Arq. Ciên. Mar, 20 (1/2): 25-32
Dezembro, 1980 — Fortaleza, Ceará, Brasil

MIGRATORY BEHAVIOUR OF THE SPINY LOBSTER PANULIRUS ARGUS (LATREILLE), OFF CEARÁ STATE, BRAZIL[1]

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Fishing is a particularly mobile means of harvesting inasmuch as the vessels are able to move a great deal in search of areas with the highest densities of fish, in order to ensure high catching efficiency. In their turn, fish populations follow migratory cycles, mainly correlated with the feeding and reproduction functions, and hence it follows that one of the requirements of a constant checking on them is to determine dispersion patterns so as to be matched with those of fishing distribution.

The process of catching, marking or tagging, releasing and collecting information on the recaptured individuals is known as tagging experiment. Data obtained on the tagged subpopulation are supposed to be representative of the whole population and therefore it is needed that experiments cover uniformly the entire area in the different seasons of a year and the number of tagged fish hold a constant proportion to the density around each release position. The success of an experiment also depends on a rapid and uniform mixing of tagged fish, and on checking possible changes in behaviour such as the tagged ones becoming more vulnerable capture and therefore undergoing a higher rate of mortality. Errors in the information on recaptured tags, inefficiency of reporting of recaptures and uneven distribution of fishing effort are liable to affect the results.

The movements of the spiny lobster *Panulirus argus* have already been studied by means of tagging experiments carried out in 1964 and 1965 (Paiva & Fonteles Filho, 1968), but the analysis was somewhat superficial in that no seasonal factors were taken into account and little quantitative significance was attached to the spatial dispersion of the tagged lobsters. In this paper, those data have been given a mathematical treatment in so far as the recapture points are considered as vectors, which allow the calculation of dispersion parameters and centres of density in different seasons whereby one can ascertain more accurately the migratory behaviour of that species, and make out its causes and consequences.

MATERIAL AND METHODS

The data used derive from three tagging experiments of 3,867 lobsters, sor-

(1) Research work of a project supported by Superintendência do Desenvolvimento do Nordeste (SUDENE).
(2) Bursar of Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

ted out as follows: Experiment no. 1: 471 individuals (230 males and 241 females, of which 117 were spawning) tagged and released around 03°37'S – 38°06'W, in the period 16-25 March, 1964; Experiment no. 2: 971 individuals (227 males and 744 females) tagged and released around 02°35'S – 40°10'W, in the period 2–9 July, 1964; Experiment no. 3: 2,425 individuals (302 males and 2,123 females, of which 1,961 were spawning) tagged and released around 02°16'S – 40°04'W, in the period 14–23 March, 1965 (table I).

A serrated spear was used as tag, being introduced in the tail's muscle, between the first and second dorsal segments to the right of the symmetry plan (Paiva & Fonteles Filho, 1968). It should be added that not all recovered tags have been reported and/or returned, some account needing be made for losses due to the tagging process itself and shedding of tags ensuing moulting.

In each experiment, the recapture points have been plotted on a chart of the continental shelf off Ceará State, by quarters of the year, the sex not being taken into account given the small number of tagged males. Data referring to recaptures made within 5 days of release have been discarded so as to avoid bias caused by the clustering of points very near the release positions.

The simplest way of displaying a set of tagged lobsters is by means of a diagram showing their liberation and recapture positions, and the period at liberty of each individual. While being very useful, such a diagram shows very little of the actual movement of the lobsters as they travel from the release to the recapture positions, since only the end points of each journey are fixed and it is left to be deduced what happened in between.

To overcome this problem, each recapture point can be looked at as a vector with a certain angle of direction (θ) and a "strength" measured by its distance from the release position (r) and thus being determined by the intersection of the lines $x = r \sin \theta$ and $y = r \cos \theta$, the longitudinal and latitudinal components, respectively. Based on an approach by Skellam (1951), who used the mathematical theory of diffusion of particles in a fluid, the method has to do with regarding each fish as moving within a circle, from any point in the circumference to its centre, with a constant probability. The formulae obtained by developing that model as an extension of Skellam's approach were modified by Jones (1966) so as to be used for the purpose of estimating a directional coefficient of dispersion, a random coefficient of dispersion and a centre of density:

$$V = \frac{\sqrt{(\Sigma\, r \sin\theta)^2 + (\Sigma\, r \cos\theta)^2}}{\Sigma t}$$

TABLE I

Details of the tagging experiments of *Panulirus argus* (Latreille) used in this investigation.

Experiment	Tagging period	Release position	Numbers tagged				
			male	female			Total
				total	spawning female n	spawning female %	
1	16-25/3/1964	03°37 ' S – 38°06 ' W	230	241	117	48.5	471
2	2- 9/7/1964	02°35 ' S – 40°10 ' W	227	744	–	–	971
3	14-23/3/1965	02°16 ' S – 40°04 ' W	302	2,123	1,961	92.4	2,425

$$a^2 = \frac{1}{n}\left[\Sigma \frac{r^2}{t} - \frac{(\Sigma r \sin\theta)^2 + (\Sigma r \cos\theta)^2}{\Sigma t}\right]$$

where,

V = directional coefficient, measured in mile/day;

r = distance of recapture from release point, in miles;

θ = angle of direction of movement;

n = number of recaptures;

t = number of days at liberty;

a^2 = random coefficient, measured in $mile^2$/day.

The resulting value of the directional velocity (V) actually determines the extent to which lobsters have moved in certain directions, so that the centre of density of the dispersing individuals is given by a point $V\bar{t}$ ($\bar{t}$ being the mean time at liberty, for each quarter of the year) and a mean angle of dispersion Ψ , according to the formula:

$$\Psi = \arctan \frac{\Sigma r \sin\theta}{\Sigma r \cos\theta}$$

The parameter *V* measures the movement of a group of fish in a particular direction, whilst a^2 measures the extent to which individual movement departs from that overall tendency, so that pairs of values of those parameters in different seasons show the type of movement fish are predominantly engaged in. However, in the absence of a gauge to measure their variability, we have resorted to a ratio of a^2 to *V*, named the *mean free path* (d), from the following development, being *n* the number of movements per unit time:

$$V = nd \therefore a^2 = Vd = nd^2$$

$$\text{Therefore,} \quad d = a^2/V$$

The proportion of lobster lying within a circle of radius *R* around their centre of density is given by the relationship:

$$P(R, t) = 1 - e^{-R^2/a^2\bar{t}}$$

Consider the situation where 95% of lobster lie within a circle of radius *R*, that is:

$$0.95 = 1 - e^{-R^2/a^2\bar{t}}$$

$$\text{Then,} \quad R = 1.73\sqrt{a^2\bar{t}}$$

gives the length of the dispersion radius of the circle that contains 95% of lobster after time $\bar{t}$.

RESULTS AND DISCUSSION

The lobsters liberated in group, on such a small area as to be taken as a point, start moving independently of one another while a gradual dispersion takes place. If there was no directional tendency, the resultant of the group's dispersion would be equal to zero, since the individual displacements would offset each other through equal vectors operating in opposite directions. However, as there is no pure random dispersion, a direction component is to be superimposed on the overall movement, with variable predominance in different seasons, according to which main biological function prevails: feeding (mainly random dispersion) or reproduction (mainly directional dispersion).

From the analysis of table II, large variations can be shown to take place between the seasonal values of *V*, a^2, *Vt* and *R*, implying that biological factors are at work which can be held responsible for them. Lobsters realesed in March (experiments nos. 1 and 3) at positions lying about 140 miles apart reveal quite similar migratory behaviours, borne out by the following features: (1) movement paralel to the coast in the second quarter, with a low random dispersion, short mean free path (especially in Experiment no. 3), centre of density near the 50-meter isobath and relatively small dispersion radius; (2) movement oblique to the coast, bringing the centres of density to a smaller depth (about 30 meters), with a large increase of the random dispersion coefficient, the mean free path and the dispersion radius in the third quarter, and a sharp decrease of those parameters in the fourth quarter; (3) outward movement to the vicinity of the 50-meter isobath, taking the centre of density nearer the release position (8 miles away), with low values of the random dispersion coefficient, mean free path and dispersion radius (table II; figures 1 and 2).

Lobsters released in early July (experiment no. 2), in general, presented higher coefficients of directional and random dispersion than the previous experiments, but quite similar values of the mean free path and dispersion radius. In the third quarter, abnormally high directional dispersion takes the centre of density some 45 miles away from the release point, despite a large random dispersion (30.631 mile^2/day) and the movement axis displays an oblique direction to the coast. In the fourth quarter, the lobsters maintain this pattern, but move back towards the release point with their centre of density now positioned about a 15-meter depth; both coefficients of dispersion have decreased, but the high values of the mean free path and dispersion radius indicate a predominance of the random movement. In the first quarter the centre of density again moves outwardly, to a depth around the 20-meter isobath, but only in the second quarter there is a change of direction, with a further offshore displacement nearer the isobath of 50 meters; the very low values of the mean free path and dispersion radius confirm the predominance of directional movement, in the fourth and first quarters of the year (table II; figure 3), as already observed in Experiments nos. 1 and 3.

The estimation of the dispersion parameters and centre of density has undoubtedly helped throwing further light on some aspects of the migratory behaviour of the lobster *Panulirus argus* which were not made evident by the previous analysis of the recapture distribution. The varying values of V (0.018 – 1.199 mile/day) and a^2 (0.080 – 35.700 mile^2/day) indicate

TABLE II

Estimates of the dispersion parameters of the population of *Panulirus argus* (Latreille) – directional dispersion coefficient (V), random dispersion coefficient (a^2), centre of density ($V\bar{t}$), mean dispersion angle (Ψ), radius of dispersion circle (R) and mean free path (d) – off Ceará State, Brazil.

Experiment no.	Quarter of the year	Number of recaptures	Dispersion parameters					
			V (mile/day)	a^2 (mile^2/day)	$V\bar{t}$ (mile)	Ψ (degree)	R (mile)	d (mile)
1 (March, 1964)	II	47	0.032	2.726	0.86	161	14.8	85.2
	III	9	0.042	14.061	9.14	141	94.9	344.8
	IV	3	0.092	0.600	21.90	150	20.6	6.5
	I	3	0.102	1.868	25.92	136	35.5	18.3
Total	–	62	0.057	4.227	4.22	145	30.6	74.2
2 (July, 1964)	III	183	1.199	30.631	26.09	21	44.9	25.5
	IV	16	0.066	7.614	10.68	11	60.8	115.4
	I	5	0.095	0.080	20.25	22	7.1	0.8
	II	13	0.063	0.491	19.34	65	21.2	7.8
Total	–	217	0.448	26.424	24.19	23	65.3	59.0
3 (March, 1965)	II	92	0.123	1.979	19.13	343	30.3	16.1
	III	17	0.311	35.700	46.52	320	126.6	114.8
	IV	3	0.049	1.914	17.63	196	45.3	39.1
	I	23	0.018	0.303	6.55	335	18.2	16.8
Total	–	135	0.100	5.938	19.40	335	58.7	59.4

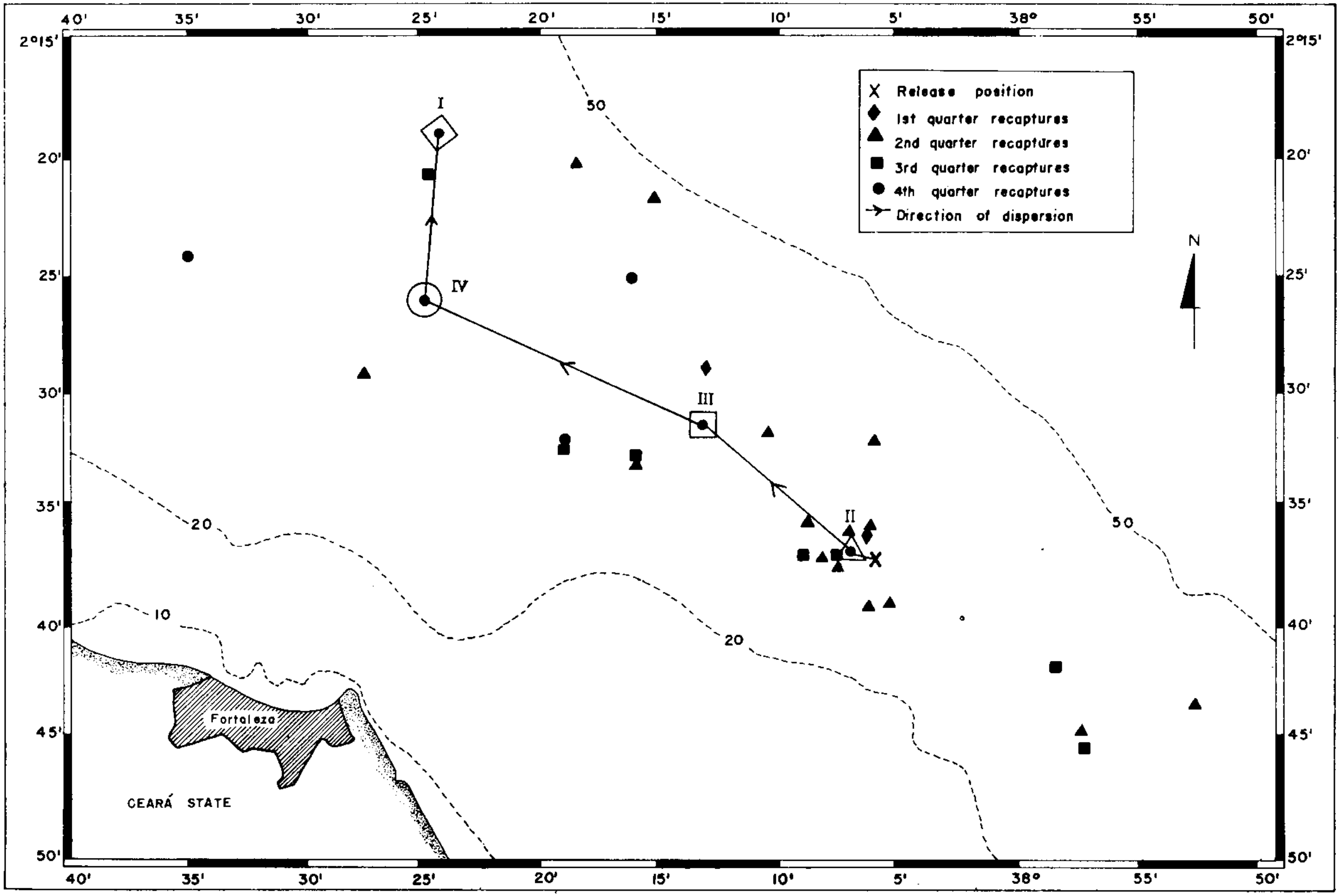

Figure 1 — Recapture distribution and centres of density, by quarters of the year, of tagged lobsters of species *Panulirus argus* (Latreille) released at 03°37'S — 38°06'W in 16 — 25 March, 1964 (experiment no. 1). One recapture, taken at 04°13'S — 37°15'W (3rd quarter). does not appear on this chart.

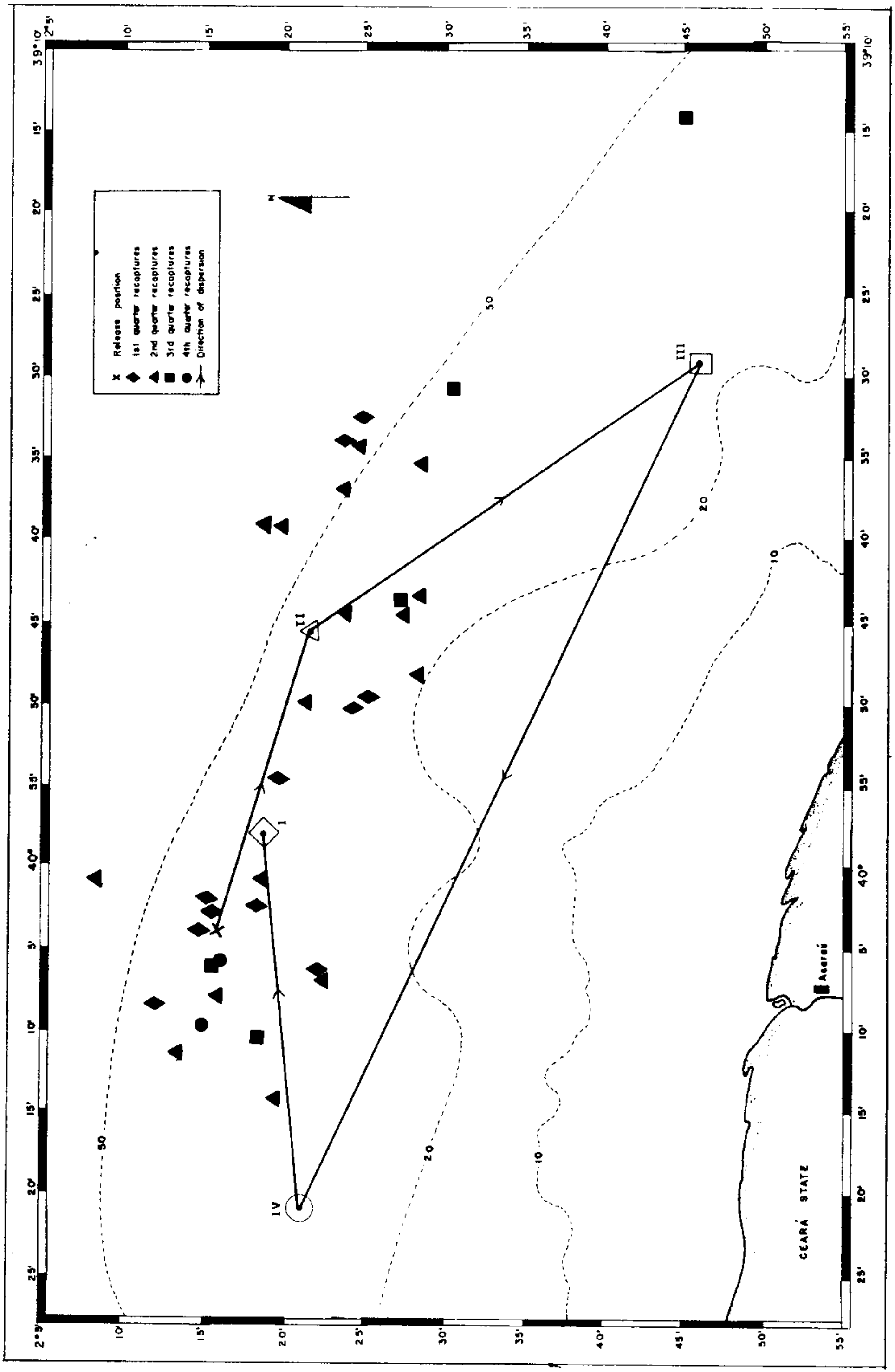

Figure 2 – Recapture distribution and centres of density, by quarters of the year, of tagged lobsters of species *Panulirus argus* (Latreille) released at 02°16'S – 40°04'W in 14 – 23 March, 1965 (experiment no. 3). Three recaptures, taken at 02°29'S – 39°01'W, 02°14'S – 40°40'W (2nd quarter) and 02°30'S – 40°49'W (4th quarter), do not appear on this chart.

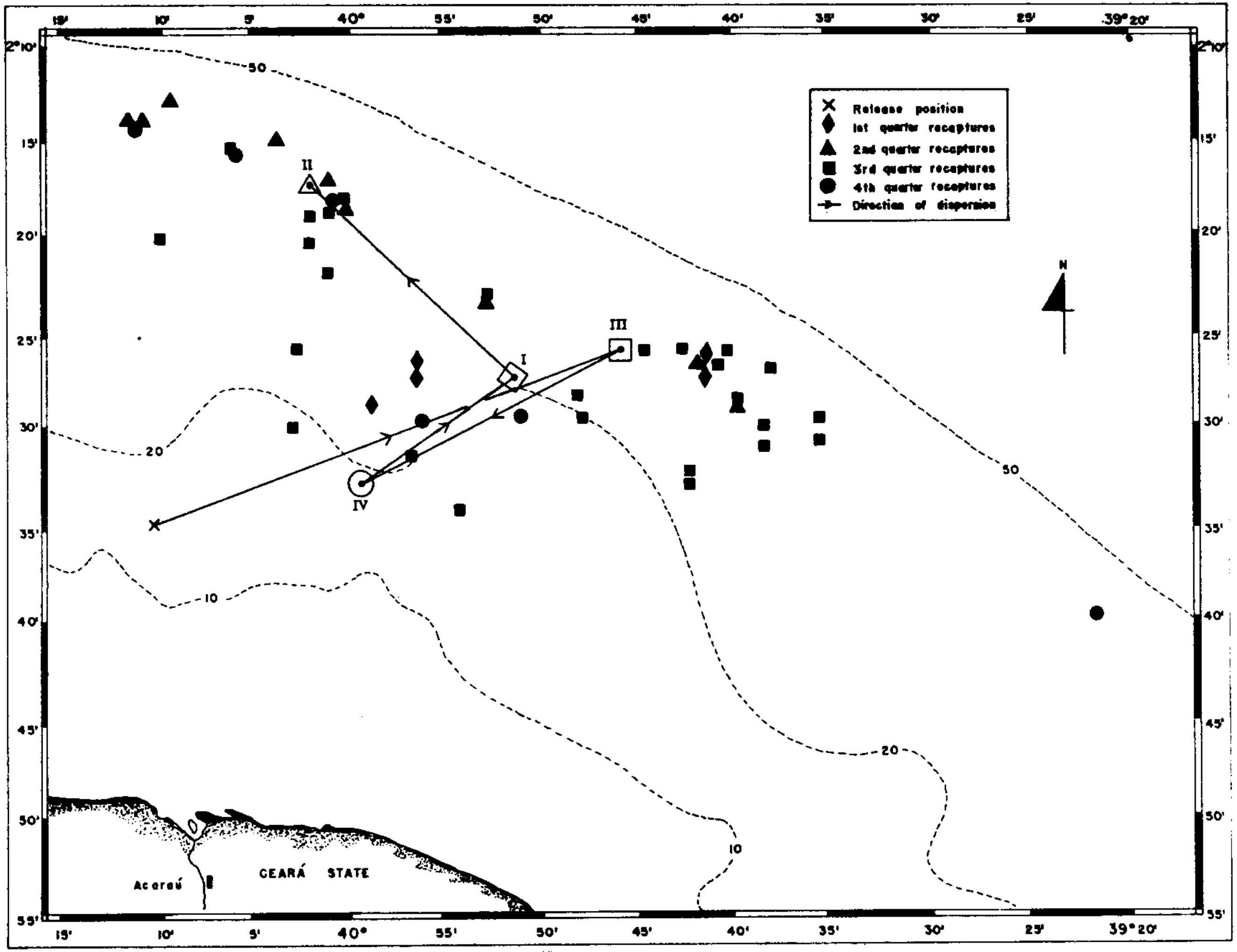

Figure 3 – Recapture distribution and centres of density, by quarters of the year, of tagged lobsters of species *Panulirus argus* (Latreille) released at 02°35'S – 40°10'W in 2 – 9 July, 1965 (experiment no. 2). Two recaptures, taken at 03°32'S – 38°24'W (2nd quarter) and 02°35'S – 49°39'W (4th quarter), do not appear on this chart.

that individuals do move as a group with changeable emphasis of the directional and random components, in direct relation to the reproductive and feeding functions, respectively. Very high values of a^2 in the two quarters after liberation are bound to be caused mainly by sampling errors because mistaken reports of the actual position of recapture after a short period of time have a much larger effect on the value of r^2/t. Estimates of a^2 are also overvalued by abnormally lengthy migrations of individuals (Jones, 1959), and some isolated cases have occurred in all experiments. However, since both V and a^2 are bound to be affected, the mean free path has been used as an indicator of the predominance of either dispersion tendency.

This evidence has been useful to show that:

(1) The directional dispersion in the first and second quarters is related to the lobsters' movement to spawning grounds — data of Experiment no. 3, particularly, support this conclusion, as 92.4% of females were spawning at the time of tagging (table I) and, according to Mesquita (1973), breeding takes place mainly in March–June; therefore, the positions of the centre of density in offshore areas, close to the 50-meter isobath, are also an indication that spawning is performed far from the coast.

(2) The paralel movement to the coast in the third and fourth quarters, with a high random dispersion coefficient, is most probably linked with the lobsters' search for food; this is further confirmed by the high frequency of molting individuals in July–August (Buesa Más *et al.,* 1968) at the onset of a growth cycle which extends itself throughout the second half on the year, coinciding with the main feeding season of *Panulirus argus* off Ceará State.

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