

Descriptive Characterization of Mass Autumnal Migrations of Spiny Lobster, *Panulirus argus*¹

WILLIAM HERRNKIND, PAUL KANCIRUK, JOSEPH HALUSKY
and RICHARD McLEAN
Department of Biological Science
Florida State University
Tallahassee, Florida 32306

INTRODUCTION

Perhaps the most striking aspect of the life history of spiny lobsters (*Panulirus argus*) is the phenomenon of mass single file movements (Herrnkind and Cummings, 1964; Herrnkind, 1969, 1970; Herrnkind and McLean, 1971). The event involves both nocturnal and diurnal movements of thousands of lobsters in chain formations (queues) across open shallow areas devoid of lobsters at other times. The movement lasts only a few days, during which all queues travel in the same general heading. The event occurs in autumn, usually after a period of stormy weather and seems to be localized according to climactic conditions. Mass queuing is reliably reported from the Florida Keys, Boca Raton, Bimini and Grand Bahama (Herrnkind, 1969). Only one-way treks have been observed and the movements presently appear to be emigrations of lobsters from certain areas to as yet undetermined destinations.

These mass migrations are unusual in several respects. First, the mode of movement in formation is unique among benthic crustaceans. Species such as the King crab (*Paralithodes camtschatica*) and some other spider crabs, the anomurans *Pleurocodes* and *Coenobita* (terrestrial), as well as some ocypodids (terrestrial and semi-terrestrial), move *en masse* and form groups but apparently do not travel in formation (Bainbridge, 1961; Allen, 1966; Herrnkind, 1972). Movements of other "lobsters," e.g., *Homarus americanus* and various palinurids, may involve clustering and travel by individuals in proximity, but queues or similar arrangements are reported only for *Panulirus argus* (Lindberg, 1955; Bainbridge, 1961). Second, the other known migrations and wanderings of *Panulirus argus* involve variable solitary movements causing shifts in the population over periods of months (Dawson and Idyll, 1951; Sutcliffe, 1952, 1953; Buesa, 1969). Such movements typically occur at night, the lobsters remaining in seclusion by day. Third, the latter movements are often associated with inshore-offshore migrations of adults during the reproductive season in the spring, whereas mass migrations occur after the main reproductive period (Allen, 1966). Hence, the functional significance of the event is not immediately apparent.

The literature on this phenomenon is sparse. Crawford and DeSmidt (1922) mention movement of *Panulirus argus* in "trains" but do not cite the source of

¹ Contribution number 21 from the Tallahassee, Sopchoppy and Gulf Coast Marine Biological Association.

this observation. Sutcliffe (1952) was told of a migration of considerable magnitude that occurred at Bermuda one autumn in the late 1940s, and he in turn suggested that it might be comparable to a migration occurring at Bimini in October 1950, as reported to him by C. M. Breder, Jr. Aside from such vague references possibly indicating occurrence of mass movements, the volumes of literature on this species included no adequate characterizing data until our recent reports. The documented occurrence of mass migration, a brief description and a photograph of a queue, was published by Herrnkind and Cummings (1964). The tactile mechanism associated with queue maintenance and evidence for an internal Zugunruhe was reported by Herrnkind (1969). More recently, the pathway and orientation vectors were described for a mass migrating population off the west coast of Bimini in 1969 (Herrnkind and McLean, 1971).

In spite of the paucity of scientific information, we found that lobstermen in migration areas have known about the phenomenon for many years and capitalize on it by making large catches. For example the lobstermen at Bimini actively monitor the past migratory pathway through the fall, and during a mass movement catch 500-1,000 lobsters (estimated) per bully-netter per day. This compares to a typical good daily catch of 100-150 at other times of the year. Some of the anecdotal information provided us by these individuals was valuable in focusing our present research in that region.

The absence of scientific information on mass migration is attributable to the following reasons. The earlier authors mentioning the event apparently presented only anecdotal descriptions and did not, themselves, witness it. Furthermore, trapping studies, the common source of data on lobster population dynamics, cannot adequately detect or discriminate a mass movement since it often occurs in areas where traps are not set and even full traps give no indication of time of entry, mode of movement, directionality or magnitude. Directly witnessing the migration is hindered by rough sea conditions and high turbidity associated with its occurrence. Chance observations are further reduced by its limited duration and localization and by the fact that few scientists until recent years actually entered the marine medium to conduct observations (Herrnkind, in press).

For the past 3 years we have undertaken *in situ* and laboratory-based research aimed at characterizing mass migrations, determining causal factors, establishing its biological function and interpreting economic and conservational implications. This paper gives the general characteristics of these events drawn from direct observations in 1963, 1965 and particularly 1969 and 1971. The other research aims mentioned above are briefly discussed but will be treated more fully in a series of detailed papers presently in preparation.

STUDY AREA

Field research was conducted primarily at Bimini, Bahamas, on the extreme western edge of the Great Bahama Bank some 50 miles (83 km) east of Miami, Florida. Bimini is particularly suitable for study of mass migrations occurring off the western side of the islands between shore and the Florida Straits (Fig. 1). The surrounding waters are clear, with visibility ordinarily exceeding 20 m along the west shore and only slightly less to the east over the bank. Even after storms

and periods of high winds cloud the shallow waters, the migratory pathway adjacent to South Bimini is quickly flushed by northward-flowing, clear Gulf Stream water washing over the bank edge. The unique combination of proximity to a migratory area, research facilities (Lerner Marine Laboratory), high probability of migration, water clarity and mild weather provides an excellent situation for *in situ* study of the phenomenon.

The benthic communities and substrate characteristics of the Great Bahama Bank, with special reference to the Bimini area, are treated by Newell *et al* (1959) and Kornicker (1958). In general, the area west of the islands (North and South Bimini and Turtle Rocks) is a gently sloping shelf dropping gradually from the shore or shallow bank area (2-5 m depth), then abruptly at approximately 30 m depth between 1 and 2 km offshore. Lobsters on the shelf live primarily below 6 m depth on hard substrate providing crevices or under isolated coral heads mostly at depths of 10-20 m. The extensive and heavily fished bank population resides mainly in the seawhip (Plexaurid) and sponge beds, although lobsters may inhabit any exposed rock shelves and undercut *Thalassia* banks. We have not observed lobsters by day over open sand, sparse grass beds or benthic *Sargassum* except at migration time. Most of the shelf area over which mass movements were noted consists of these typically uninhabited bottom types.

The hydrographic conditions of the shelf area, according to past studies and our observations, are influenced by the conservative characteristics of the Gulf Stream and the more variable water mass over the shallow bank. Water clarity, temperature and salinity vary according to tidal phase, wind direction and other climactic factors. The waters of the shelf and bank area near Bimini during mild weather in late summer and early fall generally have high clarity (visibility in excess of 20 m), temperatures about 28C (83F) and salinities near 35 parts per thousand (‰), the highest salinities being found in the Bimini lagoon outflow and over the bank (Kornicker, 1958). According to Newell and Imbrie (1955), the Great Bahama Bank water flows generally westward with current vectors varying with tides and displacement, or channeling, of water flowing around the islands. Periods of high winds and thermal perturbations have a rapid and marked influence on the shallow bank. Heavy wave turbulence increases turbidity and sediment disturbance, while the dynamics of heat exchange result in considerable fluctuation in water temperature, especially as compared to the Gulf Stream.

METHODS

Our field research was designed to monitor the lobster populations adjacent to Bimini concurrently with hydrographic and climactic conditions from the premigratory period in early fall through a mass movement (usually in late October - mid November) and subsequently for several weeks. In the premigratory period, we surveyed the general region to determine the distribution of the resident populations and characterized them by number, number per den, size frequency, sex ratio, molt condition, reproductive state and degree of fouling by epifauna and eiflora. As many individuals as possible were tagged with sphyryion type back tags for later identification and released in the area of capture.

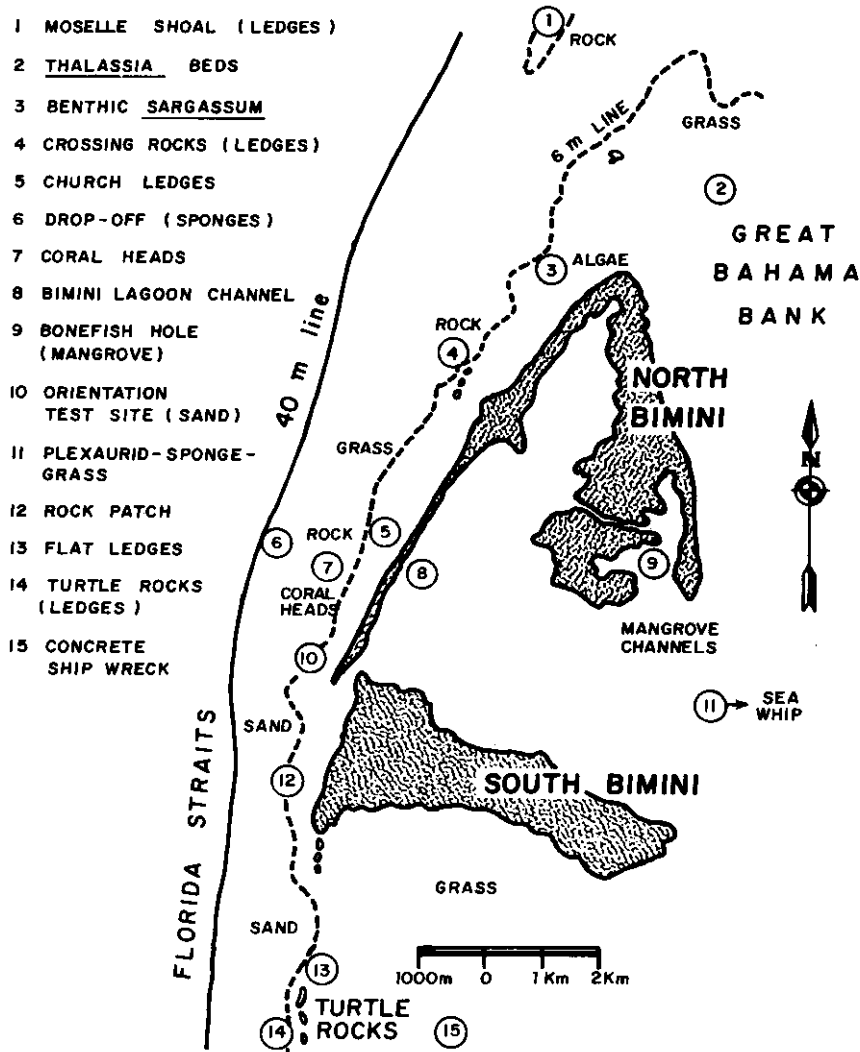


Fig. 1. Bottom characteristics in the Bimini region and areas (1-15) frequently sampled for spiny lobster in 1969 and 1971.

Environmental conditions were monitored by constant recording thermographs (General Oceanics and Ryan) and current sensor (General Oceanics) emplaced on the bottom by divers at such locations as the past migratory pathways, suspected pathways and source areas, and the edge of the shelf in deep water (40 m). Daily thermometer casts were made in the Bimini lagoon and surf.

Specific locations chosen to grid the area were checked on a periodic 4-7 day basis throughout the fall to document any changes in population distribution or

condition. The sphyron tags allowed recognition and monitoring of individual movements while an advertised reward program provided for further information through local divers and lobstermen. Ordinarily we merely recorded the number of a resighted, tagged lobster but did not capture or physically disturb them. Throughout the fall specimens were collected and sacrificed for gut content and hemolymph analyses.

Survey, capture and tagging were conducted exclusively by diving techniques to assure a thorough sample in selected areas and to facilitate behavioral observations. The techniques resemble those described by Cooper and Herrnkind (1971). During daylight, lobsters were visually located (by closely examining the substrate) then captured by tail-snare to avoid injury (to both lobster and diver). When convenient, lobsters were measured and tagged underwater and immediately replaced in their dens. Otherwise, they were placed in mesh bags for measurement and tagging at the surface and subsequent release in the general capture area.

Additional survey outside the selected area was accomplished by boat-towing an observer on a diving plane (Kumpf and Randall, 1961). The plane allowed a snorkler to travel 3-4 knots and dive with little effort to 10 m. Deeper depths down to 30 m were covered by towing a diver with SCUBA. The dive plane technique was especially valuable during mass movements and when water clarity was reduced or surface ripples precluded observing through the air-water interface. Spotting lobsters in dens was facilitated by the ability to control both depth and horizontal scope when operating the plane.

The onset of a mass migration was determined from visual observations of queues moving during daylight. During the periods of probable massing, divers surveyed the general area beginning at dawn, keeping in communication with Bimini lobstermen, who usually dispersed and monitored the shallower depths to 5-6 m (within range of their bully-nets). Upon occurrence of mass queuing, we recorded the number of lobsters per queue and its compass bearing, as well as the location, depth, substrate type, temperature, visibility and general behavior. Samples of the migratory group were tail-snared, measured, sphyron-tagged and released. Behavior and interesting events were photographically documented by 35mm underwater camera whenever possible.

Some migrants were sonic-tagged and tracked as far as possible to determine the pathway at night and in deep or turbid water. Each saddle-shaped transmitter pulsed a 70KHz signal at an individually identifiable periodicity detectable up to 250 m by diver-carried or surface-operated directional receiver (Smith-Root). The general technique is given by Herrnkind and McLean (1971) and further elaborated in Herrnkind *et al* (in prep.). The tracking program was just initiated and results are not included in this paper. However, the method is potentially significant because, by sonic telemetering migrants over long duration (30-day tag life), we hope to determine the population movement presently escaping investigation. Knowledge of resultant changes in population distribution and structure is necessary to interpret the functional significance of the event to the species.

DESCRIPTIVE CHARACTERIZATION

PREMIGRATORY PERIOD

Figure 1 shows the main areas surveyed regularly during the early fall along the shelf area west of Bimini where past mass queuing was observed (Herrnkind and Cummings, 1964; Herrnkind and McLean, 1971).

The region is mostly open sand, sparse grass, benthic *Sargassum* or hard substrate with few ledges, and lobsters were not observed by day in these habitats. Some rocky areas in shallow depths (5-8 m) providing ledges were occasionally inhabited by a small number of lobsters (areas 4, 5, 12 on Fig. 1). Several areas of coral heads and rock outcrops 10-20 m in depth were inhabited at this time, but the regions were relatively confined (totaling approximately 20 hectares) and we estimate they contained only a few hundred lobsters on any sampling day. The main channels in the Bimini lagoon had a small population of young mature lobsters while juveniles were found in the shallow sand flats and mangrove areas. The migratory pathway was relatively devoid of both lobsters and suitable habitat, especially in depths less than 10 m.

Numbers increased in sparsely populated locations in early October some 1-3 weeks prior to mass queuing. This is shown in Figure 2 for two areas (5 and 12 on Fig. 1) several kilometers apart off the west shores of North and South Bimini. These increases occurred both during periods of uninterrupted mild weather (1969) and during periods of intermittent, brief storms (1971). Lobsters moved in by night and during the crepuscular hours, queues being observed at these times. Thereafter, large clusters of lobsters (up to 70 individuals per den) were noted in areas formerly containing few or none. The recently arrived immigrants sometimes emerged from dens by day under provocation of capture and formed queues. More typically they retreated into the crevices, the common response of lobsters other than mass migrants. While we cannot accurately estimate the numerical increase in the population for the total area, it was certainly manifold. Additionally, the behavior suggests a propensity for queuing and daytime locomotion not seen during the preceding period and more typical of the mass movement.

MASS MIGRATION

Severe squalls lasting several days with high winds from the northerly quadrants and cool temperatures occurred during late October-mid-November. Mass queuing was observed after such storms in 1961, 1963, 1969 and 1971 off Bimini (and 1965 off Boca Raton, Florida). In all cases, queues were seen on the shelf west of North and South Bimini in those areas where water clarity permitted. The lobsters were observed to move southerly, generally along shore, across depths ranging from 5-20 m in 1963, 2-10 m in 1969 and 1971, and as deep as 40 m in 1961. Figure 3, a composite scatter diagram of queue headings taken in 1969, shows a strong southerly direction over a 10 km distance during a 4-day period (see Herrnkind and McLean, 1971, for further details). Queues followed a shallow S-shaped track over distances of several hundred meters, thus accounting for some of the apparent deviation from the resultant southerly path. Despite the essing and gross deviations of queues and individuals dispersed by bully-

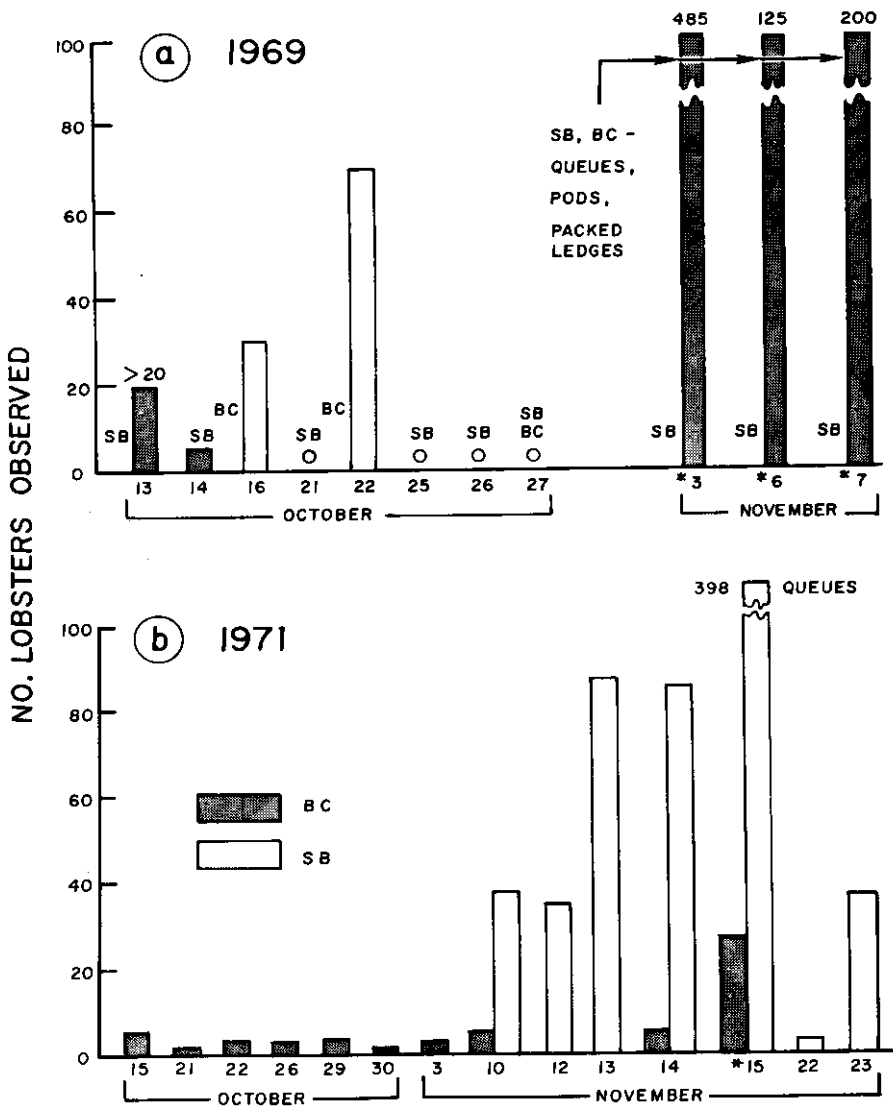


Fig. 2. Numbers of spiny lobsters observed in selected pathway sample areas during autumn 1969 (a) and 1971 (b). Asterisk indicates dates when mass daytime queuing was observed. SB - South Bimini patch reef (12 on Fig. 1), BC - Church ledges (5 on Fig. 1).

netters, all 1,638 lobsters comprising 230 queues and 39 individuals were observed within a narrow corridor some 400 m wide for 5-6 km as they passed Bimini.

The bulk of the migrants (98%) moved in queues rather than individually as shown in the frequency plot in Figure 4. Most solitary lobsters were recorded near bully-net operations which caused fragmentation of queues and subsequent

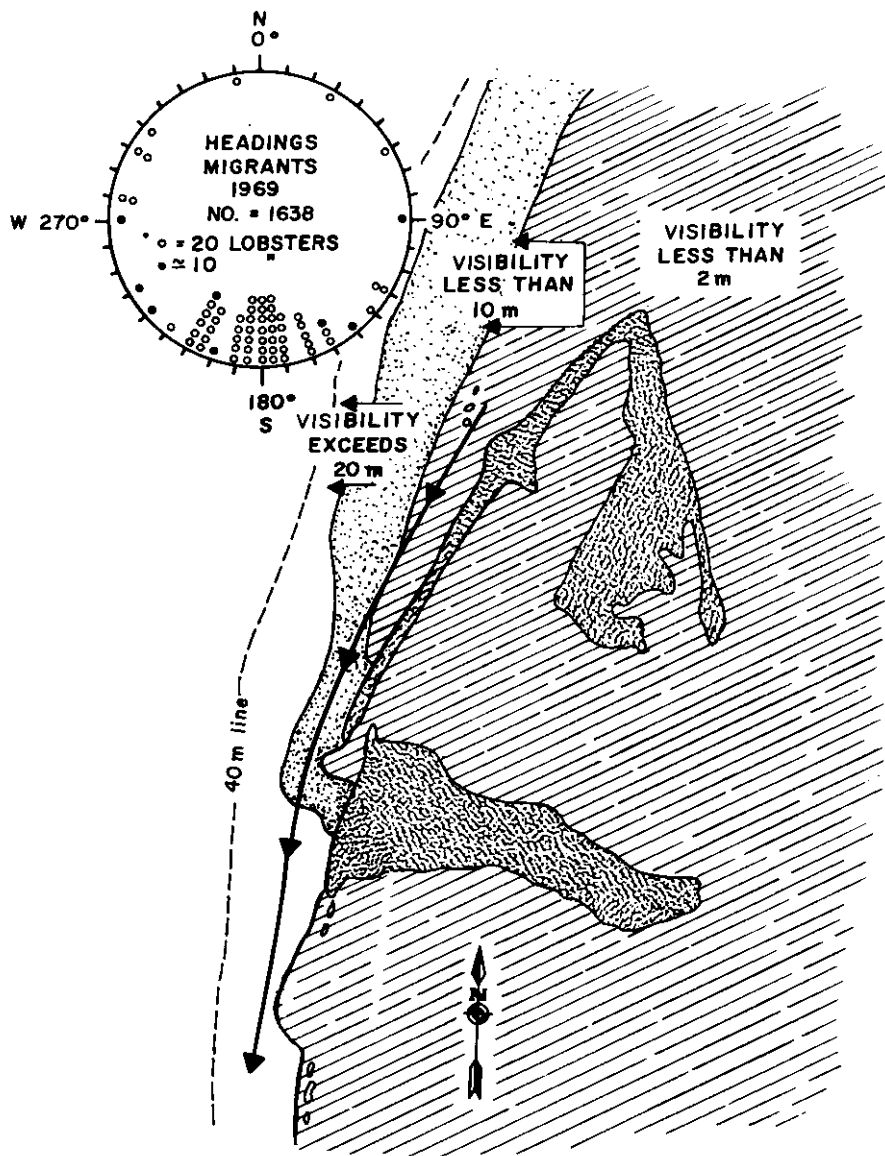


Fig. 3. Migratory pathway (arrows) observed in 1969 (including portions observed in 1961, 1963 and 1971) in relation to Bimini and the principal water masses, as defined by turbidity characteristics, at the time of mass migration. The scatter diagram gives the compass headings recorded for migrants observed in 1969 ($n = 1638$).

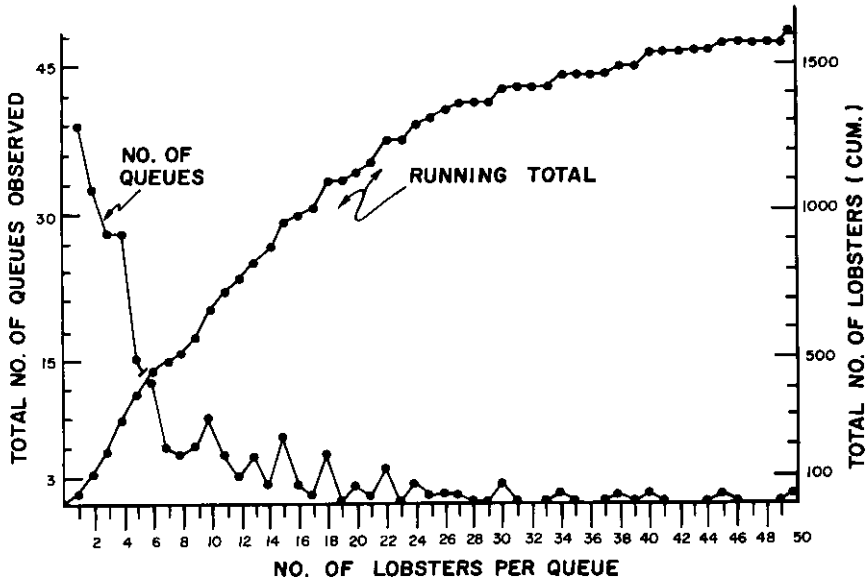


Fig. 4. Frequency profile of number of spiny lobsters per queue observed in 1969 (left scale) and the cumulated number of spiny lobsters represented (right scale). Total number of queues plus solitary migrants = 230; total number of individuals = 1638.

brief dispersal. As many as 65 lobsters were observed in a single queue (1971) and 34 queues of 13 or more individuals made up 18% of the queues but approximately 50% of the population on which we were able to record data in 1969. The higher frequency of smaller queues accounted for the remaining 50% of the total population as queues less than 13 individuals; i.e. 82% of the queues. Queuing, therefore, was the major mode of movement, the larger queues occurring with lower frequency. Yet large queues were not infrequent and represented a significant proportion of the emigrants (20% of all moving lobsters travelled in queues of 25 or more individuals).

When not queuing, migrants either formed large congregations (pods) in areas devoid of cover or packed into any available crevices. During 1969, for example, data were recorded on 2,365 lobsters, 1,638 (69%) of which were observed as queues (including 39 solitary moving lobsters), 449 (19%) under ledges, 265 (11%) in pods and 13 solitary resting individuals. Apparently, the quiescent periods do not last more than a few hours, since any pod was observed only once although repeated surveys were made throughout the day. In addition, queues entered ledges already packed with lobsters, some of which emerged, formed new queues and moved off. Stable congregations that did not emerge by day, even under provocation, occurred more frequently toward the end of the movement. At that time lobsters were found only in dens rather than in pods in open areas. In summary, the bulk of the population passed through the area as queues, although some lobsters established apparent residency, especially toward the end of the movement.

No specific attempt was made to measure the total number in past migratory populations and we can only offer an estimate based on our counts in the field and the catch by Bimini bully-netters, the latter reported to us verbally by several of them and by a commercial wholesaler (we witnessed the catches prior to shipment but did not make counts). The lobstermen claimed catches of 500-1,000 lobsters per boat per day over a 4-day period (3,4,6,7 November 1969), while the wholesaler estimated a total shipment of 20,000 lobsters for that period. This latter estimate seems reasonable since a catch of 500 lobsters per boat, with up to 13 boats fishing each day (from our notes), over 4 days gives a figure near 20,000 lobsters. We know the bully-netters fished only from daylight until late afternoon, approximately 10 hours, but the migration occurs at night as well. Also, we counted 256 lobsters over a 2-hour period directly down the pathway from the fishermen and 338 lobsters in a similar period in an area unfished by them. Obviously large numbers either escaped capture while amidst the lobstermen, moved through the area outside the fishing period or moved by outside the fished region. Consequently, we suggest the lobstermen fished less than half the migratory period and likely missed at least half of those lobsters present in the area observed during the fished period. Thus, an estimate of 100,000 lobsters seems appropriate although it might be orders of magnitude low if the movement occurred over the large regions we were unable to monitor. Hopefully, our present tagging program and the cooperation of the lobster wholesalers will permit more reliable future estimation.

Duration of the observed daytime mass queuing varied from approximately 5 hours (1971) to 4-5 days (1969). However, the actual starting time could not be determined because the point(s) of origin was not ascertained and the turbid water conditions north of Bimini prevented visually backtracking along the migratory pathway. The final stages of past movements, at least over the 10 km distance between Crossing Rocks and North Turtle Rocks, was associated with decreasing occurrence of queues. Additionally, an increasing number of lobsters resided by day under nearby ledges at this time. Apparently, the number in the pathway area decreased and/or those remaining ceased diurnal locomotory activity. The true termination of mass queuing also cannot be established, since movement may continue past the southernmost point we have tracked queues (i.e., 1-2 km south of South Bimini).

Samples of migrants for characterization by biological condition were taken either from queues, pods or crevices during the main period of daytime movement in areas known from preceding surveys to be otherwise uninhabited. Data taken on 200 lobsters in 1969 and 1971 are given in Figure 5 and Table 1. The size frequency over both years shows a range in carapace length (measured from between the rostral horns to the posterodorsal margin of the cephalothorax) of 55-126 mm, and a relatively symmetrical distribution around means of 84.6 mm (1969) and 82.1 mm (1971). The larger individuals tended to be males, and the only lobsters over 110 mm were a queue of five captured in 1969. Leader lobsters from queues (n=39) showed the same size frequency distribution and sex ratio as the total group (Fig. 5a) and were morphologically indistinguishable from the followers. Overall the migration lacked both young juveniles, typical of

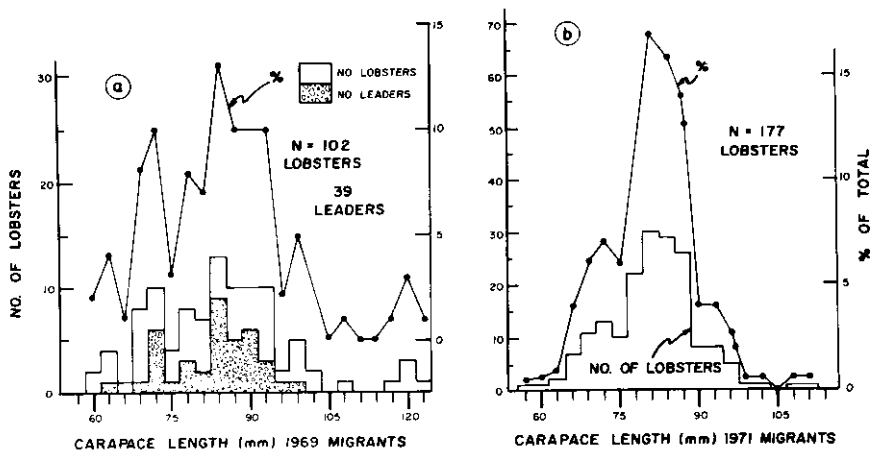


Fig. 5. Size frequency distribution of carapace lengths (measured from between the rostral horns to the posterodorsal margin of the cephalothorax) plotted as 3 mm intervals for 102 migrants in 1969 (a) and 177 migrants in 1971 (b). Shaded portion of 1969 migrants (a) indicates size frequency of queue leaders ($n = 39$).

the Bimini lagoon and Bank area, and older matures common to deeper reef habitats (Sutcliffe, 1952; Cooper and Herrnkind, 1971). Rather, most were individuals of initial reproductive age (Sutcliffe, 1952).

The sex ratio for the migrant sample was not significantly different from 1:1 either in 1969 or 1971. Only one female with spermatophores or eggs was taken from these collections (or observed in queues), although some were found in the pre-migratory build-up. Ecdysial state (molt or intermolt) classified by the carapace condition was also recorded. Pre-molt lobsters showing a dark line and flexing along the ventrolateral cephalothoracic margins, and post-molt lobsters with still flexible carapaces were considered in the molt category. Lobsters with hard carapaces resisting flexure when grasped firmly were considered intermolts. The migratory group showed a significant portion (20%) of recent and incipient molters.

Color notes and photographs revealed nearly the full range of variation reported for the species; i.e., from light tan through brownish-red to dark purple. The extremes of either light or dark color did not make up a large proportion of the samples. One striking color variation consisting of a violet hue noticeable over the entire dorsal and lateral carapace and appendages was recorded with variable frequency both during the premigratory period and from queues. We have not yet determined whether this violet cast is specific to any particular populations at other times or represents a peculiarity of fall migrants. As we obtain further samples from various populations before and after migration, we hope to correlate color, fouling organisms or some other biological feature with such attributes of mass migrants to infer their possible origin.

Table 1. Migrant sex ratios, carapace length, reproductive condition and molt state (1969 and 1971)

Year	♂	CL mm	♀	CL mm	♂+♀ CL mm	Eggs or Spermat	Pre- or post- molt	Inter- molt	Total
1969	53(52%)	87.9	49(48%)	81.1	84.6	0	—	—	102
1971	89(50%)	84.1	88(50%)	80.0	82.1	1(0.6%)	36(20%)	141(80%)	177

GENERAL BEHAVIOR

A number of behavioral aspects including the striking queue formations characterize the mass movements. Lobsters in queues, especially in open areas, may move continuously for at least several hours. The locomotory rate was estimated from tracking studies to be about 1 kilometer per hour over distances of at least 1-2 km over unobstructed bottom topography. When moving rapidly, the queue members usually maintained single-file formation with physical contact by the antennular inner rami and/or the anteriormost pereopods, as described for queues in laboratory pools (Herrnkind, 1969). A line retained its integrity through turns analogous to a railway train, further reflecting the close contact between individuals. Breaks in rank occasionally occurred, resulting in either increased locomotory rate of the trailing individuals, who remained in line and eventually re-established contact, or divergence in pathways of the separated groups.

Disturbances by a diver or obstruction in the path caused piling up of queue members into a pod. As this occurred, whole lengths of queues sometimes moved abreast to give a double or triple-file appearance. Groups at rest in areas devoid of ledges were seen in rosette formations, the members facing outward with abdomens in contact. Pods and rosettes did not immediately disperse as individuals unless physically scattered; instead, queues formed as lobsters began to move away. Leadership of queues generally changed both during pod disruption and queue-splitting, yet queues in the area retained the appropriate heading. Apparently, a number of individuals, perhaps all, are capable of the necessary orientation.

We witnessed feeding of emigrants by day although they probably fed nocturnally as well. At times, queue members fed while marching by manipulating the food object with the anterior pereopod pair while walking on the remaining posterior pairs, presumably retaining alignment by antennular contact and/or vision. The food in each case was probably recently obtained from the substrate. For example, holothurians and asteroid starfish common to the open sand were often carried by lobsters moving through those areas. Otherwise, lobsters milled about briefly in sea grass and algal beds apparently searching for food, although we didn't chance to see actual feeding at such times. Stomach content analysis also showed recently ingested material in a significant proportion of migrants. The range of items was typical of the normal diet but reflected the biota of the

pathway and included polychete, pelecypod, gastropod, crustacean and echinoderm material (n=29).

ASSOCIATED PHYSICAL CONDITIONS

Mass migrations typically occurred following frontal storms in an area according to our observations, reliable reports and island legend. Since such atmospheric disturbances modify the shallow water environment where migrations appear (and perhaps originate), both meteorological and hydrological conditions before and during the migratory period are of interest. Air and water temperatures were obtained from Lerner Marine Laboratory daily records and from our thermographs. Underwater visibility as an indication of turbidity was estimated by divers using a measured line.

Weather, in late September and early October, prior to population increases in the pathway and adjacent areas, was characteristically mild with air temperatures in the mid 80's (F) and with light winds predominately from the east and south quadrants. Our records from Bimini show the shallow waters (3-30 m) were generally calm with few large swells, temperatures in the low 80's (F) and useful diver visibility exceeding 20 m even in the lagoon and bank areas, which are usually slightly more turbid than the shelf area. Influx of lobsters to the pathway area occurred during such conditions in early October 1969. Build-up occurred during intermittent brief periods of squalls and gusty winds in late October 1971; the latter conditions being more typical for this period than earlier in the month. During squalls, wind comes mainly from the northerly quadrants, and higher velocities cause chop over the bank and larger waves seaward of Bimini. Turbidity usually increases, reducing visibility to 5 m or less on the bank as well as on the shelf where bank water is carried by tide, wind and currents, and where surge action stirs the substrate (Fig. 3). The turbid condition lasts only a day or so and is least apparent to the south and west of the islands.

The stormy periods we observed immediately prior to mass queuing lasted at least several days. Sustained winds from the NE and NW often exceeded 15 mph (22km/hr), and air temperatures dropped as much as 10-15F for several days. Sea conditions included heavy chop on the bank with intense wave action along the west shores, carrying onto the fringe of the bank north and south of Bimini. At such times, water visibility was less than 1 m. With return of mild weather and light breezes came the initial observations of daytime queuing in pockets of clear Gulf Stream water washing over the shelf along the southwest shore of North Bimini (Fig. 3). Water temperature drops of up to 5C also occurred on the bank and shelf during the storms as shown in Figure 6. Cold water was especially noticeable below thermoclines that formed at this time west of the islands in depths of 5-40 m.

The period following the onset of mass queuing varied from mild and calm to moderately stormy and was often followed by another storm within a few weeks. This pattern became characteristic of the late fall and winter. We have reports of several mass movements occurring in some regions between September and December but have not witnessed more than one major fall movement at Bimini.

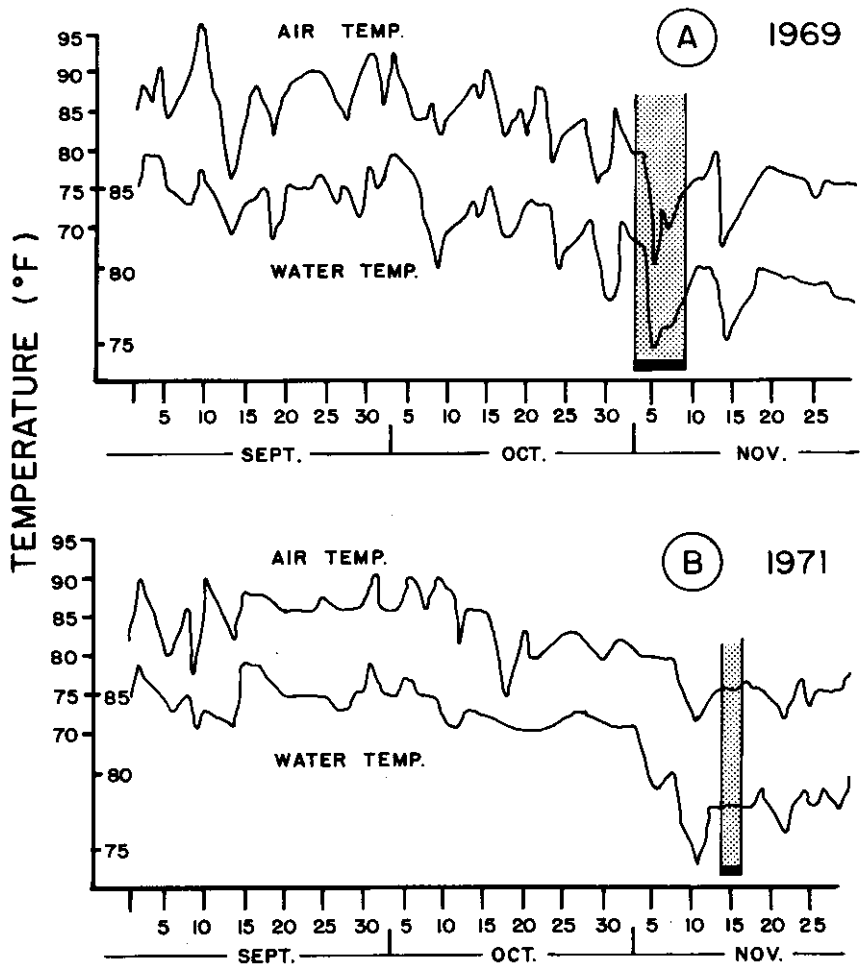


Fig. 6. Daily air temperatures (upper line each graph) and water temperatures (lower lines) plotted for the 3 month period preceding and including observed mass queuing (shaded area) in 1969 (a) and 1971 (b). Water temperatures were taken in the surf along the west shore of North Bimini contiguous with the migratory pathway.

DISCUSSION

The major sequential events of the mass migratory phenomenon may be summarized as follows: An influx of lobsters to the shelf area west of Bimini occurs during nocturnal movements over several weeks in October, causing a manifold increase in local population size. A severe autumnal squall causing high water agitation, increased turbidity and a temperature drop on the bank and shelf area, is followed by appearance of up to 100,000 migratory lobsters. The migrants off Bimini are observed to move almost exclusively in queue forma-

tions, day and night, southward along the shelf area. The mass migration lasts up to 5 days, most lobsters moving through the area but some taking up at least temporary residence. The aspects bearing discussion are: (1) the change in population distribution in the region, (2) the apparent nexus with autumnal storms, (3) the significance of sociality to the mass migration, (4) the localized nature of the migratory direction and (5) the economic and conservational implications.

The autumnal pattern seems to involve two possibly related phases: first, a gradual movement of lobsters into the shelf region over several weeks, increasing both the population number and density in confined areas of suitable habitat; second, a synchronous mass movement including those lobsters from the previous period still residing in the pathway at the time but not excluding recruitment from as yet undefined areas. Certainly the pathway area population prior to the initial influx period was too small to generate the mass migrant group. The resultant effect in the pathway adjacent to Bimini following the migration is at least a temporary increase in population size made up of remnants of the migrant group; most migrants having emigrated from the area. Assuming no adult return movement (although lack of observations does not disprove occurrence of such an event) a significant seasonal redistribution of the local adult population occurs over an area of at least 20 km², but likely much larger.

We cannot as yet define and prove the functional significance of the mass migration and resultant population shift, but some inferences may be drawn. Reproductive aggregation is apparently not the immediate function. The frequency of occurrence of females in reproductive condition was low in the pathway throughout the fall and less than 1% for the mass queuing samples. Additionally, timing of mass migration mismatches the reported spring-summer reproductive period for other areas of similar environmental conditions, e.g., in Florida and Bermuda (Sutcliffe, 1953). Unless there exists an undiscovered winter breeding period or area, we suggest the mass movement affects reproduction only in an indirect, but perhaps crucial, way.

The area's potential reproductive population is increased, since a large number of young mature lobsters are redistributed along the shelf in habitats characteristic of adult habitation (Sutcliffe, 1952) and at a location adjacent major oceanic currents where larval release likely occurs (Allen, 1966). Such relocation occurs also in the U.S. Virgin Islands under quite different ecological conditions (Herrnkind and Olsen, 1971, unpublished report). There, the juvenile habitats are devoid of lobsters over 80 mm carapace length (c.l.), whereas the reefs from shore out to 20 m depth show a paucity of lobsters under 80 mm c.l. Obviously the life history of the Virgin Island lobsters includes a shift in habitat from the nursery areas to the reefs at about the age of sexual activity. We are presently sampling the reef (adult) and shallow bank (nursery) areas near Bimini to establish the general characteristics of those populations and to determine whether mass movements produce a similar effect.

The correlative evidence suggests that autumnal frontal storms trigger and synchronize the mass migratory population, but occurrence of influxes during preceding calm periods indicates the storms are not necessarily the only stimulus for migration. Other information implicates a probable change in internal state

and other causal factors associated with migratory behavior. For example, lobsters in the field, and others taken from the migration and placed in laboratory pools, continued diurnal and locomotory activity under non-storm conditions. Queues off Bimini in 1969 and 1971 continued migrating in clear warm water, mostly of Gulf Stream origin. Lobsters captured from queues off Boca Raton, Florida, in 1965 continued daytime locomotion and frequent queuing for several weeks in an indoor pool (Herrnkind, 1969). Lobsters collected at other times remained active for only several hours. In a recent study, we found the duration of diel locomotory activity varies seasonally, probably in response to shifting photoperiod (Kanciruk and Herrnkind, in press). Such long term factors as photoperiod, gradual thermal change, nutrition and population density effects are now under study as possible influences on Zugunruhe.

Present information does not rule out the possibility that the physical disturbances from storms stimulate both queuing and a long lasting Zugunruhe. However, it is necessary to discriminate between stimuli evoking migration and stimuli evoking queuing, a behavior also exhibited under certain non-migratory conditions (although number of individuals, duration and orientation of queues in the latter case are much less impressive). We plan to test the effect of storm-related factors including sharp temperature changes, severe water agitation, decreased light levels and increases in suspended particles in the laboratory and, whenever possible, in the field.

The behavior of mass migrants shows an extremely strong tendency for sociality, even for a species congregative at other times. Lobsters living on reefs, for example at St. John, U.S. Virgin Islands, typically reside by day in specific dens with one or more other lobsters (Cooper and Herrnkind, 1971; Herrnkind *et al.*, in prep.). Yet, nocturnal feeding forays as well as occasional long distance movements are performed solitarily, and single resident dens are not infrequent. The excessive sociality during mass migration is demonstrated by the close physical contact during queuing, resistance by grouped lobsters to a separation when disturbed by divers or bully-netters, and the strong tendency to reform queues or pods after forced dispersal. This is reflected in the fact that solitary lobsters made up less than 3% of observed migrants in open areas.

It presently appears that queues, pods and rosettes serve a protective function (Herrnkind, 1969). Additionally, queues possibly provide a mechanism assuring appropriate orientation of the entire population, facilitating establishment of congregations immigrating into areas low in population density. The strong social tendency at this time provides the necessary basis for these, or any other, consequential group behavioral adaptations.

The observed migratory pathway in 1961, 1963, 1969 and 1971 was southerly although the depth range and area covered varied somewhat among these years. Reports from other areas also suggest local directionality repeated at each migration; e.g., northward along the southeast Florida coast (Herrnkind and Cummings, 1964; Herrnkind, 1969) and westward at Grand Bahama (B. Rose, personal communication). No clear pattern of offshore or onshore movement has emerged, but all observed pathways included a definite along-shore component. Regardless, the differences in direction from place to place, and the slight year-to-year variability of the pathway at Bimini, suggest local guideposts

rather than regional navigation cues. Our orientational research is presently focused on hydrodynamic cues such as current and wave surge since lobsters can orient accurately without vision and must do so during much of the migration (Herrnkind and McLean, 1971). Mechanisms involving visual cues (landmark, polarization and astronomical-compass orientation), magnetic cues, topographic gradients, kinesthesia, inertial guidance or chemotaxis are under scrutiny but seem less likely to operate under the known range of migratory conditions.

The economic and conservational implications are obviously important in each locality presently fishing the migrations. The Bimini lobstermen bully-net daily catches up to tenfold that normally caught at other times; i.e., 3 or 4 migration days are equivalent to a month's work. Diving lobstermen also make large catches as one of us (Herrnkind) observed off Boca Raton in 1965 when two free divers took over 200 lobsters in 1 hour. Hence, the catch per unit effort is exceedingly high for net, gig and snare capture methods where lobsters are actively sought. The process is further facilitated by the strong congregative behavior of the migrants. While the mass queuing may last only a few days, the population during the preliminary influx period and the remaining migrants are congregated in large groups, facilitating capture, and are available over periods of up to a month. The influence of the fall migration is therefore more extensive than suggested by its short duration.

The mass migrations are reportedly fished throughout the Bahamas (Herrnkind and Cummings, 1964) as are apparently similar movements in British Honduras (Allsopp, 1968). It seems likely the localized occurrences are weather dependent but cover the distributional range of the species in areas with appropriate ecological conditions. Also, the massive redistribution of lobsters may be consequential to the existing fisheries the remainder of the year and certainly for the month-long period bracketing mass queuing. Taking these points into consideration, the total migratory catch may reflect a significant component of the total spiny lobster fishery. Overfishing the mass queuing migrants could possibly result in regional depletion. Moreover, the phenomenon is a regularly occurring one of massive proportions and it is therefore reasonable to assume that its function (whatever) is of considerable importance to the species. If concentrated unregulated fishing occurs at this time, it might detrimentally influence the migration function, and thereby adversely affect the population as a whole.

In our opinion the potential economic and ecological implications of this phenomenon are not recognized by most marine scientists and fisheries experts. Hopefully the information and discussion presented here will serve to increase interest in the further research of mass migrations within the milieu of lobster population dynamics and behavior. We believe the coordination of broad based fisheries research techniques with the *in situ* and laboratory methodology partly elaborated here is necessary to ultimately elucidate this problem.

ACKNOWLEDGEMENTS

We gratefully acknowledge the field assistance of M. Sinclair; M. Halusky; R. Matusalem and R. Bill, who also prepared the sonic transmitters; the analytical

assistance of D. Sandberg and D. Olsen; and aid provided by W. Hamner and his research team. The facilities and support of R. Mathewson, Director of the Lerner Marine Laboratory, and his staff are sincerely appreciated. The research was variously supported by the following: 1969, ONR Grant (552-07) through the American Museum of Natural History; 1969-70, COFRS Grant from Florida State University; 1970-71, NSF-NOAA Sea Grant (GH-86); 1971-72 NSF Grant (GA-30813). We thank the Psychobiology Research Center at Florida State University for continued support and facilities.

LITERATURE CITED

- Allen, J.
1966. The rhythms and population dynamics of decapod crustacea. *Oceanogr. Mar. Biol. Ann. Rev.* 4:247-265.
- Allsopp, W.
1968. Investigations into marine fishery management, research and development policy for spiny lobster fisheries. Report to the government of British Honduras. Based on the work of W. H. L. Allsopp, FAO, TA-2481. 86 p.
- Bainbridge, R.
1961. Migration. *In* *Physiology of Crustacea* (T. Waterman, ed.) Vol. 2. Academic Press, New York. p. 431-463.
- Buesa, R.
1969. Biology and fishing of spiny lobsters, *Panulirus argus* (Latreille). *In* *Soviet-Cuban Fishery Research* (A. Bogdanov, ed.). Published for U.S. Dept. of Interior and NSF by Israel Program for Scientific Translation. U.S. Dept. Commerce Clearinghouse, p. 62-78.
- Cooper, R. and Herrnkind, W.
1971. Ecology and population dynamics of the spiny lobster, *Panulirus argus*, of St. John Island, U.S. Virgin Islands. *In* *Scientists in the Sea*, (Miller, J., J. VanDerwalker and R. Waller, eds.). IV:34-57.
- Crawford, D. and W. DeSmidt
1922. The spiny lobster, *Panulirus argus*, of southern Florida: its history and utilization. *Bull. U.S. Bur. Fisheries*, 38:281-310.
- Dawson, C. and C. Idyll
1951. Investigations on the Florida spiny lobster, *Panulirus argus* (Latreille). University of Miami Mar. Lab. Tech. Ser. No. 2:1-39.

- Herrnkind, W.
1969. Queuing behavior of spiny lobsters. *Science*, 164:1425-1427.
- Herrnkind, W.
1970. Migration of the spiny lobster. *Natural History*. 79:36-43.
- Herrnkind, W.
1972. Orientation in shore-living arthropods, especially the sand fiddler crab. *In Behavior of Marine Animals*, (H. Winn and B. Olla, eds.). Vol. I. Plenum Press, p. 1-59.
- Herrnkind, W.
In press. *In situ* approach to marine behavioral research. *In Experimental Marine Biology* (R. Mariscal, ed.).
- Herrnkind, W. and W. Cummings
1964. Single-file migrations of the spiny lobster, *Panulirus argus* (Latreille). *Bull. Mar. Sci. Gulf and Carib.* 14:123-125.
- Herrnkind, W. and R. McLean
1971. Field studies of homing, mass emigration, and orientation in the spiny lobster, *Panulirus argus*. *Annals N.Y. Acad. Sci.* 188:359-377.
- Herrnkind, W. and D. Olsen
1972. Ecological study for the development of lobster management techniques. Final report on Sea Grant GH-86. 51 p., 24 figs.
- Herrnkind, W., J. Vanderwalker and L. Barr
In prep. Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S. V.I.: (4) Habitation, patterns of movement and general behavior.
- Kanciruk, P. and W. Herrnkind
In press. Preliminary investigations of the daily and seasonal locomotory activity rhythms of the spiny lobster, *Panulirus argus*.
- Kornicker, L.
1958. Ecology and taxonomy of recent marine ostracodes in the Bimini area, Great Bahama Bank. *Inst. Mar. Sci. U. of Texas*, 5:194-300.
- Kumpf, H. and H. Randall
1961. Charting the marine environments of St. John, U.S. Virgin Islands. *Bull. Mar. Sci. Gulf and Carib.*, 11:543-551.

- Lindberg, R.
1955. Growth, population dynamics and field behavior in the spiny lobster, *Panulirus interruptus* (Randall). Univ. Calif. Publ. 2001, 59:157-248.
- Newell, N. and J. Imbrie
1955. Biological reconnaissance in the Bimini area, Great Bahama Bank. Trans. New York Acad. Sci. ser. 2, 18:3-14.
- Newell, N., J. Imbrie, E. Purdy and D. Thurber
1959. Organism communities and bottom facies, Great Bahama Bank. Bull. Amer. Mus. Nat. Hist. 117:177-228.
- Sutcliffe, W.
1952. Some observations of the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. Proc. Gulf Carib. Fish. Inst. 4:64-69.
- Sutcliffe, W.
1953. Further observations on the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. J. Marine Res., 12:173-183.