Breeding and larval distribution of the pteropod *Clione limacina* in the North Atlantic, Subarctic and North Pacific Oceans

S. A. Mileikovsky

Institute of Oceanology of the Academy of Sciences of USSR, Moscow, USSR

**Abstract**

The pteropod *Clione limacina* (Phipps, 1774) is an arctic-boreal, circumpolar species, which is widely distributed in the North Atlantic and Subarctic Oceans; it also occurs in the North Pacific Ocean (in the Oyashio and neighbouring waters) and along the Atlantic coast of North America in the waters of the cold Labrador current to the Cape Hatteras region (35° N). The distribution of *C. limacina* larvae in the plankton of the Norwegian, Barents and White Seas, the Bear Island-Spitsbergen region of the Greenland Sea, the Newfoundland Grand Bank and the Flemish Cap Bank region of the North-western Atlantic Ocean, and the Kurile-Kamchatka region of the North-western Pacific Ocean has been studied, and information from literature concerning the reproduction and larval occurrence of the species is summarized. Throughout its distributional area, spawning of *C. limacina* is characterized by the same general ecological pattern. This species breeds and spawns in all types of water masses occurring within the vertical range which it commonly inhabits — from surface layers to 500 m water depth. In all local populations of the species, the most intensive spawning is correlated with the spring/summer period of annual heating of the local waters, and the highest abundance parallels maximum growth of phytoplankton which serves as food for veligers and early polytrochous larvae. After the end of this period, spawning intensity in all local *C. limacina* populations declines sharply, but spawning continues at low intensity during the autumn/winter season, being practically continuous throughout the year. Distribution patterns of *C. limacina* larvae are determined by those of their parental forms (the parental forms spawn in the zones permanently inhabited). The earliest larval stages of *C. limacina* (veligers) are present predominately in the upper 100 or 200 m water layer, i.e. in the zone of high phytoplankton abundance. Polytrochous larvae, after becoming predaceous feeders, are distributed throughout the whole water column from the surface to 500 m depth, similar to adult *C. limacina*. As with the adults, larvae are present (within the species’ distribution area) in all types of water masses. Since the beginning of the twentieth century, in the course of the warming of the Arctic Ocean, the southern race of *C. limacina* (formerly a summer/autumn seasonal invader in the Norwegian Sea) has become a permanent component of the plankton fauna of the Norwegian and Barents Seas in regions influenced by the Norwegian-Northcape Current System.

**Introduction**

Despite the fact that the pteropod *Clione limacina* (Phipps, 1774) is mentioned in practically all text books on invertebrate zoology, and in very many popular scientific books about life in the sea, the biology of this species, which is a very common holo-plankter (the “sea angel”), has, up to date, been incompletely studied.

Even the systematic status of this species, its zoogeographical origin, and the characteristics of its geographical distribution, can no longer be considered as settled. In the Soviet and pre-revolution Russian literature on marine biology and planktonology, *Clione limacina* is described as a widely distributed Arctic and Atlantic arctic-boreal, circumpolar species (Linko, 1913; Mankiewicz, 1937; Jaschnow, 1948), or as a typical cold-water or arctic form (Derugin, 1915; Zenkevitch, 1947, 1963) which also inhabits the Antarctic (Kisselev, 1969) and the deep waters of the Sargasso Sea (Zenkevitch, 1951). On the basis of all these data, *C. limacina* can be characterized as a bi-polar species with cosmopolitan distribution in cold and temperate waters. Such characteristic of the species was adopted in the author’s early papers (Mileikovsky, 1958, 1960a, 1962a).

The above-named authors do not, however, report on the systematics of Pteropoda. Those authors who do examine the problem do not provide conclusive evidence. Massy (1932) and Tesch (1950) write that there is some doubt as to the taxonomic validity of the Antarctic “species” *Clione antarctica* E. A. Smith, 1902, and that, probably, this form is only a variety of the species *Clione limacina* (Phipps, 1774); neither author, however, reached a final conclusion on this problem. There is also no definite conclusion (only a discussion, Tesch, 1950) on the taxonomic position of the problematic species *Clione minuta* Pruvot, 1929, found within the North Atlantic and North Pacific parts of the distribution area of *C. limacina* — whether it is a separate species, or whether it is synonymous with *C. limacina* (Phipps, 1774).

Summarizing the data of authors dealing especially with the systematics of Pteropoda, or with the biology of *Clione limacina* (Lebour, 1931; Massy, 1932; Tesch, 1950; Morton, 1958; Kramp, 1961), it can be concluded that *C. limacina sensu stricta* is an arctic-boreal, circumpolar species, which is widely distributed in the North Atlantic and Arctic Oceans, and present in the North Pacific Ocean, which is transported along the Atlantic coast of North America to the region of...
Cape Hatteras (35° N) by the waters of the cold Labrador Current. Within this range of distribution the species will be discussed in this paper. The populations most studied are those which inhabit the open oceanic waters and the Atlantic and Subarctic Seas. In various separate regions of this area, the distribution of *Clione limacina*, its seasonal occurrence, and its annual fluctuations have been studied from year to year (Boas, 1886; Meinert-Thieme, 1905; Damas and Kofoed, 1905; Linke, 1907, 1913; Massy, 1909; Paulsen, 1909; De Ryugin, 1915, 1928; Wirketiss, 1926; Chmyznikova, 1931; Lebour, 1931; Thorson, 1936; Mantefel, 1937; Lemche, 1938; Jaschnov, 1948; Tesch, 1950; Morton, 1958; Glover et al., 1961; Kram, 1961; Vane and Colebrook, 1962). The complete cycle of the larval development of the species has also been studied in these waters (M'Intosh, 1898; Lebour, 1931; Mileikovsky, 1958, 1962a). For these aquatories, data have been summarized characterizing, distinctively, general biology, life-cycle, feeding and behavior, not only of local populations of *C. limacina* but, also, of the species as a whole (Lebour, 1931; Mantefel, 1937; Morton, 1958; and others). For the North Pacific populations of the species, however, such data are practically absent in the literature.

Information on the breeding and spawning ecology of *Clione limacina* is even poorer, despite the fact that the reproductive seasons and periods of larval occurrence in various regions of the North-east Atlantic and Subarctic areas of its distributional range have received far more attention (Boas, 1886; M'Intosh, 1898; Damas and Kofoed, 1905; Paulsen, 1909; Wirketiss, 1926; Lebour, 1931; Thorson, 1936; Mileikovsky, 1958, 1960a, 1962a; Morton, 1958; and others) than those of 2 other common pteropods of the area: the cold-water *Limacina helicina* Phipps and the temperate-water *L. retroversa* Fleming (Lebour, 1932; Hsiao, 1939; Redfield, 1939; Mileikovsky, 1958, 1960a, 1962a; Paranjape, 1968; and others) on which *C. limacina* herds permanently in the cold and temperate-water regions of its range (Paulsen, 1909; Lebour, 1931; Mantefel, 1937; Morton, 1958; Glover et al., 1961; Vane and Colebrook, 1962; and others). All these data have been collected from totally different and widely separate regions and have not yet been summarized as a whole.

The author has studied the reproduction and larval development of *Clione limacina* in the Kandalaksha Bay of the western White Sea (Mileikovsky, 1958, 1960a, 1961a, 1962a) and, in the course of further work with plankton samples from the Barents and Norwegian Seas, the Bear Island-Spitsbergen region of the Greenland Sea (Mileikovsky, 1960b, 1961b, 1962b, 1965, 1966, 1968a, b), the Newfoundland shallows of the Northwestern Atlantic (Mileikovsky, 1965), and the Kurile-Kamchatka region of the North-western Pacific (Mileikovsky, 1968a, 1969, 1970a); he has collected data which, added to those from the White Sea, characterize the reproductive ecology and larval distribution of *Clione limacina* within the largest part of its distributional area.

On the basis of these data, and a summarizing of the literature data available, the present paper will attempt to analyze the reproductive ecology of *Clione limacina* and its larval distribution patterns for the whole distribution range of the species.

**Material and methods**

This paper is based on the results of the author's work with samples of plankton from the following areas:

1. The region of the White Sea Biological Station of Moscow State University, on the Velikaya Salma Sound of the Kandalaksha Bay of the White Sea, collected by the author in June to September, 1957.

2. The whole area of the Norwegian Sea, including the Faroe-Shetland region, the Bear Island-Spitsbergen region of the Greenland Sea, and the whole southern part of the Barents Sea, collected during the 16 cruises of various research vessels of the Polar Research Institute of Marine Fisheries and Oceanography, in Murmansk, in 1958 to 1960.


From the Velikaya Salma Sound, 63 quantitative samples of plankton were examined from one restricted region. Samples were collected from the 0 to 8 m, and 8 to 16 m water layers by Juday net (No. 43 silk, 0.1 m² entrance diameter).

From the Norwegian, Greenland and Barents Seas, 3,803 quantitative samples were examined from 1,481 stations, collected from standard horizons (0 — 25 m, 25 — 50 m, 50 — 100 m, 100 — 200 m, 200 — 500 m, 0 — 50 m, 50 — 100 m, 100 or 200 m bottom, where the depth was less than 500 or 300 m) by Juday net (No. 38 silk, 0.1 m² entrance diameter), by Nansen and, rarely, by Hensen nets (No. 23 silk, having the largest mesh size from all three: 0.2 m²).

From the Newfoundland region, 202 quantitative samples were examined from 67 stations, collected by Juday net (No. 38 silk, 0.1 m² entrance diameter). From the Kurile-Kamchatka region, 33 samples were examined from 3 deep-sea stations, collected on 2 of them with the Juday net oceanic model — JOM (No. 38 silk, 0.5 m² entrance diameter) and on 1 with the Bogorov-Rass net (No. 140 mesh with larger mesh size: 1.0 m²).

Full details of all these samples are given in Mileikovsky (1968a, 1969, 1970a). All samples were examined thoroughly.