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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.

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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. Numerial 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.

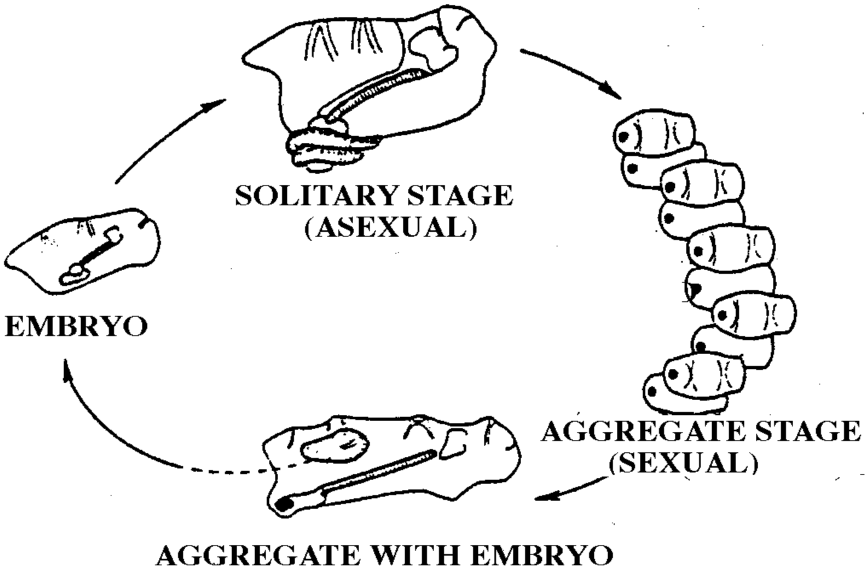

Figure 1. The life cycle of salps. (from Alldredge and Madin 1982)

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 a 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.

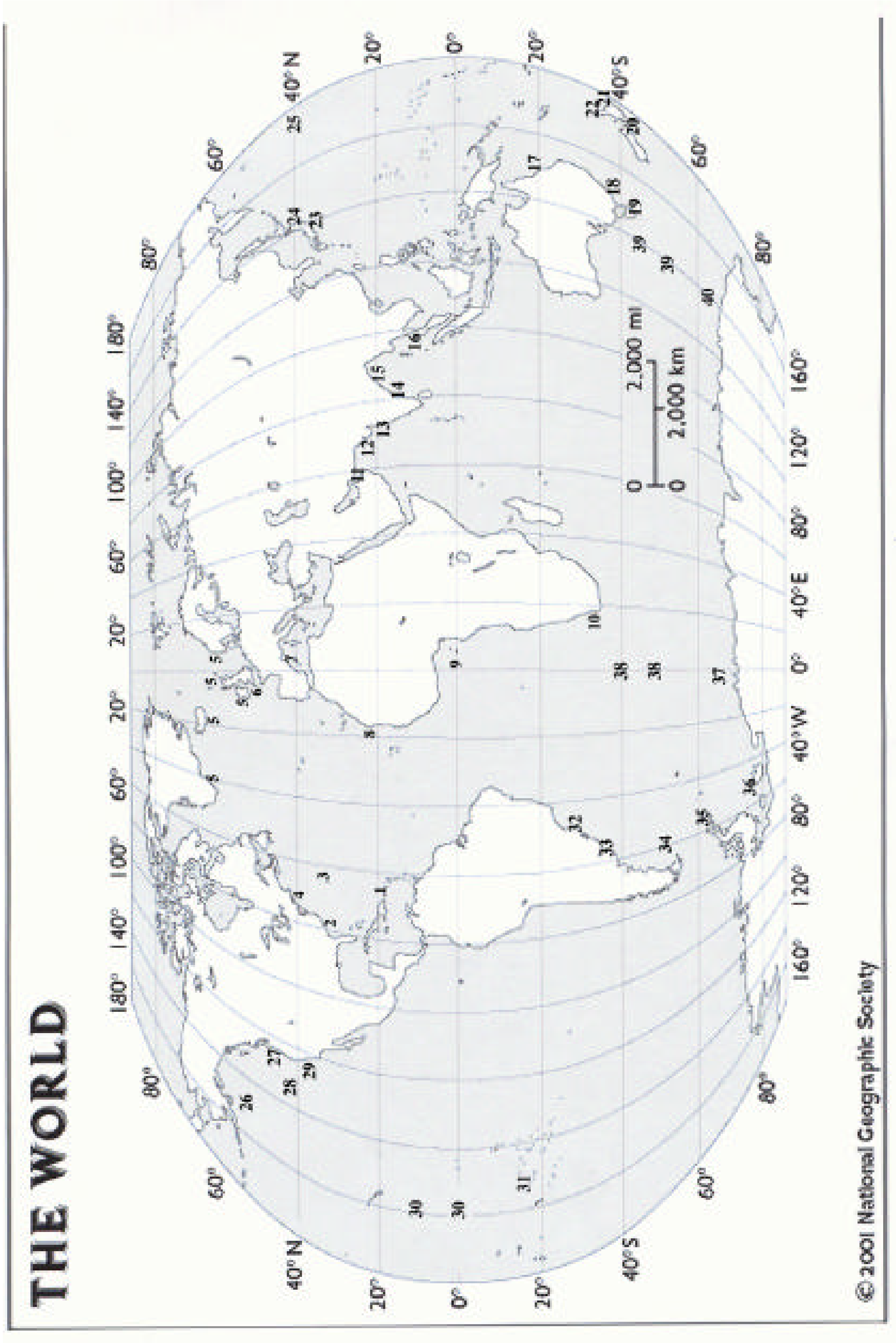

Figure 2. Global distribution of documented salp swarms. Details in Table 1 (following 2 pages)

Table 1. Details for areas described in published accounts of salp swarms including: salp species; season of swarm formation; related hydrography (if studied); quantity of biological and physical information (range 1-4 from single observation to well documented); reference. Abbreviations for species: *Salpa fusiformis* (SLF); *S. aspera* (SLA); *S. thompsoni* (SLT); *S. cylindrica* (SLC); *Iasis zonaria* (IAZ); *Thalia democratica* and other *Thalia spp*. (THD); *Pegea confoederata* (PCO); *Traustedtia multitentaculata* (TRM); *Cyclosalpa bakeri* (CBA); *Ihlea spp.*

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 shelf	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
5	Eastern-North Atlantic	SLF	spring-summer	North Atlantic Drift	4	Brattstrom 1972, Hunt 1968, Fraser 1949, Fraser 1969
6	North Atlantic near Europe	THD	late summer-fall	Mediterranean outflow to Atlantic	2	Hunt 1968
7	Western Mediterranean	THD SLF	spring/summer early spring	east wind, advection west wind, upwelling	4	Braconnot et al. 1990, Menard et al. 1994
8	N. W. Africa	THD	late spring	shelf-slope front, coastal upwelling	2	Blackburn 1979
9	Gulf of Guinea West Africa	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
11	Gulf of Oman, Arabian Sea	PCO, THD, SLC, IAZ		none given	1	Sewell 1953
12	Pakistan	?	Nov., March	continental shelf, postmonsoon	1	Haq et al. 1973
13	N. W. India	PCO, THD	Sep't.-Dec.	postmonsoon	2	Mohan 1965, Lodh et. al 1988 Krishnapillai and Subramonia 1981
14	Madras, E. India	THD	Sep't - Oct. Jan. - March	none given	1	Menon 1931, Nair 1949
15	Bay of Bengal	IAZ	Feb.-March	invasion of oceanic water on broad cont'l shelf	3	Nagabhushanam 1960, Madhupratap et al. 1979
16	Burma	THD	Jan.-March	correlation w/ high salinity	1	Sewell 1926
17	N.E. Australia	THD	summer	none given	1	Mullin 1983
18	S. E. Australia	THD	spring-sum.	slope water intrusions	2	Heron and Benham 1984, Humphrey 1963
19	Storm Bay, Tasmania	THD, SLF	spring-sum.	destratification from upwelling, mixing of subtropical water at subtropical convergence	4	Tranter 1962, Clementson et al. 1989, Harris et al. 1991
20	Wellington, New Zealand	THD, Ihlea sp.	late summer to fall	water >15°C	1	Wear 1965
21	East Cape, New Zealand	THD, SLF	summer	topographically induced warm-core eddy	3	Bradford and Chapman 1988
22	Hauraki Gulf, New Zealand	THD, SLF	summer	intrusions of shelf water to the Gulf	3	Zeldis et al. 1995
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	SLA	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	summer-fall	upwelling	3	Hubbard and Pearcy 1971
28	NE Pacific, off California	SLF(?)	December	none given, upwelling filament (?)	1	Mansueda et al. 1986
29	Cal. Current, off So. Calif.	SLF, THD	spring-summer	upwelling	4	Berner 1967, Blackburn 1979

30	E. Pacific Ocean so. from Hawaii	THD, SLF		Equatorial upwelling; shear region between N. Eq. Current and C.C.	3	Yount 1958
31	Rangiroa Atoll Central Pacific		THD	mixing of oceanic and lagoon water	1	Michel et al. 1971
32	S. Brazil. cont'l shelf	THD	April-July, fall	onwelling of oceanic water onto shelf	2	Tavares 1967
33	Argentina, cont'l shelf	IAZ	May	salinity front, Rio de la Plata	3	Mianzan et al. 2001
34	So. Atlantic, off S. Argentina	SLT	summer	none available	2	Kashkina 1978
35	Antarctic Penn., So. Ocean	SLT	austral summer		4	Mackintosh 1934, Hardy and Gunther 1935, Caldwell 1966, Huntley et al. 1989, Nishikawa et al. 1995, Siegel and Loeb 1995
36	Weddell Sea	SLT	summer	ice cover	2	Boysen-Ennen et al. 1991
37	Lazarev Sea, So. Ocean	SLT	austral summer	marginal ice zone	2	Perissinotto and Pakhomov 1998
38	S. of Africa					
	40°S	IAZ	summer	warm-core eddy, near STC	3	Pakhomov et al. 1994
	50°S	SLT	summer	Antarctic Polar Front	3	
39	S. of Australia		summer			
	45°S	IAZ				
	55°S	SLT		Polar Front	3	Casareto and Nemoto 1986
40	Adelie Coast, Antarctica	SLT	austral summer		2	Chiba et al. 1999

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 confoederata, Ihlea spp.,Cyclosalpa backeri, and Traustedtia multitentaculata.* 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.

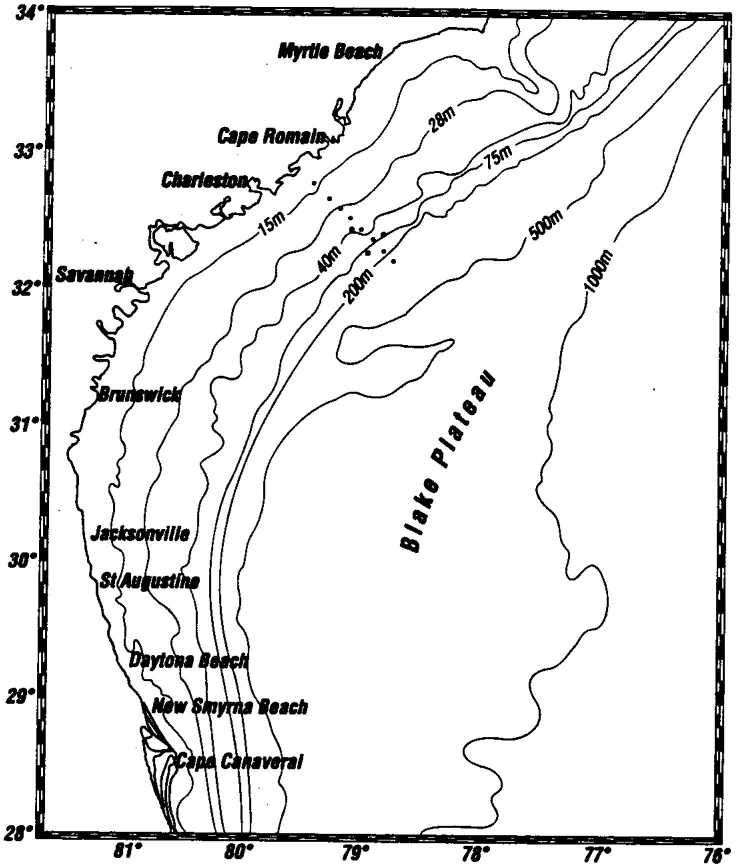

Figure 3. The continental shelf of the southeastern United States. (from Paffenhofer et al. 1995)

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 km^2 (Paffenhofer and Lee 1987). High densities of salps have been documented in this region with regularity.

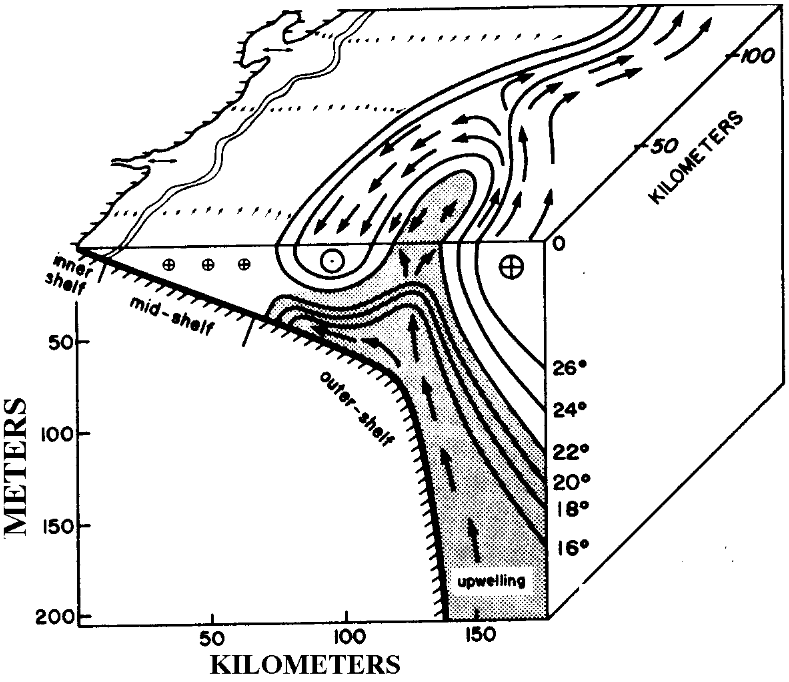

Figure 4. Schematic of a Gulf Stream frontal eddy on the shelf of the southeastern shelf of U. S. (from Lee et al 1981)

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 *Salp*a 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/m^3, with a maximum of 608 salps/m^3 (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 km^2 (Fig. 5).

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 a 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).

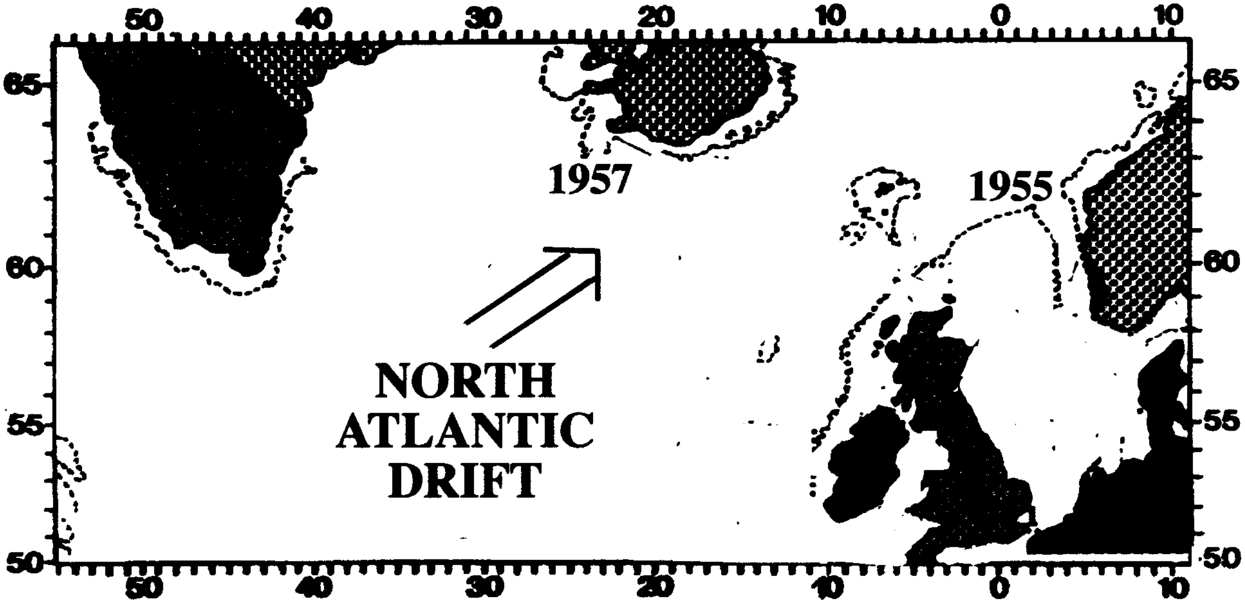

Figure 6. Map of the North Atlantic. Note the contrast in locations of swarms of *Salpa fusiformis* in 1955 and 1957, presumably due to differences in the North-Atlantic Drift.

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

Alldredge, A. L. and L. P. Madin. 1982. Pelagic tunicates: Unique herbivores in the marine plankton. Bioscience. 32:655-663.

Atkinson, L.P., G.-A. Paffenhofer, and W. M. Dunstan. 1978. The chemical and biological effect of a Gulf Stream intrusion off St. Augustine, Florida. Bull. Mar. Sci. 28(4): 667-679.

Atkinson, L. P., E. Oka, S. Y. Wu, T. J. Berger, J. O. Blanton, and T. N. Lee. 1989. Hydrographic variability of Southeastern United States shelf and slope waters during the genesis of Atlantic lows experiment: Winter 1986. J. Geophys. Res: 94:C8:10,699-10,713.

Berner, L. 1967. Distributional atlas of Thaliacea in the California Current region. Calif. coop. ocean. Fish. Invest. (CalCOFI) Atlas 8:1-322.

Binet, D. 1976. Contribution a l'ecologie de quelques taxons du zooplancton de Cote d'Ivoire. II. Dolioles - Salpes - Appendiculaires. Doc. Sc. C. R. O. Abijan. 7:45-61.

Blackburn, M. 1979. Zooplankton in an upwelling area off northwest Africa: composition, distribution and ecology. Deep-sea. Res. 26:41-56.

Blackburn, M. 1979. Thaliacea of the California current region: Relations to temperature, chlorophyll, currents, and upwelling. CalCOFI Rep. 20:184-214.

Boysen-Ennen, E., W. Hagen, G. Hubold, and U. Piatkowski. 1991. Zooplankton biomass in the ice-covered Weddell Sea, Antarctica. Mar. Biol. 111:227-235.

Braconnot, J. C., M. Etienne, M. Moite. 1990. Distribution du tunicier pelagique *Salpa fusiformis* Cuvier a Villefranche: 13 annees d'observations. Rapp. Comm. int. Mer Medit. 32:225.

Bradford, J. M. and B. E. Chapman. 1988. Epipelagic zooplankton assemblages and a warm-core eddy off East Cape, New Zealand. J. Plank. Res. 10:601-619.

Brattstrom, H. 1972. On *Salpa fusiformis* Cuvier (Thaliacea) in Norwegian coastal and offshore waters. Sarsia. 48:71-90.

Caldwell, M. C. 1966. The distribution of pelagic tunicates, family Salpidae in Antarctic and Subantarctic waters. Bull. So. Calif. Ac. Sci. 65. 15p.

Caron, D. A., L. P. Madin, and J. J. Cole. 1989. Composition and degradation of salp fecal pellets: implications for vertical flux in oceanic environments. J. Mar. Res. 47:829-850.

Casareto, B. E. and T. Nemoto. 1986. Salps of the Southern Ocean (Australian Sector) during the 1983-84 summer, with special reference to the species *Salpa thompsoni*, Foxton 1961.

Chiba, S., T. Ishimaru, G. W. Hosie, and S. W. Wright. 1999. Population structure change of *Salpa thompsoni* from austral mid-summer to autumn. Polar Biol. 22:341-349.

Clementson, L. A., G. P. Harris, F. B. Griffiths, and D. W. Rimmer. 1989. Seasonal and inter-annual variability in chemical and biological parameters in Storm Bay, Tasmania. I. Physics, chemistry and the biomass components of the food chain. Aust. J. Mar. Freshw. Res. 40:25-38.

De Decker, A. 1973. Agulhas Bank plankton. p.189-219. *In* B. Zeitschel (ed.) The Biology of the Indian Ocean. Springer, Berlin.

Deevey, G. B. and A. L. Brooks. 1971. The annual cycle in quantity and composition of the zooplankton of the Sargasso Sea off Bermuda. II. The surface to 2000m. Limnol. Oceanogr. 16:927-943.

Deibel, D. 1985. Blooms of the pelagic tunicate, *Dolioletta gegenbauri:* are they associated with Gulf Stream frontal eddies? J. Mar. Res. 43:211-236.

Fraser, J. H. 1949. Distribution of the Thaliacea (salps and doliolids) in Scottish waters, 1920-1939. Scient. Invest. Fish. Div. Scot. Home Dep. 1949. No. 1:1-44.

Fraser, J. H. 1962. The role of ctenophores and salps in zooplankton production and standing crop. Int. Coun. Explor. Sea. 153:121-123.

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

Haq. S. M., J. Ali Kahn, and S. Chugtai. 1973. The distribution and abundance of zooplankton along the Coast of Pakistan during postmonsoon and pre-monsoon periods. p.257-272. *In* B. Zeitschel (ed.) The Biology of the Indian Ocean. Springer, Berlin.

Harbison, G. R., and V. McAlister. 1979. The filter-feeding rates and particle retention efficiencies of the species of *Cyclosalpa* (Tunicata: Thaliacea). Limnol. Oceanogr. 24:517-528.

Hardy, A. C. and E. R. Gunther. 1935. The plankton of the South Georgia whaling grounds and adjacent waters 1926-1927. Discovery Reports 11:1-456.

Harris, G. P., F. B. Griffiths. L. A. Clementson, and H. Van der Doe. 1991. Seasonal and interannual variability in physical process, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. J. Plank. Res. 13:109-131.

Heron, A. C. and E.E. Benham. 1984. Individual growth rates of salps in three populations. J. Plank. Res. 6:811-828.

Hubbard, L.T. and W. G. Pearcy. 1971. Geographic distribution and relative abundance of Salpidae off the Oregon coast. J. Fish. Res. Bd. Canada. 28:1831-1836.

Humphrey, G. F. 1963. Seasonal variations in plankton pigments in waters off Sydney. Aust. J. Mar. Freshw. Res. 14:24-36.

Hunt, H. G. 1968. Continuous plankton records: contribution towards a plankton atlas of the North Atlantic and the North Sea. Part XI: The seasonal and annual distributions of Thaliacea. Bull. Mar. Ecol. 6:225-249.

Huntley, M. E., P.F. Sykes and V. Marin. 1989. Biometry and trophodynamics of *Salpa thompsoni* (Tunicata: Thaliacea) near the Antarctic Peninsula in austral summer, 1983-4. Polar Biol. 10:59-70.

Iseki, K. 1981. Particulate organic matter transport to the deep sea by salp fecal pellets. Mar. Ecol. Prog. Ser. 5:55-60.

Kashkina, A. A. 1978. Areas of concentration and abundance of salps in the Atlantic Ocean. Soviet J. Mar. Biol. 4(3):643-648.

Kashkina, A. A. 1986. Feeding of fishes on salps (Tunicata, Thaliacea). J. Ichthyol. 26:57-64.

Kremer, P. and L. P. Madin. 1992. Particle retention efficiency of salps. J. Plank. Res. 14:1009-1015.

Krishnapillai, S., and G. Subramonia Bhat. 1981. Note on the abundance of zooplankton and trawler catch during the postmonsoon months along the northwest coast of India. J. Mar. Biol. Ass. India. 23:208-214.

Lazarus, B. I. and D. Dowler. 1979. Pelagic tunicata off the west and south-west coasts of South Africa, 1964-1965. Fish. Bull. S. Afr. 12:93-119.

Le Borgne, R. 1983. Note sur les proliferations de Thaliaces dans le Golfe de Guinee. Oceanogr. Trop. 18:49-54.

Lee, T. N. and L. P. Atkinson. 1983. Low frequency current and temperature variability from Gulf Stream frontal eddies and atmospheric forcing along the Southeast U. S. outer continental shelf. J. Geophys. Res. 88: C8: 4541-4567.

Lee, T. N., L. P. Atkinson, and R. Legeckis. 1981. Observations of a Gulf Stream frontal eddy on the Georgia continental shelf, April 1977. Deep-Sea Research. 28A: 347-378.

Lodh, N. M. , S. N. Gajbhiye and V. R. Nair. 1988. Unusual congregation of salps off Veraval and Bombay, west coast of India. Ind. J. Mar. Sci. 17:128-130.

Mackintosh, N. A. 1934. Distribution of the macroplankton in the Atlantic sector of the Antarctic. Discovery Reports 9:65-160.

Madhupratap, M., V. P. Devassy, A. R. Sreekumaran Nair, and T. S. S. Rao. 1979. Swarming of pelagic tunicates associated with phytoplankton bloom in the Bay of Bengal.

Madin, L. P. 1982. Production, composition and sedimentation of salp pellets in oceanic waters. Mar. Biol. 67L:39-45.

Madin, L.P. and Deibel, D. 1998. Feeding and energetics of Thaliaceans. pp. 43-60. *In* The Biology of Pelagic Tunicates. Q. Bone (ed.). Oxford University Press, Oxford, England.

Madin, L. P. and J. E. Purcell. 1992. Feeding, metabolism and growth of *Cyclosalps bakeri* in the Subarctic Pacific. Limnol. Oceanogr. 37:1236-1251.

Madin, L. P., C. M. Cetta and V. L. McAlister. 1981. Elemental and biochemical composition of salps (Tunicata: Thaliacea). Mar. Biol. 63:217-226

Madin, L. P., P. Kremer, J.E. Purcell, and D. A. Nemazie. 1994. Vertical migration of a large *Salpa aspera* population in the North Atlantic slope water. EOS 75:90 (abstract).

Mansueda, H., N. Handa, I. Inoue and H. Takano. 1986. Ecological significance of salp fecal pellets collected by sediment traps in the eastern North Pacific. Mar. Biol. 91:421-431.

Menard, F., S. Dallot, G. Thomas, J. C. Branconnot. 1994. Temporal fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. Mar. Ecol. Prog. Ser. 104:139-152.

Menon, K. S. 1931. A preliminary account of the Madras plankton. Rec. Ind. Mus. vol. 33.

Mianzan, H., M. Pajaro, G. Alvarez Colombo, and A. Madirolas. Feeding on survival-food: gelatinous plankton as a source of food for anchovies. Hydrobiol. 451:45-53.

Michel, A., C. Colin, R. Desrosieres et C. Oudot. 1971. Observations sur l'hydrologie et le plancton des abords et de la zone des passes de l'Atoll de Rangiroa (Archipel des Tuamotu, Ocean Pacific Central). Cah. O.R.S.T.O.M., Ser. Oceanogr. 9(3):375-402.

Mohan, R. L. L. 1965. On a swarm of salps, *Pegea confoederata* (Forskal), from the Gujarat coast. J. Mar. Biol. Ass, India. 7:201-202.

Moore, H. B. 1949. The zooplankton of the upper waters of the Bermuda area of the North Atlantic. Bull. Bingham Oceanogr. Coll. 12(2):1-97.

Mullin, M. M. 1983. *In situ* measurement of filtering rates of the salp, *Thalia democratica,* on phytoplankton and bacteria. J. Plank. Res. 5:279-288.

Murray, J. and J. Hjort. 1912. *Atlanterhavet.* Aschehoug & Co. Kristiania. 595 pp.

Nagabhushanam, A. K. 1960. Observations on some pelagic tunicates in coastal water of the Bay of Bengal. J. Mar. Biol. Ass. India. 2:263.

Nair, R. V. 1949. The Thaliacea of the Madras plankton. Bull. Madras Gov. Mus. Nat. Hist Section. 6(1).

Nishikawa, J., M. Naganobu, T. Ichii, H. Ishii, M. Terazaki, and K. Kawaguchi. 1995. Distribution of salps near the South Shetland Islands during austral summer, 1990-91 with special reference to krill distribution. Polar Biol. 15:31-39.

Paffenhofer, G. -A., and T. N. Lee. 1987. Development and persistence of patches of Thaliacea. S. Afr. J. mar. Sci. 5:305-318.

Paffenhofer, G. -A, L. P. Atkinson, T. N. Lee, P. G. Verity and L. R. Bulluck. 1995, Distribution and abundance of thaliaceans and copepods off the southeastern U.S.A. during winter. Cont. Shelf. Res. 15:255-280.

Pakhomov, E. A., R. Perissinotto, and C. D. McQuaid. 1994. Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. Mar. Ecol. Prog. Ser. 111:155-169.

Perissinotto, R. and E. A. Pakhomov. 1998. Contribution of salps to carbon flux of marginal ice zone of the Lazarev Sea, Southern Ocean. Mar. Biol. 131:25-32.

Ryan, J. P., J. A. Yoder, P. C. Cornillon. 1999. Enhanced chlorophyll at the shelfbreak of the Mid-Atlantic Bight and Georges Bank during the spring transition. Limnol. Oceanogr. 44:1-11.

Sars, M. 1846. Beobachtungen uber die Organisation der Entwickelung der Salpen. Fauna littoralis Norwegiae. 1:63-85.

Sewell, S. R. B. 1926. The salps of Indian Seas. Rec. Ind. Mus. 28(2):65-126.

Sewell, S. R. B. 1953. The pelagic tunicates. Juhn Murray Expedition 1933-34, Scientific Rep. Brit. Mus. Nat. Hist. 10:90p.

Siegel, V. and V. Loeb. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. Mar. Ecol. Prog. Ser. 123:45-56.

Tavares, D. Q. 1967. Occurrence of doliolids and salps during 1958, 1959, and 1960 off the Sao Paulo coast. Bolm. Inst. oceanogr. S. Paulo. 16(1):87-97.

Tokioka, T. 1937. Notes on salps and doliolums occurring on the Pacific coast of middle Japan. Annot. Zool. Japan. 16(3):219-235.

Tokioka, T. and P. B. Bhavanarayana. 1979. Notes on the occurrence of a swarm of *Salpa cylindrica* Cuvier (Tunicata: Salpidae) in Sardinera Lagoon, Puerto Rico. Proc. Biol. Soc. Wash. 92:572-576.

Tranter, D. J. 1962. Zooplankton abundance in Australasian waters. Aust. J. Mar. Freshw. Res. 13:106-142.

Tsuda, A. and T. Nemoto. 1992. Distribution and growth of salps in a Kuroshio warm-core ring during summer 1987. Deep-sea Res. 39(suppl.1):S219-S229.

Van Soest, R. W. M. 1975. Thaliacea of the Bermuda area. Bull. Zool. Museum. Univ. Amsterdam. 5(2).

Van Zyl, R. P. 1960. A preliminary study of the salps and doliolids off the west and south coasts of South Africa. Investigational Rept. Div. Fisheries, Union of South Africa. v.40, 31p.

Wear, R. G. 1965. Zooplankton of Wellington Harbour, New Zealand. Zool. Publ. Victoria,Univ. Wellington. 38. 31pp.

Wiebe, P. H., L. P. Madin, L. R. Haury, G. R. Harbison and L. M. Philbin. 1979. Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate matter transport to the deep sea. Mar. Biol. 53:249-255.

Yount, J. L. 1958. Distribution and ecologic aspects of Central Pacific Salpidae (Tunicata). Pac. Sci. 12:111-130.

Zeldis, J. R., C. S. Davis, M. R. James, S.L. Ballara, W. E. Booth, and F. H. Chang. 1995. Salp grazing: effects on phytoplankton abundance, vertical distribution and taxonomic composition in a coastal habitat. Mar. Ecol. Prog. Ser. 126:267-283.