Towards an understanding of salp swarm dynamics
by Patricia Kremer

ABSTRACT
Species of salps are characterized by intermittent blooms. Several studies have documented the importance of physical processes both in providing seed stocks of salps and creating an environment that is favorable for the rapid increase of salp populations. Although salps are typically oceanic, most observations of bloom dynamics have been made in more accessible inshore waters, so it is difficult to assess how frequent and widespread these swarms are. A review and comparison of existing data is helping to define geographic “hot spots” for salp blooms as well as the necessary physical and biological precursors. Although at this point, the review is far from complete, several generalities are emerging. The details of the physical forcing functions vary, but the overall physical regime seems to require a region of pulsed mixing of oceanic water that results in a relatively high standing stock of autotrophs. For a salp bloom to occur, there also needs to be an adequate seed population of salps and sufficient sustained primary production to support the biomass of the salp population as the bloom develops. As non-selective filter feeders, salps are able to remove a wide range of particulates from the water column, transforming the undigested portion into fast sinking feces. Therefore, when salps occur at high densities, the water is characterized by low abundance of other plankton, with obvious trophic implications.

Patricia Kremer: Marine Sciences, University of Connecticut, Groton CT 06340-6097, USA [tel: +1 860 405 9140; fax: +1 860 405 9153; e-mail pkremer@uconn.edu]

INTRODUCTION
Salps are holoplanktonic grazers that have a life history, feeding biology, and population dynamics that contrasts sharply to copepods and other crustacean zooplankton (Madin and Deibel 1998). These pelagic tunicates, as all of the gelatinous zooplankton, are watery and therefore large in size relative to their organic content (Madin 1981). This affords them several advantages:
• large size results in a larger search volume when feeding, than their crustacean counterparts of comparable organic content
• large size limits the number of predators that can feed on salps
• somatic growth in terms of increase in organic matter, represents a disproportionately large increase in physical size

The life history of salps also makes them suited to rapid population growth given
favorable conditions. In the aggregate part of the life cycle, salps occur in chains, further limiting the potential predators due to the increased size. Each of these individual aggregates is internally fertilized, and does not release the embryo until it is fairly large relative to its mother. The solitary salp then reproduces asexually releasing the aggregates as a chain (Fig. 1) Although the sizes of the aggregates and solitaries for various species of salps varies considerably, they all have this life cycle in common. Numerical increases in the salp population are produced asexually each generation, and the survival of sexually produced embryos is enhanced through internal brooding by the aggregate salps.

![Image of the life cycle of salps.](from Alldredge and Madin 1982)

Figure 1. The life cycle of salps. (from Alldredge and Madin 1982)

Salps sometimes occur in high densities that cover large areas, but the conditions that initiate and support these blooms are not generally well understood, and there has not been a synthesis of what seems to be the necessary and sufficient conditions for salps to become very abundant. Most observations of salp swarms have taken place without much of an understanding of the hydrographic and biological context in which these blooms occur. Over the past fifty years, however, there have been enough salp collections in areas where the hydrographic conditions have also been systematically studied that a global synthesis can begin to be made.

This study consists of an ongoing effort to review information on salp swarms. Of particular interest are those geographic areas where there are both time series data on salps and also information on the associated hydrographic conditions and florestics/primary productivity. The goal of this work is to formulate testable hypotheses about why some areas have salp swarm with regularity, while other areas have high densities of salps only irregularly, and other places seem to experience blooms rarely if ever. Comparisons of these regions in terms of their physical and biological settings should enable us to better understand and predict when and where salp swarms occur.
Figure 2. Global distribution of documented salp swarms. Details in Table 1 (following 2 pages)
<p>| Map  | Region          | Species       | Season  | Related Hydrography                                      | Info. Index | Reference                                      |
|------|-----------------|---------------|---------|----------------------------------------------------------|-------------|------------------------------------------------||
| 1    | Puerto Rico     | SLC           | July    | none given                                               | 1           | Tokioka and Bhavanarayana 1979                |
| 2    | S.E. U.S.A      | THD           | late winter-summer | Gulf Stream intrusions; stimulated by topography | 4           | Paffenhofer and Lee 1987, Paffenhofer et al. 1995 |
| 3    | Bermuda         | SLA, SLF, THD | winter-summer | advection                                              | 2           | Moore 1949, Deevey and Brooks 1971, Van Soest 1975 |
| 4    | Mid-Atlantic Bight slope | SLA          | spring-summer | shelf-slope front upwelling (warm core rings) | 3           | Wiebe et al. 1979, Madin et al. 1994          |
| 6    | North Atlantic near Europe | THD | late summer-fall | Mediterranean outflow to Atlantic | 2           | Hunt 1968                                    |
| 7    | Western Mediterranean | SLF    | spring/summer | early spring, west wind, upwelling                      | 4           | Braconnet et al. 1990, Menard et al. 1994      |
| 8    | S.W. Africa     | THD           | late spring | shelf-slope front, coastal upwelling                    | 2           | Blackburn 1979                               |
| 9    | Gulf of Guinea  | SLF           | variable  | front, upwelling                                        | 1           | Binet 1976, LeBorgne 1983                     |
| 10   | South Africa    | THD           | spring   | So. Atlantic Convergence (Sep’t-Nov.)                   | 3           | Van Zyl 1960, DeDecker 1973, Lazarus and Dowler 1979 |
| 12   | Pakistan        | ?             | Nov., March | continental shelf, postmonsoon                          | 1           | Haq et al. 1973                              |
| 13   | N. W. India     | PCO, THD      | Sep’t.-Dec. | none given                                               | 2           | Menon 1931, Nair 1949                         |
| 14   | Madras, India   | THD           | Sep’t - Oct. | invasion of oceanic water on broad cont’l shelf         | 3           | Nagabhushanam 1960, Madhupratap et al. 1979   |
| 15   | Bay of Bengal   | IAZ           | Feb.-March | correlation w/ high salinity                            | 1           | Sewell 1926                                  |
| 16   | Burma           | THD           | Jan.-March | none given                                               | 1           | Mullin 1983                                  |
| 17   | N.E. Australia  | THD           | summer    | correlation w/ high salinity                            | 1           | Heron and Benham 1984, Humphrey 1963          |
| 18   | S. E. Australia | THD           | spring-sum. | slope water intrusions                                   | 2           | Tranter 1962, Clementson et al. 1989, Harris et al. 1991 |
| 19   | Storm Bay, Tasmania | THD, SLF | spring-sum. | destratification from upwelling, mixing of subtropical water at subtropical convergence | 1           | Wear 1965                                    |
| 20   | Wellington, New Zealand | THD, Ihaea sp. | late summer | to fall                                                  | 3           | Bradford and Chapman 1988                    |
| 21   | East Cape, New Zealand | THD, SLF | summer    | topographically induced warm-core eddy                  | 3           | Zeldis et al. 1995                           |
| 22   | Hauraki Gulf, New Zealand | THD, SLF | summer    | intrusions of shelf water to the Gulf                   | 3           | Iseki 1981                                   |
| 23   | Japan           | SLF           | spring    | none given                                               | 1           | Tokioka 1937                                 |
| 24   | Kuroshio cur., off Japan | THD, TRM, SLF | Sep’t. | warm core ring                                          | 2           | Tsuda and Nemoto 1992                        |
| 25   | North Pacific   | SFA           | May       | none given                                               | 1           | Iseki 1981                                   |
| 26   | Subarctic Pac.  | CBA           | late summer | permanent halocline                                     | 2           | Madin and Purcell 1992                      |
| 27   | Cal. Current, off Oregon | SLF, CBA | summer-fall | upwelling                                                | 3           | Hubbard and Pearly 1971                     |
| 28   | NE Pacific, off California | SLF(?) | December  | none given, upwelling filament (?)                       | 1           | Mansueda et al. 1986                         |</p>
<table>
<thead>
<tr>
<th>#</th>
<th>Location</th>
<th>Season</th>
<th>Hydrology</th>
<th>Reference</th>
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<tr>
<td>30</td>
<td>E. Pacific Ocean THD, SLF so. from Hawaii</td>
<td>Equatorial upwelling; shear region between N. Eq. Current and C.C. mixing of oceanic and lagoon water</td>
<td>3</td>
<td>Yount 1958</td>
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<td>31</td>
<td>Rangiroa Atoll Central Pacific THD</td>
<td>Apri-July, fall</td>
<td>1</td>
<td>Michel et al. 1971</td>
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<tr>
<td>32</td>
<td>S. Brazil, cont’l shelf</td>
<td>May</td>
<td>2</td>
<td>Tavares 1967</td>
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<tr>
<td>33</td>
<td>Argentina, cont’l shelf</td>
<td>May</td>
<td>3</td>
<td>Mianzan et al. 2001</td>
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<tr>
<td>34</td>
<td>So. Atlantic, off S. Argentina</td>
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<td>None available</td>
<td>2</td>
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<tr>
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<td>Weddell Sea SLT</td>
<td>summer</td>
<td>Ice cover</td>
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<td>S. of Lazarev Sea, So. Ocean SLT</td>
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<td>38</td>
<td>S. of Africa 40°S</td>
<td>summer</td>
<td>Warm-core eddy, near STC</td>
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<td>39</td>
<td>50°S SLT</td>
<td>summer</td>
<td>Antarctic Polar Front</td>
<td>3</td>
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<tr>
<td>40</td>
<td>Adelie Coast, Antarctica 45°S</td>
<td>austral</td>
<td>Polar Front</td>
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**RESULTS**

Salp swarms have been reported from all the major oceans and seas, over a wide range of latitudes (Fig. 2). The apparent association of these swarms with oceanic regions relatively near the coast is undoubtedly partly due to a sampling bias in waters on or near the continental shelves, and areas near oceanographic centers and marine laboratories. In addition, however, the development of a salp swarm requires a sufficient food source, constraining salp blooms in both space and time. The locations of documented salp blooms presented in Fig. 2, undoubtedly represent only a small subset of the blooms that actually occur in the ocean. At this time, it is impossible to estimate the magnitude of this underestimate. Nevertheless, these limited observations can be useful in helping to synthesize overall patterns.

For each of the locations identified in Fig. 2, information is summarized (Table 1) about the salp species, seasonal occurrence, associated hydrography, the quantity of available information, and key reference(s). This summary shows that only a relatively few species of salps are responsible the overwhelming majority of the observed swarms, specifically: *Thalia democratica* (and closely related species); *Salpa fusiformis, S. aspera, S. thompsoni*; and occasionally *Iasis zonaria, S. cylindrica, Pegea confoderata, Ihlea spp., Cyclosalpa backeri, and Traustedtia multitenaculata*. Hydrographic conditions associated with these swarms (e.g. pulsed upwelling, convergence, divergence, eddy intrusion, water mass interleafing) lead to temporary destratification of the water column. The season for salp blooms is typically in the spring-summer in higher latitudes, when solar radiation is sufficient to result in the critical depth for phytoplankton productivity being lower that the mixed layer depth (Svedrup model). Salp blooms typically do not appear to develop, however, unless there is a physical mechanism that
sustains high productivity through periodic destratification, allowing nutrient-rich water to reach the photic zone.

Several locations within the ICES area of the North Atlantic offer interesting and contrasting case studies of different hydrographic conditions that can lead to salp blooms. Four areas are summarized here, illustrating a range in regularity of the appearance of salp swarms and the underlying hydrographic forcing.

Figure 3. The continental shelf of the southeastern United States. (from Paffenhofer et al. 1995)

The continental shelf of the Southeastern United States (Fig. 3) is one of the best studied shelf regions in the world. Intensive investigations of the physical, chemical and biological oceanography of this region (Atkinson et al. 1978, Lee et al. 1981, Lee and Atkinson 1983, Deibel 1985, Paffenhofer and Lee 1987, Atkinson et al. 1989, Paffenhofer et al. 1995) reveal that this area is particularly prone to intrusions of oceanic water from the Gulf Stream. Frontal eddies appear to enlarge in northern Florida, where the continental shelf widens, resulting in elongated tongues of warm Gulf Stream water 100-200 km in length. The Gulf Stream is observed to have a quasi-permanent eastward displacement downstream of the “Charleston Bump”, a topographic anomaly of the continental slope at 32°N. This is believed to further enhance the meanders and eddies of this region. As eddies move onshore onto the continental shelf, they result in upwelling near the shelf break, intrusions of deep water, and generalized vertical mixing of the outer shelf waters (Fig. 4). This leads to increased primary production.
Especially if winds are weak and the water is transported shoreward across the shelf as it stratifies, an environment favorable for the development of high densities of Thaliaceans is produced. During July-August 1981, in less than a month, an area with high densities of salps (*Thalia democratica*) and doliolids, grew from 2800 km² to more than 9300 km² (Paffenhofer and Lee 1987). High densities of salps have been documented in this region with regularity.

![Figure 4. Schematic of a Gulf Stream frontal eddy on the shelf of the southeastern shelf of U. S. (from Lee et al 1981)](image-url)

In contrast to the regularity in the appearance of salps in the continental shelf region discussed above, salps blooms in the region of Bermuda are much more irregular and sporadic. Moore (1949) noted a winter maximum of *Thalia democratica* and one dense swarm of *Salpa* sp. (probably *S. aspera*) in May. Deevey and Brooks (1971) collected high numbers of salps only in April. Van Soest (1975) working with collections from the Ocean Acre project did not specifically focus on the timing of swarms of salps, but noted that the most common salps, *Thalia spp, Salpa spp and Iasis zonaria* were most common in the spring and summer. Biggs and Dam (unpublished) recorded a swarm of *S. aspera* in July of 1983, but not in 1984, 1986, or 1987. Monthly sampling at the Bermuda-Atlantic Time Series (BATS) has shown that both *T. democratica* and *Salpa spp.* can occur in swarms. More than 60 times from 1991-1999 densities of salps were greater than 0.1 salps/m³, with a maximum of 608 salps/m³ (Ranelletti and Steinberg unpublished). The waters around Bermuda are generally oligotrophic and the densities of salps are generally low. Salp swarms are likely the result of productive waters containing salps being advected near the island.
The slope water of the **Mid-Atlantic Bight** has been sampled for salps only infrequently and intermittently. Nevertheless, large areas of high densities of *S. aspera* have been documented in the summers of 1975, 1986, 1993, and 2002 and this salp species has been shown to be a strong vertical migrator (Wiebe et al. 1979, Wiebe unpublished, Madin et al. 1994, Kremer personal observations) Recent observations in June 2002 showed that the swarm extended from at least the shelf break to the Gulf Stream, and from off Virginia (37°N) to south of Woods Hole (71°W), a minimum of 15,000 km² (Fig. 5).

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![Map of the Mid-Atlantic Bight region](image)

**Figure 5.** Map of the Mid-Atlantic Bight region where swarms of *Salpa aspera* have been observed. ● = Sampling in 1975 (Wiebe et al. 1979); X = 1986 (Wiebe unpublished); § = 1993 (Madin et al. 1994); Shaded area = 2002 (75 stations, Madin and Kremer pers. observation); ? = potential extent of bloom in 2002

There is evidence for a zone of enhanced chlorophyll along the Mid-Atlantic shelfbreak that may be important in providing the organic matter necessary to produce these massive salp blooms. During the spring transition between winter (when the shelfbreak front extends from surface to bottom) and summer (when the front extends only between the bottom and the seasonal thermocline), the pigment enhancement was observed during all the years examined (1979-1986) (Ryan et al. 1999). The overall pigment levels were twice the levels in both the adjacent slope and shelf waters during this season, and the enhancement zone was observed to extends long as 1100 km along the entire Mid-Atlantic Bight shelfbreak. The alongshelf orientation of the pigment enhancement is facilitated by alongshelf advection to the southwest in
the frontal jet.

This pigment enhancement is distinct from and occurs later than the winter-spring phytoplankton bloom that usually occurs during March-April. This pigment enhancement of the later period comes after the surface shelf waters have become stratified and nutrient limited. Disturbance of the frontal region by winds or warm-core rings can upwell deep-shelf nutrients, and transport water along the frontal pycnals that shoal in the offshore direction and mix with offshore water. If the waters are not too strongly stratified, the nutrient enriched water may reach the surface and the resulting chlorophyll detected by satellites. The process can also occur during strongly stratified conditions in summer, increasing subsurface nutrients and primary production, but not reaching to the surface. Even though the pigment enhancement is not expressed at the surface, and therefore is not detectable to satellite remote sensing, the increased primary productivity at the shelf-slope break may be important in helping to produce and sustain summer salp blooms of *S. aspera* in the slope waters.

Salp swarms are well documented for the **Eastern North Atlantic**, with published observations dating back more than one hundred fifty years. (Murray and Hjort 1912 p.452, Sars 1829 p.51, Sars 1846. In some years *S. fusiformis* has been observed in very high densities west of the United Kingdom and Ireland, and even as far north as the northern part of Scotland, the Faroe-Shetland channel, the coast of Norway and even into the southern Norwegian Sea (Fraser 1949, Fraser 1962, Hunt 1968, Brattstrom 1972). In other years *S. fusiformis* has been observed in swarm densities in Icelandic waters and even in the waters south of Greenland. These swarms do not occur every year in these regions and seem to be strongly associated with warmer Atlantic Ocean waters of the North Atlantic Drift. When salps were abundant off Iceland or Greenland, there were none in coastal Norway, implying large interannual variability in the pattern of the flow of the North Atlantic Drift (Fig. 6).

![Figure 6. Map of the North Atlantic. Note the contrast in locations of swarms of *Salpa fusiformis* in 1955 and 1957, presumably due to differences in the North-Atlantic Drift.](image-url)
These swarms may cover larger areas as they move with the water masses. Fraser (1962) estimated that in 1961 there was a swarm of *S. fusiformis* that covered over 20,000 sq. miles and continued for several months.

**CONCLUSION**

Relatively few species of salps account for most of the observed swarms. *Thalia democratica*, *Salpa fusiformis*, *S. aspera*, *S. thompsoni* are the most common species observed in high densities. Salp swarms are found in all oceans and from the Arctic to the Antarctic Circle. These swarms appear to be associated with regions of sustained high productivity such as regions of pulsed upwelling, and water-mass fronts which cause nutrient-rich water into the photic zone. Blooms of the *Salpa spp.* are typically found along the continental shelf break and slope waters, at the subtropical convergence in the Southern Hemisphere, and along the Antarctic Polar Front. Blooms of *Thalia democratica* are most commonly found in relatively warm waters, often on the continental shelf, where offshore waters intrude regularly. In subtropical and tropical waters, where light is not seasonally limiting, salp swarms are not particularly seasonal. At higher latitudes, however, salps are most common during the spring and summer, the time when the phytoplankton are the most productive.

Salp swarms are ephemeral, lasting a few months at the most. Some swarms are relatively small, and may represent physical aggregations resulting from currents and winds. The larger swarms, however, are clearly “blooms” with the salp population growing rapidly in situ. Although these blooms are not the typical conditions for most environments, this literature review has shown that they are not uncommon in many locations, and seem to be directly linked with the physical circulation and mixing.

Salps have been shown to ingest a wide range of small particles (2 um to 1 mm) with high efficiency (Harbison and McAlister 1979, Kremer and Madin 1992). Salp feces are generally large and fast-sinking compared with other zooplankton (Madin 1982, Caron et al. 1989). Therefore salps have a potentially important role in the transport of organic matter from the photic zone to the benthos. They also are potentially important in reorganizing trophic pathways, and facilitating changes in species composition of the phytoplankton. Larger fauna, which generally grow more slowly than the opportunistic salps, are at a competitive disadvantage during the time the salp population is growing. Typically copepods are in low abundance when salps densities are high.

The relationship between salps and fish is complex. Although there is evidence that fish consume salps (Kashkina 1986, Mianzan et al. 2001), there is also evidence that fish densities are adversely affected during salp swarms (Harris et al. 1991, Zeldis et al. 1995). The precise details are not yet well understood, but it is likely that salps consume much of the organic matter that otherwise might support a crustacean-fish food chain, resulting in a lower harvestable stock of fish.
REFERENCES


Fraser, J. H. 1969. Variability in the oceanic content of plankton in the Scottish area. Prog. Oceanogr. 5:149-159.


