WHOI-75-48

Woods Hole Oceanographic Institution

BEHAVIOR OF LOBSTERS (HOMARUS AMERICANUS) IN A SEMI-NATURAL ENVIRONMENT AT AMBIENT TEMPERATURES AND UNDER THERMAL STRESS

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Lauren Stein, Stewart Jacobson
and Jelle Atema

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TECHNICAL REPORT

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Approved for Distribution ______________________
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Department of Chemistry

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ABSTRACT

In January, 1974 we established semi-natural habitats in two 10ft. diameter, octagonal aquaria, with five lobsters (*Homarus americanus*) each, and several *Cancer irroratus*, *Anguilla rostrata*, *Pseudopleuronectes americanus*, and *Tautoglabrus adspersus*. The lobsters, with respect to size and sex, were identical as possible between tanks, as were the numbers of other species. The aquaria, which received ambient seawater, were arranged identically with an oyster shell substrate, and cement blocks, rocks and ceramic pipes to provide a surplus of shelters. Observations, spanning from February through August, were made both during the day, following feeding, and (using red light) just after sunset, when lobsters are active under natural conditions. Types of behavior we were able to quantify included occupation of specific shelters, feeding, activity and social behavior.

In our large aquaria the lobsters appeared to be much less aggressive than generally has been reported. Aggression was most frequent during feeding. Observations at night revealed few encounters, and these were usually either one sided avoidance without pursuit, or mutual ritualized displays.

Neither an animal's size nor sex seemed to determine its relative dominance. Dominance shifted somewhat between different animals during the study, and complicating this picture was possible territorial behavior in the larger individuals. In one tank, only the two adult females were territorial from February through mid May, following which no lobster showed stability of residence. In the second tank, only one animal, a female, was territorial for more than several weeks, until early June, when the largest male established a reproductive territory lasting until the end of August. Even in our large aquaria space may have been too

limited for all animals to be territorial.

Lobsters appeared to lose their position in the hierarchy just prior to, and for up to a month or more following the molt. Such animals were often observed on top of shelters, in exposed locations, where other lobsters apparently did not harass them. Although captive lobsters are considered quite cannibalistic, we lost only one animal, a juvenile female, out of six molts.

In our large aquaria, female lobsters about to molt sought out, took up residence, and actively courted the tank's largest male. The males were very non-aggressive toward these females, and yet during this period made violent attacks against other males as well as fish. In each case following mating, the males retired to the shelter and fed on the cast shell. Cohabitation, in or around the males' residences, continued for several days following mating.

Diurnal activity, which was evoked by the presence of food, showed little change over the range of 5-28°C. Nocturnal activity, which was more spontaneous, was similar in both tanks through mid June (temp. range 5-18°C). The level of activity was as high in late February - early March as in late May, with a dip in activity in late March - late April, a period marked by storms. From mid June on, the nocturnal activity in tank I increased with the increasing temperature, leveling off approximately when the peak temperature of 28°C was reached. In contrast, activity in tank II did not increase at temperatures above 20°C, and remained at a much lower level than in tank I.

Although patterns of residence and dominance in the lobsters changed seasonally, the direction of change was rather different in each tank and did not seem correlated with temperature. Other factors, such as molting and loss of dominance prior to mating in previously aggressive females, were probably more important than temperature effects. The frequency of aggressive behavior in the temperature range 22-28°C was similar to levels at ambient temperatures.

Interspecific relations between lobsters and the other species were mainly pacific, although predation on *Cancer* by *H. americanus* may have occurred.

The response of the eels (*Anguilla rostrata*) to temperature increases was consistent between tanks. Swimming was first observed at 8°C, and feeding at 10°C. Further, the eels in both tanks became markedly aggressive when the temperature reached 26°C.

INTRODUCTION

The American lobster (*Homarus americanus*) is a marine inshore crustacean both of major economic importance and of intrinsic interest. Two approaches have contributed to the knowledge of lobster behavior. One is comprised of laboratory studies under controlled and structured conditions. For instance, Cobb (1971) studied shelter-related behavior and activity in *H. americanus*. Aggressive communication and interactions in *H. americanus* has been described quantitatively by Scrivener (1971). Dunham (1972) observed effects of isolation vs. group-holding conditions on lobster aggressive behavior. Finally, a relationship between dominance and molting patterns in pairs of juvenile lobsters has been demonstrated by Cobb and Tamm (1974). However, as in most laboratory studies of behavior, application of findings to the natural environment may be limited.

At the other extreme are studies of lobster activity, migration and shelter-related behavior under field conditions (Wilder, 1962; Cooper and Uzmann, 1971; Stewart, 1971). Lobsters are nocturnal, however, and direct observation of behavior is difficult under field conditions. Questions such as whether lobsters are territorial can be approached only in an indirect manner. For instance, through repeated observations of lobsters in the same burrows, rather than of defense of territory.

We felt an approach which bridged the gap between these two types of studies was needed. Our interest was in a long-term view of the behavior of individual lobsters living in an environment with as much space as possible, ample shelter, and a variety of other organisms which co-occur with *H. americanus* locally. This necessitated a compromise between a field study and a more highly structured laboratory approach to behavior.

The primary objective of this study was to observe the behavior of

Homarus americanus under conditions approximating the natural state. A second objective was to observe effects of higher than normal temperatures on the behavior of lobsters and other organisms in our naturalistic habitat.

We feel that our approach has rewarded us with information about lobster behavior which would have been difficult to obtain by other methods. Perhaps more important than the data *per se*, however, are the questions we have raised which are of interest to the student of lobster behavior and ecology, and those interested in lobster culture.

MATERIALS AND METHODS

1. The Aquaria

In January of 1974, we established two semi-natural subtidal habitats in 10-foot diameter, octagonal aquaria of 1500 gallon capacity inside an aquarium room (Fig. 1). The two aquaria, which were provided with large windows (4 ft x 4 ft) were arranged identically with oyster shell substrate, and concrete blocks, ceramic pipes, and rocks to provide surplus shelters for lobsters and other species (Fig. 2). There were at least 22 possible shelters which could be utilized by lobsters, although all were not equally suitable, some being apparently too small for the larger lobsters. The arrangements of blocks and pipes, and particularly a large center structure of 9 concrete blocks, provided visual complexity and opportunity for smaller or subordinate individuals to remain out of visual range of larger lobsters.

The aquaria continuously received sea water from nearby Vineyard Sound with filtration only through Troy Felt (dacron polyester). The flow rate varied seasonally, with a maximum of 3 to 4 l/min. Four airstones in each tank provided aeration (Conde air compressor, graphite lubricated).

The aquarium room was moderately illuminated with incandescent bulbs located away from the aquaria and from ambient daylight through several windows. The overhead lighting was controlled by a timer adjusted weekly to turn the lights on 15 minutes after sunrise and turn them off 15 minutes before sunset. Thus, the lobsters experienced a gradual increase and decrease in light as in nature. Five 60 watt red light bulbs, suspended two feet over the three-foot deep water, were on continuously and provided illumination at night.

2. Heating Methods

Figures 4 and 5 show the temperature regime for both aquaria. During the winter months the inflow was reduced in order to keep the water tempera-

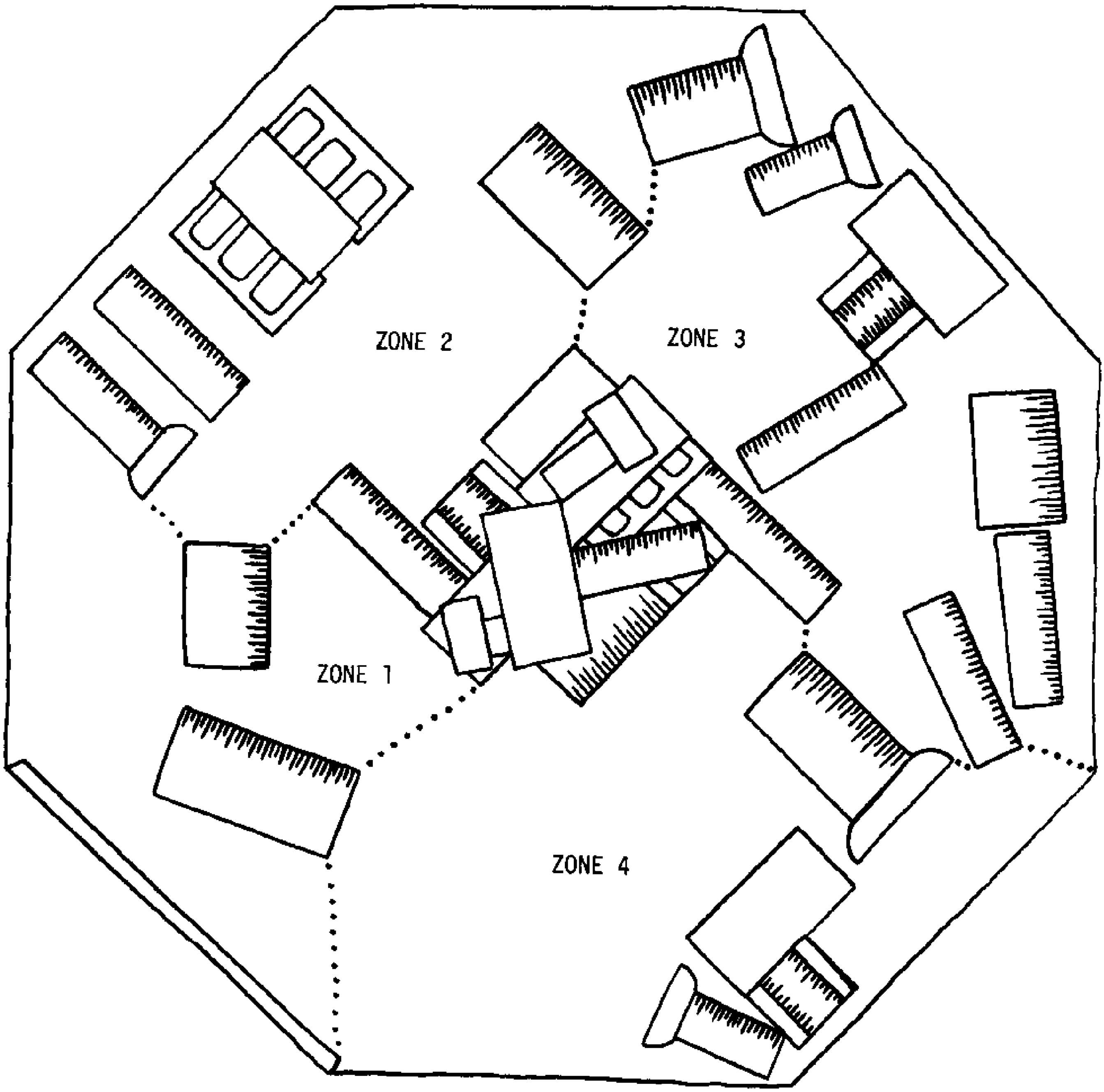

Fig. 1 Diagram of aquaria, showing numbered zones.

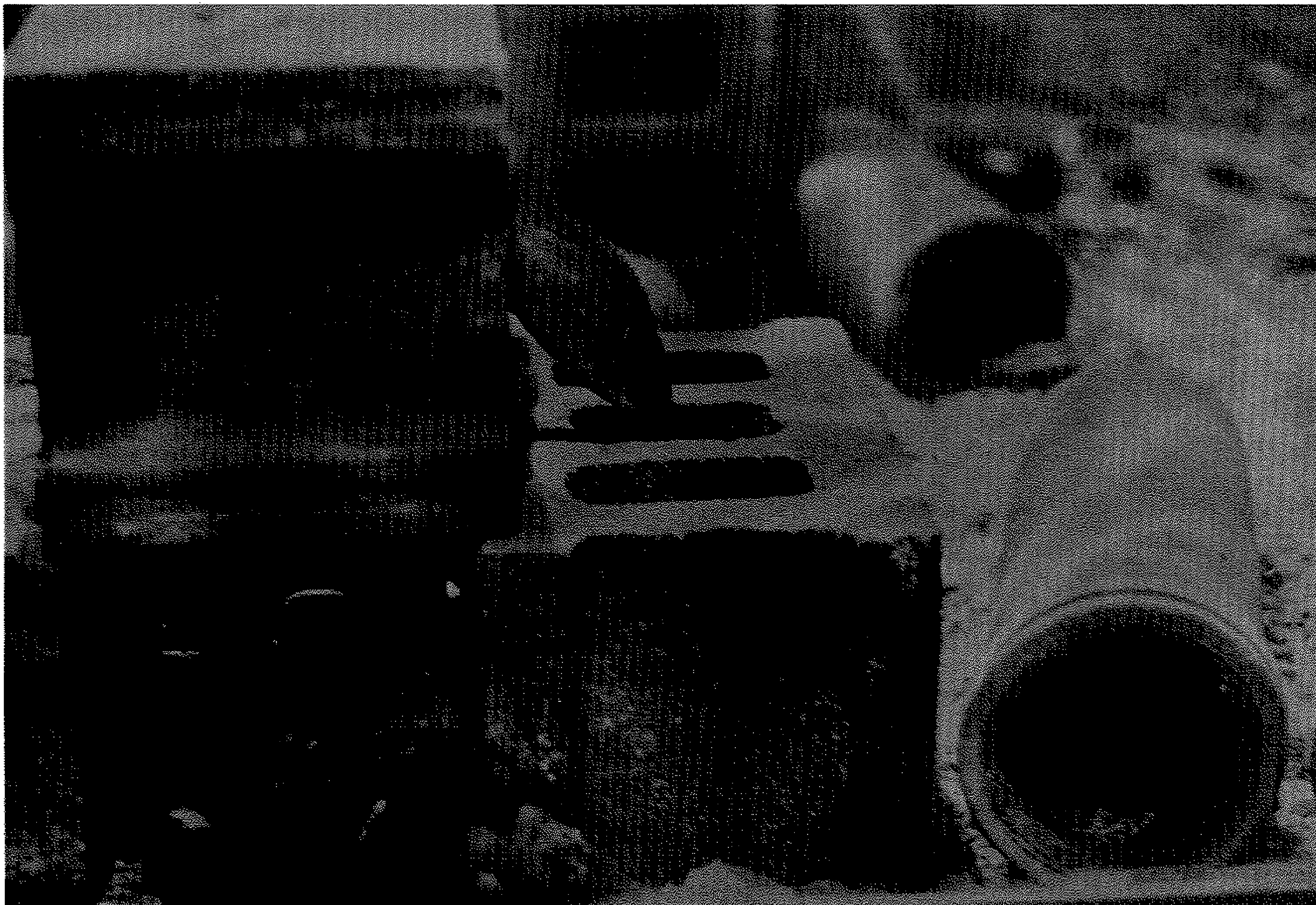

Fig. 2 View through window of aquarium, showing lobsters in shelters.

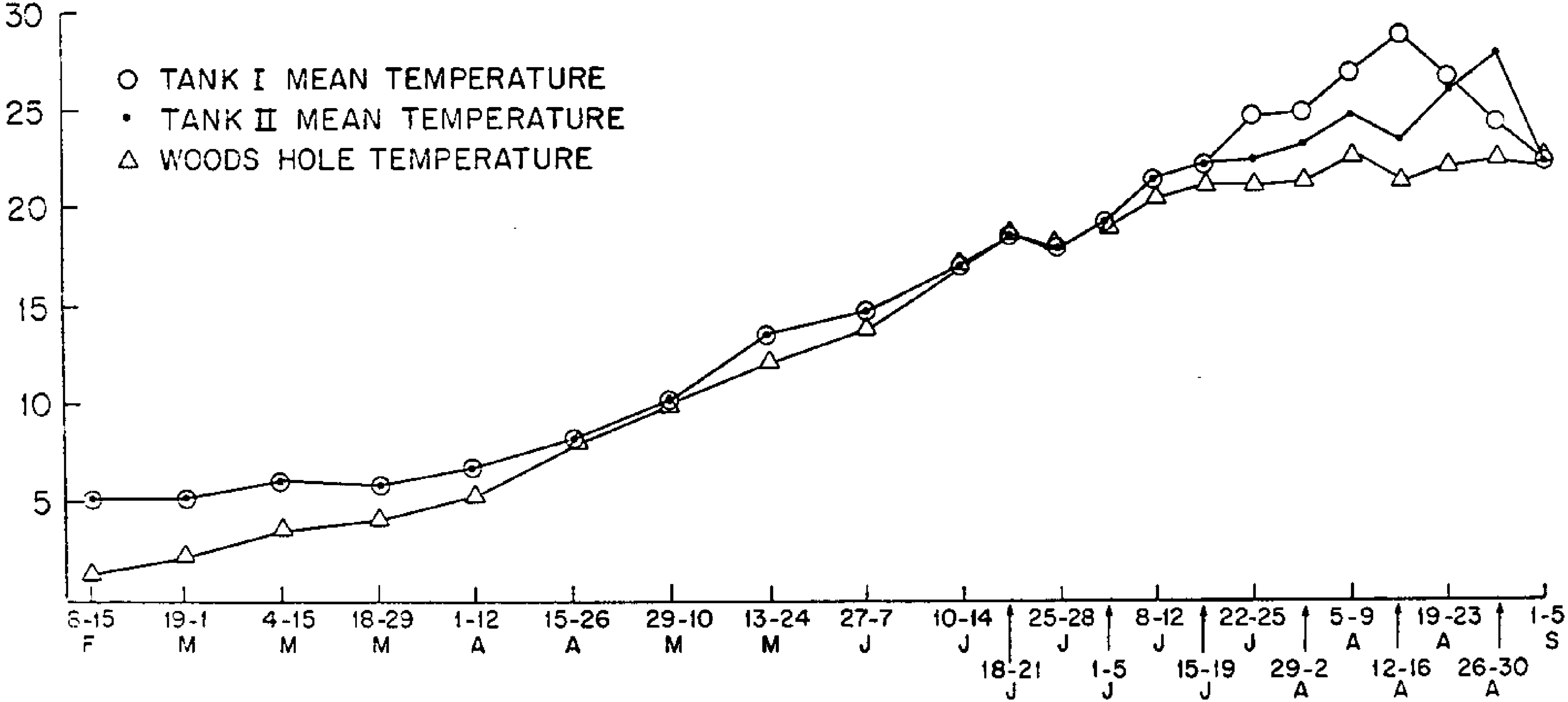

Fig. 3 Comparison of temperature regimes for both aquaria with ambient temperatures.

ture above $4^{o}C$, so as to resemble temperatures in deeper water, where lobsters migrate during this season. Approximately seven months after introduction of the lobsters into the aquaria, when the ambient sea water began to reach its normal summer peak temperature, we began heating the incoming sea water (Figs. 4 and 5). A titanium heat exchanger was used to heat the incoming sea water in a 180-gallon tank from which the water was pumped (using two March pumps containing no exposed metal parts) to a bucket containing a Troy Felt Filter. Here it was first mixed with ambient sea water before actually entering the aquarium (see Figure 1 for location of sea water inputs). The sea water in the heating tank itself was aerated so as to release super-saturated gas resulting from rapid heating.

3. The Lobsters and Other Species Stocked

Each 1500-gallon aquarium was stocked with matched groups of 5 lobsters, both mature and immature, of both sexes (Table 1). For purposes of identification, a day-glow orange letter on Neoprene rubber was glued on the back of each lobster; each animal also had a color-coded rubber band on the merus of the cheliped. In addition to lobsters, each aquarium was provided with several species of fish, crustacea and other invertebrates characteristic of subtidal environments of Cape Cod, and based in part on Cobb's (1969) study (Table 2). Although we introduced no species predatory on lobsters, the large edible crab Cancer borealis is a potential competitor of the lobster for food and shelter (Cobb, 1969), and eels (Anguilla rostrata) occur with and perhaps compete with lobsters in habitats locally. Mussels, sea urchins and seastars were stocked to provide possible food for the lobsters.

4. Recording Methods and Feeding

Because our past experience with lobster behavior has shown them to be relatively inactive animals, day-time observations of lobster behavior

TABLE 1

Lobster Vital Statistics

Animal, sex	Jan 29 wt.	Oct 30 wt.	% increase	Molt or egg extrusion date
A (f)	574 gm	625 gm	9%	eggs, June
G (m)	542			No molt
B (f)	388	568	46%	molt, 22 July
L (m)	339			molt, 24 June
D (f)	192			molt, 6 June dead
C (f)	581	625	8%	eggs, June
K (m)	588			no molt
F (f)	423	653	54%	molt, 24 June
S (m)	306			molt, 17 June
J (f)	177	312	76%	molt, 16 July

TABLE 2

Species Selected for Marine Inshore

Community in 1500 Gallon Aquaria

Taxon	Species and Common Name	No. Stocked Per Tank
Pisces	*Tantoglabrus adspersus*, cunner	8
	Anguilla rostrata, American eel	3 (41 to 58 cm, std. length)
	Pleuronectes sp., flounder	3 (8 to 14 cm, std. length)
	Fundulus heteroclitus, killi fish	50 (mostly adults)
Crustacea	*Cancer borealis*, edible crab	6 (adults)
	Homarus americanus, American lobster	5 (see Table 1)
Mollusca	*Mytilus edulis*, blue mussel	2 clumps of ca. 25
Echinodermata	*Asterias forbesi*, *A. vulgarus*, starfish	8
	Stronglocentrotas sp.	8

were made immediately following introduction of food, when activity was assured. Day-time records were made between the hours of 1430 and 1630 from three to five times weekly, depending on the weekly rate of temperature change. Recording sessions which totalled 20 minutes began with the introduction of food and comprised 10 minutes at each of two opposite windows picked in random order. Since the lobsters usually returned to their shelter after searching and feeding, longer periods of observation would have yielded little more in the way of behavior.

The lobsters and other animals were fed alternately with pieces of mussel and herring, and occasionally cut-up green crabs or other small crabs. From January 29 until June 7, the animals were fed 3 times a week, from June 10 until termination of the experiment 6 times a week. The amount of food varied at different times of year, and was based largely on how much the animals would consume within an hour.

In addition to day-time observations, we recorded lobster behavior at night, for a total of 40 minutes per tank per session. Since, Cobb (1969) has shown that an increase in lobster activity occurs shortly following a decrease in light level, the recording was timed so as to commence 40 minutes after sunset. Each aquarium was recorded by a single observer for 10 minutes at each of 2 windows (order randomly chosen), and then the second aquarium was recorded. After a 15 to 20 minute interval, the procedure was repeated.

The recording techniques used were those used by Atema and Stein (1973), and utilized a list of well-established behavioral units (Table 3). This list of units is similar to the one published by Scrivener (1971), but with modifications as noted. Recordings of social behavior were made by writing down a sequential record of behavioral units as they appeared, with information on the actors and place of interaction. Activity and feeding behavior were noted once a minute. The location of behavior or activity was noted with respect to one of four zones arbitrarily dividing up the floor of each tank (Fig. 1). The recordings were made by three observers who had initially recorded together and matched their records.

A second type of record consisted of marking the location of individual lobsters twice a day, between 0900 and 1000, and 1400 and 1500 (before the afternoon feeding and recording). This provided a record of the animals' locations during periods of quiescence, when they might be expected to occupy a "home" shelter.

TABLE 3

LIST OF UNITS USED FOR RECORDING LOBSTER BEHAVIOR

Notations under the unit names indicate whether the term is the same as used by Scrivener (1971). If it is different, the term used by Scrivener is noted, in parenthesis. If it is the same,"(Scrivener)" appears under the unit name. No notation appears when the unit was not used by Scrivener.

UNIT	DESCRIPTION	CODE
NON SOCIAL BEHAVIOR		
Groom	Rub, scratch or pick at parts of the body with the walking legs	Gr
Rake	Back & forth movement of one or more walking legs across the substrate while the body is still	R
Walk	A series of uninterrupted steps, forward or backward	W
SOCIAL BEHAVIOR		
Advance	While in a Face Off, one animal move closer to the other	Adv
Antenna Feel (antenna whip)	Quick Successive movements of the antennae over another lobster-occurs in an aggressive encounter (ie. Face Off) or in mating	F
Approach (Scrivener)	Forward movement directed toward another lobster greater than 1 lobster length away	App
Chase	Quick movement of lobster in persuit of another, during an interaction.	Ch

Claw Lock	Hand-shake position (crusher locked oncrusher) while animals are in a Face Off position	L/C
Defensive Posture	Tail tucked under body, body slightly raised, claws open and raised in front of the body, as a shield	Def
Face Off	Head to head confrontation within one body length distance	FO
Flee (Running away)	One animal quickly moving forward in an opposite direction from another during an encounter, usually following a Face Off and ending the encounter	Fl
Follow (Scrivener)	Slow movement of one animal after another which has moved away	Foll
Jab (boxing)	Poking at other animals' body or claws with own claws	Ja
Lunge	Fast extension of claws, usually accompanied by a run	Lu
Meral Spread (Scrivener)	Claws raised and spread apart - usually a defensive posture	MS
Near	One animal walking close to another unintentionally - i.e. not to "purposefully" initiate an encounter	Near
No response	No reaction to an initiating response of another animal	Ø
On Guard	Defensive body position where seizer claw is raised and extended and crusher claw is close to the body	OG

Push (Scrivener)	One animal extending claws against another & maneuvering him backwards	Pu
Retreat (backing)	A direct consequence of advance or approach - a reverse walk or movement away from another animal (occurs within one body length distance)	Ret
Rip	Quick jerk of body while in claw lock - a very high intensity pull using the whole body	Rip
Sideways (Scrivener)	Forward and lateral walk simultaneously - crablike movement usually as avoidance	SA
Snap	Quick opening and closing of seizer claw, usually without contact (often follows a lunge)	SN
Swat	Swinging of seizer claw of one lobster toward the other - as in a "right hook" usually occurs during a claw lock	Swat
Tail Flip (abdomen flex)	Rapid flexing of the abdomen under the body so as to propel the animal backwards - an escape movement	TF

REPRODUCTIVE BEHAVIOR

Dismount	Disengaging from a mount	Dism
Ejaculate	Thrust of abdomen of male, to deposit sperm, during the mating	Ejac
Mount	Positioning of one animal completely on and over another to begin the mating process	M
Turn Animal Over	After mounting, turning the submissive animal over, so as to mate	TAO

RESULTS AND DISCUSSION

1. Growth, Molting and Survival

Table 1 shows the dates of molting of those animals which did molt. The growth data, which fall within the range reported by Wilder (1963) and Thomas (1973) for inshore lobster populations, suggest that the experimental lobsters received ample food. The other important information in the table is that although captive lobsters are considered quite cannibalistic, five out of six molts survived. The single death was a small, probably immature, female (D), which disappeared without a trace. It is not clear whether other lobsters, or such predaceous species as crabs (*Cancer borealis*) or eels (*Anguilla rostrata*), may have eaten this individual. The three other females molted (B in tank I, F and J in tank II) and then mated with the largest male in their respective tanks. For more information on their behavior, see the section on reproductive behavior.

2. Activity and Shelter Occupancy

Figures 4 and 5 present the temperature and activity data for tanks I and II, respectively. Mean temperatures are shown for each approximate one or two-week period over which the data were summarized. In tank II, the dip in the temperature increased from 12 to 16 August, and the sudden drop during 26 to 30 August, were due to malfunctions of the heating system and were not an intentional part of the thermal regime.

The activity data in Figures 4 and 5 are represented as means of the mean frequencies for each tank per one- or two-week period. The amount of day-time activity (given as the number of minutes in which Walk was recorded) appears similar in both tanks and did not differ greatly from January through September. Note that the night recording sessions lasted 40 min. per tank, vs. 20 for day-time, and thus the data represent double the amount of recording relative to that for day-time activity. Even so, at least for

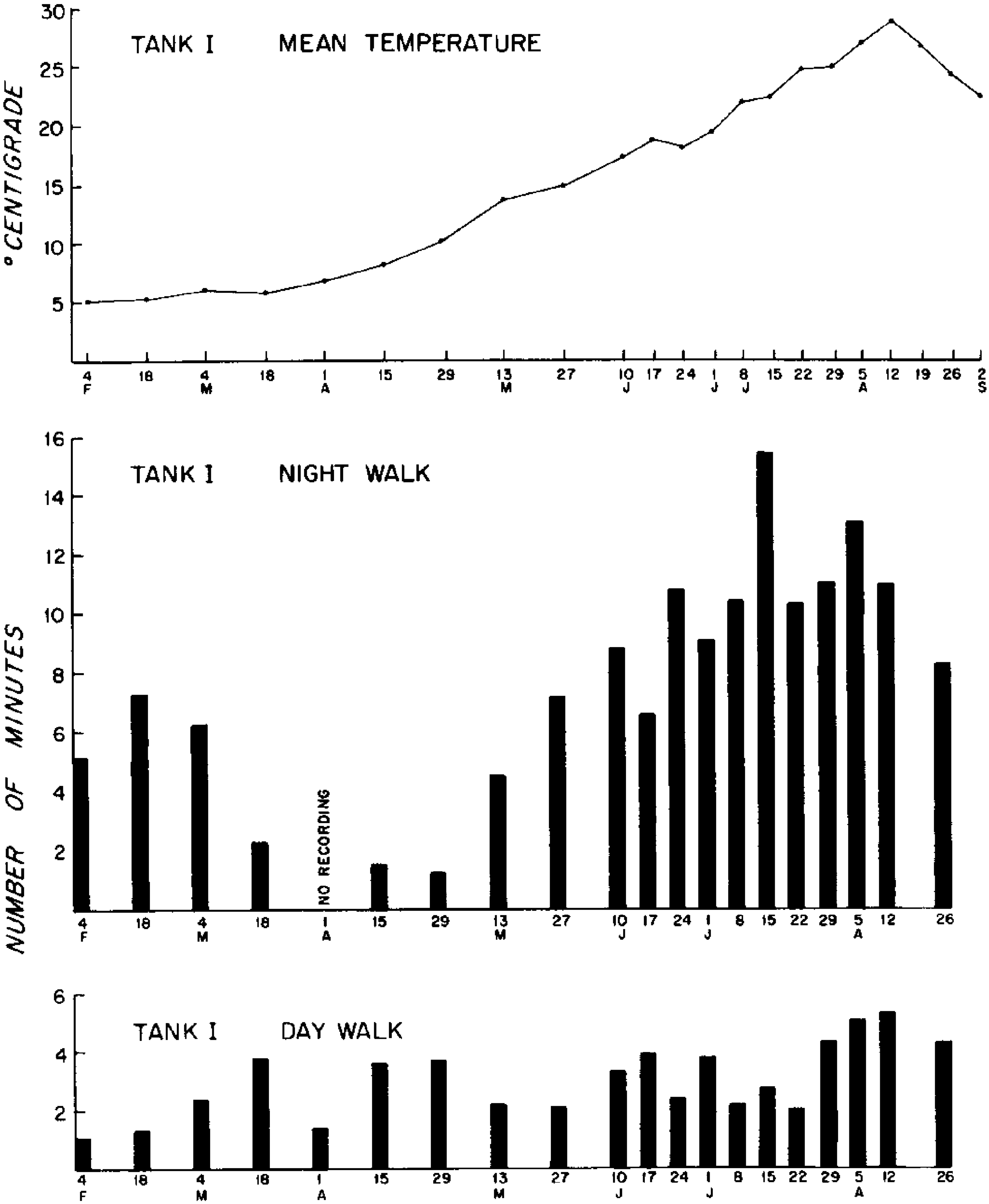

Fig. 4 Tank I, day and night activity and temperatures.

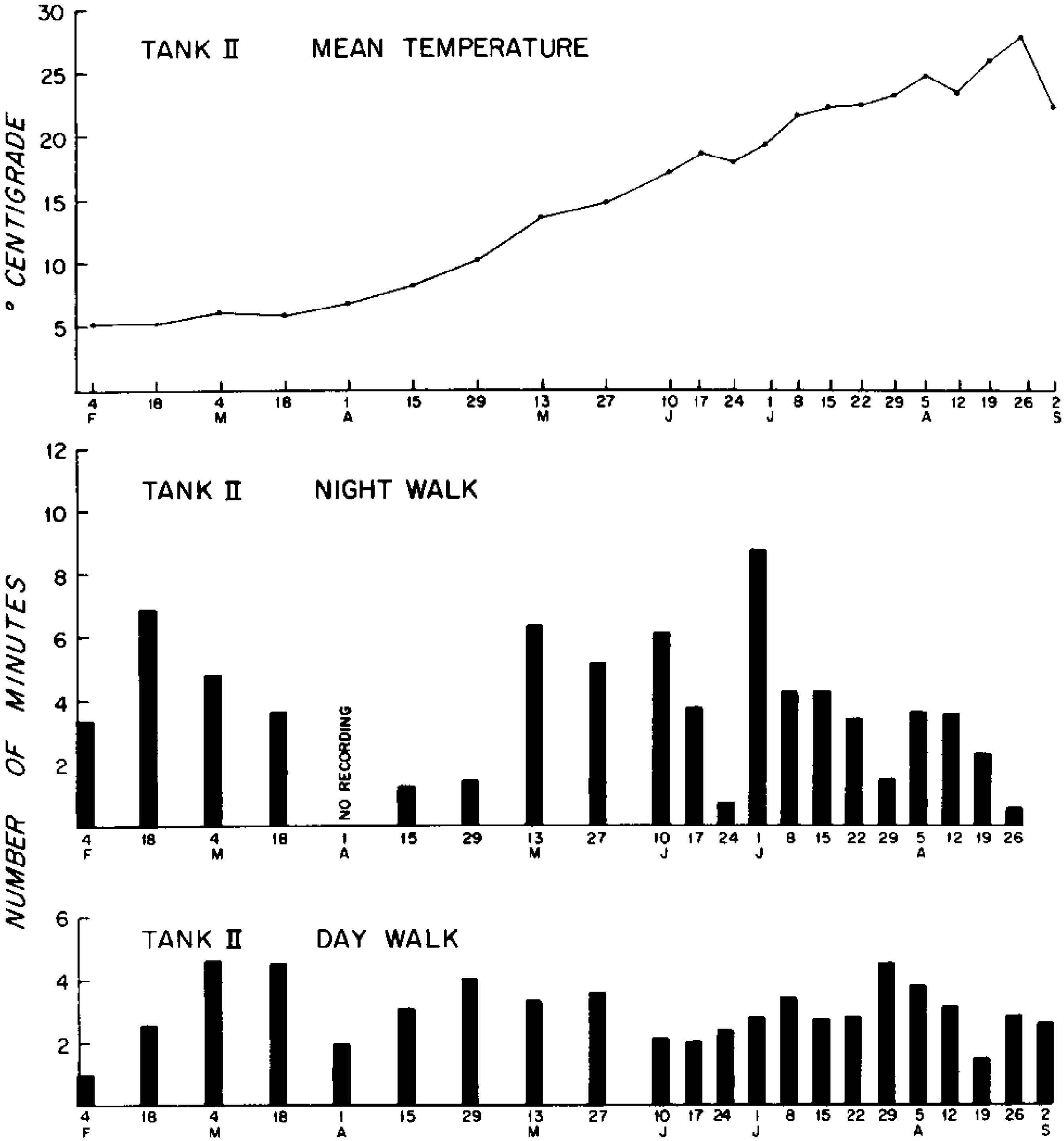

Fig. 5 Tank II, day and night activity and temperatures.

tank I, there appeared to be considerably more activity during the night than the day. This was especially true during the period 10 June to 2 August.

Day-time activity in the experimental animals was stimulated by the presence of food. In comparison, the nocturnal activity was more spontaneous, and more truly represented the natural seasonal activity patterns of H. americanus. Therefore, we should focus analysis of activity in relation to seasonal variables (such as temperature) largely on night activity. Nocturnal activity in both tanks shows similar patterns through about 21 June (Figs. 4 and 5). Interestingly, the activity during late February to early March was not much lower than that in middle May to middle June. More striking still is the dip in activity levels for late March to early May. The month of April was marked by numerous storms which greatly increased turbidity in the sea water supply. When visibility was reduced so that individuals were not clearly visible half-way across the aquarium (a distance of 5 ft), we did not record behavior. Thus, the apparent decrease in activity during April is felt to be a real phenomenon, and perhaps based on the lobster's perception of storm conditions, decreasing their activity as an adaptive response.

On June 27, the night recording showed little activity in tank II. While activity recovered for the next time period (2-3 July) and was similar to tank I, after that date the general activity in tank II was less than the average over the previous 1½ months. In comparison, the overall nocturnal activity in tank I was somewhat greater. The contrast is noticeable in comparing the activity during the periods when we began artifically heating the sea water; nocturnal activity increased to its greatest level in tank I but decreased substantially in tank II. In tank I, the activity level remained relatively high during the period of artificially increased temperatures;

after the temperature began to decrease gradually, the activity also decreased somewhat. In tank II, nocturnal activity under thermal stress remained at a level similar to that seen in the previous three weeks. Lobster activity in tank II also decreased with the decrease in temperature, which was marked by a sudden drop due to a failure of the heating system.

3. Residence and Dominance

Figures 6 and 7 present residence data both for before and after imposition of thermal stress. These data are based on the twice-daily observations for five-day periods of the locations of lobsters. The lobsters were not always visible or identifiable at every observation. Residence during a given week was defined as seventy percent of observations, maximum 10 per week, minimum 3, in or immediately adjacent to the same shelter. Residence for each animal during any given week (five days) is indicated by a line spanning the week period; dots indicate periods when residency could not be ascertained, and serve to lead the eye from one period of residency to another. Initial absence of lines or dots indicates no residence was established until the date indicated. The ticks above and below the residency lines indicate winning and losing encounters, respectively, in the individual's zone of residence. Zone of residence refers to the area surrounding a specific shelter, and which includes the numbered zone (Fig. 1) containing the shelter, and the border areas of adjacent zones. The different shelters used as residences by the lobsters are given in Figures 6 and 7 (see also Fig. 1).

As can be seen in Figure 6, the residence behavior and relations (winning and losing) between lobsters in Tank I differed substantially between the periods separated by the arrows at top and bottom. Based on the lobsters' behavior, we divided the time during which the lobsters were

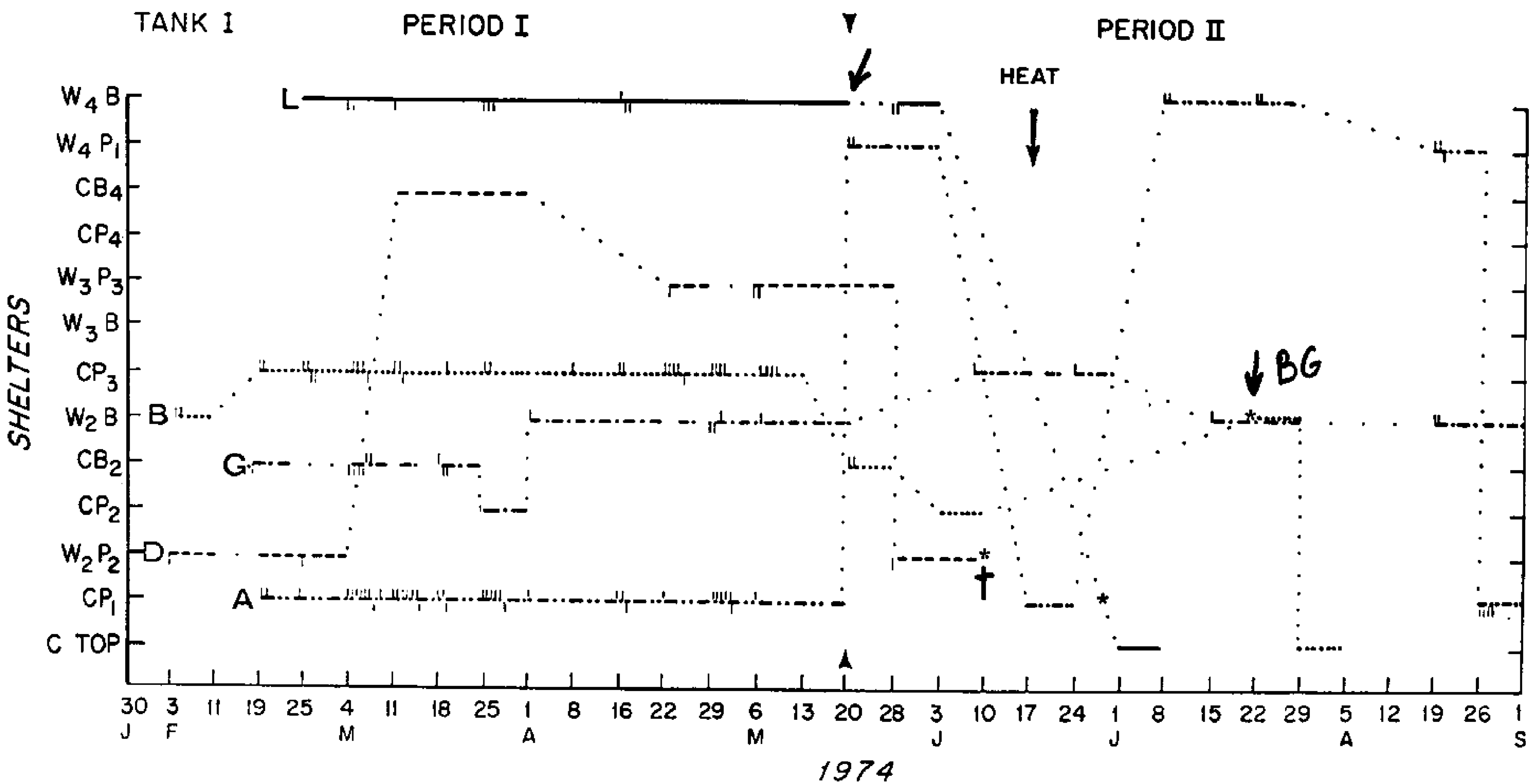

Fig 6 Tank I, residency and dominance within zone of residence. Lines indicate residency; spaced dots, residency not established. Encounters won or tied are indicated by ticks above the lines, losses by ones below the lines. * indicates time of molt.

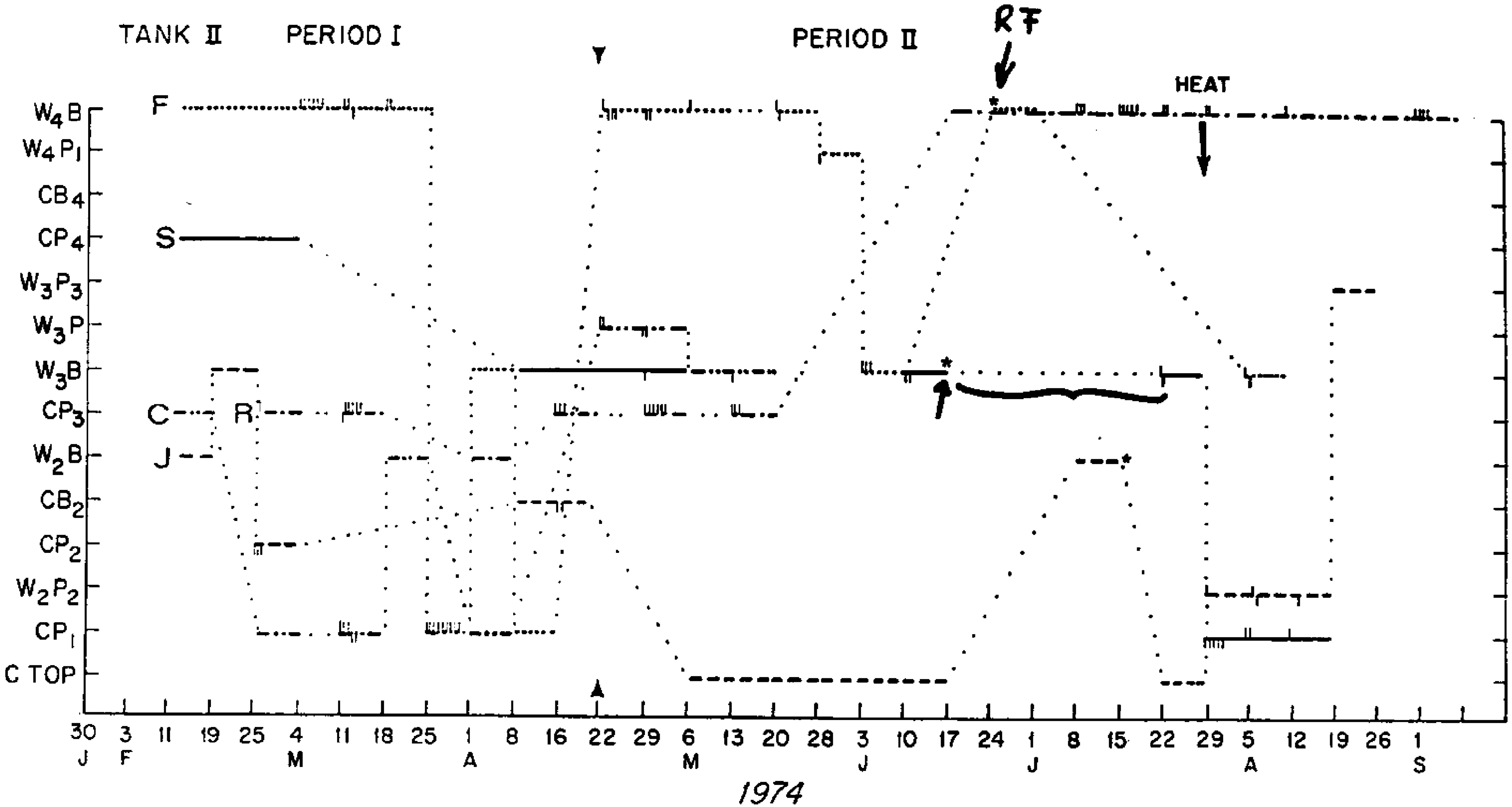

Fig. 7 Tank II, residency and dominance within zone of residence (see Fig. 6 for explanation).

observed into periods I and II. Period I was characterized by a relatively stable residence pattern for animals A, B and L, and a somewhat less stable period for G. (As shown in Table 1, the lobsters listed in order of decreasing size are A, G, B, L, D.) During period I, A and B, both females, were largely victorious within their residence zones; in contrast, the males G and L lost far more encounters than they won.

The lobster behavior was quite different during period II, when none of the lobsters showed long-term stability of residence. Lobster G's residence in shelter W4 B for several weeks coincided with his mating with B in that shelter. As to effects of thermal stress on residence patterns, there were no obvious changes following heating. Part of the difficulty in discerning changes could be due to the above-mentioned lack of a stable pattern during the month or so preceding the date we began heating.

Figure 7 shows the residence pattern for lobsters in tank II. During the first period, the lobsters showed much less stability than those in tank I. A change in lobster behavior, exemplified perhaps most dramatically by F's failure to dominate in her zone of residence after about 16 April, suggested that we use this date to demarcate two periods of contrasting behavior in tank II. (The lobsters in order of decreasing size were C, R, F, S, J - Table 1.) In contrast to tank I, period II in tank II was more stable than the first period in either tank. This is true even if one only looks at residence patterns after May 20, the date demarcating period II from I in tank I. A further feature of period II in tank II is that the stability of residence maintained by the large male R occurred during the time when he mated with two females.

Examination of Figure 7 does not suggest any obvious effects of heat on residence patterns in tank II. For example, R continued to use and to "defend" the same shelter before and after heating. Animals S and J did establish residences shortly after imposition of thermal stress, however, it seems improbable that this was related to increased temperatures.

Figures 8 and 9 present data which further demonstrate the differences in the lobsters' behavior between the periods designated I and II for each tank. These data are based on the twice daily observations made during quiescent periods of the day. All observations were classified as to whether an individual was in a shelter, open (in an unprotected location which was judged as being used as a shelter, such as on top of cinder blocks), or walking.

For tank I, it can be seen that during period I almost all day-time observations were made of lobsters in shelters (Fig. 8). During period II, a much larger percentage of observations were made for animals B and L in open locations or walking. As shown in Figure 5, these two animals molted and subsequently failed to establish residences.

Figure 9 gives similar data for tank II. The three animals which molted (F, S and J) also show a greater tendency to be observed in open locations following the molt. Comparison with Figure 7, showing the residency data for tank II, shows that these three animals also failed to establish stable residences during period II.

Dominance relations between the different lobsters in tank I are shown in Tables 4 and 5 for period I and II, respectively. The vertical columns show the number of times an animal has been defeated; the horizontal rows the number of times an individual has defeated or tied the animal whose column the row intersects. For each row, the numbers above the line indicate wins or ties in an animal's zone of residence, the numbers below, wins or ties in all other areas. Examination of Table 4 shows that the large male G was an exception to the general trend of larger animals dominating smaller. Further, while G did defeat or tie A and B in a number of encounters, these were almost always outside his zone of residence, which

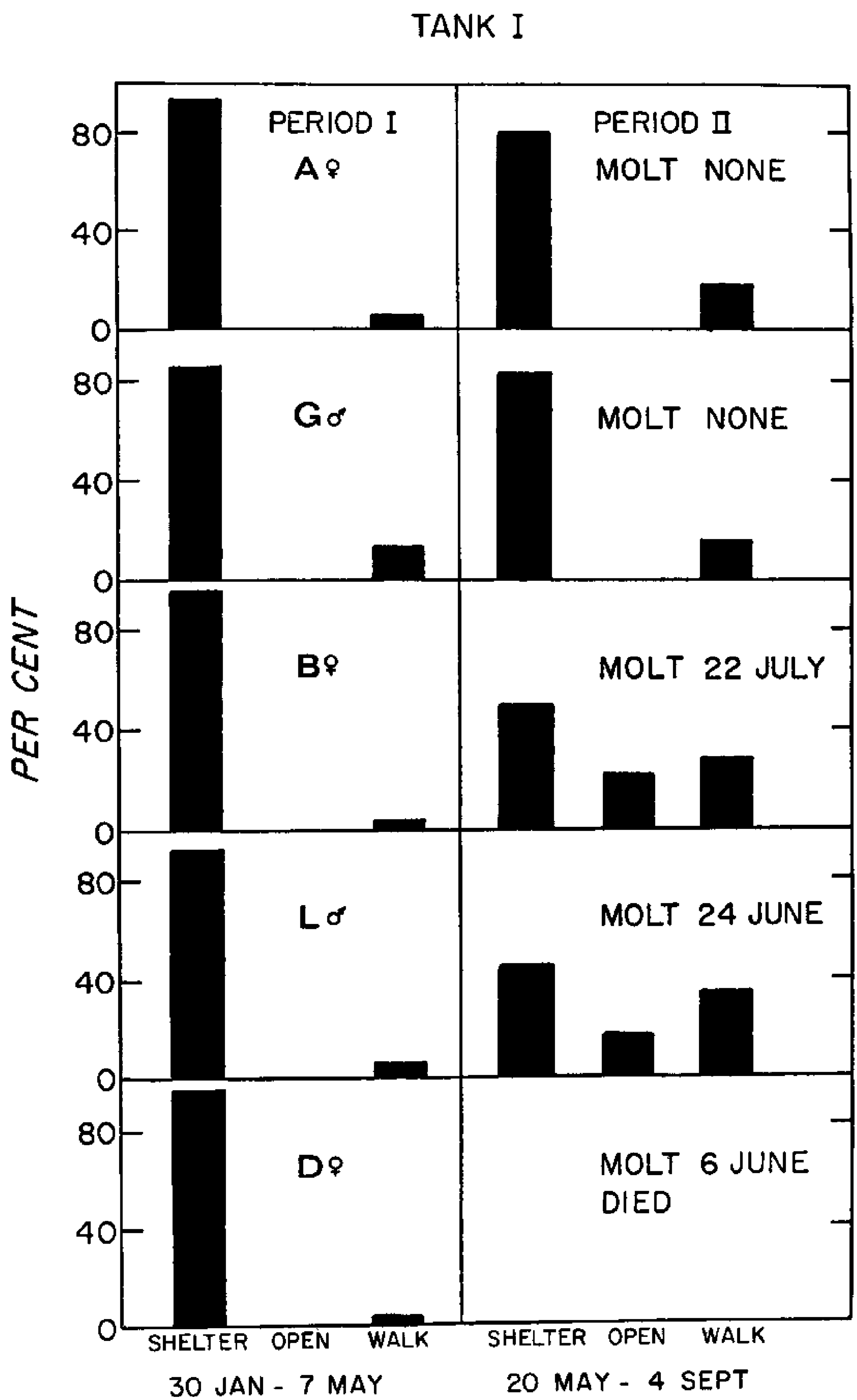

Fig 8 Tank I, percent of observations in shelter, resting in the open, or walking.

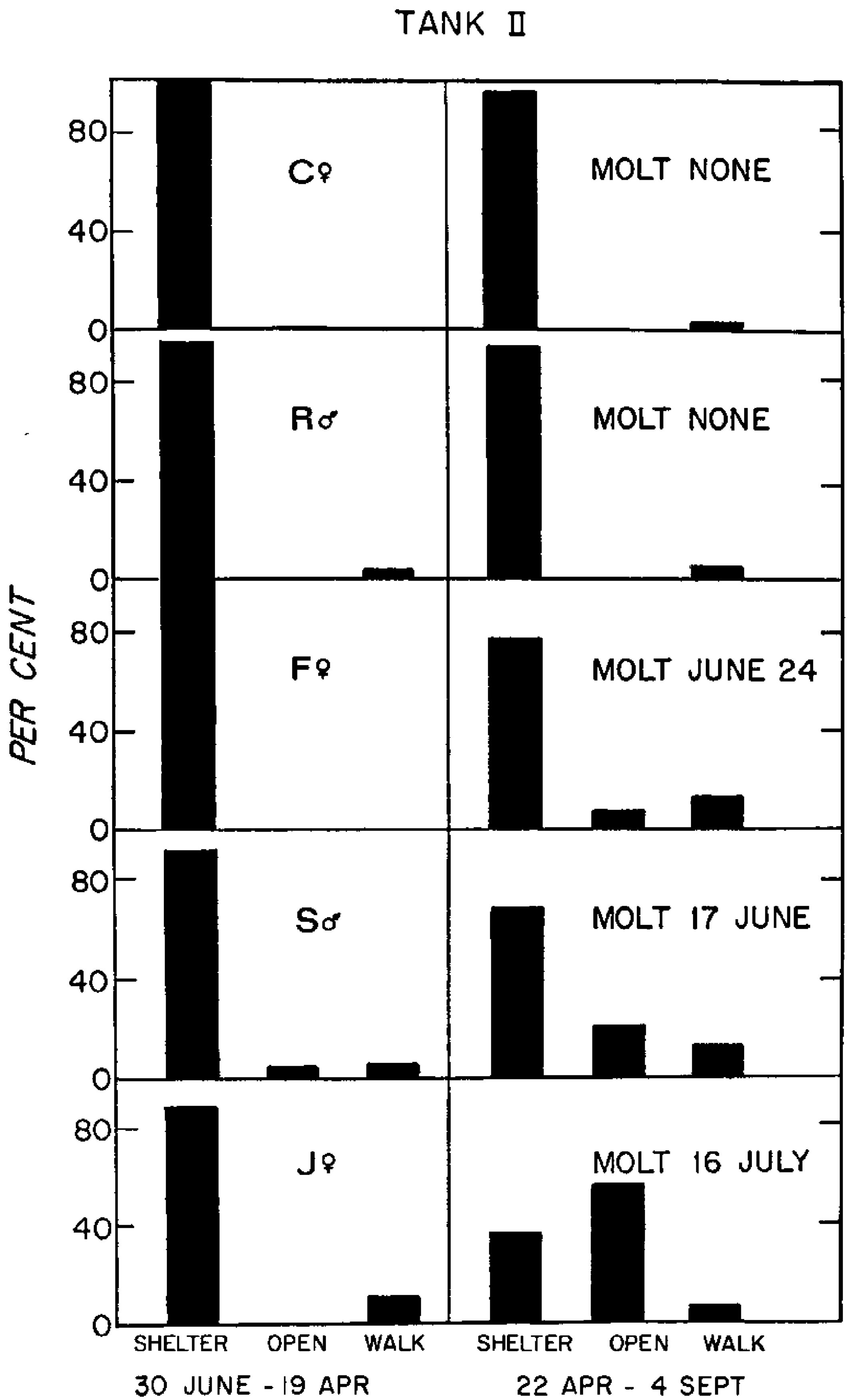

Fig 9 Tank II, percent of observations in shelter, resting in the open, or walking.

TABLE 4

Dominance relations in Tank I lobsters, 4 Feb. to 20 May (period I). Denominators of the fractions are the number of times the lobsters listed vertically were dominant to those at the heads of columns. Numerators are the number of encounters in the dominants' zones of residence. Lobsters are described in Table 1.

	SUBORDINATE				
DOMINANT	A	G	B	L	D
A		9/16	9/11	8/10	4/5
G	1/9		4/13	2/5	0/2
B	3/6	16/19		9/15	2/2
L	0/1	0/2			0/3
D	0/0	0/0	0/0	0/0	

TABLE 5

Dominance relations in Tank I lobsters, (period II) 20 May to 4 Sept.
For legend, refer to Table 4.
* Lobster D died on or before 20 June.

	SUBORDINATE				
DOMINANT	A	G	B	L	*D
A		$\frac{0}{1}$	$\frac{0}{4}$	$\frac{8}{14}$	$\frac{0}{0}$
G	$\frac{0}{9}$		$\frac{4}{8}$	$\frac{0}{13}$	$\frac{0}{0}$
B	$\frac{0}{2}$	$\frac{1}{3}$		$\frac{0}{8}$	$\frac{1}{1}$
L	$\frac{0}{7}$	$\frac{0}{1}$	$\frac{0}{6}$		$\frac{0}{0}$
D	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	

TABLE 6

Dominance relations in Tank II lobsters, 4 Feb. to 20 Apr. (period I). For legend, refer to Table 4.

DOMINANT	SUBORDINATE C	R	F	S	J
C		$\frac{1}{9}$	$\frac{0}{1}$	$\frac{0}{2}$	$\frac{1}{7}$
R	$\frac{4}{5}$		$\frac{0}{4}$	$\frac{1}{1}$	$\frac{4}{7}$
F	$\frac{10}{11}$	$\frac{5}{10}$		$\frac{3}{5}$	$\frac{1}{7}$
S	$\frac{0}{1}$	$\frac{0}{0}$	$\frac{0}{0}$		$\frac{0}{0}$
J	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	

TABLE 7

Dominance relations in Tank II lobsters, 22 Apr. to 1 Sept. (period II). For legend, refer to Table 4.

DOMINANT	SUBORDINATE				
	C	R	F	S	J
C		$\frac{1}{3}$	$\frac{1}{10}$	$\frac{0}{9}$	$\frac{0}{2}$
R	$\frac{7}{20}$		$\frac{13}{24}$	$\frac{1}{8}$	$\frac{5}{11}$
F	$\frac{0}{0}$	$\frac{1}{3}$		$\frac{3}{12}$	$\frac{1}{2}$
S	$\frac{0}{3}$	$\frac{0}{0}$	$\frac{0}{4}$		$\frac{2}{6}$
J	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{0}{1}$	

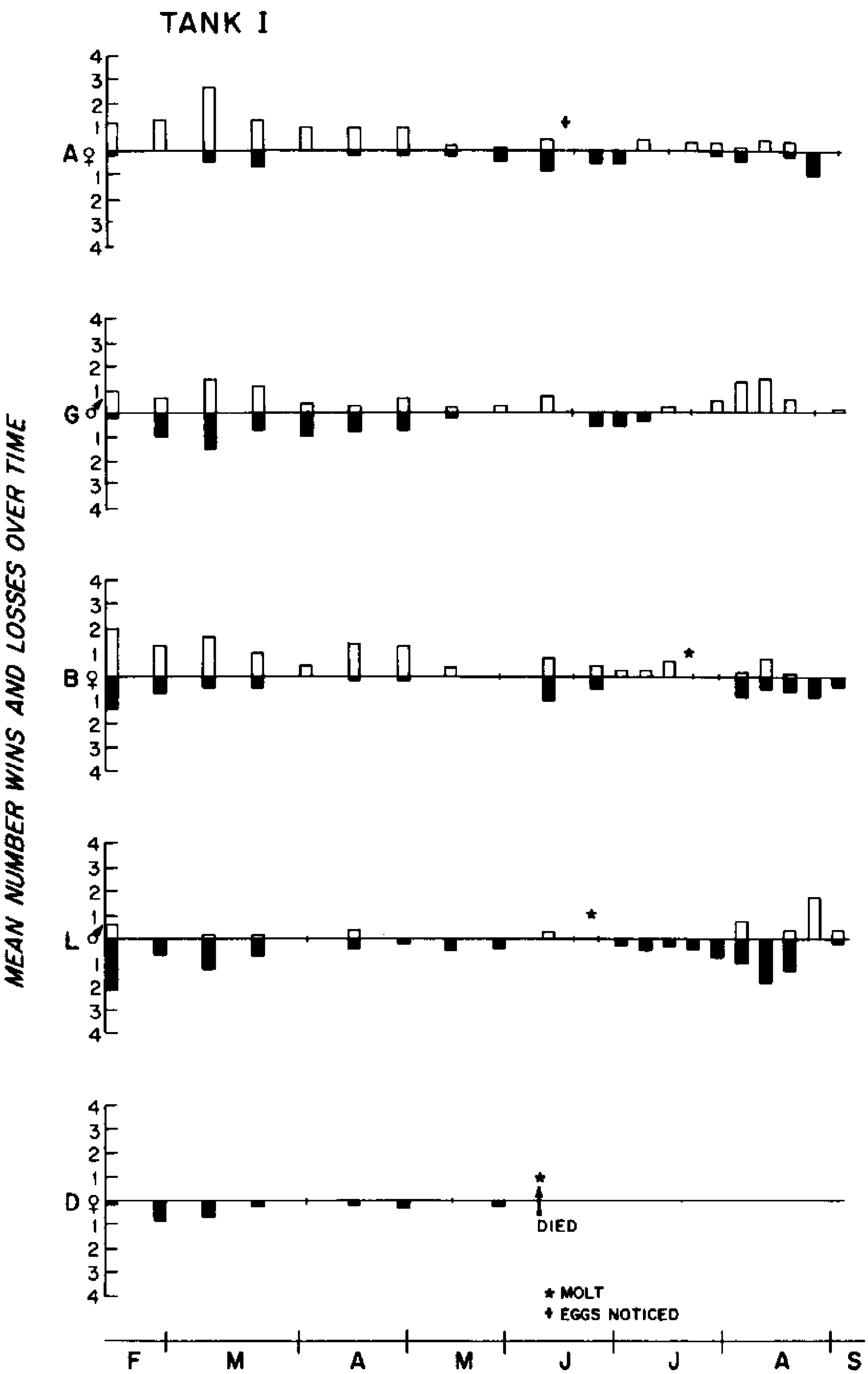

Fig 10 Tank I, dominance and subordinance over time. Number of wins and ties are indicated above the line, losses below. * indicates time of molt.

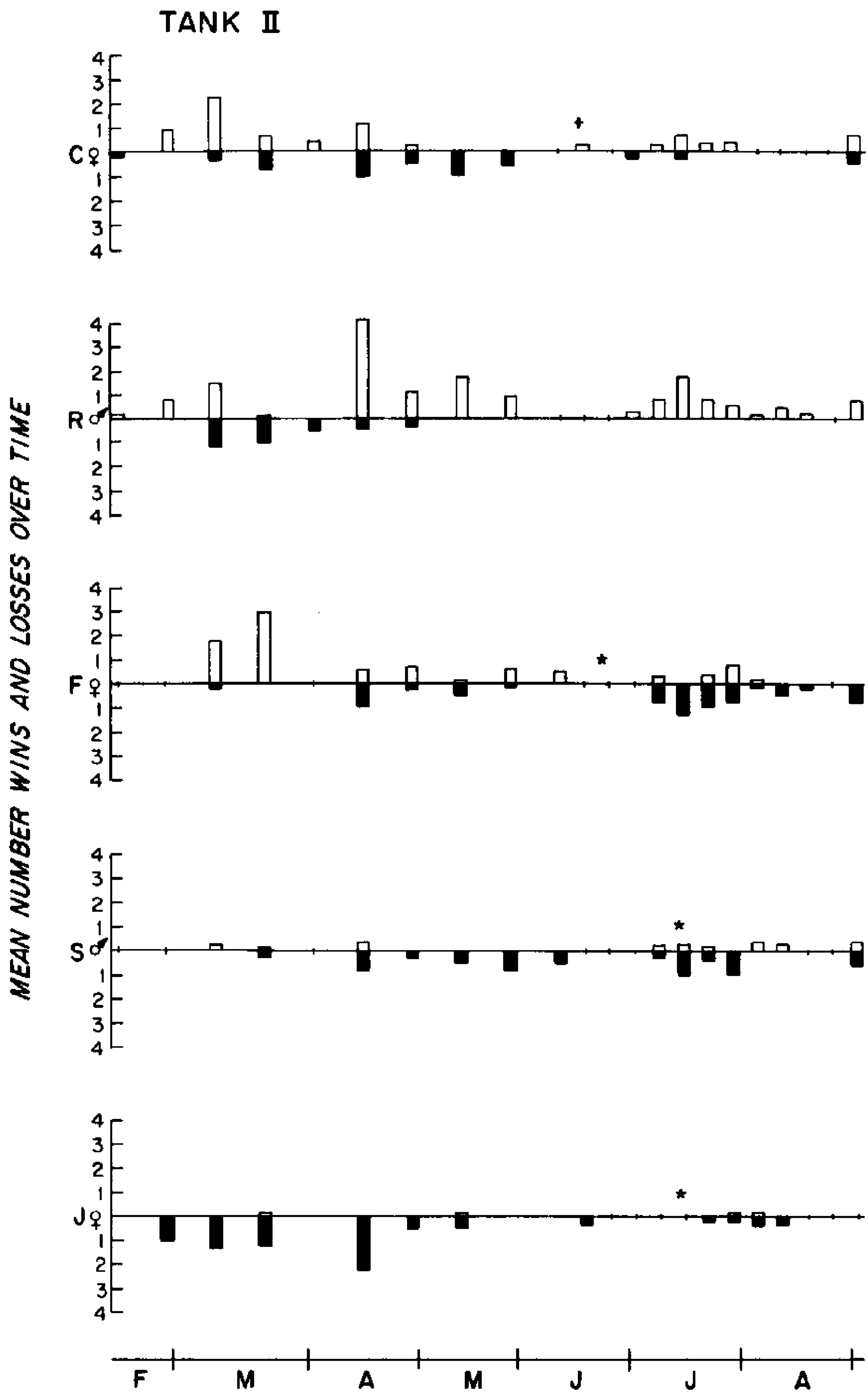

Fig. 11 Tank II, dominance and subordinance over time. (See Fig. 10 for explanation.)

overlapped (during April 1 to May 20) with that of B, as can be seen in Figure 5. During period II (Table 5) the male lobsters G and L increasingly won encounters and the females A and B appeared to have lost status.

Tables 6 and 7 present similar data for tank II. In comparison to tank I, relatively fewer animals seemed to win encounters during period I in their zones of residency, probably reflecting the unstable residency patterm (Table 6). The relatively stable residence pattern for R during period II (Table 6) coincides with the large number of wins within his zone of residence.

Further aspects of dominance relations in the lobsters are presented in Figures 10 and 11. These graphs show the number of wins and ties (above the line) vs. losses (below the line) for each animal throughout the course of the study. Shifts in relative dominance through time are illustrated in these graphs. For instance, in tank I (Fig. 10), G eventually became a winner with no losses, coincident with the period of thermal stress; in contrast, animal B molted and became more of a loser. A somewhat more consistent pattern following heating is shown in Figure 11 for tank II. Here there seemed to have been a trend toward fewer social encounters in comparison to the previous month or so.

4. Pair Bonding and Reproductive Behavior in Lobsters

Table 8 is a time table of major events of pairing, mating and the post-mating bond. The focal point is the mating act, around which the timing of other events is organized. By comparing the three matings, one can gain an idea of the normal course of events in our aquaria. The following is a general description of reproductive behavior in *H. americanus*, including aspects of pair bonding, and based on observations of the three pairs listed in Table 9.

Male lobsters established residences about one week before mating

<u>TABLE 8</u>

Pair bonding, mating, and post-mating events in three pairs of lobsters. Solid lines indicate probable continuation of bonding; broken lines indicate duration of the bond unknown. Italicized letters refer to individual lobsters listed in Table 1.

Pair	*F* and *R*	*J* and *R*	*B* and *G*
	♀ ♂	♀ ♂	♀ ♂
Day			
-4			Not together
-3	Together in shelter	Not together	No recordings made
-2	No recordings made	No recordings made	
-1			Together in shelter
0	24 June 1528h, F begin molt 1600h, mating	15 July, Together 1714h, J begin molt 1800h, mating	23 July post 1700h, probable mating
+1		1430, Together	0850, molt shell observed
+2		Separated	
+3	900, Together 1000, Separated		Together
+4			
+5			
+6			Separated

actually occurred (Figs. 6 and 7). In the weeks prior to molting, female lobsters showed unstable residence patterns (Figs. 6 and 7). About three to four days before mating, the female lobsters appeared to seek out the largest male in the tank. Initial contacts between the pair involved the female approaching the male with her claws down and the male non-aggressively repelling her, usually pushing with claws closed and held low. This continued for a variable period of time, but eventually the female gained entrance to the male's shelter and was tolerated even though she sometimes appeared to push him out of the shelter. During this period, however, the female was not always in the shelter with the male, but was often seen on the opposite side of the tank.

In H. americanus, the actual mating is preceded by the female molting. In the two instances we observed, the interval between completion of the molt and the mating was between 20 and 45 min. At least 7 hours before the mating, the female displayed a series of behavior patterns not seen in other contests. The female repeatedly Approached the male rapidly and placed her outstretched but closed claws on the meropodite of his cheliped. The male then lifted the female's claws up and Pushed her away, but gently and with claws closed. The female then turned around and backed up to the male, who placed his claws on her abdomen. The female Walked away, faced the male again, and Approached with claws outstretched. This pattern occurred repeatedly, although not continuously, prior to the molt. During intervals in activity, the male stood high on his legs and Antenna Felt her carapace.

The female would either molt inside the male's shelter or outside adjacent to it. She began molting laying on her side in front of the male, who faced her with claws down. After molting the female was very weak and supine; during this interval the male stood and placed his closed claws over her and often engaged in mutual Antenna Touching with her. The female then

Fig. 12 Lobster pair in male's shelter the day following mating. The female is beneath, and a portion of her molted chelae is to the left.

began alternately approaching and tail flipping away from her suitor.

Mating appears to be initiated by the female who, as before the molt, repeatedly backed up to the male, who placed his claws over her thorax. The male then turned the outstretched female over with his walking legs, and mounted and ejaculated, as evidenced by repeated tail thrusts. The male then dismounted and the female tail flipped away. Shortly, the female began again her seductive backing up to the male, and mated again one or more times. The male then began feeding on the female's molt shell (although isolated, recently molted females almost always eat their own shell).

One further aspect of male lobster behavior is especially interesting. In spite of the male's non-aggressive tolerance of the female for a week or so encompassing the mating, his behavior towards other intruders, inter- or intraspecific, was highly aggressive. Often a mating was interrupted by the male attacking Cunners (Tautoglabrus adspersus) in a very aggressive manner not previously observed. These fish seemed especially attracted to the molting process, and fed on the molt shell before the male took it into his shelter. In tank II, equally unusual aggression was directed at the other, smaller male who seemed inquisitive and came over near the molted female.

The pair bonding remained intact for three or more days following mating and then broke up (Table 8). Figure 12 shows the pair J (female) and R together in his shelter the day following the mating. The male's protective attitude in response to the photographer is well conveyed by this photograph. The female can be seen beneath the male, and a portion of her molted chela is to one side.

5. Comparison of Intra- and Interspecific Behavior Involving Lobsters

Table 9 presents a comparison between intra- and interspecific encounters involving Homarus americanus. All interactions were classified as to

TABLE 9

Total number for both tanks of intra- and interspecific encounters of different intensities involving lobsters. L refers to low intensity, M to medium intensity, and H to high intensity encounters (see text).

		Lobster
	L	274
lobster	M	82
(*Homarus americanus*)	H	31
	L	11
crab	M	3
(*Cancer borealis*)	H	0
	L	39
eel	M	34
(*Anguilla rostrata*)	H	1
	L	22
flounder	M	3
(*Pleuromectes sp.*)	H	0
	L	8
cunner	M	3
(*Tantoglabrus adspersus*)	H	0

intensity, depending on the behavior patterns displayed by the lobsters. Low intensity encounters were characterized by the units Approach, Advance, Retreat, Flee and Defensive Posture, as well as No Response (Table 3). Middle intensity encounters involved these units, but also the more aggressive Lunge and Snap. High intensity interactions between lobsters were relatively prolonged and frequently included Claw Locks and Rips.

It is clear from Table 9 that the vast majority of recorded interactions involving lobsters were intraspecific. In tank I, there were a total of 137 low, 43 medium and 9 high intensity intraspecific interactions recorded; a similar breakdown for tank II gave 137, 39 and 22, respectively.

Of the total number of interactions for both tanks, 92% were of low or medium intensity, and only 8% were classed as high intensity encounters.

Encounters between crabs (Cancer borealis) and lobsters appeared relatively pacific (Table 9). By the time we began heating the aquaria, all crabs had died, so that we have no data for the period of thermal stress. The cause of death is unknown, although one male lobster (R in tank II) was observed eating at least two of the crabs, one of which may have been alive at the time. In the same tank, other crabs died and were untouched, or only eaten by lobsters after several days. Of the 14 crab-lobster interactions recorded, two were initiated by crabs. On one occasion, a crab displaced one of the smallest lobsters, J. Intraspecific relations in C. borealis were much less aggressive than in lobsters, and the former often aggregated in groups of two or three.

Table 10 shows that most interspecific interactions involving lobsters were of low intensity with all species except eels (Anguilla rostrata). The single high intensity interspecific interaction recorded involved an eel and a lobster. The eels were not active during the first third of the study (see section on eel behavior), and thus had a shorter overall period to interact with the lobsters than either of the other two species of fish.

Interactions between flounders and lobsters usually consisted of a flounder swimming over a lobster and the latter displaying a Defensive Posture, apparently in reaction to the shadow of the fish. Frequently, the lobster's response was to retreat to its shelter. The flounders either fled or paid little notice to the lobsters, who, however, may have been reacting to the former as they would a predator. In contrast, almost all cunner-lobster interactions stemmed from cunner curiosity towards recent female molts and the male's aggressive defense previously referred to in the section on reproductive behavior.

6. Effect of Temperature on the Behavior of Eels, *Anguilla rostrata*

Of all the species in the large aquaria, the eels showed the most clear-cut response to temperature. Prior to about the middle of April (temp., $8^{o}C$), the three eels in each tank were inactive and remained in the holes in the center cement blocks. From mid April on the eels became increasingly active, and were first observed to feed on May 8 (temp., $10^{o}C$).

Because lobster behavior was the major focus of our study, we did not systematically record eel behavior when the lobsters were active. The eels' pattern of activity was similar to the lobsters', although they were rather less active when food was not present. Social behavior in the eels consisted largely of momentary contact while searching for food, with one animal brushing another and neither appearing to take much notice. Such contacts were frequent in spring and early summer, when no aggressive interactions were noted between eels.

On July 17, we began heating the sea water entering tank I, and by August 5 the temperature in this tank was $26.5^{o}C$. On this latter date, the eels first displayed overt aggression, consisting of circling behavior, biting, open mouth displays, and mouth locks (perhaps analogous to Claw

Locks in lobsters). Also observed were one-sided encounters, when one eel repeatedly chased and nipped the other. Interestingly, aggressive behavior in tank II eels was first noted on August 20, when the temperature was 26°C. Aggressive encounters were last noted in tank I on August 21, when the temperature had decreased to 26°C from a high of 28°C.

A total for both tanks of 4 low intensity (physical contact without overt aggression), 2 medium intensity (chasing behavior) and 13 high intensity (including mouth locking) aggressive interactions were observed during the period in which the temperature was 26°C or greater, and no medium or high intensity interactions were observed below 26°C. Although they were not systematically recorded, low intensity interactions were not uncommon between eels at ambient seawater temperatures.

Our results on temperature effects on behavior of the eel, *Anguilla rostrata*, can be contrasted with those of Nyman (1973) for the European eel (*A. anguilla*). This author found that the European eel was totally inactive from 5 to 8°C, and began swimming only at about 14°C (vs. 10°C in the present study). Feeding also did not occur below 14°C, although this may have been due to too short an acclimatization period (Nyman, 1973). Elsewhere the European eel has been cited as feeding at 10°C (Brunn, 1963). Nyman also observed aggressive "territorial" behavior which began at 17°C and was most pronounced at temperatures above 21°C. In the present study, aggression was first observed at 26°C, and there was no evidence of territorial behavior, although lack of identifying marks may have made territorial behavior difficult for observers to recognize.

CONCLUDING DISCUSSION

Our results do not support the highly aggressive and cannibalistic reputation of *Homarus americanus*. Of the six animals which molted in both tanks, only one did not survive, possibly due to predation by the crabs (*Cancer borealis*) or by the eels, or through inability to molt. Although there were no losses of claws, the dactylopodite of the crusher claw of one lobster (F) was damaged following the molt; also, the large male C initially damaged the dactylopodite of his crusher claw, and this probably occurred in the fighting following introduction in January.

Another indication of the relatively non-aggressive behavior of *H. americanus* in our study is given by the comparatively small number of interactions involving lobsters (Tables 4, 5, 6 and 7). Further, Table 9 shows that the number of lobster interactions of high intensity were few. Although the data are not analysized here, in spite of the relatively high night-time vs. day-time activity in the lobsters (especially Tank I), there were very few interactions at night, and most were mutual or one-sided avoidances.

Our data suggest that if given enough space and shelter, the American lobster is much less aggressive than has been previously supposed. However, when forced to interact in small quarters, especially with strangers, as in Scrivener's (1971) study, lobsters are quite aggressive. Aggressitivity in lobsters is also increased by isolation (Dunham, 1972) and probably by hunger, as in hermit crabs (Hazlett, 1966).

Compared to many captive studies of lobster behavior, or conditions under which mass culture has been attempted, our animals were given a large amount of space. In the present study, there were 1.4 m^2 of bottom area per lobster (area of tank bottom, 6.8 m^2). The density of lobsters may have been similar to that found in natural reef habitat areas (Richard Cooper, personal communication), although our lobsters had no large adjacent area ("home range") in which they could forage.

When we began this study, we were very much interested in the question of territoriality in lobsters. Some of the lobsters did show patterns of stable residency for up to 3 months, particularly in Tank I (Figs. 6 and 7). This, coupled with the information in Tables 4 through 7 (showing the number of times an individual was dominant in encounters inside vs. outside his "zone of residence") strongly suggests that several individuals were territorial. For example, the female lobsters A and B in tank I were territorial, but not the males G, who was unstable in residence, or L, who lost a high percentage of encounters around his shelter. The large male R in tank II was clearly territorial from about June 17 until the end of the study. Restricted space, forcing foraging lobsters to come close to others residences may have allowed only the largest and most aggressive to hold territories. If this were true, fewer (or smaller) animals, or more space would have resulted in a higher percentage of territorial animals.

A disturbing feature of our study is that the groups of lobsters in the two tanks were so dissimilar in behavior, although they had been carefully size and sex matched. These differences are perhaps most apparent in Figures 6 and 7. As previously mentioned, the activity response to artificial increase in temperature in the two tanks was the opposite (Figs. 4 and 5). Although it does not clarify the issue, our impression is that the lobster behavior in the two aquaria reflected the "personalities" of the most dominant two or three individuals in the tanks.

A related issue is the "intentional" dissimilarity of the different individuals within each tank. Apart from possible "personality" quirks, the normal biological processes of molting and egg-bearing doubtless strongly influenced certain individual's behavior, clouding any interpretation of the lobsters' response to an external perturbation, such as the super-normal temperature increase. Figure 6 for tank I best illustrates the possible effect of molting or egg-bearing on residence patterns in lobsters.

In spite of the difficulties outlined above, we can make some statement about super-normal temperature effects on behavior of H. americanus. The most obvious point is that the artificial temperature increase did not have an effect on activity, especially "spontaneous" nocturnal activity, consistent between tanks (Figs. 4 and 5). Further, while the artificial temperature increase coincided with a decrease in the number of encounters in tank II, this was not true in tank I. In tank I, the temperature increase did not seem to bring about changes in the residence pattern established (Fig. 6) during period II. In tank II, the relatively long-term, stable residence pattern of R did not appear to be changed much after heating. In conclusion, super-normal temperatures, within a few degrees of the lethal temperatures for H. americanus (Todd et al., 1972), did not alter lobster behavior in adults or juveniles in any clear, consistent manner. The same basic conclusion was reached by Todd et al. (1972) in a comparatively short-term, more artificial study in which lobsters were placed together in a 30-gallon aquarium and allowed to interact at a progressive series of super-normal temperatures.

As stated in the introduction, the major focus of this study was to observe lobster behavior in a semi-natural habitat. This necessitates a complex environment, and one in which variables are difficult to control. The results of the present study, together with the results of Todd et al.'s study (1972), do not show any dramatic thermal effects on lobster behavior within the temperature ranges studied. We must be cautious, however, in assuming that without studying other life stages of lobsters, including embryonic, larval, post-larval, as well as small juveniles, we can rule out possible deleterious effects of thermal stress on lobster populations.

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