

Riding Langmuir circulations and swimming in circles: a novel form of clustering behavior by the scyphomedusa *Linuche unguiculata*

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Date of final manuscript acceptance: September 6, 1991. Communicated by J. M. Lawrence, Tampa

Abstract. *Linuche unguiculata* (Schwartz) seasonally forms patches in the Caribbean Sea and Indo-Pacific Ocean. Eighteen patches of medusae varying from about 500 m² to nearly 1 km² in area, were documented along the Belize barrier reef in March and April 1987, April 1988, and March and April 1990. The shape of each patch and the inter-medusa distances varied with wind velocity. At low wind speed (< 4 m s⁻¹) patches were elliptical or circular and the individual medusae were separated by distances of 0.5 m, whereas at higher speeds windrows were evident and medusae were closer together. Windrows probably form by horizontal advection owing to convergence by Langmuir circulations. Because individual patches might exist for up to 4 mo as they drift downwind, and because winds of sufficient speed to produce Langmuir circulations do not always occur, a mechanism is necessary to maintain patch integrity during calms. In situ observations and in vitro video recording showed that the medusae swam in horizontal, near-surface, circular, clockwise trajectories. Although swimming speed was relatively high (up to 8 cm s⁻¹), net displacement velocity can be low (< 1 cm s⁻¹). Thus, circular swimming probably reduces cluster breakup. Patch formation probably improves reproductive success by reducing sperm dilution.

Introduction

Zooplankton patchiness may be caused by: (1) vectoral-physical gradients in a vertical plane; (2) stochastic-vectoral-advection by currents; (3) social-active schooling or swarming for social reasons; (4) reproductive-aggregation of young due to spawning activity of adults; (5) coactive-aggregation for trophic interactions (Stavn 1971).

Although physical factors are important in regulating zooplankton distributions (e.g. Longhurst 1981, Zeldis and Jillett 1982, Mackas et al. 1985), behavior may be even more significant in patch formation, at least at smaller spatial scales (Hauray and Weibe 1982, Hamner et al. 1983, O'Brien 1988 a, b, Price 1988). Most studies on zooplankton patchiness have been indirect, using nets. Consequently, much is known about some aspects of patchiness, e.g. spatial scales of patches, but little is known about how individual behavior is involved. Direct observation, when possible, can lead to a better understanding of patchiness since behavior of individual animals, or at least subpopulations, can be quantified (e.g. Hamner and Carlton 1979, Hamner et al. 1983, 1987, O'Brien 1988 a, b).

Gelatinous zooplankton, because of their large size, low swimming speeds, and lack of highly complex behavior, lend themselves to the study of clustering (herein the terms aggregations, clusters, and patches are used interchangeably). Many reports of aggregations of ctenophores, medusae, and salps, have appeared in the literature (e.g. Stevensen 1962, Lal Mohan 1965, Zelickman 1969, Russell 1970, Yasuda 1970, Malej 1989); however, little is known about the underlying causes and effects. Physical factors, especially Langmuir circulation, are perhaps the primary mechanism responsible for patch formation in medusae (Kikinger 1983, Hamner and Schneider 1986, Zavodnik 1987). Additionally, aggregations could be formed by inshore surface currents causing the medusae to collect near shore, or in the lee of islands, i.e., "island effect" (probably associated with Von Karman vortices), or by oceanographic fronts, or internal waves. A unique type of clustering in medusae was described by Hamner and Hauri (1981), whereby the rhizostome *Mastigias* sp. performed diel migrations to opposite ends of a marine lake in Palau. The significance of behavior in clustering is not well documented for gelatinous zooplankton. Gelatinous zooplankton have relatively "simple" neuro-sensory and locomotory systems, and therefore probably do not swarm in the sense defined by Wittmann (1976) for crustaceans, whereby inter-individual

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ual distances are closely maintained. Yet, it is often assumed that these patches are social in nature and are for reproductive purposes, implying some active involvement in patch formation.

The "thimble jellyfish" *Linuche unguiculata*, a species of small coronate scyphomedusa, forms conspicuous patches in the Caribbean Sea and Indo-Pacific Ocean (Roberts 1827, Fewkes 1882, Agassiz and Mayer 1899, Conklin 1908, Mayer 1910, Beebe 1928, Bigelow 1928, 1938, Larson 1982, Kremer et al. 1990). Roberts (1827) stated that in April through June, along the Caribbean coast of Nicaragua, "...the sea is covered with what fisherman call thimbles - a small blubber fish, in shape not unlike a tailor's thimble. ..." He noted that green turtles fed on the abundant *L. unguiculata* at that time. Mayer (1910) wrote: "In the Bahama region in the spring these medusae form swarms, miles in extent, filling the water with myriads of brown thimbles. ..." "I have seen hundreds of such swarms all composed of but one species." Fewkes (1882) reported, "In the tide eddies near the Tortugas Islands (the Dry Tortugas), we passed through long windrows of medusae, reaching as far as the eye could follow." Beebe (1928) described finding *L. unguiculata* so dense off Haiti, that a pail full contained "...3 solid quarts of medusae." Few observers have considered the possible causes and effects of *L. unguiculata*

patches. The present study was undertaken in an attempt to better understand patch formation in *L. unguiculata*.

Materials and methods

Studies were conducted in the western Caribbean at Carrie Bow Cay, Belize (Fig. 1) in March and April 1987, April 1988, and March and April 1990. The cay is located along the Belizian barrier reef. No medusae were seen after late May. Clusters of *Linuche unguiculata* (Schwartz) were searched for during daylight hours along about 10 km of the barrier reef using a small outboard motorboat. Medusae were hunted by patrolling perpendicular to the wind. Because *L. unguiculata* was often associated with surface slicks, such slicks were investigated whenever present. The amount of glare and wave action determined the visibility of the patches, but generally they could be seen at distances of 10 to 50 m.

The size and shape of each patch was ascertained by slowly driving the boat around the perimeter of each patch. Small buoys were placed at several points around the patch so that its morphology could be determined. Approximate patch dimensions and distance between medusae in the patch were estimated by eye and from in situ and above-surface photographs. The behavior of medusae in each cluster was observed from the boat and by snorkeling. Wind velocities were measured using a hand-held anemometer (Weather Measure Co., Model 131).

For in vitro observations, *Linuche unguiculata* medusae were dipped from near the surface with a cup attached to a long handle

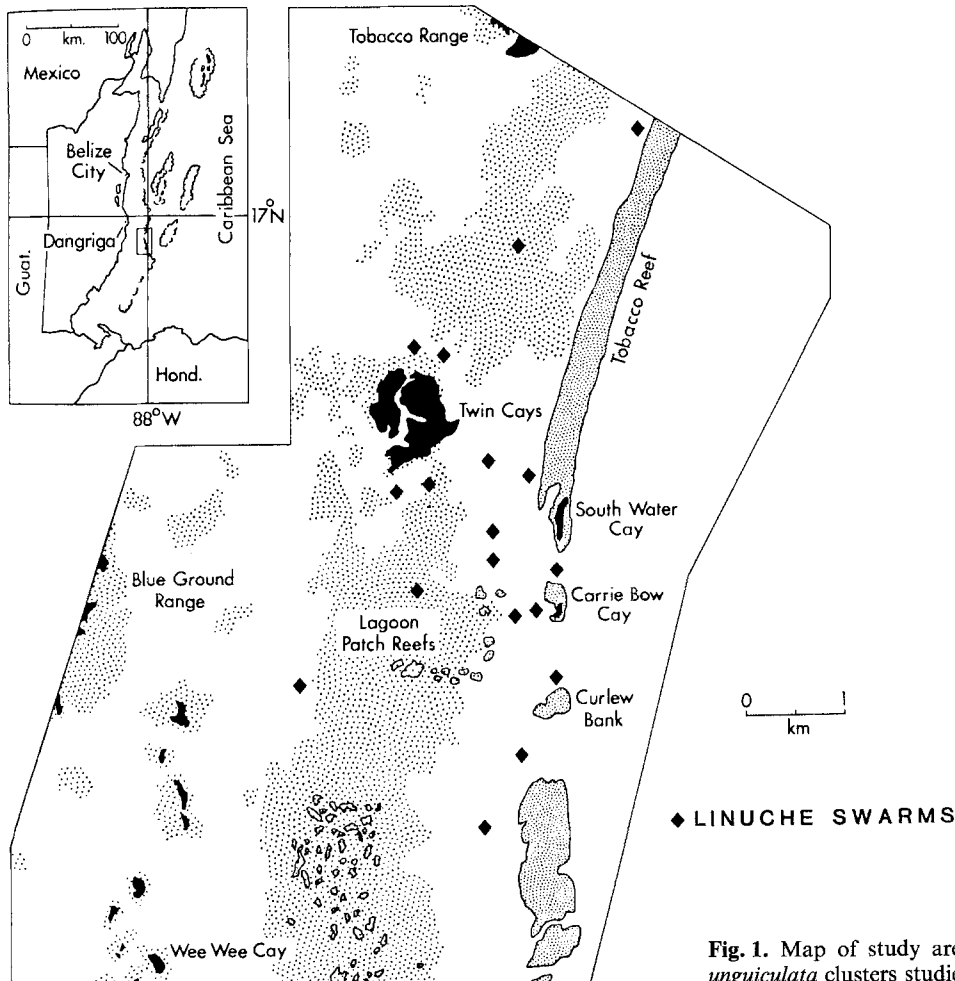


Fig. 1. Map of study area showing locations of the 18 *Linuche unguiculata* clusters studied

and then transported back to the laboratory in 20-liter plastic buckets. Others were collected with a dipnet and fixed using 5% formalin. Measurements of bell diameter (at the coronal groove) were made on about 50 preserved specimens from each cluster using a dissecting microscope with an ocular micrometer, or using calipers. Shrinkage of tissues occurred following fixation so that reported sizes are conservative.

In the laboratory, 5 to 7 mm-diam. medusae were observed in a 90-liter aquarium (60 × 40 × 40 cm). Larger medusae were placed in a plastic pool (35 cm high by 2 m diam) placed outdoors in a partially shaded situation. Water pumped from the reef-flat entered the aquarium and pool (when observations were not being made), keeping temperatures within 2°C of those in situ.

Determination of swimming speeds and paths was made using two methods. In 1987, swimming paths of small medusae (5 to 7 mm diam), were determined by placing a 6 mm-thick acrylic sheet over the aquarium and tracing the swimming path of a near-surface medusa, using a felt-tipped marker. The medusa was followed until it contacted an aquarium wall. A stopwatch was used to record the time. A map-distance measuring device was then used to determine the total length of the marked swimming path.

In 1988, swimming paths were documented using video. A video camera was attached to a tall tripod 1.8 m above the pool. A field of view of 1.2 × 1.5 m was attained over the center of the pool. About 50 medusae were placed in the pool. A 10 cm rule was placed in the pool for size reference. Analysis of video recordings to determine swimming path and velocity was done using a video-analysis system (Micro-Comp Corporation), consisting of: (1) a microcomputer and software, (2) a video-cassette recorder, (3) a video monitor, and (4) a digitizing tablet. After calibration this system could automatically determine distances along a digitized swimming course. A stopwatch was used to obtain the time for a particular swimming event to occur. Swimming velocity was obtained by dividing the distance swam by the time taken to cover the distance. A hard copy of the digitized path was made by tracing the digitized path onto clear vinyl sheets.

Results

In situ observations

Linuche unguiculata medusae were mostly seen in clusters. Isolated medusae were extremely rare and were most often associated with a cluster that had been dispersed by going around an island or over a reef. More than 20 patches were seen within 5 km of Carrie Bow Cay. Data were obtained on 18 of these (Fig. 1; Table 1). Six clusters were observed in March and April 1987; two were found in April 1988; and more than ten were seen in March and April 1990.

Patch size varied from <100 to >300 m (Table 1). Patch shape was variable but could be approximately described as one of three categories: (1) rows, (2) circles, (3) ellipses. Rows consisted of narrow bands, 1 to 3 m wide, associated with surface slicks and flotsam (mostly pieces of *Syringodium* sp., a sea grass; fragments of *Turbinaria* sp., a brown macroalga; and pieces of discarded plastic). Also often present in windrows were *Trichodesmium* sp., a buoyant cyanobacterium; and various weakly-swimming zooplankton including tornaria larvae, cerianthid larvae, hydromedusae, and chaetognaths. In windrows, medusae of *Linuche unguiculata* were sometimes so dense that they touched one another, forming brown, ribbon-like patches which were visible from a distance of 25 m or more (Figs. 2 and 3). Windrows reached lengths of more than 100 m and were parallel to the wind. Medusae in windrows were often seen maintaining their surface position by upwards swimming.

Table 1. *Linuche unguiculata*. Characteristics of 18 patches studied. S, M, L: maximum patch sizes of <100 m, 100 to 300 m, and >300 m, respectively. nd: not determined

Date	Bell diam, mm (mean ± SE)	Wind speed (m s ⁻¹)	Patch size	Distance between medusae (cm)	Patch shape
1987					
15 Mar.	nd	nd	M	1–50	nd
21 Mar.	nd	nd	M	50–100	nd
22 Mar.	11.6 ± 0.1	2–4	S	50–100	elliptical
3 Apr.	18.8 ± 0.2	4–7	S	1–25	3 rows parallel to wind
4 Apr.	18.7 ± 0.2	2–5	L	1–50	elliptical, 1 row
7 Apr.	19.7 ± 0.2	1–4	S	25–200	elliptical
1988					
14 Apr.	13.5 ± 0.4	0–2	M	25–1000	circular
16 Apr.	13.8 ± 0.4	0–3	M	25–2000	circular
1990					
23 Mar.	6.4 ± 0.1	5–6	S	5–50	2 rows parallel to wind
25 Mar.	7.4 ± 0.1	4–5	M	2–20	1 row parallel to wind
28 Mar.	8.6 ± 0.1	3	M	5–20	wide row parallel to wind
28 Mar.	8.2 ± 0.1	2–3	L	25–2000	elliptical
29 Mar.	8.2 ± 0.1	3	L	5–25	row 20 m wide, parallel to wind
30 Mar.	8.3 ± 0.1	3	L	25–50	? circular
1 Apr.	9.1 ± 0.1	3–5	M	5–20	2 rows parallel to wind
3 Apr.	9.6 ± 0.1	0–1	L	10–50	circular
4 Apr.	9.8 ± 0.1	5–6	L	10–5000	elliptical
4 Apr.	9.3 ± 0.1	4–5	S	5–15	1 row parallel to wind



Fig. 2. *Linuche unguiculata*. A small portion of a dense windrow in which medusae were touching one another (3 April 1987). Pieces of floating *Syringodium* sp. sea grass are also visible

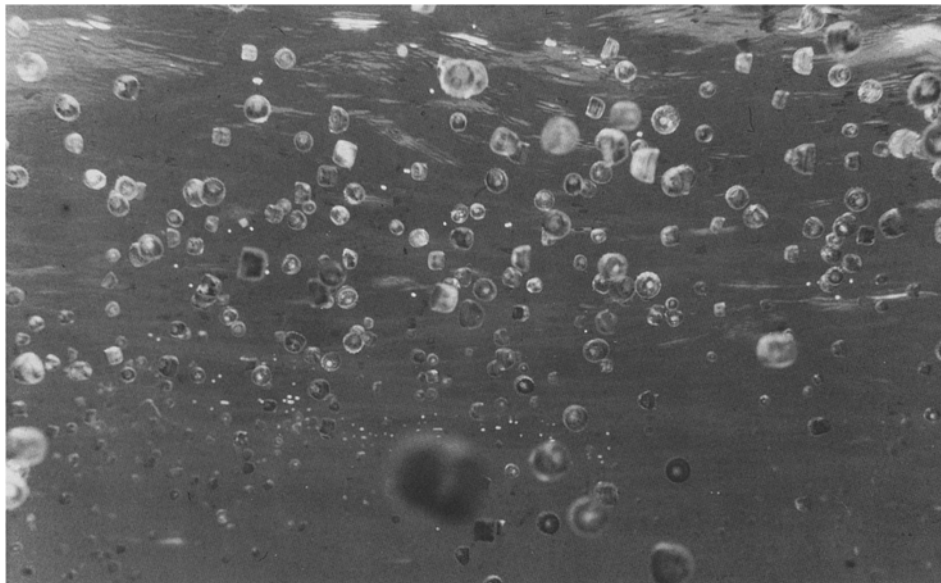


Fig. 3. *Linuche unguiculata*. Medusae swimming near the surface. They are from 1 to 5 cm apart (4 April 1987)

Patch shape and spacing of medusae was related to wind velocity (Table 1). At speeds of $>4 \text{ m s}^{-1}$, medusae were mainly in windrows and inter-medusa spacing was mostly $<25 \text{ cm}$. At wind speeds of $<4 \text{ m s}^{-1}$, they were often more dispersed and the shape of the patch was less linear (Table 1). Because wind speed was often variable over short time-periods, some windrows of medusae were found at low wind-speeds, and circular patches were found at higher wind-speeds. When there was sufficient wind, the medusae were seen drifting down-wind. One patch moved about 300 m in 1 h.

Medusae were not evenly distributed throughout the water column. Mostly they occurred in the upper 10 to 25 cm (Fig. 3), but some were deeper (1 to 5 m). Their vertical distribution was not related to wind speed or wave heights; although in windrows, many medusae were at the surface.

The medusae swam actively. Viewed from above, they usually swam in clockwise, circular paths of $<25 \text{ cm}$ to $\sim 1 \text{ m}$ diam; depending on the size of the medusa. Seen underwater from the side, most of the swimming was horizontal, with little variability ($<5 \text{ cm}$ mostly) in depth. However, some medusae were seen swimming upwards at the surface, especially when concentrated in windrows, and others descended $\geq 10 \text{ cm}$ on a given swimming path.

Laboratory observations

Many of the medusae in the pool swam down to the bottom where they stayed. For those in the water column, bell pulsations were rapid (from 3 to 6 pulsations s^{-1} for 5 to 18 mm-diam medusae) and swimming velocities were

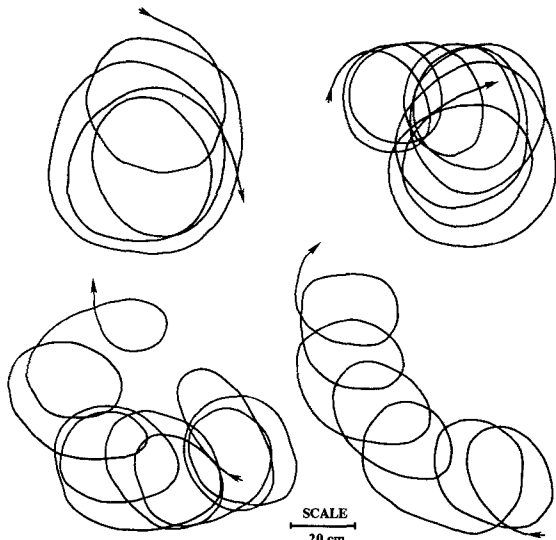


Fig. 4. *Linuche unguiculata*. Examples of clockwise swimming paths of four medusae (from video)

high. Swimming speeds increased with bell diameter. Medusae 5 to 7 mm in diameter swam at speeds of 3.5 ± 0.1 (mean \pm SE) ($n=19$); those 10 to 12 mm in diameter swam at speeds of 4.4 ± 0.2 ($n=14$); and those 15 to 22 mm in diameter swam at speeds of 7.2 ± 0.2 ($n=24$).

Swimming was in clockwise, circular paths. Only rarely ($<5\%$ of the time) was swimming otherwise. In the aquarium, 5 to 7 mm-diam medusae swam in circles of about 13 ± 0.5 cm ($n=97$). In the pool, 14 to 22 mm-diam medusae swam in circles, 41 ± 1 cm in diameter ($n=125$). In both cases, a few medusae attempted to swim in larger circles but were confined by the size of the container. In any one swimming sequence, the degree to which each circular path overlapped with previous paths varied. Some medusae swam for several minutes with little net displacement; for example, one medusa in the pool swam for 4 min with a net displacement (distance from a starting point, picked at random, to the time it went out of the field of view) of only 33 cm. Other medusae swam in a series of circles that overlapped less (Fig. 4). Sometimes these circles consisted of a series of small circles forming a larger one. For medusae of 14 to 22 mm diam, the mean rate of displacement from a given point was 1.4 cm s^{-1} (range = 0.13 to 8.3 cm s^{-1}) (Fig. 5).

The medusae spun clockwise (around their oral-aboral axis), viewed from the subumbrellar side. This rotation was a result of the asymmetry of the lappets, which act like the blades of a propeller.

There was no visible difference in the behavior of medusae at different times of the day, either in the field or in the pool. Medusae were continuously swimming clockwise in circles and spinning counterclockwise.

Population structure

Linuche unguiculata medusae in any one patch were of uniform size (Figs. 6, 7; Table 1). For 16 patches, the

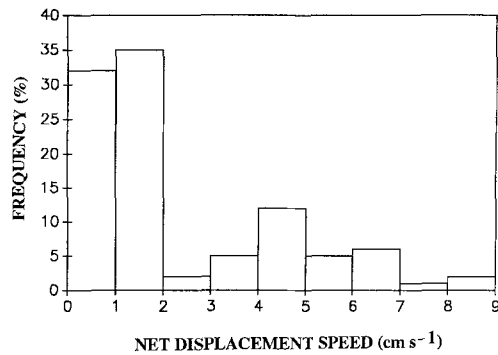


Fig. 5. *Linuche unguiculata*. Frequency of net displacement speed for medusae of 14 to 22 mm bell diam ($n=84$)

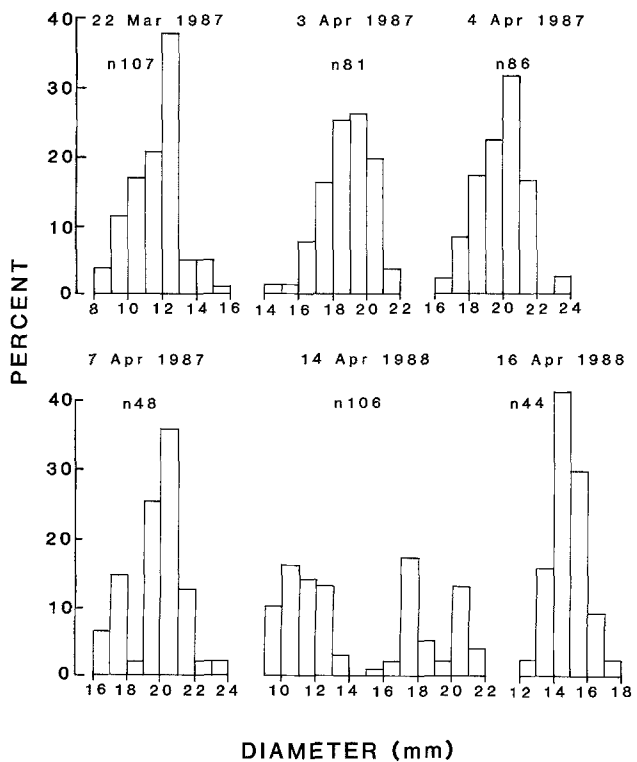


Fig. 6. *Linuche unguiculata*. Size-frequency of bell diameters of medusae collected from six different patches. Each date represents an individual patch

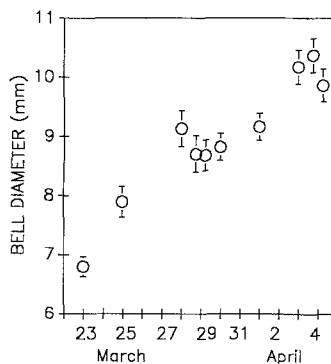


Fig. 7. *Linuche unguiculata*. Scatter plot of bell diameters (mean \pm 95% CL) from clusters collected in March and April 1990

coefficient of variation of bell diameter averaged $10 \pm 1\%$ (mean \pm SE). The major exception was the population sampled on 14 April 1988. The size-frequency diagram for this cluster showed two modes at about 10 to 12 mm diam and at 17 to 21 mm diam. The CV was $\sim 9\%$ for each group (8 to 13 mm and >14 mm diam).

Discussion

These observations confirm previous accounts that describe *Linuche unguiculata* as a patch-forming medusa. I suggest that these patches result primarily from two factors, one physical and the other biological. Inshore, aggregations of hydromedusae and scyphomedusae often occur in areas where tidal eddies or Von Karmen vortices form. Dense aggregations of *Aurelia aurita* form near coral reefs off Puerto Rico where tidal eddies occur (own unpublished observations). Yet, swarms of *L. unguiculata* showed no fixed relationship to reefs or other bottom topography that might produce eddies. Instead the patches occurred randomly and moved over time. These observations suggest that other mechanisms cause clustering. The apparent aggregations of *L. unguiculata* near Carrie Bow Cay is probably an artifact due to the greater amount of time spent searching in that area. Little searching was done on the seaward side of the reef.

Linuche unguiculata are often found in windrows with flotsam and associated slicks oriented parallel to the wind. These conditions are indicative of Langmuir circulations, in which floating debris and organic films accumulate in the downwelling convergence zones (Weller and Price 1988). The prevalence of windrows in the Caribbean Sea during the spring when the NE trade winds are evident, suggests that these circulations are common. *L. unguiculata* probably become aggregated in windrows by being laterally advected into convergence zones between adjacent Langmuir cells (Fig. 8). Once in a convergence, medusae are apparently maintained there by upwards swimming. Spacing of adjacent cells, which can vary from 5 to >50 m, is a function of water and thermocline depth (Weller and Price 1988), and thus the larger patches of *L. unguiculata* were probably formed offshore rather than in the shallow (<10 m) areas inside the reef. Langmuir circulations have been implicated as the primary mechanisms responsible for patch formation



Fig. 8. *Linuche unguiculata*. Possible mechanism of medusae aggregations in convergence zones of Langmuir circulations. Medusae swimming near surface are advected horizontally into convergence zone. They swim upwards, and remain in convergence. As a result, windrows of medusae occur parallel to wind direction

in other medusae (Kikinger 1983, Hamner and Schneider 1986, Zavodnik 1987), and for other zooplankton (e.g. Stavn 1971).

During March and April, the months when adult *Linuche unguiculata* appear off Belize, calms occur during 5 to 10% of the time (Rützler and Ferraris 1982). During calm periods, a patch of *L. unguiculata* could disperse and eventually breakup. This could be accelerated by the swimming of the medusae. Assuming linear swimming at 5 cm s^{-1} , a patch could disperse at a rate of $>300 \text{ m h}^{-1}$. Although dispersion in the absence of Langmuir circulations does happen, as evidenced by the low densities of medusae in aggregations at slight wind speeds, patches persist longer since isolated medusae are rare. This is evidently because circular swimming behavior reduces the rate of dispersion.

Patches of *Linuche unguiculata* may exist for months, but move spatially. Ephyrae first appear off Belize in January (Larson 1982) and adults are seen up to May. During this time a cluster would drift hundreds of kilometers. The most plausible explanation for original patch formation is that ephyrae are simultaneously released, in large numbers, from a localized population of polyps. The small temporal variation in bell diameter within a patch suggests a cohort; however, since the diameter variance of medusae from different patches sampled on the same day was small the entire *Linuche unguiculata* population possibly was a cohort. Nonetheless, medusae in a patch may be more closely related to one another than those from other patches.

Patch-maintenance behavior of *Linuche unguiculata* appears to be a primitive form of social swarming that could significantly increase reproductive success by reducing inter-mate distances, as suggested by Conklin (1908). Sperm dilution has been shown to be highly important in determining fertilization success in free-spawning invertebrates, including medusae (e.g. Roosen-Runge 1962, Pennington 1985). Additionally, aggregation in Langmuir circulations could provide *L. unguiculata* with increased prey densities if upwardly migrating zooplankton became concentrated (Hamner and Schneider 1986). Doubtless, there must be trade-offs for clustering. For example, predators such as turtles could follow a patch and gorge themselves. Yet, because these patches are relatively rare, few predators may find them. The advantages of clustering to increase reproductive success apparently outweigh the disadvantages.

Linuche unguiculata appears to be unique among zooplankton in its apparent dependence on Langmuir circulations to effect relatively stable clustering. Further studies seem warranted on this unique form of patch formation. Long-term observations on *L. unguiculata* clusters are needed to document their longevity and changes in patch shape and density of medusae as a function of wind speed. Additionally, studies of the genetics of medusae taken from different swarms may clarify the amount of gene flow between swarms.

Acknowledgements. This study was generously supported by funding from the Caribbean Coral Reef Ecosystems (CCRE) Program, Smithsonian Institution. I would like to thank M. Carpenter of the Smithsonian and the staff at Pelican Beach Resort in Belize for

logistical support. K. Larson and P. Willenz provided photographs, and T. Smoyer printed photographs. This is CCRE Contribution No. 345, and Contribution No. 885 of Harbor Branch Oceanographic Institution.

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