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Spatial aggregations of the swarming jellyfish *Pelagia noctiluca* (Scyphozoa)

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Abstract

In the Adriatic Sea, the spatial distribution and aggregation aspects of swarming *Pelagia noctiluca* (Forskål, 1775) were studied by SCUBA divers from August 1984 to November 1985. Medusae were usually distributed in the upper 20- to 30-m layer. Dense aggregations caused by wind, currents and tidal phenomena occurred only in shallow coastal waters. Maximum population densities of swarms drifting freely near the shore were estimated at about 20 individuals per cubic meter, but when they had drifted ashore jellyfish could reach concentrations of 150 to 600 individuals in the same volume of sea water. Some peculiar forms of aggregations could be distinguished: couples, clusters, and surface and bottom aggregations. The effects of wind, currents and geomorphological features of the shore on passive aggregations of jellyfish are presented.

Introduction

During the past decade or so, outbreaks of the pelagic swarming scyphozoan *Pelagia noctiluca* have been noted in many areas of the Mediterranean (Vučetić, 1985). In the Adriatic Sea, this jellyfish has been known since 1911 (Babić, 1913) but for over half a century it was considered a rather rare species (Riedl, 1970; Vučetić, 1983). However, since 1977 (Rottini Sandrini *et al.,* 1980), *P. noctiluca* swarms have been reported in offshore and coastal waters. Recently, many papers have appeared regarding regional distribution, temporal appearances, reproductional biology, physiology and other aspects of the natural history of the Adriatic *P. noctiluca* (Bratina *et al.,* 1981; Malej, 1982; Rottini Sandrini and Avian, 1983; Vučetić, 1983, 1984, 1985; Piccinetti Manfrin and Piccinetti, 1983–84; Benović, 1984; Malej and Vuković, 1984; Stravisi, 1984). Apparently, however, the now frequently dense aggregations of this species have never been subject to field studies.

Materials and methods

The present results refer exclusively to field observations by SCUBA divers at 52 localities in the Adriatic Sea: mostly around the islands of Lošinj and Susak, in the area of the marine National Park "Kornati Islands", and in the coastal and offshore waters of the Istrian Peninsula. Diving operations were conducted from August 1984 to November 1985, at irregular intervals depending on swarm appearances. Diving was always during daylight hours (mostly between 10:00 and 17:00 hrs), and never at depths below 65 m. Occasionally, basic hydrographic data, such as sea currents, tidal phenomena, temperature and salinity were noted. Occurrences of *Pelagia noctiluca* (Forskål, 1775) were noted by divers as "few" (scattered individuals), "moderate" (approximative distances between medusae about 5 to 15 m) and "dense" (medusae less than about 5 m apart). On occasion swarms were sampled with a hand net, and later approximate densities per cubic meter were calculated.

Results and discussion

Vertical distribution

In the Mediterranean the jellyfish *Pelagia noctiluca* has been reported to be distributed between 0 and 640 meters depth (Stiasny, 1921). According to our observations, this species was most abundant in the upper 20- to 30-m layer, in all seasons, at least during the daytime. The temperature structure of the water column did not appear to be a major factor affecting the vertical distribution of the jellyfish populations. It was found, however, that buoyancy of *P. noctiluca* beyond its active movements depends also on the specific density of the individual (which perhaps varied according to its physiological state: A. Malej, personal communication).

Population density

We observed that swarms drifting offshore rarely contained more than 20 individuals per cubic meter. This agrees with a critical swarm density computed by Legović and Benović (1984). When the swarm had drifted ashore, however, the population maximum was between about 150 to 600 individuals per cubic meter in the surface layer. It should be added that *Pelagia noctiluca* has enough mobility so that it never stays more than a few minutes just at the sea surface. Also the jellyfish very rarely touch the bottom. Some individuals which lacked a manubrium exhibited unusual behavior, and usually increased rates of pulsation, however, they were unable to control their buoyancy. Presumably the manubrium had been bitten off by a predator, which in the Adriatic Sea may be the mackerel (*Scomber scombrus*) or the horse mackerel (*Trachurus* spp.).

Aggregation aspects

Swarming jellyfish aggregated by active swimming, or drifted together by abiotic agents, such as water currents. Aggregations of maximum population densities were only noted in shallow water.

Couples. Sometimes two or three *Pelagia noctiluca* were swimming – or drifting – in close association, i.e. one near the other. Such couples were encountered in all water layers, although they occurred very rarely near the bottom. The reasons for coupling are not known, but in all probability couples are formed by active movement of the individuals, perhaps in relation to feeding or reproductive behaviour.

Surface aggregations. Under normal (offshore) conditions, *Pelagia noctiluca* tended not to swim right at the sea surface, probably to avoid the possible damaging effects of waves. When nearing the shore, and struggling to escape undesirable contact with the bottom, a jellyfish was forced to approach sea surface where its swimming efficiency was reduced until it was damaged by hitting nearshore rocks or floating refuse. It then usually drifted ashore. When floating at the surface under crowded conditions, jellyfish could not help touching each other, which probably also contributed to lesions of their umbrellas. In the Northern Adriatic, we observed that maximum surface aggregations, when the free water literally could not be seen, seldom occupied a surface area bigger than six square meters.

Mid-layer clusters. They are extremely rare. We only once observed such a cluster, about 0.5 m in diameter at a depth of 10 m in an area populated with "few" medusae (Fig. 1). The cluster exhibited a perfect buoyancy, although hundreds of medusae had contacted and interlaced by their manubria and tentacles. The jellyfish pulsated at a normal frequency. No explanation for this cluster could be given.

Fig. 1. *Pelagia noctiluca.* A mid-layer cluster

Bottom aggregations. They were noted several times. While drifting towards the shore, the jellyfish assembled just above the bottom (or 80 to 100 cm above it) in a sheet about 50 cm or more thick, in an effort to escape contact with the bottom. Though very numerous (probably more than 100 individuals per cubic meter), the jellyfish appeared to avoid mutual contacts. In other cases, however, medusae were passively concentrated by retreating water on the ebb tide, in densities of hundred or more individuals per cubic meter.

Swarming aspects

The reasons and mechanisms of offshore swarming in *Pelagia noctiluca* have still not been adequately explained. It is known that the transport of swarms is the result of wind and sea currents, as related to their direction, speed and endurance (Rottini Sandrini *et al.,* 1980; Legović and Benović, 1984; Vučetić, 1985). During our observations several aspects of *P. noctiluca* massing in the coastal area investigated were noteworthy.

Wind effects. These are a most conspicuous aspect of swarming. It was observed that after a few days of continuous winds, large assemblages of jellyfish appeared along the mainland and island shores of the region (Fig. 2). In the Adriatic Sea, the areas most affected by jellyfish swarms are exposed to the open sea, particularly in the Quarner and Istrian regions. However, surface swarms of medusae are also driven to the windward shore of bays and islands after a few hours of the daily maestral, a north-western offshore wind. In the afternoon, after the maestral dies down, the medusae that had accumulated in shallow water usually gradually disappeared. On small islands or in the bays, the regularity of this phenomenon

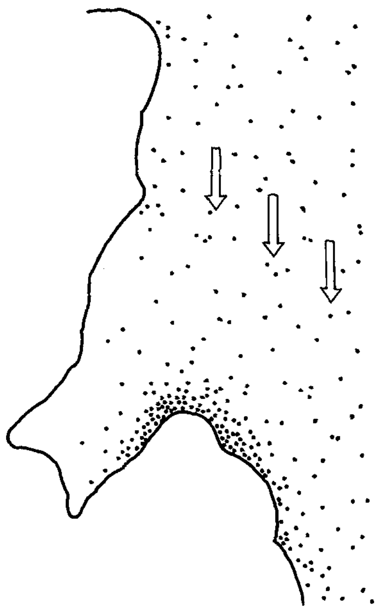

Fig. 2. *Pelagia noctiluca.* Coastal aggregations at wind drift

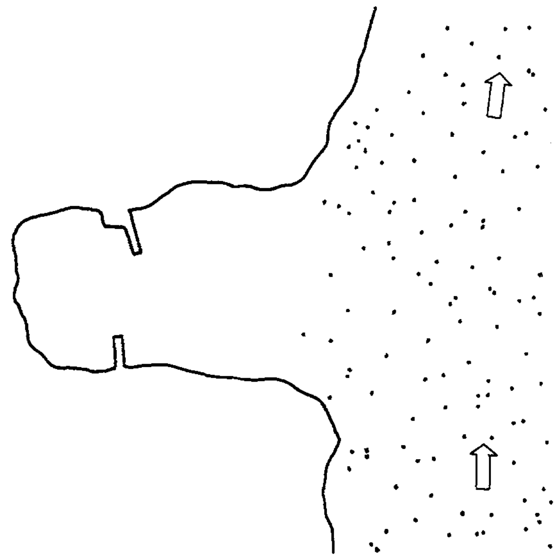

Fig. 4. *Pelagia noctiluca.* Steady current drift

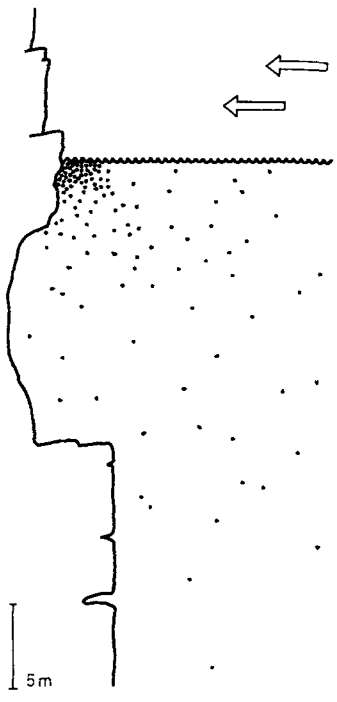

Fig. 3. *Pelagia noctiluca.* Surface drift effect at a gentle breeze (maestral)

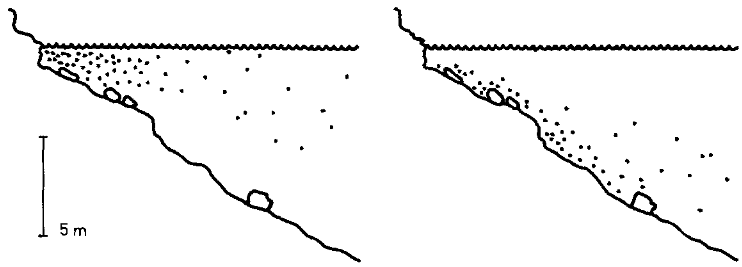

Fig. 5. *Pelagia noctiluca.* Tidal effect. Distribution at the tide (left) and ebb (right) time

led to a clear correlation between wind direction and daily movements of tourists in search of "clear and healthy" swimming places. It should be noted that wind accumulations of jellyfish along windward shores were limited to about 2 to 5 meters' depth (Fig. 3). The maximum aggregation noted was about 500 *Pelagia noctiluca* per cubic meter, stretching along the shore as a belt about 10-m-wide and more than 200-m-long.

Current effects. These could easily be noted as the movement of a jellyfish swarm past a point on land or an anchored boat (Fig. 4). We never observed that this kind of steady current transportation, near the surface and in the middle layers of the sea, resulted in increased aggregations of medusae. On the other hand, the importance of tides and tidal currents in concentrating *Pelagia noctiluca* populations right at the shore was evident (Fig. 5). It was repeatedly observed during the flooding tide, with jellyfish accumulating near and on the sea surface in hundreds per square meter. On the ebbing tide, they disappeared from the surface, and were driven, en mass, along the sloping bottom into deeper layers. Sometimes many of the medusae being moved away from the shore were in poor condition, perhaps damaged when they had surfaced or had come into contact with floating refuse or shore cliffs.

Island effect. When transported by currents, or drifted by wind, medusae can accumulate behind large obstructions, such as a cliff, a small island, or a pier. Accumulations form in the shelter of these objects, due to whirls and

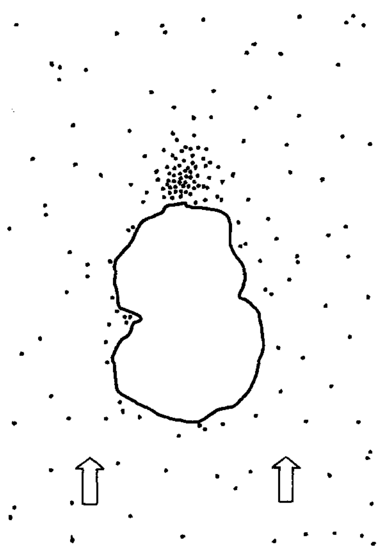

Fig. 6. *Pelagia noctiluca.* Steady current drift: island effect

eddies in the water body; and for the same reason, floating refuse, together with jellyfish, also accumulated at such sites (Fig. 6).

Trap effect. The shoreward drift of jellyfish swarms caused by tidal phenomena is also affected by the interaction of the shore line and the shallowing sea bottom. During the shoreward movement jellyfish were trapped between the sea surface and shallowing bottom, and the swarms were forced to concentrate in maximum aggregation densities. Through pulsing pumping, the jellyfish tended to avoid contact with the surface and bottom, thus accumulating just below the surface and 0.5 m or so above the shallow bottom (Fig. 7). However, very near the surface, and the bottom, they could not avoid contact, even by active swimming, and the jellyfish were inevitably damaged, especially under conditions where waves occurred.

Conclusions

When swarming in shore areas, *Pelagia noctiluca* often accumulated in aggregations in which population densities could exceed 500 individuals per cubic meter.

Pelagia noctiluca was primarily passively aggregated, due to the drift effects of wind, sea currents and tidal phenomena. Active coupling and clustering were also noted.

Jellyfish aggregations mostly occurred in shallow water, especially at the sea surface and in the near vicinity of the bottom when depths were less than 10 m deep.

When densely aggregated, medusae were subjected to lesions by mutual contacts, or contacts with the sea bottom, shore cliffs, and/or floating refuse.

Jellyfish aggregations were temporary: they disappeared after the main drift agents (e.g. wind, currents) had been reduced.

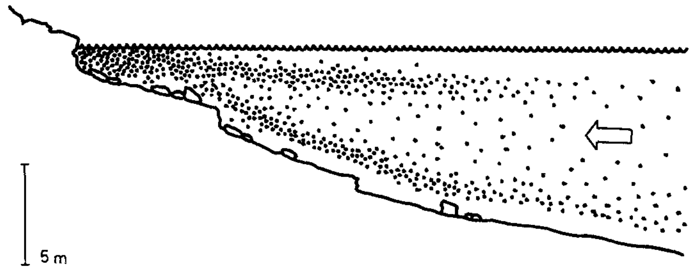

Fig. 7. *Pelagia noctiluca.* Tidal drift: trap effect in calm sea conditions

Characteristic forms of aggregation distributions in swarming medusae were formed in relation to the geomorphological and hydrological characters of the swarm area.

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