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MICHAEL GRAHAM'S BAY OF FUNDY *SAGITTA* PATCH REVISITED; ARE THERE "STOCKS" OF ZOOPLANKTON ANIMALS?

by

T. D. Iles
Department of Environment
Fisheries and Marine Service
Biological Station, St. Andrews, New Brunswick
Canada EOG 2XO

INTRODUCTION

Michael Graham was a visiting scientist at the St. Andrews Biological Station between September 1931 and November 1932. He carried out an investigation of the herring of Passamaquoddy and adjacent region, the site of a weir fishery for juvenile ("sardine") herring which was one of the oldest, large-scale fisheries in eastern Canada (Graham 1936; Iles 1975a - this meeting). Graham surveyed the Bay of Fundy and adjacent waters for larval herring over the period December 1931 to September 1932, using a Petersen net with an 1/30-in mesh size (lumen about 0.7 sq. mm) fished obliquely from the bottom to the surface. While valuable observations on the distribution of larval herring were made, of more immediate interest are the references by Graham to the occurrence and distribution of ctenophores and of *Sagitta* in the Bay of Fundy area. These were found throughout the survey period, i.e., almost throughout the year, and they occupied what appeared to

Graham as characteristic, and distinct and different areas. That for ctenophores was localized in the Digby Neck-St. Mary's Bay-Cape St. Mary area; that for *Sagitta* lay off Digby, further in the Bay of Fundy, and extended across the Bay towards Saint John. Figures 1 and 2 illustrate Graham's results, taken from his figures 11 and 12 (Graham 1936, pages 117 and 118). The apparent persistence of these populations over the year in these more or less distinct and separate areas led Graham to suggest that absence of water circulation was the readiest explanation, but he realized that this was by no means the only possible one.

Since 1969 the Bay of Fundy area has been surveyed regularly to determine the distribution and abundance of herring larvae (Iles 1971: Stobo and Iles 1973). In the initial surveys in 1969 and 1971, an Isaacs-Kidd trawl with small-mesh lining was used; from 1972 onwards, paired Bongo nets (505 and 333 μ mesh size) were used and both the area covered and the intensity of coverage were increased. Over the whole period, however, sampling was designed to cover as much of the water column as possible.

RESULTS

Some of the results of the analysis of zooplankton samples taken over the period 1969-1974 are shown in Fig. 3-6 as distributional maps for ctenophores (*Pleurobrachia* sp.), *Sagitta (elegans)* and the general categories of "euphausids" and "copepods". Those for *E. E. PRINCE* cruises 57 and 58 (October and November 1969) are derived from counts of individuals from station samples or sub-samples and converted into numbers per square metre surface. Those for *E. E. PRINCE* cruise 145 were obtained from formalin wet weights for the total zooplankton, and visual estimates of proportions of the different categories for each sample. For the euphausids a more detailed analysis was also made, including breakdown by species and the incorporation of data from a larger number of cruises. This is reported on elsewhere (Kulka and Iles 1975, this meeting).

For both *Sagitta* and Ctenophores the distribution found by Graham in 1931 and 1932 conforms to that found in the late 1960's and early 1970's. That of *Sagitta* (Fig. 4) lies very largely within an area extending from Digby Neck, along the Nova Scotia coast past the Annapolis Basin, and across the Bay of Fundy to the New Brunswick side. There are indications that there are year-to-year differences in the area of concentration, but there is little overlap with the area of distribution for ctenophores. The results shown in Fig. 5 for ctenophores confirm that the Digby Neck-St. Mary's Bay area is an area of distribution but indicate that it can extend farther south on the southwest Nova Scotia shelf.

Both the localization and persistence of these populations found by Graham on a seasonal basis appear to be continued over a time period of years that must cover a large number of generations of the animals concerned. For *Sagitta elegans*, for instance, Sameoto (1971) lists estimates of generation time for a St. Margaret's Bay, Nova Scotia population of from 91 to 206 days.

In addition, it appears that characteristic local distributions of populations of other zooplankton species occur in the area. That for euphausids involves two sympatric species, *Meganyctiphanes norvegica*, and *Thysanoessa inermis*, with an area of winter concentration in the Grand Manan basin, and seasonal movements from this centre (Kulka and Iles, this meeting). There is a high degree of overlap in distribution throughout the year for the two species. Two fall-spawning herring stocks occur in the area, one off southwest Grand Manan and one off the Nova Scotia coast in the Yarmouth area. In the fall, certainly, the larval populations from these spawning stocks occupy largely different and characteristic areas and, even after the overwintering period, it appears likely that physical mixing of the products of spawning between the two groups is not at a high level (see Fig. 1 from Stobo and Iles 1973; Iles 1975, this meeting). There are indications from material collected from these plankton cruises and not reported on here that the distribution of other zooplankton species in this area is localized, characteristic, and persistent. This material includes mysids, amphipods and pelagic gasteropod snails, all of which appear to be shallow-water forms with a near-shore distribution.

It will be remembered that the "obvious" explanation drawn by Graham was that there was little water circulation in the area. This, of course, cannot be true as Graham suspected. The Bay of Fundy is extremely energetic hydrographically, arguably one of the most turbulent bodies of water in the world and, besides very strong tidal forces, there are well marked, residual, non-tidal patterns (Hachey and Bailey 1952). It has been suggested that the distribution of larval herring in the Bay of Fundy is the result of the interaction of behavioural factors and these water movements - a process of transport and retention (Iles 1975b, this meeting). It can now be suggested that the maintenance of characteristic distributional areas for the other species is another aspect of the phenomenon of retention.

Vertical movement and distribution of zooplankton populations

For herring it has been demonstrated by Graham (1972) (not incidentally, the same Graham') that retention of a herring larval population within an estuary, despite tidal flow and a net seaward residual flow, is achieved by adjusting larval depth during the tidal cycle to take advantage of differential flow rates at ebb and flood. This involves depth selection in relation to differential flow in the water column to maintain position. The well known Hardy hypothesis (Hardy and Gunther 1935), of course, maintains that an analagous behavioural mechanism can result in net horizontal transport of zooplankton in the open sea. Iles (1971, 1975b, this meeting) maintained that the characteristic distribution of larval herring in the Bay of Fundy and southwest Nova Scotia resulted from depth selection in both the transport phase and the retention phase, and this is now extended to account for the distribution of other zooplankton species in the area. This carries the implication that each species has its own characteristic vertical behavioural pattern interacting in its own way with features of the hydrographic system of the area to result in the final distinctive distribution.

Biological status of the populations

It is a reasonable inference that at least some of these zooplankton populations are "local" and "persistent". The question then arises whether they are also "self-replicating", whether the life history can be, or is, completed within the Bay of Fundy itself or whether recruitment from outside the area is regular enough and at a sufficiently high level to prevent the setting up of genetic isolation. For the euphausid species *M. norvegica* and *T. inermis* it is known that reproduction takes place in the Bay of Fundy and that both larval and juvenile stages are found in a spatial pattern that suggests a "closed" life-history cycle (Kulka and Iles 1975, this meeting).

For *Sagitta* and ctenophores there is no direct evidence one way or another as yet. Sameoto (1971) detected incursion of *Sagitta* from outside St. Margaret's Bay by analysis of length-frequency data, suggesting that the question is amenable to relatively simple testing in the Bay of Fundy area by a similar analysis.

It is possible however to indicate the type of biological interaction that occurs between the various elements of the zooplankton fauna in the area and between the zooplankton and, particularly, some important components of the fish fauna.

It is well known that both ctenophores and *Sagitta* are predators of larval fish, including herring (Bigelow 1926). The areas of concentration of both these predators is within the boundaries of the distribution of larvae produced by the

Nova Scotia herring stock. That of the ctenophores includes part of the spawning area itself and extends along the relatively narrow corridor on the Bay of Fundy side of Digby Neck through which larvae pass from the spawning ground to the Bay of Fundy section of the retention area (Iles 1975b, this meeting). *Sagitta* is not found in numbers on the spawning ground or along the "transport corridor" but occurs in greatest numbers inside the Bay of Fundy. This is, perhaps, an example of exclusion on the part of two species each taking the same prey organism.

The euphausid distribution, certainly over the winter period, does not overlap to any degree with that of the herring larval population. On the other hand, euphausids are preyed on by herring, by adults in the fall, which have moved across the Bay from the Nova Scotia spawning ground, and, by juveniles in the summer in the general Passamaquoddy area.

It does not seem very likely that the combined patterns of distribution, seasonal movements and biological relationships can be accounted for by the action of purely physical factors on passively drifting, inert organisms. Rather, the high degree of structure shown in the Bay of Fundy macrozooplankton argues for a well integrated and ecologically balanced system, resulting from subtle and sophisticated adaptations. The analysis of this Bay of Fundy ecosystem in detail should contribute greatly to our knowledge of marine ecology.

SUMMARY

The late Michael Graham spent over a year at the St. Andrews Biological Station in 1928 and 1929, studying the juvenile herring fisheries of the area in relation to a proposed power dam scheme for Passamoquoddy Bay. One typical Graham excursion into a related field, one that demonstrates the breadth of his knowledge and interest and the questing nature of his approach to marine science, can now be discussed in a wider biological context.

Graham recorded the existence of concentrations of *Sagitta (elegans)* and of ctenophores in the Bay of Fundy, whose location was both specific and persistent. This he recognized as a phenomenon of great interest but which could not at the time be explained, although he suggested possibilities and drew implications. The Bay of Fundy area has been surveyed regularly since 1969 by the St. Andrews Biological Station to determine herring larval distribution and abundance. The surveys have covered a grid of closely set stations and the phenomenon described by Graham has been confirmed as to its occurrence, and in finer detail. In the light of improved knowledge of hydrographic conditions in the area and other biological information, it is possible to suggest that these concentrations can be described as "local, persistent, self-replicating, biological units at the infraspecific level". Their existence, and that of similar ones of other zooplankton species in the Bay of Fundy area, suggests a picture of a complex ecological structure of zooplankton units related to specific hydrographic features. A more detailed study of one of these units is submitted as another communication to this meeting.

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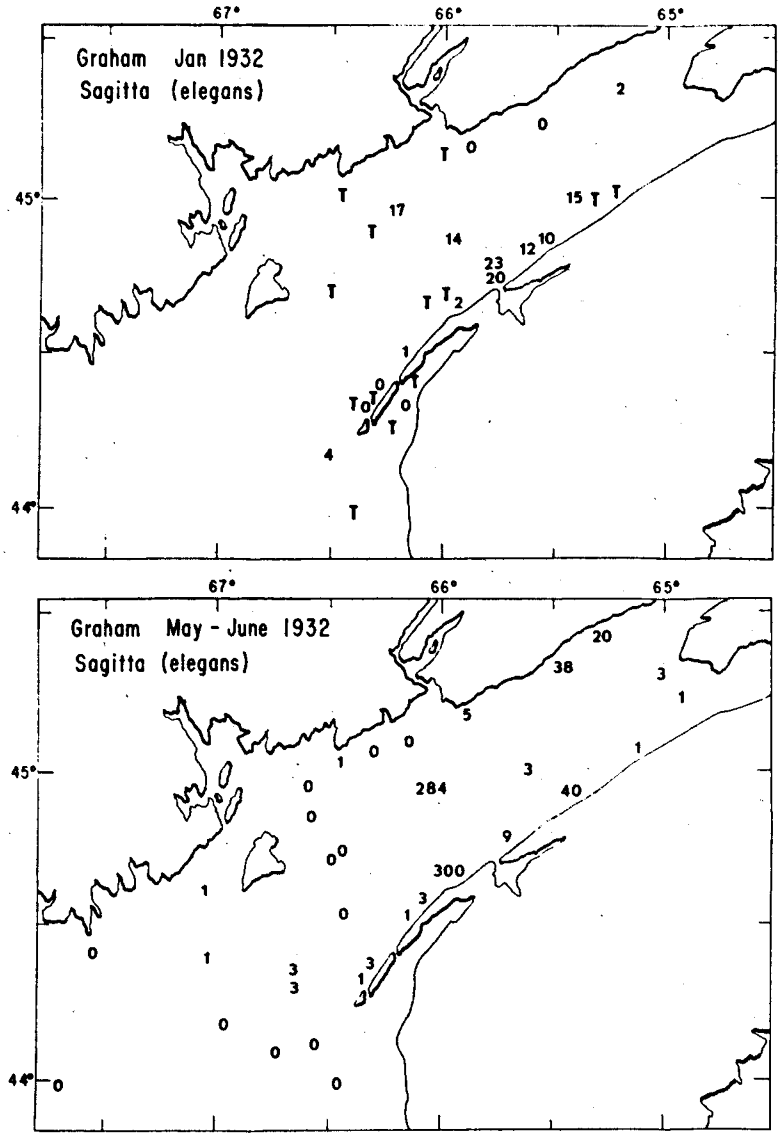

Figure 1. Bay of Fundy distribution of *Sagitta*, 1932 as shown by Graham 1936 (estimated by Graham in volume units/standard tow).

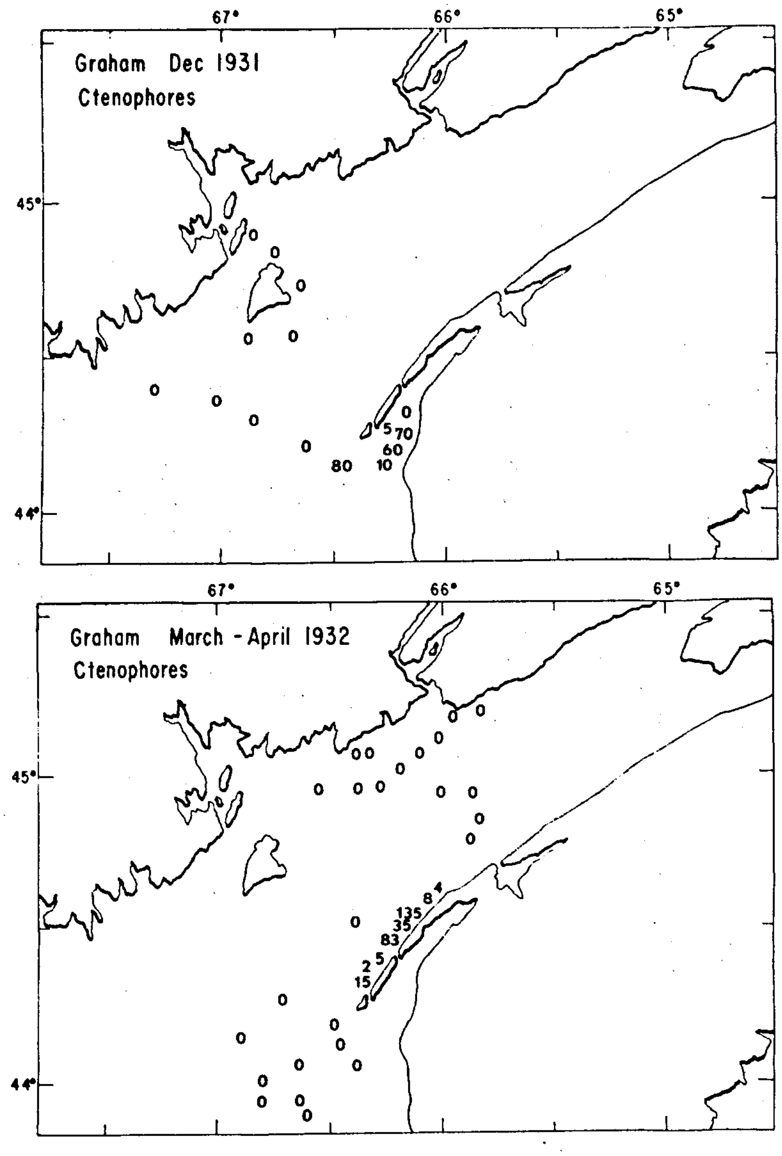

Figure 2. Bay of Fundy distribution of ctenophores, 1931 and 1932 (Graham 1936).

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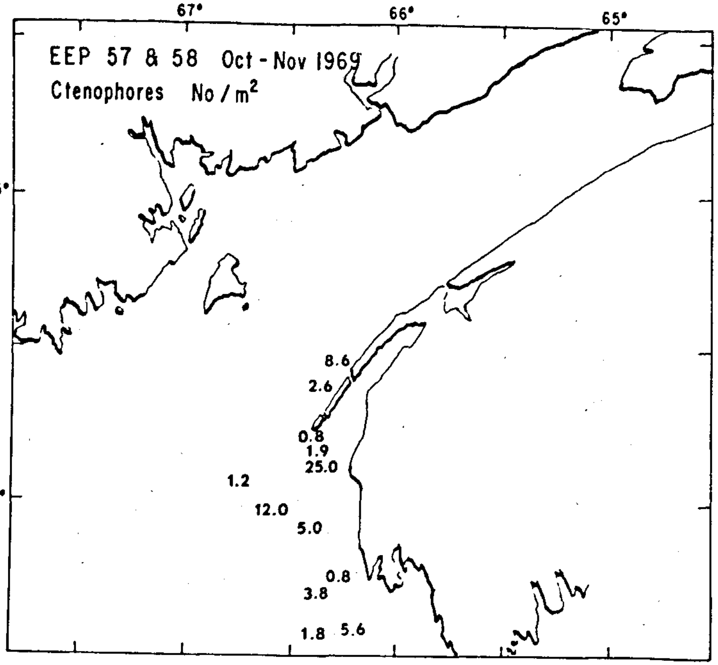

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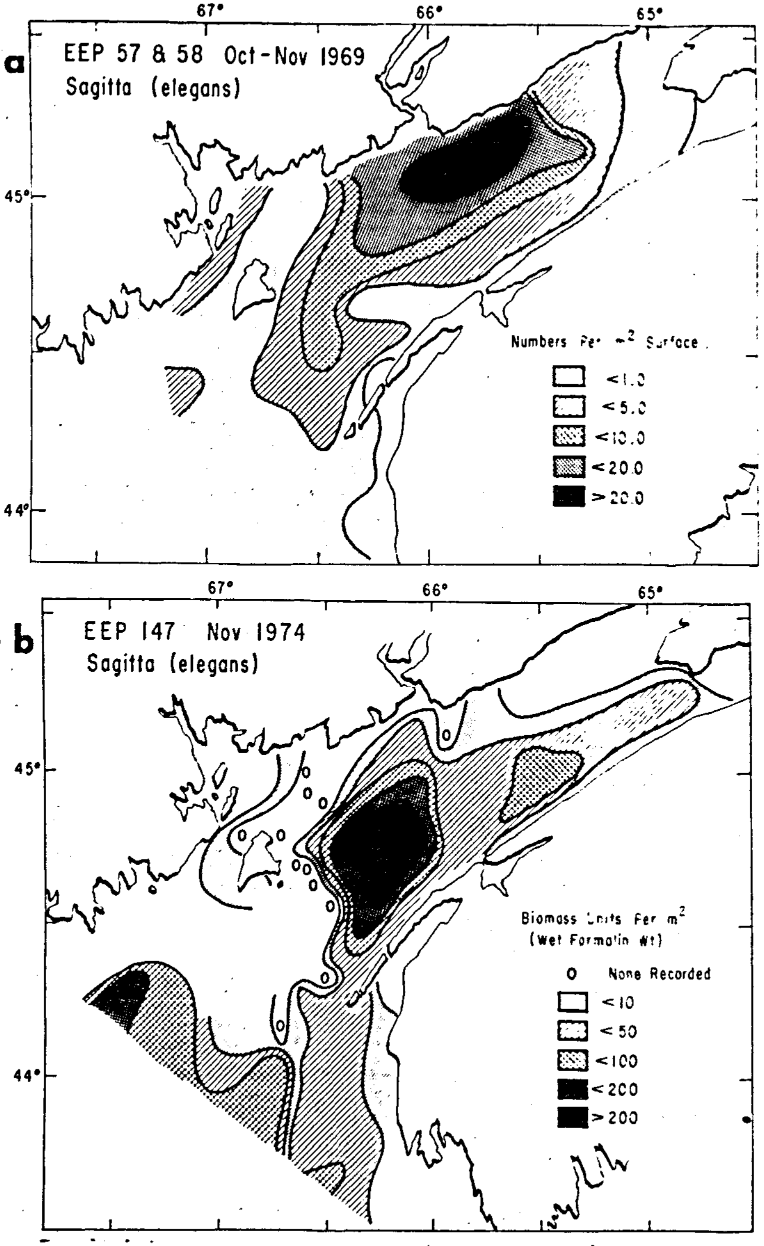

Figure 3. Bay of Fundy distribution of ctenophores October-November, 1969.

Figure 4. Bay of Fundy distribution of *Sagitta*
(a) October-November 1969
(b) November 1974

Figure 5. Bay of Fundy distribution of euphausids October-November 1969.

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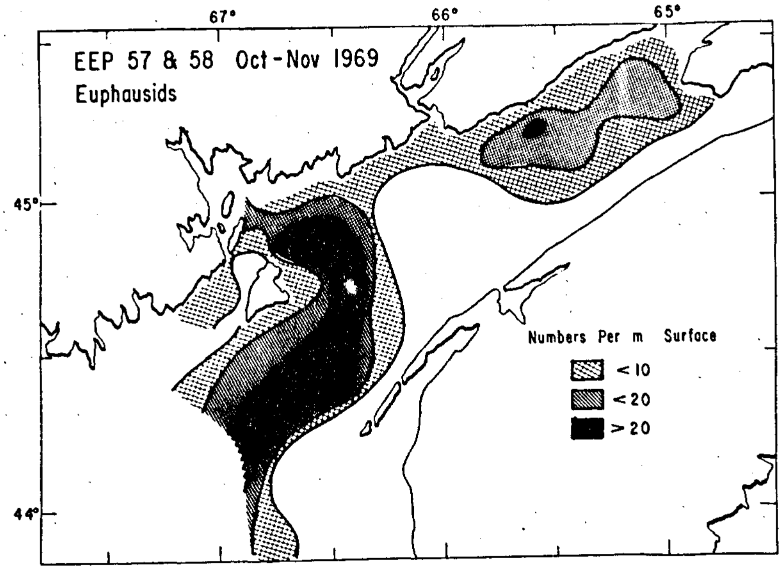

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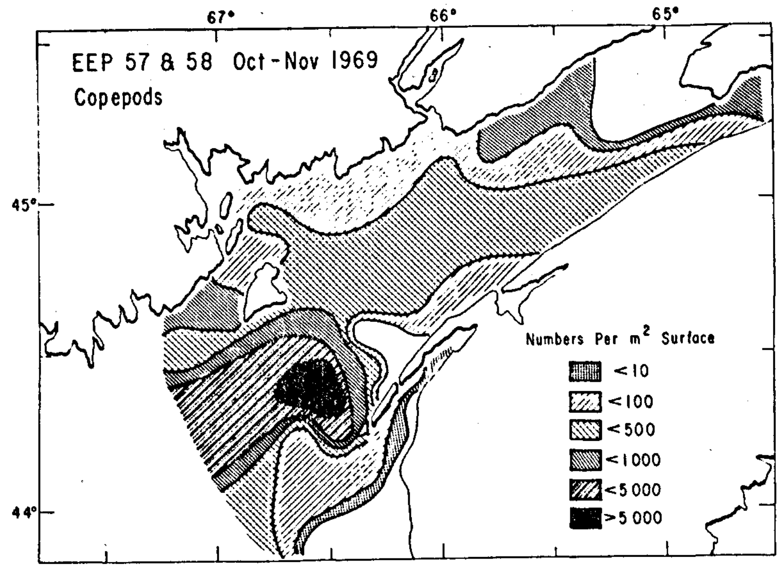

Figure 6. Bay of Fundy distribution of copepods October-November 1969.