LABORATORY STUDY OF BEHAVIORAL INTERACTIONS BETWEEN THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, AND THE CALIFORNIA SPINY LOBSTER, *PANULIRUS INTERRUPTUS*, WITH COMPARATIVE OBSERVATIONS ON THE ROCK CRAB, *CANCER ANTENNARIUS*[1]

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ABSTRACT

Behavioral interactions between *Homarus americanus* and *Panulirus interruptus*, with comparative observations on *Cancer antennarius*, were studied in order to determine the possible effects an introduced population of *H. americanus* would have on the southern California population of *P. interruptus*. Subjects were placed in tanks 3 m in diameter with observational windows equally spaced around the tank perimeter. Three 30-min observation periods were conducted on the lobsters each day for a 5-day precontrol period (*H. americanus* absent), a 10-day experimental period (*H. americanus* present), and a 5-day postcontrol period (*H. americanus* absent). Five replicates of a shelter and no shelter condition were made with five naive *P. interruptus* and one *H. americanus* for each replicate. Agonistic action patterns were recorded for actors and reactors, along with various other behaviors, on data sheets partitioned into 1-min intervals. A large percentage of *Homarus*-initiated behavioral actions in the shelter (44%) and no shelter (39%) conditions involved threat and attack by *H. americanus*. In *Homarus*-initiated interactions, *P. interruptus* was displaced by *H. americanus* 61% of the time in the shelter condition and 63% of the time in the no shelter condition. Although *Panulirus*-initiated interactions occurred much less frequently, the results were similar to the *Homarus*-initiated interactions in that *P. interruptus* was ultimately displaced by threatening and attacking *H. americanus* 92% of the time in the shelter condition and 76% of the time in the no shelter condition. Our results, and those of other studies, are discussed with respect to the potential adverse effects of introducing *H. americanus* into southern California waters. The evidence suggests that such an introduction is inadvisable.

At the present time, there is strong interest from the private sector in introducing the American lobster, *Homarus americanus*, into California waters. This interest arises primarily from the marked downward trend in annual landings of the California spiny lobster, *Panulirus interruptus*, and the high unit value and continuing demand for lobster species in general and in particular for the American lobster, which supports one of the most valuable fisheries in North America. Conditions along the entire California coast appear well within the limits tolerated by larvae, juveniles, and adults of *H. americanus*. Thus, with the recent development of successful mass culture techniques (Hughes, 1968; Ghelardi and Shoop, 1968; Kensler, 1970), the species probably could be established, at least by means of continued stocking (Ghelardi and Shoop, 1972).

Despite the apparent value of the American lobster as a Pacific Coast fishery, there are several potential detrimental effects of introducing it into the Pacific which must be considered (Rathbun, 1888; Ghelardi, 1967). These are: 1) the introduction of disease, parasitic organisms, or other microfauna and microflora harmful to native species and 2) the elimination or reduction in abundance of ecologically similar forms, such as *P. interruptus*, in areas where *H. americanus* might become established.

Introductions of some foreign animals and plants have had very serious effects on native species (Elton, 1958). Thus, there is a great need for effective evaluation and control of exotic species introductions, as recently discussed by Lachner, Robins, and Courtenay (1970). There have been at least 23 attempts to introduce

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H. americanus between Monterey Bay and British Columbia (Ghelardi and Shoop, 1968). The exact reasons for the failure of these introductions are unknown. However, three possible causes were: 1) low stocking density, 2) unsuitability of the locations used for introductions, and 3) possible injuring or weakening of lobsters through mishandling or disease before the introductions (Ghelardi and Shoop, 1968). In the lobster transplants, as in virtually all other attempts to transplant species, there has been little or no effort to evaluate the impact the exotic would have on native species or to control pathogens and other potentially harmful organisms associated with it. Only the recent pilot introduction in British Columbia by Ghelardi and Shoop (Ghelardi, 1967; Ghelardi and Shoop, 1972) considered potential detrimental effects and was conducted on a truly scientific basis.

While it might be argued that one can never determine what the effects of an exotic introduction will be until it takes place, we feel that a serious attempt must be made to evaluate potential adverse effects by laboratory studies before even a small-scale pilot transplant is attempted. During the period 1970-73 we, and others of our group, have conducted a series of studies on the social interactions of *H. americanus* with ecologically similar decapod crustaceans from southern California waters. This paper describes the results of one of our studies concerning interactions between *H. americanus* and *P. interruptus* with comparative observations on *P. interruptus* and the rock crab, *Cancer antennarius*. In it, we have primarily considered agonistic interactions. Other studies have shown that interspecific aggression can be important in regulating the lives of sympatric species (see Aspey, 1971; also Myreberg, 1972a).

METHODS AND MATERIALS

American lobsters were purchased in San Diego from the Gulf of Maine Lobster Corporation. They were quarantined 2 wk in a large holding tank (0.5 × 1.2 × 2.3 m) for effects of gaffkemia or other diseases before being introduced to experimental tanks. California spiny lobsters and rock crabs were trapped in shallow water off the San Diego coast and were either introduced directly into experimental tanks or maintained for short periods in holding tanks of the same size employed for *H. americanus*.

Holding tanks were supplied with fresh running seawater from the Scripps Institution system. The temperature of the water in tanks varied throughout the year in close correspondence with ambient ocean temperatures, from a minimum of 14°C in January to a maximum of 23°C in August. The study began in July 1972 and ended in April 1973. Lobsters and crabs in holding tanks were fed frozen squid, *Loligo opalescens*, and northern anchovy, *Engraulis mordax*, twice a week. No attempt was made to control the photoperiod for these individuals while in the holding tanks. However, they were exposed to the normal day-night cycle during this period from light entering through the walls, roof, and building openings.

Three experimental tanks were used, each 3.04 m in diameter and 1.22 m in height, with a capacity of approximately 9,000 liters. Each tank had four observation windows 68.5 × 48.0 cm positioned equidistant around the perimeter. The tanks were enclosed in lightproof tents made of black Mobil Kordite[3] polyethylene sheeting of 6-mil thickness. Lobsters in the experimental tanks received 11 h of light daily from 0400 to 1500 P.s.t. (Pacific standard time), supplied by two 75-W General Electric floodlights. The experimental subjects were not fed while in the experimental tanks so as to eliminate the variable of interactions for food.

Three experimental conditions were studied. These were: 1) social interaction between *P. interruptus* and *H. americanus* in the absence of shelter, 2) social interaction between *P. interruptus* and *H. americanus* with more shelters than lobsters, and 3) social interaction between *P. interruptus* and *C. antennarius* without shelter. Seven shelters were provided for the experimental condition involving interaction between *P. interruptus* and *H. americanus* with shelter. The shelters, which measured 25 cm in width, 38 cm in length, and 14 cm in height, were made by cutting 76-cm sections of concrete conduit lengthwise and then into 38-cm lengths.

In each experimental condition, five California spiny lobsters and either one American lobster or one rock crab were employed. Five replicates of each experimental condition were made using naive animals for each replicate. The 5:1 ratio used for the *P. interruptus* and *H. americanus*

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

interactions was a compromise between a representative density which might result from a large stocking of *H. americanus* in natural habitats on the southern California coast and the physical limitations of the experimental tanks which prevented using more *P. interruptus*. Both males and females of each lobster species were used for experiments. However, only male *C. antennarius* were used because all females obtained were carrying eggs at the time these experiments were conducted.

Interaction experiments involving *P. interruptus* and *C. antennarius* were employed to help in the process of assessing potential effects *H. americanus* might have on *P. interruptus*. That is, we wanted to establish a behavioral base line by using a clawed decapod crustacean which is naturally sympatric with *P. interruptus*. Thus, the 5:1 ratio used for the *C. antennarius* and *P. interruptus* interactions was employed for comparative purposes.

The *P. interruptus* subjects used ranged in weight from 209 to 911 g, with a mean of 436 g. *Homarus americanus* used weighed from 417 to 635 g, with a mean of 471 g. *Cancer antennarius* used ranged in weight from 560 to 840 g, with a mean of 673 g. California spiny lobsters were assigned to groups by a randomization process. Each group usually consisted of both sexes and individuals which were larger, smaller, and the same size as the single American lobster tested. *Cancer antennarius* used in the experiments weighed more than most of the California spiny lobster subjects with which it was tested. An attempt was made to use *P. interruptus* that weighed between 400 and 600 g for all experiments so that their weight matched the weight of the *H. americanus* available to us. As a result of poor trap catches, however, we were sometimes forced to use *P. interruptus* that were either smaller or larger than the *H. americanus* subjects.

Each of the 15 separate experiments consisted of three observation periods. These were called the precontrol, experimental, and postcontrol periods. For the social interaction experiments involving *P. interruptus* and *H. americanus*, precontrol observations were taken for 5 days, experimental observations were taken for 10 days, and postcontrol observations were taken for 5 days. For the experiments involving social interactions between *P. interruptus* and *C. antennarius*, the precontrol, experimental, and postcontrol observation periods were all 5 days in duration. For the precontrol observation period, only individuals of *P. interruptus* were present in the experimental tanks. Upon completion of the precontrol period, an *H. americanus* or *C. antennarius* was introduced into the tank. Following the experimental observation period, the *H. americanus* or *C. antennarius* was removed and the postcontrol observations of *P. interruptus* taken.

For *P. interruptus* and *H. americanus* experiments, three 30-min observation periods were conducted daily for each tank. These 30-min observation periods were taken between 0800 and 1000 (4-6 h after the onset of the lights), 1200 and 1400 (8-10 h after the onset of the lights), and 1510 and 1700 h (10 min-1 h 50 min after the lights went off) P.s.t. for precontrol, experimental, and postcontrol periods. In the experiment involving *P. interruptus* and *C. antennarius*, only two 20-min observation periods were taken daily. One was taken between 0800 and 1000 and the other between 1510 and 1700. The 1200-1400 observation period was omitted because of the low frequency of interactions shown by these species during initial observations. Table 1 summarizes the experimental paradigm used for this study.

Observations taken between 1510 and 1700 were made using two 100-W red lights with a spectral distribution between 550 and 720 nm. Most of the red light (75%) fell within 600-650 nm. Spectral sensitivity of *H. americanus* ranges from 400 to 600 nm with peak sensitivity at 520-525 nm (Kennedy and Bruno, 1961). At present no information exists on the spectral sensitivity of *P. interruptus*, but the assumption was made that this species also is insensitive to light within this spectral range. During the study, we observed no evidence that movement and social behavior of either species was inhibited by the use of red lights.

TERMINOLOGY

The frequency and type of behavioral interactions between *P. interruptus* and *H. americanus* or *C. antennarius* were recorded on a data sheet which was partitioned into 1-min intervals. The behavior of the actor (the individual presenting the stimuli or initiating the interaction) and the subsequent response of the reactor (the individual

TABLE 1.—Experimental paradigm for social interaction study between *Homarus americanus*, *Panulirus interruptus*, and *Cancer antennarius*

Experimental condition	Precontrol			Experimental			Postcontrol		
	Number of days	Length of observation periods (min)	Time of observations	Number of days	Length of observation periods (min)	Time of observations	Number of days	Length of observation periods (min)	Time of observations
H. americanus vs. *P. interruptus* No shelter	5	30	0800-1000 1200-1400 1510-1700	10	30	0800-1000 1200-1400 1510-1700	5	30	0800-1000 1200-1400 1510-1700
H. americanus vs. *P. interruptus* Shelter	5	30	0800-1000 1200-1400 1510-1700	10	30	0800-1000 1200-1400 1510-1700	5	30	0800-1000 1200-1400 1510-1700
P. interruptus vs. *C. antennarius* No shelter	5	20	0800-1000 1510-1700	5	20	0800-1000 1510-1700	5	20	0800-1000 1510-1700

responding to the stimuli) were both recorded in the predetermined categories described below. In addition, the amount of locomotion displayed by subjects, their location in the tank with respect to the wall, and the number of individuals in shelters, when present, were recorded. The behavioral action patterns of *P. interruptus, H. americanus,* and *C. antennarius* described by previous workers were employed in this study where possible.

I. The following categories were employed for the actor: A) Approach, B) Threat, C) Attack, and D) Social contact. These terms are defined, in most cases, separately for each of the three species considered.

A) Approach—Movement of the actor directly toward a moving or stationary heterospecific. During approach, the actor compensates for changes in the direction of movement of a moving heterospecific so that the actor is always moving directly toward the heterospecific. No implication of function is intended in our use of the term approach.

B) Threat

1) *Homarus americanus*

Meral spread—In this study only the display described by Schrivener (1971) as meral spread was recorded as threat. Schrivener's description of this behavior is as follows: "During meral spread, the lobster stands on its walking legs with its body raised from 4 to 5 cm off the bottom. The abdomen is usually fully extended, with the cephalothorax angled slightly upwards from the horizontal. The chelae are held about 5 cm off the bottom spread wide apart with their long axes pointing directly at the opponent. Some animals hold the claws fully extended, wide apart, and as high off the bottom as possible."

2) *Cancer antennarius*

Lateral Merus Display—The merus of the chelipeds is extended laterally, with the distal end of the meri raised and extended somewhat anteriorad. The higher the intensity of the display, the greater is the lateral spreading of the chelipeds (Schone, 1968; Wright, 1968). Wright (1968) subdivides the Lateral Merus Display into three subtypes based on the position of the chelae. These are: 1) the High-Intensity Merus Display in which the chelae are unflexed (maximum adduction) with the tips held laterally; 2) the Mid-Intensity Merus Display in which the chelae are half flexed so that the tips point forward; and 3) the Low-Intensity Merus Display in which the chelae are flexed, with their tips medial. All intensities of the meral spread were observed, but these were simply recorded together as threat in our study.

3) *Panulirus interruptus*
   Two of the aggressive postures described by Roth (1972) were used in this study. These aggressive postures are body raise and rear-up. We observed that these are the most common and morphologically distinct aggressive postures exhibited by *P. interruptus*.
   a) Body raise—Raising the body off the substrate by partial extension of the walking legs. This corresponds to Roth's term Rise Up (R_1).
   b) Rear-up—Raising the body off the substrate by full extension of the third, fourth, and fifth walking legs. The anterior part of the body is raised much higher than the posterior part of the body. This was also called Rise Up by Roth (R_2 and R_3). However, we have combined his R_2 and R_3 into a separate category, rear-up, because they appear to be different intensities of the same behavior action pattern, which is distinct from R_1.

C) Attack
   1) *Homarus americanus* and *Cancer antennarius*
      Four actions were included under attack. These were pinch, push, scissoring, and chase.
      a) Pinch—Rapid gripping and release of any part of a California spiny lobster's body with one or both chelipeds.
      b) Push—Contact between the chelipeds and any part of a California spiny lobster's body when the chelipeds are thrust forward while the body remains stationary or the chelipeds are extended or in a meral spread in a stationary position during locomotion.
      c) Scissoring—As described by Schrivener (1971) for *H. americanus*, "This occurs when one lobster faces its opponent, with the chelae in the meral spread posture (spread wide apart, long axes of the palms pointing at the adversary). The chelae are then rapidly brought together in a scissoring motion. As a result, they either strike or pass rapidly in front of the other animal."
      d) Chase—During chase the actor moves rapidly toward a heterospecific that in turn is usually moving rapidly and is obviously trying to remove itself from the vicinity of the lobster following it. Chase was recorded only after the actor and reactor had been within 30 cm from one another. Frequently, chase precedes a push or pinch and follows an initial lunge by an actor towards the reactor. During chase *H. americanus* usually displays meral spread.
   2) *Panulirus interruptus*
      Two actions were included under attack. These were physical contact and chase.
      a) Physical contact—This involves colliding with some part of a heterospecific's body; in some cases clasping of the opponent with the first three pairs of walking legs or a bite may occur. This includes Roth's (1972) low intensity attack (A_1), high intensity attack (A_2), and clasp (CL).
      b) Chase—Rapid locomotion toward a reactor while it is removing itself from the vicinity of the lobster following it.

D) Social contact—Two heterospecifics were recorded as having social contact when one of the following events occurred.
   1) Two or more heterospecifics came within 30 cm of one another during movement about the tank without aggressive interaction occurring. This category was recorded

whether one or both animals were moving, and in some cases direct physical contact was made.

2) Two or more heterospecifics were touching or within 30 cm of one another, were not moving, and exhibited no aggressive interaction. Social contact during movement was distinguished from approach by the absence of direct movement of heterospecifics toward one another. That is, the animals were not on a collision course.

II. The following categories were employed for the reactor: A) No response, B) Walk away, C) Abdomen flex, D) Threat, and E) Attack.

A) No response—No change in the overt behavior of the reactor.

B) Walk away—Movement away from an approaching, threatening, or attacking heterospecific, using the walking legs.

C) Abdomen flex—Movement away from an approaching, threatening, or attacking heterospecific, using rapid flexion of the abdomen.

D) Threat—The description(s) of threat used for *H. americanus, P. interruptus*, and *C. antennarius* provided above for actors (I-B) was also used for the reactor.

E) Attack—The description(s) of attack used for *H. americanus, P. interruptus*, and *C. antennarius* provided above for actors (I-C) was also used here for the reactor.

III. Additional categories used on the data sheet and their definitions were as follows:

A) Roaming—Slow or moderate walking about the tank. During roaming, direct interaction between heterospecifics or conspecifics does not occur. For *P. interruptus*, roaming by an individual was recorded only if it occurred for 31 s or more during a 1-min interval. For *H. americanus* and *C. antennarius*, the amount of time they were observed roaming during each 1-min interval was recorded.

B) Wall—Like many decapods, *P. interruptus* exhibits thigmotactic behavior. When shelter is absent individuals are found with their bodies in contact with a solid object. In our no shelter condition, the tank wall was the only solid object present. A lobster that had some part of its body, excluding the antennae, within 30 cm of the side of the tank for 31 s or more of each 1-min interval was recorded as wall. The location of a lobster within the tank that was greater than 30 cm from the side of the tank for 31 s or more of each 1-min interval was recorded as no wall.

C) Group—A congregation of two or more subjects, each within 30 cm of one another. Thus, in a group of five *P. interruptus*, a maximum distance of 120 cm would separate lobsters at opposite ends of a group.

RESULTS AND DISCUSSION

Agonistic Behavior

The frequency and outcome of agonistic behavioral interactions between *H. americanus* and *P. interruptus* for conditions involving shelter and no shelter are shown in Table 2. Similar data also are presented in this table for interactions between *P. interruptus* and *C. antennarius*.

Homarus vs. *Panulirus* with No Shelter

There were a total of 2,515 *Homarus*-initiated behavioral interactions by actors for the five replicate *H. americanus-P. interruptus* no shelter experiments. Twenty percent of the behavioral interactions were classed as social contact, 40% as *Homarus* approach, 24% as *Homarus* threat, and 15% as *Homarus* attack (Table 2). Sixty-eight percent (1,700) of the *Homarus*-initiated behavioral interactions occurred during the 1510-1700 h observation period (lights off).

There were a total of 1,683 responses by reactors to *Homarus*-initiated interactions. Thirty seven percent of these were classed as no response, 49% *Panulirus* walk away, and 14% *Panulirus* abdomen flex (Table 2). Thus, *P. interruptus* was displaced a total of 63% of the time when *H. americanus* initiated a behavioral interaction. *Panulirus interruptus* was never observed to threaten or attack *H. americanus* in *Homarus*-initiated behavioral interactions.

A total of 227 *Panulirus*-initiated behavioral interactions were recorded in the five replicate

TABLE 2.—The total number of behavioral interactions between *Homarus americanus* and *Panulirus interruptus* during 10-day experimental periods for the shelter (n = 5 groups) and no shelter (n = 5 groups) conditions, and between *P. interruptus* and *Cancer antennarius* during 5-day periods for a no shelter condition (n = 5 groups). Social contact (SC) and no response (NR) for *Homarus*-initiated interactions include both *Homarus* and *Panulirus* actions where only social contact occurred. HA = *Homarus* approach; HT = *Homarus* threat; HAT = *Homarus* attack; PWA = *Panulirus* walk away; PAF = *Panulirus* abdomen flex; PA = *Panulirus* approach; PT = *Panulirus* threat; PAT = *Panulirus* attack; HWA = *Homarus* walk away; HAF = *Homarus* abdomen flex; CA = *Cancer* approach; CT = *Cancer* threat; CAT = *Cancer* attack; CWA = *Cancer* walk away.

Homarus-initiated interactions

		Actor					Reactor			
P.s.t.	Experimental condition	SC	HA	HT	HAT		NR	PWA	PAF	
0800	No shelter	177	172	106	56		207	156	24	
	Shelter	7	6	1	2		8	5	1	
1200	No shelter	97	97	63	47		128	92	43	
	Shelter	6	2	1	1		7	3	1	
1510	No shelter	238	748	438	276	Σ = 1,700 (68%)	299	572	162	Σ = 1,033 (61%)
	Shelter	24	104	74	41	Σ = 243 (90%)	53	72	27	Σ = 152 (86%)
Totals	No shelter	512	1,017	607	379	Σ = 2,515	634	820	229	Σ = 1,683
	Percent	20	40	24	15		37	49	14	
	Shelter	37	112	76	44	Σ = 269	68	80	29	Σ = 177
	Percent	14	42	28	16		38	45	16	

Panulirus-initiated interactions

		Actor			Reactor				
P.s.t.	Experimental condition	PA	PT	PAT	NR	HWA	HAF	HT	HAT
0800	No shelter	36	0	0	3	1	0	29	16
	Shelter	3	0	0	0	0	0	3	0
1200	No shelter	83.	1	0	7	3	1	65	26
	Shelter	3	0	0	1	0	0	2	1
1510	No shelter	107	0	0	6	41	4	54	21
	Shelter	22	0	0	0	2	0	20	5
Totals	No shelter	226	1	0	16	45	5	148	63
	Percent	100	0	0	6	16	2	53	23
	Shelter	28	0	0	1	2	0	25	6
	Percent	100	0	0	3	6	0	74	18

Cancer-*Panulirus* interactions

		Actor							Reactor							
P.s.t.	Experimental condition	SC	CA	PA	CT	PT	CAT		NR	CWA	PWA	PAF	CT	PT	CAT	
0800		130	4	16	2	0	5		145	0	6	0	2	0	2	
1510		37	8	20	2	3	2		49	0	15	0	9	0	3	
Total	No shelter	167	12	36	4	3	7	Σ = 229	194	0	21	0	11	0	5	Σ = 231
	Percent	73	5	16	2	1	3		84	0	9	0	5	0	2	

experiments. Of these, 226 were *Panulirus* approach while only 1 was *Panulirus* threat (Table 2). There was a total of 277 responses by the reactors (*Homarus*). Sixteen (6%) of these were classed as no response, 45 (16%) as *Homarus* walk away, 5 (2%) as *Homarus* abdomen flex, 148 (53%) as *Homarus* threat, and 63 (23%) as *Homarus* attack (Table 2). Thus, 76% of *H. americanus* responses to *P. interruptus* approach were threat and attack. These threats and attacks by *H. americanus* subsequently resulted in displacement of *P. interruptus* from the immediate area.

The number of behavioral actions by both the actor (primarily *Homarus*) and reactor (primarily *Panulirus*) decreased with time, as shown in Table

3. There was a significant reduction in *Homarus*-initiated actions with time as indicated by the results of a Spearman Rank Correlation Analysis ($r_s = -0.66$, $P < 0.05$; Siegel, 1956). Social contact was excluded from the statistical analysis of actor actions because it included and did not differentiate *H. americanus* and *P. interruptus*-initiated interactions. Most social contact, however, was initiated by *H. americanus*. There also was a significant decrease in behavioral actions with time for *P. interruptus* responses ($r_s = -0.82$, $P < 0.01$). Only *Panulirus* walk away and abdomen flex were considered. No response was excluded from the statistical analysis of reactor actions because it included both *H. americanus* and *P. interruptus* responses.

In the absence of shelter, some *H. americanus* excavated a depression in the sand where they remained when they were not roaming. When a *P. interruptus* approached an *H. americanus* in its sand depression, the likelihood of attack increased, and the attacks appeared to last longer and involve more pinching.

Homarus vs. *Panulirus* with Shelter

The addition of seven shelters reduced the number of *Homarus*-initiated interactions as compared with the no shelter condition. A comparison of all *Homarus*-initiated interactions (both actor and reactor) between the shelter and no shelter conditions indicated that *Homarus*-initiated interactions for the shelter condition were significantly reduced ($P = 0.01$, Wilcoxon matched-pairs test; Siegel, 1956). There were a total of 269 behavioral actions by actors and 177 by reactors (Table 2). Ninety percent (243) of the behavioral actions by actors and 86% (152) of behavioral actions by the reactors occurred in the 1510-1700 h observation period.

Fourteen percent of the *Homarus*-initiated interactions of actors were classed as social contact, 42% as *Homarus* approach, 28% as *Homarus* threat, and 16% as *Homarus* attack. The behavioral actions of the reactors were 38% no response, 45% *Panulirus* walk away, and 16% *Panulirus* abdomen flex.

There was a total of 28 *Panulirus*-initiated behavioral actions for the five replicate experiments. All were classed as *Panulirus* approach. Thirty-four behavioral actions by *H. americanus* (reactor) resulted. Of these, 1 was classed no response, 2 *Homarus* walk away, 25 *Homarus* threat, and 6 *Homarus* attack. Thus, 92% of these responses of *H. americanus* to *Panulirus* approach involved threat and attack.

Most of the behavioral interactions that occurred in the *Homarus-Panulirus* shelter condition took place when the lobsters were out of their shelters. On some occasions, however, *H. americanus* attacked *P. interruptus* while they were in shelters. When this occurred *H. americanus* entered the shelter through the front entrance, the attack ensued, and *P. interruptus* fled through the back entrance which was nearly flush against the side of the tank. The amount of time *H. americanus* remained in the shelter of the displaced *P. interruptus* varied greatly. Some *H. americanus* left the shelter within 1 min and either roamed or displaced another *P. interruptus* from its shelter. Others remained in the shelter longer, and some for the duration of the observation period. *Panulirus interruptus* that approached *H. americanus* in a shelter were usually

TABLE 3.—The total number of *Homarus americanus*-initiated behavioral interactions with *Panulirus interruptus* by day for the no shelter condition ($n = 5$ groups). These totals include data from morning, noon, and evening observations. Social contact (SC) and no response (NR) totals include both *H. americanus* and *P. interruptus* actions. However, the great majority of SC is *Homarus* initiated, and the great majority of NR is derived from *Panulirus*. HA = *Homarus* approach; HT = *Homarus* threat; HAT = *Homarus* attack; PWA = *Panulirus* walk away; PAF = *Panulirus* abdomen flex.

	Actor						Reactor				
Day	SC	HA	HT	HAT	Total	Total[1]	NR	PWA	PAF	Total	Total[2]
1	113	234	116	65	528	415	146	185	38	369	223
2	48	112	93	61	314	266	59	92	22	173	114
3	25	85	56	37	203	178	32	78	29	139	107
4	32	85	73	55	245	213	42	72	28	142	100
5	49	79	18	15	161	112	53	68	12	133	80
6	40	92	51	26	209	169	45	84	16	145	100
7	37	108	59	36	240	203	54	72	29	155	101
8	93	109	72	48	322	229	105	75	32	212	107
9	53	75	46	19	193	140	66	65	10	141	75
10	22	38	23	17	100	78	34	29	13	76	42

[1]These totals exclude SC.
[2]These totals exclude NR.

quickly threatened or attacked. However, this event was rare.

When *H. americanus* pinched *P. interruptus*, in both the shelter and no shelter condition, the pincer claw appeared to be the only one used. *Panulirus interruptus* that had been attacked, and especially those pinched by *H. americanus*, appeared to move away from an approaching *Homarus* in subsequent encounters at greater distances than they did initially before they had been attacked.

***Panulirus* vs. *Cancer* with No Shelter**

There was little aggression shown in behavioral interactions between *P. interruptus* and *C. antennarius*, species which commonly occur together in nature. A total of 229 behavioral actions were initiated by actors. Of these, 73% (167) were classed as social contact, 5% (12) as *Cancer* approach, 16% (36) as *Panulirus* approach, 2% (4) as *Cancer* threat, 1% (3) as *Panulirus* threat and 3% (7) as *Cancer* attack (Table 2). There was a total of 231 responses by the reactors. Eighty-four percent (194) of these were classed as no response, 9% (21) were classed as *Panulirus* walk away, 5% (11) as *Cancer* threat, and 2% (5) as *Cancer* attack.

One of us (Krekorian) observed *P. interruptus* walk over *C. antennarius* 21 times with no response from the latter species. This was never observed between *P. interruptus* and *H. americanus*. In addition, on 63 occasions noninteracting groups were observed composed of two or more *P. interruptus* and *C. antennarius* within 30 cm of one another, and on 50 other occasions similar groups were observed consisting of *C. antennarius* and one *P. interruptus*. In contrast, we never observed groups composed of *H. americanus* and *P. interruptus*.

Discussion of Agonistic Behavior

These results show that a large percentage of *Homarus*-initiated behavioral interactions in the shelter (44%) and no shelter (39%) conditions involved aggressive behavior (*Homarus* threat + *Homarus* attack, Table 2). The response of *P. interruptus* to *Homarus* approach and aggressive acts was usually defensive. In the shelter condition *P. interruptus* was displaced by *H. americanus* 61% of the time. *Panulirus* either walked away or used an abdomen flex to remove itself from the area occupied by *Homarus*. In the no shelter condition *P. interruptus* was displaced 63% of the time. Although shelter reduced the total number of behavioral interactions initiated by *H. americanus*, the percentages for aggressive and defensive acts remained about the same (Table 2).

The number of *Panulirus*-initiated behavioral interactions was far less than the number of behavioral interactions initiated by *Homarus*. However, the result of the interactions which followed were qualitatively the same. That is, *P. interruptus* was ultimately displaced by threatening and attacking *H. americanus* in the shelter (92% of the time) and no shelter (76% of the time) conditions.

Grasping of one *H. americanus* by another was rarely involved in the agonistic encounters observed by Schrivener (1971). In contrast to this, we frequently observed *H. americanus* pinching *P. interruptus*. Pinching by *H. americanus* is typical of its predation behavior. At no time in our study did we observe *P. interruptus* attack *H. americanus* or *C. antennarius*.

Studies by other members of our group have shown that the laboratory activity rhythms of *P. interruptus* and *H. americanus* over a 24-h period are very similar, both species exhibiting their highest levels of activity during the first 4 h of darkness (Van Olst and Carlberg, pers. commun.). This similarity in the timing of activity probably would intensify interactions between the two species in the field. Such interactions could result in *P. interruptus* being displaced from areas occupied or frequented by *H. americanus*, and/or being placed under considerable stress due to possible competition for food, suitable refuges, or other aspects of space within the habitat. In the laboratory, *H. americanus* displaced *P. interruptus* when there was only one shelter for two lobsters (Lester, pers. commun.) and inhibited *P. interruptus* from feeding when food was limited (Neëdham, pers. commun.).

Assuming that the behavior displayed by the two lobster species in the laboratory would be similar to that occurring in the field, one would expect considerable agonistic interaction between the two species if they were to occupy the same habitat. Although there have been few studies that have thoroughly compared the behavior of animals in the laboratory with their behavior in the field, there are some data that suggest the two are very similar, at least where species other than primates are involved. For example, a recent study by Myrberg (1972b), involving such a direct comparison, showed that the agonistic and other social behavior of the bicolor damselfish, *Eupomacentrus partitus*, in the laboratory was very similar to its field behavior both qualitatively and quantitatively. In another study, Hazlett and Bossert (1965) similarly detected no qualitative differences between the laboratory and field behavior of some pagurid and diogenid crabs. As a result of this, they chose to study the behavior of these crabs in the laboratory where conditions were more uniform and controllable.

There have been surprisingly few studies concerned with interspecific aggression. This is especially true of many decapod crustaceans for which most of the studies have been rather superficial (Reese, 1964). It is rapidly becoming apparent from the few studies that have been made, however, that interspecific aggression may be very important in regulating the distribution and abundance of many marine animal populations. Myrberg (1972a) has found that in the bicolor damselfish interspecific chases accounted for approximately 40% or more of the chases carried out by territorial males. Interspecific aggression was displayed by both sexes and occurred throughout the year.

In laboratory experiments, Teal (1958) found that the fiddler crab, *Uca pugnax*, reduced the number of burrows dug by *U. pugilator* and *U. minax*. In field studies, described by Aspey (1971), it was found that where *U. pugnax* and *U. pugilator* existed in overlapping areas, the number of burrows per square meter was significantly less than in areas inhabited only by *U. pugilator*. The reduction in the number of burrows dug by other species of *Uca* when paired with *U. pugnax* appears to be due to the greater frequency of agonistic display exhibited by *U. pugnax* (Aspey, 1971).

In contrast to the results of the *Panulirus-Homarus* experiments, very little behavioral interaction or aggression occurred between *C. antennarius* and *P. interruptus*. Seventy-three percent of actor behavior involved nonaggressive actions (social contact), and 84% of the reactor responses involved no change in behavior (no response). In addition, *C. antennarius* frequently remained in close proximity to *P. interruptus*, and *P. interruptus* frequently walked over *C. antennarius* when moving from one area in the tank to another area. These events were never observed in *Homarus-Panulirus* experiments. The laboratory observations on *Panulirus-Cancer* interactions agree with observations made in the field where *C. antennarius* is sometimes found sharing the same refuges with *P. interruptus*.

Our data also show that even though the number of *Homarus-Panulirus* interactions decreased with time, there was still a large number of behavioral interactions between *P. interruptus* and *H. americanus* on day 10 in the no shelter condition. This is most clearly seen when the number of interactions on day 10 are compared with the total number of *Cancer-Panulirus* interactions. The percentage of aggression shown by *Homarus* (*Homarus* threat + *Homarus* attack) on day 10 (40%) was very similar to the total percentage of aggression (39%). Likewise, the amount of fleeing (*Panulirus* walk away + *Panulirus* abdomen flex) shown by *Panulirus* on day 10 (55%) was similar to the total percentage of fleeing (63%). Thus, although the absolute number of behavioral interactions decreased with time, the relative amounts of *Homarus* aggression and *Panulirus* fleeing remained the same as the total percentages. These data suggest that, even if the number of encounters in the field between introduced *H. americanus* and *P. interruptus* were small, the behavioral actions by *H. americanus* would be largely aggressive and the responses by *P. interruptus* defensive.

Locomotion

Homarus vs. *Panulirus* with No Shelter

The total numbers of *P. interruptus* observed roaming during the three observation periods, precontrol 1,277, experimental 1,271, and postcontrol 1,171, were not significantly different (Table 4; $P < 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). A comparison of the three observation periods showed that the majority of this roaming by both *P. interruptus* and *H. americanus* occurred during the 1510-1700 h observation period. In *P. interruptus*, 62% of the roaming occurred during this period. In *H. americanus*, 81% of the roaming occurred during the 1510-1700 h observation period.

The relationship between the amount of time spent roaming by *H. americanus* and the number of *Homarus*-initiated behavioral actions is shown

TABLE 4.—The total number of *Panulirus interruptus* roaming during precontrol (*Homarus* absent), experimental (*Homarus* present), and postcontrol (*Homarus* absent) periods for shelter and no shelter conditions. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable. The maximum number of roaming lobsters possible for each group, during each period and for each condition (shelter or no shelter) was 2,250.

Group	Precontrol		Experimental		Postcontrol	
	Shelter	No shelter	Shelter	No shelter	Shelter	No shelter
1	27	214	97	197	30	308
2	99	361	56	252	12	125
3	168	55	132	213	106	358
4	282	89	156	207	63	62
5	129	558	125	402	154	318
Totals	705	1,277	566	1,271	365	1,171

in Table 5. There was a significant correlation ($r_s = +0.90, P = 0.05$) between the total roaming time of each *H. americanus* ($N = 5$) and the number of *Homarus*-initiated behavioral actions. That is, the greater the total roaming time, the greater was the number of behavioral actions.

TABLE 5.—Total *Homarus*-initiated behavioral actions and roaming time for shelter and no shelter conditions. *Homarus*-initiated behavioral actions include social contact, *Homarus* approach, *Homarus* threat, and *Homarus* attack. Social contact includes some *Panulirus*-initiated actions; however, the great majority of the total is due to *Homarus*-initiated actions.

Group	Shelter				No shelter			
	Sex	Size (g)	Roaming (s)	Behavioral actions	Sex	Size (g)	Roaming (s)	Behavioral actions
1	♂	419	6,435	72	♀	480	15,665	442
2	♀	469	2,785	84	♀	635	33,590	541
3	♂	457	1,650	55	♂	467	20,005	514
4	♂	471	1,735	26	♂	457	23,125	725
5	♀	430	2,025	32	♀	417	9,435	293

Homarus vs. *Panulirus* with Shelter

The numbers of *P. interruptus* roaming during the three observation periods were: precontrol 705, experimental 566, and postcontrol 365 (Table 4). The differences between the three test periods were not significant ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

The majority of roaming that occurred in both *P. interruptus* and *H. americanus* took place during the 1510-1700 h observation period as in the no shelter condition. Seventy-seven percent of *P. interruptus* roaming and 78% of *H. americanus* roaming occurred during this period. The amount of roaming done by *H. americanus* in the shelter condition was not significantly correlated with the number of *Homarus*-initiated behavioral actions (Table 5; $r_s = +0.60, P > 0.05$).

The amount of *P. interruptus* roaming without shelter was significantly greater than the amount of roaming with shelter (Table 4; $P = 0.028$, Mann-Whitney *U* test). Similarly, the amount of *H. americanus* roaming without shelter was also significantly greater than the amount of roaming with shelter (Table 5; $P = 0.004$, Mann-Whitney *U* test).

Panulirus vs. *Cancer* with No Shelter

The number of *P. interruptus* roaming during the three observation periods was: precontrol 532, experimental 534, and postcontrol 549 (Table 6). There were no significant differences in the amount of roaming during the three observation periods ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

TABLE 6.—The total number of *Panulirus interruptus* roaming and within 30 cm of the wall during the precontrol (*Cancer* absent), experimental (*Cancer* present), and postcontrol (*Cancer* absent) periods for the *Panulirus* vs. *Cancer* no shelter condition. The maximum number of roaming lobsters for each group during each period was 1,000. The maximum number of wall + no wall positions for each group during each period was also 1,000.

Group	Precontrol		Experimental		Postcontrol	
	Wall	Roaming	Wall	Roaming	Wall	Roaming
1	967	11	956	44	997	20
2	873	168	828	169	748	196
3	925	127	952	112	901	104
4	922	160	913	118	909	76
5	953	66	865	91	810	153
Totals	4,640	532	4,514	534	4,365	549

Distribution of *Panulirus*

Homarus vs. *Panulirus* with No Shelter

The displacement effect *H. americanus* had on *P. interruptus* is clearly shown in Table 7. During the precontrol observation period (*Homarus* absent) *P. interruptus* was most frequently found within 30 cm of the wall. In all five replicate experiments the subjects spent the majority of their time near the wall. Group 5 was observed within 30 cm of the wall three times more frequently than it was observed away from the wall. The other groups exhibited even greater wall—no wall differences. For example, Group 3 was observed within 30 cm of the wall 13 times more frequently than it was observed away from the wall (Table 7).

TABLE 7.—The total number of *Panulirus interruptus* within 30 cm of the wall during the precontrol (*Homarus* absent), experimental (*Homarus* present), and postcontrol (*Homarus* absent) periods for the no shelter condition. The maximum number of positions (wall + no wall) for each group during each period was 2,250. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable.

	Precontrol		Experimental		Postcontrol	
Group	Wall	No wall	Wall	No wall	Wall	No wall
1	1,998	252	360	1,890	1,959	291
2	1,967	283	500	1,750	713	1,537
3	2,094	156	723	1,527	1,592	658
4	2,011	239	964	1,286	2,162	88
5	1,684	566	1,496	754	1,432	818

During the experimental observation period (*Homarus* present) *P. interruptus* was usually found in the center of the tank (no wall). Four of the five groups were observed more frequently in the center of the tank than within 30 cm from the wall. Only Group 5 was observed near the wall more frequently than in the center. However, Group 5 spent less time near the wall during the experimental period than in the precontrol period.

During the postcontrol period, four out of five groups were observed within 30 cm of the wall more frequently than in the center (Table 7). Group 2 spent approximately twice as much time in the center than within 30 cm of the wall.

The wall-no wall distribution of *P. interruptus* during the three observation periods was significantly different ($P = 0.009$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). The sums of ranks for the three observation periods were: precontrol 59, experimental 19, and postcontrol 42. These sums of ranks indicate that the differences are between the experimental and control periods. There were no significant differences between the precontrol and postcontrol periods ($P > 0.05$, Mann-Whitney U test; Siegel, 1956).

Homarus vs. *Panulirus* with Shelter

In the shelter condition individuals of all five groups spent most of their time in the shelters (Table 8). There were no significant differences between the precontrol, experimental, and postcontrol observation periods for the number of *P. interruptus* observed in shelters ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

TABLE 8.—The total number of *Panulirus interruptus* in shelters or within 30 cm of the wall during the precontrol (*Homarus* absent), experimental (*Homarus* present) and postcontrol (*Homarus* absent) periods for the shelter condition. The maximum number of positions (shelter + wall + no wall) for each group during each period was 2,250. Values for the experimental period are one-half the 10-day total so that the totals shown for the three periods are comparable.

	Precontrol		Experimental		Postcontrol	
Group	Shelter	Wall	Shelter	Wall	Shelter	Wall
1	2,217	23	2,036	166	2,163	86
2	2,076	110	1,635	434	2,160	66
3	1,372	694	1,449	643	1,982	255
4	1,639	490	1,714	427	1,780	298
5	1,862	356	1,893	285	1,966	252

The wall-no wall distribution of *P. interruptus* for the three observation periods also was not significantly different (Table 8; $P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks). The greatest number of *P. interruptus* found outside the shelters (wall and no wall condition) occurred during the 1510-1700 h observation period.

Panulirus vs. *Cancer* with No Shelter

During the precontrol, experimental, and postcontrol periods, individuals of all five groups of *P. interruptus* were observed within 30 cm of the wall much more frequently than in positions 30 cm away from the wall (Table 6). The groups were observed near the wall from approximately 3 (Group 2 postcontrol) to 332 (Group 1, postcontrol) times more frequently than away from the wall. Group 1 spent nearly all its time near the wall during the postcontrol period. There were no significant differences in the number of lobsters found near the wall for the three periods ($P > 0.05$, Kruskal-Wallis One-Way Analysis of Variance by Ranks).

Discussion of Lobster Distribution and Locomotion

The effect of the presence of *H. americanus* on the distribution of *P. interruptus* in a tank without shelter is quite evident. *Homarus americanus* displaced *P. interruptus* from its preferred areas (areas within 30 cm of the wall). There was a reversal of the precontrol wall position of four out of five *P. interruptus* groups during the experimental period (Table 7). When *H. americanus* was removed for the postcontrol period, three of the four groups which had reversed their precontrol position during the experimental period moved back to the wall position. Group 2 remained in the no wall position during the postcontrol. The exact reason for this is unknown, but perhaps this group's encounters with *H. americanus* were somehow more intense and thus the enounters had a more lasting effect on the behavior of Group 2. The individual used in this group was by far the most active *H. americanus* tested for both the shelter and no shelter condition and initiated the second highest number of behavioral actions (Table 5).

Group 5 remained in the wall position more than the no wall position during all three test periods. Thus, the *H. americanus* introduced to this group had little effect on its distribution within the tank. The reason for this is probably the low level of activity and aggression shown by this individual. It showed the least amount of roaming (approximately one-half the value shown by the next least active individual) and the lowest number of behavioral actions of any lobster in the no shelter condition. It directed only 16 attacks at *P. interruptus*, less than one-half of those shown by the next least aggressive *H. americanus*.

In contrast to the above, *C. antennarius* had no effect on the distribution of *P. interruptus* in the absence of shelter. All five groups of *P. interruptus* spent nearly all their time near the wall during each of the three test periods (Table 6). That is, *P. interruptus* groups were never observed spending more time in the no wall position than in the wall position when paired with *C. antennarius*.

Douglis (1946) found that when *H. americanus* was present in a large aquarium tank with one or more blue crab, *Callinectes sapidus*, spider crab, *Libinia emarginata*, or hermit crab, *Pagurus polycarus*, "it tended by pushing and fighting to keep the crabs on the opposite side of the tank from itself." Thus, although details were not given, it appears that *H. americanus* displaced crabs that, by virtue of their claws, would seem to be much better prepared to cope with *H. americanus* than is *P. interruptus*.

The presence of more shelter than was necessary for the number of lobsters in a tank substantially decreased the number of *P. interruptus* displaced from the wall position. This was primarily due to the fact that when shelter was present, all lobsters spent the majority of their time in the shelter. This interpretation is supported by comparing data on the roaming time for the shelter and no shelter conditions. The presence of shelter significantly reduced the amount of roaming in both *P. interruptus* and *H. americanus*.

The greater frequency of agonistic interactions observed between *H. americanus* and *P. interruptus* during the 1510-1700 h observation period, as compared with the 0800-1000 and 1200-1400 h observation periods, was also no doubt due to the higher level of locomotion during this period.

A great amount of variability in the activity and aggression of individual *H. americanus* was also observed in our study. Some individuals were very active and aggressive, while others were neither. In our study these variables were not related to the sex or size of *H. americanus*. In the shelter condition, a female exhibited the greatest number of behavioral actions, while in the no shelter condition, it was a male. Of the 10 *H. americanus* tested, these lobsters ranked fourth and seventh in size (Table 5).

CONCLUSIONS

Although we cannot predict with certainty the effect a large introduced population of *H. americanus* would have on *P. interruptus* and other decapod crustaceans native to southern California, our data suggest that an adverse outcome from such an introduction could occur. The types of behavioral interactions we observed in the laboratory between *H. americanus* and *P. interruptus* would most likely also occur in the field. This conclusion is strengthened by the studies and observations of other workers who have compared and found close agreement between the laboratory and field behavior. Our data show that a large percentage of the behavioral actions of *H. americanus* toward *P. interruptus* probably would involve aggressive actions. Assuming that individuals of these two species came in contact with one another in nature, these aggressive actions could have direct or indirect effects on the distribution and abundance of *P. interruptus*. Thus, our evidence suggests that it would be inadvisable to introduce *H. americanus* into southern California waters.

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