

DAYTIME SURFACE SWARMS OF *THYSANOESSA SPINIFERA*
(EUPHAUSIACEA) IN THE GULF OF THE
FARALLONES, CALIFORNIA

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ABSTRACT

Daytime surface swarms of the euphausiid *Thysanoessa spinifera* were observed and sampled in spring 1985 in the Gulf of the Farallones off San Francisco, California. Samples were dipnetted at the surface from nine discrete swarm patches; and depth-stratified plankton tows were made before, during, and after swarm activity. Analyses of sex and maturity stage of surface patch samples showed that 94% of all euphausiids were in breeding condition. Sex ratios differed significantly in six of the nine patches, with males dominating four and females dominating two patches. This sexual segregation is thought to be related to differences in size between sexually mature males and females. Biological and oceanographic observations at the swarm site, and examinations of food baskets of swarm individuals, gave little indication that the animals were passively transported to the surface, or that they were there to feed or avoid predators. *T. spinifera* eggs and Stage I nauplii were numerous in plankton collections taken the night following, and day after surface swarming was observed. It is concluded that swarming in this species is related to reproduction. Its adaptive value in regard to different breeding-related activities is still unclear, but probably involves a combination of factors that relate to the timing of sexual maturation, egg release, and larval dispersal in the changeable upwelling environment off central California.

The neritic euphausiid *Thysanoessa spinifera* aggregates in conspicuous daytime swarms at the ocean surface along the California coast during spring and summer. Little is known about these surface swarms or what triggers their formation, probably because of the unpredictable nature of their onset and duration. The behavior occurs during daylight when most vertically migrating euphausiids, including *T. spinifera* (Alton and Blackburn, 1972), are usually found at greater depths.

In general, upwelling centers have been associated with highest densities of *T. spinifera* (Brinton, 1962); and in the Gulf of the Farallones, daytime swarms occur sporadically from about April to July, when upwelling events are the most frequent and intense along the central California coast (Bakun, 1975). During this time, northwest winds intensify, triggering the offshore transport of warm surface waters, which are then replaced by cool, nutrient-rich water from the depths (Bolin and Abbot, 1962). Periodically during the upwelling season, northwesterly winds slacken, the process temporarily subsides, and surface temperatures may rise due to solar radiation or intrusion of warmer offshore water (Bolin and Abbot, 1962; Hatfield, 1983).

When the rust-colored patches appear, many of the commercial sport fishing boats, guided by flocks of feeding seabirds, seek them out in search of salmon, which we have found to feed heavily on euphausiids at this time of year. Although this daytime swarming is often highly visible and appears to be a relatively common event off central California, very little information is available on swarm population structure. The only published reports consist of brief accounts of swarms that washed ashore at La Jolla, California (Boden et al., 1955), and Bandon, Oregon (Percy and Hosie, 1985), which were composed entirely of spent females, and those observed in Monterey Bay by Barham (1956) for which sex and maturity composition are not known.

Over a dozen species of euphausiids from various parts of the world are known to appear in similar aggregations at the sea surface during the day (Komaki, 1967; Mauchline, 1980), but the frequency of swarming varies from species to species. *Euphausia superba* of the Antarctic may swarm at the surface during the day throughout most of its life cycle (Marr, 1962) and is the best studied euphausiid; other species, such as *T. spinifera*, appear to swarm only seasonally or intermittently (Mauchline, 1980). The mechanism that brings about the formation of these swarms is not clear and may differ according to species. Theories proposed to account for daytime surface swarming of various euphausiid species generally fall into the following categories: (1) the animals actively congregate at the surface for some biological purpose—to feed (Paulsen, 1909; Brown et al., 1979), reproduce (Ponomareva, 1966; Mauchline, 1980; Nicol, 1984a; Endo, 1984; Endo et al., 1985) or escape predators (Komaki, 1967); (2) they are passively transported to the surface by water currents or turbulence (Aitken, 1960; Forsyth and Jones, 1966; Brown et al., 1979; Terazaki, 1980); or (3) a breakdown of an environmental barrier, such as the thermocline, enables them to expand their vertical distribution to the surface (Komaki, 1967; Endo, 1984). These theories have proven difficult to substantiate since many aspects of the swarming phenomenon are not open to experimental investigation. Also, existing published accounts lack direct hydrographic evidence and comparative information on the vertical distribution of various components of the population before, during and after swarm activity.

It is not known which of the above factors are implicated in *T. spinifera* swarming activity, but the dominance of spent females in swarms that washed ashore in southern California (Boden et al., 1955) and Oregon (Percy and Hosie, 1985) suggests that swarming may be related to reproduction. In the more northern part of its range in subarctic waters, this species is reported to have a 2-year life cycle, reaching sexual maturity in its second year, with a one-time breeding season (Nemoto, 1957). Males must transfer a pair of spherical spermatophore packets to females for fertilization to take place, and in members of this genus, females shed their fertilized eggs freely in the water (Boden et al., 1955). The length of time between spermatophore transfer and release of eggs is not known.

The goal of the present study was to identify factors associated with swarming of *T. spinifera* off central California. We made observations of swarms and associated biological activity in a swarm area, collected oceanographic information, and examined samples from individual swarm patches and plankton collections obtained before, during and after swarm activity. In this paper, we describe our results and discuss the possible adaptive significance of swarming in this species.

MATERIALS AND METHODS

Swarms were observed and sampled between 1300 and 1530 h on 31 May 1985 in the Gulf of the Farallones (37°48.3'N, 122°56.3'W). Individual patches were sampled using a hand-held dip net (mouth area = 0.1 m², mesh width = 1.0 mm). Each sample came from a discrete patch, the size of which was estimated visually. These samples were then preserved in 10% neutralized formalin and seawater. Water temperature profiles were obtained with an expendable bathythermograph (XBT).

We were able to obtain depth-stratified plankton samples in the swarm area before, during, and after surface swarm activity. This was possible because the swarms occurred in the same area (within 1.5 km) in which we had been monitoring *T. spinifera* springtime relative abundance since 1983. A set of horizontal tows of 15-min duration was made at the swarm site 12 h prior to and 12 and 24 h after swarm activity was observed. Each set consisted of tows made at 55, 37, and 18 m over bottom depths of 68–70 m. During the day of swarm activity, one tow at 55 m was completed while dipnet samples were being collected from surface waters. These collections were made with an opening-closing Tucker net (described by Hopkins et al., 1973) with an effective mouth opening of 1 m² and a mesh size of 0.335 mm. The net was towed at 1.3 m sec⁻¹. Controlled test runs using a digital flowmeter in the mouth of the net indicated this procedure strained roughly 74 m³ of water per minute, assuming

Table 1. Sex ratios, χ -square values, and significance levels of *Thysanoessa spinifera* swarm patch samples collected by dip net from the sea surface

Patch sample number	Patch area (m ²)	N	% Females	χ^2	P
1	1.0	239	0.30	38.56	<0.01
2	1.5	136	0.31	19.12	<0.01
3	4.0	147	0.12	85.34	<0.01
4	1.5	133	0.38	6.76	<0.01
5	2.0	167	0.50	0.00	N.S.
6	3.0	154	0.65	13.16	<0.01
7	2.0	179	0.55	1.82	N.S.
8	5.0	116	0.76	30.02	<0.01
9	1.0	33	0.64	1.94	N.S.

the absence of net clogging. Organism counts were standardized for 1,000 m³ of water strained by the net.

Swarm samples containing 200 euphausiids or less were examined in their entirety; larger samples were divided with a Folsom plankton splitter. Total length was measured to the nearest millimeter from the tip of the rostrum to the tip of the telson. Body length, from the base of the eye to the junction of abdomen and telson, was also measured to allow comparison with other data. These lengths were highly correlated ($r^2 = 0.957$, $P < 0.0001$). A least-squares fit of 1,304 comparisons gave the equation

$$Y = 0.742X + 0.26$$

where Y = body length and X = total length. An analysis of variance showed that variation due to regression is significant, and therefore the true slope differs from zero ($F = 29,051$; $df = 1, 1302$; $P < 0.001$). Females were classified as (1) with spermatophores attached, with ripe or ripening eggs (0.2–0.4 mm in diameter); (2) without spermatophores, with ripe or ripening eggs; (3) without spermatophores, with early developing eggs (<0.2 mm); and (4) with spermatophores attached, but with no eggs discernible in the thoracic cavity (spent). Females with spermatophores attached to the thelycum will be termed "fertilized," even though actual fertilization of eggs may not take place at the time of spermatophore transfer. Males were classified as (1) with ripe spermatophores protruding or internal; and (2) without ripe spermatophores. All specimens were grossly examined for the presence of parasites. In addition, the ventral food basket between the thoracic appendages of each specimen was examined, and contents of food boluses were identified to the lowest possible taxonomical level.

RESULTS

Nine patches, 1–5 m² in size (Table 1), each approximately 137 m apart, were sampled over an area of about 1 km². The aggregations occurred from the surface to a maximum depth of about 37 m in 71 m of water, based on echosounder readings (Fig. 1A).

Weather and sea conditions at the swarm site were seasonally mild: wind speed = 8 knots, wind direction = 270°, sea state = 2 on Beaufort scale, swell height = 1 m, swell direction = 255° mag., cloud cover = 2 (1/8 sky covered). During the cruise period (30 May–5 June), oceanographic conditions were characterized as transitional, marked by persistent south winds, relaxation of upwelling, and warming and stratification of upper surface layers.¹ Coastal Upwelling Index values (Bakun, 1975) for the central California coast were well below average for the last week in May, indicating an absence of strong upwelling during and preceding swarm activity.²

Observations of swimming behavior and patch shape were made while the ship

¹ K. Briggs, University of Santa Cruz, Santa Cruz, CA 95064, pers. commun. June 1985.

² Andrew Bakun, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93942. Unpubl. data.

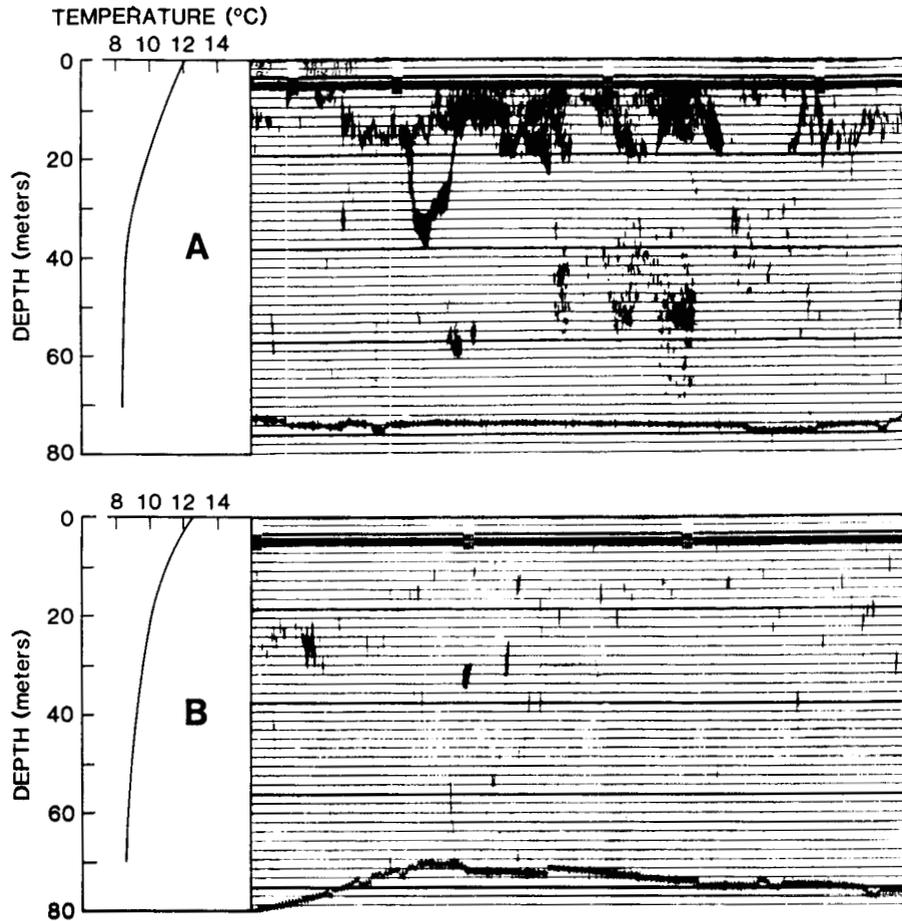


Figure 1A. Echogram (38 kHz) and XBT temperature profile obtained at the surface swarm site on the day of swarm observations, 31 May 1985; Figure 1B. Echogram and XBT temperature profile obtained at the surface swarm site the night following swarm activity, 1 June 1985.

drifted into the swarming area and during sampling. Some of the patches were roughly circular and contained tightly spaced individuals without parallel orientation. Others were ribbonlike streams of individuals, which swam parallel to each other at an estimated 0.3 m sec^{-1} . The animals often sounded rapidly as a group when disturbed, and some individuals even vaulted from the water in an effort to escape the dip net or the samplers' boat. Isolated individuals were also observed swimming at the surface outside the dense patches.

Although feeding activity of fishes has been associated with surface swarming of *T. spinifera* in Monterey Bay (Harvey³) and in the Gulf of the Farallones (by the salmon sportfishing fleet⁴), we saw no evidence of this at the swarm site. The

³ Harvey, J. T. Daytime surface swarming of euphausiids in Monterey Bay, California. Unpubl. manusc., Hatfield Marine Science Center, Oregon State University, Newport, OR 97365.

⁴ Roger Thomas, Captain *Salty Lady*, Harbor Drive, Sausalito, CA 94965, pers. commun. May 1985.

Table 2. Estimated number per 1,000 m³ (N) and percent sample volume (%) of *T. spinifera* eggs, nauplii, and adults taken in plankton tows at the swarm site before, during, and after swarm activity

Tow depth (m)	Tow duration (min)	Eggs		Nauplii		Adults			Total sample volume (ml)
		N	%	N	%	Ripe ♂	Fert. ♀	%	
Night before swarm activity (0150–1340 hr)									
18	15	19,533	0.01	—	—	91	40	0.12	183
37	16	744	<0.01	—	—	18	10	0.05	94
55	15	689	<0.01	—	—	15	1	0.05	56
Day of swarm activity (1400 hr)									
55	15	3,217	<0.01	64	<0.01	—	*	—	109
Night following swarm activity (0200–0350 hr)									
18	15	17,235	0.05	—	—	3	3	0.01	63
37	15	28,151	0.20	—	—	—	2	0.01	43
55	15	18,269	0.13	—	—	1	1	0.01	31
Day after swarm activity (1240–1400 hr)									
18	15	4,600	0.01	1,181	<0.01	—	—	—	47
37	15	24,129	0.30	—	—	—	—	—	23
55	15	9,566	0.07	—	—	—	—	—	46

* A single, unfertilized female with early stage eggs was taken in this collection.

only predators evident in the area were western gulls (*Larus occidentalis*) which were observed on the water singly or in pairs, feeding on individual patches.

There was no evidence, either in our plankton collections (Table 2) or in echosounder tracings (Fig. 1B), that the surface swarming persisted after nightfall. Euphausiid eggs, however, were numerous in plankton collections taken that night and the next day (Table 2). Although positive identification could not be made of the eggs or of the Stage 1 nauplii found in near-surface samples the following day, the size of the egg embryos and the shape of the nauplii differed from those of *Euphausia pacifica*, the only other abundant euphausiid in the area.⁵ We therefore assume that the eggs and nauplii were those of *T. spinifera*. Egg numbers may have been underestimated because of possible extrusion through the net meshes (mean egg diameter = 0.41 mm; mesh width = 0.335 mm; mean diagonal mesh width = 0.42 mm).

Analyses of sex and maturity stage of the dipnetted samples from surface patches showed that 94% of all euphausiids were either males with fully developed spermatophores or fertilized females with ripe or ripening eggs. The sex ratio, however, differed from patch to patch. Six of the nine collections differed significantly from the expected 1:1 male : female ratio, with males dominating in four collections and females dominating in two collections (Table 1). Analyses of length frequencies by maturity stage helped to distinguish major components of the swarms (Fig. 2). Overall, sexually mature males (TL mean = 20.7 mm) and large fertilized females with eggs (TL mean = 25.4 mm) comprised 55.7% and 38.0%, respectively, of the sampled population. A third, lesser group (4.8% of individuals), which occurred strongly only in patch sample 2, was composed of smaller developing females (TL mean = 19.9 mm). The remainder (1.5%) consisted of unfertilized ripe females (8 individuals), spent females (6), and males without spermatophores (5).

⁵ Margaret Knight, Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. March 1986.

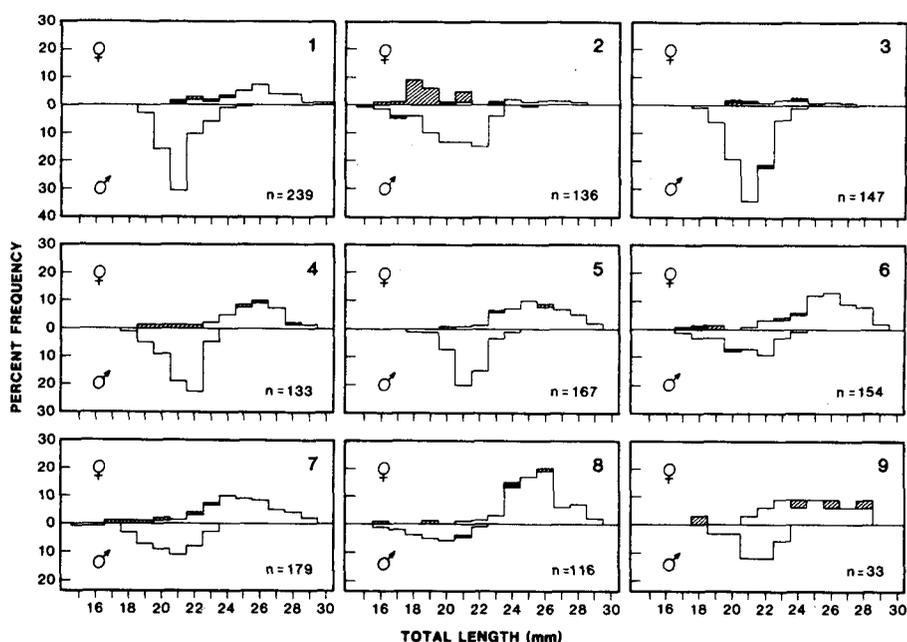


Figure 2. Length frequency histograms of the nine sampled swarm patches of *Thysanoessa spinifera*. Crosshatching = unfertilized developing females; open = fertilized females with ripe or ripening eggs and males with spermatophores; solid = other (males without spermatophores, fertilized females without eggs, and ripe, unfertilized females).

Examination of food baskets of swarm individuals indicated little feeding activity, but some cannibalism was evident. The only recognizable items were euphausiid ommatidia and other optic material. Of the 1,304 specimens examined; 81.1% had empty food baskets, 17.6% contained euphausiid ommatidia, and the remainder contained unrecognizable material.

Suctorian protozoans infested the exoskeletons of 75.2% of the euphausiids examined.⁶ The thoracic cavity of three female individuals each contained a single larval nematode, identified as *Anisakis* sp.⁷

DISCUSSION

The results provide evidence of sexual segregation in *T. spinifera* and strongly indicate that swarming is related to reproduction. It is unlikely that the euphausiids were transported to the surface by some physical force, judging from the stratified temperature profiles and mild oceanographic conditions, and we found no evidence that they were there to feed or avoid predators.

Some of these findings are very similar to those of others who have recently studied daytime swarming of temperate water euphausiids on other coasts. Nicol (1984a) found that reproductive adults dominated swarms of *Meganycitiphanes norvegica* in the Bay of Fundy, and that sex ratios from patch to patch were highly skewed. He also found a high degree of suctorian infestation in swarm samples

⁶ Identified by S. K. Johnson, Texas A&M University, 111 Nagle Hall, College Station, Texas 77843, pers. commun. May 1986.

⁷ Identified by Mike Moser, University of California, Santa Cruz, CA 95064, pers. commun. April 1986.

compared to those taken at depth offshore (Nicol, 1984b). Endo (1984) and Endo et al. (1985) concluded that swarming of *Euphausia pacifica* in Sendai Bay, Japan, was related to reproduction, although the majority of ripening females they sampled were as yet unfertilized. They also found a predominance of euphausiid spines and eye parts in guts of swarm individuals and a similar infestation of suctorian epibionts.

Adult male euphausiids and the larger adult females may segregate by sex to facilitate schooling (Nicol, 1984a). Those patches in which the sexual segregation was not pronounced may represent the convergence of male and female aggregations and, indeed, swarm patches have been seen to merge and separate.⁸ The fertilized mature females and sexually mature males are assumed to represent the 1983 year class because they correspond to individuals classified as Age 2 by Nemoto (1957). If so, the smaller developing females are likely sexually precocious individuals of the 1984 year class. Their association with the more sexually advanced males may be based on corresponding size and therefore swimming efficiency, rather than corresponding reproductive stage.

Surface swarming may relate to reproduction in one or more of the following ways: (1) for more effectual transfer of spermatophores from males to females, (2) for release of eggs at the surface, or (3) for maturation of sexual products in adults and/or incubation of eggs in warm surface layers. There are arguments for and against all of these possibilities.

Swarming for the purpose of spermatophore transfer seems likely, considering the range of sex ratios in individual patches and observations of swarms merging. But the virtual absence in our samples of mature but as yet unfertilized females suggests otherwise. We have also found a similar absence of unfertilized females in plankton samples and chinook salmon (*Oncorhynchus tshawytscha*) gut contents collected throughout the swarm season. This suggests that the bulk of spermatophore transfer takes place prior to the surface swarming season, and that refertilization of molted females, if it does occur, takes place in areas less accessible to our collecting gear and to salmon predation. Nicol (1984a) also found very few unfertilized mature females in swarming *Meganyctiphanes norvegica* in the Bay of Fundy.

Although the intermolt period for nonreproductive *T. spinifera* has been estimated at 5 to 6 days (Jerde and Lasker, 1966), molting may be delayed or suspended during the reproductive period or upon reaching sexual maturity (Dexter, 1977; Nicol, 1984b). This would further explain why an overwhelming majority of females carry intact spermatophores throughout the breeding season, and may account for the high incidence of exoskeleton infestation by suctorians. Suspension of ecdysis would seem an adaptive means to alleviate the need for segregated males to relocate and refertilize females with each molt.

The presence of eggs in the swarm area suggests that egg release may be an important function of swarming. This hypothesis is supported by the reports of swarms composed entirely of spent female *T. spinifera* (Boden et al., 1955; Percy and Hosie, 1985). Egg incubation, however, is probably not a factor, since euphausiid eggs, being denser than seawater, tend to sink when broadcast freely in the sea (Mauchline and Fisher, 1969). Even so, neritic species such as *T. spinifera* would benefit from releasing eggs high in the water column, thus providing more time for eggs to develop and hatch before reaching the sea floor. After hatching, the larvae are thought to ascend to surface waters where food supplies are abundant

⁸ Peggy Gamin, vessel *Salty Lady*, Harbor Drive, Sausalito, CA 94965, pers. commun. May 1985.

(Mauchline and Fisher, 1969) and the greater average velocity of surface currents can disperse them away from the area and potential cannibalism by adults. But the advantage gained by suspending or reversing normal diel migratory behavior by aggregating at the surface during daylight hours is still not clear. As with other breeding-related activity, egg release could occur during crepuscular or nocturnal periods, presumably with the same benefits mentioned above with the added protection from diurnal predators that darkness would provide. In addition, less than 1% of females in our swarm samples were spent, which indicates that egg release may not be the primary swarm activity during the day, or at least during the afternoon period that we sampled.

Perhaps one of the functions of daytime surface swarming is to prolong exposure of reproductive individuals to the warmer surface layers, where maturation of sexual products would be accelerated. Lindley (1978), working with *Thysanoessa longicaudata*, found that timing of reproduction in spring was correlated with sea surface temperature, and concluded that the rate of sexual maturation is controlled mainly by temperature. The animals may take advantage of interim warming periods between upwelling events to accelerate gonadal development in the warm surface layers. But again, the advantage gained by this strategy would have to outweigh the disadvantage of being highly vulnerable to predation at the sea surface during the day.

Most likely, the adaptive significance of *Thysanoessa spinifera* surface swarming encompasses more than just one factor, since the selective forces acting upon breeding adults would differ from those acting upon eggs and larvae (Dingle, 1980). Both the timing of sexual maturation and the timing of egg release and subsequent larval dispersal would seem crucial, since these events occur during the upwelling season when water temperature and sea surface current velocity and direction can change over a short period of time. Success, however, would seem to depend largely on the rapid behavioral responses of breeding adults. Swarming may be such a response. Although the cost of being at the surface in daylight would seem high for adults because of their greater visibility, the intermittent formation of dense schools, and the rapid response to stimuli that schooling facilitates, may offer the needed edge over predators to ensure that sufficient numbers of adults survive to breed and release their eggs under favorable environmental conditions. The small-scale patchiness revealed by this study re-emphasizes the importance of direct sampling of these reproductive swarms, the dynamics of which may be masked by more conventional sampling with towed plankton nets.

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