnson, 1956; 1960), but recently Serfling and Ford (1975a) demonstrated that pueruli are capable of continuous and directed swimming within a few centimeters of the ocean surface. Efficient forward motion is achieved by synchronously beating the heavily setose pleopods that interlock pairwise by means of minute coupling hooks.

Panulirus interruptus pueruli are strongly attracted to bright underwater lights at night and can be collected in certain areas using floating habitat traps containing surf grass (Parker, 1972; Serfling and Ford, 1975a). These studies indicate that pueruli

first enter coastal waters off San Diego during May and appear regularly through September. Peak abundance seemed to be correlated with seasonal surface temperature maxima, but showed no apparent relationship to lunar cycles. Pueruli were not known to feed during their two- to three-month stay in the plankton. Serfling and Ford (1975a) concluded that the puerulus stage represents a transitional pelagic phase specifically adapted to return larvae to near-shore habitats after they had spent approximately one year in the open sea (see Fig. 1).

Panulirus interruptus pueruli may be capable of selecting or rejecting certain benthic habitats. Parker (1972) tested small numbers of pueruli (9-20 individuals per test) in laboratory habitat choice experiments and found that pueruli prefer artificial consolidated substrate over sand, and Phyllospadix over Macrocystis or rubble rock. "Presettlement" pueruli, provided with an acceptable substrate, undergo within 48 hours a series of behavioral and morphological changes including reversal of phototaxis from positive to negative, reduction in activity from swimming to clinging, loss of the distal halves of the antennae through breakage, and gradual accumulation of pigment (Parker, 1972; Serfling and Ford, 1975a). Following this irreversible settlement, the "postsettlement" pueruli become fully pigmented in six to eight days; at nine to eleven days,

ecdysis has transformed the larvae into benthic juveniles (also called postpueruli).

Previous to the work of Serfling (1972) and Parker (1972), the only known collections of early juvenile P. interruptus were of a few specimens found infrequently in intertidal pools (MacGinitie and MacGinitie, 1949). The inability to locate juveniles led Lindberg (1955) to speculate that pueruli settle to the bottom in deep water, and that juveniles "probably do not reach inshore waters in concentration until their second to sixth year." Qualitative sampling of intertidal and subtidal habitats near San Diego by Serfling (1972) revealed that large juveniles were common in adult habitats, but juveniles less than 40 mm carapace length* rarely were encountered there. However, small lobsters were found in a semi-protected area (Big Fisherman Cove and Bird Rock) on the leeward side of Santa Catalina Island, 137 km northwest of San Diego. Juvenile P. interruptus were collected in shallow (0-4 m) rock rubble habitats containing the algae Sargassum, Pterocladia, and Plocamium and in consolidated rock habitats dominated by Phyllospadix (Ford and Serfling, 1970; Serfling, 1972). As a result of exploratory dives at Bird Rock, Santa Catalina Island from 1970 to 1972 (in which 334

*Hereafter, "carapace length" has been abbreviated to "CL."

juveniles were encountered and 130 were captured), Parker (1972) predicted that small P. interruptus would be found in high densities in surf grass beds and that they would remain in this nursery habitat for two years before moving subtidally. He also demonstrated in preliminary habitat-choice tests that juveniles prefer angular rocks over sand and cobbles; surf grass over Zostera, red algae, and Macrocystis; and long, low profile shelters with blocked rear entrances over short, high, and open shelters.

Growth

From newly settled juveniles weighing less than a gram (7 mm CL), the California lobster can grow to adults weighing 16 kg (282 mm CL), although individuals over five kilograms are rare (Lindberg, 1955). Natural growth rates have been estimated by several workers (Barnhart, unpublished, reported by Lindberg, 1955; Lindberg, 1955; Backus, 1960; Mitchell et al., 1969; Serfling, 1972; Odemar et al., 1975; Ford and Farris, 1977). Comparison of results is difficult since different methods were used to estimate growth; some workers used total length instead of carapace length to measure size increases, and different molting frequencies were assumed when figuring annual growth. As can be seen from the summarized information in Table 1, much of the past work is not in agreement. The discrepancies become even more apparent when

TABLE 1.-Comparison of annual natural growth rates and critical age predictions for the California spiny lobster, Panulirus interruptus

Size Range (mm CL)	Molts per Year	Mean Growth per Year (mm CL) M F	Age at Sexual Maturity (Yr)* M F		Age at Legal Size* M F		Growth Study Methods	Reference
			5	6-7	8	9		
19-73**	2-5	10.6**	10.6**	5	6-7	8	9	LC Harnhart, in Lindberg, 1955
50-160**	2	6.2-9.3**		4-5	5-6	7-8	LC, LF, MR Lindberg, 1955	
84-124	1	6.3	6.2				LF Backus, 1960	
50-80	1	4.1***	5.0***	5	7	11	10 LF Mitchell et al., 1969	
7-60		18-20		3-4	5-6		LC, LF Serfling, 1972	
40-111	1	3.6	2.5	6-6	8-9	11	13 MR Odernar et al., 1975	
60-140	1	6.0				8	LC, MR Ford and Ferris, 1977	

*All ages were determined from the time of egg hatching. Sexual maturity = 58 mm CL (M) and 70 mm CL (F) (Lindberg, 1955). Legal size = 83 mm CL.

**Data were converted from total length (TL) to carapace length (CL) by the equation CL = 0.31 TL (Bakus, 1960).

***Calculations were corrected for error in molt frequency count by Mitchell et al. (1969).

LC = Laboratory Culture LF = Length Frequency MR = Mark-Recapture

individuals larger than legal size are considered; Lindberg (1955) predicted that an animal 140 mm CL was 15 years of age while Odemar et al. (1975) estimated that a 114 mm CL male would be 24 years old! Table 1 also shows that Backus (1960) and Mitchell et al. (1969) reported faster rates of growth in females compared to males, based on size-frequency analysis, but Odemar et al. (1975) found the opposite to be true based on mark-recapture studies.

Lindberg (1955) synthesized growth predictions from laboratory culture, length-frequency, and mark-recapture studies (Table 1). Natural variation in growth rates was ascribed to the effects of diet, regeneration of lost appendages, and possibly the attainment of some maximum size. Observations on a few juveniles revealed that growth per molt was roughly 3.1 mm CL and molting frequency was much higher than in adults. Mitchell et al. (1969) employed scuba diving techniques to monitor a population of P. interruptus at San Clemente Island from 1964 to 1967. Results confirmed that legal-sized animals (83 mm CL) molt only once per year after completing the reproductive cycle in late summer. Recently the California Department of Fish and Game used this information to design a mark-recapture study at Santa Catalina Island (Odemar et al., 1975). Of 1,760 lobsters marked with coded holes punched into the tail fan before the summer molt, 434 molted animals later were recaptured.

Growth in both sexes was size dependent with small lobsters growing the most (5.6 mm for males 50 mm CL) and large lobsters the least (1.3 mm for females 104 mm CL). Ford and Farris (1977) compared growth rates of lobsters (marked with Floy anchor tags; Floy Tag & Mfg. Inc., Seattle, WA) held in concrete pools with those recaptured in the field and found that the rates were generally similar.

Until the work of Serfling (1972) and Blecha (1972) practically no information was available on growth in P. interruptus less than 50 mm CL. Serfling (1972) attempted to measure natural growth using three methods: culture in cages suspended from floating docks; laboratory culture; and field size-frequency studies. Unfortunately, the following problems ensued: the live cages either were lost or empty after two months; only five juveniles lived for four months in aquaria; and the 240 individuals used in size-frequency plots represented accumulated field visual size estimates and measured collections from various localities (San Diego, Dana Point, Santa Catalina Island) in four different years (1969-1972). Using pooled results, juveniles were estimated to reach 24 mm CL after one year and 44 mm CL after two years of benthic life.

Blecha (1972) looked at the effect of temperature on biomass production in juvenile P. interruptus and found that the relative

increase in biomass per molt averaged 55% at 16°C, 38% at 21-22°C, and 41% at 26-27°C, and intermolt time averages 67, 44, and 33 days for the three temperature regimes, respectively. Considering all factors, the optimal temperature for increased biomass production for this species was predicted to be about 24°C.

Serfling and Ford (1975b) cultured puerulus through juvenile stages of California lobster at constant temperatures of 22°C and 28°C in closed-system aquaria. The resulting growth rates were two and three times greater than the estimated rates for natural growth at ambient temperatures in southern California (12-20°C).

The California Lobster Fishery

The fishery for P. interruptus in southern California extends from Pt. Arguello to the Mexican border, including the Channel Islands; in Baja California it ranges from the Coronados Islands south to Punta Abreojos. The history of the fishery in southern California has been reviewed by Wilson (1948) and Odemar et al. (1975). Basically, a long period of relative catch stability (157,400 kg/yr avg; 1918-1943) was followed by a series of increased landings (330,700 kg/yr avg; 1944-1956); subsequently, the catch has declined steadily despite increased fishing effort, to the point where the 1974 harvest of 86,000 kg was the second smallest since 1888 (U.S. National Marine Fisheries Service, 1975). The severity of

this decline prompted a California Department of Fish and Game investigation (Odemar et al., 1975), from which it was concluded that, in addition to commercial fishing pressure, stock reduction has been accelerated by the following:

1. the illegal taking of undersized lobsters (<83 mm CL), which is estimated to exceed legal landings
2. the tremendous increase in sport diving in recent years, reflected by partyboat catch increases from 248 lobsters in 1958-59 to 6,734 in 1973-74 (while the number of lobsters caught per diver-day declined from 0.90 to 0.42)
3. the loss of habitat due to environmental degradation and coastal development

The California fishery primarily is operated by independent fishermen who set lines of two-chambered rectangular wire mesh traps (46 x 71 x 91 cm) from power skiffs during the open season, October through March. As of 1976, each trap must have an escape port of specific size such that legal lobsters are retained while most sublegals (approx. 80%) can escape. Log book data demonstrate that the use of escape ports has caused a substantial decline in the sublegal to legal capture ratio; for example, from 5.4:1 in 1973-74 to 0.8:1 in 1976-77 (J. Carlisle, personal communication). High proportions of sublegals are captured from La Jolla to Point Loma

and at San Clemente and Santa Catalina Islands. Relatively few are reported from the Santa Barbara coast and the other channel islands. Overall, an average of 0.52 legals of mean weight 0.76 kg were captured per trap lift during the 1973-74 season (Odemar et al., 1975). Highest fishing effort and catch occur early in the season, after which both decline considerably. For example, 36% of the catch for 1973-74 was taken in October. Effort declined 86% by March, 1974, when only 6% of the catch was fished. Odemar et al. (1975) also found that the most productive lobster grounds are in the southernmost areas of California; the mainland coast from Encinitas to San Diego and San Clemente Island accounted for over 60% of the 1973-74 catch.

Because the California spiny lobster fishery is a relatively minor commercial enterprise (total value of 1973-74 catch was \$474,000), research effort has been confined to monitoring the catch, leaving the aspects of population structure, annual recruitment, and reproductive strategy largely unstudied. Even less is known about the populations of P. interruptus in Baja California despite the fact that Mexican landings represent more than seven times the California catch (Martinez et al., 1973).

MATERIALS AND METHODS

Juvenile Habitat

Puerulus Recruitment

Puerulus larvae were collected to confirm the settling period reported by Serfling and Ford (1975a), to test for larval habitat selection, and to acquire animals with a known time of settlement for growth studies. Following methods modified from Serfling and Ford (1975a), two types of equipment were employed to collect pueruli--an underwater night-light and Phyllospadix habitat traps. The light was constructed from a T-shaped arrangement of PVC pipe. Two standard 500 w motion picture projector lamps and 0.5 kg of lead were sealed into the ends of the "T" with silicone glue. The apparatus was clamped onto a dock or pier (provided with 120 v electricity) so that the lamps were about 30 cm below the water surface. In this position, the lamps emitted a hemisphere of bright light approximately 8 m in diameter. Pueruli attracted to the illuminated area, although transparent, were easily seen and netted due to the side- and back-lighting effect of the lamps. Night-lighting was used to collect pueruli from the vicinity of the floating dock at

the Catalina Marine Science Center (CMSC), located in the northeast corner of Big Fisherman Cove near the Isthmus on Santa Catalina Island, and from the Marineland of the Pacific pier, located on the Palos Verdes peninsula of Los Angeles (Fig. 2). Water depths at collecting locations were 3-6 m. Occasionally the night-light was used from boats with generators along the leeward side of Santa Catalina Island.

Serfling and Ford (1975a) tested five types of habitat traps and found that a nylon mesh bag filled with Phyllospadix worked best in terms of puerulus catchability, ease of use, durability, and cost. For the present study, modified floating bag traps were constructed by mounting an 0.8 m diameter plywood disk on top of an automobile inner tube by means of a central bolt connected to two crossed blocks of wood beneath the tube. Suspended under the tube was a 38 mm mesh nylon fishing net bag, 1 m in diameter, filled with fresh surf grass. Some traps were anchored to large rocks with heavy link chain. Four traps, placed in various habitats near CMSC (Fig. 2; Table 2), were checked weekly from June through September 1975 for the presence of pueruli. New surf grass was added to the traps every two weeks.

Puerulus recruitment to the Phyllospadix habitat at Bird Rock was monitored indirectly by means of monthly scuba searches

Figure 2. Location of sampling sites for puerulus larvae and primary study sites for juveniles of P. interruptus.

- = 20 m depth contour
- X = puerulus night-lighting site
- O = puerulus habitat trap site
- △ = juvenile study site in Phyllospadix habitat
- = juvenile study site in Halidrys habitat

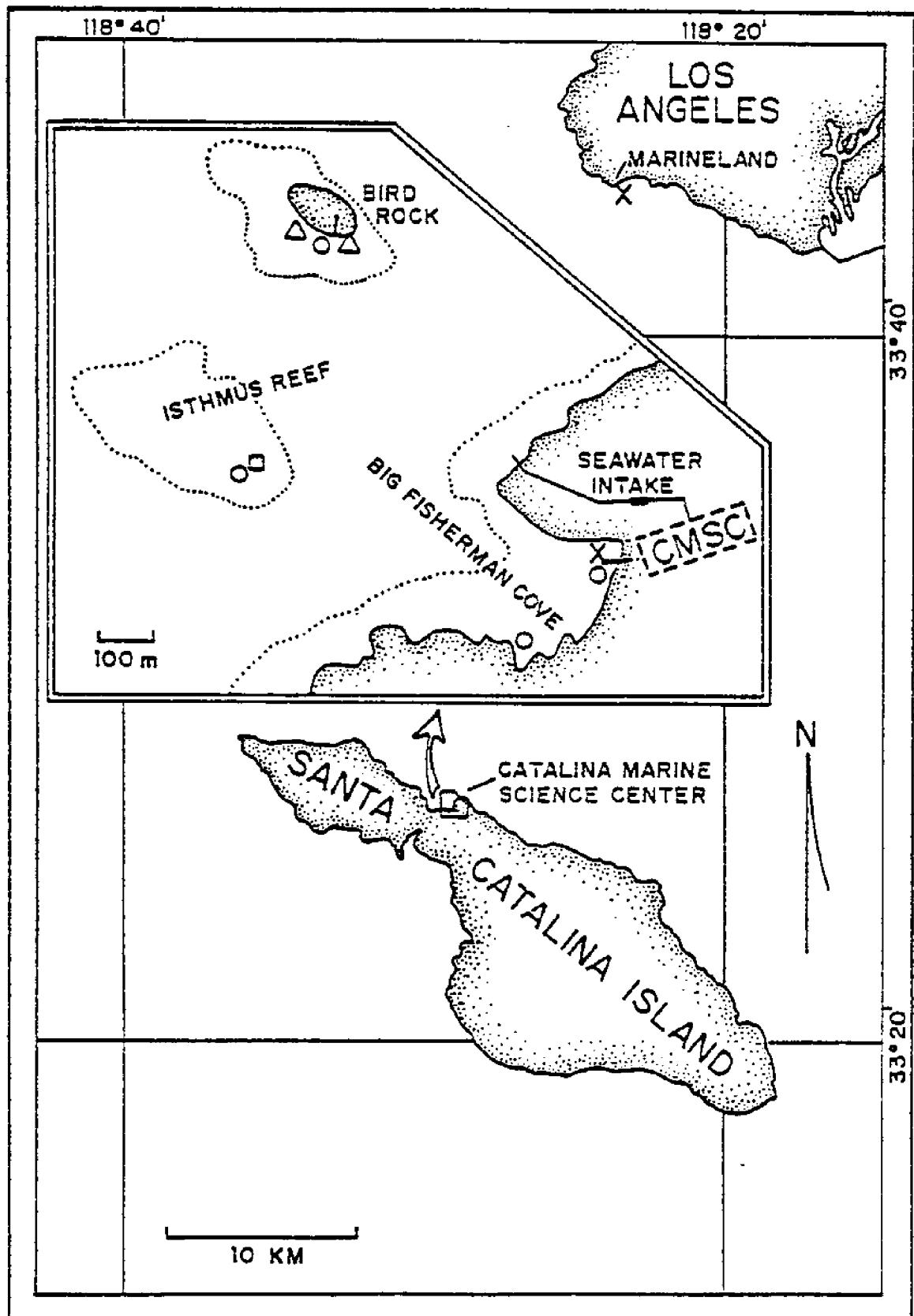


TABLE 2. -- Distribution of floating Phyllospadix traps monitored for the recruitment of
P. interruptus pueruli (see also Fig. 2)

Location	Depth (m)	Habitat	
		Immediate Area	Nearby Area
1. Under CMSC Dock, Big Fisherman Cove	4	Muddy Sand, <u>Sargassum</u>	Cobble, Boulders, <u>Macrocystis</u>
2. Southeast Corner, Big Fisherman Cove	4	Sand, Boulders, Low Brown Algae	Bedrock, <u>Phyllospadix</u>
3. East End, Isthmus Reef	5	Bedrock, Sand Channels, Low Brown Algae	Reef Pinnacle, <u>Halidrys</u> , <u>Macrocystis</u>
4. East End, Bird Rock	5	Shelly Sand, Boulders, Coraline Algae	Bedrock, <u>Phyllospadix</u> , <u>Macrocystis</u>

for recently settled juveniles from October 1974 through December 1976, supplemented by occasional dives in 1977 (see below for details).

Puerulus Metamorphosis

Morphological and behavioral changes associated with puerulus metamorphosis into the first juvenile stage were observed and recorded for all pueruli captured by night-lighting.

Puerulus Habitat Preference

Recently captured puerulus larvae were held in separate 1 liter beakers containing sea water only, then tested for habitat preferences by introducing single animals into 65 liter aquaria (87 x 58 x 13 cm) containing two different representative substrates located at opposite ends of the test chambers. Ten choice tests were run simultaneously (five paired-habitat trials and five control trials) in a uniformly darkened room for periods of not less than five hours. All larvae were used only once per choice situation and were tested individually to prevent social interactions from interfering with substrate selection.

Each lobster was placed inside a Plexiglas ring in the center of the noncirculating sea water test tank for five minutes before starting the trial, to reduce possible effects of handling on

choice behavior. Subsequent to removal of the rings, the larvae were left undisturbed until the end of the test period when their positions in the tanks were scored. Between tests all aquaria were drained and scrubbed, then refilled with clean sea water. Fresh substrates were obtained locally for each series of trials and prepared for testing by rinsing them thoroughly with sea water to remove debris and epiphytes.

Pueruli were scored as choosing a substrate if they were found within or under the material on that particular half of the aquarium. Control aquaria contained either no introduced substrate or the same substrate in each half.

Juvenile Habitat Surveys

Parker (1972) and Serfling (1972) conducted intertidal and subtidal exploratory searches to locate juvenile lobsters in southern California. In the present study, an extensive program of subtidal day and night scuba surveys (plus occasional intertidal searches) of various physical and biological habitats within the depth range 0-30 m was undertaken for representative areas throughout the geographical range of P. interruptus (Fig. 3). Islands surveyed include: Santa Cruz, Santa Barbara, San Nicolas, Santa Catalina, and San Clemente in southern California, and Los Coronados, San Martin, Sacramento Reef, San Benitos, and Cedros in Baja California.

Figure 3. Geographic locations of subtidal and intertidal surveys for juvenile Panulirus interruptus and Phyllospadix spp.

□= subtidal
△= intertidal



These islands were visited one or more times from November 1974 through October 1978 during cruises of the vessels Westerly, Briva III, Ellen B. Scripps, Sand Dollar, Disappearance, and Cormorant.

Mainland locations proved to be considerably more difficult to explore because of limited access to rocky beaches, harsh surf conditions, and poor underwater visibility. Thus, mainland surveys were limited to coastal areas in the vicinity of Los Angeles (intertidal), La Jolla, and Point Loma in southern California, and Ensenada and Puerto Tomas (intertidal) in Baja California. Permission to investigate lobster habitats along the central coast of Baja California in association with Mexican fisheries researchers was denied (by the Mexican federal government).

Scuba surveys consisted of randomly-oriented, detailed explorations of benthic microhabitats within a particular dive area, concentrating on juveniles less than 60 mm CL. Physical and biological characteristics of each dive area were recorded (i.e., depth, temperature, substrate types, and dominant plant cover). The number of juveniles encountered during a dive and the time spent searching were noted so that "catch per unit effort" (CPUE) could be compared for different areas.

Juvenile Habitat Preference

Within two weeks after their metamorphic molt, the lobsters captured by night-lighting at Marineland pier were retested for habitat preferences using the same experimental procedures described above. Unlike the pueruli, postpuerulus juveniles always walked along the bottom during the choice trials.

Surf Grass Distribution Surveys

Since the San Diego team of researchers (Blecha, 1972; Parker, 1972; Serfling, 1972) were most successful in finding juvenile P. interruptus within shallow Phyllospadix habitats (at Bird Rock, Santa Catalina Island), special emphasis in the present study was placed on locating and exploring surf grass habitats in all the areas listed above for juvenile surveys (Fig. 3). Physical habitat characteristics, such as bed size, depth range, degree of wave exposure, and thickness of sediment layers were noted and compared to the abundance of young lobsters.

In order to estimate whether there were sufficient surf grass areas in one locality to serve as nurseries for the resident lobster population, a detailed survey of the distribution and density of surf grass habitat for a 9 km section of shoreline along the leeward side of Santa Catalina Island (from Blue Cavern Point to Arrow Point) was undertaken during the spring of 1976. The number of

adult lobsters within the central half of this area had been determined previously from a mark-recapture program conducted by the California Department of Fish and Game (Odemar et al., 1975). In the present study, surf grass beds were observed by free-diving with diver propulsion vehicles (DPV's) along the shoreward edge of Macrocystis beds. Location and abundance information was relayed to an aide following on the surface in a small skiff.

The Primary Study Site

Evaluation of the Phyllospadix habitat as a possible lobster nursery required long-term studies of one representative surf grass/lobster system. Bird Rock, Santa Catalina Island, was chosen as the primary site for these studies for the following reasons:

1. availability of juveniles--Bird Rock is one of the few locations where young lobsters have been found consistently in previous investigations (Blecha, 1972; Parker, 1972; Serfling, 1972)
2. abundance of surf grass--healthy, discrete beds of Phyllospadix are present along both the south and east sides of Bird Rock
3. protection from extensive wave exposure--Bird Rock's location on the north side of Santa Catalina Island protects it from the commonly occurring westerly swells, thus permitting year-round in situ studies

4. accessibility--small skiffs can easily traverse the 750 m from the CMSC dock to Bird Rock by day or night any time of the year
5. ecological isolation--this small island (9,800 m² in area) is separated from Santa Catalina Island by a channel 475 m wide and 55 m deep, and from Isthmus Reef by another channel 420 m wide and 38 m deep; therefore, the shallow surf grass/lobster complex is essentially a closed system (see Fig. 2, insert).

Juvenile lobster habitat, growth, density, mortality, food habits, and behavior studies were based primarily on the Bird Rock surf grass system, which then was compared with other P. interruptus habitats and localities. The shallowest part of Isthmus Reef (0-1 m in depth) was chosen as a secondary study site because it was similar to the Bird Rock site except that Phyllospadix was absent. Instead, the reef top was covered by a dense bed of Halidrys dioica Gardner, a perennial brown alga of the family Fucaceae. As preliminary background for the above studies, a comprehensive map of the Phyllospadix beds around Bird Rock was constructed from in situ measurements, taken every 3 m along the shoreline, of grass bed perimeter depths and distances from shore. Water depth and Halidrys bed diameter measurements were taken at the single small Isthmus Reef site.

The Bird Rock Surf Grass Ecosystem

If Phyllospadix is a lobster nursery habitat, then field observations of its characteristic abiotic and biotic organization should suggest reasons why this system is favorable for juvenile survival and growth. Preliminary studies showed that temperatures in the Bird Rock grass beds were identical to daily surface water measurements recorded by CMSC personnel for Isthmus Channel (240 m from Bird Rock), so the latter temperature readings were used throughout the rest of this study. During each dive, tidal phase, wave surge, underwater light level, and water turbidity (horizontal visibility) were estimated visually.

Macro-organisms (>1 cm) associated with surf grass were recorded systematically and pertinent ecological and behavioral information was noted in the field. Clumps of Phyllospadix were collected periodically and sorted for micro-mollusks (<1 cm) which were identified to genus. The following associated studies provided additional information on surf grass community inhabitants:

1. micro-mollusk diversity within the Bird Rock Phyllospadix bed was compared to that within the Isthmus Reef Halidrys bed, at similar water depths (G. Brown, personal communication)
2. a species list of Phyllospadix bed invertebrates was compiled from collections at Lunada Bay and Flat Rock Cove, Los Angeles (R. Miracle and G. Brown, personal communication)

3. the infaunal community of the rhizome-sediment mat of Phyllospadix from Point Fermin and Flat Rock Cove, Los Angeles, was characterized by Rischen (1976)

Stable Carbon Isotope Analysis

In evaluating the importance of surf grass for juvenile P. interruptus, it would be useful to know more about the trophic pathways through which young lobsters derive energy for maintenance and growth. More specifically, is Phyllospadix the primary source of energy for juvenile lobster growth, either directly by lobster consumption of live or dead surf grass, or indirectly through one or more intermediate levels of the food chain? Comparison of the stable carbon isotope composition of animals with that of their presumed food can answer this question if the carbon isotope ratios for the potential diet sources are sufficiently distinct (Haines, 1976; De Niro and Epstein, 1978).

Carbon isotope fractionation accompanying photosynthetic carbon fixation yields plants which are depleted in the mass-13 isotope of carbon relative to the starting carbon dioxide (Pardue et al., 1976). Carbon isotope ratios are calculated by the equation:

$$\delta^{13}\text{C} \text{ (in ‰)} = \left[\frac{(\text{13C}/\text{12C})_{\text{sample}}}{(\text{13C}/\text{12C})_{\text{standard}}} - 1 \right] \times 1000 \quad (1-0)$$

The standard is carbonate from the fossil skeleton of Belemnitella americana from the Peedee formation of South Carolina (abbreviated as "PDB").

Smith and Epstein (1971) reported that $^{13}\text{C}/^{12}\text{C}$ ratios for plants fall into three general categories:

1. vascular plants utilizing the Calvin (C_3) biochemical pathway of photosynthesis have low $\delta_{\text{PDB}}^{13}\text{C}$ values (-24 to -34 ‰)
2. vascular plants utilizing the Hatch-Slack (C_4) biochemical pathway of photosynthesis have high $\delta^{13}\text{C}$ values (-6 to -19 ‰)
3. algae have intermediate $\delta^{13}\text{C}$ values of -12 to -23 ‰

Since lobster carbon derived from surf grass (a vascular plant) should be different from lobster carbon derived from algae, a preliminary study of carbon isotope ratios was undertaken. Muscle and exoskeleton samples were taken from various sizes of lobsters from the surf grass habitat at Bird Rock and the Halidrys habitat at Isthmus Reef. In addition, samples were taken from Phyllospadix and Halidrys, and from two common surf grass bed inhabitants, the kelp snail Norrisia norrisi and the fish Gibbonsia elegans. All 500 mg tissue samples were dried in small Whirl-Pak bags containing silica gel and sent to the laboratory of Dr. P. L. Parker at the University of Texas Marine Institute, where carbon isotope ratios were measured as described by Calder and Parker (1973).

Juvenile Growth

The natural growth of juvenile P. interruptus was estimated from molt increment and molt frequency data gathered using a combination of the following four techniques:

1. analysis of monthly shifts in length-frequency modes of individuals captured in the field
2. evaluation of molt increments from various sizes of freshly caught lobsters which molted shortly after capture
3. measurements of juveniles which were captured, individually marked, released, then recaptured on one or more occasions after varying periods of time in the field
4. laboratory culture of juveniles from the time of puerulus metamorphosis through the second year of benthic life.

Field Capture Techniques

Juveniles for the above growth studies were obtained from Bird Rock, with the exception of a small field-monitored sample from Isthmus Reef. Attempts were made to trap juveniles from Bird Rock using concrete habitats and PVC pipe habitats similar to ones described by Sweat (1968), and miniature commercial-type lobster traps (50 x 50 x 20 cm) constructed from 12 mm wire mesh, but these designs were unsuccessful. Ultimately, all juveniles were hand-captured by scuba diving within the shallow (0-3 m) surf grass

beds. Methodical searching, despite moderate to heavy wave surge conditions, was facilitated by the addition of 4-9 kg of lead weights to a normally-weighted diver's weight belt and by the attachment of a 1.4 kg lead weight to each ankle by means of Velcro straps. Most juveniles were captured with bare hands; some larger individuals (>30 mm CL) were entrapped with a small hand net. Captured specimens were accumulated in 2 liter plastic bottles clipped to weight belt rings, then transferred to 19 liter buckets after the dive for transport to CMSC aquaria.

Lobster Measurements

For every field animal captured from November 1974 until November 1975, the following information was recorded in duplicate on preprinted data forms: capture date, capture locality, individual identification code number, carapace length, wet weight, antennae lengths, sex, body color, and condition of appendages. Any injuries, areas of regeneration, or other unique characteristics were noted. Carapace length, defined as the length from the mid-dorsal anterior carapace edge between the rostral spines to the mid-dorsal posterior carapace edge, was used as the standard measurement of size because of its accuracy and practicality. Carapace lengths were measured to the nearest 0.05 mm with vernier calipers by taking the mean of three readings. Wet weight was measured by shaking

the lobster (held in an anterior end down position) five times to remove excess water from the branchial chamber, damp drying the exoskeleton with a paper towel, and weighing the animal to the nearest 0.1 g on a triple beam balance. Antennal length, defined as the length from the distal edge of the carpus of the second antenna to the flagellum tip, was recorded for both antennae to aid in characterization of individual lobsters and to determine the effect of antennal injury on juvenile growth. Postmolt individuals with soft exoskeletons were held until hardened (2-3 days) before measuring; otherwise, juveniles were returned to the area of capture within one day.

The above recording system was used also to monitor juveniles raised in laboratory aquaria. During the first two months of this study, all individuals were measured once every two weeks in order to determine the range of measurement variability within intermolt animals. Later, only juveniles which had molted since the previous two-week examination period were measured.

Length-Weight Relationships

Relationships between carapace length and wet weight were determined for different size groups and sexes of field-captured and laboratory-raised juveniles so that lobster growth, measured as incremental increases in carapace length, could also be expressed

as changes in biomass per unit time. Length-weight relationships can be affected by such variables as missing appendages, degree of water retention in the branchial chambers, changes in weight during the intermolt period, allometric growth of the carapace, and changes in tissue density. The first variable was eliminated by using only data from intact lobsters. The second and third variables were reduced by standardization of measuring techniques (see above). For juvenile lobsters, carapace growth was assumed to be isometric, and changes in tissue density were assumed to be relatively unimportant.

By October 1975, sufficient length-weight data were accumulated; thereafter, wet weight was no longer measured for field-captured individuals.

Sex Determination

The sex of juvenile P. interruptus was determined primarily by the presence or absence of the male gonopores on the coxae of the fifth pereopods. In the smallest males (7-15 mm CL), the gonopore is barely visible as a tiny slit amidst a slight irregularity on the ventral surface of the coxa. The gonopore of larger juveniles (25-45 mm CL) is readily apparent as a shallow concavity of uncalcified cuticle covering 50-90% of the coxal surface. Males approaching sexual maturity (>55 mm CL) have swollen, glandular

gonopores suitably modified for spermatophore formation.

In females, the ventral surface of the coxa of the fifth pereopod is smooth and similar in appearance to those of the other pereopods. Small chelae on the tips of the fifth pereopods are evident in females larger than 35 mm CL. Allometric enlargement of pleopodal exopods is barely noticeable at 35 mm CL, but both pleopodal exopods and endopods are considerably larger in females greater than 35 mm CL than in correspondingly sized males.

Size-Frequency Distributions

From October 1974 through December 1976, carapace lengths were recorded for juveniles captured from the surf grass habitat at Bird Rock at irregular times during each month, determined by the presence of favorable sea conditions. In principle, it was considered desirable to obtain at least 100 single year class juveniles per month for the two years combined, so the diving effort was planned with this goal in mind. All juveniles captured were used in the size-frequency analyses, including those with broken or missing appendages, but nonmolted recaptured individuals were recorded only once per month. Recaptured individuals measured for two different instar sizes during a given month were recorded as follows: if the first measurement was taken on or before the 15th of the month, the premolt size was assigned to the previous month

and the postmolt size to the current month; but if the first measurement was taken after midmonth, the premolt size was assigned to the following month. The same system was used for laboratory-raised lobsters, for which more accurate molt dates were available.

Carapace length data were compiled into monthly histograms which were analyzed for progressive shifts of size modes toward larger animals, presumably indicative of growth.

Field Molt Increments

Exact growth per molt for juveniles which undergo ecdysis shortly after capture can be determined if one assumes that capture stress and laboratory handling do not affect short-term growth processes. Individuals collected from Bird Rock which were close to molting (late proecdysis) were held in aquaria for a period no greater than one week to record the increase in size at ecdysis. Premolt lobsters could be recognized in two ways:

1. by the darkened appearance of the branchiostegal reabsorption line (normally pale yellow) located along the ventro-lateral area of the carapace. In late proecdysis this line is softened, allowing the branchiostegites to move easily when touched
2. by the presence of a dark lining around the perimeter of the cut surface when a rostral spine was removed (for the mark-recapture study, discussed below). This pigmentation results

from chromatophore development in the exocuticle of the soft, underlying "postmolt" exoskeleton.

Mark-Recapture Growth

Marking adult lobsters by punching holes in the tail fan (uropods and telson) and/or cutting pleopods has been used successfully in field recapture studies to measure total growth (molt increment plus molt frequency) over varying intercapture periods (Odemar et al., 1975; Chittleborough, 1976; Winstanley, 1976). In the present study, juveniles between 10 and 60 mm CL captured from Bird Rock (plus a few from Isthmus Reef) were marked in three ways:

1. combinations of one, two, or three of the five tail fan sections were punched with a spring-loaded leather punch or a common paper punch
2. combinations of one or two of the eight pleopods were clipped off at the coxae with scissors
3. one of the two rostral spines was removed

The leather punch had a revolving head with six cylinders that enabled circular holes between 2 and 5 mm in diameter to be made; the paper punch made 6 mm diameter holes. Lobsters were marked with as large a hole as possible (without ruining the appendage) to delay occlusion of the mark by regenerating tissue, so that

the code would still be recognizable after numerous molts. Recaptured juveniles which had molted in the field were remarked with the same code to remove regenerated tissue.

The tail fan/pleopod marks permitted 1,050 combinations. Rostral spine marks, sex, and other unique characteristics served to double-check the tail fan/pleopod code when identifying recaptured individuals. In addition, the rostral spine cuts were used to approximately determine intermolt phases. The cut surface of the rostral spine was colorless to pink on postmolt juveniles, light red to red on mid intermolt juveniles, and dark red to dark brown on premolt juveniles.

Laboratory Culture

Growth programs based on laboratory rearing of captive individuals may yield dubious information if the animals are crowded, kept in unnatural surroundings, or not given adequate food; however, carefully administered culture studies can provide natural growth data not available from field programs, i.e., lengthy individual sequences of size increases separated by known intermolt periods (see, for example, Chittleborough, 1975; Phillips et al., 1977). Also, laboratory-raised juveniles can be used to evaluate the effects of a marking system on lobster survival and growth.

From October 1974 through April 1975, 33 juveniles ranging in size from 12 to 28 mm CL were collected from surf grass habitats in the vicinity of CMSC for laboratory culture studies. Lobsters were marked using the same techniques applied to field animals except for one juvenile left unmarked (as a control). In addition, laboratory juveniles were marked with underwater epoxy (Sea Goin' Poxy Putty, Permalite Plastics Corporation, Newport Beach, CA) on the dorsal surface of the carapace, so that newly molted individuals could be recognized quickly. Eleven lobsters were kept in each of three 140 liter Plexiglas aquaria (87 x 58 x 27 cm) supplied with unfiltered, ambient temperature sea water flowing through the system at a rate of roughly 200 liter/h. The aquaria were light-sealed with black plastic film and covered with plywood lids, each containing a 20 w cool white fluorescent lamp. The lamps were connected to a 24 hour on/off timer set to simulate the day/night cycle occurring in the field.

All three aquaria were provided with den-like shelters made of rocks, bricks, shells, and clay tiles. Natural habitat biota, including clumps of surf grass, coralline algae, and mussels (Mytilus spp.), were added to the system as needed to provide additional shelter and live food items. To ensure an abundance of food, fresh cracked mussels and occasional chunks of fish and abalone were presented two or three times per week. In order to minimize

disturbance, juvenile lobsters were examined only once every two weeks when the aquaria were cleaned. Measurements were taken at this time, as described above. Molt dates were determined from the presence of fresh exuviae, or by extrapolating from the condition of late premolt or early postmolt animals.

By November 1975, the 31 surviving juveniles had reached a size range of 26-41 mm CL; to avoid crowding, they were transferred to a 1,285 liter outdoor tank (280 x 102 x 45 cm) with a sea water flow rate of approximately 2,500 liter/h. In addition, a submerged pump, connected to a one hour on/off timer, sucked up water from the tank bottom and sprayed it over the surface for 10 minutes every hour to prevent the formation of oxygen-deficient pockets. Habitat conditions and feeding regimes were identical to those in the indoor aquaria, except that the timer-controlled light cycle no longer was necessary. Also, in November 1975, 28 newly settled juveniles, captured as pueruli by night-lighting, were established in the three indoor tanks. These animals were raised to provide growth information from a known starting point, the time of settlement (puerulus metamorphosis). Juveniles were maintained in the indoor and outdoor systems until January 1977, when the laboratory growth study was terminated.

Growth Analysis

Data from size-frequency, field molt increment, mark-recapture, and laboratory culture studies were analyzed with respect to sex, size, and temperature for both lab and field populations. Specific year class size ranges were established for the first two years of benthic life from graphic plots of carapace length against time. Multiple regression analysis was used to generate predictive equations relating changes in molt increments and molt frequencies to changes in premolt size and water temperature. Initially, these equations made it possible to estimate field molt frequencies for re-captured individuals with long intercapture intervals. Finally, they permitted the construction of generalized instar-size and age-size tables under given seasonal settlement periods and yearly temperature regimes.

Results from the above analyses then were fitted to adult P. interruptus growth estimates to produce a more complete picture of lobster growth, especially with respect to age at sexual maturity and age at legal size.

Juvenile Abundance

Information obtained from the juvenile growth study dives in the Phyllospadix beds at Bird Rock also was used to estimate the size of the juvenile population. Two methods were utilized: catch

per unit effort (CPUE), in the form of catch per diver-hour of searching; and mark-recapture analysis. Problems in interpreting CPUE data are generally associated with biased collections caused by variable diver search and capture abilities, patchy lobster distributions, and changing underwater environmental conditions (e.g., wave surge, tide level, light, and turbidity). The first problem was reduced by adjusting dive partner performance to my own performance (see Results, p. 91). The second and third problems were reduced by summing all dives for each month of the study.

Mark-recapture abundance determinations were based on a multiple capture scheme in which all new individuals were marked each time the population was sampled for the growth studies (see above). For unbiased results, the following assumptions must be met (see Pope, 1963):

1. marked lobsters which are recaptured are correctly recognized as such
2. new recruitment and immigration are insignificant, and any mortality or emigration affects marked and unmarked animals equally
3. marked and unmarked animals are randomly distributed within the sampling area so that both have equal chances of being captured

Some of the above conditions were not known a priori, nor could they be tested within the scope of this project. Also, the sampling scheme was limited (by strong surge and by difficulty in seeing and capturing juveniles) to the collection of relatively few lobsters per dive at irregular intervals, so a simple direct method of population size estimation was chosen which would provide at least "order of magnitude" information. Capture-recapture data were combined for each month, then population estimates were computed for three- or four-month periods using the method of Schumacher and Eschmeyer (1943). This method is more efficient than Schnabel's (1938) formula when the percentage of marked individuals in the field population exceeds 25% (see Ricker, 1945).

Observations of juvenile lobster distributional patterns within the Phyllospadix habitat were made during field survey dives. Numbers, sizes, and age class composition of aggregations were noted when possible.

Juvenile Activity Patterns

Spatial and temporal aspects of juvenile P. interruptus locomotor activity were divided into four topics for investigation: den residency, diel activity rhythms, home range, and seasonal movement patterns. To determine whether lobsters repeatedly return to the same den after each foraging period, five juveniles

occupying specific crevices within small patches of Phyllospadix at depths of 0.5-1.0 m in Big Fisherman Cove (see Fig. 2, insert) were monitored for periods up to seven months. The first two juveniles were individually recognizable from the pattern of light bands on the antennae. Later, four of the five juveniles were captured and marked as described above, except that thin aluminum wire was wound around the base of one antenna to permit quick field identification with minimal observer disturbance. Immediately after marking, the juveniles were returned to their crevices. Den monitoring was continued at irregular intervals until all juveniles no longer could be found.

Day and night observations of activity rhythms were made on laboratory-raised and on field-surveyed juveniles. In addition, on two occasions, an underwater television camera and 250 w mercury vapor lamp (Hydro Products Corp., San Diego, CA) were mounted above the crevice containing a juvenile marked for the den residency study. The camera and lamp were connected by 450 m of cable to a dry station at CMSC, where a television monitor and a timer-controlled videotape recorder automatically displayed and recorded a view of the den for five minutes of every hour.

The spatial extent of juvenile movements (home range) was determined by comparing capture locations with recapture locations

for the individually marked juveniles at Bird Rock and Isthmus Reef. Specific capture and recapture localities also were used to ascertain whether seasonal movements occurred. Monthly size-frequency plots and CPUE and mark-recapture abundance estimates were evaluated for seasonal variation which would reflect mass movement patterns (i.e., migrations).

Juvenile Food Habits

Gut content or fecal content analyses are useful techniques for indirectly determining the natural diet of field animals when their feeding habits make direct observations difficult or impossible. A preliminary evaluation of gut content versus fecal content techniques for use with juvenile P. interruptus resulted in the following observations:

1. gut contents already were so macerated by the combined action of the mandibles, gastric mill, and digestive enzymes that food item identification was no easier than that for fecal contents
2. fecal content samples were easier to compare on a relative quantitative basis because all food items were exposed to approximately the same amount of digestion
3. fecal content analysis did not require killing lobsters (often for no benefit since roughly 20% of the guts essentially were empty), so the same animals could be used for other concurrent studies.

Food items in the diet of all lobsters collected between November 1974 and May 1975 from the Bird Rock Phyllospadix beds (and a few from the Isthmus Reef Halidrys habitat and the CMSC sea water intake Macrocystis habitat) were identified by fecal content analysis. Freshly captured juveniles were isolated for 24 hours in one liter beakers containing filtered sea water, after which the fecal material was concentrated and preserved in 70% isopropyl alcohol. A preliminary study of 16 juveniles checked at 8-, 12-, and 24-hour intervals for two days revealed that over 90% of the fecal material was eliminated within the first 24 hours.

Each food item was identified to the lowest taxon possible by comparing fragments to whole animals collected from the surf grass rhizome-sediment mat. For all recognizable food materials, sizes and numbers of individuals or fragments and visual estimates of biomass percentage were recorded. Dry weights of fecal material were not taken because of errors relating to differential digestibility and because of the small amounts of material per sample (< 0.1 g). For gastropod mollusks, the number and size range of opercula were recorded for each genus consumed.

A measure of the relative importance of individual food items was obtained by multiplying their frequency of occurrence among samples by their mean abundance within samples (% visual

biomass). Food habits were analyzed with respect to lobster size and habitat. Results were compared to field observations of foraging behavior and food availability.

Juvenile Mortality

Instances of lobster mortality related to handling and marking stress, ecdysis, and other factors were recorded for laboratory-raised juveniles. Natural mortality trends for Bird Rock surf grass juveniles were determined from changes in the monthly catch per unit effort and the mark-recapture abundance estimates.

Mortality due to predation was documented by means of serendipitous and controlled observations of predator-prey interactions and actual attacks on juvenile lobsters, by personal communications with investigators identifying gut contents of suspected lobster predators, and by examining the ingested material collected from the stomachs of Scorpaena guttata and Scorpaenichthys marmoratus (two fish known to prey on benthic crustaceans) using the double tube flushing technique of Seaburg (1957). After collecting stomach contents, the fish were marked with numbered plastic garment tags inserted into the dorsal musculature with a spring action applicator, then released at the area of capture.

RESULTS

Juvenile Habitat

Puerulus Recruitment

Night-Lighting

Night-lighting for the puerulus larvae of Panulirus interruptus was carried out intermittently during the months of June through November, 1974-1976. The results are listed in Table 3. Additional data for CMSC were provided by J. Wible (personal communication) for June 1977 and M. Ninos (personal communication) for July-November 1978. In total, 65 pueruli were collected during 168.5 hours of night-lighting, resulting in a catch per unit effort (CPUE) of 0.4 larvae per hour. Seventy-seven percent of all pueruli were captured at Marineland in 55.5 hours during 10 nights from August through October 1975 (0.9 larvae/h CPUE). Thirty-seven percent of the total were captured in one night at Marineland (4.0 larvae/h CPUE). Pueruli rarely were captured at CMSC during 1974, 1975, or 1976. Ten of the 12 pueruli found there were collected during one 11-day period in June 1977. One puerulus was captured within 10 m of the surf grass beds at Bird Rock on August

TABLE 3. -- Night-light sampling for the puerulus larvae of *P. interruptus* at Santa Catalina Island and Marineland of the Pacific, Los Angeles [1977 data from J. Wible (personal communication); 1978 data from M. Ninos (personal communication)]

Year	Date	Location	Observation		Water			
			Time (h)	Pueruli Collected	CPUE (#/h)	Temperature (°C)	Tide Phase	Moon Phase
1974	10- 5	CMSC pier	1	0	0	19.5	R	LQ
	10- 6	" "	2	0	0	19.5	R	LQ
	10- 7	" "	1	0	0	19.0	L	LQ
1975	6-24	CMSC pier	2	0	0	16.5	H	F
	6-25	" "	2	0	0	17.0	H	F
	7- 4	" "	2	0	0	18.5	E	LQ
	7-12	" "	1.5	0	0	19.0	R	N-FQ
	7-18	" "	2	0	0	18.0	E	FQ
	7-19	" "	1.5	0	0	18.0	E	FQ-F
	7-29	" "	2.5	0	0	19.5	L	LQ
	8- 4	" "	5	0	0	20.5	E	N
	8- 5	" "	2.5	0	0	20.5	H	N
	8- 7	" "	3.5	0	0	20.0	H	N
	8- 8	Bird Rock	2	0	0	20.5	H	N
	8-14	CMSC pier	2.5	0	0	19.0	E	FQ
	8-18	" "	3.5	0	0	19.0	H	FQ-F
	8-20	" "	2.5	0	0	20.0	H	F
	8-21	" "	3	0	0	20.0	H	F
	8-25	" "	3	0	0	20.5	R	F-LQ
	8-26	" "	3.5	0	0	19.5	R	LQ
	8-29	Marineland	3.5	3	0.9	16.0	E	LQ
	9- 4	CMSC pier	3.5	0	0	20.0	H	N
	9- 5	Marineland	5	3	0.6	16.5	R-H	N
	9- 6	"	5	24	4.0	16.5	R-H	N
	9- 7	"	5.5	4	0.6	17.0	H-E	N
	9-16	"	6	8	1.3	17.5	H-E	FQ-F
	9-17	"	4	0	0	17.0	H	F
	10- 6	"	6	3	0.5	16.5	R-H	N
	10- 7	"	6.5	5	0.8	16.0	R-H	N
	10-24	"	6	0	0	15.0	R	F-LQ
	10-25	"	6	0	0	15.0	R	LQ
1976	5-14	CMSC pier	2	0	0	20.0	R	F
	6-25	" "	2.5	0	0	20.5	H	N
	7-19	" "	2	0	0	21.0	E	LQ
	7-29	" "	1.5	0	0	20.5	R	N
	8-18	Bird Rock	2	1	0.5	20.0	E	LQ
	8-24	Arrow Point	3	2	0.7	20.5	H	N
	9-12	CMSC pier	2	0	0	21.5	R	F-LQ

TABLE 3.--Continued

Year	Date	Location	Observation		Water		Tide Phase	Moon Phase
			Time (h)	Pueruli Collected	CPUE (#/h)	Temperature (°C)		
1977	5- 6	CMSC pier	3	0	0	18.5	L	LQ
	6- 7	" "	2	3	1.5	17.5	L	LQ
	6- 8	" "	3	2	0.7	17.5	E	LQ
	6-11	" "	2	4	2.0	17.5	E	LQ
	6-18	" "	1	1	1.0	18.5	R	N
1978	7- 7	CMSC pier	1	0	0	19.0	R	N
	7-15	" "	2	0	0	20.5	E	FQ
	7-29	" "	1.5	1	0.7	19.0	E	LQ
	7-31	" "	1	0	0	17.5	H	LQ-N
	8- 1	" "	1.5	0	0	20.0	H	N
	8- 3	" "	1	0	0	20.5	R	N
	8- 4	" "	1.5	1	0.7	20.5	R	N
	8- 5	" "	2.5	0	0	20.0	R	N
	8-19	" "	1	0	0	21.0	R	F
	8-26	" "	1.5	0	0	20.0	E	LQ
	8-29	" "	1.5	0	0	20.0	E	LQ-N
	9- 2	" "	1	0	0	19.5	H	N
	9- 3	" "	1	0	0	19.5	H	N
	9-13	" "	1	0	0	19.0	E	FQ-F
	9-14	" "	1	0	0	18.5	H	F
	9-28	" "	1	0	0	21.5	H	LQ-N
	9-30	" "	1	0	0	21.0	H	N
	10- 3	" "	1	0	0	20.5	R	N
	10-16	" "	1	0	0	20.0	R	F
	10-18	" "	1	0	0	20.0	R	F
	10-19	" "	1	0	0	20.0	R	F
	10-27	" "	1	0	0	20.0	E	LQ-N
	10-28	" "	1	0	0	19.0	H	N
	10-29	" "	1	0	0	18.5	E	N
	11- 6	" "	1	0	0	18.0	L	FQ
	11- 8	" "	1	0	0	18.0	E	FQ
	11-13	" "	1	0	0	17.5	H	F
	11-14	" "	1	0	0	17.0	H	F

Tides:

L = Low
 R = Rising
 H = High
 E = Ebbing

Moon Phases:

N = New
 FQ = First Quarter
 F = Full
 LQ = Last Quarter

18, 1976. Six days later, two pueruli were collected approximately 1 km offshore from Arrow Point, Santa Catalina Island.

Pueruli were captured as early in the year as June 7 (in 1977) and as late as October 7 (in 1975). The general period of puerulus catchability corresponded to the season of highest water temperatures for both Santa Catalina Island and Marineland (see below); however, the months December through May were not sampled. The limited number and variable catchability of pueruli precluded correlation with specific water temperatures, tide heights, or moon phases (Table 3).

Night-lighting was successful in attracting numerous organisms visible to the naked eye, including swarming polychaete worms, ostracods, copepods, mysids, stomatopod synzoea, isopods, brachyuran zoea and megalopa, caridean shrimps, squid, and fish larvae, juveniles, and adults (e.g., Hypsoblennius larvae, Atherinops juveniles, and Cypselurus adults). Amidst this cloud of organisms, the appearance of puerulus larvae was readily apparent because of their size (20 mm total length, 30-70 mm antennae length), shape (like miniature adult lobsters), color (pale translucent white when side- or back-lit by the underwater light), and behavior (forward swimming at the water surface).

Interlocking endopods of opposing pleopods facilitate the forward locomotion of pueruli. When swimming, the anteriorly

pointing pereopods were appressed to the lateral carapace, and the long antennae were held together, projecting ahead of the larvae. Periodically, the larvae would cease swimming, separate their antennae (producing an elongated "V-shaped" appearance), and slowly sink 0.5-1.0 m before resuming forward motion. Pueruli did not show rapid escape responses when dip-netted, but were capable of backward abdominal flipping when forward motion was blocked.

Roughly one-fourth of the larvae had one or both antennae partially broken at the time of capture. Complete antennae had a slightly swollen, red pigmented area at their tips. Within 12 hours of capture, all antennae had broken off to 30-50% of their former length. Captured pueruli, placed in a 20 liter bucket, remained motionless around the bottom edge with their abdomens tucked under their bodies. They clung tenaciously to any introduced object, including air stones and other pueruli.

Phyllospadix Habitat Traps

Four surf grass habitat traps were monitored weekly from June through September 1975 for the presence of settled pueruli (see Fig. 2; Table 2). No lobster larvae were captured using this technique.

Puerulus Metamorphosis

"Settlement" of the puerulus larvae of P. interruptus was defined behaviorally by the absence of pleopodal swimming and morphologically by the loss of the distal half of the second antennae and the appearance of white pigment in the "V"-shaped median hepatic lobes. The latter characterized the first of three progressive pigmentation stages of the post-settlement larvae described by Parker (1972). In addition to the white hepatic lobes, Stage 1 larvae have traces of rose tint at the antennal bases and along the lateral edge of the cephalothorax. Stage 2 larvae have increased reddish color on the dorsolateral sides of the cephalothorax and abdomen, except for a pair of large white spots on the carapace and a smaller pair on the first abdominal segment. A median dorsal white band extends the length of the body. By Stage 3, the pigmented areas are fully darkened to a reddish brown color. The white band and spots clearly are evident.

Table 4 shows the times required for 27 pueruli captured within a three-day period at Marineland to reach each pigmentation stage and the metamorphic molt. Larvae were kept in separate ambient sea water temperature beakers (avg T = 20°C). Sixteen larvae had settled and reached Stage 1 within four days. Six more individuals reached Stage 1 within a week of capture, but the

TABLE 4.--Time after capture for 27 *P. interruptus* pueruli, collected at Marineland on September 4-6, 1975, to reach three post-settlement pigmentation stages and the metamorphic molt [see text and Parker (1972) for description of pigmentation stages]

Puerulus	Post-capture Time (days)			Molt
	Stage 1	Stage 2	Stage 3	
2A	4	8	12	13
3A	4	6	10	11
4A	4	6	8	10
5A	7	9	11	12
6A	4	7	11	12
7A	4	7	D	D
8A*	29	32	35	39(D)
A13	4	6	9	10
B13	7	9	13	15
C13	4	7	10	11
H13	3	5	7	9
I13*	13	15	16	19
J13*	15	17	20	22
L13	7	8	10	11
N13	7	9	11	12
O13	4	11	13	15
P13	4	8	11	12
Q13	5	6	9	11
R13	4	9	13	15
S13*	11	13	14	15
T13	3	5	7	9
U13*	10	11	13	15
W13	7	8	9	10
X13	3	5	7	10
Y13	4	5	7	12
A14	3	5	8	10
C14	3	5	7	11
<hr/>				
N	22	22	21	21
Mean	4.5	7.0	9.7	11.5
SD	1.5	1.8	2.1	1.8
95% Cf	0.7	0.8	1.0	0.8

*Larvae which settled later than one week after capture were not included in the descriptive statistics.

D = Died

remaining five larvae did not begin to acquire pigment until 10-29 days after capture. One of the latter individuals, puerulus 8A, died during the metamorphic molt, which occurred 39 days postcapture. The mean time to molting for those larvae which settled within one week of capture was 11.5 days.

Freshly molted "postpueruli" appear similar to the pigmented pueruli since the postsettlement pigment had been incorporated in the newly developing cuticle underlying the clear larval exoskeleton. In this first juvenile stage, the cephalothorax is less flattened and the pleopods are reduced and no longer interlocking. In addition, numerous 1 mm high, thin white featherlike projections are evident on the dorsal surface of the carapace. Their detailed structure and function are unknown.

Bird Rock Recruitment

From 1974-1977, 205 recently settled juvenile lobsters (7-12.9 mm CL) were captured from the Phyllospadix beds at Bird Rock. These small, well-camouflaged individuals were difficult to locate and capture by hand in the shallow, surgy grass beds, so the number captured probably represents only a minor fraction of those present during the settlement season. No major differences were noted between years; however, the data were insufficient to determine the extent of yearly variation in recruitment. Table 5 shows

TABLE 5. -- Monthly captures of 7-12.9 mm CL juvenile P. interruptus from Phyllospadix beds at Bird Rock for the combined years 1974-1977

	NUMBER OF JUVENILES						Total 10-12.9 mm CL	
	7-7.9 mm CL		8-8.9 mm CL		9-9.9 mm CL			
	Total mm CL	7-9.9 mm CL	Total mm CL	7-9.9 mm CL	Total mm CL	11-11.9 mm CL		
JAN	0	0	0	0	0	3	4	
FEB	0	0	0	0	0	2	3	
MAR	0	0	0	0	0	2	6	
APR	0	0	0	0	0	0	2	
MAY	0	0	0	0	0	0	0	
JUN	0	0	0	0	0	0	0	
JUL	1	7	11	19	1	1	0	
AUG	0	4	2	6	14	4	6	
SEP	2	1	2	5	8	4	16	
OCT	1	1	7	9	8	15	8	
NOV	0	0	1	1	5	6	10	
DEC	0	0	0	0	1	3	7	
						3	11	

the monthly captures of these small juveniles for 2 mm length groups for all years combined. Results from laboratory growth studies of pueruli caught at Marineland revealed that, in general, juveniles less than 10 mm CL must have settled within the month previous to their capture (see below). Juveniles from 10 to 12.9 mm CL most likely settled from one to two months previous to their capture during warm water periods, or from three to four months previous to capture during cold water periods.

Juveniles less than 10 mm CL were found from early July through late November; therefore, puerulus recruitment ranged from June to early November. Juveniles from 10 to 12.9 mm CL were collected during all months except May and June. Subtracting an average of 1.5 months from individuals captured during July through November, and an average of 3.5 months from those caught between December and April, the settling season was found to extend from May to December. With the above assumptions applied to the data of Table 5, the main settlement period was July, August, and September. Mid-August represents the median as well as the apparent peak time of puerulus recruitment at Bird Rock.

Age at Settlement

For this investigation, the time of hatching of the phyllosoma larva from the egg was considered the birth date. As

reasoned by Chittleborough (1974a), hatching time can be taken as the midpoint of the breeding season prior to larval settlement. Mitchell et al. (1969) found that 78% of adult female P. interruptus were berried in June, but only 8% were berried in August. Thus, hatching was taking place mainly during July and August. On this basis, I considered the birth month for California lobster to be August. Since the midpoint of the settling season and the peak settling time also occurred during August at Bird Rock, newly settled larvae were assumed to be one year old. Therefore, post-settlement juveniles represent age 1+, 2+, 3+,...year classes.*

Sea Water Temperatures

Surface sea water temperatures recorded by CMSC personnel in the vicinity of Bird Rock ranged from 12 to 23°C for the period 1970-1977. Mean annual temperature for this eight-year period was 16.9°C. In general, December through May were cold water months (avg T = 15.0°C), and June through November were warm water months (avg T = 18.9°C).** Temperatures for different depths, locations, and times were compared using seasonal means

*Hereafter, all ages have been expressed in this shortened form, e.g., age 2+ lobsters = lobsters between 2 and 3 years of age.

**These definitions of warm and cold water periods have been used hereafter.

(Table 6). Mean temperatures at 20 m depth for the eight-year period were 0.5°C colder than surface water during cold months and 1.9°C colder during warm months.

Surface temperature data taken by the County Sanitation Districts of Los Angeles County at White's Point, 6 km south of Marineland, from December 1974 through November 1975 (J. Parkhurst, personal communication), were similar to Bird Rock temperatures at 20 m depth for the same time period. Bird Rock surface temperatures for 1975 (avg T = 16.2°C) averaged 0.7°C lower than the 1970-1977 period, while 1976 temperatures (avg T = 18.2°C) were 1.3°C higher than the eight-year mean. Semimonthly surface temperature means and ranges for Bird Rock during 1975 and 1976 are shown in Figure 4. Seasonal temperature maxima for both years (July-September) correspond with the peak settlement period of P. interruptus pueruli.

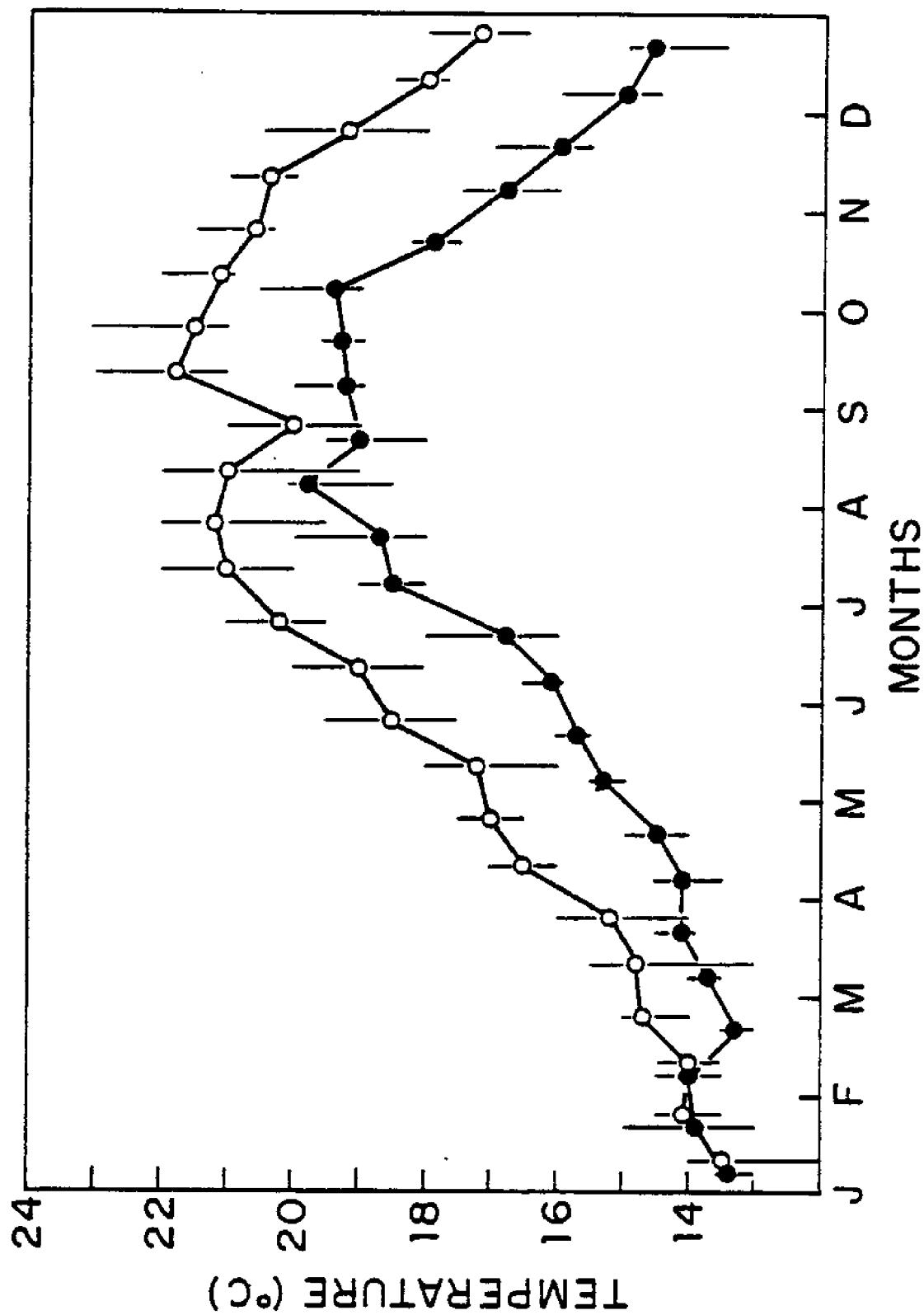
The CMSC flow-through sea water system pumps water from a depth of 7 m near the field temperature recording station. Temperatures within laboratory aquaria averaged 0.4°C higher than field surface temperatures, and were more variable since the water warmed up 0.5-1.5°C on sunny days and cooled off by a similar amount on clear, cold nights.

TABLE 6. -- Mean seasonal temperatures for surface sea water near Marineland during 1975, and for two depths (0, 20 m) and three time periods (1975, 1976, 1970-1977) near Bird Rock, Santa Catalina Island

Location	Time Period	Depth (m)	Mean Sea Water Temperature (°C)				
			DEC-FEB	MAR-MAY	JUN-AUG	SEP-NOV	
Bird Rock Area	DEC 1975-NOV 1976	0	14.3	16.5	20.4	20.8	
Bird Rock Area	DEC 1974-NOV 1975	0	14.3	14.6	18.2	18.1	
Bird Rock Area	DEC 1974-NOV 1975	20	14.0	14.1	15.9	16.5	
Marineland Area	DEC 1974-NOV 1975	0	13.9	13.9	16.5	16.6	
Bird Rock Area	1970-1977	0	14.7	15.3	19.1	18.6	
Bird Rock Area	1970-1977	20	14.4	14.6	16.9	17.0	

Figure 4. Mean semimonthly surface sea water temperatures at Bird Rock, Santa Catalina Island, during 1975 and 1976. Vertical lines represent the range of daily temperature values.

● = 1975
○ = 1976



Puerulus Habitat Preference

Laboratory Substrate-Choice Tests

Results from the paired substrate-choice experiments were evaluated for significance using the binomial goodness of fit test* (Siegel, 1956) (Table 7). Pueruli preferred Phyllospadix over rubble rock, the large kelp Macrocystis pyrifera, and brown alga Halidrys dioica. No preference was shown between Phyllospadix and the red alga Plocamium cartilagineum. These results agree with those of Parker (1972), who used similar substrates (see Table 7).

Pueruli in control aquaria (no introduced substrates) were found along the walls and corners. A few reacted to the turning on of room lights by rapid walking or swimming. In control aquaria with the same substrate at both ends, and in mixed-substrate test aquaria, over 95% of the pueruli were found either clinging to or directly underneath the selected substrate.

Field Observations

Postsettlement pueruli were not seen during any dives at Bird Rock. On several occasions recently molted first instar juveniles were found concealed within clumps of Phyllospadix brought

*The following criterion for significance has been adopted for all statistical tests throughout this study: If $P \leq 0.05$, the numerical distributions are nonrandom.

TABLE 7. -- Results of habitat preference experiments on the puerulus larvae of Panulirus interruptus from this study and from Parker (1972)

	Choice A	Number Choosing	Choice B	Number Choosing	P	Results
	A		B	B		
Parker (1972)	Control	10	Control	16	>0.30	A = B
	<u>Phyllospadix</u>	24	Rubble Rock	2	<0.01	A > B
Parker (1972)	<u>Phyllospadix</u>	9	Rubble Rock	0	<0.01	A > B
	Control	11	Control	21	>0.10	A = B
Parker (1972)	<u>Phyllospadix</u>	26	<u>Macrocytis</u>	6	<0.01	A > B
	<u>Phyllospadix</u>	10	<u>Macrocytis</u>	1	<0.01	A > B
Parker (1972)	Control	8	Control	9	>0.90	A = B
	<u>Phyllospadix</u>	10	<u>Plocamium</u>	6	>0.40	A = B
Parker (1972)	<u>Phyllospadix</u>	8	Red Algae	4	>0.10	A = B
	Control	16	Control	16	>0.90	A = B
Parker (1972)	<u>Phyllospadix</u>	24	Halidrys	8	<0.01	A > B

to the laboratory. One sample of Plocamium cartilagineum collected by T. Audesirk (personal communication) on September 19, 1975, contained two first instar juveniles.

J. Morin (personal communication) collected a transparent puerulus while diving in 7 m of water on a shelly debris plain near Habitat Reef, Big Fisherman Cove, on July 17, 1976. The larva was found on an isolated rock, 15 cm in diameter, covered with encrusting and erect coralline algae. The distal halves of both antennae were missing, but no other signs of settlement were evident.

Juvenile Habitat Surveys

From 1974 to 1978, 2,357 P. interruptus less than 60 mm CL were seen or captured in various localities throughout southern and lower California during 330 diver-hours of scuba search effort. In addition, juvenile presence or absence was noted during 178 non-survey diver-hours during this same period. Fifteen percent of the total survey search effort took place at night. Table 8 summarizes the survey results with respect to dominant plant cover, depth range, relief, substrate, day and night search times, and number of lobsters encountered per diver-hour (CPUE) for two size classes of juveniles. Most of the search time was spent exploring different sites at Santa Catalina Island (Fig. 5). Due to related concurrent studies, 55% of all search efforts were directed at the Phyllospadix beds of Bird

TABLE 8.--Results of scuba surveys for juvenile lobsters in various locations throughout the geographic range of *P. interruptus*

Location	Plant Cover	Depth Range (m)	Relief	Substrate	Search Time (Diver Hrs)*		Juveniles			
					Day	Night	# Seen	CPUE	# Seen	CPUE
<u>Santa Catalina Island</u>										
Bird Rock	Phy	0-2.5	Low	Bd, Sh	209.7	5.1	1733	8.1	118	0.6
" "	Ela	0-4	Med	Bd, Cr	4.3	20.0	33	1.5	34	3.5
" "	Mac	4-10	Med	Bd, Sh	2.4	12.4	16	1.1	23	1.8
" "	Aga	23-28	High	Bd, Bo	1.9	0	0	0	18	9.4
Isthmus Reef	Hai	0-1.5	Med	Bd, Cr	17.2	0	61	3.6	9	0.5
" "	Aga	13-18	Med	Bd, Sh	3.4	4.3	0	0	48	5.3
Other Sites	Phy	0-4	Med	Bd, Bo	15.2	1.5	23	1.5	4	0.2
" "	Zos	4-11	Low	Mud	2.9	0	0	0	0	0
" "	Bro	4-8	Med	Bd, Bo	3.3	0	0	0	1	0.3
" "	Mac	4-16	Mix	Bd, Bo	12.5	10.1	0	0	26	1.2
" "	Aga	18-28	Med	Bd, Bo	1.5	0	0	0	0	0
<u>Other Channel Islands</u>										
Santa Cruz	Mac	3-17	Mix	Mix	2.8	0	0	0	0	0
Santa Barbara	Phy	1-3	Med	Bd, Bo	1.1	0	0	0	2	1.9
" "	Bro	4-8	High	Bo, Sh	1.0	0	0	0	10	10.0
" "	Mac	8-20	Mix	Mix	9.8	0	0	0	1	0.1
" "	None	5-11	Low	Sa	0	2.3	0	0	0	0
San Nicolas	Mac	7-22	Mix	Mix	13.8	1.0	0	0	0	0
San Clemente	Phy	1-4	Med	Bo, Sh	2.0	0	2	1.0	9	4.5
" "	Mac	7-14	Mix	Mix	3.3	0	0	0	3	0.3
<u>Southern California Mainland</u>										
Laguna Beach	Phy	0-3.5	Med	Bo, Sa	0.7	0	0	0	0	0
La Jolla	Phy	0-4	Mix	Mix	6.8	0	3	0.4	14	2.1
<u>Baja California Mainland</u>										
Ensenada	Phy	0-4	Med	Bo, Sa	1.7	0	0	0	0	0
<u>Baja California Islands</u>										
Los Coronados	Mac	9-14	High	Bo, Sh	0.7	0	0	0	0	0
San Martin	Phy	1-3.5	Low	Sa	0.4	0	0	0	0	0
" "	Mac	5-10	Med	Bd, Bo	0.4	0	0	0	0	0
" "	Aga	11-14	High	Bd	0.5	0	0	0	0	0
Sacramento Reef	Phy	0.5-4	Med	Bd, Cr	1.5	0	2	1.3	13	8.7
" "	Mac	9-19	Mix	Bd, Bo	1.1	0	0	0	0	0
San Benitos	Hai	0-2	Low	Bd, Cr	0.3	0	0	0	5	16.7
" "	Phy	0-2.5	Med	Bd, Bo	1.3	0	2	1.2	13	8.2
" "	Ela	3-21	High	Bd, Cr	2.1	0	1	0.5	2	1.0
" "	Mac	7-18	Mix	Mix	2.9	1.4	0	0	21	4.9
Cedros	Phy	0-2.5	Low	Bd, Cr	0.3	0	12	19.0	5	9.5
" "	Ela	1-3.5	Med	Bd, Cr	0.5	0	2	4.0	15	30.0
" "	Mac	6-14	Med	Bd, Bo	0	0.7	0	0	14	21.0
Total:					330.4	58.8	1895		462	

*Diver Hrs does not represent my dive partners' times, except for certain Bird Rock *Phyllospadix* dives (see text).

Table 8. --Continued

Plant Cover (Assemblage dominants):

Aga = Agarum fimbriatum, Laminaria farlowii, and Eisenia arborea (deep)
Bro = Brown algae, including Cystoseira spp., Sargassum spp., Dictyosperis
 undulata, and Colpomenia sinuosa
Eis = Eisenia arborea (shallow) and erect coralline algae
Hal = Halidrys dioica
Mac = Macrocystis pyrifera, including brown algae understory
Phy = Phyllospadix spp.
Zos = Zostera marina

Relief (Substrate elevations):

Low = ~0-0.5 m
Med = ~0.5-2.0 m
High = >2.0 m
Mix = Mixture of several types

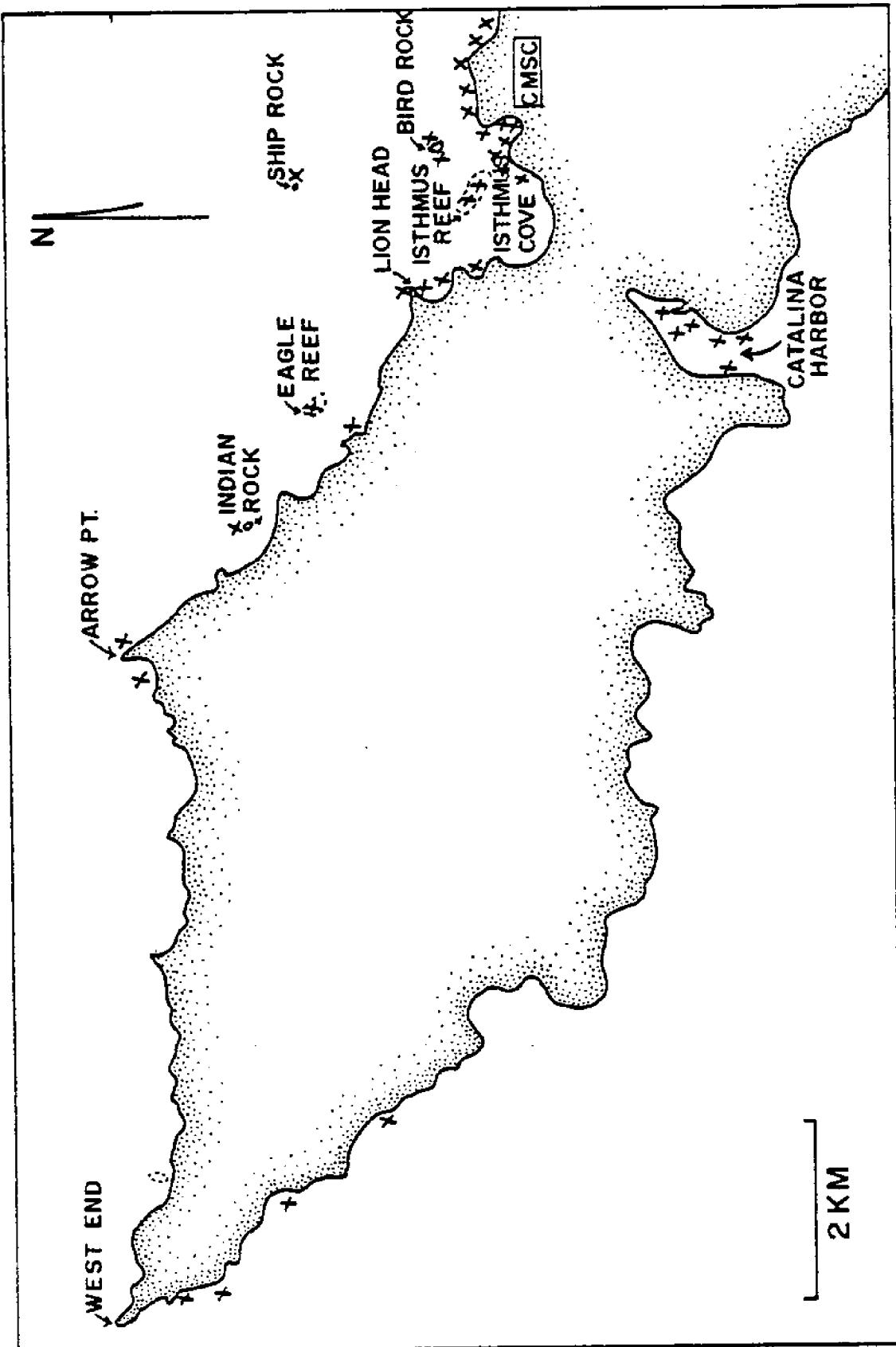
Substrate (Physical types):

Bd = Bedrock
Bo = Boulders
Cr = Crevices
Sa = Sand
Sh = Shelly debris
Mix = Mixture of several types

CPUE = mean number of juveniles caught per hour for Bird Rock Phyllospadix; for all other dives, the number of juveniles seen but not caught also were included.

Figure 5. Location of juvenile P. interruptus scuba survey sites at western Santa Catalina Island.

X = scuba survey site



Rock. Results from this area represent minimum CPUE values since only juveniles actually captured were counted. As a general approximation, one-third more juveniles were seen than were captured. Bias due to the varying experience of my dive partners in seeing and capturing juveniles was reduced by relating their captures to mine as follows: if my dive partner caught less than 10% of my total, his/her diver-hours were not counted; if 10-50%, then 0.5 diver-hours were counted; and if greater than 50%, then all partner diver-hours were counted.

Total encounters per diver-hour were threefold higher in shallow rocky habitats (Halidrys, Phyllospadix, Eisenia, and mixed brown algae) than in deeper rocky habitats (Macrocystis and Agarum). Except for night dives at Bird Rock during late summer and fall, all juveniles in deeper areas were greater than 30 mm CL. Juveniles less than 30 mm CL were consistently found only in the shallowest rocky habitats (0-4 m in depth) possessing dense plant cover and narrow bedrock crevices. Often these areas were exposed to such harsh surf conditions that proper search efforts were not possible. In the few shallow areas calm enough for careful searching, maximum CPUE for juveniles less than 30 mm CL occurred in Phyllospadix habitats. At Isthmus Reef, where Phyllospadix was absent, juveniles were consistently found at the shallowest location--an 81 m² bed of Halidrys 0-2 m in depth.

No P. interruptus were found during intertidal searches of surf grass and tide pool habitats along the rocky shores of Palos Verdes Peninsula in Los Angeles County, and Ensenada and Puerto Santa Tomas in Baja California.

Relationship of Body Color to Habitat

Both laboratory-raised and field-captured juveniles retained the light and dark color pattern characteristic of postpueruli up to 12-15 mm CL; in larger animals the body color was uniform. Exoskeleton colors for 10 mm size groups of juveniles from the Bird Rock Phyllospadix habitat and the Isthmus Reef Halidrys habitat are shown in Table 9a. Of 332 individuals less than 30 mm CL from Bird Rock, 240 were olive green, 23 chestnut brown, and 69 intermediate between these two colors. Of 20 small juveniles from Isthmus Reef, none were green, 14 were brown, and the rest were intermediate or brown red. Chi-square tests of the proportions of greenish (green or green brown) and brownish (brown or brown red) individuals for Bird Rock and Isthmus Reef showed significant differences between the two areas for all 10 mm size groups from 10-40 mm CL (Table 9b). Laboratory-raised juveniles, captured as pueruli from Marineland, had been provided with Phyllospadix but not Halidrys. Ninety-two percent of the small ones were green. This correlation of body color with juvenile habitat was observed during survey dives in all localities.

TABLE 9. -- Body coloration changes with increasing size for juvenile *P. interruptus* from the Bird Rock *Phyllosstadix* habitat and from the Isthmus Reef *Halidrys* habitat

a. Percentage Data

Location	Size Range (mm CL)	N	Exoskeleton Color				Abdominal Spots		
			% Green	% Green-Brown	% Brown	% Brown-Red	% Present	% Reduced	% Absent
Bird Rock	<9.9	4	75	0	25	0	100	0	0
	10-19.9	186	78	17	3	1	98	2	0
	20-29.9	142	64	26	7	3	64	30	7
	30-39.9	62	35	44	6	15	24	25	51
	40-49.9	20	5	40	15	40	0	0	100
	50-59.9	4	0	0	0	100	0	0	100
Isthmus Reef	10-19.9	6	0	33	67	0	83	17	0
	20-29.9	14	0	0	64	36	36	38	28
	30-39.9	6	0	0	17	83	0	0	100
	40-49.9	1	0	0	0	100	0	0	100

b. Chi-square (χ^2) Tests of Binomial Proportions*

1) Bird Rock (BR) versus Isthmus Reef (IR)

Size Range (mm CL)	Exoskeleton Color **			Abdominal Spots ***		
	χ^2	P	Result	χ^2	P	Result
10-19.9	28.7	<0.005	BR ≠ IR	1.06	>0.250	BR = IR
20-29.9	64.3	<0.005	BR ≠ IR	3.06	>0.050	BR = IR
30-39.9	13.3	<0.005	BR ≠ IR	0.69	>0.250	BR = IR

2) Juveniles <30 mm CL (Sm) versus Juveniles >30 mm CL (Lg)

Location	Exoskeleton Color **			Abdominal Spots ***		
	χ^2	P	Result	χ^2	P	Result
Bird Rock	37.2	<0.005	Sm ≠ Lg	134.3	<0.005	Sm ≠ Lg
Isthmus Reef	0.76	>0.250	Sm = Lg	5.55	<0.025	Sm ≠ Lg

*Yates' correction for continuity applied except where total N < 40 (Sm vs Lg : IR)

**Two categories: 1) Green or Green-Brown; 2) Brown or Brown-Red

***Two categories: 1) Present; 2) Reduced or Absent

Juveniles from both populations darkened with increasing size toward the brown or brown red coloration typical of adult lobsters; however, only the Bird Rock juveniles showed significant changes from greenish to brownish colorations. At all sizes, laboratory-raised juveniles were consistently paler than field individuals.

Most juveniles from Bird Rock and Isthmus Reef retained the pair of white spots on the first abdominal segment up to 30 mm CL (Table 9a, b). By 40 mm CL, the spots were gone. Compared to Bird Rock juveniles, those from Isthmus Reef lost their spots at a smaller size. Fifty-two percent of Marineland laboratory juveniles still had their spots at 30-39 mm CL.

Juvenile Habitat Preference

Laboratory Substrate-Choice Tests

Paired substrate-choice tests for first instar juveniles were run in the same manner as those for pueruli, using the same animals after their metamorphic molt. Early juveniles preferred Phyllospadix over rubble rock and Macrocystis, but did not significantly choose surf grass over Halidrys, and Plocamium was chosen over Phyllospadix (Table 10). These results agree with those of Parker

TABLE 10.--Results of habitat preference experiments on early juvenile Panulirus interruptus from this study and from Parker (1972)

	Choice A	Number Choosing		Number Choosing	P	Results
		A	B			
Parker (1972)	Control	16	Control	12	>0.50	A = B
	<u>Phyllospadix</u>	27	Rubble Rock	1	<0.01	A > B
	Control	13	Control	15	>0.80	A = B
Parker (1972)	<u>Phyllospadix</u>	22	<u>Macrocytis</u>	6	<0.01	A > B
	<u>Phyllospadix</u>	9	<u>Macrocytis</u>	0	<0.01	A > B
	Control	14	Control	14	>0.90	A = B
Parker (1972)	<u>Phyllospadix</u>	8	<u>Plocamium</u>	20	<0.05	A < B
	<u>Phyllospadix</u>	13	Red Algae	2	<0.01	A > B
	Control	14	Control	13	>0.90	A = B
	<u>Phyllospadix</u>	17	<u>Halidrys</u>	10	>0.20	A = B

(1972), except that his juveniles preferred Phyllospadix over assorted red algae.

Microhabitat Observations

Juveniles held in laboratory aquaria utilized any protective cover available to them. Commonly occupied shelters included cylindrical glass jars (4 cm diam) covered with black plastic tape, low arcuate clay roof tiles, and rectangular dens (6 x 5 x 21 cm) formed by alternately stacking clay bricks. Juveniles encountered during diurnal scuba surveys sometimes were found under movable objects, such as mussel shells or small rocks, but most inhabited narrow bedrock crevices and circular solution pockets. In flat, well-sedimented Phyllospadix beds, undisturbed juveniles were found burrowed among the roots and debris of the surf grass rhizome-sediment mat.

Surf Grass Distribution Surveys

Intertidal searches and scuba surveys from Santa Cruz Island, California, south to Cedros Island, Baja California (see Fig. 3), revealed the presence of Phyllospadix spp. at every major locality (Table 11). However, within any particular region, Phyllospadix was not distributed uniformly. When present, surf grass was confined to a shallow subtidal zone (usually 0-3 m in depth),

TABLE 11.--Results of scuba surveys for Phyllospadix in various locations throughout the geographic range of P. interruptus

Location	Scuba Survey Time (h)	<u>Phyllospadix</u> Abundance	Distance Offshore (m)	Depth Range (m)	Substrate	Wave Exposure
<u>California Channel Islands</u>						
Santa Cruz	2.8	0-2	0-15	0-3	Bo	M
Santa Barbara	11.7	0-2	0-18	0-3	Bo, Bd	L-M
Santa Catalina	316.7	0-3	0-15	0-4	Bo, Bd	L-H
San Nicolas	14.8	0-3	0-30	0-3.5	Bo, Bd	M-H
San Clemente	5.8	0-2	0-16	0-4	Bo, Bd	M-H
<u>Southern California Mainland</u>						
Laguna Beach	0.7	0-4	0-100+	0-3.5	Bo, Sa	M-H
La Jolla	5.4	2-4	0-75+	0-4	Bd, Sa	M-H
Point Loma	1.4	4-5	0-250+	0-3.5	Bd, Sa	H
<u>Baja California Mainland</u>						
Ensenada	1.7	3-5	0-300+	0-4	Bo, Sa	H
<u>Baja California Islands</u>						
Los Coronados	0.7	0-1	0-5	0-2	Bd	M
San Martin	0.8	1-4	0-50	1-3.5	Sa	L-M
Sacramento Reef	2.6	4-5	-	0.5-4	Bd	M-H
San Benitos	8.3	0-2	0-25	0-2.5	Bo, Bd	L-M
Cedros	1.8	0-4	0-20	0-2.5	Bd, Sa	M

Phyllospadix Abundances:

- 0 = Absent
- 1 = Occasional patches (2-4 m diam)
- 2 = Patches common; occasional beds (5-15 m diam)
- 3 = Beds common
- 4 = Beds abundant; occasional meadows (>15 m diam)
- 5 = Extensive meadows

Substrates:

- Bo = Boulders
- Bd = Bedrock
- Sa = Sand

Exposures:

- L = Low ; minimal surge ; swell <0.5 m
- M = Medium ; moderate surge ; swell 0.5-1.0 m
- H = High ; strong surge ; swell >1.0 m

associated with rocky substrata, although the rock surfaces often were covered by varying amounts of sand or shelly debris. Rocky areas with high wave exposure could not be searched adequately using scuba. Generally, the greatest abundances of Phyllospadix were associated with areas of high water movement which were partially protected from the highest wave exposure, such as the leeward sides of islands or along coasts with offshore kelp reefs. The presence of Macrocystis beds offshore was a good indicator of potential surf grass habitats inshore.

Beaches of gradual slope with kelp beds 0.5-1.0 km offshore (e.g., Point Loma and Ensenada) had the most extensive surf grass meadows (dense Phyllospadix from 0 m to over 250 m offshore). The rhizome mats of these meadows were covered with 10 to 30 cm of sand. Steeply sloping coastal areas characteristic of the offshore islands contained grass patches and small beds confined to the narrow zone of shallow water (patchy Phyllospadix commonly 0-15 m offshore). The rhizome mats either were exposed or covered with approximately 5-10 cm of sand or shelly debris.

Figure 6 shows the results of a continuous coastal survey using diver propulsion vehicles to map Phyllospadix beds from Blue Cavern Point to Arrow Point, Santa Catalina Island. Phyllospadix was absent in many shallow areas and patchy in most others. Only a few locations contained beds similar in size to those at Bird Rock.

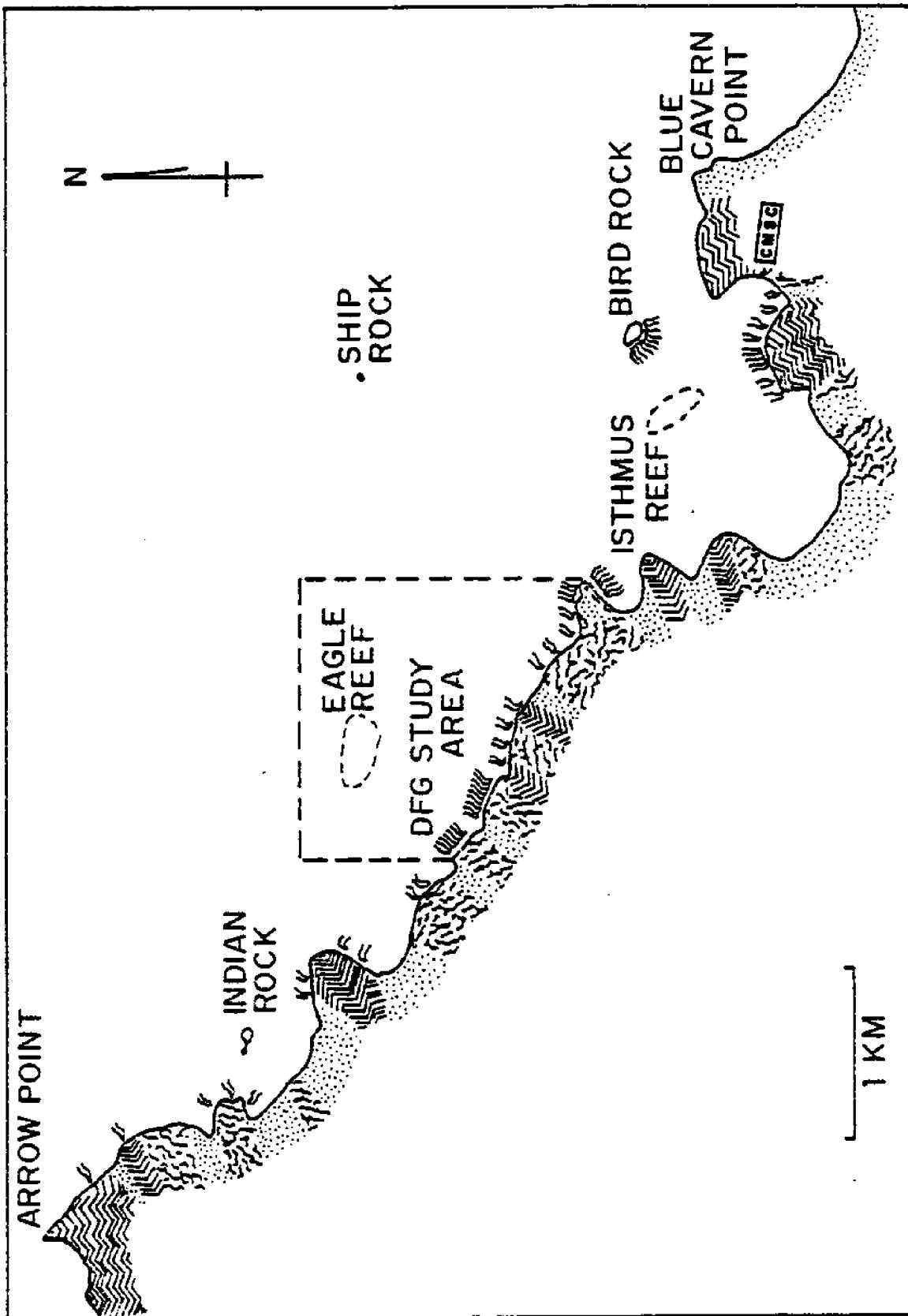
Figure 6. Distribution of Phyllospadix torreyi from Blue Cavern Point to Arrow Point, Santa Catalina Island. Geological information modified from Dykzeul and Given (1978). The area marked by dotted lines was the site of adult lobster population studies by the California Department of Fish and Game (DFG) from 1973 to 1974 (Odemar et al., 1975).

Phyllospadix abundance:

No mark = absent
↗ = occasional patches
(2-4 m diam)
↖ = beds common
(5-15 m diam)

Intertidal geology:

☰ = solid rock
✖ = boulders
◎ = sand



Offshore rocks and reefs, such as Ship Rock, Indian Rock, Isthmus Reef, and Eagle Reef, were all inhabited by P. interruptus, but had no surf grass habitat. Phyllospadix habitat within the California Fish and Game lobster survey region was more common than in adjacent areas (which had more sandy beaches), but most of the surf grass was in isolated 0.5-2.0 m patches located on boulder tops.

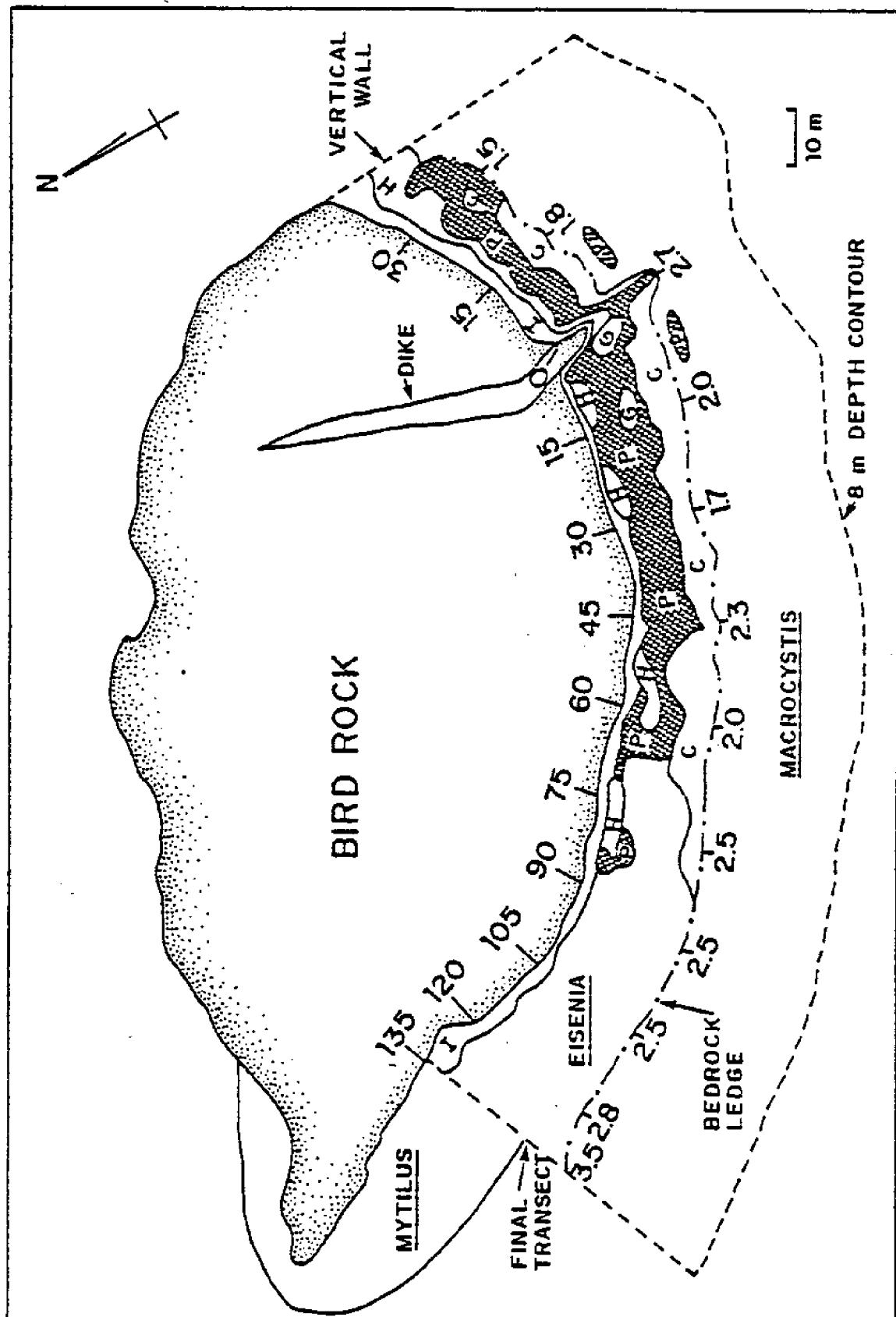
Bird Rock and Isthmus Reef Habitat Surveys

Figure 7 shows the results of habitat survey transects taken at 3 m intervals along the southwestern shore of Bird Rock. An intrusion of igneous rock (dike) provided a partial underwater barrier separating the Phyllospadix habitat into two major beds. East of the dike, Phyllospadix covered 296 m² from 0.3 to 1.5 m in depth. West of the dike, surf grass beds covered 598 m² from 0.2 to 1.8 m in depth. Isolated patches of surf grass (0.5-2 m in diameter) were found as deep as 3.5 m.

Just inshore of the grass beds were patches and beds of Halidrys dioica covering a total area of 181 m². The lower vegetative stipes of Halidrys (0.5 m in length) were perennial while the upper reproductive stipes (0.5-1.5 m in length) were present only from May through October. Immediately inshore of the Halidrys habitat was a relatively plant-free intertidal zone composed of

Figure 7. Map of Phyllospadix beds and nearby shallow habitats at Bird Rock, Santa Catalina Island. Onshore numbers indicate 15 m shoreline distances from the dike. Offshore numbers indicate water depths along the top of the bedrock ledge.

Habitats: C = coralline algae (mostly Lithothrix aspergillum)
G = gravel
H = Halidrys dioica
I = intertidal algae (mostly Pelvetia fastigiata)
P = Phyllospadix torreyi



volcanic breccia upon which were clumps of Mytilus californianus, Tetraclita squamosa rubescens, erect coralline algae, and Pelvetia fastigiata.

Adjacent to the Phyllospadix beds, in slightly deeper water, was a uniform carpet of 4-8 cm high coralline algae, composed mostly of Lithothrix aspergillum. The lower edge of this zone was delineated by a bedrock ledge, 1-1.5 m high, below which the dominant vegetation was Macrocystis pyrifera with an understory layer of Dictyopteris undulata, Dictyota flabellata, Cystoseira neglecta, Sargassum spp., and various erect corallines.

The eastern extent of the Phyllospadix and Halidrys areas ceased abruptly at the edge of a vertical rock wall, the bottom of which was 25-30 m in depth. This flat rock wall, dominated by the pelecypod mollusk Chama arcana and various low encrusting organisms, extended along the entire northeastern half of Bird Rock. The westernmost Phyllospadix bed graded into a medium relief Eisenia/coralline algae habitat, which itself graded into an extensive Mytilus californianus bed at the west end of Bird Rock.

The shallow site at Isthmus Reef (Fig. 2, insert) also was surveyed and found to be an ovoid, uniform bed of Halidrys covering 81 m² of bedrock 0-1 m in depth. This "high spot" was 1.5 m above the surrounding Eisenia/coralline algae habitat, which graded into a Macrocystis/understory brown algae forest below 4 m in depth.

The Bird Rock Surf Grass Ecosystem

The Phyllospadix habitat at Bird Rock was located in a shallow subtidal zone characterized by high water motion yet partially protected from the prevailing westerly oceanic swells hitting the Mytilus beds at the opposite end. Breaking waves were rare at Bird Rock, except during winter storms, but strong surge from long wavelength swells was common, especially during the period November to April.

Typical tidal fluctuations at Bird Rock were 1-2 m (U. S. Dept. of Commerce, NOAA Tide Tables). The shallowest Phyllospadix beds were exposed for short periods (approx. 1 h/day) at negative tides, which occurred during the two weeks of spring tides each month. Even when exposed, the grass frequently was wetted by the surge. Spring tides produced moderately strong longshore currents (2-4.5 km/h), causing the grass to flatten against the substrate. Inside the Phyllospadix beds, wave, surge, tide, and current effects were mollified by the dampening effects of the dense grass. Typically, grass beds thicken by means of vegetative growth along creeping rhizomes, creating a tough interwoven horizontal mat from which numerous wiry leaf-blades 0.5-2 m long arise. Particles of sand and shell bits collect at the interface of the surf grass rhizome mat and the vertical leaf-blades. Consequently, turbidity

levels are higher and light levels are lower here than just outside the grass bed. Within or upon this dim, relatively calm micro-habitat lived the majority of small motile animals characteristic of the Bird Rock Phyllospadix ecosystem, including juvenile P. interruptus.

Although extensive work has not been done on the assemblage of organisms associated with Phyllospadix, a considerable number of species has been recorded (Table 12). The most species-rich group is mollusks. In a preliminary study by G. Brown and myself, the micro-mollusk (< 1.5 cm) genera found within Bird Rock Phyllospadix beds were compared with those present in Isthmus Reef Halidrys beds by collecting and identifying all mollusks taken from three 1/3 m² benthic quadrats at both sites (Table 13). The Phyllospadix habitat samples contained 2,210 micro-mollusks (2,155 gastropods and 55 pelecypods) representing 34 genera. Seventy-nine micro-mollusks (5 gastropods and 73 pelecypods) representing nine genera were obtained from the Halidrys samples. The most important mollusks at Bird Rock (Amphithalamus, Barleeia, and Tricolia) were small gastropods of less than 5 mm in height found within the organic material of the rhizome mat. In contrast, the small Halidrys holdfasts attached to bare rock had little entrapped sediment and few tiny gastropods.

TABLE 12.--The number of species known from Phyllospadix habitats for major phylogenetic groups [represents results from this study combined with the following: B. Draper (personal communication), R. Miracle and G. Brown (personal communication, Barnard (1969), Smith and Carlton (1975), Abbott and Hollenberg (1976), Rischen (1976), and McLean (1978)]

Phylogenetic Group	Number of Species	Phylogenetic Group	Number of Species
Division Chlorophyta	2	Suborder Natantia	3
Division Phaeophyta	11	Suborder Reptantia	
Division Rhodophyta	13	Section Brachyura	9
Phylum Porifera	6	Section Anomura	5
Phylum Cnidaria		Subphylum Chelicerata	
Class Anthozoa	5	Class Pycnogonida	3
Class Hydrozoa	4	Phylum Mollusca	
Phylum Platyhelminthes	?	Class Gastropoda	94
Phylum Nemertea	2	Class Pelecypoda	29
Phylum Nematoda	?	Class Polyplacophora	3
Phylum Sipunculida	3	Class Scaphopoda	?
Phylum Annelida		Class Cephalopoda	1
Class Oligochaeta	6	Phylum Ectoprocta	?
Class Polychaeta	45	Phylum Entoprocta	?
Phylum Arthropoda		Phylum Echinodermata	
Subphylum Mandibulata		Class Asteroidea	4
Class Crustacea		Class Echinoidea	3
Subclass Ostracoda	7	Class Ophiuroidea	6
Subclass Copepoda	2	Class Holothurioidea	3
Subclass Cirripedia	3	Phylum Chordata	
Subclass Malacostraca		Subphylum Urochordata	2
Order Isopoda	11	Subphylum Vertebrata	
Order Amphipoda	72	Class Chondrichthyes	2
Order Cumacea	3	Class Osteichthyes	36
Order Decapoda			

TABLE 13.--Comparison of micro-mollusk (<1.5 cm) genera between the Bird Rock Phyllospadix habitat and the Isthmus Reef Halidrys habitat, from three $1/3 \text{ m}^2$ benthic quadrat samples at each site [combined results from this study and from G. Brown (personal communication)]. Bird Rock mollusk genera are listed in order of decreasing importance

Importance Index = Mean Number of Individuals \times Frequency of Occurrence among Samples

Genus	BIRD ROCK			ISTHMUS REEF		
	Mean Number of Mollusks	Standard Deviation	Importance Index	Mean Number of Mollusks	Standard Deviation	Importance Index
<u>Amphithalamus</u>	575	585	575	0	0	0
<u>Barleeia</u>	51	45	51	0	0	0
<u>Tricolia</u>	35	5	35	1	1	0.2
<u>Bittium</u>	18	12	18	0	0	0
<u>Littorina</u>	12	11	12	0	0	0
<u>Caecum</u>	7	8	7.0	0	0	0
<u>Mitrella</u>	10	9	6.5	0	0	0
<u>Norfolkia</u>	9	9	5.0	0	0	0
<u>Tegula</u>	8	8	5.6	0	0	0
<u>Alvinia</u>	7	12	4.5	0	0	0
<u>Epilucina</u>	3	3	3.3	0	0	0
<u>Lasaea</u>	3	3	3.3	0	0	0
<u>Lima</u>	2	1	2.0	0	0	0
<u>Epitonium</u>	3	3	1.8	0	0	0
<u>Tellina</u>	3	4	1.8	1	1	0.5
<u>Crepidula</u>	2	2	1.3	0	0	0
<u>Mitrella</u>	2	2	1.3	0	0	0
<u>Nassaria</u>	2	2	1.1	0	0	0
<u>Halodakra</u>	1	1	0.9	0	0	0
<u>Hiatella</u>	1	1	0.9	0	0	0
<u>Leptopecten</u>	1	1	0.9	0	0	0
<u>Cypriscus</u>	1	1	0.7	0	0	0
<u>Mytilus</u>	1	1	0.7	15	14	9.8
<u>Nassaria</u>	2	3	0.7	1	1	0.5
<u>Clathurella</u>	2	3	0.6	0	0	0
<u>Lacuna</u>	1	2	0.3	0	0	0
<u>Chama</u>	0.3	0.3	0.1	1	1	0.2
<u>Acteocina</u>	0.3	0.6	0.1	0	0	0
<u>Collisella</u>	0.3	0.6	0.1	0	0	0
<u>Conus</u>	0.3	0.6	0.1	0	0	0
<u>Crepipatella</u>	0.3	0.6	0.1	0	0	0
<u>Ocostomia</u>	0.3	0.6	0.1	0	0	0
<u>Teinostoma</u>	0.3	0.6	0.1	0	0	0
<u>Volvarina</u>	0.3	0.6	0.1	0	0	0
<u>Callostoma</u>	0	0	0	0.3	0.6	0.1
<u>Philobryva</u>	0	0	0	0.3	0.6	0.1
<u>Siliqua</u>	0	0	0	0.3	0.6	0.1

Within the Bird Rock surf grass ecosystem, the abundant micro-mollusks as well as polychaete worms, amphipods, etc., represent potential food for larger animals. Table 14 lists the macro-organisms (> 1 cm) commonly encountered in the Phyllospadix study site, with their typical microhabitats and their apparent trophic categories. Most of these larger organisms also were found in a variety of other subtidal habitats, but a few either were unique to or most abundant in surf grass beds. These include juvenile Cancer antennarius, majid crabs (unidentified species), P. interruptus, Gibbonsia elegans, Paraclinus integripinnis, and Syngnathus arctus. Predator-prey relationships between the organisms listed in Tables 13 and 14 and juvenile lobsters are presented below in the sections on juvenile lobster mortality and food habits.

Stable Carbon Isotope Analysis

Carbon isotope analysis could potentially shed light on trophic relationships within the surf grass ecosystem. Individual $\delta_{\text{PDB}}^{13}\text{C}$ values for P. interruptus and several other organisms from surf grass and non-surf grass habitats in southern California for this study and from Smith and Epstein (1971) are listed in Table 15. The $\delta_{\text{PDB}}^{13}\text{C}$ values for muscle and exoskeleton tissues taken from the same lobster differed by 0.5‰. All of the $\delta^{13}\text{C}$ values for lobsters from Phyllospadix beds at Bird Rock were higher

TABLE 14. -- Macro-organisms (>1 cm) commonly associated with the Phyllospadix habitat at Bird Rock, Santa Catalina Island

		Micro-habitat	Apparent Trophic Type
Division Phaeophyta (Brown Algae)			
<u>Colpomenia sinuosa</u>		Sc	
<u>Dictyopteris undulata</u>		Sc	
<u>Eisenia arborea</u>		Sc	
<u>Halidrys dioica</u>		Sc	
Division Rhodophyta (Red Algae)			
<u>Chondria californica</u>		Ep	
Encrusting corallines		Sc	
<u>Lithothrix aspergillum</u>		Sc	
<u>Melobesia mediocris</u>		Ep	
Small reds		Ep	
Phylum Cnidaria			
Class Anthozoa (Anemones)			
<u>Anthopleura elegantissima</u>		Sc	Mc
<u>Corynactis californica</u>		Sc	Mc
Phylum Arthropoda			
Class Crustacea (including Crabs, Hermit Crabs)			
<u>Cancer antennarius</u>	In, Eb	O	
<u>Cycloanthrops novemdentatus</u>	Sf, Eb	O	
Majid Crab	Eb	O	
<u>Paguristes ulreyi</u>	Eb	O	
<u>Pagurus</u> sp.	Eb	O	
<u>Panulirus interruptus</u>	Sf, Eb	O	
<u>Paraxanthias taylori</u>	Sf	O	
<u>Pugettia producta</u>	Eb, Ep	H	
<u>Taliepus nuttalli</u>	Eb, Ep	H	
Phylum Molluska			
Class Gastropoda (Snails, Sea Slugs)			
<u>Aplysia californica</u>	Eb	H	
<u>Astraea undosa</u>	Eb	H	
<u>Ceratostoma nuttalli</u>	Eb	Mc	
<u>Conus californica</u>	Eb, Ep	Mc	
<u>Haliotis cracherodii</u>	Sc, Sf	H	
<u>Haliotis fulgens</u>	Sf	H	
<u>Kelletia kelletii</u>	Eb	O	
<u>Norrisia norrisi</u>	Eb, Ep	H	
<u>Tegula aureotincta</u>	Eb, Ep	H	

TABLE 14. --Continued

		Micro-habitat	Apparent Trophic Type
Class Pelecypoda (Bivalves)			
<u>Mytilus californianus</u>	Sc	Mc	
Class Cephalopoda (Including Octopus)			
<u>Octopus bimaculatus</u>	Sf, Ep	C	
Phylum Echinodermata			
Class Asteroidea (Sea Stars)			
<u>Patiria miniata</u>	Eb	O	
<u>Pisaster giganteus</u>	Eb	C	
Class Echinoidea (Sea Urchins)			
<u>Strongylocentrotus franciscanus</u>	Sf	H	
<u>Strongylocentrotus purpuratus</u>	Sf	H	
Class Holothuroidea			
<u>Parastichopus parvimensis</u>	Eb	D	
Class Ophiuroidea			
<u>Ophioderma panamense</u>	Sf	O	
<u>Ophiopterus papillosa</u>	Sf	O	
<u>Ophiothrix spiculata</u>	Sf	Mc	
Phylum Chordata			
Subphylum Urochordata			
Class Asidiacea (Tunicates)			
<u>Euherdmania claviformis</u>	Sc	Mc	
Subphylum Vertebrata			
Class Chondrichthyes (Sharks and Rays)			
<u>Heterodontus francisci</u>	Sf, Eb	C	
Class Osteichthyes (Bony Fishes)			
<u>Artedius corallinus</u>	Eb	Mc	
<u>Atherinops affinis</u>	Ne	Mc	
<u>Damalichthys vacca</u>	Ne	Mc	
<u>Embiotoca jacksoni</u>	Ne	Mc	
<u>Gibbonsia elegans</u>	Eb	Mc	
<u>Girella nigricans</u>	Ne	H	
<u>Hypsoblennius jenkinsi</u>	Sf	Mc	
<u>Oxyjulis californica</u>	Ne	O	
<u>Paraclinus integripinnis</u>	Sf, Eb	Mc	
<u>Paralabrax clathratus</u>	Ne, Eb	C	

TABLE 14. --Continued

	Micro-habitat	Apparent Trophic Type
<u>Scorpaena guttata</u>	Eb	C
<u>Scorpaenichthys marmoratus</u>	Eb	C
<u>Sebastes atrovirens</u>	Eb	Mc
<u>Sebastes rastrelliger</u>	Eb	C
<u>Syngnathus arctus</u>	Eb	Mc

Micro-habitats:

Eb = Epibenthic (motile)

Ep = Epiphytic

In = Infaunal

Ne = Nektonic

Sc = Saxicolous

(living on rocks)

Sf = Saxifragous
(crevice-dwelling)

Apparent Trophic Types:

C = Carnivore (food items

>1 cm)

D = Deposit feeder

H = Herbivore

Mc = Micro-carnivore (food
items <1 cm)

O = Omnivore

TABLE 15.-- $\delta^{13}\text{C}$ values for P. interruptus and several other marine organisms from southern California [results from this study and from Smith and Epstein (1971)]

Specimen	Size (mm CL)	Sample	Habitat	Location	$\delta_{\text{PDB}}^{13}\text{C} (\text{o/oo})$	
					This Study	Smith and Epstein(1971)
Phylum Arthropoda						
<u>P. interruptus</u>	12	muscle and exoskeleton	Phy	BR	-14.6	
" *	23	muscle	Phy	BR	-17.3	
" *	23	exoskeleton	Phy	BR	-16.8	
"	32	muscle	Phy	BR	-17.0	
"	20	muscle	Hal	IR	-18.1	
"	69	muscle	Hal	IR	-17.6	
Division Rhodophyta						
<u>Corallina chilense</u> [sic]						-18.6
Division Phaeophyta						
<u>Halidrys dicica</u>		blades	Hal	BR	-16.0	
<u>Macrocystis pyrifera</u>						-17.5
<u>Sargassum</u> sp.						-16.3
Division Tracheophyta						
<u>Phyllospadix torreya</u>		leaves	Phy	BR	-13.8	-14.0
Phylum Mollusca						
<u>Norrisia norrisi</u>		muscle	Phy	BR	-17.4	
Phylum Chordata						
<u>Gibbonsia elegans</u>		muscle	Phy	BR	-21.3	

*Different samples were taken from the same animal.

Habitats:

Phy = Phyllospadix
Hal = Halidrys

Locations:

BR = Bird Rock
IR = Isthmus Reef

than values for lobsters from the Halidrys habitat at Isthmus Reef.

The $\delta^{13}\text{C}$ value for surf grass, although closely corresponding to that obtained by Smith and Epstein (1971), was only a few parts per thousand larger than the data for Halidrys (this study), and for Macrocystis and Sargassum (Smith and Epstein, 1971).

Juvenile Growth

From October 1974 to August 1978, 2,145 Panulirus inter-
ruptus less than 60 mm CL were hand-captured at Santa Catalina Island for studies of juvenile sex ratios, length-weight relationships, monthly length-frequency distributions, molt increments, molt frequencies, and long-term growth of marked individuals.

Sex Ratios

Of 1,475 first-capture juveniles collected at the Bird Rock study site between November 1974 and December 1976, 701 (48%) were males and 774 (52%) were females. Sex ratios for 10 mm CL classes, evaluated using the chi-square goodness of fit test, revealed no significant differences between the number of males and females for any size class (Table 16).

Length-Weight Relationships

Measurement Precision

The precision for carapace length and wet weight values was

TABLE 16.--Sex composition of 10 mm size classes of juvenile
P. interruptus from Bird Rock Phyllospadix beds

Size (mm CL)	Sex	N	%	χ^2	P
<10	M	26	46	0.44	>0.50
	F	31	54		
10-19.9	M	369	47	3.17	>0.05
	F	419	53		
20-29.9	M	223	50	0.02	>0.80
	F	220	50		
30-39.9	M	61	46	0.91	>0.30
	F	72	54		
40-49.9	M	22	41	1.85	>0.10
	F	32	59		
Total	M	701	48	3.61	>0.05
	F	774	52		

determined from repeated measurements of laboratory-raised and field-recaptured lobsters that had not molted between measurements. Carapace length error for 100 paired measurements of juveniles from 9 to 50 mm CL ranged from -1.1% to +0.6% (avg error = $\pm 0.2\%$), and wet weight error ranged from -16.7% to +9.3% (avg error = $\pm 3.3\%$). Fifty-four percent of the lobsters showed no change in carapace length between measurements, while 75% were heavier on the second weighing. Weight errors were due to measuring device imprecision, variable water or food retention, and gradually increasing body weight during the intermolt period as water was replaced by denser living tissue. Ideally, the weight of the animal which most accurately represents accumulated biomass within the molt cycle is the weight at intermolt Stage C, since body weight does not increase after that point until just prior to ecdysis when water is taken up (Travis, 1954).

Regression Equations

The regression of wet weight versus carapace length was calculated for 820 lobsters (368 males and 452 females) ranging in size from 7 to 50 mm CL. Only lobsters which had no missing appendages were considered. The equation used was:

$$W = aL^b \quad (2-0)$$

where W = wet weight in grams, L = carapace length in millimeters, and a and b are fitted constants. The regression was fitted by the method of least squares using the logarithmic transformation:

$$\ln W = \ln a + b \ln L \quad (3-0)$$

where $\ln a$ = y-intercept and b = slope.

Because any length-weight allometry may be affected by factors such as growth conditions, sex, or size, regressions also were calculated for various subgroups of juveniles. These included individuals raised in laboratory aquaria (hereafter designated as lab juveniles), juveniles captured within Bird Rock Phyllospadix beds (hereafter designated as field juveniles), males, females, juveniles less than 30 mm CL (hereafter designated as small juveniles), and juveniles greater than 30 mm CL (hereafter designated as large juveniles). Groups with greatly unequal size-frequency distributions were normalized for similar frequencies by randomly eliminating excess measurements from high frequency size classes. For each group, the sample size (N), constants a and b , and the coefficient of determination (r^2) are shown in Table 17a. In every case, the r^2 values are close to unity, indicating that nearly all of the variation has been explained by the regression. The mathematical relationships for juvenile males and females are represented in Figure 8.

TABLE 17.--Carapace length vs. wet weight regressions for various groups of juvenile *P. interruptus* (see text for meanings of group designations)

a. Regression constants

Equation Number	Group	N	$W = aL^b$		
			$a \times 10^{-6}$	b	r^2
2-1	Total	820	626	3.098	0.998
2-2	Lab*	300	634	3.091	0.999
2-3	Field*	200	627	3.101	0.998
2-4	Male*	225	666	3.076	0.999
2-5	Female*	225	527	3.148	0.998
2-6	Small	571	547	3.148	0.996
2-7	Large	249	672	3.074	0.989
2-8	Small Male	272	637	3.096	0.997
2-9	Small Female	299	476	3.195	0.996
2-10	Large Male	96	664	3.074	0.993
2-11	Large Female	153	668	3.078	0.988

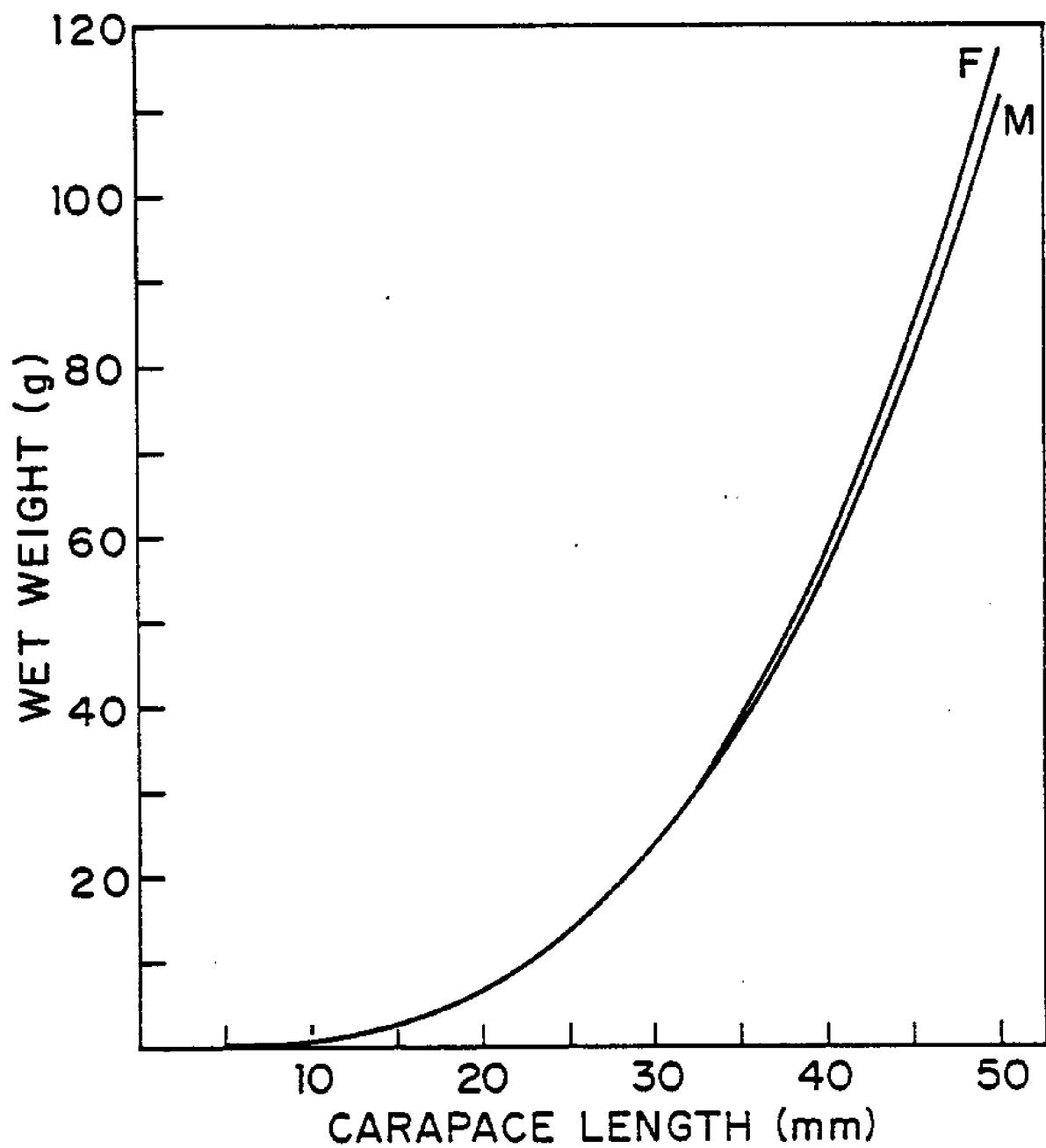
b. t-tests for equality of slopes

Groups Compared	df	<u>t</u>	P
Lab vs. Field*	496	0.81	>0.400
Male vs. Female*	446	6.24	<0.001
Small vs. Large	816	2.63	<0.010
Small Male vs. Small Female	567	6.21	<0.001
Large Male vs. Large Female	245	0.11	>0.900
Small Male vs. Large Male	364	0.57	>0.500
Small Female vs. Large Female	448	3.13	<0.010

*Normalized for similar frequencies of carapace lengths

Figure 8. Relationship between carapace length and wet weight for male and female juvenile P. interruptus. The curves were plotted from Equations 2-4 and 2-5, respectively (see Table 17 and text).

M = male
F = female



Females were slightly heavier than males having the same carapace length.

Log-transformed equations for pairs of groups were compared using t-statistics to test for slope equality. For each comparison, the degrees of freedom (df), t-values, and level of significance (P) are shown in Table 17b. Regression slopes were not significantly different for lab versus field juveniles. On the other hand, despite the small numerical differences in slopes between males and females, sex related length-weight differences were significant. Sex differences were most pronounced in small juveniles. Carapace length-weight allometry also was different for small versus large juveniles. These size differences were most evident in females.

Size-Frequency Distributions

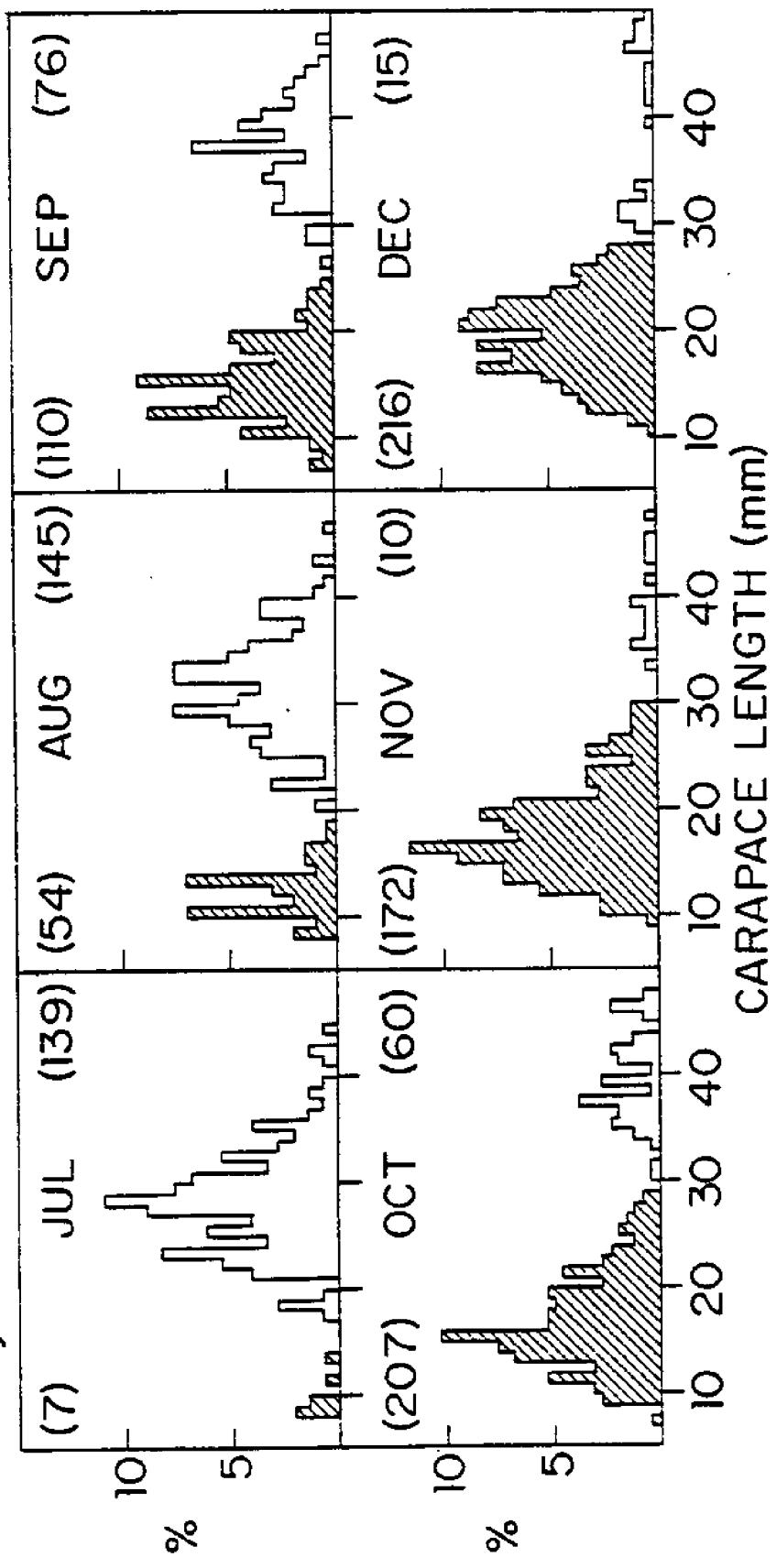
Monthly size-frequency distributions were calculated on the basis of 1 mm carapace length class intervals for 2,068 juveniles captured from the Bird Rock site during the period October 1974 through December 1976 (Fig. 9a, b). Because of difficulty in catching sufficient juveniles during each month of the study and since yearly trends were similar, each month represents combined data for the different years. Throughout the year, the lobster population within the Phyllospadix habitat has recognizable and regular

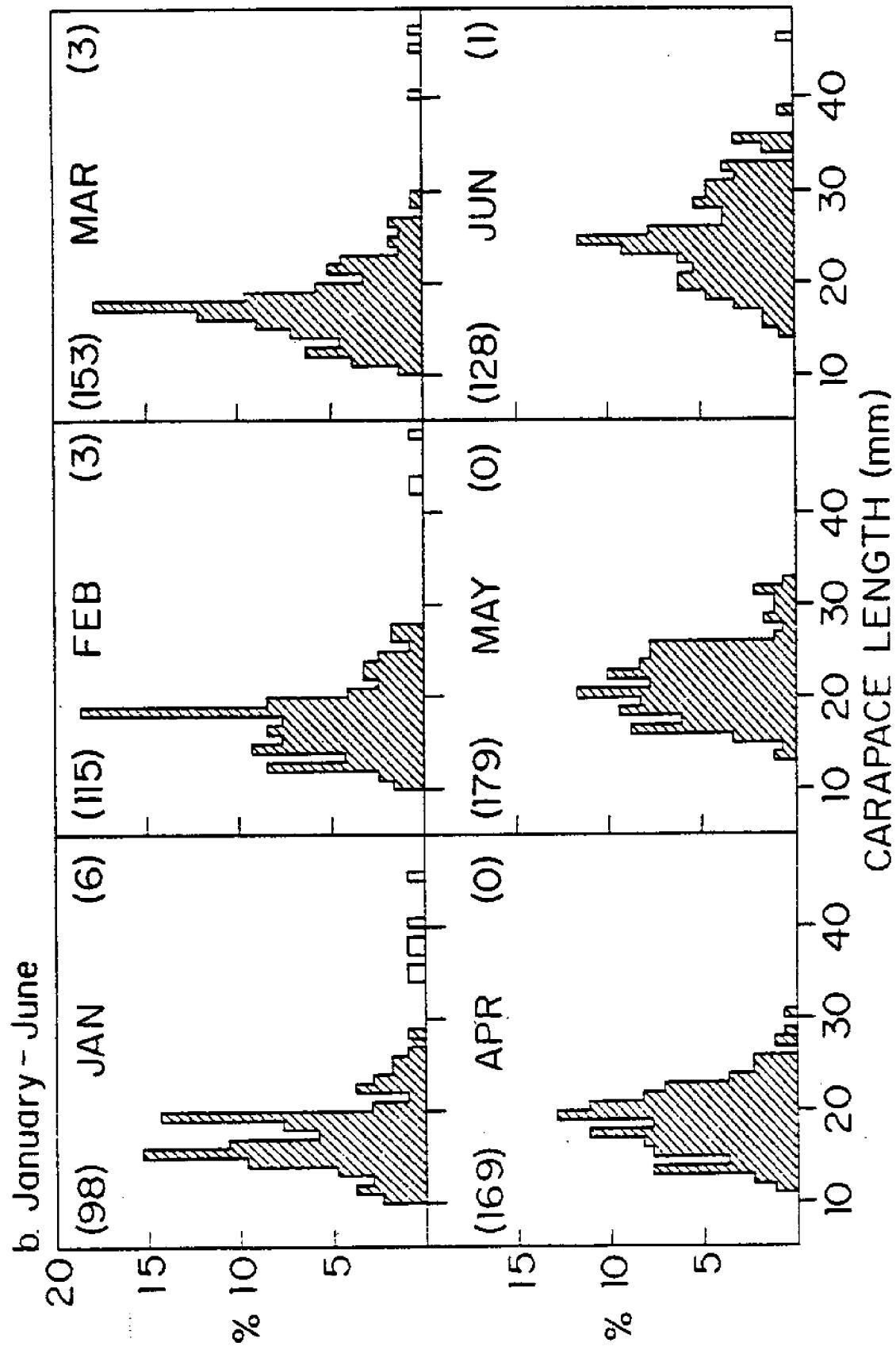
Figure 9. Monthly size frequencies for 1 mm size classes of juvenile P. interruptus captured at Bird Rock from October 1974 to December 1976:

- a. = July-December
- b. = January-June

- = age 1+ year class juveniles
- = age 2+ year class juveniles
- () = number of individuals

a. July - December





bimodal or unimodal length distribution patterns. Each clearly defined modal group comprises a year class; the lined modal group represents age 1+ year class juveniles and the unlined group, age 2+ year class individuals.

Starting from the first occurrence of age 1+ juveniles in July, two trends are apparent:

1. the progressive monthly increase in the proportion of small juveniles due to cumulative settlement
2. the shifting of secondary modes to larger sizes, due to growth (and possibly differential mortality)

The corresponding monthly decrease in numbers of age 2+ juveniles, culminating in their complete absence by April and May was due partly to growth beyond the size which could be reasonably captured by hand and partly to mortality, but mainly to a fall emigration from the surf grass habitat to deeper water (see below). A relatively large rightward shifting of secondary modes for both year classes occurred during warm water months. Considerably less rightward shifting was evident for cold water months.

To determine whether the secondary modes represent separate instars, as has been suggested for adult lobsters (Lindberg, 1955; Bakus, 1960; Mitchell et al., 1969), size-frequency distributions were plotted for 0.6 mm CL classes of all field and lab

lobsters measured during this study (Fig. 10). The highest peak in the lab histogram represents the combined values for puerulus and postpuerulus stages, between which only a minor increase in carapace length occurred. Despite the fact that the same lab juveniles were plotted for each molt stage, separate peaks were readily apparent only for the first four instars.

Mean instar values for lab juveniles collected as pueruli from Marineland also were marked on the field size-frequency histogram. Consistent correspondences between frequency modes and instar means were not evident.

Monthly Mean Size Analysis

Monthly mean sizes of juvenile P. interruptus collected during 1975 and 1976 (representing settlement year classes 1974, 1975, and 1976) were calculated to evaluate yearly trends in the population structure within the Phyllospadix habitat (Fig. 11). Over threefold more juveniles were captured during 1976 than in 1975 due to my increased ability to see and capture the well-camouflaged lobsters.

Mean carapace lengths for age 1+ juveniles were significantly different between 1975 and 1976 for all months from September to February and for the month of April (Table 18). Comparisons for

Figure 10. Size frequencies for 0.6 mm size classes of all laboratory-raised and field-captured juvenile P. interruptus measured during the growth study. Marks indicate consecutive mean instar sizes for lab juveniles (J) captured as pueruli (P) from Marineland.

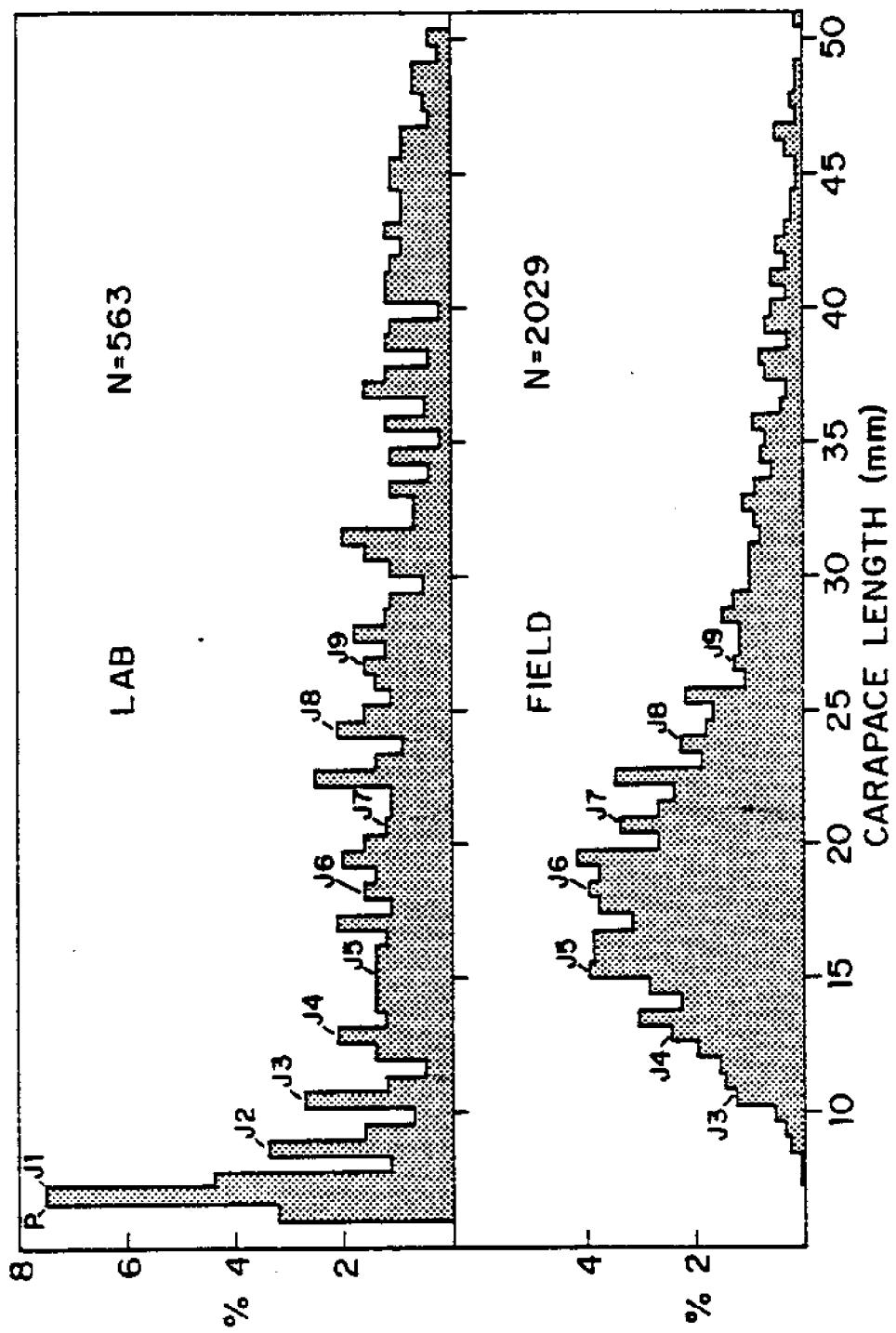


Figure 11. Monthly mean sizes of juvenile P. interruptus collected at Bird Rock during 1975 and 1976. Vertical lines represent 95% confidence limits.

- = 1975 (N = 428)
- = 1976 (N = 1,560)

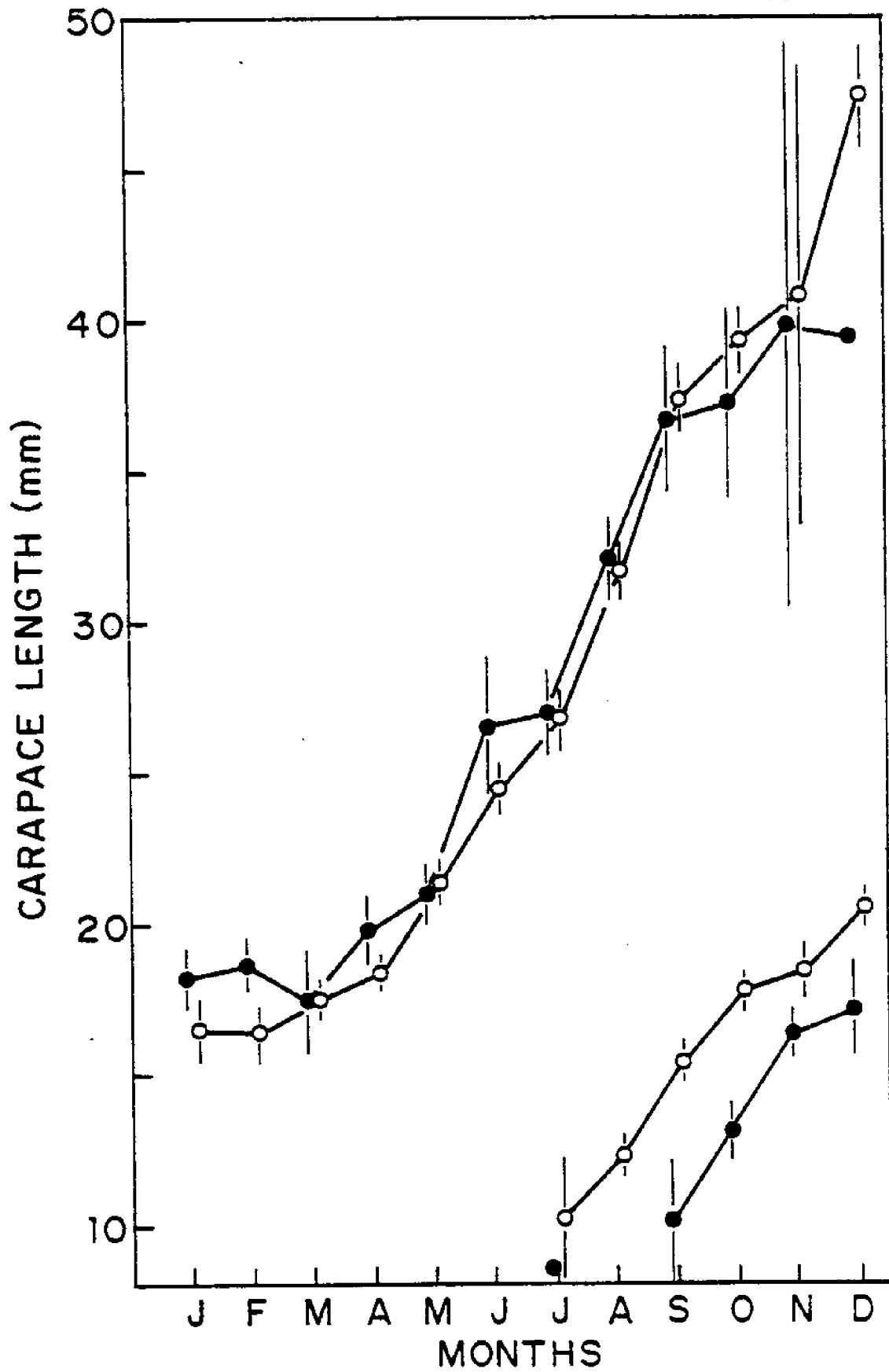


TABLE 18. t -test comparisons between the monthly mean sizes of juvenile P. interruptus captured during 1975 and 1976 at Bird Rock, Santa Catalina Island

Month	Age (yr)	Settlement			1975			Settlement			1976		
		Year Class	N	Mean Size (mm CL)	Year Class	N	Mean Size (mm CL)	Year Class	N	Mean Size (mm CL)	t	P	
SEP	1+	1975	4	10.1			1976	106	15.4	3.02	<0.01		
OCT			34	13.1				158	17.7	5.75	<0.001		
NOV			34	16.3				121	18.4	2.41	<0.02		
DEC			17	17.1				176	20.5	2.76	<0.01		
JAN	1974		43	18.2	1975		55	16.5		2.34	<0.02		
FEB			58	18.7			57	16.4		3.44	<0.001		
MAR			16	17.5			136	17.5	0.01	>0.90			
APR			47	19.8			122	18.4		2.36	<0.02		
MAY			46	21.0			133	21.4	0.59	>0.50			
JUN			18	26.6			110	24.5	1.70	>0.05			
JUL			43	27.0			94	28.8	1.94	>0.05			
AUG	2+		41	32.1			106	31.7	0.44	>0.60			
SEP			17	36.7			59	37.4	0.59	>0.50			
OCT			4	37.2			51	39.3	0.99	>0.30			
NOV			4	39.8			4	40.8	0.26	>0.70			

other months and for age 2+ juveniles showed no significant differences between the two years.

Sexual differences in the monthly mean sizes of field juveniles were evaluated for all months for which there were adequate data (Table 19). No significant differences were found for any month between mean sizes of male and female lobsters.

Monthly mean carapace lengths for lab juveniles (combined Marineland pueruli and Bird Rock juveniles; see below) and for field juveniles (combined 1975 and 1976) illustrate trends similar to those in the field size-frequency distributions (cf. Figs. 9 and 12). For most months, mean sizes in the field were similar to the dominant secondary frequency modes. Age 1+, 2+, and 3+ field juvenile means are clearly distinguishable. Field mean sizes at ages 2 and 3 years (August) were 32 mm CL and 56 mm CL, respectively, while lab mean sizes were 26 mm CL and 46 mm CL for the same ages. Few field individuals greater than 35 mm CL were captured after December of either sampling year (since most larger animals had emigrated from the surf grass habitat; see below). Size decreases in field animals from December and January represent the effects of combination of data from different settlement year classes (see Table 18).

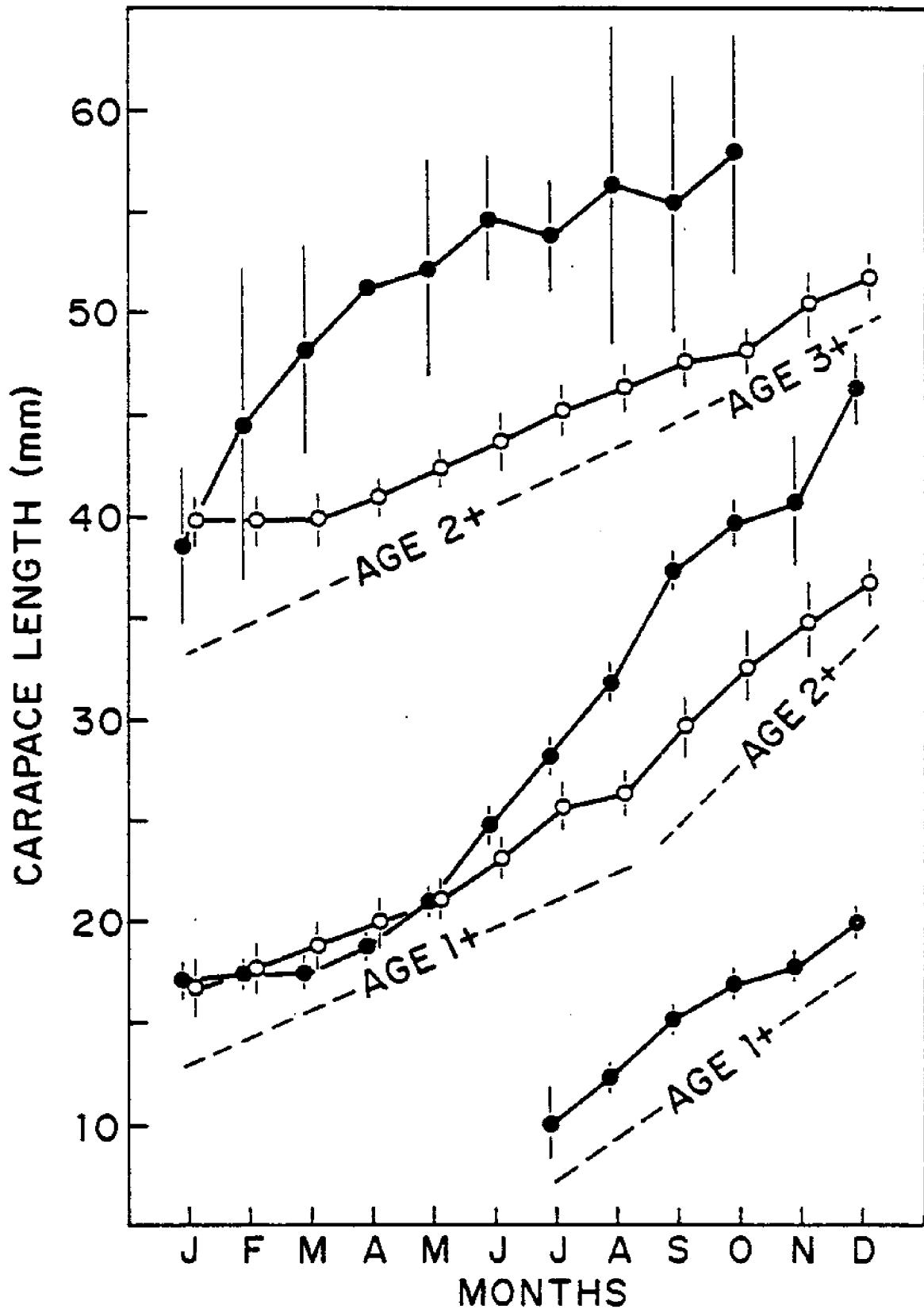
Mean sizes of laboratory juveniles increased less from month to month than did the corresponding mean sizes of field

TABLE 19.--*t*-test comparisons between the monthly mean sizes of male and female juvenile P. interruptus from Bird Rock, Santa Catalina Island

Month	Age (yr)	MALES		FEMALES		<i>t</i>	P
		N	Mean Size (mm CL)	N	Mean Size (mm CL)		
SEP	1+	51	15.6	49	15.4	0.22	>0.80
OCT		93	17.3	112	16.6	1.20	>0.20
NOV		80	17.9	86	17.8	0.21	>0.80
DEC		89	20.6	113	20.0	0.89	>0.30
JAN		49	17.4	48	17.1	0.31	>0.70
FEB		65	17.5	47	17.5	0.07	>0.90
MAR		69	17.9	82	17.2	1.11	>0.20
APR		83	19.2	79	18.3	1.67	>0.05
MAY		87	21.4	91	21.3	0.23	>0.80
JUN		59	25.1	66	25.0	0.11	>0.90
JUL		61	28.7	75	27.9	0.90	>0.30
AUG	2+	65	31.9	79	31.9	0.01	>0.90
SEP		29	37.4	47	37.2	0.21	>0.80
OCT		30	39.5	30	39.8	0.29	>0.70
NOV		3	41.3	7	40.3	0.32	>0.70
DEC		4	45.4	11	46.6	0.61	>0.50

Figure 12. Monthly mean sizes of laboratory-raised and field-captured juvenile P. interruptus. Vertical lines represent 95% confidence limits.

- = field (N = 2,113)
- = lab (N = 538)



juveniles. From January to June, mean carapace lengths of age 1+ laboratory individuals were not significantly different from those of field animals (Table 20). However, from July of age 1+, all (except for January) through age 2+, and at least the first three months of age 3+, the means of the two groups were significantly different from each other. Mean annual growth, calculated from differences between the average sizes of age 1+ and age 2+ lobsters each month from January through August, was 28 mm CL for field juveniles and 20 mm CL for lab juveniles.

Field Molt Increments

During the period of growth investigations, 157 juvenile P. interruptus (8-56 mm CL) from Bird Rock Phyllospadix beds and one juvenile from the Isthmus Reef Halidrys bed molted in laboratory aquaria within a week of capture. Individual growth records are listed in Appendix II. Increase in carapace length per molt ranged from 3.4% to 23.7% and averaged 14.1%. Mean size increase was 12.7% in cold water months and 15.1% in warm water months. Small juveniles grew 14.4% per molt, and large juveniles grew 12.0% per molt.

TABLE 20.--t-test comparisons between the monthly mean sizes of laboratory-raised and field-captured juvenile P. interruptus

Month	Age (yr)	LAB		FIELD		<u>t</u>	P
		N	Mean CL (mm)	N	Mean CL (mm)		
JAN	1+	31	16.8	98	17.2	0.62	>0.50
FEB		31	17.7	115	17.5	0.24	>0.80
MAR		31	18.9	152	17.5	1.92	>0.05
APR		31	20.1	169	18.8	1.89	>0.05
MAY		31	21.4	179	21.3	0.10	>0.90
JUN		31	23.2	128	24.8	1.73	>0.05
JUL		31	25.7	137	28.2	2.59	<0.01
AUG	2+	31	26.3	147	31.8	5.87	<0.001
SEP		30	29.7	76	37.3	7.99	<0.001
OCT		29	32.5	60	39.7	7.30	<0.001
NOV		29	34.8	10	40.6	3.46	<0.001
DEC		29	36.8	15	46.3	9.39	<0.001
JAN		15	39.8	6	38.6	0.86	>0.30
FEB		15	39.8	3	44.5	3.16	<0.01
MAR		15	39.9	6	48.1	5.14	<0.001
APR		15	40.9	1	51.2	4.88	<0.001
MAY		15	42.3	7	52.1	6.08	<0.001
JUN		14	43.7	8	54.6	7.81	<0.001
JUL		14	45.2	16	53.8	5.88	<0.001
AUG	3+	14	46.3	3	56.3	7.55	<0.001
SEP		14	47.6	6	55.4	4.42	<0.001
OCT		14	48.1	7	57.9	5.41	<0.001
NOV		14	50.5				
DEC		14	51.7				

Mark-Recapture Growth

The Marking System

Marked lab and field juveniles showed no obvious ill effects from the marking system. There was no evidence of decreased mobility, infection, or mortality due to the coded marks. Lab juveniles, whose marks ranged from none to the maximum amount (3 tail fan sections punched, 2 pleopods clipped, and 1 rostral spine removed) showed no differences in growth attributable to the marking system.

Body injuries of various types were commonly found on field juveniles captured for the first time. Thirty-eight percent of all individuals captured and measured for the first time had notched or ragged uropodal margins. Besides some minor injuries which occurred during capture and handling (recognizable as unscarred wounds), approximately 20% of all first-captures had one or more legs injured or missing, 14% had broken or missing antennae, and 2% were missing pleopods. Thus, regeneration of damaged body parts was almost a continual process for many field juveniles.

Marks on lab juveniles were allowed to be repaired by regeneration until they were barely legible before remarking. In general, regeneration time was not an absolute time period; rather, it was dependent on the molt frequency (Table 21). The three

TABLE 21. -- Minimum time intervals and numbers of molts after which mark code components were still recognizable, for 5 mm size classes of juvenile P. interruptus raised in laboratory aquaria. "+" indicates that marks were still readable when the study was terminated, hence these are minimum values

TAIL FAN				PLEOPOD				ROSTRAL SPINE			
Size Range (mm CL)	Number of Lobsters	Mean Time Interval (months)	Number of Molts	Mean Time Interval (months)	Number of Molts	Mean Time Interval (months)	Number of Molts	Mean Time Interval (months)	Number of Lobsters	Mean Time Interval (months)	Number of Molts
<9.9									8	11.7+	7.4+
10-14.9	14	6.9+	4.5+	17	6.5+	4.2+	9	15.2+	9.6+		
15-19.9	17	8.7+	5.2+	14	7.1+	4.6+	9	18.3+	9.0+		
20-24.9	8	9.5+	4.8+	12	8.9+	4.7+	7	21.7+	9.0+		
25-29.9	2	8.0+	3.5+	5	10.4+	4.6+	2	14.5+	7.5+		
30-34.9	1	14.5+	6.0+	4	14.4+	5.5+					
35-39.9	2	14.5+	5.0+	1	15.5+	5.0+					

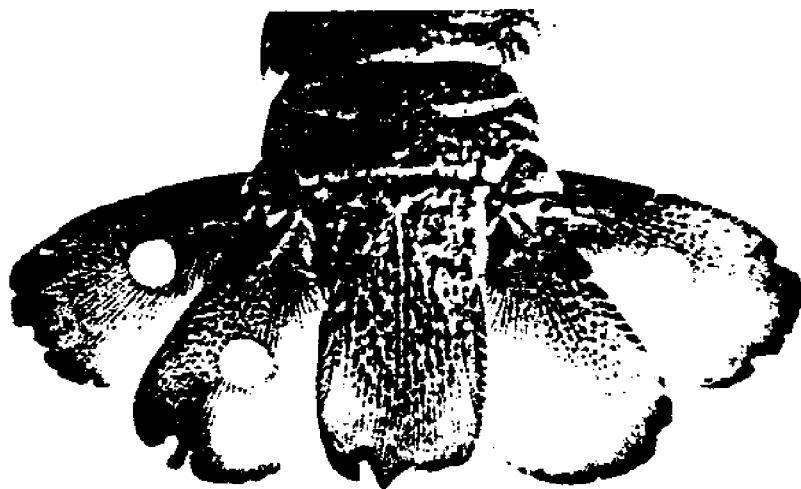
components of the marking code lost legibility at different rates. Regenerated pleopods became hard to read first, because there was less material to regrow and because no malformation occurred. Figure 13a-d shows the typical regeneration pattern for the holes punched in the tail fan after 0, 1, 2, and 5 molts. The circular hole tears out distally during the first exuviation, producing a "key-hole" appearance. Newly regenerated tissue appears proximally after each subsequent molt. At first, the tail fan marks on lab juveniles were repunched at the same time as the pleopods were re-clipped (see Table 21), but later it became evident that uropod and telson marks were recognizable for a longer period of time because the pattern of regrowth eventually produced slight malformations or scars which were readable long after the original mark was filled in (Fig. 13d). Rostral spine ablations were recognizable twice as long as the other marks in laboratory lobsters (Table 21). For individuals 10-30 mm CL, rostral spine marks were legible after a minimum average of 8.8 molts (17.4 months), and pleopod and tail fan marks lasted at least 4.5 molts (8.3 months).

To recognize individual field-captured juveniles, all three marks had to be legible. The number of lobsters identified after more than six months at large, along with the maximum intercapture times for 5 mm size classes are shown in Table 22. Only 34

Figure 13. Appearance of the holes punched in the uropods and telson of typical laboratory-reared juvenile P. interruptus:

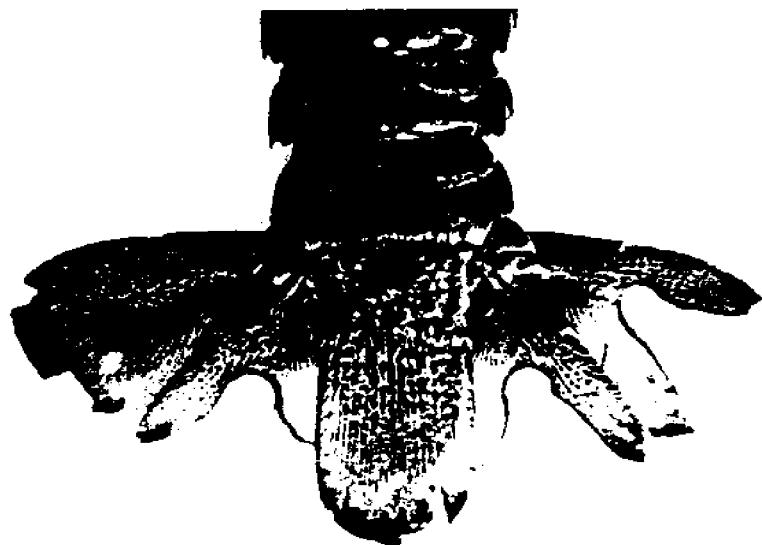
- a. before the first ecdysis
- b. after the first ecdysis
- c. after the second ecdysis
- d. after the fifth ecdysis

a. Juvenile K8 (27 mm CL): punch code 1-2-5 initial marks.



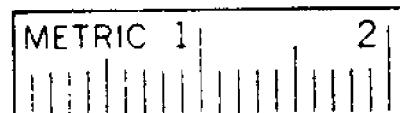
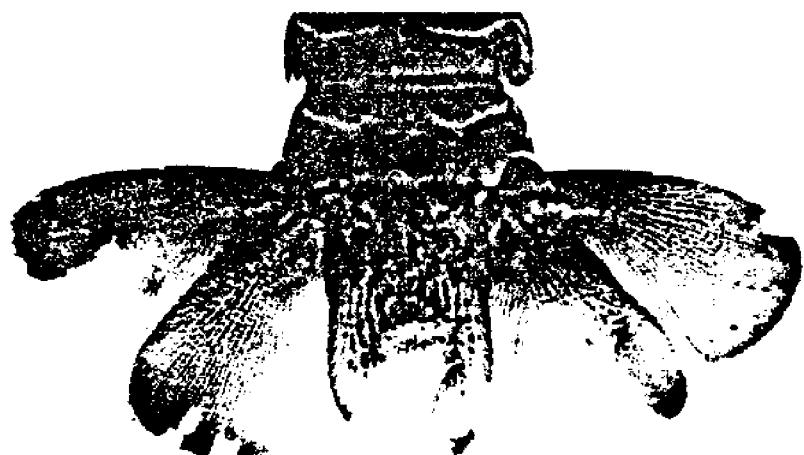
METRIC	1	2

b. Juvenile B6 (23 mm CL): punch code 2-4-5 after 1 molt.

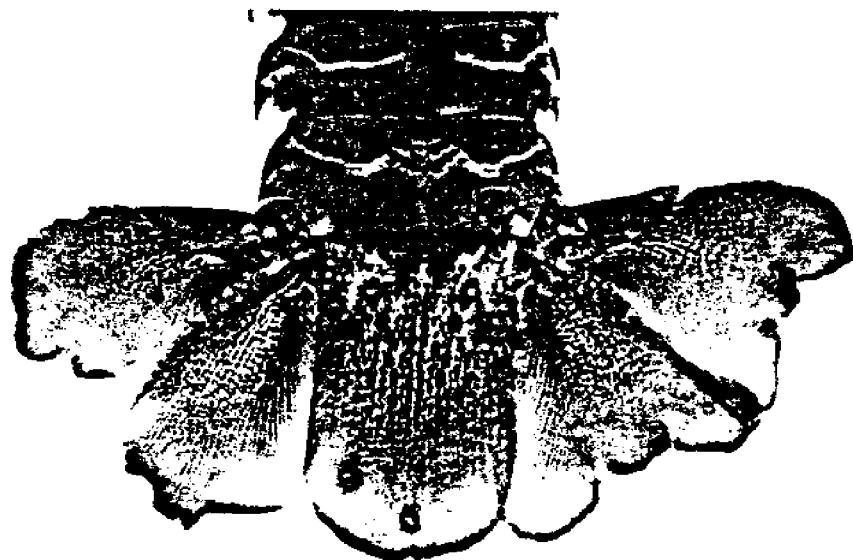


METRIC	1	2

c. Juvenile T (22.3 mm CL): punch code 1-3-4 after 2 molts.



d. Juvenile T7 (52.0 mm CL): punch code 1-4-5 after 5 molts.



10 11 12 13 14 15 16 17 18 19

TABLE 22. --Intercapture intervals after which individual mark codes were still recognizable, for 5 mm size classes of juvenile P. interruptus from Bird Rock and Isthmus Reef

Size Range (mm CL)	Number of Juveniles Recaptured After More Than Six Months at Large						Recaptured Juveniles with Maximum Time at Large		
	6-8.9	9-11.9	12-14.9	15-17.9	18-20.9	21-23.9	Time at Large (Days)	Estimated Number of Molts	Recapture Size (mm CL)
<9.9	1	-	-	-	-	-	204	4	16.9
10-14.9	9	-	-	-	-	-	267	9	45.8
15-19.9	11	1*	-	-	-	-	288	6	39.0
20-24.9	3	-	-	-	-	-	240	6	47.7
25-29.9	1	-	-	-	-	-	205	4	40.5
30-34.9	-	-	1	-	-	-	409	4	50.5
35-39.9	1	1	1	-	-	2	649	5	57.8
40-44.9	1	-	-	-	1	-	613	4	63.0

*from Isthmus Reef

lobsters were recaptured after intervals greater than six months because juveniles remaining within the confines of the Phyllospadix and Halidrys beds often were recaptured within shorter periods of time and remarked, and probably because mortality and emigration gradually removed marked juveniles from the local population. In general, small juveniles remained recognizable through 4-6 molts (6-9 months). Large juveniles were recognizable after 4-5 molts (9-24 months).

Molt Stage Determination

During the marking process, I noticed that the wound color of the rostral spine cut varied from colorless to dark brown. Six juveniles, ranging in size from 10 to 43 mm CL were monitored for spine wound color changes by cutting off a thin section of a rostral spine every ten days. The results indicate that spine wound color was a crude indicator of intermolt stage (Table 23). The colorless-pink condition occurred during 20% of the intermolt period, light red-red during the next 65% of the time, and dark red-dark brown during the final 15% of the intermolt period. Colorless-pink, light red-red, and dark red-dark brown phases roughly corresponded to molt stages A-C₁, C₂-D₀, and D₁-E of Passano (1960).

Recapture of Marked Individuals

Table 24 shows the size and sex distribution of juvenile

TABLE 23. - Sequential color changes in the developing exocuticle, viewed from the cut surface of a rostral spine, during intermolt for various sizes of juvenile *P. interruptus*

Day	Female		Male		Female		Female		Female	
	10.4 mm CL	14.4 mm CL	19.6 mm CL	24.4 mm CL	37.4 mm CL	42.7 mm CL	10.4 mm CL	14.4 mm CL	19.6 mm CL	24.4 mm CL
0	Light Red	Light Red	Pink	Red (M : Day 8)	Dark Brown (M : Day 4)	Light Red	Dark Brown (M : Day 4)	Colorless	Colorless	Light Red
10	Red (M : Day 18)	Red	Red	Red	Colorless	Colorless	Colorless	Colorless	Colorless	Light Red
20	Colorless	Dark Red (M : Day 22)	Dark Red (M : Day 25)	Pink	Pink	Pink	Pink	Pink	Pink	Red
30	Light Red	Pink	Colorless	Light Red	Light Red	Light Red	Light Red	Light Red	Light Red	Red
40	Red	Red (M : Day 47)	Light Red (M : Day 47)	Red (M : Day 46)	Red (M : Day 46)	Red	Red	Red	Red	Red
50	Dark Red (M : Day 56)	Colorless	Red	Colorless	Colorless	Red	Colorless	Colorless	Colorless	Dark Red
60	Colorless	Light Red	Red	Pink	Pink	Dark Red	Dark Brown (M : Day 62)			

M = Molt (Ecdysis)

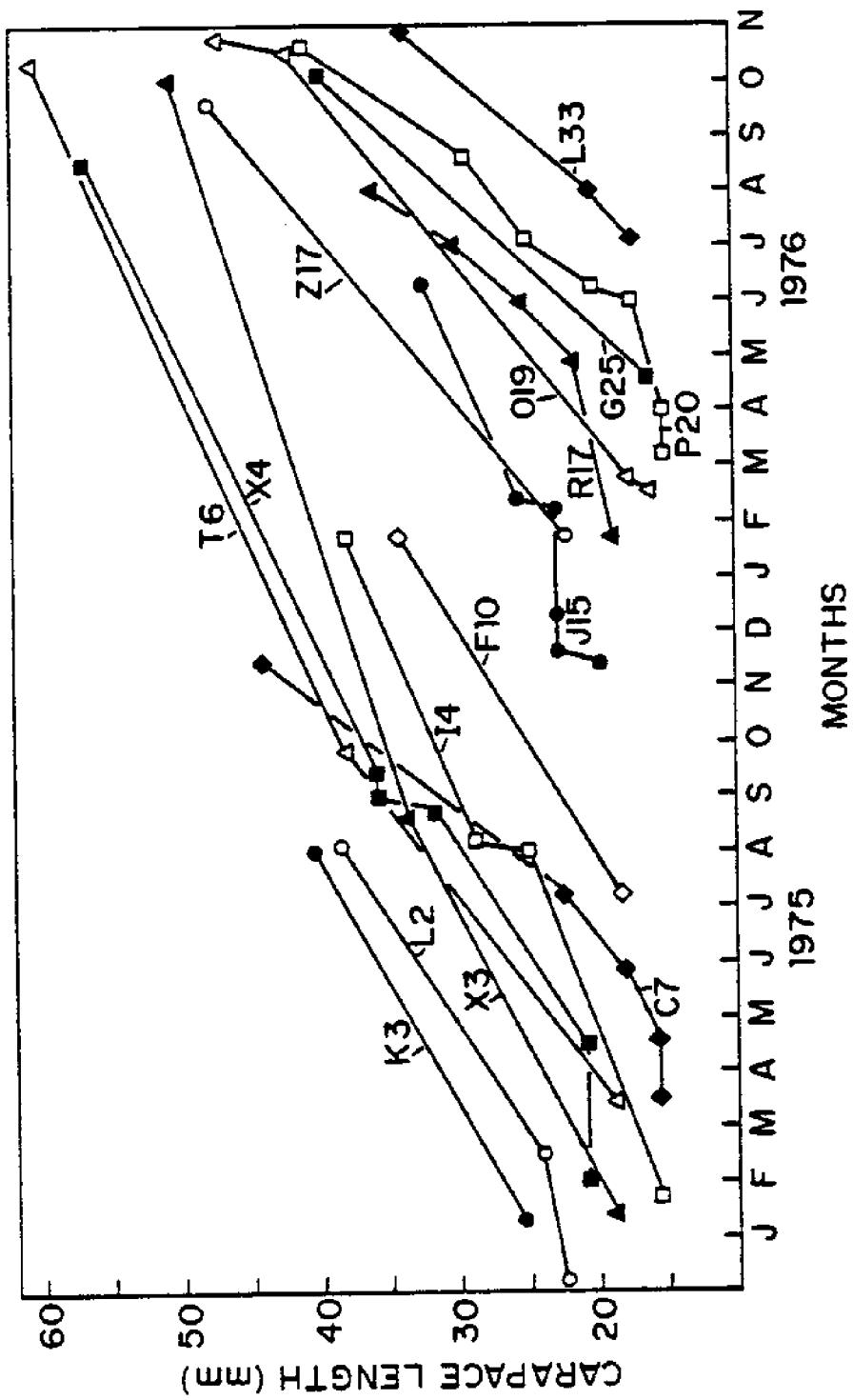
TABLE 24.--Size and sex distributions of juvenile P. interruptus
individually marked and released at Bird Rock and Isthmus Reef

Size Range (mm CL)	Punch Hole Diameter (mm)	Number of Juveniles Marked and Released					
		Bird Rock			Isthmus Reef		
		Males	Females	Not Sexed	Males	Females	
10-19.9	2.0-2.5	196	209	7	6	4	
20-29.9	2.5-3.5	130	121	7	16	8	
30-39.9	3.5-4.0	52	63	0	4	3	
40-49.9	5.0	17	28	0	1	1	
50-59.9	6.0	8	5	0	0	0	
Total:		403	426	14	27	16	

P. interruptus marked and released at Bird Rock (843 lobsters) and Isthmus Reef (43 lobsters) from November 1974 to November 1976. Individual recapture records are listed in Appendix III. Thirty-five percent of the marked juveniles at Bird Rock and 9% of those at Isthmus Reef were recaptured one or more times. Of the 292 juveniles recaptured at Bird Rock, 187 were recaptured once, 69 twice, 28 three times, 7 four times, and 1 five times. At Isthmus Reef, three juveniles were recaptured once and one individual twice.

The variety of growth patterns for juveniles recaptured from the Bird Rock Phyllospadix beds is depicted in Figure 14, in which postcapture and postmolt measurements of 15 representative individuals are plotted over time. Nearly all other mark-recapture growth records fell within the extremes shown here. The most realistic growth curves are those of juveniles recaptured frequently, at regular time intervals (i.e., C7, R17, P20). The 1974 settlement year class juveniles are readily separated from those which settled in 1975, with two exceptions: age 3+ juvenile X3, who was only a few millimeters larger than age 2+ juvenile Z17, and juvenile F10, who probably settled late in 1974, after water temperatures declined. Slow growth during the cold water season is apparent for juvenile J15, who had an exact intermolt period (bounded by postcapture laboratory molts) of 84 days between November and February.

Figure 14. Growth of 15 representative marked juvenile P. inter-
ruptus recaptured one or more times from Phyllospadix
beds at Bird Rock during 1975 and 1976. Each mark
represents a measurement after a field capture or after
a laboratory molt occurring within a week of capture.
Nearly vertical growth lines characterize the single
laboratory molts.



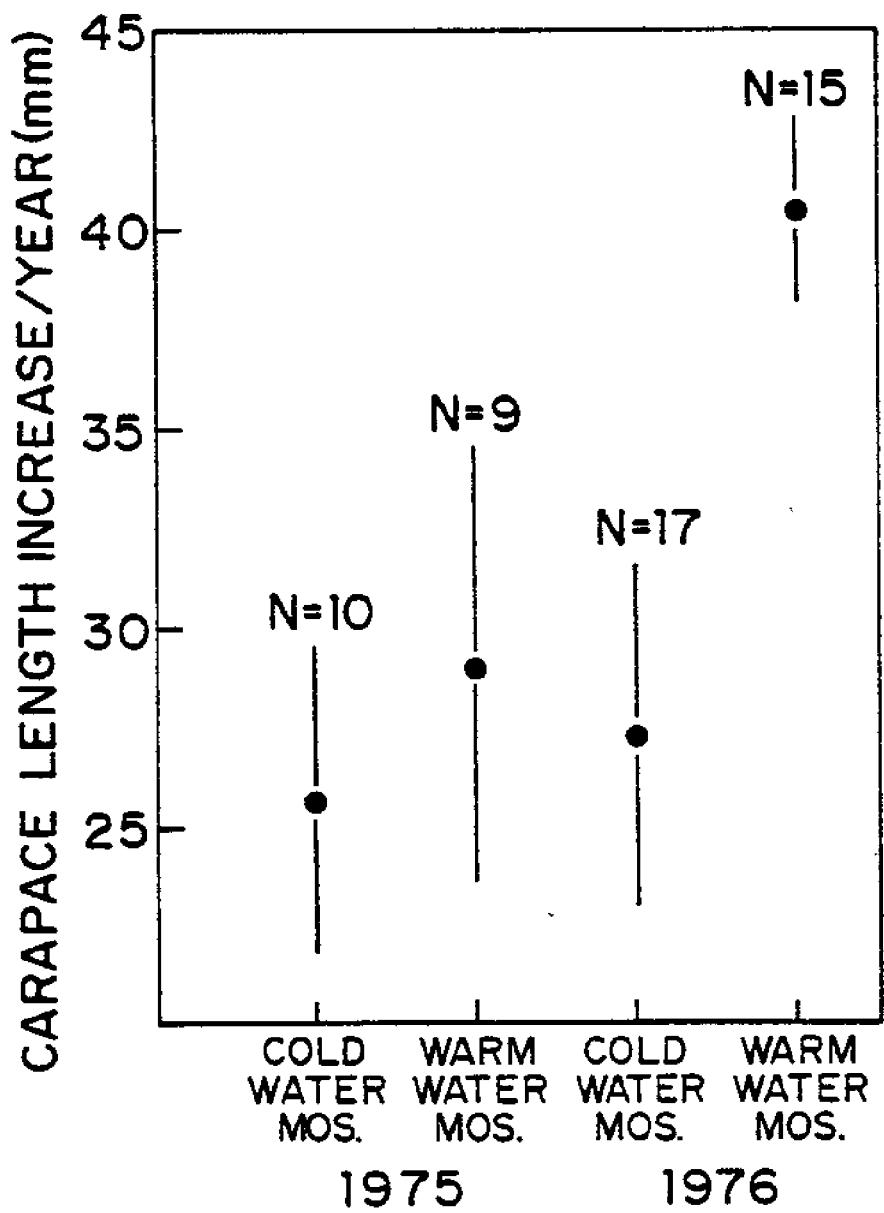
Only seven marked juveniles (three males and four females) which had grown to sizes greater than 50 mm CL were recaptured (including juveniles X3, X4, and T6 shown in Fig. 14). The largest recapture, female E39, was carrying eggs when collected on July 6, 1978.

Annual growth, calculated for 54 marked juveniles which were recaptured one or more times over periods greater than six months (see Appendix III), ranged from 12 to 46 mm CL (avg = 30 mm CL/yr). In 1976 mean annual growth for individuals at large predominantly during cold water months was significantly lower than for those at large during warm water months (t-test, $P < 0.001$) (Fig. 15). In 1975 the differences were noticeable, but not significant ($P > 0.2$). Mean annual growth for juveniles at large during warm water months in 1976 was significantly higher than during the same time in 1975 ($P < 0.001$), but long-term cold water growth was similar in both years ($P > 0.6$).

Laboratory Culture

Of 42 juvenile P. interruptus captured from surf grass beds at Bird Rock and Ripper's Cove from October 1974 to April 1975, 28 survived in laboratory aquaria through December 1976 (hereafter these will be designated as Catalina lab juveniles). Of 51 puerulus larvae captured by night-lighting from the marineland

Figure 15. Mean increases in size per year for marked juvenile *P. interruptus* recaptured one or more times in the Phyllospadix beds at Bird Rock after time periods greater than six months. Separate means are shown for cold water months (December- May) and warm water months (June- November) for 1975 and 1976. Vertical lines represent 95% confidence limits.



pier during August-October 1975, 14 survived in aquaria through December 1976 (hereafter these will be designated as Marineland lab juveniles).

Individual growth records for 29 Catalina and 16 Marineland lab juveniles are listed in Appendix IV. Since no significant differences were found between the annual growth rates of males and females, combined data were used for all lab growth analyses. Monthly mean growth data for 15 Catalina lab juveniles captured before December 1974 and for 16 Marineland lab juveniles are summarized in Tables 25 and 26. Maximum mean size increases and mean numbers of molts per month generally occurred during the months July to December, a period which lagged the warm water season by one month. Except for temperature trends, mean numbers of molts per month gradually declined with age.

Average intermolt times for 2 mm size groups of Catalina and Marineland lab juveniles are shown in Figure 16. The plots have the appearance of a sine wave of progressively increasing amplitude, an indication that two variables had affected intermolt times. Generally, intermolt times lengthened with increasing size. Within this trend, intermolt times were short during warm water months and long during cold water months.

Mean growth per year for age 1+ Catalina lab juveniles (20.8 mm CL) was similar to that for age 1+ Marineland lab

TABLE 25.--Monthly mean sizes, size increases, and molt frequencies for laboratory-raised juvenile *P. interruptus* collected from *Phyllospadix* habitats at Santa Catalina Island

Year	Month	Age (yr)	N*	Mean Size (mm CL)	95% CI	Mean Size Increase (mm CL)	Mean Number of Molts per Month	Seawater Temperature (°C)
1974	DEC	1+	15	18.8	1.8			16.1
1975	JAN		15	19.6	1.8	0.8	0.4	14.1
	FEB		15	20.2	1.9	0.6	0.3	14.1
	MAR		15	20.8	1.9	0.5	0.3	14.3
	APR		15	21.7	1.8	0.9	0.5	14.7
	MAY		15	22.5	1.9	0.3	0.3	15.0
	JUN		15	24.4	1.7	1.9	0.7	16.0
	JUL		15	28.2	1.8	3.8	1.0	19.0
	AUG	2+	15	29.3	1.5	1.1	0.3	19.8
	SEP		15	33.0	1.6	3.7	0.4	19.7
	OCT		15	36.0	1.4	3.0	0.7	19.1
	NOV		15	39.4	1.3	2.4	0.5	16.3
	DEC		15	38.9	1.2	0.5	0.1	15.2
1975	JAN		15	39.8	1.2	0.9	0.3	14.2
	FEB		15	39.8	1.2	0	0	14.8
	MAR		15	39.9	1.4	0.1	0.1	15.4
	APR		15	40.9	1.1	1.0	0.3	17.2
	MAY		15	42.3	0.9	1.4	0.4	18.3
	JUN		14	43.7	1.5	1.4	0.3	20.0
	JUL		14	45.2	1.1	1.5	0.4	21.5
	AUG	3+	14	46.3	1.1	1.1	0.4	20.9
	SEP		14	47.6	1.3	1.3	0.5	22.1
	OCT		14	48.1	1.1	0.5	0.2	21.2
	NOV		14	50.5	1.7	2.4	0.6	20.2
	DEC		14	51.7	1.2	1.2	0.4	18.0

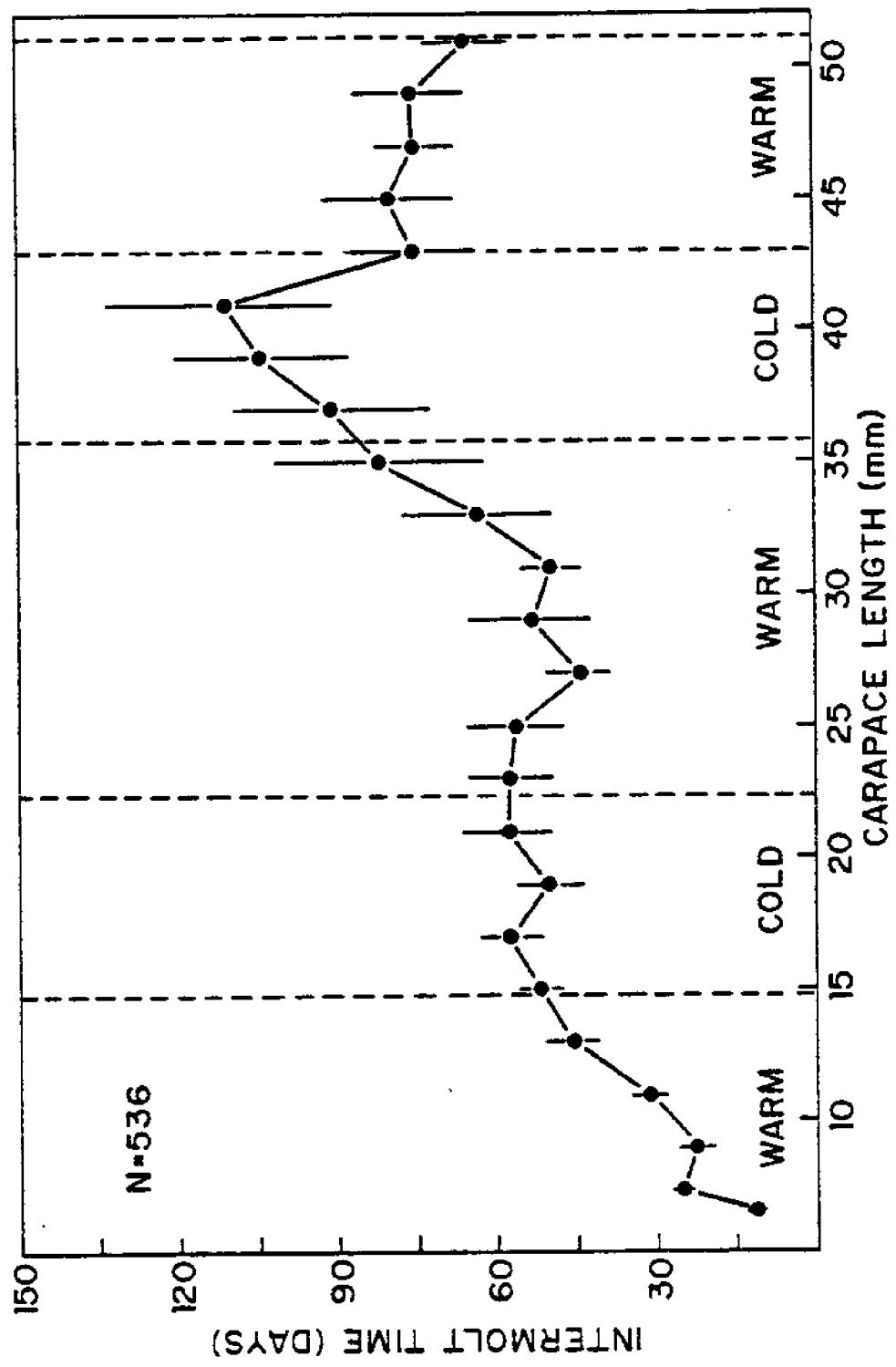
*Includes only those lab juveniles which were captured before December 1974.

TABLE 26. -- Monthly mean sizes, size increases, and molt frequencies for laboratory-raised juvenile *P. interruptus* collected as puerulus larvae from Marineland

Year	Month	Age (yr)	N	Mean Size (mm CL)			95% Cf	Increase (mm CL)	Mean Size	Number of Molts	Mean Seawater Temperature (°C)
				1975	1+	15					
	AUG		16	7.2		0.1			0.5	0.9	19.7
	SEP		16	8.6		0.3			1.4	0.9	19.1
	OCT		16	10.5		0.4			1.9	1.0	16.8
	NOV		16	12.8		0.5			2.3	0.9	15.2
	DEC		16								
1976	JAN		16	14.1		0.9			1.3	0.5	14.2
	FEB		16	15.4		0.4			1.3	0.6	14.8
	MAR		16	17.0		1.0			1.6	0.6	15.4
	APR		16	18.5		0.8			1.5	0.5	17.2
	MAY		16	20.4		0.8			1.9	0.8	18.3
	JUN		16	22.1		1.0			1.7	0.6	20.0
	JUL		16	23.4		0.8			1.3	0.4	21.5
	AUG	2+	16	23.4		0.8			0	0	20.9
	SEP		15	26.4		0.9			3.0	1.0	22.1
	OCT		14	28.6		1.6			2.2	0.6	21.2
	NOV		14	31.0		1.7			2.4	0.6	20.2
	DEC		14	34.6		1.2			3.6	0.9	18.0

Figure 16. Mean intermolt times for 2 mm size groups of juvenile P. interruptus raised in laboratory aquaria. Vertical solid lines represent 95% confidence limits. Dashed lines indicate mean juvenile sizes between six-month temperature periods.

Cold = cold water months (December-May)
Warm = warm water months (June-November)



juveniles (20.0 mm CL), but was significantly different from age 2+ Catalina lab juveniles (12.8 mm CL) (t-test; $P < 0.001$). Age 1+ lab juveniles averaged 3.9 molts per year. Mean annual growth for all lab juveniles during warm water months (25.1 mm CL; 6.9 molts) was over twice as high as the growth during cold water months (12.0 mm CL; 4.6 molts).

An inverse relationship existed between initial size (CL_0) and total increase in size (ΔCL) after two years of growth in laboratory aquaria for Catalina lab juveniles (Fig. 17). Linear regression analysis of the form:

$$y = a + bx \quad (4-0)$$

resulted in the relationship:

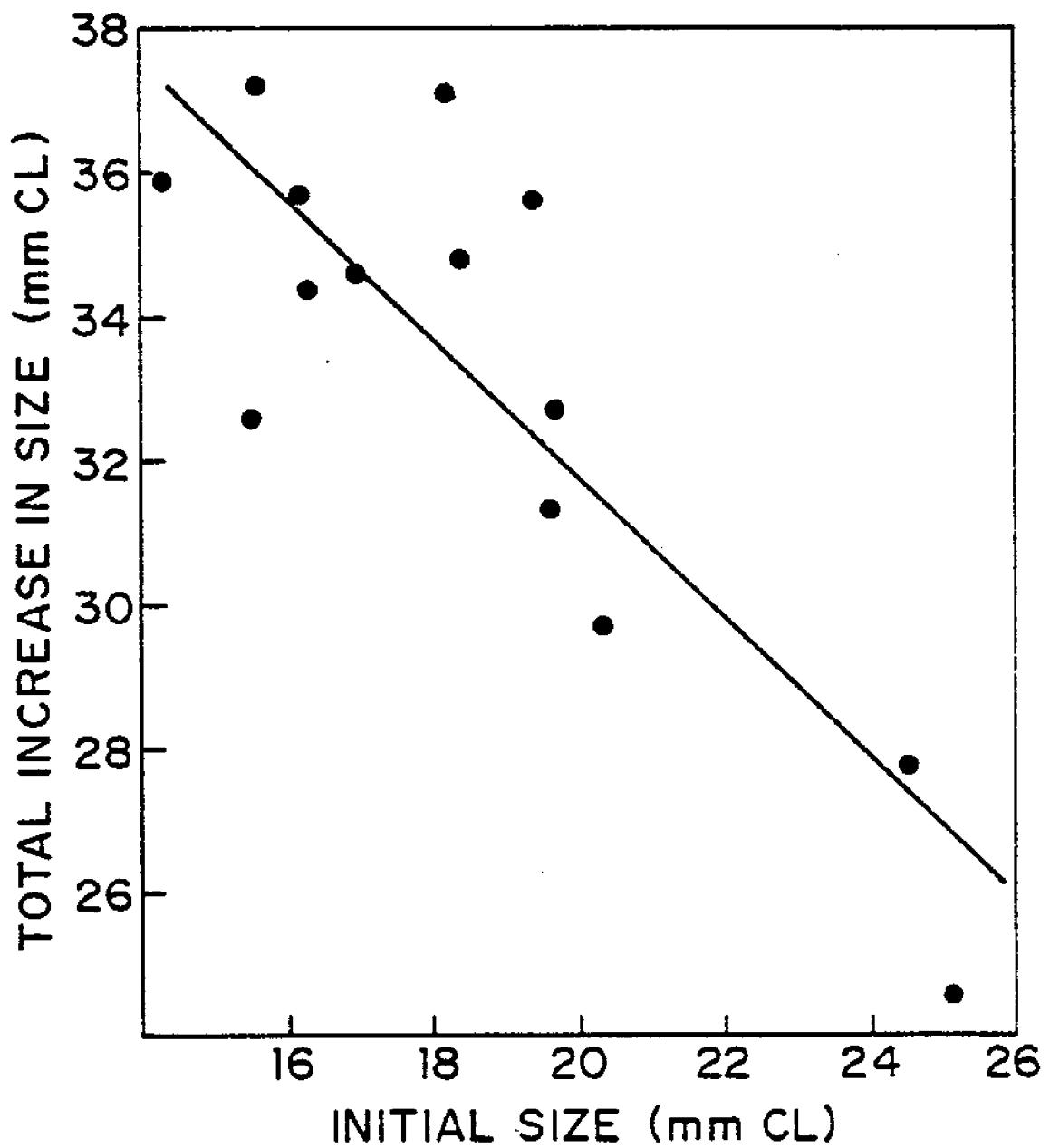
$$\Delta CL = 51.0 - 0.966 CL_0 \quad (4-1)$$
$$r^2 = 0.707$$

Growth Analysis

Field Single Molt Determination

Determining single molt increments for recaptured lobsters presented problems because molting activity during the intercapture interval could not be monitored directly. For the initial characterization of single field molts, only those individuals recaptured after

Figure 17. Relationship between initial size and total increase in size after two years of growth in laboratory aquaria for 14 P. interruptus collected as juveniles from Bird Rock. The line was fitted by linear regression analysis (Equation 4-1).



short intercapture intervals were utilized. Of 115 Bird Rock juveniles (12-38 mm CL) recaptured within one month of release (see Appendix III), 68 showed no change in carapace length and 47 showed increased size and had keyhole-shaped tail fan marks, indicating that one molt had occurred. Increase in carapace length for the single-molt juveniles ranged from 8.3% to 19.4%.

Mean percentage increase in size per molt for the above juveniles (14.9) was tested for equality with the mean percentage increase for 132 similarly-sized field juveniles which molted in laboratory aquaria within a week of capture (14.5; see Appendix II) using the t-statistic (after all percentages had been converted to angles by means of the arc sine transformation*). Since the two means were not significantly different ($P > 0.4$), the data were combined.

Individuals recaptured more than one month after release which exhibited single-molt mark regeneration and the relative increase in size of which fell within two standard deviations of the above combined mean also were considered single field molts. Of 332 total single field molts, mean relative increase in size for the premolt range 8-46 mm CL was 15.0%.

*Hereafter all parametric statistical tests of percentage data have been so transformed.

Effect of Appendage Regeneration on Molt Increment

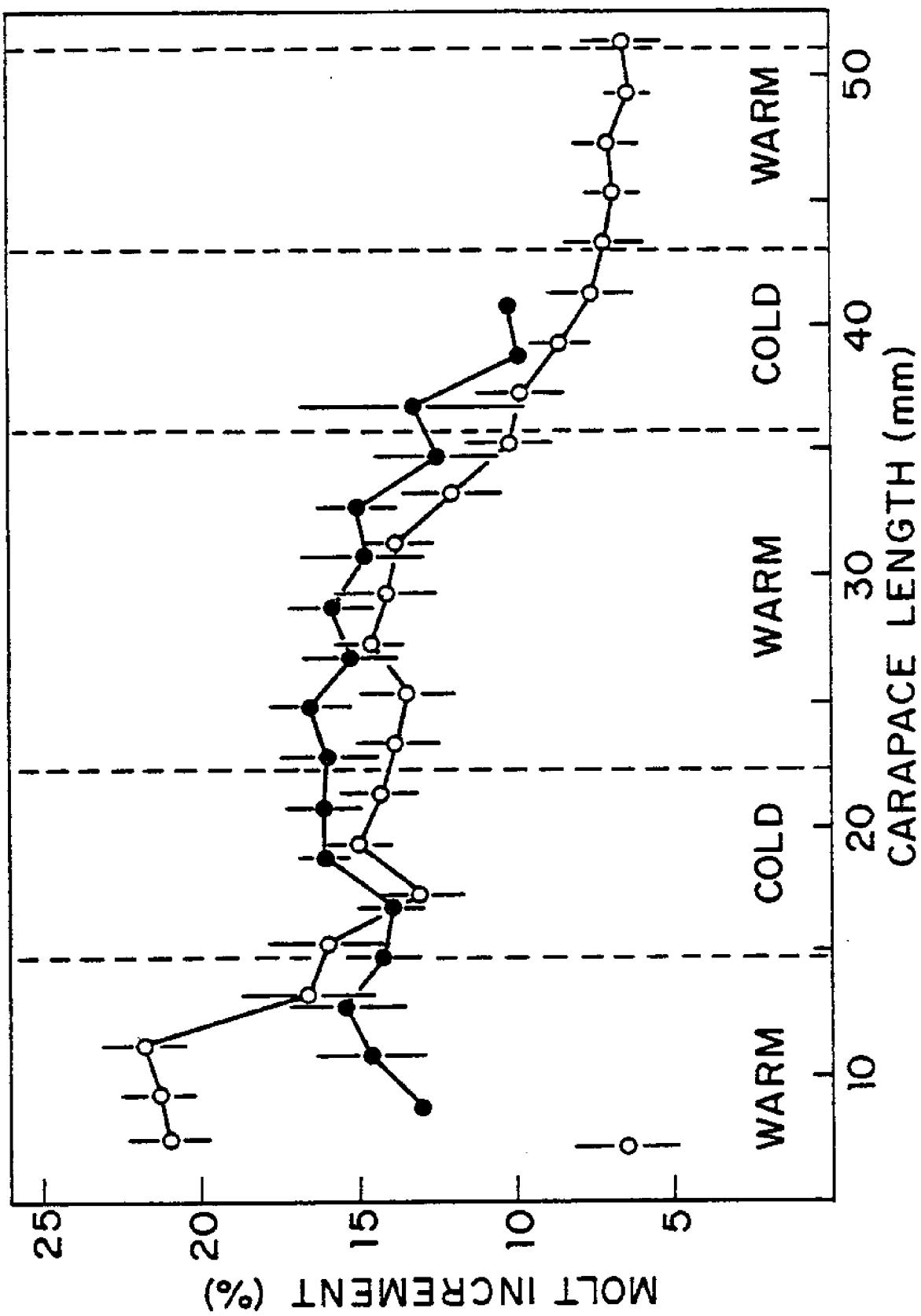
Juvenile P. interruptus found missing one or more pereopods or antennae regenerated the lost appendages within two or three molts usually, depending on when during the intermolt period the loss occurred. Mean percentage increase in size per molt for 234 intact field juveniles within the range 12-32 mm CL (15.7) was compared with that for 31 similarly sized individuals partially regenerating one appendage (14.7), for 11 individuals regenerating two appendages (14.2), and for 13 individuals regenerating more than two appendages (10.5). No significant differences (t-test; $P > 0.1$) were found between intact lobsters and those missing either one or two appendages. Those missing more than two appendages grew relatively less per molt ($P < 0.001$) than intact lobsters. Therefore, the former animals were omitted from all comparative growth analyses in this study.

Effect of Premolt Size on Molt Increment

Mean percentage increases in size for 2 mm CL groups of 332 single field molts and for 532 single lab molts are shown in Figure 18. Marineland pueruli grew little during the metamorphic molt (the isolated lab value), but small Marineland juveniles grew 21.3% per molt during an exceptional warm water period

Figure 18. Mean single molt percentage increases in carapace length for 2 mm size groups of laboratory-raised and field-captured juvenile *P. interruptus*. The isolated lab mean represents the metamorphic molt from puerulus larval to first juvenile stage. Vertical solid lines represent 95% confidence limits (calculated from arc sine transformations). Dashed lines indicate mean lobster sizes between six-month temperature periods for lab juveniles.

Cold = cold water months (December-May)
Warm = warm water months (June-November)
○ = lab (N = 532)
● = field (N = 332)



($T = 20.9^{\circ}\text{C}$). In animals from 12 to 32 mm CL, lab and field relative size increases were fairly constant, averaging 14.4% and 15.3%, respectively. Percentage size increments decreased for larger juveniles of both groups.

Mean actual molt increments for lab and field juveniles increased with increasing size up to 31 mm CL (lab) and 37 mm CL (field) (Fig. 19). Larger lab juveniles (35-51 mm CL) maintained a nearly constant increase in size per molt (3.3 mm CL). Linear regression analysis (Equation 4-0) of the data from 8 to 32 mm CL resulted in the following equations:

$$\text{Lab} \quad . \quad CL = 0.838 + 0.108 \quad CL \quad (4-2)$$

$$r^2 = 0.546$$

$$\text{Field} \quad CL = -0.255 + 0.168 \quad CL \quad (4-3)$$

$$r^2 = 0.621$$

The slopes of the two regression lines were significantly different (t-test; $P < 0.001$).

Equations 4-2 and 4-3 were used to construct plots of generalized instar sizes for lab and field juveniles, starting from the known mean size of Marineland puerulus larvae (instar 0; 6.7 mm CL) and first instar juveniles (7.1 mm CL) (Fig. 20). Lab juveniles were larger at each instar than field lobsters because of the high

Figure 19. Mean single molt increments for 2 mm size groups of laboratory-raised and field-captured juvenile P. interruptus. The isolated lab mean represents the metamorphic molt from puerulus larval to first juvenile stage. Vertical solid lines represent 95% confidence limits. Dashed lines indicate mean lobster sizes between six-month temperature periods for lab juveniles.

Cold = cold water months (December-May)
Warm = warm water months (June-November)
○ = lab (N = 532)
● = field (N = 332)

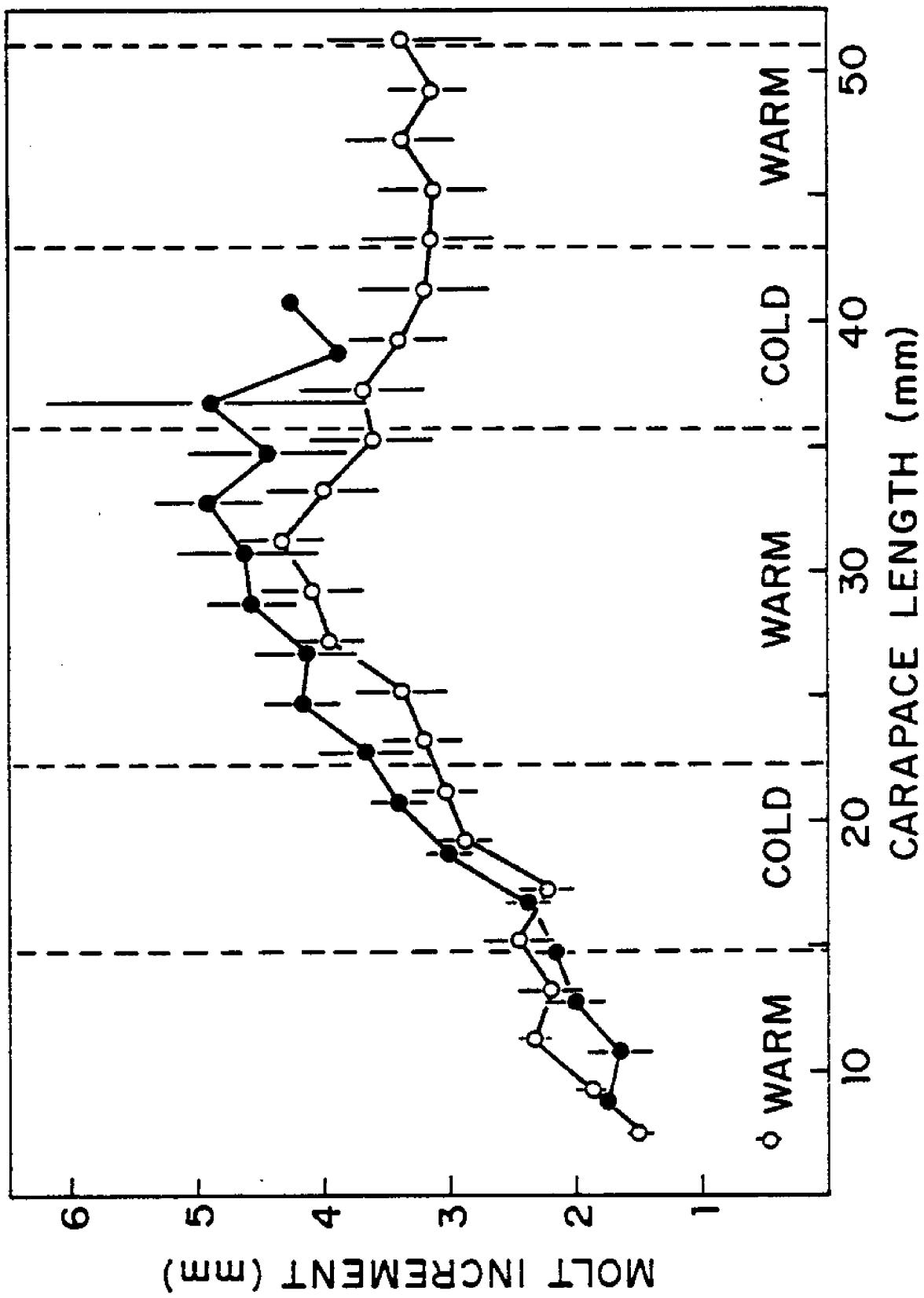
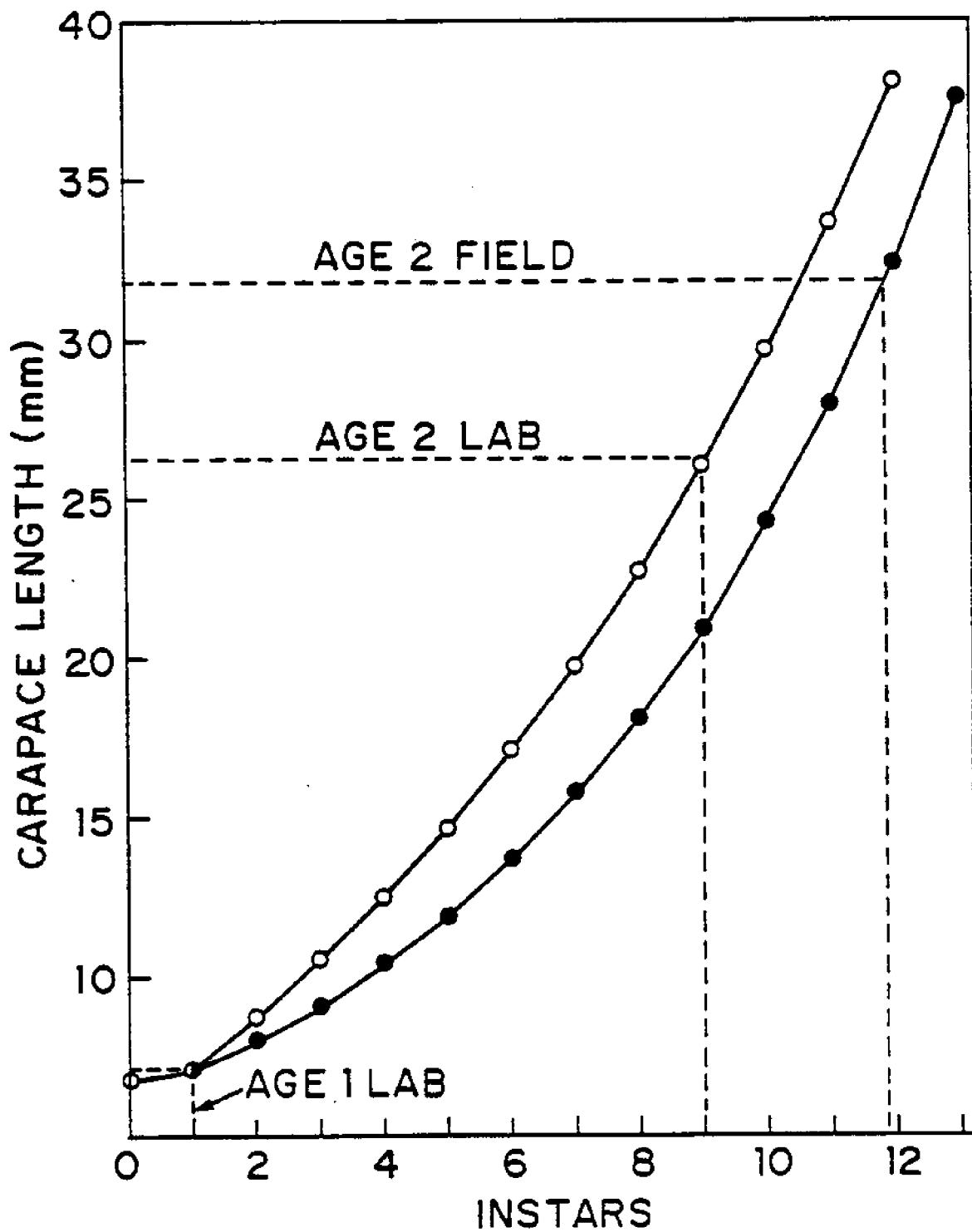


Figure 20. Instar sizes of laboratory-raised and field-captured P. interruptus calculated from linear regressions of single molt increment on carapace length (Equations 4-2 and 4-3, respectively). Instars 0 and 1 represent mean sizes for Marineland puerulus larvae and first juvenile stages, respectively. Dashed lines show mean sizes for lab and field juveniles on their first and second August birth dates (see Fig. 12; Table 20).

○ = lab (N = 311)
● = field (N = 303)



growth increments of Marineland juveniles during the exceptional warm water period (see above). Lab juveniles reached instar 9 (8.1 molts) at age 2. Field juveniles molted 33% more frequently, approaching instar 12 (10.8 molts) within the same time period.

Effect of Temperature on Molt Increment

Single-molt field animals (8-46 mm CL) recaptured after cold water periods grew 13.9% per molt, and those at large during warm water months grew 16.2% per molt. The differences were significant (t -test; $P < 0.001$). Similarly sized lab juveniles also showed this dichotomy (cold months, 12.1%; warm months, 14.3%; $P < 0.001$). Variations in lab relative and actual molt increments corresponding to seasonal water temperature differences can be seen in Figures 18 and 19. Molt increments generally decreased immediately prior to or during cold water months and increased just before or during warm water months.

Growth Equations

From the above results (Figs. 15, 16, 18, 19; Tables 25, 26), it became apparent that molt increment and molt frequency were influenced by two variables--premolt size and water temperature. Multiple linear regression analysis was used to evaluate the relationship of the two variables to lab juvenile intermolt time, lab

juvenile molt increment, and field juvenile molt increment. The equation used was:

$$Y = a + b_L L + b_T T \quad (5-0)$$

where Y = intermolt time in days or molt increment in mm CL, L = premolt carapace length in mm, T = water temperature in $^{\circ}\text{C}$, and a , b_L , and b_T are fitted constants. Water temperature data are mean intermolt temperature for lab animals, mean temperature for one month preceding capture for field molts in the lab, and mean intercapture temperature for recaptured field animals. In addition to the regression constants, the following values were calculated:

1. r^2 , the coefficient of multiple determination, represents that fraction of the total variation in Y which is associated with variations in L and T
2. b'_L and b'_T , the standard partial regression coefficients, provide a comparison of the relative importance of L and T to the regression
3. r_L and r_T , the partial correlation coefficients measure the relationship between L and Y , and T and Y , independent of L and T interactions
4. SE, the standard error, provides a measure of the accuracy of the regression equation in predicting actual values of Y

Table 27 shows the multiple regression analysis results for different size and temperature ranges. The constants b_L and b_T were associated positively with Y for all molt increment regressions. For lab intermolt time regressions, b_L was positively proportional and b_T was negatively proportional to Y . All r^2 , r_L , and r_T values were significantly different from zero (F tests; $P < 0.001$). In general, the regression equations fit the data better (higher r^2 values and lower SE values) when records for periods when water temperature was greater than 20°C were deleted, and when premolt juveniles greater than 32 mm CL were omitted. Deletion of high temperature records greatly increased r^2 values for lab intermolt time regressions, especially for small juveniles, but had little effect on field molt increment regressions. Omission of large juveniles greatly increased r^2 values for lab molt increment regressions, but decreased r^2 values for lab intermolt time regressions. Too few data were available to determine the effects of field juveniles larger than 32 mm CL on regression equations.

Premolt size was more important than water temperature (cf. b'_L and b'_T) in the small juvenile molt increment regressions in Table 27. Full size range molt increment regressions showed little differences in importance between the two variables. Premolt size was more important for 8-55 mm CL juveniles in the lab

TABLE 27. -- Multiple regression coefficients for the relationship of premolt size and water temperature to intermolt time and molt increment for lab and field juvenile *P. interruptus* (see Equation 5-0 and text for details)

	Equation Number	Size Range (mm CL)	Temp. Range (°C)	N	a	b_{L_1}	b_T	r^2	b_L'	b_T'	r _L	r _T	SE
Lab	5-1	8-55	13-22	460	140.4	2.07	-7.78	0.61	0.86	-0.63	0.77	-0.66	18.2
Intermolt	5-2	8-55	13-20	372	107.3	2.29	-11.03	0.77	0.82	-0.68	0.85	-0.80	15.0
Time	5-3	8-32	13-22	310	104.4	1.84	-5.45	0.43	0.67	-0.65	0.61	-0.59	14.4
(Days)	5-4	8-32	13-20	275	148.1	1.94	-8.32	0.73	0.72	-0.85	0.78	-0.83	9.8
Field	5-5	8-55	13-22	460	0.19	0.02	0.13	0.26	0.29	0.30	0.28	0.30	0.86
Molt	5-6	8-55	13-20	372	-1.62	0.04	0.23	0.42	0.38	0.41	0.43	0.46	9.79
Increment	5-7	8-32	13-22	310	-0.86	0.09	0.12	0.60	0.60	0.27	0.64	0.35	0.64
(mm CL)	5-8	8-32	13-20	275	-1.94	0.09	0.19	0.65	0.59	0.36	0.67	0.48	0.60
Field	5-9	9-45	13-22	332	-2.15	0.09	0.20	0.69	0.53	0.42	0.63	0.54	0.64
Molt	5-10	9-45	13-20	279	-3.07	0.09	0.25	0.68	0.51	0.48	0.64	0.62	0.60
Increment	5-11	9-32	13-22	300	-2.38	0.13	0.17	0.72	0.60	0.36	0.70	0.51	0.58
(mm CL)	5-12	9-32	13-20	265	-3.25	0.13	0.22	0.74	0.58	0.43	0.72	0.61	0.53

a = Regression constant

b_{L_1}, b_T = Partial regression coefficients

r^2 = Coefficient of multiple determination

b_L', b_T' = Standard partial regression coefficients

SE = Standard error of multiple regression predictions

intermolt time regressions, but equal or less important than temperature for 8-32 mm CL lab juveniles.

Equations 5-4 and 5-12 from Table 27 were applied to representative premolt size and water temperature data in order to demonstrate the relative effects of molt frequency and molt increment on juvenile lobster growth when either size or temperature is held constant. Table 28 shows that temperature affects growth primarily by means of changes in molt frequency. If temperature is held constant, the greater size increase per molt related to larger premolt size is counterbalanced by decreased molt frequency; therefore, no net change in the overall rate of growth occurs.

Molt Frequency Predictions

Equation 5-9 (Table 27) was used to estimate the number of molts for recaptured individuals which had molted more than once between captures (see Appendix III). Temperature values used were three-month field temperature means assigned sequentially throughout the intercapture period such that intermolt times were consistent with those plotted for lab juveniles in Figure 16.

The accuracy of the above estimation procedures was tested by applying Equation 5-7 to 352 haphazardly chosen pairs of measurements from each of 45 lab juveniles. Actual numbers of molts during these laboratory "intercapture" periods ranged from

TABLE 28. -- Example of the relative effects of molt frequency and molt increment on juvenile *P. interruptus* growth when either premolt size or water temperature is held constant. (See Table 27 for details on multiple regression Equations 5-4 and 5-12)

Growth Equations:

$$\text{Molt Frequency} = 148.1 + 1.94 \text{ CL}_0 - 8.32 \text{ T} \quad (5-4)$$

$$\text{Molt Increment} = -3.25 + 0.13 \text{ CL}_0 + 0.22 \text{ T} \quad (5-12)$$

	Molt Frequency			Molt Increment		
	CL ₀ (mm)	T (°C)	Intermolt Time (Days)	Relative Growth Enhancement (%)	Size Increase Per Molt (mm CL) (%)	Relative Growth Enhancement (%)
Constant CL ₀	20	14	70	+ 141	2.4	+ 46
	20	19	29		3.5	
Constant T	15	17	36	- 81	2.4	+ 83
	30	17	65		4.4	

CL₀ = Premolt carapace length (mm)

T = Water temperature (°C)

two to eight. Equation 5-7 was able to estimate the actual number of molts for lab juveniles which molted two to five times with 85% accuracy, and for those molting six to eight times with 70% accuracy. All estimations were correct to plus or minus one molt with 99% accuracy.

Molt frequency predictions for 296 field-recaptured juveniles are summarized in Table 29. Annual molt frequency, calculated for 51 marked juveniles which were recaptured one or more times over periods greater than six months, ranged from 5 to 14 molts per year for juveniles less than 30 mm CL₀. Mean annual molt frequency for small field animals (9.0 molts/yr) was significantly greater (t-test; P < 0.001) than that for small Catalina lab juveniles (6.6 molts/yr) (Table 30). Too few large field juveniles were recaptured for adequate molt frequency comparisons to be made between age 2+ field and lab lobsters.

The Generalized Pattern of Growth

Generalized P. interruptus growth for the first two years of benthic life was estimated for an average lobster settling at Bird Rock in mid August and exposed to yearly temperature cycles represented by eight-year semimonthly means (1970-77) for the CMSC area. The simplified growth model, based on the combined effects of temperature and premolt size on growth, was made as accurate

TABLE 29.--Summary of intercapture molt frequencies for 296 marked field juvenile P. interruptus recaptured one or more times from Bird Rock and Isthmus Reef

Number of Molts Estimated from Equation 5-9	Number of Separate Intercapture Intervals	Number of Initial- capture to Final- recapture Intervals
0	76	26
1	185	92
2	72	43
3	48	43
4	32	33
5	14	25
6	13	17
7	4	9
8	2	3
9	1	3
10	0	1
11	0	0
12	0	1

TABLE 30. --Annual molt frequencies for two size groups of field-captured and laboratory-raised juvenile *P. interruptus*

Group	Initial Size Range (mm CL)	N	Mean Initial Size (mm CL)	SD	Mean Time Interval (days)	SD	Mean Number of MoltS per Year	SD
Field	<30	61	17.0	4.2	256	127	9.0	2.0
Catalina Lab	<30	14	16.5	2.6	365	0	6.6	0.8
Marineland Lab	<30	15	7.2	0.2	365	0	8.0	0.4
Field	>30	3	38.0	2.9	515	198	2.8	0.9
Catalina Lab	>30	14	37.3	2.0	365	0	3.9	0.4

as possible by setting the following conditions:

1. intermolt times and molt increments for the puerulus larva and for juvenile instars 1-4 were represented by the means for Marineland lab juveniles
2. multiple linear regression Equations 5-9 (field molt increment) and 5-2 (lab intermolt time) (Table 27) were split into two size ranges, resulting in the following equations:

12-31.9 mm CL juveniles

$$\text{Molt increment} = -2.38 + 0.126 \text{ CL}_0 + 0.173 \text{ T} \quad (5-13)$$
$$r^2 = 0.69$$

$$\text{Intermolt time} = 150.9 + 2.02 \text{ CL}_0 - 8.60 \text{ T} \quad (5-14)$$
$$r^2 = 0.62$$

32-55 mm CL juveniles

$$\text{Molt increment} = 1.12 - 0.023 \text{ CL}_0 + 0.216 \text{ T} \quad (5-15)$$
$$r^2 = 0.32$$

$$\text{Intermolt time} = 225.9 + 1.72 \text{ CL}_0 - 11.57 \text{ T} \quad (5-16)$$
$$r^2 = 0.55$$

3. lab intermolt time was converted to field intermolt time by reducing calculated values for juveniles larger than 15 mm CL by 75% (based on 8.1 molts/yr lab juveniles versus 10.8 molts/yr field juveniles; see Fig. 20).

The generalized lobster grew from 7.1 to 33.7 mm CL in 10 molts during its first year of benthic life, and from 33.7 to 53.51 mm CL in 5 molts during its second benthic year (Fig. 21).

Juvenile Abundance

Catch per Unit Effort

Catch per diver-hour of age 1+ juvenile Panulirus interruptus from the Phyllospadix habitat at Bird Rock increased for each new settlement year class surveyed (Fig. 22). Monthly mean catch per unit effort (CPUE) was nearly constant (avg = 4.4 juveniles/diver-hour) from December 1974 to May 1975, after which CPUE declined gradually to zero by December 1975. CPUE for juveniles which settled in 1975 and 1976 increased consistently to peaks of 22.3 juveniles per diver-hour (April 1976) and 27.4 juveniles per diver-hour (December 1976; end of study). Equally consistent decreases in CPUE for the 1975 settlement year class occurred from April 1976 to August 1976. After reaching 2 years of age in August, larger juveniles were captured in low numbers during September and October; age 2+ juveniles rarely were encountered in the Phyllospadix habitat during other months of the year.

Figure 21. Growth of a generalized juvenile P. interruptus from settlement (age 1 year) to age 3 years at Bird Rock, Santa Catalina Island, calculated from molt increment and intermolt time means for small Marineland lab juveniles and from multiple linear regression Equations 5-13, 5-14, 5-15, and 5-16 (see text). Numerals represent consecutive juvenile instars. Dashed lines divide water temperature seasons.

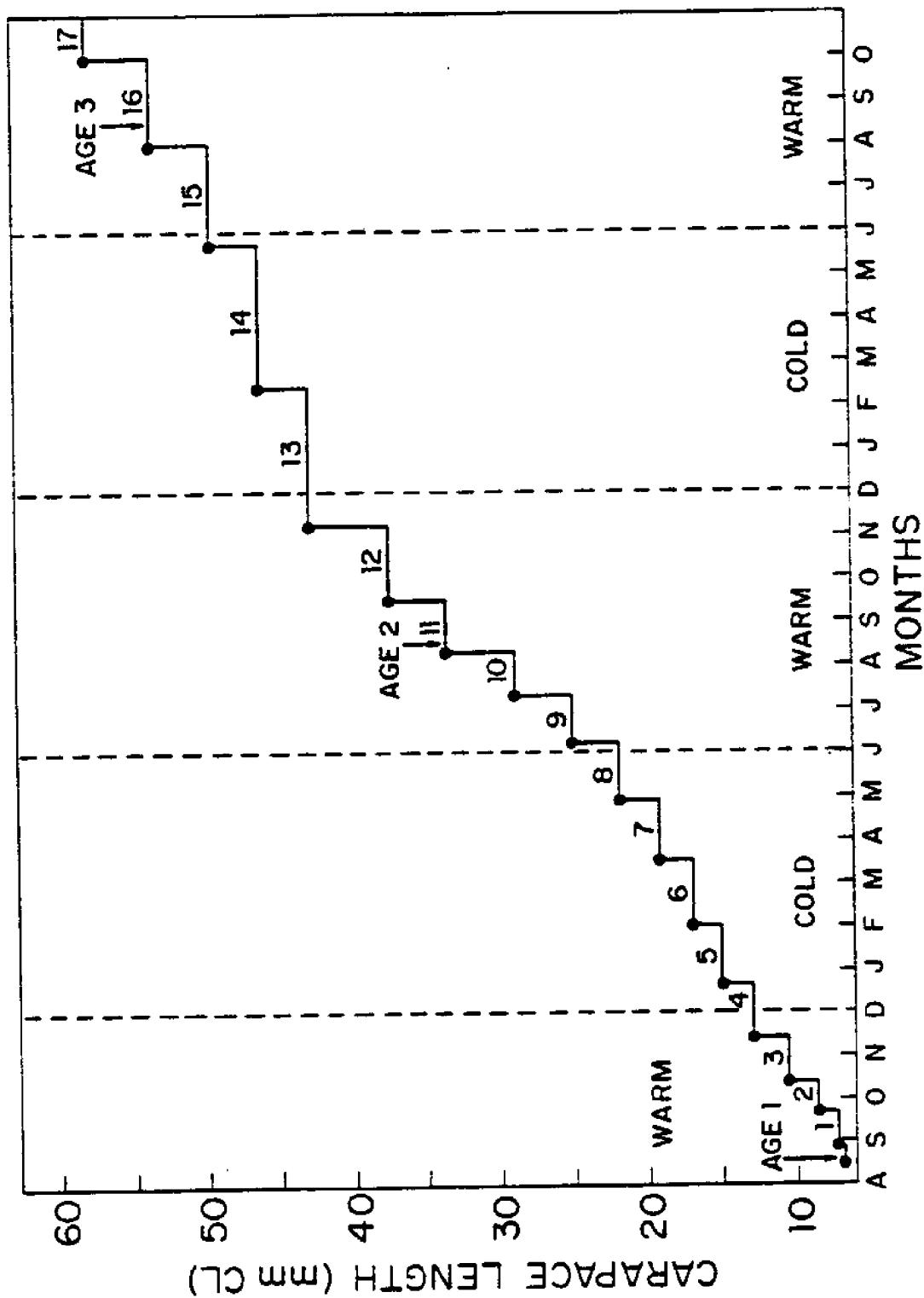
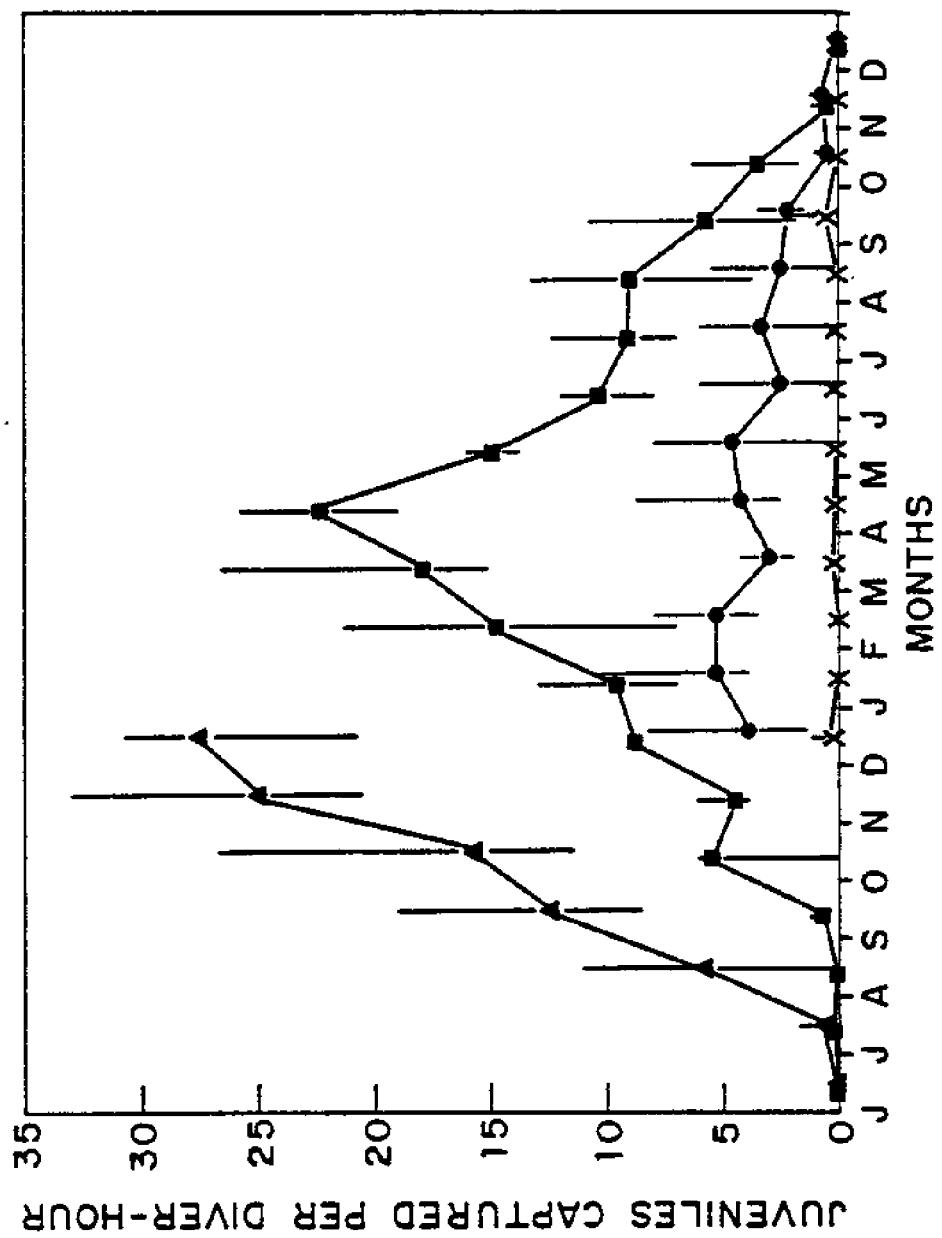


Figure 22. Monthly means and ranges of catch per diver-hour for juvenile P. interruptus at Bird Rock from December 1974 through December 1976.

- X = 1973 settlement year class (age 2+)
- = 1974 settlement year class (age 1+)
- = 1975 settlement year class (age 1+)
- ▲ = 1976 settlement year class (age 1+)



Mark-Recapture Population Size Estimates

The formula devised by Schumacher and Eschmeyer (1943) for determining population size (N) from multiple mark-recapture data is:

$$N = \frac{\sum M^2 n}{\sum Mm} \quad (6-0)$$

where M = the number of marked lobsters at large, n = the number of lobsters in a sample, and m = the number of marked lobsters in a sample. The standard error (SE) of N is:

$$SE = \sqrt{\frac{N^3 s^2}{\sum Mm}} \quad (7-0)$$

$$s^2 = \frac{1}{K-1} \left(\sum \frac{m^2}{n} - \frac{1}{n} \sum Mm \right)$$

where s^2 = the variance of N and K = the number of samples.

Monthly compilations of capture-recapture data and three or four month population estimates for age 1+ juvenile lobster populations on either side of the dike at Bird Rock are shown in Table 31. As with CPUE, population estimates increased for each new settlement year class surveyed. Similar abundance trends occurred on both sides of the dike. Population estimates declined slightly during

TABLE 31.--Population estimates, using the computation method of Schumacher and Eschmeyer (1943), for three settlement year classes of age 1+ juvenile *P. interruptus* from two *Phyllospadix* beds at Bird Rock, Santa Catalina Island (see Equations 6 and 7 and text for details)

Year	Month	West of Dike						East of Dike					
		M	n	m	N	SE		M	n	m	N	SE	
1975*	JAN	21	51	2				0	0	0			
	FEB	68	34	11				0	14	0			
	MAR	90	10	2	269	65		12	5	2			
	APR	97	19	7				15	11	2			
	MAY	104	20	9				27	17	7			
	JUN	115	4	2	245	16		37	6	5	68	5	
	JUL	115	11	6				40	27	19			
	AUG	120	19	10				48	16	10			
	SEP	128	0	0				55	13	10			
	OCT	127	3	2	218	9		59	0	0	67	6	
1976**	JAN	63	26	1				30	24	1			
	FEB	88	30	5				53	8	5			
	MAR	113	76	4	1368	717		56	51	4	715	2	
	APR	185	66	26				103	38	10			
	MAY	226	80	31				130	43	20			
	JUN	274	58	17	649	125		152	42	21	308	24	
	JUL	315	39	14				173	35	16			
	AUG	342	18	3				190	67	33			
	SEP	357	16	7				223	29	21			
	OCT	363	13	9	868	193		234	12	8	358	26	
1976***	OCT	69	79	6				83	58	7			
	NOV	142	66	5				134	44	3			
	DEC	203	89	5	2564	987		175	87	8	1617	526	

*1974 settlement year class juveniles

**1975 settlement year class juveniles

***1976 settlement year class juveniles

1975 for age 1+ juveniles (which settled in 1974). From March to June 1976, the estimated population size for 1975 settlement year class lobsters declined by more than 50%. From June to October 1976, a slight increase in the population was projected.

Substantial mark-recapture data for early juveniles (within a few months of settlement) was obtained only for the 1976 year class. The size of this population was approximately 70% larger than that for the 1975 year class after one year of benthic life.

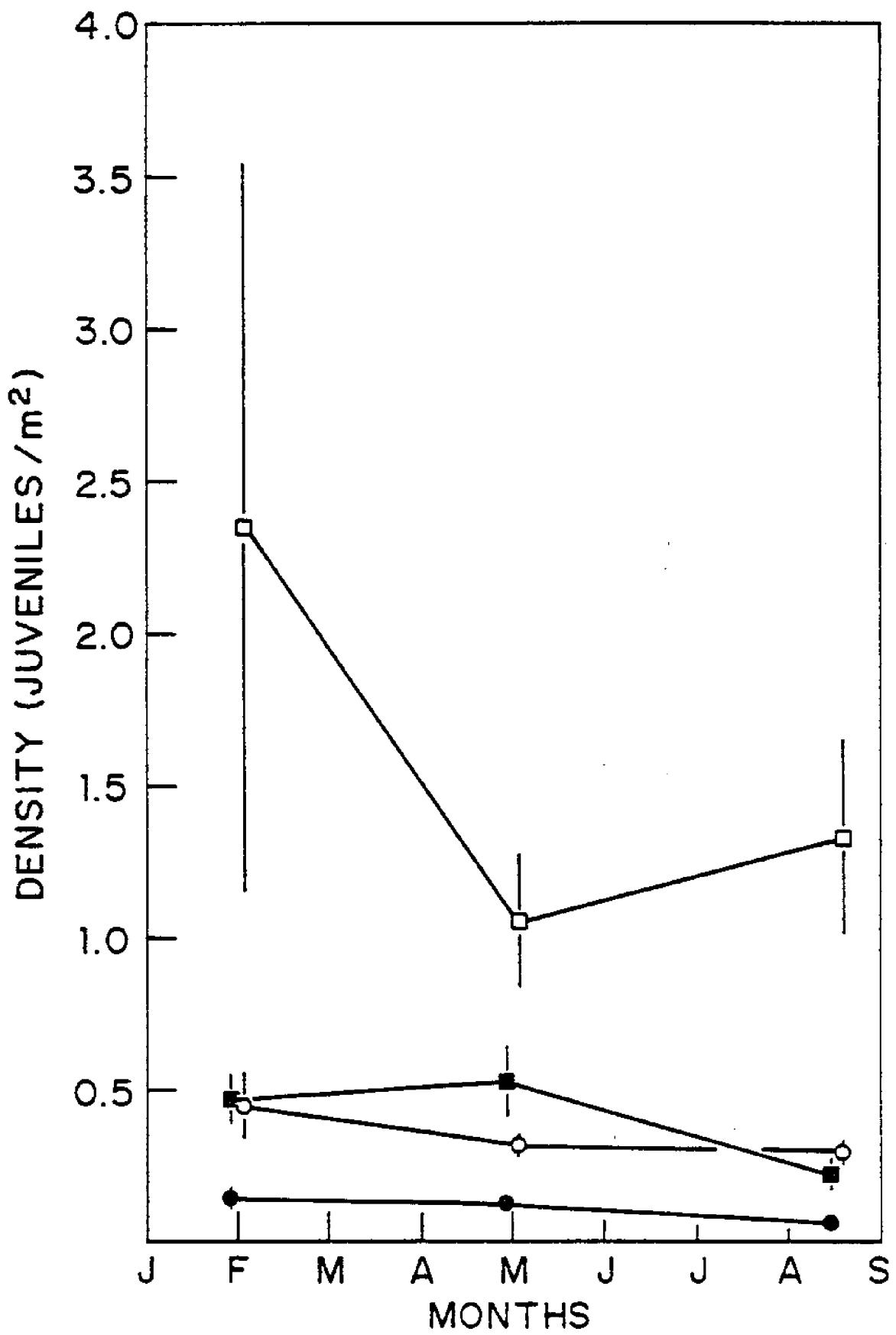
Population Density

Relative population estimates calculated from CPUE were converted to relative densities by dividing all estimates by 30 m^2 , the approximate area of surf grass habitat searched per diver-hour. Population estimates based on mark-recapture results were converted to densities by dividing all values by the areas of the two major surf grass beds (west of dike, 598 m^2 ; east of dike, 296 m^2).

Mark-recapture age 1+ juvenile densities in the two major grass beds never varied by more than 0.3 lobster/m^2 , so the data were combined. Mark-recapture juvenile density estimates were higher than CPUE estimates by averages of 0.2 and 1.2 lobsters/m^2 for the 1974 and 1975 year classes, respectively (Fig. 23). Relative density differences within and between year classes were similar to the relative abundance trends above. Mean densities for the 1976

Figure 23. Catch per diver-hour and mark-recapture population density estimates for two settlement year classes of age 1+ P. interruptus at Bird Rock. Vertical lines represent standard errors of three or four month means.

- = 1974 year class catch per diver-hour
- = 1974 year class mark-recapture
- = 1975 year class catch per diver-hour
- = 1975 year class mark-recapture



year class juveniles during the period October-December were 0.8 ± 0.1 and 4.9 ± 1.8 juveniles/ m^2 for CPUE and mark-recapture methods, respectively.

Aggregations

Divers crawling through the grass beds often caused lobsters to flee, thus making observations of natural density patterns difficult. Despite this problem, as search and capture techniques improved, it became apparent that the lobsters were not distributed uniformly throughout the Phyllospadix habitat. At least 29% of all age 1+ juveniles and 38% of all age 2+ juveniles were found in aggregations composed of 2-16 individuals. Small groups of 2-4 juveniles were most common, accounting for 92% of age 1+ groups and 87% of age 2+ groupings. Most of the aggregations were associated with microhabitats which provided shelter, such as crevices, solution pockets, or thick rhizome-sediment mats. However, aggregations of age 2+ juveniles with larger lobsters, not associated with specific shelters, were commonly encountered during August, September, and October.

Juvenile Activity Patterns

Den Residency

Most juvenile lobsters in the Phyllospadix beds at Bird Rock were found partially buried within the rhizome-sediment mat;

however, the few juveniles encountered at Isthmus Reef and Big Fisherman Cove were occupying narrow vertical bedrock crevices or small solution pockets. Five crevice dens containing individually identifiable 12-18 mm CL lobsters in the Big Fisherman Cove area were monitored for periods of four months (juveniles M5, N5, and O5), six months (juvenile CC), and seven months (juvenile P5) (Table 32). Juvenile P5 was present in its den on 65% of the observation dates between November 1974 and April 1975. On June 2, 1975, the den was occupied by an octopus, and so the monitoring study was terminated. Juvenile CC was present each time the den was checked over an eight-day period, then was never seen again. Juvenile M5 occupied the same den off and on for 72 days, then disappeared. Juveniles N5 and O5 occupied their crevices for 13 days and 29 days, respectively, before the television camera and light apparatus were fixed above them (see below). Subsequently, both left and never returned.

Diel Activity Rhythms

Most of the juvenile lobsters encountered during surf grass survey dives at Bird Rock were inactive during daylight hours. Those few which were found walking on the rhizome-sediment mat may have been disturbed by the diver search efforts. Night surveys proved to be difficult because of the limitations of hand-held lights in the dense,

TABLE 32.--Temporal den residency patterns for five juvenile P. interruptus in the Big Fisherman Cove area, Santa Catalina Island

Year	Date	JUVENILE				
		P5	CC	M5	N5	O5
1974	11- 2	+				
	11- 6	+				
	11- 7	+				
	11-15	-*				
	11-28	+	+			
	11-29	+	+			
	12- 3	+	+			
	12- 5	+	+			
	12- 9	-	-			
	12-10	-	-			
1975	1- 8	+	-			
	1-21	-	-			
	1-29	-**	-	+	+	+
	2- 5***	+	-	+	+	+
	2-11	-	-	-	+	+
	2-19	-	-	-	-	+
	2-22	+	-	-	-	-
	2-27	-	-	+	-	+
	3-15	+	-	+	-	-
	4-11	+	-	+	-	-
	4-20	+	-	-	-	-
	5- 4	-	-	-	-	-
	6- 2	-	-	-	-	-

*Night dive; P5 found foraging 3 m away from crevice.

**P5 discovered in a different crevice 1 m away from den.

***P5, M5, N5, and O5 captured, marked, and returned to dens.

+= Present

-= Absent

continuously swaying Phyllospadix. Nevertheless, nearly all juveniles found at night were moving actively. Along the deeper edge of the grass beds, larger age 1+ and age 2+ lobsters often were seen foraging in the adjacent coralline algae habitat by combing through the tufts of calcareous algae with their pereopods.

Observations of the diel activity rhythms of juveniles raised in laboratory aquaria equipped with timer-controlled lights agreed with the above field observations, except that the lab juveniles would search actively for and consume food placed in the aquaria at any time of the day or night.

Remote underwater television monitoring of the diel activity patterns of juvenile N5 was begun at 1315 hours on February 11, 1975. At 1337 hours, N5 left the crevice and did not return until 2030 hours. At 0230 hours the following morning, N5 again left the den. Monitoring was continued for two days until a storm occurred, but N5 had not returned. At 1330 hours on February 27, monitoring of juvenile O5 was begun. Juvenile O5 occupied the den until 2030 hours, at which time it emerged from the crevice and walked away. The den remained empty for the following twelve days. Since both juveniles had been occupying the same dens faithfully before the television study (see Table 32), I suspect that some disturbance created by the installation of the underwater camera

caused the juveniles to leave the area and, therefore, the study was terminated.

Home Range

Of 430 recaptures of individually marked juveniles at Bird Rock, 88% were recovered from the same general surf grass areas where originally captured (beds west of dike or east of dike; see Fig. 7). Small juveniles rarely were captured outside the Phyllospadix habitat, but 31% of the large juveniles recaptured were found in other habitats (Table 33). Eighty-one percent of the latter were caught at night foraging 2 to 140 m away from the nearest Phyllospadix beds, in depths ranging from 1 to 16 m. Compared to small juveniles, fewer large individuals that were recaptured in the same grass beds as originally captured had intercapture intervals longer than two months (Table 33).

Additional capture-recapture evidence for the relatively small home ranges of age 1+ juveniles came from 13 survey dives within a 25 m² isolated patch of Phyllospadix located 85 m west of the dike at Bird Rock (see Fig. 7), and from 14 dives in the 81 m² patch of Halidrys at Isthmus Reef. Between January and August 1975, four of the 11 juveniles marked and released in the isolated patch of Phyllospadix were recaptured once, two others were recaptured twice, and another was recaptured three times (see

TABLE 33. -- Net movement patterns and relative home ranges for two size classes of juvenile *P. interruptus* at Bird Rock, Santa Catalina Island, determined from capture and recapture location data

Size Range (mm CL)	#	Recap.	Non-surf Opposite Grass Bed Recap.	% Opposite Grass Bed Recap.	Same Grass Bed Recap.	% of "Same Grass Bed Recap." ¹ at Different Intercap. Intervals			
						0-2	2-4	4-6	>6
<30	342	1		5	94	35	38	17	10
30- 60	88	31		8	61	60	19	13	8

Recap. = total number of recaptures of marked juveniles.

% Non-surf Grass Recap. = percentage of total recaptures that were not recaptured within the Phyllospadix habitat.

% Opposite Grass Bed Recap. = percentage of total recaptures that were recaptured in surf grass beds on the opposite side of the dike from which they were originally captured.

% Same Grass Bed Recap. = percentage of total recaptures that were recaptured in surf grass beds on the same side of the dike as originally captured.

Appendix III). From January to November 1975, four of the 21 marked individuals at Isthmus Reef were recaptured one or more times (see Appendix III).

Seasonal Movement Patterns

Analysis of size-frequency, CPUE, mark-recapture, and home range data indicated that juvenile home range expanded with increasing lobster size, resulting in gradual dispersion of age 1+ individuals from the Phyllospadix habitat beginning in April and May (Figs. 9, 22, 23; Tables 31, 33). During June, July, and August, increasingly frequent observations of brown or brown red juveniles (see Table 9), including a few marked ones, suggested that some lobsters were periodically leaving and returning to the surf grass beds. During the period September-November, rapid decreases in the relative frequency of captures (Fig. 9) and the CPUE (Fig. 22) of now age 2+ juveniles (to the point where large individuals rarely were encountered during surf grass survey dives) indicated that these lobsters were leaving the Phyllospadix habitats.

On September 21, 1976, an aggregation of 50-100 lobsters, including numerous age 2+ and age 3+ juveniles, was discovered 70 m north of the Halidrys habitat at Isthmus Reef in a large crevice in 16 m of water. Five subsequent dives in 1976, and several dives in 1977 and 1978, documented the presence of variable numbers of

large juveniles and adults in this crevice during the day. Only a few lobsters occupied the crevice at night; most were encountered 1-10 m away, foraging under the low canopy created by the brown kelps Agarum fimbriatum, Laminaria farlowii, and Eisenia arborea.

On December 8, 1976, several aggregations of large juveniles and adults were encountered in a boulder pile in 27-30 m of water at the base of the vertical wall 60 m east of the dike at Bird Rock (see Fig. 7). Several marked juveniles were seen and one (O20) was captured. On six subsequent dives in this area during December, age 2+ juveniles were commonly seen, but I was able to collect only one marked (W32) and one unmarked juvenile using two small-mesh lobster traps. Also in December, at the west end of Bird Rock, three age 2+ juveniles were found foraging in the brown alga Cystoseira sp. in 12-18 m of water at night. One of these was a recapture (X29) which had moved at least 260 m from the surf grass beds east of the dike when last captured on July 3, 1976.

Age 2+ juveniles again were encountered (but rarely captured) in the Phyllospadix, Halidrys, Eisenia, and Mytilus habitats at Bird Rock during May-August, coincident with the occurrence of adult lobsters in these shallow areas.

Juvenile Food Habits

Of 200 P. interruptus (198 juveniles and 2 adults) held for fecal content analysis, 37 produced little or no fecal material. Examination of the feces of the other 163 lobsters revealed unrecognizable debris (averaging approximately 40% of each sample), as well as undigested or partially digested remains representing a variety of prey taxa (Table 34). Most food items were identifiable only to major group, but the majority of mollusk material was identifiable to genus by means of shell fragment or operculum characteristics (Table 35).

Mollusk shell bits were the most important items represented in the feces of 150 small juveniles captured in surf grass beds at Bird Rock, followed by calcified segments (intergenicula) of coralline algae, and to a lesser extent, egg membranes of the spotted kelpfish Gibbonsia elegans (Clinidae), segments of crustacean exoskeletons, foraminiferan tests, and fragments of Phyllospadix (Table 36a). The most important mollusks ingested were 1-2 mm Amphithalamus, followed by 1-5 mm Halodakra, Tricolia, and Bittium (Table 36b).

Major emphasis was placed on characterizing the food habits of lobsters from the Phyllospadix habitat; however, seven

TABLE 34.--Major groups of organisms represented in the fecal material of juvenile P. interruptus from Santa Catalina Island. Predominant items are shown in parentheses after each phylum

Rhodophyta (coralline algae)	Arthropoda (exoskeletons)
Tracheophyta (surf grass)	Pycnogonida
Protozoa (foraminiferans)	Crustacea
Porifera (spicules)	Ostracoda
Annelida (worm tubes)	Copepoda
Mollusca (shell bits)	Cirripedia
Gastropoda	Cumacea
Pelecypoda	Tanaidacea
Polyplacophora	Isopoda
Ectoprocta (zooecia)	Amphipoda
Echinodermata (ossicles)	Decapoda
Chordata (clinid eggs)	

TABLE 35. --Identifiable mollusk genera in the fecal material of juvenile P. interruptus from Santa Catalina Island

	Life Stage	Adult Size (mm)*
Class Gastropoda		
<u>Alvinia</u> (+ <u>Merelina</u>)	J, A	1-3
<u>Amphithalamus</u>	J, A	1
<u>Barleeia</u>	J, A	2-3
<u>Bittium</u>	J, A	7-12
<u>Caecum</u>	J, A	2-6
<u>Calliostoma</u>	J	8-35
<u>Collisella</u>	J	8-40
<u>Crepidula</u>	J, A	15-40
<u>Cystiscus</u>	J, A	3-6
<u>Fissurella</u>	J	20-35
<u>Littorina</u>	J	8-18
<u>Mitrella</u> (+ <u>Alia</u>)	J, A	3-11
<u>Nassarina</u>	J, A	5
<u>Norrisia</u>	J	45-55
<u>Parviturbo</u>	J, A	3
<u>Serpulorbis</u>	J	6-9 (diam)
<u>Tricolia</u>	J, A	2-11
<u>Volvarina</u>	J, A	7-10
Class Pelecypoda		
<u>Glans</u>	J, A	7-10
<u>Halodakra</u>	J, A	2-3
<u>Hiatella</u>	J	15-25
<u>Lasaea</u>	J, A	2
<u>Leptopecten</u>	J	10-30
<u>Mytilus</u>	J	70-130
<u>Philobrya</u>	J, A	5-6
Class Polyplacophora		
<u>Callistochiton</u>	J	10-30

*After McLean (1978).

J = Juvenile

A = Adult

TABLE 16. - Frequencies of occurrence, mean percent abundances, and relative importance values for major groups of organisms and major mollusk genera found in the fecal material of *L. littoralis* from three different habitats.

a. Major groups		150 Lobsters (12-28 mm CL)			7 Lobsters (13-32 mm CL)			3 Lobsters (56-84 mm CL)				
		from the Bird Rock Phyllopondix Habitat			from the Isthmus Reef Habitat			from the Isthmus Macrocystis Habitat				
Group		Freq.	Abln.	Impo.	Freq.	Abln.	Impo.	Freq.	Abln.	Impo.	Rank	
		%	%		%	%		%	%			
Mollusks		0.973	29.4	29.6	1	0.373	31.4	17.9	2	1.000	79.7	1
Coralline Algae		0.813	19.0	15.4	2	0.143	0.1	0.01	5	0.667	0.7	5
Crab/Eggs		0.267	6.3	1.7	3	0	0	0	0	0	0	-
Crustaceans		0.287	3.2	0.9	4	1.00	32.3	32.3	1	1.000	9.0	2
Foraminiferans		0.019	0.9	0.0	5	0.429	0.4	0.2	3	1.000	0.7	4
Sand Grains		0.227	1.2	0.3	6	0	0	0	0	0	0	-
Heterozoa		0.213	0.3	0.1	7	0.286	0.4	0.1	4	0.333	0.3	3
Exchocoenont		0.127	0.2	0.03	8	0.246	0.3	0.1	4	0	0	-
Spores		0.067	0.2	0.01	9	0.13	0.7	0.1	4	0.333	0.3	1
Polyellidaea		0.053	0.1	0.005	10	0	0	0	2	1.000	1.3	3

b. Major mollusk genera		150 Lobsters (12-28 mm CL)			7 Lobsters (13-32 mm CL)			3 Lobsters (56-84 mm CL)					
		from the Bird Rock Phyllopondix Habitat			from the Isthmus Reef Habitat			from the Isthmus Macrocystis Habitat					
Genus		Freq.	Abln.	Impo.	Freq.	Abln.	Impo.	Freq.	Abln.	Impo.	Rank		
		%	%		%	%		%	%				
<u>Anoplithaerus</u>		0.640	6.0	1	0	0	0	-	0.8	0.3	0	-	
<u>Hedistidium</u>		0.553	3.5	1.9	2	0	0	-	0	0	0	-	
<u>Triticella</u>		0.420	3.0	1.3	3	0	0	-	0.667	22.0	14.7	2	
<u>Hittia</u>		0.406	2.4	1.1	4	0	0	-	0	0	0	-	
<u>Fasciolaria</u>		0.278	1.9	0.5	5	0	0	-	0	0	0	-	
<u>Norfolkia</u>		0.246	1.1	0.3	6	0	0	-	0.333	0.7	0.2	5	
<u>Ceramus</u>		0.207	1.0	0.2	7	0	0	-	0	0	0	-	
<u>Nassarius</u>		0.207	0.0	0.2	7	0	0	-	0.333	0.7	0.2	5	
<u>Callianassa</u>		0.120	0.7	0.1	8	0	0	-	0.667	3.7	2.5	4	
<u>Pisidium</u>		0.080	0.7	0.1	8	0	0	-	0.667	3.7	2.5	4	
<u>Mytilus</u>		0.073	0.9	0.1	8	0.246	0.4	2.5	2	0.333	17.0	5.7	3
<u>Nucella</u>		0	0	0	7	0.571	20.7	11.9	1	0	0	-	
<u>Cerithidea</u>		0.040	0.1	0.004	9	0	0	-	0.667	20.3	10.5	1	

Data taken from operculum counts because the shell bits of the two genera were indistinguishable.

Freq. = Frequency of occurrence among fecal samples.

% Abln. = Mean percent abundance (% visual biomass) within fecal samples.

Impo. = Importance value (frequency of occurrence X mean percent abundance).

individuals from the Halidrys habitat at Isthmus Reef and three larger lobsters from the CMSC sea water intake Macrocystis habitat were analyzed for comparative purposes (Table 36). Mollusks and crustaceans were the most important food items for these non-surf grass habitats. Juvenile bivalves of the genera Hiatella and Mytilus were the major mollusks consumed in the Halidrys habitat, and adult gastropods of the genera Crepidula and Tricolia were most important for the Macrocystis habitat lobsters.

Phyllospadix habitat fecal content results were analyzed for three size classes of juveniles, although few large individuals were captured (Table 37). Major groups of prey items were consumed in approximately the same proportions for all size classes. Mollusks less than 1-3 mm maximum size as adults (see Table 35), such as Amphithalamus, and to a lesser extent Halodakra, Barleeia, and Caecum, were most important in the diet of the smallest juveniles. The same trend is apparent in Table 38, which shows the importance values of gastropod opercula for the three size classes. Operculum counts revealed that one 17.5 mm CL lobster (Q3) had consumed at least 98 Amphithalamus, 11 Caecum, 2 Bittium, and 1 Barleeia (representing 39% of the feces). In addition, juvenile Q3 produced shell fragments from Mytilus, Halodakra, Tricolia, Callistochiton, and Crepidula (representing 32% of the feces) in the same sample.

TABLE 37.—Percents of occurrence, mean percent abundances, and relative importance values for major groups of organisms and major mollusk genera found in the fecal material of three size classes of juvenile *P. interruptus* from the Bird Rock *Phyllospadix* habitat.

a. Major groups		107 Small Juveniles (12-19 mm CL)			43 Medium Juveniles (20-28 mm CL)			3 Large Juveniles (41-46 mm CL)				
Group	Freq.	Abun.	Impo.	Rank	Freq.	Abun.	Impo.	Rank	Freq.	Abun.	Impo.	Rank
Mollusks	0.963	30.0	28.9	1	1.000	26.1	20.1	1	1.000	15.0	15.0	1
Coralline Algae	0.794	20.1	16.0	2	0.860	16.4	14.1	2	1.000	3.0	3.0	3
Clad Egg's	0.271	6.1	1.6	3	0.256	6.7	1.7	4	0.333	13.3	4.4	2
Foramoliferans	0.889	0.9	0.8	4	0.889	0.9	0.8	5	1.000	1.0	1.0	4
Crustaceans	0.234	1.6	0.4	5	0.419	6.9	2.9	3	0.333	1.7	0.6	6
Surf Grass	0.243	1.3	0.3	6	0.186	1.0	0.2	6	0.333	2.3	0.0	5
Hydrozoans	0.215	0.3	0.1	7	0.209	0.3	0.1	7	0.333	0.3	0.1	8
Echinoderms	0.112	0.1	0.01	8	0.163	0.3	0.05	8	0	0	0	-
Sponges	0.056	0.2	0.01	9	0.093	0.1	0.01	9	0.333	0.3	0.1	6
Polychaetes	0.037	0.1	0.004	10	0.093	0.1	0.01	9	0.333	0.7	0.2	7

b. Major mollusk genera		107 Small Juveniles (12-19 mm CL)			43 Medium Juveniles (20-28 mm CL)			3 Large Juveniles (41-46 mm CL)				
Genus	Freq.	Abun.	Impo.	Rank	Freq.	Abun.	Impo.	Rank	Freq.	Abun.	Impo.	Rank
<u>Amphithalamus</u>	0.731*	11.9*	6.7	1	0.444*	1.3*	0.6	6	0*	0*	0*	-
<u>Intodakra</u>	0.617	3.6	2.2	2	0.395	3.1	1.2	2	0	0	0	-
<u>Bilium</u>	0.495	2.4	1.2	3	0.395	2.4	1.0	3	0.333	0.7	0.2	4
<u>Tricolla</u>	0.420	2.0	1.2	3	0.442	3.1	1.4	1	0.667	1.3	0.0	2
<u>Barleefia</u>	0.315*	2.1*	0.7	4	0.178*	1.3*	0.2	9	0*	0*	0	-
<u>Caeclum</u>	0.234	1.2	0.3	5	0.140	0.5	0.1	10	0	0	0	-
<u>Norrisia</u>	0.196	0.9	0.2	6	0.372	1.8	0.7	5	0.333	0.3	0.1	5
<u>Nassaria</u>	0.140	0.4	0.1	7	0.372	2.1	0.8	4	0.667	0.7	0.5	3
<u>Callistochiton</u>	0.075	0.2	0.02	8	0.232	1.6	0.4	8	0.333	6.7	2.2	1
<u>Fissurella</u>	0.037	0.2	0.01	9	0.106	1.9	0.4	6	0	0	0	-
<u>Mytilus</u>	0.028	0.2	0.01	9	0.106	2.5	0.6	7	0	0	0	-

*Data taken from operculum counts because the shell bits of the two genera were indistinguishable.

Freq. = Frequency of occurrence among fecal samples.

% Abun. = Mean percent abundance (% visual biomass) within fecal samples.

Impo. = Importance value (frequency of occurrence X mean percent abundance).

TABLE 38.--Frequencies of occurrence, mean numbers, and relative importance values for the opercula of major mollusk genera found in the fecal material of three size classes of juvenile *P. interruptus* from the Bird Rock Phyllospadix habitat.

Genus	Freq.	# of Opercula	Impo.	Rank	43 Medium Juveniles (20-28 mm CL)			3 Large Juveniles (41-46 mm CL)				
					Freq.	# of Opercula	Impo.	Rank	Freq.	# of Opercula	Impo.	Rank
<u>Amphithalamus</u>	0.731	8	6	6.3	1	0.444	1.8	0.8	1	0	0	-
<u>Berleseia</u>	0.315	1	5	0.5	2	0.178	0.9	0.2	3	0	0	-
<u>Bitium</u>	0.315	0	7	0.2	3	0.333	1.0	0.3	2	0.333	0.3	0.1
<u>Caecum</u>	0.194	0	5	0.1	4	0.111	0.3	0.03	5	0	0	-
<u>Tricolla</u>	0.222	0	6	0.1	4	0.222	0.8	0.2	3	0.667	0.7	0.5
<u>Norrlisia</u>	0.194	0	3	0.1	4	0.267	0.4	0.1	4	0	0	-
<u>Alvinia</u>	0.157	0	2	0.03	5	0.133	0.1	0.01	6	0	0	-
<u>Nassarina</u>	0.092	0	2	0.02	6	0.200	0.4	0.1	4	0	0	-

Freq. = Frequency of occurrence among fecal samples.

of Opercula = Mean number of opercula within fecal samples.

Impo. = Importance value (frequency of occurrence X mean number of opercula).

All of the above prey items presumably were consumed within one foraging period.

Juvenile Mortality

Mortality of Laboratory-Raised Juveniles

Loss of 51 puerulus larvae and juveniles held in aquaria during a two-year period resulted from the following conditions: sea water system malfunctions (20%), handling shock (8%), cannibalism (8%), ecdysis complications (6%), accidental fish predation (4%), and unknown causes (55%). The suspected cause of mortality during sea water system breakdowns was low oxygen concentration, since intermolt juveniles in aerated aquaria survived despite exposure to water temperatures as high as 25°C.

Small juveniles were most susceptible to shock from air exposure and handling while being measured and marked. Juveniles typically remained "stunned" for 15 seconds when returned to sea water after 90-second air exposures. Most individuals recovered quickly, but four small juveniles autotomized appendages and died.

Three lab juveniles died midway through ecdysis, and two others were eaten when a mussel blenny, Hypsoblennius jenkinsi, accidentally was introduced into a culture tank. Most of the unexplained mortality was reflected in the disappearance of small

juveniles. Although cannibalism may have accounted for some of this loss, documented cannibalism occurred only when juveniles molted in a tank in which lobster density was temporarily high and little shelter was available, or when temperatures rose above 23°C during sea water system breakdowns.

CPUE and Mark-Recapture Mortality Trends

Field observations indicated that mortality was high in age 1+ juveniles, and that it was inversely proportional to lobster size, but these observations could not be quantified accurately by CPUE or mark-recapture techniques because of the combined effects of recruitment, differential catchability, and migrations. Declines in CPUE and mark-recapture abundance estimates which occurred after recruitment ceased (and despite increased catchability of medium-sized juveniles) probably reflect some emigration (see above), but mostly reflect high mortality (Fig. 22; Table 31).

Predation

Eighteen species of fishes and two species of invertebrates representing potential predators of juvenile P. interruptus were encountered during 124 survey dives in the Phyllospadix habitat at Bird Rock (Table 39). Three benthic macro-carnivores, Scorpaena guttata, Scorpaenichthys marmoratus, and Octopus bimaculatus,

TABLE 39. -- Frequency of occurrence and typical size of potential predators of juvenile *P. interruptus* encountered during survey dives in the *Phyllospadix* habitat at Bird Rock (documented records of predation on juvenile and adult lobsters from this and other studies are presented)

Scientific Name	Common Name	Size at Bird Rock (cm SL)	Freq. at Bird Rock (%)			Documented Predation Adult Lobster	Documented Predation Juvenile Lobster
			AI	LI	Tr		
<i>Panulirus interruptus</i>	California Spiny Lobster	7.5*	100			TS (Lab)	
<i>Gibbonsia elegans</i>	Spotted Kelpfish	12	100			TS	
<i>Scorpaenichthys guttatus</i>	Sculpin	10-30	60	1A, 1A,		TS	
<i>Scorpaenichthys marinaratus</i>	Cabezon	33	31				
<i>Octopus bimaculatus</i>	Twospot Octopus	35**	16	AI, LI, Tr		TS (Lab)	
<i>Oxyjella californica</i>	Señorita	16	12				
<i>Artedius coralliculus</i>	Coralline Sculpin	10	10			TS (Lab)	
<i>Paracanths integrifinis</i>	Reef Flinspot	6	9				
<i>Embletoeca jacksoni</i>	Black Surfperch	10	8				
<i>Hypsoblennius Jenkinsi</i>	Mussel Blenny	9	8			Co	
<i>Parahabrax californicus</i>	Kelp Bass	30	5	1A,		TS (Lab)	
<i>Damalichthys vaccinus</i>	Pile Surfperch	13	4			Co, Tr	
<i>Girella nigricans</i>	Opal Eye	25	4				
<i>Heterostichus rostratus</i>	Grant Kelpfish	31	4				
<i>Sebastodes atriventris</i>	Kelp Rockfish	30	3				
<i>Heterodontus francisci</i>	Horn Shark	75	2				
<i>Placelometopon pilchrum</i>	California Sheephead	28	2				
<i>Pleuronichthys coenosus</i>	C-O Turbot	22	2				
<i>Rhaeocochilus toxotes</i>	Rubberlip Surfperch	20	2				
<i>Schistes radiatus</i>	Grass Rockfish	41	2				
<i>Gymnothorax mordax</i>	California Moray	-	0	AI, LI			

*cm CL for typical adults present during warm water months

**cm total length

SL = Standard Length

Freq. = Frequency of occurrence among 124 *Phyllospadix* habitat dives at Bird Rock

(Lab) = Predation documented in laboratory aquaria only

AI = Allen (1916)

Co = Coyer (Personal Communication)

LI = Lindberg (1955)

Tr = Tricas (Personal Communication)

TS = This Study

all of which are known to prey on lobsters (Lindberg, 1955; Winget, 1968), frequently were found resting on or foraging along the surf grass rhizome-sediment mat. Typical daytime densities, based on encounters per diver-hour, were $0.1/m^2$, $0.01/m^2$, and $0.008/m^2$, respectively.

Stomach contents flushed from a live Scorpaena (23 cm standard length) captured in the surf grass habitat consisted of one majid crab (22 mm carapace width) and one xanthid crab (15 mm carapace width). On two occasions, during Bird Rock survey dives, inactive juvenile lobsters caused to flee by my search efforts were eaten immediately by nearby Scorpaena. Stomach contents flushed from four Scorpaenichthys ranging in size from 30 to 38 cm standard length (SL) contained the following: four crabs, three caridean shrimps, one juvenile lobster, two octopuses, one abalone, and one fish. One Scorpaenichthys, captured and tagged on December 3, 1974, was recaptured on January 16, 1976 in the same location.

Octopuses were not observed preying on juvenile lobsters in the field; however, they readily captured small juveniles when both were placed in aquaria containing no shelters. Small juveniles reacted to contact with a live or dead octopus by rapidly tail-flipping away, but juveniles larger than 30 mm CL usually charged forward, thrust their finely serrate antennae at the octopus, and

rasped them back and forth across its body until the octopus retreated. If several large juveniles were present, they prodded and rasped in unison. If the octopus began attaching its tentacular suckers to the lobsters, they would stridulate and tail-flip away, then initiate exploratory movements until contact again was made with the octopus. On two occasions in the field, I watched the above "offensive" behavior by adult lobsters successfully drive octopus away from lobster dens. On the other hand, a healthy 85 mm CL lobster was seen at midday vigorously struggling in the grip of a large octopus (T. Tricas, personal communication). The octopus nearly killed the lobster before it was chased away by the divers.

Other records of predation on juvenile P. interruptus include the following:

1. on two occasions, the spotted kelpfish Gibbonsia elegans attacked and killed small juveniles (< 10 mm CL) that were "flushed out" during surf grass surveys.
2. the cephalothorax of a small juvenile was found in the mouth of a 16 cm SL sheephead (Pimelometopon pulchrum) gill-netted from Bird Rock on August 22, 1976.
3. a 16 mm CL lobster was found in the gut of a grass rockfish (Sebastes rastrelliger) captured on January 17, 1976, near the CMSC sea water intake pipes in 5 m of water (T. Tricas, personal communication).

4. the gut of a 21 cm SL kelp bass (Paralabrax clathratus) speared on October 21, 1976, in Big Fisherman Cove contained a 12 mm CL lobster (J. Coyer, personal communication).
5. the gut of a 47 cm SL Paralabrax speared 5 km east of Bird Rock on April 6, 1977, contained an intact 57 mm CL lobster (T. Tricas, personal communication).
6. eight postsettlement puerulus larvae were found in the guts of five large black surfperch (Embiotica jacksoni) (avg size = 22 cm SL) collected from Santa Barbara and Santa Cruz Islands during July and August 1977 (J. Coyer, personal communication).

DISCUSSION

Puerulus Recruitment

No Panulirus interruptus pueruli were captured using floating Phyllospadix habitat traps and few were collected by night-lighting at Catalina Island, yet the presence of recently settled juveniles at Bird Rock confirmed the fact that recruitment was occurring. Also, during part of the same "settlement season," pueruli frequently were captured by night-lighting at the Marineland pier. Mean CPUE for August and September, 1975, at the Marineland pier (1.4 larvae/h) was similar (considering the large nightly variability) to mean CPUE for night-light collections during August and September of the years 1969-1971 at the Scripps Institution pier in La Jolla (2.3 larvae/h) by Parker (1972) and Serfling and Ford (1975a). The latter investigators also collected pueruli using floating Phyllospadix habitat traps at the Scripps pier, but similar traps anchored in water 3 to 15 m deep off Point Loma, San Diego, and at Big Fisherman Cove (Santa Catalina Island) during August and September, 1969, failed to catch any pueruli. Trap failure was thought to be due to the presence of large quantities of floating surf grass and algae in these areas, but no pueruli were found associated

with these drifting plants (Serfling and Ford, 1975a).

The Marineland pier and the Scripps pier are situated on the open mainland coast, where surf-washed sand plains are the most common inshore habitats. Although Marineland is located on the rocky Palos Verdes Peninsula, both the Marineland pier and the Scripps pier are surrounded by sand, with patchy kelp-rock reefs located 100-500 m away. Since sand habitats are unsuitable for *puerulus* settlement (Parker, 1972), more swimming (unsettled) *pueruli* may be present in these areas than at Santa Catalina Island, where the larvae could settle immediately in the dense rocky habitat vegetation covering nearly all shallow subtidal regions.

For the years 1976-1977, the settling season determined from night-light captures (June-October; Table 3) fit within the broader season extrapolated from the captures of recently settled juveniles at Bird Rock (May-December; Table 5). Parker (1972) and Serfling and Ford (1975a) documented the presence of P. interruptus *pueruli* in nearshore waters from May to October for the years 1969-1971. Both their findings and results from this study show that peak recruitment occurs during July, August, and September. This period corresponds to the season of highest water temperature in southern California (Fig. 4).

Since the growth rate of juvenile P. interruptus varies directly with temperature (Table 27), lobsters settling during

the warmest water periods will grow the fastest, thus minimizing the time spent in small-sized instars which apparently are subject to high mortality (see p. 207). Of course, other factors may affect the seasonal pattern of larval recruitment. For example, settling periods may reflect the timing of egg hatching or the duration of larval life, either of which could be adapted to patterns of food availability, predator abundance, and water currents necessary for returning larvae to nearshore areas.

Panulirus japonicus from Japan and P. longipes cygnus from western Australia, two subtropical species considered to be in the same evolutionary group as P. interruptus (George and Main, 1967), recruit during warm water seasons. Like P. interruptus, the pueruli of P. japonicus are most common in nearshore waters from July to October (Nakamura, 1940; Okada and Kubo, 1948; Harada, 1957). Peak periods of P. longipes cygnus settlement on rope tassel collectors occurred between September and January, coincident with rising water temperatures in the southern hemisphere (Chittleborough and Phillips, 1975; Phillips and Hall, 1978). In addition, pueruli of the rock lobster Jasus lalandii from South Africa are netted in greatest quantities from December to April (Pollock, 1973).

Recruitment in two other palinurids does not correspond to warm water seasons. Little (1977) summarized data from various

recruitment studies of the tropical lobster P. argus. Pueruli (called postlarvae) were collected throughout the year, with recruitment peaks generally more frequent during spring and fall. Pueruli of the rock lobster J. novaehollandiae in southern Australia settled on pallet collectors in greater numbers during periods of low water temperatures and low salinities (Lewis, 1978).

Results from the paired habitat-choice experiments conducted in this study and by Parker (1972) (see Table 7) demonstrate that P. interruptus pueruli can discriminate between different habitat materials and that they preferred Phyllospadix over all other plants (and rubble rock) tested, except for the feathery red algae Plocamium. Since freshly captured pueruli exhibited persistent clinging and contact-oriented behavior, reticulate or matted plants providing extensive surface area for body contact and grasping may be preferred for settlement. Other characteristics of the plants may or may not be important; monofilament nylon webbing and synthetic rope tassels are acceptable substrates for the settlement of P. argus (Witham et al., 1968) and P. longipes cygnus (Phillips, 1972), respectively, but Serfling and Ford (1975a) found that P. interruptus settled in significantly higher numbers in floating Phyllospadix/red algae habitat traps than in Witham nylon webbing collectors.

Selection of matted plants, such as Phyllospadix, for settlement by P. interruptus larvae not only would allow the clinging pueruli to remain in place despite inshore water currents and turbulence, but also would conceal the inactive larvae from visual predators during the period of time between settlement and metamorphosis. The presence of post-settlement pueruli in the guts of black surfperch (Embiotoca jacksoni) provides evidence that predation of small lobsters by epibenthic carnivores does occur (J. Coyer, personal communication).

Early Juvenile Habitats

Scuba surveys conducted throughout southern and Baja California during this study have confirmed the initial observations of Parker (1972) and Serfling (1972) that small juvenile Panulirus interruptus are consistently found in the shallowest (0-4 m) subtidal rocky habitats covered with surf grass or various algae. Lack of familiarity with this narrow surf-swept zone, the cryptic behavior of juveniles, and the inability to trap them explain why previous investigators, such as Lindberg (1955), could not locate small lobsters (and thus mistakenly believed that juveniles lived in deep water).

My inability to find juveniles during many of the survey dives (Table 8) does not necessarily mean that they were absent.

Considerable survey experience was required before an adequate "search image" could be formed for the well-camouflaged juveniles. In addition, surveys were less meticulous when strong surge and poor visibility conditions prevailed. Nevertheless, whenever thorough habitat searches were possible at any survey locality, more small juveniles were encountered per diver-hour in Phyllospadix beds than in any other habitat.

Substrate-choice behavior of recently metamorphosed juveniles indicated significant preferences for Phyllospadix over rubble rock and Macrocystis, but no preference between Phyllospadix and Halidrys (Table 10). Survey dives at Isthmus Reef and at the San Benitos Islands revealed juvenile lobsters inhabiting crevices within thick beds of Halidrys (Table 8). At Bird Rock, age 2+ juveniles were observed moving freely back and forth between the Phyllospadix and the Halidrys habitats (Fig. 7). In additional laboratory tests, tufts of Plocamium were preferred over surf grass; however, Parker (1972) reported opposite results using unspecified red algae. The overall pattern of habitat choice for small juveniles was similar to that of pueruli; both sets of results suggest that structural cues are important in habitat selection.

Within shallow water plant/rock habitats, juvenile P. interruptus were associated with certain physical microhabitats,

including narrow bedrock crevices, sedimentary rock solution pockets, and surf grass rhizome-sediment mats. Behavioral observations indicated that active juveniles became inactive when maximal contact between body (especially the abdomen) and substrate was established. Parker (1972) evaluated juvenile shelter selection in the same manner as the substrate-choice tests; small lobsters preferred long shelters (20 cm) over short shelters (10 cm), and shelters with a single entrance over those with a second rear opening. Juveniles occupying such shelters not only would be protected from the effects of wave action, but also would be effectively hidden from visual predators. Should discovery occur, the lobster could retreat to the rear of the den, while warding off the attacker with its antennae. Juveniles buried in loose sediment do not have the protective advantages of a den, but they can escape by "tail-flipping" through the grass thicket.

Characterization of the habitat occupied by age 1+ P. inter-
ruptus during this study provides additional data for the growing list of palinurid species known to settle and live for some period of time in shallow subtidal "nursery" habitats (Table 40). These habitats have particular physical formations, plant associations, or animal assemblages that provide numerous microhabitats suitable for sheltering juvenile lobsters. Examples of microhabitats occupied by those species listed in Table 40 include ledges, crevices,

TABLE 40. --Habitat characteristics reported for the early juvenile stage of various Palinurid species

Species	Location	Depth (m)	Substrate	Vegetation	Reference
<i>J. edwardsii</i>	New Zealand	<1	Boulders	Low Algal Turf	Kensler, 1967
<i>J. Islandii</i>	South Africa	<5	Concrete Blocks	Low Algal Turf	Heydorn, 1963b; Pollock, 1973
<i>J. novachollandiae</i>	S. Australia	<2	Rocks, Caves	Sea Grass, Algal Turf	Lewis, 1978
<i>P. argus</i>	Brazil	4	Sand, Mud	Sea Grass, Erect Algae	Costa et al., 1969
" "	Florida	<3	Sand, Mud	Sea Grass, Erect Algae, Mangroves	Witham et al., 1964; Sweat, Eldred et al., 1972; Little, 1977
" "	Jamaica	sh	Sand, Mud	Sea Grass	Herrill, 1975
" "	Virgin Islands	<10	Sand, Mud	Sea Grass, Man-groves	Davis, 1971; Olsen et al., 1975
<i>P. japonicus</i>	Japan	2-3	Rocks	Erect Algae	Okada and Kubo, 1950; Ibaruda, 1957
<i>P. longipes cygnus</i>	W. Australia	<9	Sand, Reefs	Sea Grass, Erect Algae	Sheard, 1949; Chittleborough, 1970
<i>P. marginatus/pencillatus</i>	Hawaii	<10	Coral, Rubble	C. MacDonald, personal communication	
<i>P. polyphagus</i>	India	2-7	Mud	Detritus	Rao and Kathirvel, 1971
<i>P. versicolor</i>	Palau	sh	Coral, Rubble	C. MacDonald, personal communication	

sh = shallow water; depth was not specified

holes, clusters of algae, and sea grass root systems. In addition, young P. argus are known to inhabit mangrove roots (Witham et al., 1964; Olsen et al., 1975), sea urchin spines (Davis, 1971), and sponges (Khandker, 1964). Small J. lalandii live within clusters of erect tunicates and mussel beds (Heydorn, 1969b).

The *Phyllospadix* Habitat

Preliminary results of extensive intertidal surveys conducted at representative locations throughout southern California by M. Littler (personal communication) indicate that Phyllospadix habitats cover an average of 4% of the rocky intertidal zone and comprise a greater biomass than any other intertidal plant, except for Egregia and Pelvetia. Based on my limited geographical surveys, combined with information reported by Dawson (1945), Den Hartog (1970), Egstrom (1974), Gordon and Fulton (1975), and Morin and Harrington (1978), Phyllospadix habitat abundance in southern California appears to be positively correlated with P. interruptus abundance. The coastal zone from La Jolla to Point Loma, which had by far the greatest abundance of surf grass habitat (Table 11), is also the area of greatest production of lobsters in California. Odemar et al. (1975) reported that of the 612 km of coastline fished for P. interruptus, over 30% of the commercial catch in 1973-74 came from this 26 km zone; this represents a catch of 1,914

lobsters per shore kilometer. In addition, 63% of all sublegal lobsters (< 83 mm CL) caught and released came from this area (21,375 lobsters/km). By comparison, the 34 km of shore along the windward side of Catalina Island produced 6% of the 1973-74 legal catch (267 lobsters/km) and 3% of the sublegal catch (694 lobsters/km). Odemar et al. (1975) concluded that "if short [sublegal lobster] production is a reasonable indicator, there is little doubt that the La Jolla-Point Loma area is the best lobster nursery in California."

In Baja California, center of the range of P. interruptus, Phyllospadix was present in every area surveyed (Fig. 3; Table 11). Surf grass beds were especially abundant along the mainland coast, where gradually sloping beaches similar to those at La Jolla and Point Loma were encountered. Nearly 50% of the total Mexican production of P. interruptus in 1971-72 came from the coastal zone extending from Punta Eugenia south to Laguna San Ignacio (Martinez et al., 1973). Although I was not able to survey this area, information from Dawson (1951, 1957) and Dawson et al. (1960a,b) confirms the occurrence of large surf grass beds throughout the region and documents the presence of additional Phyllospadix habitats along the coast south of Laguna San Ignacio at least to Punta del Conejo.

The leeward side of Catalina Island has been closed to commercial lobster fishing since 1917. Except for unknown quantities

caught by sport divers and illegal trappers, the lobster population in this area can be assumed to represent an unharvested condition. Results of a mark-recapture trapping program carried out by the California Department of Fish and Game (DFG) during 1974 showed that the population size of trap-vulnerable lobsters for one 2 km coastal zone (see Fig. 6) was 4,781, or 2,390 lobsters/km (Odemar et al., 1975, p. 86). My continuous diver propulsion vehicle survey from Blue Cavern Point to Arrow Point revealed that only two locations within the DFG study area had Phyllospadix beds similar in size and density to those at Bird Rock (Figs. 6, 7). Even less Phyllospadix habitat was found along the rest of the 9 km coast surveyed; none was present at offshore reefs or rocks (except Bird Rock), yet small lobsters were present at these locations. The relative abundance of lobsters throughout the survey area, coupled with the scarcity of large surf grass beds, indicate that Phyllospadix is not the sole nursery habitat for P. interruptus at Catalina Island.

Juvenile Growth

Length-Weight Relationships

The equations listed in Table 17 demonstrate that for every subgroup of juvenile lobsters, wet weight was proportional to the cube of the carapace length; therefore, juvenile Panulirus

interruptus growth tends to be isometric with respect to these parameters. Significant regression slope differences for logarithmic plots of male versus female and small versus large juvenile length-weight data were not expected in immature lobsters. It was the small (< 30 mm CL) female subgroup which accounted for these dissimilarities; large females were proportioned similarly to large males and so were small males compared to large males. Fielder (1964), Heydorn (1969a), and Olsen and Koblic (1975), working with lobsters in Australia, South Africa, and Florida, respectively, found insignificant differences in length-weight relationships between the sexes, even of mature individuals. Nakamura (1940) reported that female P. japonicus were slightly heavier than males of similar carapace length for 30-60 mm CL juveniles, but no sexual differences were evident when the size range was expanded to 18-112 mm CL. Lindberg (1955) found similar length-weight relationships for 56-87 mm CL male and female P. interruptus, but at greater sizes the males were heavier--a fact that he attributed to their disproportionately widened carapaces.

Irrespective of statistical significance, actual regression slope differences between subgroups of juvenile P. interruptus shown in Table 17 were so minor that for practical purposes, the data can be combined to yield Equation 2-1. The regression

constants of Equation 2-1 ($a = 0.00063$; $b = 3.098$) are similar to those calculated from a length-weight plot of 44* juvenile P. interruptus measured by Blecha (1972) ($a = 0.00060$; $b = 3.109$), and to those calculated from a length-weight table** of 342 adult female P. interruptus measured by Lindberg (1955) ($a = 0.00076$; $b = 3.057$); 240 adult males were relatively heavier ($a = 0.00032$; $b = 3.275$), as mentioned above. Comparable regression constants also are reported by Nakamura (1940) for P. japonicus (2,103 males: $a = 0.00098$; $b = 2.974$) (1,331 females: $a = 0.00093$; $b = 2.994$).

Year Class Growth

Single year (age) classes are recognizable as distinct modal size groups in plotted size-frequency distributions if the species has a well-defined settling period and rapid post-larval growth (Heydorn, 1969a). The year class (primary) mode would have secondary modes corresponding to instars if there is little variation in size at settlement and in size increments per molt. Most spiny lobster species only partially meet these ideal criteria. Age-size relationships could not be determined accurately from size-frequency plots for adult Jasus lalandii (Heydorn, 1969b), P. interruptus (Mitchell et al., 1969) or P. homarus (Heydorn, 1969a; Berry, 1971).

*Four apparently erroneous data points were omitted.

**Total lengths were converted to carapace lengths by the equation $CL = 0.31 TL$ (Backus, 1960). Length and weight values listed in the table were means.

However, monthly size-frequency studies of juvenile P. japonicus (Nakamura, 1940), P. argus (Eldred et al., 1972), and J. lalandii (Pollock, 1973) have been successful in identifying different year classes.

In P. interruptus, due to variability in the time of hatching of the phyllosoma larvae (June-August) (Mitchell et al., 1969) and in the length of planktonic life (approx. 9-14 months) (Johnson, 1960; Serfling and Ford, 1975a) benthic recruitment is spread out in time from at least June through October. Nevertheless, the rapid growth of early juveniles (Fig. 21) and the symmetrical distribution of primary size-frequency modes permitted clear distinction of the first two benthic year classes (Fig. 9a, b). This, in turn, made it possible to calculate monthly means and size ranges for each year class (Figs. 11, 12). However, variation in the size of newly settled postpueruli (6.3-7.7 mm CL) and in size increases per molt, mostly due to the effects of temperature on growth (Table 27), precluded accurate distinction of instar groups by size-frequency analysis (Fig. 10).

Palinurid year class growth can be determined by following the passage of separate modal size groups through the population with time if large samples are taken from a homogeneous assemblage in which there is no appreciable differential immigration,

emigration, mortality, or catchability. In general, the assemblage of age 1+ P. interruptus in the surf grass habitat at Bird Rock was residential (see Table 33). The following variables affected year class growth estimates for this discrete population:

1. recruitment added variable numbers of small juveniles to the Bird Rock population throughout the 5-7 month settling season
2. since home range expanded with increasing size of an individual, a net loss of larger juveniles from the Phyllospadix beds may have occurred
3. CPUE and mark-recapture data (Fig. 22; Table 31) coupled with in situ observations suggested that juvenile mortality was inversely proportional to size
4. the smallest juveniles (< 10 mm CL) were difficult to find in the dense grass; reduction of this capture bias with increasing search experience probably explains why juveniles captured during January, February, and April, 1975, were significantly larger than those caught during the same months in 1976
(Table 18)
5. the largest juveniles (> 35 mm CL) also were difficult to capture because they tended to escape by tail-flipping great distances upon the slightest provocation.

The progressive upward shifts in both means and modes of monthly field-captured age 1+ and 2+ juveniles with time (Figs. 9,

11, 12; Tables 18, 20) were consistent with the growth of individually marked juveniles (Appendix III) and with the growth effects of water temperature seasons determined from molt increment and molt frequency analyses (Figs. 16, 19). Since size-frequency and mean size analyses resulted in a reasonable estimate of juvenile year class growth, the five variables outlined above either were inconsequential or resulted in opposing biases that produced, in effect, "suitable" monthly size values.

Assuming average birth and settlement dates of mid-August (see p. 79), juvenile P. interruptus grew from 7 to 32 mm CL during their first year of benthic life (age 1+ years) and from 32 to 56 mm CL during their second benthic year (age 2+ years) (Fig. 12). This constant annual growth, averaging 25 mm CL/yr, was lower than either the 28 mm CL/yr calculated from mean monthly size differences between the two year classes, or the 30 mm CL/yr determined from recaptures of marked individuals at large for more than six months. The latter two values do not include recently settled juveniles whose growth rate was slightly depressed relative to larger animals (Table 26). Also, mark-recapture annual growth was biased toward warm water periods--68% of the individuals used in this analysis originally were captured between January and March, just before water temperatures began rising; only 7% were

initially captured during July-September, prior to the autumnal cooling period.

Serfling (1972) used limited field data gathered from various sources (see p. 32) to fit a growth curve for juvenile P. interruptus that indicated sizes of 24 mm CL and 44 mm CL after one and two years of benthic life. These age-size relationships were based on June (the beginning of the settling season) as a starting point. Converting this start point to the middle of the settling season in August, Serfling's size estimate for age 2 juveniles becomes 29 mm CL; an age 3 size estimate is not possible because the data do not extend past June of the second benthic year.

The little information that is available on natural age-size relationships in other juvenile palinurids is comparable to that for P. interruptus. Nakamura (1940) estimated that 6 mm CL P. japonicus reached a modal size of 30 mm CL by age 2 years and 50 mm CL by age 3 years. Chittleborough (1976) found that P. longipes cygnus in high density areas grew from 8.3 to 36 mm CL in one year and from 36 to 49 mm CL during the second year. The latter size was considerably smaller than that reached by juveniles raised under near-optimal laboratory conditions. Postsettlement J. novaehollandiae in southern Australia grew from 10.3 mm CL to approximately 37 mm CL in one year (Lewis, 1978). J. lalandii

from South Africa had the slowest juvenile growth; modal year class size increased from 10 to 23 mm CL during the first year of benthic life (Pollock, 1973).

Field versus Laboratory Growth

Juvenile lobster growth monitored in laboratory systems often does not reflect normal field growth due to the unnatural environmental conditions provided or the insufficient quantities of animals cultured. Because of these problems, many laboratory culture studies have yielded growth rates much lower than those measured in field populations (Lewis et al., 1952; Sutcliffe, 1957; Sweat, 1968; Heydorn, 1969b; Pollock, 1973). On the other hand, recent studies have shown that under favorable conditions (e.g., abundant food, shelter, and space), the growth rates of laboratory-raised juveniles can equal or even exceed those which are found in nature (Chittleborough, 1974a, 1975, 1976; Phillips et al., 1977).

In this study, reduced growth rates of lab juveniles relative to field juveniles became evident after the first six months of culture (Fig. 12; Table 20). Field juveniles were, on the average, 5.5 mm CL larger than lab lobsters at age 2; by age 3, this differential was 10 mm CL. The retarded growth of lab juveniles was reflected in decreased molt frequency (Fig. 20) and in depressed growth increments per molt (Fig. 19).

Chittleborough (1975) demonstrated that young P. longipes cygnus offered food less frequently than once per day experienced a food shortage. The first effect of a mild food shortage was lengthened intermolt periods. More severe shortage of food not only delayed molting further, but also lessened the increase in size per molt. If daily feeding is also necessary for optimum growth of P. interruptus, then lab juveniles raised on two or three feedings per week (plus a constant supply of natural habitat biota) may have experienced a gradual food shortage that stunted long-term growth.

Chittleborough (1976) suggested that the retarded growth (compared to optimal lab growth) characteristic of young lobsters living on high density reefs in Western Australia was due to limited food resources. By reversing this logic, one can speculate that since food probably was not limiting for juvenile P. interruptus living in the Phyllospadix beds at Bird Rock (see below), the depressed growth of lab juveniles may be similar to lobster growth in central Baja California, if high lobster densities there result in competition for limited food resources.

Factors Affecting Growth

Numerous physiological and environmental factors affect lobster growth (see, for reviews, Passano, 1960; Aiken, 1977; Dall, 1977; Ford, 1977). One major factor, food supply, is

discussed below in connection with juvenile food habits. Four other factors which often have important effects on lobster growth include sex, appendage regeneration, premolt size, and water temperature (Chittleborough, 1976; Phillips et al., 1977).

In this study, a 1:1 ratio between the sexes was found for all 10 mm size groups of field juveniles (Table 16); no growth differences were detected between males and females reared in laboratory aquaria (Appendix IV); and all monthly mean sizes for age 1+ and 2+ juveniles were similar for both sexes (Table 19). Since sexual maturity is not reached until 60-70 mm CL in P. interruptus (see below), depressed female growth attributed to the "antagonism between somatic and reproductive growth" (Aiken, 1977) was not expected in juvenile lobsters. Evidence supporting this view is provided by Nakamura (1940), Lewis et al. (1952), Sutcliffe (1957), Heydorn (1969b), and Phillips et al. (1977). Chittleborough (1976) discovered that although no growth differences were evident between laboratory-raised males and females, wild males larger than 40 mm CL grew faster than similarly sized females in areas where food resources were limiting.

Because "natural" bodily injuries were a common occurrence in wild juvenile P. interruptus (see p. 138), and since injuries due to handling and marking were inevitable, evaluation of the impact of regenerative growth on carapace length growth is warranted.

On the average, relative molt increments in field lobsters were progressively lessened when one, two, or more limbs were missing prior to ecdysis. However, unless more than two appendages were being regenerated, these decreases were not significantly different from intact animal growth per molt (p. 163). Controlled limb removal studies on juvenile P. longipes cygnus by Chittleborough (1975) yielded comparable relative molt increment reductions. In addition, he found that single loss of up to four appendages had no immediate effect on molt frequency, but repetitive removal of two or more limbs led to precocious molting. Thus, repeated autotomy of only two limbs by P. longipes cygnus paradoxically could result in a slight overall increase in short-term growth rate.

Premolt size and water temperature together accounted for more than 60% of the growth rate variation in young P. interruptus, through their effects on both size increases per molt and on the period of time between successive molts (see Figs. 15, 16, 19, 21; Tables 27, 28, 30). Relationships between each of the growth-controlling variables and each of the components of lobster growth were relatively linear for sizes less than 32 mm CL and temperatures less than 20°C (Table 27). Limited data for larger juveniles indicates that they apparently have entered a different phase of growth (Figs. 16, 19). In this new phase molt increments

no longer increase proportionally with greater premolt size; instead, growth increments appear to remain relatively constant or even decline slightly with increasing carapace length. The effects of temperature tend to obscure the molt frequency trends in age 2+ juveniles; however, Serfling and Ford (1975b) raised young P. interruptus at a constant temperature of 22°C and found a frequency of molting pattern consisting of two distinct sigmoid curves of lengthening intermolt duration with increasing size. Transition between the two growth phases occurred at 28 mm CL. Significantly, the fundamental changes in both molt increment and molt frequency growth patterns occur at the same size (age) as when juveniles migrate from shallow, warm-water Phyllospadix beds to deeper, cool-water habitats. The implications of these coincident phenomena will be discussed below.

Phillips et al. (1977) described four growth phases in juvenile P. longipes cygnus raised at constant and ambient temperatures. Phase I was a short period of slow growth following settlement. Phase II (9-15 mm CL) was characterized by gradual increases in molt increments, but few changes in intermolt duration. Phase III juveniles (15-41 mm CL) showed consistent increases in molt increment and intermolt time. Phase IV juveniles (> 41 mm CL) had smaller increases in molt increment and variable intermolt

duration. The general nature of this "quadriphasic" growth pattern is similar to that found for P. interruptus in this study, although I could not interpret minor differences in growth patterns (especially in the smallest juveniles) because of concomitant water temperature changes.

The general effects of temperature on lobster growth have been well studied, especially with regard to the mariculture of Homarus americanus (Aiken, 1977; Ford, 1977). However, the physiological mechanisms often are complex because temperature not only can influence molting through changes in metabolic rates, but also can affect molt-control processes by influencing neurosecretory and endocrine phenomena (Passano, 1960). Marked increases in molt frequency associated with rising temperatures (within certain temperature limits) are characteristic for juvenile palinurids (Sweat, 1968; Heydorn, 1969b; Berry, 1971; Chittleborough, 1975; Serfling and Ford, 1975b; Phillips et al., 1977). On the other hand, molt increment changes monitored in laboratory aquaria appeared either to be independent of temperature (Serfling and Ford, 1975b; Phillips et al., 1977) or inversely correlated with temperature (mostly at high culture temperatures) (Blecha, 1972; Chittleborough, 1975). In this study, the temperature effect on molt increment was obvious, but small, relative to the temperature

effect on molt frequency (Table 28). Also, the effect was more pronounced in field juveniles than lab juveniles (Table 27). Perhaps some condition associated with culturing P. interruptus in the laboratory, e.g., slightly reduced availability of fresh food items, might explain the discrepancies between my findings and those of Blecha (1972) and Serfling and Ford (1975b).

In analyzing the growth of P. interruptus with respect to temperature, an implied assumption was that temperature effects on growth components were independent of any particular stages within the molt cycle. Since the growth data were averaged, failure of this assumption would not seriously affect results; however, individual variability in molt frequency seemed to be higher than usual during periods of relatively rapid changes between summer and winter water temperatures. Growth rates may differ between P. interruptus cultured at a constant temperature and those reared at varying temperatures even if the same average temperatures are maintained in both regimes (Ford, personal communication).

Phillips et al. (1977) noted that P. longipes cygnus which failed to molt before the winter drop in water temperatures had an extra long intermolt period, but those molting just before the summer temperature rise often molted more frequently than others of the same carapace length. This phenomenon also might explain many of the growth irregularities in juvenile P. interruptus.

Temperature variations not only caused seasonal fluctuations in the growth rate of California spiny lobsters (Figs. 16, 19), but also may have caused differences in growth between the two field-sampling years. Surface water temperatures averaged 2.7°C warmer during the months September-December 1976, than during the same period in 1975 (Fig. 4). All monthly mean sizes of juveniles captured during the four-month period in 1976 were significantly larger than the corresponding sizes of juveniles caught during the autumn of 1975 (Table 18). Similarly enhanced growth for marked juveniles at large during warm water months in 1976 compared to 1975 is evident in Figure 15. Feasibilities for using elevated temperatures to increase the biomass production of P. interruptus in potential mariculture programs are discussed by Blecha (1972) and Serfling and Ford (1975b).

Adult Age-Size Relationships

The results of this study indicate that juvenile P. interruptus in the field reach 56 mm CL by age 3 years. This represents a larger size than the 48-52 or 44 mm CL previously estimated by Mitchell et al. (1969), and Serfling (1972), respectively, for three year old California spiny lobsters. The new information on growth rates of juveniles resulting from the present study may help to reduce some of the confusion concerning the time required

for P. interruptus to reach sexual maturity and legal size; however, the differing techniques used to measure growth and the highly variable growth rates subsequently recorded do not permit the establishment of detailed age-size relationships for larger lobsters at the present time (see Table 1).

Ninety percent of all female P. interruptus were found to be sexually mature (evidenced by the presence of eggs attached to the abdomen) at 68 mm CL by Wilson (1948), 73 mm CL by Lindberg (1955), or 69 mm CL by Odemar et al. (1975). Sexual maturity in males is more difficult to determine due to the lack of reliable external indications. Lindberg (1955) used plots of relative testes weight to estimate that most males should be mature at approximately 58 mm CL.

Ford and Farris (1977) compared the growth of four size groups of P. interruptus (ranging from 50-142 mm CL) raised in large concrete pools with ones marked and recaptured in the field. Both molt increment and molt frequency were highly variable in both studies (e.g., percentage increase in size per molt varied from 1 to 16), but mean values were comparable. The results suggest that annual growth rates of lobsters larger than 60 mm CL are low, averaging only 6 mm per year. If four year old lobsters are approximately 60-70 mm CL, then males would be sexually mature by age 4 years and most females by age 5 years. These estimates are

consistent with data from recaptures of several marked juveniles that had grown to sizes greater than 56 mm CL (juveniles T6, K21, Z35; see Appendix III). The youngest age for female sexual maturity probably was represented by juvenile E39, who grew from 41 mm CL on October 30, 1976 (age 2+) to 63 mm CL on July 6, 1978 (age 3+), at which time she was carrying a small cluster of eggs.

If the 6 mm CL annual adult lobster growth rate estimated by Ford and Farris (1977) is further extrapolated, legal size (83 mm CL) would be reached by age 7-8 years. This age estimate is identical with that of Lindberg (1955), but it is far lower than the estimates of Mitchell et al. (1969) and Odemar et al. (1975) (Table 1). Both of the latter studies appropriately analyzed growth separately for males and females, but other basic assumptions appear to be untenable. Mitchell et al. (1969) assumed that peaks in size-frequency plots represented single year classes; however, results from this study and from Ford and Farris (1977) indicate that the wide variability of P. interruptus growth would tend to obscure any year class groupings in adult lobster size-frequency distributions. Odemar et al. (1975) assumed that 50 mm CL lobsters were age 4 years (3rd benthic year). They actually are age 2+ years. In addition, they assumed that lobsters larger than 50 mm CL molted only once per year, in the autumn, so growth per molt was considered

to be annual growth. Observations made during this study and data from Ford and Farris (1977) indicate that, between 50 mm CL and at least 70 mm CL, individuals molt two or possibly more times per year, hence, Odemar et al. (1975) underestimated annual growth. The retarded growth of females compared to males, found by Odemar et al. (1975) for every 3 mm size group between 63 and 93 mm CL, may be due to reduced molt increments associated with energy allocation for egg production, or to reduced molt frequency (of 60-70 mm CL lobsters) caused by inhibition of molting for approximately seven months of the year while carrying the spermato-phore or the eggs.

Juvenile Food Habits

The diet of juvenile Panulirus interruptus ascertained in this study generally was comparable to that determined for adult California spiny lobsters by Lindberg (1955) and Winget (1968), except that juveniles consumed proportionately smaller food items (see Tables 35, 36, 37). Winget (1968) found that mollusks were the major diet component for 60-90 mm CL lobsters collected from rubble rock and surf grass habitats. Smaller adults utilized mollusks to a greater extent than larger adults, possibly because larger individuals were more capable of capturing and consuming crabs and sea urchins. The major contribution of mollusks to the diet

did not appear to vary with season. Next to mollusks, crustaceans (mostly crabs) and echinoderms (mostly sea urchins) were the most important food items, followed by algae and Phyllospadix. Mussels were heavily favored over all other food items presented in laboratory food preference trials, followed by sea urchins, crabs, and coralline algae.

The proportions of various organisms consumed by lobsters usually reflects the relative abundance of potential prey items within a particular area (Lindberg, 1955; Winget, 1968; Heydorn, 1969b; Berry, 1971). Limited investigation of the abundance of micro-mollusks within Phyllospadix and Halidrys habitats by G. Brown (personal communication) and myself confirmed that mollusk genera were consumed according to their relative availability (cf. Tables 13, 36). Observations made during survey dives at Bird Rock indicated that this relationship generally holds for other prey types. Thus, the relatively large proportion of Gibbonsia eggs consumed was correlated with high densities of these fish, and the low abundance of small sea urchins was reflected by their relative scarcity in juvenile fecal material. However, consumption of crustaceans appeared to be low compared to their abundance in the Bird Rock Phyllospadix beds. Since crustacean parts present in fecal material usually were well-digested, the importance of this group of organisms in the diet of young lobsters probably was underestimated.

The same bias would exist for any soft-bodied organisms consumed. Conversely, the importance of largely undigestible materials would be overestimated. Some calcareous materials, such as coralline algae, may have been ingested for reasons unrelated to caloric value. Lindberg (1955), Heydorn (1969b), and Berry (1971) have suggested that these items may provide the calcium required for hardening the postmolt exoskeleton.

In this study, juvenile lobsters generally had the same activity rhythms, foraging tactics, and modes of prey consumption as adult P. interruptus (cf. Lindberg, 1955; Winget, 1968). Two differences between juvenile and adult foraging behavior were evident: the nightly foraging range of juveniles was considerably smaller than that observed for adults; and small juveniles did not appear to be attracted to food (bait) at a distance, as is characteristic for adults. Both of the above behavioral differences would tend to confine juvenile movements to a relatively small area, thus possibly reducing the chances of encountering a lurking predator, such as Scorpaena guttata (see Table 39).

Field and laboratory studies by Chittleborough (1975, 1976) have indicated that food supply is a major determinant of the growth and survival of juvenile Panulirus longipes cygnus in Western Australia. Food resources available to juvenile P. interruptus

were abundant in the Phyllospadix habitat at Bird Rock, but the Halidrys habitat at Isthmus Reef contained considerably fewer potential prey items (Table 13). Phyllospadix habitats in other localities also support a high diversity of small organisms (Rischen, 1976; G. Brown and R. Miracle, personal communication). Although quantitative information is not available for other shallow water habitats, their apparent lack of microhabitats suitable for supporting large assemblages of small gastropods suggests that these habitats may not be capable of sustaining densities of juvenile lobsters comparable to those found in Phyllospadix beds (see Fig. 23).

Identification of Phyllospadix as the primary source of energy (carbon) for juvenile P. interruptus and several other animals collected at Bird Rock by stable carbon isotope analysis was not possible because the $\delta^{13}\text{C}$ values for surf grass and algae were not sufficiently different (Table 15). Several sources of error were possible:

1. in a similar study, the analytical error for $\delta^{13}\text{C}$ values was approximately $\pm 0.5\text{‰}$ (Haines, 1976)
2. in a controlled diet study using various animals, including brine shrimp (Artemia salina), the $\delta^{13}\text{C}$ values for different individuals of a species with the same diet varied from 0.2 to 1.8 ‰ (De Niro and Epstein, 1978)

3. in the above study, animal carbon was found to be enriched in $\delta^{13}\text{C}$ relative to the diet carbon by $0.8 \pm 1.1\text{‰}$.

The $\delta^{13}\text{C}$ values for lobsters from Bird Rock may have been higher because they had acquired surf grass carbon; however, other sources of carbon were available to lobsters at Bird Rock, including benthic and epiphytic algae, benthic diatoms, tidal input of detritus, and organisms located just beyond the perimeter of the grass beds (including Halidrys). The smallest lobster, presumably with the least foraging range, had the $\delta^{13}\text{C}$ ratio closest to that of Phyllospadix, but both Norrisia and Gibbonsia from the surf grass habitat had $\delta^{13}\text{C}$ ratios more indicative of algal-derived carbon.

The results of this preliminary carbon isotope analysis did not warrant further investment of effort at this time; nevertheless, this technique would be valuable for ecological studies in an area where the dominant plants have sufficiently disparate $\delta^{13}\text{C}$ values. Haines (1976) was able to correlate carbon isotope ratios for fiddler crabs (Uca pugnax) with ratios of monospecific species stands of C₃ and C₄ plants in Georgia salt marshes. Research currently is in progress on shrimp utilization of turtle grass (Thalassia testudinum) carbon in the Gulf of Mexico (P. Parker, personal communication).

Juvenile Population Dynamics

The investigation of juvenile Panulirus interruptus population dynamics at Bird Rock was necessarily limited in scope for the following reasons:

1. physical conditions prevailing at the shallow, turbulent Phyllo-spadix habitat placed considerable restraints on the timing of survey dives and the catchability of juveniles
2. detailed exploration of the assumptions underlying the abundance estimation methods was not possible within the scope of this project (see p. 63).

The data obtained from CPUE and mark-recapture studies reflect the combined effects of a number of variable factors, including differential catchability, recruitment, immigration, emigration, and mortality (Fig. 22; Table 31). Low CPUE values for the 1974 year class resulted from lack of experience in catching juveniles, and adverse weather conditions during the months February-April. Increased CPUE and mark-recapture abundance values for each successive juvenile year class resulted from greater experience in catching juveniles. As an example of the tremendous effect of diver experience on catchability, on four consecutive survey dives during November and December 1976, each with a different dive partner, I caught 37, 41, 38, and 43 juveniles,

respectively; my dive partners (all competent divers but with relatively limited lobster survey experience) caught 0, 3, 0, and 9 juveniles, respectively. Because of these experience-dependent catchability differences, variation in the levels of recruitment for each year could not be estimated; however, variable annual recruitment would be expected since southern California is near the periphery of the geographic range of P. interruptus (see Chittleborough, 1970).

High CPUE and mark-recapture values for September-December 1976, compared to the same period in 1975, probably were related to the significantly larger monthly mean juvenile sizes (since larger juveniles were more easily seen and captured), which in turn were associated with elevated water temperatures (Fig. 4; Table 18). Population densities calculated from abundance data were low for CPUE values compared to mark-recapture values due to the dependence of CPUE density estimates on catchability (Fig. 23). Rising monthly CPUE and high mark-recapture population size estimates for 1975 and 1976 year class juveniles were associated with the cumulative effects of recruitment (Fig. 22; Table 31). Although the settlement season extended from June to November (see Tables 3, 5), CPUE abundance values continued to rise until April 1976 (for the 1975 year class) because the effects of

recruitment did not become evident until juveniles grew large enough to be seen and captured. Presumably mortality was high during this period, since predators capable of capturing the smallest juveniles were common at Bird Rock (Table 39); however, any mortality effects were obscured by the effects of recruitment. After April, the cumulative effects of mortality of small juveniles were reflected in the rapid decline in monthly CPUE abundance values and the substantially lower (halved) mark-recapture abundance estimates (Fig. 22; Table 31). Expanded home ranges for larger juveniles also may have accounted for a small portion of the population loss (see Table 33).

Somewhat higher estimates of juvenile mark-recapture abundance for July-October compared to April-June probably do not reflect real differences; instead, they may be due to a net loss of marked juveniles from the survey areas since both marked and unmarked animals could leave the grass beds, while only unmarked animals could enter the Phyllospadix habitat from surrounding areas. The latter individuals were recognized during survey dives by their dark brown coloration (see Table 9). Some further declines in CPUE abundance estimates during the summer months may have been related to my decreased ability to capture larger, more agile individuals and to the patchy distribution of larger juveniles as levels of aggregation increased (see p. 191).

CPUE monthly population size estimates for 1975 year class juveniles fell to near zero levels as age 2+ individuals emigrated from the Phyllospadix habitat during the months August-November. Only a few large juveniles remained in the shallow grass beds during their second benthic year (Fig. 22; 1973 settlement year class).

Serfling (1972) conducted juvenile lobster surveys within the same Phyllospadix habitat at Bird Rock during the months of February, June, and September 1971, and February 1972. Densities of juveniles encountered were estimated to range from 0.2 to 1.0 juvenile/m². These values are comparable to the 1975 CPUE density estimates in this study (Fig. 23). Since both age 1+ and 2+ juveniles were encountered, Serfling (1972) concluded that young P. interruptus remain in the Phyllospadix habitat for two years before migrating to deeper areas. In actuality, the majority of his age 2+ juveniles were encountered during the month of September, when both age classes are present in the surf grass beds. Those second year benthic juveniles found during the other sampling months represented the few larger juveniles (which tend to be more conspicuous) that did not migrate to deeper areas.

Little information is available concerning the population dynamics of other first year benthic palinurids. Quantitative information on the annual recruitment of Panulirus longipes cygnus

pueruli to artificial habitat traps has been collected for the past ten years in Western Australia, but the relationship between abundance of trap-settled pueruli and density of juveniles on the nursery reefs has not yet been established (Phillips and Hall, 1978). Heydorn (1969b) recorded monthly catches per diver-hour of 20-70 mm CL Jasus lalandii living on a shallow breakwater, but was unable to draw any conclusions from the highly variable results.

Chittleborough (1970) monitored the population densities of two to five year old P. longipes cygnus on shallow test reefs in Western Australia using a semi-annual single census trapping scheme. Population densities, on the order of 0.1-0.5 lobster/m², varied widely from year to year, indicating variable recruitment. Mortality was density dependent; for the highest recruitment year, the population size was reduced to one-third its initial size after 35 weeks. Very little dispersal or migration of the reef juveniles occurred during most of the year, but in early summer the larger individuals (age 5-6 years) moved to deeper water. New age 2+ juveniles (36 mm CL) appeared on the reefs shortly thereafter. The movement of age 2+ juveniles away from the shallow sea grass beds and onto the slightly deeper reefs takes place at approximately the same time the new year class of puerulus larvae are settling into the sea grass habitat (Phillips and Hall, 1978). These seasonal size-class replacement fluxes are comparable to that which occurred

in the P. interruptus population at Bird Rock each year. Similar "ontogenetic" migrations also are reported in P. argus (Witham et al., 1968; Olsen et al., 1975; Davis, 1976). The phenomenon of smaller size (age) class recruitment to a particular habitat occurring coincidentally with larger size (age) class migration from that same habitat suggests that a major adaptive value for such ontogenetic migrations is to reduce intraspecific competition for the available resources.

Juvenile Survival and Growth Tactics

Two fundamental principles governing life history "strategies" are:

1. an individual must survive until it grows large enough to reproduce in order to pass on its genetic material to future generations
2. the sooner an organism matures the less likely it is to die before reproducing (Williams, 1966).

With these tenets in mind, certain adaptive values can be inferred from the biological information on juvenile Panulirus interruptus presented in this paper. Of course, further observations and considerable experimentation are needed to confirm or deny these inferences.

Size-dependent predation probably is the most important factor determining the life history strategy of juvenile P. interruptus.

Since the smallest juveniles are subject to the greatest risk of predation, natural selection would favor any adaptations having anti-predatory value, including those adaptations promoting rapid growth to sizes beyond which predation is negligible. Rapid juvenile growth would have additional adaptive value in decreasing the length of time required to reach sexual maturity.

Puerulus larvae of P. interruptus that settle into Phyllospadix habitats apparently are better able to avoid predators and grow rapidly compared to those settling in other habitats for the following reasons:

1. the dense thicket of surf grass effectively conceals the clinging larvae and cryptic juveniles from visual predators
2. the turbulent, often turbid, shallow subtidal zone occupied by Phyllospadix appears to exclude most large predatory fish
3. since water temperature has a considerable direct effect on juvenile growth, the warmer surface waters bathing the surf grass habitat promote maximal growth rates
4. the highly productive Phyllospadix habitat supports an abundant supply of food resources, especially small mollusks, which sustain optimum juvenile growth rates

Juvenile P. interruptus show adaptive traits which tend to complement the beneficial growth and survival qualities of the

Phyllospadix nursery habitat. These include:

1. settling during the season of highest water temperatures, thus maximizing growth of the smallest instars
2. preferentially selecting Phyllospadix as a substrate for settlement and metamorphosis
3. acquiring green exoskeleton coloration, matching that of Phyllospadix, for more effective camouflage
4. occupying small bedrock crevices or shelter holes dug into the surf grass rhizome-sediment mat
5. aggregating in small clusters for mutual defense
6. remaining inactive during the day when visual predators are most active
7. confining nightly foraging to a small home range to reduce chances of being encountered by predators

During the first postsettlement year in the Phyllospadix habitat, juvenile P. interruptus grow rapidly to larger instars, and consequently become more heavily spined and acquire greater mobility. The risks of predation now are greatly reduced because relatively few predators are large enough to successfully attack the well-defended juveniles. Characteristic changes in life history traits apparently associated with larger size and decreased probability of predation include:

1. the nightly foraging range expands to include areas beyond the

perimeters of the surf grass beds

2. exoskeleton color changes gradually from green to brown, and the pair of white abdominal spots disappear
3. diurnal gregariousness increases as individuals outgrow the size of most crevices within the grass beds--these aggregations often consist of mixed size classes, including adults which enter shallow habitats in the summer
4. an autumnal migration to deeper water gradually occurs (in association with adults) coincidently with recruitment of the new year class of pueruli into the Phyllospadix habitat

Offshore migrations of age 2+ P. interruptus may be related to the lack of adequate dens in the grass beds for protection from winter storms or they may serve to reduce competition with first year benthic juveniles. Characteristic changes in growth patterns accompany this change of habitat. The resulting new growth phase, distinguished by more constant size changes, is not due to temperature differences, since temperature varies little with depth during late fall and winter; instead, it may be due to changing life history tactics associated with larger size or to physiological constraints imposed by physical size phenomena. Return migration to shallow water in late spring again permits rapid growth during the summer months in the warm water above the thermocline.

During the second year of benthic life and thereafter, juvenile ecological and behavioral patterns are similar to those of adults, except for the lack of sexual activities. Presumably the onset of sexual maturity is accompanied by a new phase of reduced growth (especially in females) as more energy is allocated to reproductive activity. Morphological and behavioral anti-predatory adaptations persist, since longer-lived lobsters can produce more annual batches of offspring; however, growth no longer plays a significant role in further reducing the risks of predation since an effective refuge in size has now been reached.

SUMMARY AND CONCLUSIONS

1. The natural history of juvenile California spiny lobster Panulirus interruptus (Randall) was investigated, with primary emphasis placed on three objectives: (1) ascertaining the habitats occupied by juvenile lobsters, including detailed examination of surf grass (Phyllospadix torreyi Watson) beds as possible lobster nurseries; (2) determining the natural growth rate and component growth processes of juvenile lobsters; and (3) evaluating the major ecological and behavioral phenomena associated with juvenile survival and growth, including food habits, activity patterns, population density, and mortality.

2. Exploratory habitat surveys were conducted at various island and mainland locations throughout southern and lower California. The primary study site was a discrete Phyllospadix habitat located at Bird Rock, Santa Catalina Island, near the Catalina Marine Science Center (CMSC).

3. Populations of juvenile P. interruptus inhabiting the surf grass beds at Bird Rock were monitored by means of frequent scuba surveys conducted during the period October 1974 through December 1976.

4. The natural growth of juvenile lobsters was evaluated using a combination of four techniques: (1) analysis of monthly shifts in size-frequency modes of field-captured juveniles; (2) measurement of single molt size increases in lobsters molting shortly after capture; (3) remeasurement of individually marked juveniles recaptured after varying periods of time at large; and (4) laboratory culture studies.

5. Collections of P. interruptus puerulus larvae attracted to underwater night-lights at various localities, and captures of recently settled juveniles at Bird Rock have confirmed previous work showing that larval settlement occurs at least from June through October, with peak recruitment taking place during July, August, and September when seasonal water temperatures are maximal. Since the midpoints of egg hatching and larval settling seasons both occur in August, newly settled lobsters are considered to be one year old.

6. Laboratory paired-substrate choice tests demonstrated that pueruli and early juveniles preferred Phyllospadix over rubble rock or the broad-bladed kelp Macrocystis. Variable choice behavior shown between Phyllospadix and Halidrys or Plocamium suggests that young P. interruptus may have a general preference for thin-bladed, densely matted plant cover.

7. Exploratory habitat surveys indicated that small juveniles, although difficult to find, commonly inhabited 0-4 m deep rocky habitats having dense plant cover. Most were encountered in Phyllospadix beds. Those found in surf grass beds were green in color, while those in other habitats were brown. Small lobsters were found in narrow bedrock crevices, circular solution pockets, or temporary burrows within the surf grass rhizome-sediment mat. Large juveniles were encountered in various rocky habitats, some as deep as 28 m.

8. Phyllospadix beds are most abundant on gradually sloping, rocky mainland beaches. Small, patchy surf grass beds are found along steeply sloping island shores. Phyllospadix habitat abundance in southern California, and possibly Baja California, appears to be positively correlated with P. interruptus abundance, based on all available information. At Catalina Island, surf grass habitats are not extensive enough to be the sole nursery areas for juvenile lobsters.

9. Carapace length versus wet weight relationships for Bird Rock juveniles fit standard power curve equations. The regression equation for small females was slightly, but significantly, different from that for either small males or large females.

10. Results from the growth studies demonstrate that a combination of growth measurement techniques can be used to determine natural growth rates. This study is the first to monitor the growth of individually marked first year benthic palinurids in a discrete field population.

11. Bird Rock juveniles grew from 7 to 32 mm CL in 10-11 molts and from 32 to 56 mm CL in 5-6 molts during the first and second years of benthic life, respectively. Growth rates were similar for both males and females. Juveniles regenerating more than two limbs grew less per molt than intact lobsters.

12. Long-term growth of laboratory-reared juveniles was 20% less than that of Bird Rock lobsters, possibly because of inadequate food.

13. Premolt size and water temperature were the most important conditions affecting the growth of young P. interruptus. In age 1+ juveniles, increasing size resulted in proportionately larger growth increments per molt for each successive instar. These effects were counterbalanced by corresponding reductions in the frequency of molting, resulting in an overall constant rate of growth. Molt frequency declined at a different rate in age 2+ juveniles, and molt increment became independent of premolt size. For all juveniles, molt frequency and molt increment varied directly

with water temperature. The effects of temperature on molt frequency and, to a lesser extent, on molt increment were so great that juvenile growth rates during warm water months were more than double those of cold water months.

14. Utilizing combined results from this study and from previous investigations, it is estimated that P. interruptus males and females become sexually mature by ages 4 and 5 years, respectively. After sexual maturity, females may grow slower than males; nevertheless, both sexes probably reach legal size by age 7-8 years.

15. Fecal content analysis showed that the most important food items consumed by juveniles living in the Phyllospadix habitat at Bird Rock were tiny mollusks, followed by coralline algae, Gibbonsia eggs, crustaceans, foraminiferans, and surf grass. Small mollusks were especially abundant in surf grass beds.

16. Juvenile P. interruptus activity patterns and foraging behavior were similar to those of adults, except that juvenile home ranges are proportional to body size, and small juveniles apparently are not attracted to food at a distance.

17. Preliminary carbon isotope analysis of juveniles living in surf grass beds failed to identify Phyllospadix as their as their primary source of energy (carbon), because the $\delta^{13}\text{C}$ values for surf grass and algae were not sufficiently different.

18. Results from investigation of juvenile population dynamics at Bird Rock by catch per diver-hour and mark-recapture analysis could only be broadly interpreted due to the combined effects of differential catchability, recruitment, immigration, emigration, and mortality.

19. Mortality levels were high, apparently accounting for a 70% or greater reduction in population size at Bird Rock one year after settlement. Size-dependent predation is inferred to be the major cause of juvenile mortality. Potential predators of juvenile P. interruptus within the Phyllospadix habitat are discussed.

20. During the summer following settlement at Bird Rock, larger juveniles tended to gather in mixed size class aggregations by day and to forage beyond the surf grass bed perimeter at night. In the autumn, age 2+ juveniles migrated out of the surf grass beds to deeper water, coincidently with recruitment of the new year class of pueruli into the Phyllospadix habitat.

21. Based on the information obtained during this study, it is inferred that size-dependent predation is the most important factor determining the life history strategy of juvenile P. interruptus. Life history tactics promoting rapid growth apparently have dual adaptive functions: (1) reducing the period of high vulnerability to predation until a refuge in size is attained; and (2) decreasing the length of time required to reach sexual maturity.

22. The shallow Phyllospadix habitat is concluded to be the major nursery for first year benthic P. interruptus. Selective advantages of inhabiting surf grass beds are discussed in terms of anti-predator and rapid growth adaptations.

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APPENDIX I

**SCIENTIFIC NAMES, GEOGRAPHIC LOCATIONS, AND
MAJOR JUVENILE STAGE REFERENCES FOR SPINY
LOBSTER SPECIES (FAMILY PALINURIDAE)
DISCUSSED IN THIS STUDY**

Species	Location	Juvenile Stage Reference
<u>Jasus edwardsii</u> (Hutton)	New Zealand	Kensler, 1967
<u>J. lalandii</u> (H. Milne-Edwards)	South Africa	Heydorn, 1969b; Pollock, 1973
<u>J. novaehollandiae</u> Holthuis	S. Australia	Lewis, 1978
<u>Panulirus argus</u> (Latreille)	Florida-Brazil	Sutcliffe, 1957; Sweat, 1968; Costa et al., 1969; Eldred et al., 1972; Berrill, 1975, 1976; Davis, 1976; Little, 1977
<u>P. homarus</u> (Linnaeus)	South Africa	Berry, 1971; Smale, 1978
<u>P. inflatus</u> (Bouvier)	S. Baja California	--
<u>P. interruptus</u> (Randall)	S. California	Blecha, 1972; Parker, 1972; Serfling, 1972; Serfling and Ford, 1975a, b
<u>P. japonicus</u> (v. Siebold)	Japan	Nakamura, 1940; Okada and Kubo, 1948
<u>P. longipes cygnus</u> George	W. Australia	Chittleborough, 1970, 1974a, b, 1975, 1976; Phillips et al., 1977.
<u>P. marginatus</u> (Quoy and Gaimard)	Hawaii	C. Mac Donald, personal communication
<u>P. penicillatus</u> (Oliver)	Hawaii	C. Mac Donald, personal communication
<u>P. polyphagus</u> (Herbst)	India	Rao and Kathirvel, 1971
<u>P. versicolor</u> (Latreille)	Palau	C. Mac Donald, personal communication

APPENDIX II

JUVENILE P. INTERRUPTUS GROWTH RECORDS
OBTAINED FROM FIELD INDIVIDUALS WHICH
MOLTED IN LABORATORY AQUARIA WITHIN
ONE WEEK OF CAPTURE

Juvenile	Sex	Molt Date	Premolt	Postmolt	Carapace Length	Carapace Length
			Carapace Length (mm)	Carapace Length (mm)	Increase (mm)	Increase (%)
F4	M	5-25-75	17.45	19.50	2.05	11.8
G4	F	1-26-75	17.90	19.55	1.65	9.2
I4	F	8- 3-75	24.95	28.40	3.45	13.8
J4	F	10-13-75	34.95	39.60	4.65	13.3
L4	M	1-27-75	16.50	17.90	1.40	8.5
L4	M	8-22-75	29.20	34.35	5.15	17.6
M4	M	1-26-75	16.20	17.60	1.40	8.6
T4*	M	6- 3-75	19.20	21.75	2.55	13.3
W4	M	7- 3-75	23.80	27.30	3.50	14.7
X4	F	8-28-75	31.60	35.50	3.90	12.3
U5	M	5-25-75	16.65	19.30	2.65	15.9
H6	F	8-24-75	29.70	33.85	4.15	14.0
I6	F	7- 3-75	24.75	28.60	3.85	15.6
P6	F	7- 3-75	28.05	32.15	4.10	14.6
M7	M	7- 2-75	25.80	29.40	3.60	14.0
G8	M	7-14-75	22.55	26.35	3.80	16.9
G8	M	11-22-75	35.70	39.35	3.65	10.2
V8	F	5-20-75	19.95	22.80	2.85	14.3
F9	F	5-25-75	21.45	23.85	2.40	11.2
L9	M	5-27-75	21.05	24.60	3.55	16.9
Q9*	F	6- 2-75	22.35	24.90	2.55	11.4
T9*	M	6- 3-75	27.80	31.65	3.85	13.8
U9	M	6- 5-75	23.00	27.50	4.50	19.6
X9*	F	6- 5-75	22.55	25.85	3.30	14.6
K10	F	8- 3-75	21.15	29.05	3.90	15.5
O10	F	8- 8-75	26.10	29.60	3.50	13.4
Z10	M	8-23-75	29.30	33.20	3.90	13.3
A11	F	8-23-75	32.30	37.10	4.80	14.9
C11	F	8-23-75	30.45	34.70	4.25	14.0
D11	F	1-25-76	40.00	43.25	3.25	8.1
N11	M	9-29-75	52.60	55.45	2.85	5.4
S11	M	9-28-75	8.30	8.95	0.65	7.8
V11	F	10-17-75	16.55	19.45	2.90	17.5
X11	M	10-12-75	14.30	16.70	2.40	16.8
B12	M	10-12-75	11.40	13.30	1.90	16.7
I12	F	10-15-75	11.40	13.55	2.15	18.9

Juvenile	Sex	Molt Date	Premolt	Postmolt	Carapace	Carapace
			Carapace Length (mm)	Carapace Length (mm)	Length Increase (mm)	Length Increase (%)
J12	M	10-16-75	16.50	18.90	2.40	14.5
P12	M	10-18-75	16.05	18.35	2.30	14.3
R12	F	10-13-75	9.00	10.75	1.75	19.4
S12	M	10-14-75	12.95	15.25	2.30	17.8
J15	F	11-16-75	19.65	22.60	2.95	15.0
J15	F	2-15-76	22.60	25.65	3.05	13.5
K15	M	11-23-75	15.45	17.40	1.95	12.6
M15	F	11-22-75	14.30	16.50	2.20	15.4
Q15	F	11-16-75	13.65	16.15	2.50	18.3
S15	F	11-26-75	15.95	18.00	2.05	12.8
T15	F	11-17-75	18.60	21.70	3.10	16.7
V15	F	11-23-75	18.30	20.80	2.50	13.7
W15	F	11-20-75	17.35	19.70	2.35	13.5
X15	M	11-17-75	14.05	16.10	2.05	14.6
O16	M	1-22-76	15.45	17.05	1.60	10.4
R16	M	1-21-76	16.85	18.95	2.10	12.5
Y16	M	1-24-76	45.10	48.10	3.00	6.6
A17	M	1-29-76	38.90	42.20	3.30	8.5
D17	F	1-24-76	11.80	13.25	1.45	12.3
S17	F	7-3-76	23.10	27.55	4.45	19.3
T17	M	1-24-76	15.20	17.10	1.90	12.5
W17	F	1-31-76	11.50	12.85	1.35	11.7
Y17	M	3-19-76	20.45	22.70	2.25	11.0
D18	M	1-24-76	23.65	26.55	2.90	12.3
I18	M	1-28-76	19.25	21.20	1.95	10.1
L18	M	1-31-76	10.45	11.90	1.45	13.9
S18	M	2-11-76	20.60	22.40	1.80	8.7
U18	F	2-15-76	14.55	16.55	2.00	13.8
W18	M	2-20-76	24.50	26.85	2.35	9.6
G19	M	2-16-76	16.00	18.50	2.50	15.6
H19	F	2-20-76	15.50	17.50	2.00	12.9
M19	M	2-21-76	14.60	16.50	1.90	13.0
N19	M	2-23-76	15.60	17.75	2.15	13.8
O19	M	2-19-76	15.75	17.55	1.80	11.4
O19	M	10-18-76	41.80	47.00	5.20	12.4
R19	F	5-9-76	15.20	18.00	2.80	18.4
U19	F	2-20-76	10.25	11.40	1.15	11.2
D20	M	3-10-76	12.35	13.65	1.30	10.5

Juvenile	Sex	Molt Date	Premolt	Postmolt	Carapace Length	Carapace Length
			Carapace	Carapace	Increase (mm)	Increase (%)
E20	M	3-15-76	18.10	21.05	2.95	16.3
H20	M	7-10-76	23.15	27.10	3.95	17.1
O20	F	12-10-76	39.50	42.55	3.05	7.7
P20	F	5-31-76	17.30	20.05	2.75	15.9
S20	F	3-10-76	18.15	20.10	1.95	10.7
W20	F	3- 5-76	18.80	21.50	2.70	14.4
Y20	M	3- 9-76	13.30	14.30	1.00	7.5
Z20	F	6-29-76	16.40	19.40	3.00	18.3
G21	F	3-19-76	15.70	17.55	1.85	11.8
J21	F	3-14-76	18.75	21.10	2.35	12.5
K21	M	7-15-76	55.85	57.75	1.90	3.4
R21	F	3-19-76	18.80	21.35	2.55	13.6
C22	M	3-20-76	26.00	29.00	3.00	11.5
L22	F	5-20-76	22.10	24.80	2.70	12.2
Q22	F	3-27-76	15.35	17.85	2.50	16.3
V22	M	4-22-76	16.55	19.30	2.75	16.6
E23	M	3-29-76	17.15	19.55	2.40	14.0
G23	F	3-28-76	19.65	22.25	2.60	13.2
G23	F	6-25-76	26.75	31.35	4.60	17.2
Q23	F	3-23-76	12.10	13.85	1.75	14.5
A24	F	3-21-76	10.65	12.15	1.50	14.1
M24	F	7- 9-76	18.90	22.45	3.55	18.8
U24	F	6- 9-76	20.00	23.60	3.60	18.0
C25	F	6-14-76	14.85	17.35	2.50	16.8
M25	F	4-22-76	16.00	18.50	2.50	15.6
Y25	M	4-22-76	17.10	19.45	2.35	13.7
A26	F	4-23-76	18.15	20.80	2.65	14.6
B26	M	5-14-76	19.40	22.50	3.10	16.0
R26	M	6-30-76	23.60	27.95	4.35	18.4
B27	F	8-20-76	26.70	31.55	4.85	18.2
F27	M	7- 9-76	19.15	22.55	3.40	17.8
N27	M	5- 9-76	21.45	24.65	3.20	14.9
X27	F	5-20-76	21.25	24.65	3.40	16.0
K28	F	5-21-76	20.45	23.95	3.50	17.1
T28	M	5-20-76	25.85	29.50	3.65	14.1
U28	F	9-24-76	32.85	37.30	4.45	13.6
Y28	M	5-21-76	19.80	22.80	3.00	15.2

Juvenile	Sex	Molt Date	Premolt	Postmolt	Carapace Length	Carapace Length
			Carapace	Carapace	Increase (mm)	Increase (%)
D29	M	5-20-76	21.05	24.20	3.15	15.0
G29	F	7- 3-76	20.90	24.90	4.00	19.1
G29	F	9-15-76	27.75	31.05	3.30	11.9
Q29	F	8-22-76	33.25	38.05	4.80	14.4
B30	F	5-31-76	16.00	18.85	2.85	17.8
Z30	F	6-14-76	23.40	27.50	4.10	17.5
C31	F	6-15-76	15.95	18.55	2.60	16.3
F31	M	6- 9-76	21.55	25.60	4.05	18.8
G31	F	6-14-76	30.95	35.90	4.95	16.0
Q31	F	6-21-76	24.45	30.25	5.80	23.7
R31	F	6-21-76	24.75	28.90	4.15	16.8
A32	F	6-25-76	17.75	21.05	3.30	18.6
N32	F	6-26-76	26.60	30.70	4.10	15.4
O32	M	6-25-76	23.80	28.50	4.70	19.7
T32	F	7- 7-76	30.30	35.70	5.40	17.8
Y32	F	7- 6-76	24.65	28.60	3.95	16.0
C33	F	7- 4-76	22.25	25.70	3.45	15.5
J34	M	7-23-76	30.75	35.05	4.30	14.0
K34	F	9-30-76	37.35	43.05	5.70	15.3
N34	M	7-24-76	28.45	32.55	4.10	14.4
P34	M	8-19-76	23.35	25.70	2.35	10.1
D35	M	8- 4-76	33.45	38.40	4.95	14.8
X35	F	8-16-76	35.55	41.20	5.65	15.9
G36	F	8-19-76	21.50	24.45	2.95	13.7
I36	M	8-20-76	34.75	39.55	4.80	13.8
E37	F	9-15-76	43.35	48.60	5.25	12.1
C39	F	10-21-76	37.40	41.75	4.35	11.6
A40	F	8-19-76	13.20	15.70	2.50	18.9
B40	M	8-23-76	13.25	15.70	2.45	18.5
C40	M	9-15-76	20.50	23.85	3.35	16.3
D40	F	10- 5-76	18.30	21.20	2.90	15.9
E40	M	10-18-76	12.30	14.10	1.80	14.6
F40	F	11- 1-76	23.70	26.70	3.00	12.7
G40	M	11- 1-76	14.65	16.25	1.60	10.9
H40	M	10-30-76	16.45	18.75	2.30	14.0
I40	F	11-11-76	23.05	26.40	3.35	14.5
J40	M	11- 4-76	20.90	23.65	2.75	13.2

Juvenile	Sex	Molt Date	Premolt	Postmolt	Carapace Length	Carapace Length
			Carapace Length (mm)	Carapace Length (mm)	Increase (mm)	Increase (%)
K40	M	11-11-76	15.50	17.40	1.90	12.3
L40	F	11-11-76	16.70	19.00	2.30	13.8
M40	F	11-12-76	14.75	16.00	1.25	8.5
N40	M	12-7-76	29.70	32.45	2.70	9.3
O40	M	12-7-76	28.30	31.65	3.35	11.8
P40	F	12-13-76	20.70	23.05	2.35	11.4
Q40	F	12-12-76	18.90	21.10	2.20	11.6
R40	M	12-12-76	18.75	20.65	1.90	10.1
S40	M	12-13-76	20.05	22.55	2.50	12.5
T40	F	12-13-76	15.20	17.05	1.85	12.2

*Juvenile was captured from Isthmus Reef Halidrys bed.

APPENDIX III

JUVENILE P. INTERRUPTUS GROWTH RECORDS OBTAINED FROM RECAPTURES OF MARKED INDIVIDUALS

Estimated numbers of molts were calculated from multiple linear regression of premolt carapace length and water temperature on increase in size per molt for 332 known single field molts of lobsters ranging in size from 9-45 mm CL (see Equation 5-9, Table 27).

Multiple recaptures include data on molts which occurred in laboratory aquaria within one week of capture.

A. One Recapture

Juvenile	Sex	Capture Date	Recapture Date	Field Interval (days)	Capture Carapace Length (mm)	Recapture Carapace Length (mm)	Carapace Length Increase (mm)	Estimated Number of Molts
Z	F	11-29-74	2-16-75	79	17.90	19.50	1.60	1
F2	F	12- 6-74	2-16-75	72	16.75	18.10	1.35	1
G2	F	12- 6-74	1-12-75	37	15.25	16.50	1.25	1
H2	F	12- 6-74	1-12-75	37	15.15	15.10	-0.05	0
K2	M	12- 6-74	1-12-75	37	22.50	24.45	1.95	1
N2	M	12- 6-74	2-16-75	72	17.45	19.55	2.10	1
D3	F	1- 8-75	1-31-75	23	19.10	19.10	0	0
E3	F	1- 8-75	5-18-75	130	16.90	22.30	5.40	2
I3	M	1- 8-75	2-18-75	41	17.00	17.85	0.85	1
K3	F	1- 8-75	8- 1-75	205	25.45	40.45	15.00	4
M3	M	1- 8-75	8-17-75	221	14.75	31.85	17.10	6
B4	M	1-14-75	4- 8-75	84	16.05	17.80	1.75	1
C4*	F	1-14-75	1-31-75	17	22.30	22.25	-0.05	0
E4*	M	1-14-75	5-18-75	124	19.10	24.05	4.95	2
J4	F	1-21-75	10-15-75	267	16.80	39.60	22.80	7
K4	M	1-21-75	2- 1-75	11	23.05	23.05	0	0
M4	F	1-21-75	4- 4-75	73	16.20	17.60	1.40	1
S4**	F	1-30-75	11-14-75	288	18.50	39.00	20.50	6
V4	F	1-31-75	5-23-75	112	18.60	21.40	2.80	1
A5	M	1-31-75	6-23-75	148	27.15	38.15	11.00	3
E5	F	2- 1-75	7-31-75	180	20.05	32.10	12.05	4
K5	M	2- 1-75	2-18-75	17	17.60	17.60	0	0
U5	M	2-16-75	5-31-75	104	14.60	19.30	4.7	2

Juvenile	Sex	Capture Date	Recapture Date	Field Interval (days)	Capture Carapace Length (mm)	Recapture Carapace Length (mm)	Carapace Length Increase (mm)	Estimated Number of Molts
A6	F	2-18-75	6-27-75	129	17.50	23.80	6.3	3
D6	M	2-18-75	4-4-75	45	18.65	21.15	2.5	1
L6	M	2-22-75	3-15-75	21	14.30	14.30	0	0
Y6	F	3-13-75	8-17-75	157	17.70	34.25	16.55	5
A7	F	3-15-75	6-28-75	105	22.25	31.00	39.3	3
E7	F	4-8-75	5-18-75	40	22.35	24.65	2.3	1
F7	M	4-8-75	7-7-75	90	14.95	21.10	6.15	3
J7	M	4-8-75	6-27-75	80	15.85	21.90	6.05	3
N7*	M	4-8-75	5-18-75	40	17.65	17.65	0	0
P7**	M	4-10-75	5-28-75	48	19.00	22.25	3.55	1
R7**	F	4-10-75	5-14-75	34	31.35	31.30	-0.05	0
C8	F	4-16-75	8-3-75	109	21.65	30.85	9.20	3
E8	M	4-16-75	9-16-75	153	25.50	42.15	16.65	4
N8	M	4-30-75	7-7-75	68	24.60	29.00	4.40	1
U8	F	5-15-75	5-23-75	8	18.20	18.20	0	0
B9*	F	5-18-75	6-27-75	40	18.15	20.65	2.50	1
J9	M	5-18-75	7-31-75	74	20.90	28.65	7.75	3
L9	M	5-23-75	7-29-75	67	21.05	29.75	8.70	2
A10	F	6-28-75	7-29-75	31	31.95	36.25	4.30	1
C10	F	7-4-75	7-29-75	25	21.50	25.10	3.60	1
D10	F	7-6-75	7-31-75	25	24.60	29.20	4.60	1
F10	F	7-6-75	1-21-76	199	18.15	34.05	15.90	5
H10	M	7-28-75	8-15-75	18	32.85	32.80	-0.05	0
X10	F	8-11-75	10-12-75	62	34.30	36.70	2.40	1

Juvenile	Sex	Capture Date	Recapture Date	Field Interval (days)	Capture Carapace Length (mm)	Recapture Carapace Length (mm)	Carcapace Length Increase (mm)	Estimated Number of Molts
C11	F	8-20-75	9-16-75	27	30.45	34.65	4.20	1
Z11	F	10-12-75	12-9-75	58	10.85	12.65	1.80	1
F12	M	10-12-75	4-19-76	190	11.55	20.85	9.30	4
H12	F	10-12-75	5-3-76	204	9.55	16.90	7.35	4
I15	F	11-13-75	2-6-76	85	15.90	18.40	2.50	1
K15	M	11-13-75	7-3-76	233	15.45	34.65	19.20	6
M15	F	11-13-75	2-6-76	85	14.30	18.55	4.25	2
S15	F	11-14-75	1-21-76	68	15.95	17.90	1.95	1
T15	F	11-14-75	7-3-76	232	18.60	42.75	24.15	7
O16	M	1-16-76	5-3-76	108	15.45	19.55	4.10	2
R16	M	1-16-75	4-7-76	82	16.85	22.00	5.15	2
B17	F	1-21-76	2-6-76	16	16.85	19.85	3.00	1
F17	M	1-21-76	3-29-76	68	14.55	16.80	2.25	1
H17	F	1-21-76	5-29-76	129	14.45	22.65	8.20	3
L17	F	1-21-76	3-5-76	44	14.00	15.60	1.60	1
P17	F	1-21-76	8-14-76	206	10.20	26.50	16.30	6
S17	F	1-21-76	7-18-76	179	14.05	27.55	13.50	5
Z17	F	1-21-76	9-17-76	240	22.10	47.70	25.60	6
W18	M	2-16-76	5-3-76	77	24.50	30.50	6.00	2
X18	M	2-16-76	5-3-76	77	20.20	27.20	7.00	2
Y18	M	2-16-76	3-13-76	26	14.75	16.70	1.95	1
A19	M	2-16-76	5-14-76	88	19.00	26.30	7.30	2
I19	M	2-16-76	4-7-76	51	17.55	19.65	2.10	2
N19	M	2-16-76	4-7-76	51	15.60	17.75	2.15	1
O19	M	2-16-76	10-21-76	248	15.75	47.00	31.25	8

Juvenile	Sex	Capture Date	Recapture Date	Field Interval (days)	Carapace Length (mm)	Carapace Length (mm)	Recapture	Carapace Length (mm)	Number of Molts	Estimated
P19	M	2-16-76	4-7-76	51	10.05	11.40	1.35	1		
Q19	M	2-16-76	9-17-76	214	14.60	38.60	24.00	7		
R19	F	2-16-76	5-16-76	90	12.80	18.00	5.20	2		
S19	M	2-16-76	4-7-76	51	11.85	13.55	1.70	1		
Y19	F	3-5-76	8-1-76	149	14.50	31.90	17.40	5		
Z19	F	3-5-76	8-1-76	149	26.30	40.45	14.15	3		
A20	F	3-5-76	5-14-76	70	18.40	21.70	3.30	1		
E20	M	3-5-76	3-29-76	24	18.10	21.05	2.95	1		
I20	F	3-5-76	4-27-76	53	11.35	13.55	2.20	1		
J20	F	3-5-76	5-29-76	85	12.25	17.15	4.90	2		
T20	M	3-5-76	6-30-76	117	17.40	28.05	10.65	3		
R21	F	3-13-76	5-3-76	51	11.65	16.05	4.40	2		
J21	F	3-13-76	5-3-76	51	18.75	21.05	2.30	1		
M21	M	3-13-76	4-19-76	37	18.00	21.05	3.05	1		
P21	M	3-13-76	9-21-76	192	18.10	39.80	21.70	6		
S21	F	3-13-76	6-8-76	87	28.55	32.00	3.45	1		
Y21	F	3-13-76	8-5-76	145	17.00	32.65	15.65	5		
D22	M	3-13-76	5-3-76	51	25.55	25.50	-0.05	0		
H22	M	3-13-76	5-3-76	51	18.20	20.85	2.65	1		
I22	F	3-13-76	5-3-76	51	19.30	22.60	3.30	1		
J22	M	3-13-76	4-7-76	25	20.00	20.00	0	0		
L22	F	3-21-76	5-26-76	66	22.10	24.80	2.70	1		
N22	F	3-21-76	12-10-76	264	15.05	47.60	32.55	8		
O22	M	3-21-76	4-19-76	29	17.50	20.75	18.60	1		
V22	M	3-21-76	4-26-76	36	16.65	19.30	2.75	1		

Juvenile	Sex	Capture Date	Recapture Date	Field Interval (days)	Capture Carapace Length (mm)	Recapture Carapace Length (mm)	Carapace Length Increase (mm)	Estimated Number of Molts
A23	M	3-21-76	4-19-76	29	16.50	16.50	0	0
B23	F	3-21-76	4-19-76	29	16.10	18.95	2.85	1
C23	F	3-21-76	4-19-76	29	17.75	17.65	-0.10	0
D23	M	3-21-76	4-19-76	29	16.10	18.90	2.80	1
E23	M	3-21-76	5-14-76	54	17.15	23.25	6.10	2
E23	F	3-21-76	7-1-76	102	19.65	31.35	11.70	3
G23	F	3-21-76	4-19-76	29	17.45	19.10	1.65	1
I23	F	3-21-76	4-19-76	29	19.75	23.50	3.75	1
J23	M	3-21-76	4-19-76	29	14.50	39.65	25.15	7
M23	M	3-21-76	10-16-76	209	15.65	21.55	5.90	2
N23	F	3-21-76	6-20-76	91	17.25	17.25	0	0
O23	M	3-21-76	4-19-76	29	15.45	18.60	3.15	1
P23	M	3-21-76	5-14-76	54	14.80	14.75	-0.05	0
R23	M	3-21-76	4-19-76	29	18.85	18.70	-0.10	0
V23	M	3-21-76	4-19-76	29	18.10	20.80	2.70	1
B24	M	3-29-76	4-19-76	21	12.60	17.55	4.95	2
D24	F	3-29-76	6-30-76	93	19.45	33.10	13.65	4
G24	M	3-29-76	8-14-76	138	15.65	37.45	21.80	6
H24	F	3-29-76	9-10-76	165	13.35	18.90	5.55	2
J24	M	3-29-76	6-30-76	93	16.95	19.10	2.15	1
T24	F	4-7-76	5-3-76	26	17.15	23.60	6.45	2
U24	F	4-7-76	6-21-76	75	13.55	13.60	0.05	0
B25	F	4-7-76	5-3-76	26	12.75	17.35	4.60	2
C25	F	4-7-76	6-21-76	75	13.45	18.95	5.50	2
F25	M	4-7-76	6-8-76	62	16.10	37.90	21.80	6
G25	F	4-19-76	10-2-76	166				

Juvenile	Sex	Capture Date	Recapture Date	Field Interval (days)	Capture Carapace Length (mm)	Recapture Carapace Length (mm)	Carapace Length Increase (mm)	Estimated Number of Molts
I25	M	4-19-76	5-14-76	25	14.60	17.10	2.50	1
K25	M	4-19-76	6-20-76	61	22.20	29.10	6.90	2
N25	F	4-19-76	7-18-76	90	18.20	25.55	7.35	2
S25	F	4-19-76	9-18-76	152	17.75	41.15	23.40	6
Y25	M	4-19-76	7-18-76	90	17.10	28.00	10.90	4
Z25	M	4-19-76	6-8-76	50	21.00	25.05	4.05	1
B26	M	4-19-76	5-16-76	27	19.40	22.50	3.10	1
D26	F	4-19-76	5-14-76	25	16.70	19.35	2.65	1
K26	M	4-27-76	5-29-76	32	21.25	21.30	0.05	0
M26	M	4-27-76	6-30-76	64	19.95	23.60	3.65	1
R26	M	4-27-76	6-30-76	64	19.45	27.95	8.50	2
T26	F	4-27-76	8-1-76	96	20.15	28.25	8.10	3
U26	M	4-27-76	5-29-76	32	18.15	18.20	0.05	0
B27	F	4-27-76	8-27-76	122	15.95	31.55	15.60	5
H27	M	5-3-76	7-28-76	86	22.60	32.30	9.70	3
Q27	F	5-3-76	7-18-76	76	19.65	31.60	11.95	3
U27	M	5-3-76	7-28-76	86	20.10	28.50	8.40	3
Z27	M	5-14-76	9-21-76	130	20.45	42.45	22.00	5
B28	M	5-14-76	6-20-76	37	18.55	22.45	3.90	1
E28	F	5-14-76	8-12-76	90	18.80	32.45	13.65	4
G28	F	5-14-76	6-20-76	37	20.35	24.75	4.40	1
H28	F	5-14-76	6-20-76	37	20.45	24.60	4.15	1
J28	M	5-14-76	6-20-76	37	19.55	23.45	3.90	1
N28	F	5-14-76	8-29-76	107	20.15	33.15	13.00	4
I29	M	5-14-76	7-18-76	65	21.55	30.80	9.25	3

Juvenile	Sex	Capture Date	Recapture Date	Field Interval (days)	Capture Carapace Length (mm)	Recapture Carapace Length (mm)	Carapace Length Increase (mm)	Estimated Number of Molts
H29	M	5-29-76	6-30-76	32	25.75	30.80	5.05	1
K29	F	5-29-76	9-10-76	104	25.20	40.45	15.25	3
L29	F	5-29-76	6-30-76	32	22.50	27.15	4.65	1
M29	M	5-29-76	8-17-76	80	14.85	25.70	10.85	3
P29	M	5-29-76	9-13-76	107	16.05	32.70	16.65	4
R29	F	5-29-76	8- 1-76	64	23.55	33.85	10.30	3
T29	M	5-29-76	8-17-76	80	22.50	32.35	9.85	3
U29	M	5-29-76	10-16-76	140	15.25	35.50	20.25	5
Y29	F	5-29-76	6-30-76	32	17.50	20.70	3.20	1
A30	F	5-29-76	7- 3-76	35	22.95	27.55	4.60	1
A31	F	6- 8-76	7-28-76	50	23.45	28.05	4.60	1
C31	F	6- 8-76	11- 4-76	149	15.95	35.55	19.60	5
V31	M	6-20-76	9-10-76	82	22.50	36.50	14.00	3
Z31	F	6-20-76	10-16-76	118	16.85	31.35	14.50	4
I32	M	6-20-76	7-18-76	28	22.20	25.60	3.40	1
P32	F	6-30-76	8-16-76	47	27.95	32.50	4.55	1
U32	F	6-30-76	7- 3-76	3	35.25	35.25	0	0
Y32	F	6-30-76	9-13-76	75	24.65	33.60	8.95	2
B33	M	6-30-76	8-14-76	45	21.10	28.70	7.60	2
D33	F	6-30-76	8-17-76	48	18.65	25.65	7.00	2
E33	M	6-30-76	8- 1-76	32	19.70	22.15	2.45	1
K33	F	7- 3-76	8-14-76	42	18.85	26.80	7.95	2
M33	F	7- 3-76	8-14-76	42	27.45	32.70	5.25	1
T33	M	7- 3-76	8-14-76	42	18.50	22.20	3.70	1
U33	M	7- 3-76	7-28-76	25	35.85	35.85	0	0

Juvenile	Sex	Capture Date	Recapture Date	Field Interval (days)	Carapace Length (mm)	Carapace Length (mm)	Recapture Increase (mm)	Carapace Length (mm)	Estimated Number of Molts
Y33	M	7- 3-76	7-18-76	15	23.30	23.30	0	0	0
P34	M	7-18-76	8-27-76	40	23.35	25.70	2.35	1	1
W35	M	8-12-76	9-18-76	37	38.10	43.35	5.25	1	1
Z35	M	8-12-76	5-18-78	644	37.80	59.25	21.45	4	4
F36	F	8-12-76	9-13-76	32	35.55	41.35	5.80	1	1
I36	M	8-14-76	9-10-76	27	34.75	39.55	4.80	1	1
J36	F	8-14-76	9-13-76	30	27.45	32.40	4.95	1	1
K36	F	8-14-76	9-10-76	27	34.40	38.95	4.55	1	1
N36	F	8-14-76	9-10-76	27	28.15	33.15	5.00	1	1
O36	M	8-14-76	9-10-76	27	32.35	37.25	4.90	1	1
B37	M	8-29-76	10-16-76	48	36.95	42.45	5.50	1	1
C37	F	8-29-76	10- 2-76	34	30.45	35.75	5.30	1	1
K37	M	9-13-76	10- 9-76	26	29.85	34.20	4.35	1	1
O37	M	9-10-76	10- 2-76	22	31.75	36.15	4.40	1	1
Q37	M	9-17-76	3-15-77	178	40.85	48.40	7.55	2	2
A38	M	9-18-76	10- 9-76	21	34.65	39.05	4.40	1	1
U38	F	10- 9-76	10-30-76	21	36.65	36.65	0	0	0
E39	F	10-30-76	7- 6-78	613	41.00	63.00	22.00	4	4

B. Two Recaptures

Juvenile	Sex	Capture Date	1st Field Interval			2nd Field Interval			Second Recapture Carapace Length (mm)
			Capture Carapace Length (mm)	Number of Days	Estimated Number of Molts	First Recapture Carapace Length (mm)	Number of Days	Estimated Number of Molts	
L2	M	12- 6-74	22.30	72	1	24.05	168	4	38.45
Q2	M	12- 6-74	21.05	131	1	22.75	32	1	25.65
B3	M	1- 8-75	18.85	24	0	18.85	21	0	18.80
N3	F	1- 8-75	16.15	90	1	17.35	90	2	22.85
X3	M	1-12-75	18.85	219	5	33.55	409	4	50.45
I4	F	1-21-75	15.50	190	4	24.95	174	3	37.90
L4	M	1-21-75	16.50	122	2	20.40	96	4	34.35
O4	M	1-21-75	18.35	26	0	18.35	73	1	20.60
T4**	M	1-30-75	16.80	119	1	19.20	42	1	21.80
W4**	M	1-31-75	19.40	107	2	23.85	51	1	27.30
Y4	F	1-31-75	16.65	18	1	18.25	49	0	18.25
Z4	F	1-31-75	15.65	18	1	16.95	23	0	16.95
H5	M	2- 1-75	17.20	62	0	17.15	41	1	18.90
J5	M	2- 1-75	16.50	15	0	16.50	88	1	18.70
B6	F	2-18-75	23.45	57	0	23.40	126	4	39.35
T6	F	3-13-75	18.70	193	6	38.05	383	4	59.60
M7*	M	4- 8-75	22.45	40	1	25.80	50	1	29.40
D8	F	4-16-75	16.60	81	3	23.05	23	0	23.05
F8	F	4-16-75	19.50	126	4	32.55	27	1	37.30
H8	F	4-16-75	19.70	29	0	19.65	50	3	28.25
I8	F	4-16-75	20.30	104	3	29.05	22	1	32.85
X8	M	5-15-75	22.70	52	1	27.65	25	1	31.80

Juvenile	Sex	1st Field Interval				2nd Field Interval			
		Capture Date	Carapace Length (mm)	Number of Days	Estimated Number of Molts	First Recapture Carapace Length (mm)	Number of Days	Estimated Number of Molts	Second Recapture Carapace Length (mm)
Y8	F	5-15-75	16.55	52	2	22.80	23	0	22.85
E10	M	7-6-75	19.45	45	1	22.40	27	1	26.25
B11	F	8-20-75	35.15	27	0	35.20	260	3	46.30
D11	F	8-20-75	29.45	34	1	35.15	127	2	43.25
A12	M	10-12-75	11.05	127	2	15.15	51	1	16.55
L12	F	10-13-75	10.95	126	2	14.00	77	2	18.95
G15	M	11-13-75	13.00	198	4	23.70	77	3	33.60
N16	M	1-16-76	15.40	5	0	15.40	103	2	20.85
P16	M	1-16-76	12.10	31	0	12.10	51	1	13.65
I17	F	1-21-76	13.45	114	2	17.90	37	1	21.55
NJ7	F	1-21-76	15.05	68	1	16.85	93	2	22.75
O17	M	1-21-76	12.25	129	2	16.05	32	1	19.25
U17	F	1-21-76	12.00	16	0	12.00	267	9	45.80
Y17	M	1-21-76	20.45	64	1	22.70	125	4	39.10
G18	F	1-21-76	15.75	52	1	17.35	137	3	27.85
L18	M	1-21-76	10.45	26	1	11.95	113	3	19.45
O18	M	1-21-76	15.20	164	4	27.30	72	2	37.90
K19	M	2-16-76	14.35	51	1	16.55	26	0	16.50
O20	F	3-5-76	15.85	192	6	35.55	90	2	42.55
V20	F	3-5-76	18.15	53	1	20.90	32	2	25.50
X21	M	3-13-76	25.15	51	1	28.45	94	3	39.55

Juvenile	Sex	1st Field Interval				2nd Field Interval				Second Recapture		
		Capture Date	Capture Length (mm)	Estimated Number of Days	Number of Molts	First Recapture Length (mm)	Number of Days	Estimated Number of Molts	Carapace Length (mm)	Carapace Length (mm)	Carapace Length (mm)	
K22	F	3-21-76	19.15	29	0	19.15	90	4	32.95			
W22	F	3-21-76	16.00	29	0	16.00	72	2	22.10			
F23	M	3-21-76	21.70	91	3	31.60	46	1	38.05			
W23	F	3-21-76	17.25	54	1	20.40	85	4	34.35			
X23	F	3-21-76	13.50	29	0	13.45	25	1	15.40			
E24	M	3-29-76	17.65	96	3	25.05	44	2	35.50			
M24	F	3-29-76	13.50	111	3	22.45	29	1	26.80			
O24	M	3-29-76	12.85	29	1	15.05	96	4	26.15			
P24	M	3-29-76	21.40	29	0	21.40	32	1	25.05			
O25	M	4-19-76	14.00	25	1	16.70	25	0	16.70			
P25	F	4-19-76	20.70	25	1	24.30	25	0	24.25			
E26	M	4-19-76	13.00	25	1	15.05	155	6	34.95			
P26	F	4-27-76	20.80	32	1	24.45	32	1	29.25			
S26	M	4-27-76	20.70	67	2	28.20	69	2	38.95			
X26	F	4-27-76	18.70	32	1	22.35	32	1	37.25			
U28	F	5-14-76	15.45	139	6	37.30	1	0	31.05			
G29	F	5-29-76	17.55	50	2	24.90	64	2	27.30			
J29	F	5-29-76	22.20	104	3	36.35	29	0	36.30			
Q29	F	5-29-76	23.10	90	4	38.05	105	2	46.35			
X29	M	5-29-76	25.60	35	1	30.30	161	3	46.00			
B30	F	5-29-76	16.00	42	2	22.55	45	1	26.45			

Juvenile	Sex	1st Field Interval				2nd Field Interval			
		Capture Date	Capture Length (mm)	Estimated Number of Days	Number of Molts	First Recapture Carapace Length (mm)	Estimated Number of Days	Number of Molts	Second Recapture Carapace Length (mm)
W32	M	6-30-76	25.95	45	1	30.55	133	3	46.25
I33	M	7-3-76	17.05	42	1	20.15	90	3	33.65
X33	M	7-3-76	22.95	69	2	31.05	29	1	34.50
G34	M	7-18-76	29.55	62	3	42.35	13	0	42.35
K34	F	7-18-76	27.95	76	3	43.05	163	2	52.80
M36	F	8-14-76	32.05	47	1	36.95	9	1	41.05

C. Three Recaptures

Juvenile	Sex	Capture Date	Capture Carapace Length (mm)	Estimate Number of Males	Estimate Number of Females	Number of Days	1st Field Interval		2nd Field Interval		3rd Field Interval	
							Days	Carapace Length (mm)	Days	Carapace Length (mm)	Days	Carapace Length (mm)
A3	M	1-8-76	24.05	24	0	24.05	17	0	24.05	49	0	24.05
F4*	M	1-14-76	15.40	124	1	17.45	50	2	23.35	35	1	28.10
Y5	M	2-10-76	16.85	23	1	18.50	22	0	18.50	65	3	27.75
F6	M	2-22-76	16.25	21	0	16.25	61	1	18.20	75	2	25.25
I6	F	2-22-76	18.15	85	1	21.20	50	2	28.60	22	0	28.60
K6	F	2-22-76	18.65	85	1	21.85	47	1	25.55	25	1	28.05
P6	F	2-23-76	21.95	84	2	28.15	50	1	32.15	44	1	38.40
I7	F	4-8-75	17.70	40	1	20.25	50	1	23.75	39	3	34.00
G8	M	4-16-75	19.35	100	2	26.35	50	1	31.15	71	2	38.35
W8	M	5-15-75	19.30	8	0	19.25	44	3	27.35	46	1	30.45
G9	F	5-18-75	25.70	41	1	30.30	33	0	30.30	20	1	33.50
J15	F	11-13-75	19.65	26	1	22.55	78	1	25.65	104	2	32.25
X15	M	11-14-75	14.05	197	4	23.85	35	2	29.20	42	1	34.35
M16	M	1-16-76	19.20	57	0	19.15	77	2	25.60	68	3	37.05
C17	F	1-21-76	19.05	97	1	21.35	32	1	24.35	32	1	25.20
W17	F	1-21-76	11.50	97	2	14.75	32	1	17.70	77	3	29.85
M18	F	1-22-76	16.00	25	0	16.00	51	1	18.10	26	1	21.00
T18	F	2-6-76	20.80	29	0	20.80	53	1	23.50	32	0	23.50
F20	F	3-5-76	12.30	120	3	21.25	42	2	29.90	3	0	29.90
H20	M	3-5-76	13.05	135	4	27.10	27	0	27.05	30	1	31.20
Z20	F	3-5-76	10.30	53	1	11.90	64	3	19.40	75	2	26.00
K21	M	3-13-76	13.25	137	6	27.50	66	2	37.65	649	5	57.75
V25	F	4-19-76	16.55	25	0	16.55	65	4	28.20	61	1	33.40
Q26	M	4-27-76	18.10	64	1	20.75	45	2	28.70	27	0	28.70
Z26	F	4-27-76	15.70	32	1	18.45	35	1	22.25	72	4	37.05
F27	M	4-27-76	13.55	32	1	16.00	50	2	22.55	30	0	22.55
S29	F	5-29-76	20.10	32	1	24.25	32	1	28.30	13	1	33.05
C33	F	6-30-76	22.25	45	1	25.70	16	0	25.70	24	1	29.45

D. Four Recaptures

Eine Wissenschaft

E. Five recaptures
F20 F 3- 5-76 15.00 24 0 14.05 66 2 20.05 31 1 24.65 45 1 29.10 60 2 40.90

* Juvenile was recaptured from isolated patch of *Phyllospadix* 85 m west of the dike at Bird Rock.

** Juvenile was recaptured from the Lathmus Reef lalidrys habitat.

APPENDIX IV

JUVENILE P. INTERRUPTUS GROWTH RECORDS OBTAINED FROM
45 INDIVIDUALS RAISED IN LABORATORY AQUARIA BETWEEN
OCTOBER 1974 AND JANUARY 1977

CL_0 CL_1 ... = Carapace length in millimeters for
capture instar and each succeeding instar.

TM_1 TM_2 ... = Time in days to first post-capture molt
and each succeeding molt.

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Preliminary measurement taken on January 6, 1977.

