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Ph.D. Thesis

Shortened binder title,

On the biology of a copepod, Anomalocera opalus

Studies on a member of the pleuston, *Anomalocera opalus* n.s. (Crustacea, Copepoda), in the Gulf of St. Lawrence.

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Abstract

Life cycle and behaviour studies were made from 1966 to 1969 on the pontellid copepod (formerly Anomalocera patersoni) in the Gulf of St. Lawrence. A new species, A. opalus, is proposed on the basis of morphological differences between specimens from the eastern and western North Atlantic. The distribution of this species in the Gulf of St. Lawrence is discussed and naupliar stages are described in detail. Notes are given for the identification of copepodites. The suggestion is made that A. opalus may overwinter as a resting egg.

A new morphological structure for surface attachment is described which, with observed behaviour, supports the classification of A. opalus as a pleuston copepod. A new pigment system is described with speculation on its use. Two other pigment systems are discussed. Notes are given on other species found at the surface interface in the Gulf of St. Lawrence.

Sommaire

Des études sur le cycle vital et le comportement d'un copépode pontellide, (auparavant Anomalocera patersoni) ont été fait dans le Golfe du Saint-Laurent. Une nouvelle espèce, A. opalus, est proposé sur la base des différences morphologiques entre des spécimens provenant de l'Atlantique nord-est et nord-ouest respectivement. La distribution de cette espèce dans le Golfe du Saint-Laurent est discutée et les stages de développement (nauplius 1-6) sont décrits en détail. Des critères sont fournis pour l'identification des stages copépodites (I-V). Il est suggéré que A. opalus survit en hiver sous forme d'une spore.

Une nouvelle structure morphologique est décrite laquelle, quand on considère le comportement observé, supporte la classification de A. opalus en-tant que copépode du pleuston. Un nouveau système de pigmentation est décrit et son rôle discuté. Deux autres systèmes de pigmentation sont également étudiés. Quelques autres espèces, qui sont trouvés dans les eaux de surface du Golfe, sont aussi étudiées.

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Introduction

The initial purpose of this study was to determine as much as possible about the life of the pontellid copepod, *Anomalocera patersoni*, in the Gulf of St. Lawrence. There was to be an emphasis on *Anomalocera's* life cycle and its relationships with the special class of surface life known as pleuston. When the study began it was uncertain that there was a significant development of pleuston in the Gulf of St. Lawrence, and it was not clear whether *Anomalocera* maintained itself in the Gulf as a true breeding population or was instead swept in from outside the Gulf as a summer immigrant. The former alternative was found to be the case (Section VI), and it was also found that *Anomalocera* lives in a very close relation to the surface interface and is therefore a pleuston animal. The first section of this work is a general review of the pleuston environment and life, and includes a discussion of latitudinal variation of the marine pleuston. The life cycle is discussed in Section VI.

To study the life cycle, extensive plankton collections were made over three years in different parts of the Gulf of St. Lawrence. During the spring, summer and fall of each year samples were taken roughly each week from shore stations; these were augmented by a number of cruises over the Gulf on ships chartered by the Marine Sciences Centre or by the

Fisheries Research Board. Three winter cruises were made on icebreakers. It was hoped initially that Anomalocera's life cycle would take the form of several relatively well defined generations which would make a number of population determinations possible, and allow interesting comparisons of a pleuston copepod with other better studied copepod species (see Cairns 1969). Before this could be done the development stages of Anomalocera had to be determined and described (Section VII).

Examination of the collected material showed a continuous breeding of Anomalocera over the summer months and a considerable patchiness of the population in terms of numbers and stage composition. This made it difficult to make any but the most general statements about the generations of this copepod in the Gulf. One surprising result of the three years work was a consistent appearance in June of Anomalocera in the form of nauplii and early copepodites, the adults not arriving for another two or three weeks. Since Anomalocera on both sides of the North Atlantic shows a northward extension of its range in the summer, it was initially thought that its introduction into the Gulf of St. Lawrence might be related to Le Danois' concept of Transgression (Le Danois 1934, Sewell 1948), but the first appearance of the copepod in the form of nauplii in June, repeated for three years, suggested something different. It was unlikely that very early developmental stages could arrive so punctually from the long distances which would be necessary. Adults would be expected and the timing would be less regular. Examination of the surface currents of the Scotian Shelf and Gulf of Maine made the introduction of surface plankton into the Gulf from outside seem very unlikely.

The hypothesis of a resting egg was seen as a more suitable means of explaining the data. The conclusion that Anomalocera is a shelf water genus (see below) is congruent with the resting egg theory; in fact both ideas are mutually supportive. Resting eggs are of most value to plankton species over shallow water and species with resting eggs are expected to have breeding centres inshore, for example the marine cladocerans.

Early in the study it became apparent that A. patersoni in the Gulf of St. Lawrence differed substantially from descriptions of the species from European waters. Later in the study specimens from other parts of the North Atlantic became available for examination with the result that a new species, Anomalocera opalus, is proposed (Sections II and III) to include the copepods from the Gulf of St. Lawrence and shelf waters of the western North Atlantic formerly classified with A. patersoni. The name, opalus, is derived from the opalescent pigment system discovered in this species (Section IX).

The morphological differences between the new species and the European form are very pronounced and could be easily seen with low power magnification. It was still necessary to demonstrate that this was not clinal variation across the North Atlantic, in which case the two forms would be merely extremes of continuous intraspecific variation. To do this the distribution of Anomalocera in the North Atlantic was reviewed from the literature and from samples made available to this study (Section IV). It became clear that Anomalocera on both sides of the Atlantic is a neritic copepod with breeding populations restricted to shelf waters and found very rarely in the open sea. Breeding populations seem unlikely in the very north of its range (south of Iceland and West Greenland), and it is highly doubtful that there is a significant connection between the populations of A. patersoni in the eastern North Atlantic and A. opalus in the western North Atlantic and Gulf of St. Lawrence.

Having proposed a new species and described its distribution, it was desirable to speculate briefly on its origin (Section V). In the literature of terrestrial biology, traditional arguments between advocates of two modes of speciation, allopatric and sympatric, have become less frequent and acrimonious than in former times. In the marine literature this is less true and there are many more proponents of sympatric speciation than elsewhere.

Consequently reasons for using the allopatric model of speciation in the speculations of Anomalocera's origins are discussed in some detail.

Very little was known about Anomalocera's behaviour before the present work. It had generally been considered a surface copepod and in the Black Sea micro-distribution studies of A. patersoni had indicated that it lived near the surface interface and belonged to the pleuston. This is an important aspect of the life history of A. opalus and it was given much attention in this study (Sections VIII and X). A surface attachment structure was discovered on the 1st prosome segment of all copepodite stages and its use observed both in the laboratory and at sea. All stages of A. opalus, except the eggs and the 1st nauplius stage, were found at the very surface only. Other observations also indicated that this species lives in close association with the interface and may too be considered a pleuston species.

Three apparently complex pigment systems were found in the adults and copepodites of Anomalocera opalus. These are described and their use to the animal considered in Section IX.

During the micro-distribution study of A. opalus, notes were made on a number of other species which had similar surface preferences. This included several larvae and eggs of commercially valuable fish, several small plankton animals, and one phytoplankton species. It is suggested that there may be a summer pleuston community in the Gulf of St. Lawrence but that it is largely made up of seasonal forms (Section XI).

The results of this study are presented below as separate sections. Sections II - X are concerned with the life of <u>Anomalocera opalus</u>. Section I is a general account of the marine pleuston, and Section XI deals with other pleuston species found during the study. Figures and tables are dispersed throughout the work as close to relevant text as possible. Materials and methods are given within each section as necessary, results are given and discussed in each section.

Section I

The Marine Pleuston

Introduction

"Pleuston" will be used here to denote any organism living by virtue of adaptation in a close relationship with the air-water interface in either fresh or salt waters. From the results of recent work, it appears that there are many such animals and plants in the seas, but details of their biology are generally scanty. Fresh water surface life has been known longer and received more study. Most of the marine studies consist of general surveys, trials of equipment, or work on a single species; there have not yet been any detailed community studies comparable to the Hardy plankton recorder work for general surface plankton (Bulletin of Marine Ecology) or the studies of intertidal life by Paine (1963, 1966). Zaitsev's work in the Black Sea (1959-1968, reviewed 1970) is the most comprehensive to date but must be regarded as a preliminary sketch of problems to be studied. Much of the available information on marine pleuston comes from observations made in the course of other work. This knowledge, although valuable, is frequently at the anecdotal level.

At present it is impossible to assign exact criteria for placing an organism under the term "pleuston." Clarification of the term should be seen as a major problem in studies of surface life instead of something done prior to research. This is not the common approach however, and terminology will be discussed below. Spatial proximity to the surface interface may indicate a role in a surface community, but many animals are distributed over a wide vertical range or come to the interface only for brief periods and have closer ties with other communities. Consequently discontinuous vertical micro-distribution with the greatest numbers closest to the interface is seen as a key feature of pleuston. There have been a number of studies on vertical distribution within the upper meter of surface water (Della Croce and Sertorio 1959, Specchi 1969, Zaitsev 1970, Champalbert 1971, Hempel and Weikert 1972), which have made clear some groups of animals found most commonly at the surface. A frequent result is a strong increase in total biomass next to the interface (David 1965, Zaitsev 1970). Micro-distribution alone, however, tells nothing of trophic or behavioural relationships between species. The siphonophore, <u>Physalia</u>, for example, floats on the surface by means of a gas bladder and is always assumed to be a pleuston animal, but its food gathering tentacles may hang several meters below the surface so that only its stomach is, trophically speaking, in the pleuston. The determination of behaviour and delineation of food webs will be major steps in the clarification of pleuston. The existence of a special community at the interface should not be assumed in advance or described simply in terms of vertical distributions centimeters from the surface.

Since animals and plants evolve into interdependencies with each other to form communities, adaptation is the key element in community relationships, otherwise the community concept or metaphor has little significance. The pleuston may turn out to be formed of two rather separate communities, one composed of predators feeding on the periphery of deeper living plankton populations, and another composed of small reducers feeding on rich organic matter at the interface. If such were true, it would make no sense to include in the pleuston any animal adventitiously found at the surface even if temporarily concentrated there. Special adaptation to interfacial life should therefore be considered a key element in the determination of pleuston life.

Two quite different schemes of terminology have been offered recently, each intending to define all modes of life near the surface interface and each failing to recognize the other. Hutchinson (1967) reviews the earlier work in fresh water and presents his own scheme which is a compilation of previous, often contradictory, terminologies. Zaitsev (1960) (reviewed by David 1967) offers a classification of marine surface life quite different from that of Hutchinson. There is no reason why one scheme of nomenclature cannot be used for both fresh and salt waters, and there is a drastic need of simplifying the existing schemes which presume ecological divisions where none have been demonstrated.

The term pleuston was first used by Schroter and Kirchner (1896) to denote floating fresh water plants such as the duckweed, Lemna. Nauman (1917) introduced the term, neuston to denote animal life at the surface film. Pleuston was re-introduced by Gams (1918) to include all life at the interface, both Schroter and Kirchner's pleuston and Nauman's neuston. Gams further broke his term down to micro-and macropleuston. Other authors have added refinements and variations; Carpenter (1928) used superneuston to designate animals living on top of the interface, such as the water striders. Hutchinson points out that animals and plants living on top of the surface film are the most important sub-division of the fresh water surface life. Gietler (1942) used the term "epineuston" for this group of organisms and "hyponeuston" for those living in the water just below the interface.

Hutchinson prefers pleuston as the general term in the sense that Gams used it. He notes that it has a definite priority in the literature and is etymologically suitable (from the Greek, pleustikos, a broad term meaning to go by sea, to float, sail or swim. Neuston, from the Greek, neustos, to swim, has no special surface connotation).

Hutchinson subdivides pleuston into neuston, all microorganisms at the interface (further broken down to hyponeuston, life beneath the interface, and epineuston, life partly above the interface). Macropleuston is used for large forms and epi-pleuston for animals living on the top of the interface but not submerged such as the water striders. Prefixes are advocated when they are necessary. At best this breakdown of pleuston is arbitrary and unwieldy. Hutchinson himself contradicts it in the same volume that he proposes it (1967, p. 146).

Terminology of marine surface life has taken another turn, and here neuston is the key term rather than pleuston which is relegated to a special role. Zaitsev (1961, 1970) appears to have been the initiator of the marine terminology; his system is summarized by David (1967). Under the term, neuston, are the large subdivisions, epineuston and hyponeuston, the former designating life on top of the interface but not submerged such as the marine water striders, Halobates, and the latter term designating all life just below the interface such as pontellid copepods. Hyponeuston is subdivided into four further categories:

Euhyponeuston - organisms living at the surface day and night.

Planktohyponeuston - organisms at the surface only by night.

Merohyponeuston - larval forms at the interface.
Benthohyponeuston - bottom animals at the surface by night.

Pleuston is retained to designate animals which rest half in and half out of the interface by virtue of a gas float (e.g. siphonophores, Vellela and Physalia). Zaitsev (1970) advocates the use of prefixes to make still more precise the relationship of species with the surface interface.

This terminology suffers from the same ills as that of Hutchinson and as well fails to observe the priority of pleuston. It would be better to have one system of nomenclature rather than two for the same thing, and, in consideration of the present state of ignorance concerning life at the air-water interface, the most desirable system would be one which pre-supposes the least. For these reasons, only the term pleuston will be used in the present work. Common English will be used to express particular relationships rather than multiple prefix sandwiches. (Zaitsev's bathyplanktohyponeuston translates to evening visitors.)

Physical conditions at the air-water interface

It should not be surprising that there is a rich development of life at the sea surface, both in biomass and diversity. Most of the earth's species do live at interfaces, perhaps because an interface provides place of orientation and accumulation of useful material. Hutchinson (1965) notes, "... although organisms can live in the free liquid phase of lakes and oceans, most species prefer an environment of interfaces; this may well have been a primitive preference." The sea surface, however, has received scant attention until recently, and much of the current work is done by physicists, not biologists. Physical conditions a few centimeters either side of the sea-air interface show steep gradients, and there is a constant two-way flow of matter important to the earth's geochemical cycles. Some of the more biologically important physical conditions of this zone are discussed below.

Solar radiation forms the most pronounced physical gradient at the surface. The filtering effect of the near interface waters is of great importance to the heat budget of the ocean depths, but it is the spectral composition within the filter itself that is of significance to pleuston life. Strickland (1958) estimates that about 15% of all wavelengths is reflected from the surface skin or scattered by small particles on the skin. This fraction may decrease to as little as 5% on a calm day or increase to 30% during very rough conditions. Once radiation has penetrated the interface, very strong extinction begins which acts differentially over the spectrum with different wave lengths. Absorption is predominant in infrared radiation but is also significant in the long ultraviolet. Zaitsev (1970) states that wave lengths greater than 1200 mu are essentially eliminated by the upper 10 centimeters of water. Most of the longest radiation disappears in the first mm. Ultraviolet light is both absorbed and scattered rapidly so that the first ten centimeters eliminate most of these wave lengths. There is also a great reduction of all visible light in the upper micro-layers which is subject to much variation from dissolved matter, bubbles, and small particles. The upper ten cm is visually the brightest region of the sea and contains nearly all of the invisible radiation in the water column; biologically there is a maximum of energy available here for photosynthesis, ultraviolet cell damage and infrared heating.

Zaitsev (1970), reviewing a number of studies in Russia, cites temperature gradients of one to two degrees Celsius over the upper half-meter during calm days. Similar results were obtained in the present study, but it was found difficult to measure temperature within well defined micro-layers during even slight winds. The first mm of water is perhaps the layer of most significant temperature change since a very great proportion of long-wave radiation is absorbed here. This creates problems in the field of remote sensing of ocean surface temperatures and may influence the biology of near surface animals such as Anomalocera, which inhabits the upper mm. Evaporation could significantly counteract the infrared heating of this water layer during windy conditions, but anyone who has read The Shadow Line by Conrad (123 knows of glassy calm seas persisting for many hot days. The action of infrared radiation may have its greatest effect on pleuston organisms through direct absorption within the body.

Ultraviolet light may prevent some organisms from inhabiting the surface zone but it appears to have little effect on true pleuston life. Zobell and McEwen (1935) found lethal effects of ultraviolet light on marine bacteria at normal daylight intensities but determined that as little as 10 mm cover of water provided significant protection. The greatest numbers of pleuston bacteria live within or on the surface film itself and so would have no such protection (Tzyban 1971, Zaitsev 1970, Harvey 1966). Short-wave radiation is also thought to be inhibitory to most phytoplankton (Steeman-Nielson 1964). Marumo, Taga, Nakai (1971) found large numbers of phytoplankton in low latitude pleuston, but reported that much of it was dead or dying, and they attributed the damage to ultraviolet light. In the present study in the Gulf of St. Lawrence, phytoplankton was generally present at the surface during times of phytoplankton increase. One species, Halosphaera sp, was found to be concentrated in the upper few cm. Dinoflagellates seem to be unaffected by ultraviolet light since they are often found at the surface interface in the day time (Pomeroy, Haskin and Ragotski 1956, Bainbridge 1957, Zaitsev 1970).

Evaporation will influence salinity at the surface as well as temperature, and, under certain conditions, an increase in salts might form near the interface. Evaporation would tend to reduce temperature as it increased salinity and this could contribute to instability and prevent micro-haloclines. One part per thousand salinity has five times the effect of one degree Celcius in determining water density. Zaitsev (1970) reports generally homogeneous salinity within the upper meter. A more likely event would be temporary freshening at the very surface after a downpour during calm conditions.

Hydrostatic pressure has been cited as a potential influence on pleuston life (David 1965, Zaitsev 1970); the greatest changes of pressure with depth are found very near the surface. There has been no work done to investigate pressure effects on near surface life, but since many animals, with and without gas-filled internal organs, migrate diurnally to the very surface from great depths, it would not seem to be an important factor.

The wind has a strong effect on the surface environment and in some instances on surface life. Micro-distributions of small animals would seem impossible during storms or even in moderate waves, but considerable work has shown that active animals such as pontellid copepods are able to maintain their positions near the interface in seas as large as five meters in height (Zaitsev 1970). Non-motile forms such as fish eggs may be dispersed throughout the surface waters by waves but will float back to the interface during calm conditions. Zaitsev states that very strong winds can cause massive fish egg and larvae destruction. He notes that fish with pleuston eggs such as <u>Mugil</u> spawn only during calm seas and during the season when storms are least frequent.

Wind may induce rapid horizontal transport of near surface waters and organisms. The transport of floating siphonophores is discussed below. Olson (1951) observed that the top inch of surface water moved faster than the water below, and in the present study it was noticed that the surface skin and various bits of trapped detritus moved rapidly before the slightest of breezes; <u>Anomalocera</u> attached to the surface film (Section X) moved with the film more rapidly than the water a few mm below the interface. Probably because of this effective wind transport, <u>Anomalocera</u> was never found under a weather shore. Zaitsev (1970) describes instances of large numbers of pleuston animals driven ashore by wind (see also Wilson 1958), but this would be of significance only in enclosed waters. In the open sea, wind systems are roughly congruent with the large current systems; Heinrich (1969, 1971) found that pontellid copepods in the Pacific had distributions similar to those of other non-pleuston copepods.

The most important effect of the wind on surface life is the Langmuir circulation found in both lakes and oceans. Under stress of wind, thermally unstable surface water breaks up into a series of linear and parallel rotating cells aligned approximately with the direction of the wind. The rotation of the cells alternates so that a clockwise cell is always bounded by two counter clockwise cells or helices; a water parcel in the outer portion of a cell describes a spiralling course with a net horizontal movement before the wind. There results an alternate divergence and convergence of surface water between pairs of cells. The convergence, where water is sinking from two cells, collects floating matter such as foam and seaweed into long parallel streaks known as wind rows, a persistent feature of the sea surface. The spacing of the wind rows varies positively with wind velocity and is an index of the size (or depth) of the cells which may be several meters in diameter (Langmuir 1938, Woodstock 1941, 1944, Faller and Woodcock 1964).

The mechanism explaining the structure of the helical cells has not been clearly formulated, although there are numerous papers offering complex models. Stommel (1947) and Faller (1964) suggested shear flow instability as a likely mechanism, but Scott, Myer, Stewart and Walther (1969), in a critical review, discuss six different mechanisms, some of which may work in concert to produce the helical structure. Owen (1966) discovered what may be another type of surface cell. He found a very much smaller spacing of rows on a windless day which had concentrated large numbers of _Oikopleura_.

In the oceans, but not evidently in lakes (Hutchinson 1957), there is an effect of the earth's rotation on the Langmuir cells. The wind rows in the northern hemisphere stream at an angle to the right of the wind direction, and the surface drift component to the right (in clockwise cells) is greater than the drift to the left (in counter clockwise cells). This makes the clockwise helices larger and gives an asymmetrical spacing to the convergences and divergences. In the southern hemisphere this situation is reversed (Woodcock 1944, Munk 1947, Faller 1964). A possible biological effect of this asymmetry was proposed by Woodcock (1944) to account for the dimorphic sails of the siphonophores, _Vellela_ and _Physalia_. The sails of these animals in the northern hemisphere are arranged so that the animal sails somewhat to the left of the wind direction. The reverse dimorph is found in the southern hemisphere. Woodcock theorized that such a path across the asymmetrical spacing of the convergences and divergences would keep the animal in the divergences longer than in the convergences. He suggested that the convergences were hazardous because of accumulated floating matter and that the divergences were plankton rich. Subsequent work on the siphonophores (Savilov 1956-1966, and a review by Edwards 1966) suggests that the dimorphism may not be entirely antimeric.

Other biological effects of the Langmuir helices result from their ability to circulate dissolved or non-buoyant particulate matter through a part of the surface waters and their tendency to concentrate particles and oils. Anything light enough to resist being pulled downward in the convergences will be concentrated there. Seaweeds, assorted flotsam, small upward swimming or floating animals are commonly seen in the wind rows which may provide shelter or food for other animals. Hutchinson (1967, p. 290) presents other models for concentration at different points in the helices. It appears that particles showing a slight tendency to sink may be kept in a retention area below the divergences (Stommel 1949), a possibility that supports Woodcock's theory of siphonophore dimorphism. Although there have been no detailed studies of the animals and plants concentrated by the convergence, scattered observations suggest that this is a common event at the surface. Dinoflagellates have frequently been seen in the wind rows (Bary 1953, Bainbridge 1957), as well as larvaeceans (Owens 1966), fish larvae, and small crustaceans (Hutchinson 1967, Cassie 1963, Zaitzev 1970).

The horizontal transport of surface water into the convergences may also result in a pile up of monomolecular layers of surface active compounds to form a wave dampening slick. A number of recent papers have shown that submerged air bubbles in the presence of surface active compounds will result in the formation of particulate detritus which may be used directly as food or as substrates for bacteria. A bubble swept downward in a convergence may dissolve leaving behind the coalesced organic compounds which were initially attached to the surface interface. A bubble may also attract dissolved organics during its passage through the water. The wind row convergence both concentrates organic compounds and provides a downward passage for small bubbles and may be important in the production of detritus in the oceans (Riley 1963, Baylor and Sutcliffe 1963, Sutcliffe, Baylor and Menzel 1963, Barber 1966, reviewed by Riley 1970).

Oils of biological origin, e.g. from phytoplankton cells, plankton animals, whales, and dissolved organics may form slicks over wide areas of the ocean surface (Dietz and Lafond 1950, Garret 1965, Zaitsev 1970, Wilson and Collier 1972). Any of these compounds may have their origins at depth but may be brought to the surface as droplets lighter than water or attach to the surface interface if they are polar, or to other molecules already at the interface (aerosols such as pesticides and hydrocarbons fall onto the interface from the atmosphere causing further accumulation). Non-particulate organic compounds (exclusive of visible slicks) are found in the surface skin in amounts as much as an order of magnitude greater than in the water just below the skin (Nishizawa 1971, Zaitsev 1970). As noted above thin layers of molecules on the interface can be concentrated by the small-scale wind rows to form slicks. The action of internal waves can have a similar effect over a wider area (Ewing 1950) and probably through other physical means such as current gyres or convergences. Local areas of intense primary production or zooplankton grazing may also produce slicks.

The general importance of slicks to pleuston life lies in their ability to damp waves (Dietz and Lafond 1950, Garret and Bultman 1963), which would have a mechanical effect on the surface environment. There would also be an albedo effect which would result in a great penetration of solar radiation through the interface and a decrease in evaporation which could promote heating at the surface. Bacteria and other heterotrophs would be expected to be concentrated in areas of rich organic matter (Harvey 1971).

The physical characteristics of the sea surface are more extreme and show a greater potential for rapid change than the same variables at greater depths. Temperature and salinity can at times be either higher or lower than in sub-surface waters, pressure changes most rapidly with depth at the surface, and turbulence is usually many orders of magnitude greater at the interface than elsewhere. The greatest amount of solar radiation in the water column, especially of the ultraviolet and infrared wavelengths, is found in the upper few centimeters. It is often assumed that life at the interface is more difficult than the less challenging existence in the physically buffered depths (David 1965, Zaitsev 1968, 1970, and elsewhere). The extremes found at the surface are not great compared to those of terrestrial deserts which have not been insurmountable to life; pelagic organisms have successfully invaded estuaries where physical change is always great. The interface is a zone of material accumulation and a plane of spatial orientation for organisms; its greatest significance lies here rather than in its extreme physical regime.

The accumulation of matter at the interface may indirectly affect life at the surface through an increase in habitat diversity. Floating seaweeds, large and small allochthonous particles ranging in size from microscopic seston to large pieces of driftwood create potential niches not found in the water column below. These materials break up the environment by creating refuges which may also permit increased diversity of species (Slobodkin 1966). There have as yet been no diversity studies comparing pleuston species with upper pelagic species. This will be most interesting work for the future.

Pleuston life

A suitably broad definition of pleuston would include organisms "... in any way associated with the water surface." (Hentschel 1933) which would include whales, turtles, birds, and all other creatures swimming or floating in the water, running over the top of the surface film or attached to it from below. There is no reason to exclude seafaring man who sails on floating ships in much the same way as the gooseneck barnacle, Lepas, attaches to light bulbs, solidified crude oil lumps and driftwood. Hentschel's liberal definition has not met with great approval (Zaitsev 1970), but it will be followed here in spirit.

Most of the plants and animals described below are assigned to the pleuston because they are found very near the surface and show some special adaptation to surface life (that is, some reason other than accident for being at the surface). Sometimes animals may seem to be part of the pleuston only because they are frequently caught at the surface and show some concentration there. Zaitsev (1970) gives vertical micro-distributions within the upper meter of surface water for several small Black Sea animals, among them copepods, cladocerans, and invertebrate larvae. These distributions show about twice as many animals in the upper five cm as in any of the layers sampled below, 5-25 cm, 25-45 cm, 45-65 cm. No data are available for distributions of these animals at greater depths. Some similar results are given by Della Croce and Sertorio (1959), and Della Croce (1962).

Zaitsev (1970) appears to consider these animals pleustonic but it is possible that the surface interface itself causes these distributions among randomly swimming animals whose vertical range terminates at the interface. Such an animal accidentally encountering the interface will be stopped there momentarily until it can change direction and move away . In the absence of the interface, its swimming path would have taken it to a further point. The result will be an accumulation of animals at the surface without entailing the continued presence of specific individuals there. In a similar way, animals with a positive phototropism may be stopped at the sea surface for a time until light conditions change or the phototropism ceases to operate (Russell 1925). In neither case would it be the intention of the animals to remain near the interface. The result would be an enrichment of biomass near the surface.

Another important source of surface enrichment is the addition to the interface of dead or dying organisms both from the atmosphere and from the water column. Probably the most important, especially in the open seas, is the antirain of Zaitsev (1970). Dead animals become buoyant as small gas bubbles released during decomposition form beneath the exoskeleton. They are brought to the interface and may collect there in large enough numbers to be an important food source for pleuston animals and a substrate for bacteria. Dead phytoplankton may also appear at the surface, but it is not certain whether they are killed before or after arrival at the surface (Marumo, Taga, Nakai 1971). Savage and Wimpenny (1956) found great concentrations of dead or dying Coscinodiscus floating at the surface in clumps at a time of maximum phytoplankton growth. Fulmars were observed eating the clumps of diatoms.

Living crustaceans with hydrofuge exoskeletons (Cladocerans, hyperiid amphipods) may become trapped in the surface tension and, although no quantitative measurements have been made, trapped animals do appear to provide food for Halobates, and David (1965b) observed a marine surface fish, Mupus, to feed on such trapped animals. The white bass, Roccus chrysops, swims beneath wind rows in lakes eating surface-trapped Daphnia in the same way (Hutchinson 1967).

Airborne seeds, pollen grains, and insects falling on the sea surface provide the second major outside source of organic particles to the pleuston, although the importance of this material is restricted to near shore or enclosed bodies of water. In the Black Sea floating insects and plant matter may become extremely important at certain times of year, and both insect fragments and pollen grains have been found in the guts of pontellid copepods; pollen is eaten by Noctiluca (Zaitsev 1970). In the Gulf of St. Lawrence during the present study, pollen frequently clogged the surface nets and lay on the water surface in widespread yellow mats. Insects often made up the bulk of pleuston samples, especially flying ants in the spring. It is not known how important this source of food may be to pleuston animals, but since most of it is unsinkable, it is likely that pleuston reducers will benefit from it if nothing else does.

Cassie (1963), David (1965b), and Zaitsev (1962, 1970) have emphasized that the usual methods of plankton collection inadequately sample the very surface. A net with a circular aperture hauled just at the surface, fishes at the interface with only a tiny proportion of its mouth area; often the surface layer rolls up and over the top of the net so that none of this layer is fished. A vertical or oblique net haul will fish the surface for only a few feet of its total run and again may push most of the encountered surface water aside without filtering it, especially if the net is partially clogged at the end of the haul. To overcome these limitations, nets have been made with rectangular apertures mounted on floats or skiis (see Figure 16), or suspended from booms. Samples are taken at various speeds, depending on net design and the organisms sought. A usual concern is to get the net away from the wake of the ship to fish undisturbed water. The use of keels, booms, or drift nets will accomplish this. Zaitsev (1970) has reviewed standard methods as well as ways of collecting special components of the pleuston such as bacteria. The following authors have described various techniques of pleuston collection: Parr(1939), Willis (1963), Zaitsev (1962, 1970), David (1965), Harvey (1966), Rivers (1966), Bieri and Newbury (1966), Marinaro and Henry (1968), Sameoto and Jaroszynski (1969), and Ben-Yami, Herzberg and Pisantry (1970).

Results from a number of studies indicate that bacteria are found in much greater numbers at the surface interface than elsewhere in the water column. Harvey (1966) was able to sample the top mm of water by pushing a slowly rotating drum ahead of a small boat and removing the thin water layer adhering to the drum. He found bacteria in much greater numbers in these samples than in samples taken with a surface bucket. The bacteria were often associated with clumps of detritus. Sieburth (1965) obtained similar results, but in another study (1971) found some areas in low latitudes with reduced bacteria, suggesting solar inhibition. Tsyban (1971) states that bacteria are common both on or within the surface film and in the two cm below it; these are considered two types of bacteria communities. Bacteria from both micro-layers are usually two orders of magnitude more numerous than elsewhere in the water column, and up to four orders of magnitude in the oceanic Pacific. Zaitsev (1970), Tsyban (1971a and b), and Tsyban and Polishchuk (1969) note that the surface bacteria is not dispersed by stormy weather and that seafoam is an important habitat for bacterial and protozoan communities. Pleuston bacteria possess strong proteolitic and lipolitic activity and bright pigmentation. There are many species, mostly of the genera Bacterium and Pseudomonas.

The composition of pleuston phytoplankton appears to differ from that of the general surface phytoplankton.

Steeman-Nielsen (1952) found that photosynthesis of diatoms could be inhibited by an excess of visible light as well as ultraviolet light, and Harvey (1966) found fewer diatoms in his interface samples than in the water taken by a surface bucket. Zaitsev (1970) notes the paucity of healthy diatoms in the pleuston and the frequency of dinoflagellates such as Noctiluca and Gymnodinium, a red-tide organism. He notes that reducers are common in the pleuston and this may be why the dinoflagellates have adapted to this environment. Motility may also be a factor. Further examples of dinoflagellates living at the surface are given above in the discussion of ultraviolet light. The unusual phytoplankton genus, Halosphaera, is discussed in Section XI.

Macrophytic algae has numerous representatives in the pleuston, but it is not certain that any of them, other than species of Sargassum, are specifically adapted to this habitat. In the Gulf of St. Lawrence, many types of seaweeds, but most commonly Fucus, were found at the surface during most of the year. No studies have been done to determine whether these plants are reproducing at the surface. Their importance in the pleuston is not known, although they give shelter to a number of animals at the surface (Section XI).

Protozoans appear to be well represented at the surface interface. Harvey (1966) found over 4000 microflagellates (less than 15 microns) per liter in the top mm of surface water but none in a surface bucket sample. Ciliates were found in nearly equal numbers in both samples. Zaitsev (1970) notes that sea foam contains many microflagellates in association with bacteria, and Cassie (1963) cites unpublished observations of Norris that the microflagellate, Chrysochrum ulina, attaches to the surface film with its haptonema. Bainbridge (1957) found flagellates concentrated in wind rows, and Bary (1953) observed Pyrosoma at the surface off New Zealand. Zaitsev (1970) reviews many other instances of protozoans found in the 'pleuston', including tintinnids which are very common in the top five cm of the surface, at times in numbers four orders of magnitude greater than in water below this level. Hutchinson (1967) describes surface film attachment by the basal stalk of the tintinnid, Epistylis fluitans in fresh waters. Pacific Radiolarians and Foraminifera have also been found at the interface (Willis 1963).

Rotifers appear often in the pleuston. Hutchinson (1967) describes fresh water species with internal floats and Zaitsev (1970) notes many instances of rotifers with marked surface concentrations. During the present study in the Gulf of St. Lawrence, rotifers were encountered frequently in the pleuston and during one summer appeared in a vast swarm almost entirely at the interface (Section XI). On some occasions small larvae of other invertebrates have been reported at the interface but not in sufficient numbers or frequently enough to make generalizations possible. A holothurian larva found at the interface in the Gulf of St. Lawrence is described in Section XI, and crab megalops are common pleuston samples. Zaitsev (1970) gives strong surface micro-distributions for larvae of Balanus, lamellibranchs and gastropods. Young Mytilus attach to the surface film with the byssus.

Eggs of both fish and invertebrates appear to be common in a variety of locations. Cod and halibut eggs in the Gulf of St. Lawrence were observed during the present study at the surface interface as well as great numbers of unidentified invertebrate eggs. Zaitsev (summarized 1970) has done much work on the vertical distribution and biology of fish eggs in the Black Sea, especially the eggs of the anchovy, red and grey mullet, dragonet, and sole, all of which have strong pleuston distributions. The need to survey fish egg densities in Russian seas was in fact the motivating force behind the first pleuston studies (Zaitsev 1959). There seems to be two methods of flotation of fish eggs; the most common is a low density caused by large amounts of fat droplets. In the case of Mugil, the action of a hydrofuge outer membrane traps the egg in the surface tension. The latter situation would appear to be an adaptation to keep the egg in the surface layer, perhaps, as Zaitsev suggests, to hasten development time by staying in the warmer surface water (and possibly by absorbing heat directly from infrared radiation). Low density could also be an adaptation to surface life, but the surface distribution could also be a non-adaptive by-product of stored fat. Zaitsev points out that fish egg surveys made with ordinary plankton nets are subject to drastic revision in the cases where eggs float at the very surface.

There is a large assortment of animals from other invertebrate phyla which are common in tropical oceanic pleuston, many of them of great beauty. Examples are the siphonophores, Porpita, Vellela, Physalia, the nudibranch Glaucus, the purple snail, Janthina, pelagic anemones, and several small squid including the paper nautilus, Argonauta. All of the above are coloured various shades of blue, purple and green (see David 1965b for colour photographs). All of these animals appear to be carnivores. The attachment to the surface is effected by gas floats (siphonophores), secreted bubbles encased in mucus (Janthina, anemones, stalked barnacles) or by gas bubbles within the body (Glaucus). By virtue of these floats they are obligatorily restricted to the surface interface. There has been no comprehensive study of all of these animals in one locality, but details of their biology can be found in a number of papers: Wilson (1956), Bayer (1963), David (1965b), Savilov (1956-66), Totten (1960), Zaitsev (1970), and in some books of general marine biology: the writings of William Beebe (e.g. 1926), Murray and Hjort

(1912), Marshall (1954).

Fish are common at the surface but it is often difficult to assign them to the pleuston because they may cruise over a greater depth range than smaller animals. Tuna, swordfish, and sailfish at times inhabit the near surface waters as does the ocean sunfish, <u>Mola mola</u>; the larvae of these fish and many others live near the interface. All species of flying fish and the needle fish, <u>Scomberesox suarus</u> (Nellen 1971), may be considered permanent members of the pleuston. Most pleuston fish keep to the surface by virtue of their behaviour rather than by special structures (it is assumed that regulation of the swim bladder comes under the heading of behaviour). Exceptions to this would be larval flying fish, and some sargasso fish. The fry of several species of mullet have been observed to hold external air bubbles between the dorsal fins. Seen from above, a school of these fry appears as a patch of silvery bubbles and it is possible that this is camouflage as well as a flotation device (Zaitsev 1970).

To return to Hentschel's broad definition of pleuston, it is necessary to consider the birds which get their food from the sea surface. Many sea birds, especially the tube nose birds (<u>Tubinares</u>) feed mainly on zooplankton near the interface. Very little is known about the actual stomach contents of petrels (Fisher and Lockley 1954, Huntington per. comm.) but the nature of their feeding suggests that they must take animals from the surface. Zaitsev (1970) has observed the feeding behaviour of several sea birds including the kittiwake, Rissa tridactyla, the shearwater, Puffinus puffinus, and several species of petrels of the genus Oceanodroma, and found them all to be feeding just at the interface. Although it is unlikely that they are feeding exclusively on true pleuston species, especially in boreal waters where deeper living zooplankton may come occasionally to the very surface, for example Calanus finmarchicus (Marshall and Orr 1954), it is likely that the birds have at least some effect on the true pleuston and may be a functional part of a pleuston community. The first efforts to study the pleuston of European seas were made to determine the amounts and types of food available to sea birds (David 1956). Zaitsev also notes that there is a bat which feeds exclusively on inshore pleuston (see Griffin 1963).

Gudkov (1962) calls attention to feeding associations of whales, birds and plankton. On one occasion, he found 15 species of birds and many whales congregated over a shoal of Galanus. Similar observations were made during the present study in the Gulf of St. Lawrence; basking sharks were often present but, although they feed at the surface, their mouths function in somewhat the same way as surface hauled conical plankton nets which, as Zaitsev notes, undersample the pleuston. It is not known whether these multi-phyletic feeding associations occur with the true pleuston.

David (1965a) notes that the pleuston largely disappears in high latitudes, but there is no obvious reason why this should be so. Zaitsev (1970) reports that there is little pleuston (diversity and biomass) in both the northwestern Pacific and the Antarctic (positions not given). He presumes water temperature to be the deciding factor but also notes that freezing air temperatures and sea ice would eliminate species with surface protrusions. It is doubtful that this virtual disappearance of pleuston is related to other species diversity gradients, because the loss of pleuston in high latitudes is so abrupt (Anomalocera is possibly the only permanent pleuston animal in the boreal North Atlantic). Low air or water temperatures should not in themselves make all pleuston life impossible.

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The overt adaptations to surface life seen in the tropics such as protective colouration, flotation devices, structural association with the interface, might be considered fine niche specializations, especially when compared to generalized species such as Calanus. This may be related to a remark by McGowan (1971), that a species can be expected to adapt more fully to particular and restricted roles in a community if there is a constancy or fidelity of other components in the community (see also Fager 1957, 1963). In the higher latitudes, pronounced seasonality creates great changes in plankton composition and there is presumably a low degree of fidelity within a given plankton community or water layer (although the changes in plankton composition may be predictable). Seasonal ontogeny, seasonal vertical migrations, and changes of biomass in the high latitudes are all in strong contrast to the steadier conditions of the tropics. The marked seasonal changes in the life of high latitudes and the more generalized niches found there, may result from the types of evolutionary strategies necessary in fluctuating environments, at least when these environments are of recent origin (Dunbar 1968).

It is also possible that there is more of a pleuston community in the high latitudes than has been suspected. Species may be present near the interface without the special features common in the tropics. Detailed work over long periods of time stressing both micro-distribution and behaviour will be necessary to determine this. More likely there is an increase of temporary forms. Many of Zaitsev's Black Sea examples of pleuston are clearly ontogenetic or seasonal. Anomalocera disappears from the northern parts of its range in the winter, and in the Arctic and Antarctic species have been found at the very surface but only during a small part of the year (Dunbar 1957, Amphipods; Marr 1962, Euphausids).

It is difficult to say where the importance of the pleuston lies; it may be both economic and environmental. Many of the substances which enter the sea from the land and from man's activities do so through the surface interface, for example, pesticide aerosols, particulate matter from soils and factories, and radioactive fall-out. Zaitsev (1970), who champions the extreme surface as a most important incubator for many commercial fisheries, also discusses the importance of radio-ecology of the sea surface. He gives data to demonstrate the concentration of strontium 90 and other radioactive products by several species of pleuston in the Black Sea, including fish eggs. No data are given for species living below the pleuston layer so that comparisons are not possible.

Contamination of the pleuston environment by oil slicks would appear an obvious influence on surface animals. Surface active compounds may persist at the interface after visible oil has disappeared into the bottom sediments. As little as 1 ppm dissolved crude oil fractions can adversely affect Calanus (Smith 1968), and it is reasonable to suspect that a species such as Anomalocera, which is in contact with the surface film, will be more vulnerable to oil and pesticide residues. Mileikovsky (1970) found A. patersoni (origin not given) was sensitive to low concentrations of crude oil (amounts not given). Any animal or eggs living near the surface will receive not only the effects of substances dissolved throughout the surface waters, but also have the closest contact with substances as they first enter the water column, and substances which become concentrated at the surface.

Section II

Description of the new species, *Anomalocera opalus*

As noted in the introduction, specimens of the new species, Anomalocera opalus, from the Gulf of St. Lawrence and western North Atlantic shelf waters (Fig. 3) differ markedly from specimens of A. patersoni (Templeton 1937) with which A. opalus was formerly classified (Willey 1919). The morphological variation was for the most part found in the genital segments, and was readily apparent under low magnification; the two forms can be easily distinguished without the need of dissection or measurements. To study these differences, collections of Anomalocera were obtained from various parts of the North Atlantic (Fig. 1 and Tables 1 and 2), and measurements were made on several body parts, mainly on the genital segments. None of the samples contained intermediate forms, and the differences found were non-overlapping between the two forms. There was also a clear geographical separation of the two forms, a point which is expanded and justified in Section IV on the geographical distribution of Anomalocera in the North Atlantic.

The measurements were made using an ocular micrometer in a dissecting microscope. Copepods were placed in lactic acid during the measuring to prevent drying. The ratio of genital segment length to prosome length of both males and females was found to be a convenient measure of the differences between the two species (Fig. 2, Appendix I), but other ratios could have been used, and in fact many other measurements were made (see Appendix I).

A description of <u>Anomalocera</u> <u>opalus</u> is given below, followed by a more detailed discussion of the differences between <u>A</u>. <u>opalus</u> and <u>A</u>. <u>patersoni</u>.

<u>Anomalocera</u> <u>opalus</u> is a large, stoutly built, carnivorous copepod of blue-green colour, resembling <u>A</u>. <u>patersoni</u>. Although the range of size overlaps, <u>A</u>. <u>opalus</u> is usually the larger of the two species and bears a more complex genital segment. Both sexes possess an opalescent pigment system underlying the dorsal and lateral surface of the prosome (Fig. 6, and Section IX, Fig. 28).

The adult female (Fig. 6) (prosome length 2.8 - 4 mm) has six prosome and three urosome segments and ~~six~~ five paired swimming legs, the last of which is reduced, but nearly symmetrical. There are two pairs of small cuticular lenses on the dorsal-lateral surface of the first prosome or head segment; on the ventral surface of the head, there is a large eye and strong paired rostral hooks. The dorsal surface of the first segment bears a flattened area used for attachment to the surface interface. There are lateral hooks on the first prosome segment, and the last prosome segment is extended in long points.

Figure 1. Map of the North Atlantic showing the 42 samples used in the study of geographical distribution of the two species, _A_. _opalus_ (circles) and _A_. _patersoni_ (crosses).

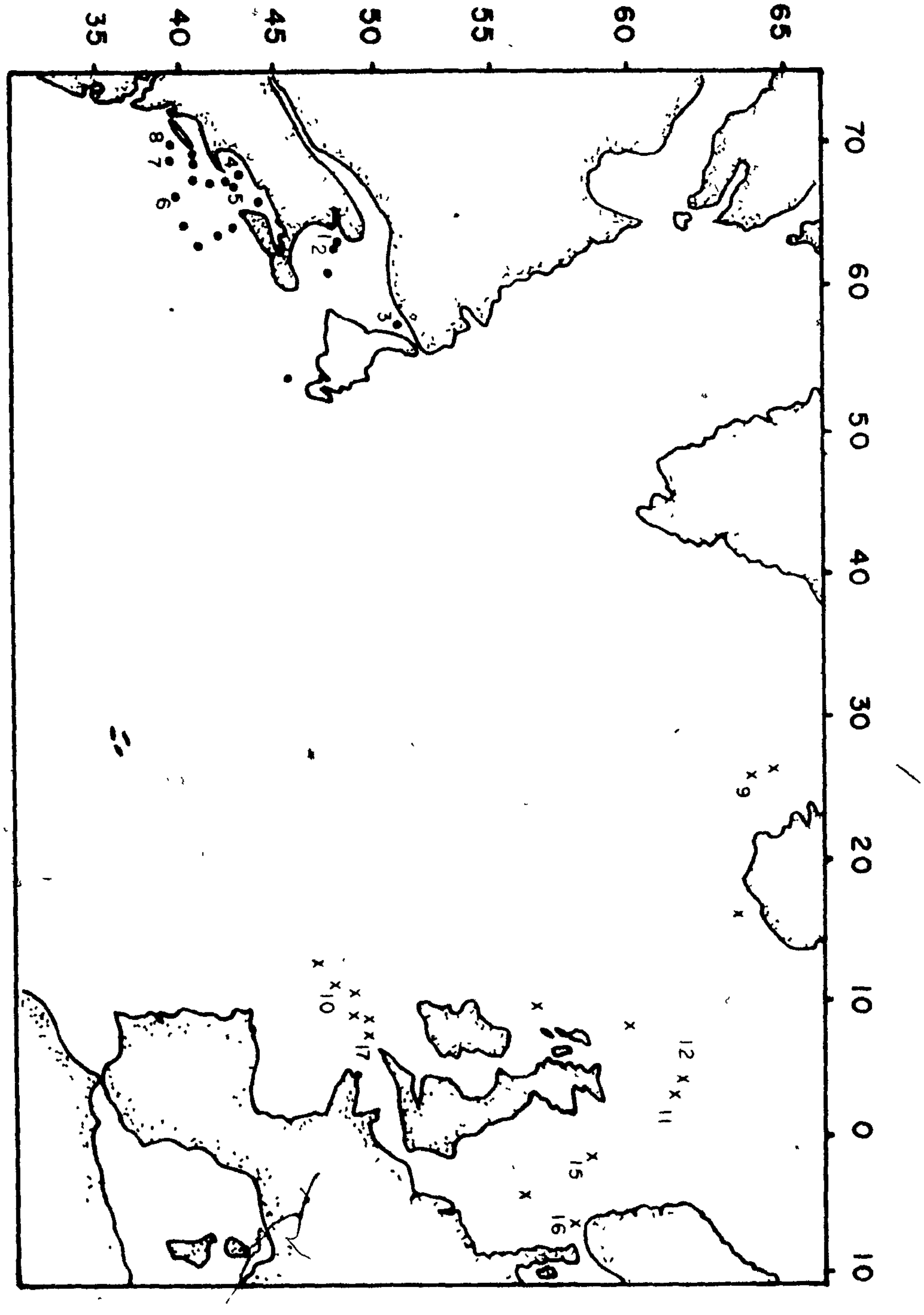
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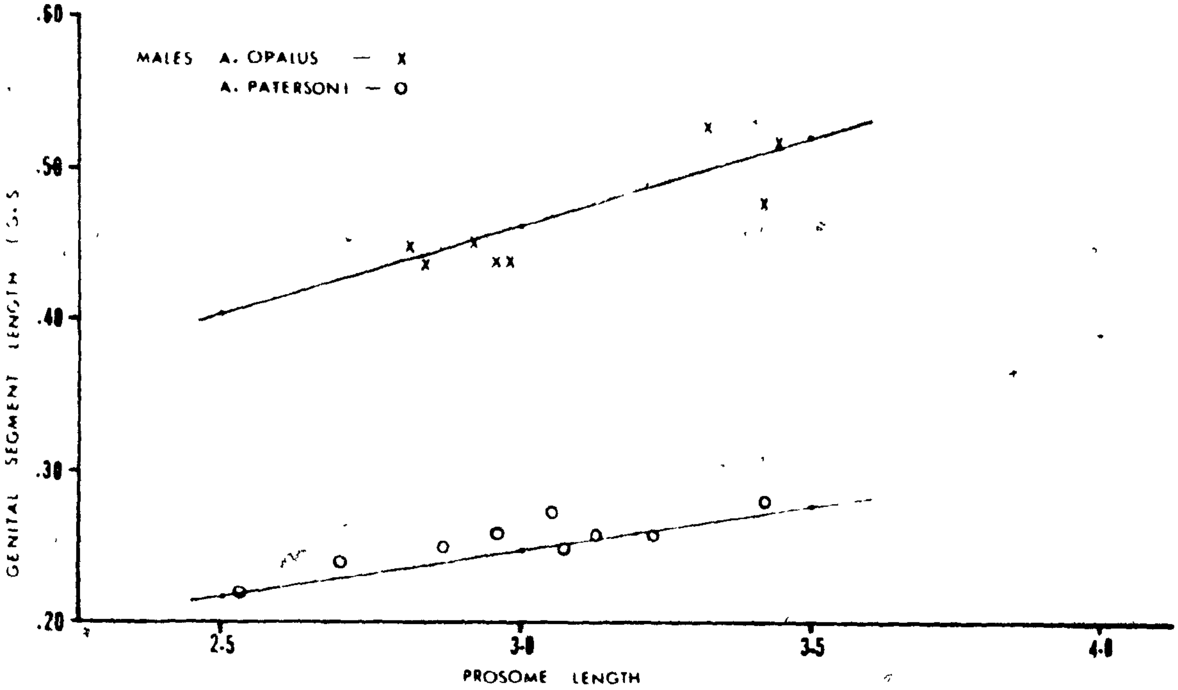
Figure 2. The regression of genital segment length on prosome length of _A_. _patersoni_ and _A_. _opalus_, males and females. Fitted by least squares regression (Stanley 1963).

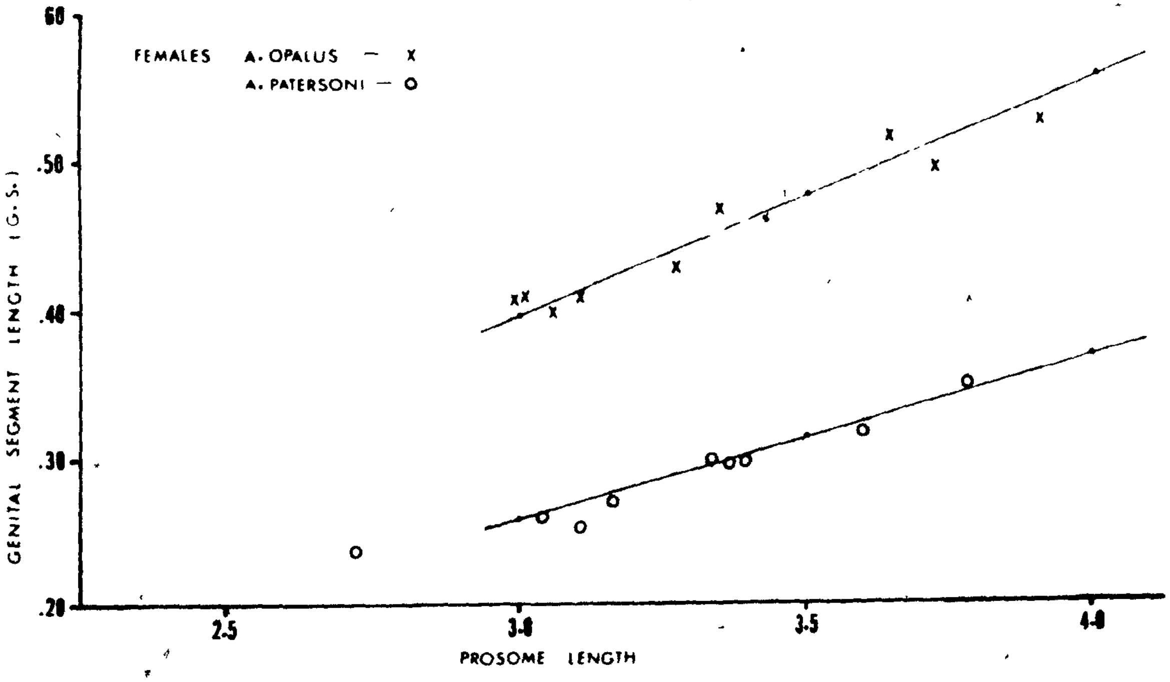


LINE = LEAST SQUARES REGRESSION

VALUES, PROSOME AND GENITAL SEGMENT LENGTH (G.S.), SEE TABLE 3

A. OPALUS — a (Y INTERCEPT) = .11
b (SLOPE) = 1179

A. PATERSONI — a = .07
b = .0604



LINE = LEAST SQUARES REGRESSION

A. OPALUS — a = -0.94
b = .1550

A. PATERSONI — a = -0.72
b = .1132

Table 1. Positions, dates of sampling, number measured, and species of those specimens used for the measurements and ratios. The positions are shown on the map. (Fig.5).

Data for samples measured.

No.	Latitude	Longitude	Date	Number in sample measured Males	Females	Species
1.	48°15'N	64°30'W	24.9.68	30	30	*A. opalus*
2.	48°15'N	64°30'W	20.8.66	30	30	"
3.	51°30'N	58°00'W	31.7.66	30	30	"
4.	43°30'N	69°30'W	29.7.66	30	30	"
5.	43°30'N	70°00'W	15.8.69	30	30	"
6.	39°35'N	71°44'W	3.8.66	30	30	"
7.	39°00'N	72°30'W	3.8.66	30	30	"
8.	40°16'N	67°30'W	31.7.66	30	30	"
9.	64°00'N	26°48'W	31.5.61	14	30	*A. patersoni*
10.	56°30'N	08°59'W	29.5.69	30	30	"
11.	61°08'N	02°10'W	19.6.65	30	30	"
12.	47°35.5'N	10°78,2'W	18.4.67	30	30	"
13.	61°21'N	03°10'W	25.11.65	14	14	"
14.	58°05'N	01°50'E	18.11.68	30	30	"
15.	59°31'N	07°05'W	11.11.65	30	30	"
16.	57°30'N	06°00'E	25.10.67	30	30	"
17.	49°00'N	06°00'W	No Date	30	30	"

Table 2. The same information for those samples for which qualitative examination only was made. Positions are shown on the map (Fig. 5).

Data for samples examined.

No.	Latitude	Longitude	Date	Number in sample examined Males	Females	Species
18.	63°48'N	15°50'W	1.8.61	30	30	*A. patersoni*
19.	64°00'N	26°48'W	31.5.61	30	30	"
20.	46°30.3'N	12°37.2'W	17.4.67	1	1	"
21.	49°28.5'N	06°28'W	18.4.67	2	-	"
22.	48°53.8'N	07°39,4'W	18.4.67	5	-	"
23.	48°38.8'N	08°20.3'W	18.4.67	1	2	"
24.	34°55.2'N	41°16.2'W	7.4.67	300	300	"
25.	55°30'N	04° E	10.63	7	4	"
26.	40°29'N	68°10.5'W	31.7.66	30	30	"
27.	40°15'N	67°30'W	30.7.66	30	30	"
28.	43°38'N	69°08.5'W	29.7.66	30	30	"
29.	41°30'N	69°32'W	28.7.66	30	30	"
30.	39°57'N	69°05'W	1.8.66	30	30	"
31.	40°29'N	68°10.5'W	31.7.66	30	30	"
32.	42°39'N	69°30'W	28.7.66	30	30	"
33.	44°00'N	68°30'W	29.7.66	30	30	"
34,	40°05'N	71°30'W	2.8.66	30	30	"
35.	40°30'N	72°30'W	3.8.66	30	30	"
36.	42°58'N	69°30'W	28.7.66	30	30	"
37.	40°31'N	69°30'W	28.7.66	30	30	"

Table 2 cont'd....

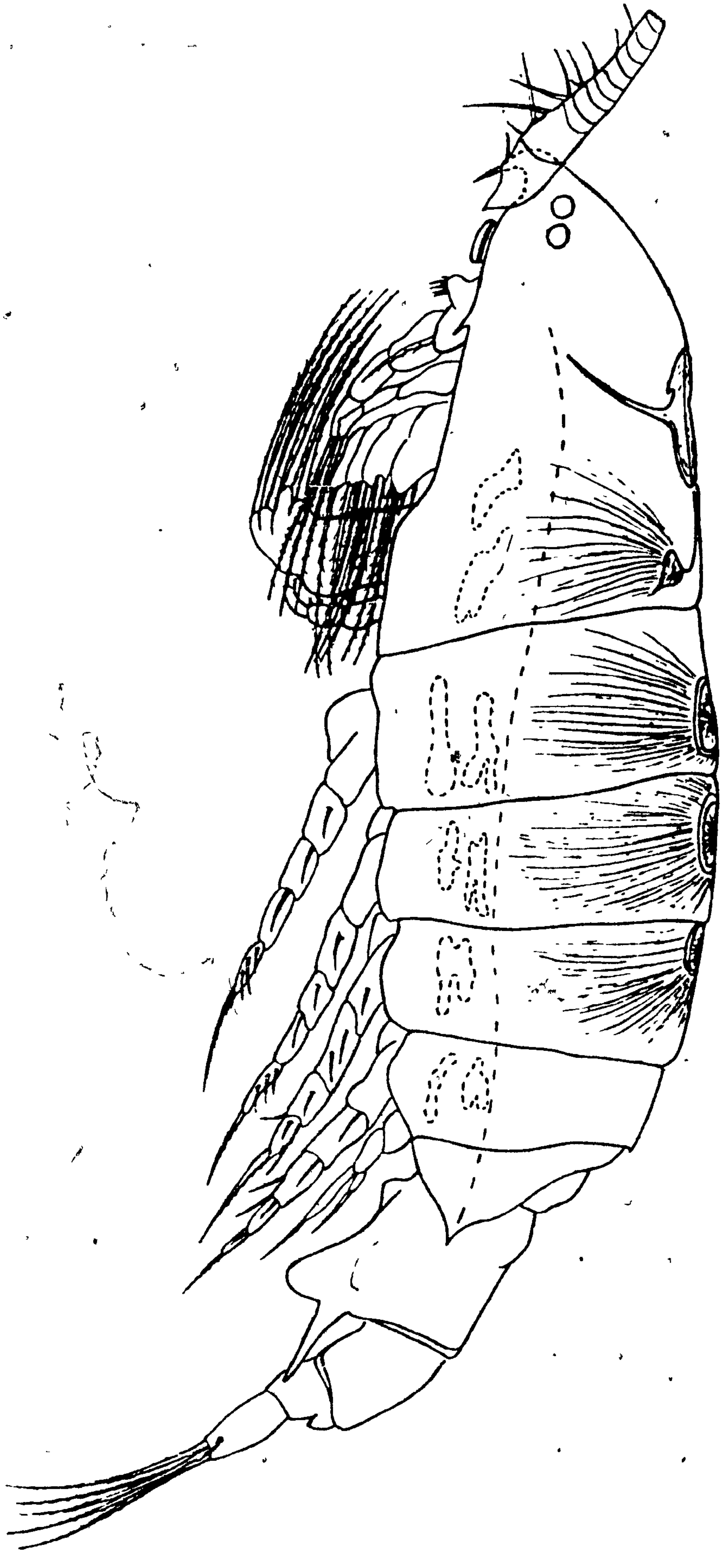
No.	Latitude	Longitude	Date	Number in sample examined Males	 Females	Species
38.	40°00'N	70°31'W	2.8.66	30	30	*A. opalus*
39.	40°12'N	69°05'W	1.8.66	30	30	"
40.	42°00'N	69°30.5'W	28.7.66	30	30	"
41.	39°35'N	71°44'W	3.8.66	30	30	"
42.	45°80'N	54°00'W	8.64	0	1	"

The female genital segment is a greatly enlarged structure with several ventral bumps and a large spine directed backward from the right posterior corner of the segment (Figs. 4, 6 and 7). The caudal rami are asymmetrical.

The adult male is somewhat smaller than the female (prosome length 2.7 - 3.4 mm), and has six prosome and five urosome segments. The prosome bears lateral hooks, dorsal lenses, ventral eye, rostral hooks, terminal points and the surface attachment area. These structures are similar to those of the female, with the exceptions that in the male, the ventral eye is more strongly developed and the right terminal point is curved. The right first antenna is highly modified as a geniculate grasping arm used for copulation. The fifth swimming legs are also modified and asymmetrical, forming a grasping hook and a claw for holding the spermatophore. The first urosome or genital segment bears a large posterior extension on the right side (Fig. 6).

In the last section, the observed differences between specimens of the proposed new species, A. opalus, and specimens of A. patersoni, are described in more detail. Figures 4 - 7 show the genital segments of both species; Figure 5 gives the origins of samples studied. Results of measurements of body proportions are given in the tables and discussed below.

Figure 3: *A*. *opalus*, stage VI, female.



Section III

Morphological comparison of A. opalus with A. patersoni

Adult female

The female first urosome or genital segment of A. opalus is relatively large and irregular, divided by a transverse cleavage. In A. patersoni, it is relatively small and smooth and not divided dorsally. This segment in both species bears a right ventral posterior process, but in specimens of A. opalus this process is relatively longer and curves more strongly to the right. It also bears a small spine at its base which is lacking in A. patersoni, but lacks a small bed of hairs found on the upper surface of the process in the latter species.

On the ventral surface of the genital segment, A. opalus bears two large protuberances, which are entirely absent in A. patersoni. One of the protuberances, located near the base of the posterior process, bears several convoluted ridges and is surmounted by a circular crater. The other is located near the mid-left lateral margin of the segment and is bounded laterally by a crescent-shaped ridge. The genital opening differs in the two species; it is oval in A. opalus and trapezoidal in A. patersoni.

The second urosome segment of A. opalus lacks spines and hairs. That of A. patersoni bears a bed of very fine hairs along its ventral surface, and a few larger hairs on the dorsal surface (shown in Fig. ~~8~~ 7c, d). Neither group of hairs was previously described.

The caudal rami are slightly asymmetrical in both species. The right lateral seta of the right ramus is shorter and more blunt in _A_. _opalus_ than in _A_. _patersoni_, and bears longer fine hairs than does that of the latter species. The left lateral spine of the left ramus of _A_. _opalus_ bears a short row of spinules; that of _A_. _patersoni_ bears spinules along nearly 2/3 of its length. There are no spines or hairs on the lateral margins of the rami of _A_. _opalus_; on each ramus of _A_. _patersoni_ is a single lateral spi~~nu~~le.

The posterior corners of the last prosome segment are more sharply pointed in _A_. _opalus_ than in _A_. _patersoni_, but otherwise are similar in both species.

Adult male

The first urosomal segment of both species is highly asymmetrical and extended laterally to the right into a pointed process which is much more pronounced in _A_. _opalus_ than in _A_. _patersoni_. This right extension of _A_. _opalus_ bears two fine hairs on the posterior margin; that of _A_. _patersoni_ bears three hairs on the posterior and one on the lateral margin. The rest of the urosome segments of A. opalus are slightly and irregularly asymmetrical and bear no hairs or spines. Those of A. patersoni bear a number of asymmetrically placed spinules (Fig. 4b), and the third segment is enlarged on the right side.

The caudal rami are similar in both species, with the exception that there are two spinules on the lateral margin of the right ramus of A. patersoni not found in A. opalus.

The last prosomal segment differs in the two species in the shape and armature of the asymmetrically extended right posterior corner. In A. opalus, this is strongly curved upward into a sickle shape and bears two hairs on the ventral surface (Fig. 3a); in A. patersoni, it is straighter and bears no hairs.

Discussion

The morphological comparisons given above reveal qualitative differences such as spines, hairs and protuberances, and proportional differences of corresponding structures. The latter observations must be freed of possible bias due to subjective interpretation, and they must be studied geographically. To do this, measurements were made on samples of adult males and females, taken from different areas in the North Atlantic (Table 1 and Fig. ~~5~~ 1).

Figure 2 shows graphically an important proportional difference, the relationship of the prosome length to the genital segment length. The genital segment is relatively longer in specimens of A. opalus (both sexes). There is no suggestion of allometry in the graphs or in any of the specimens examined in the study. The lines are fitted by least squares regression and the number of animals for each point is 30 (with three exceptions where N-14, see Table 1). (Stanley 1963).

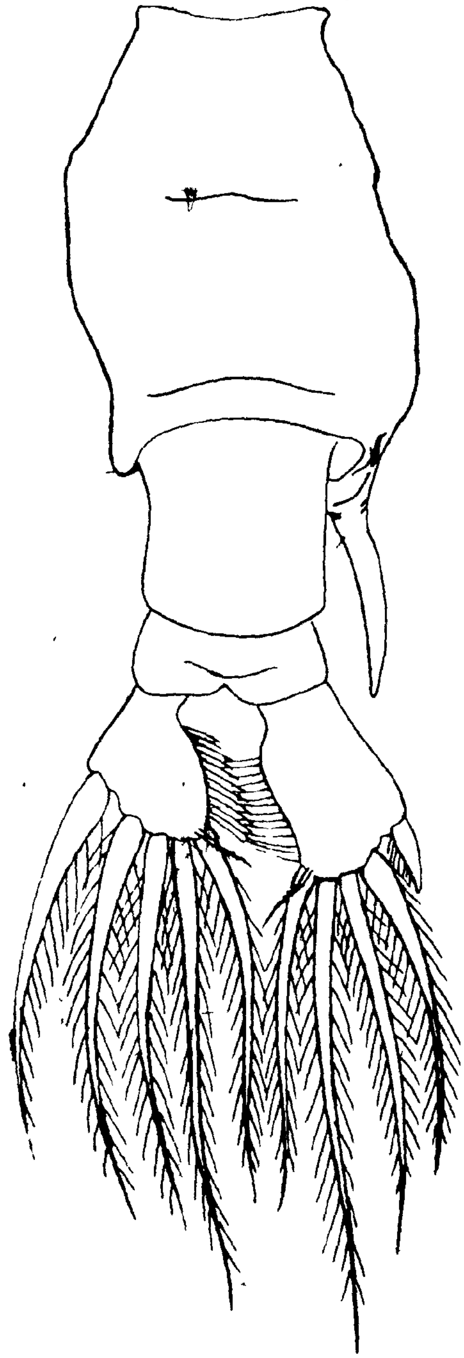
Of the 42 samples examined in the study of geographical variation, 17 were suitable for detailed measurement (Nos. 1-17 in the tables and map) and were used for the calculations of the regression lines. The remaining 25 samples (Nos. 18-42 in the tables) were examined for the qualitative features described above in the comparative description of A. opalus and A. patersoni. On the basis of these features, the specimens of each sample were assigned to the appropriate species. This was also done in the first 17 samples prior to measurement. The results are shown on the map (Fig. 1) and are also given in Tables 1 and 2.

All samples were monospecific. Those of A. opalus were from the western North Atlantic and the Gulf of St. Lawrence. Those of A. patersoni were from the eastern North Atlantic and the North Sea (including the three samples from waters near Iceland).

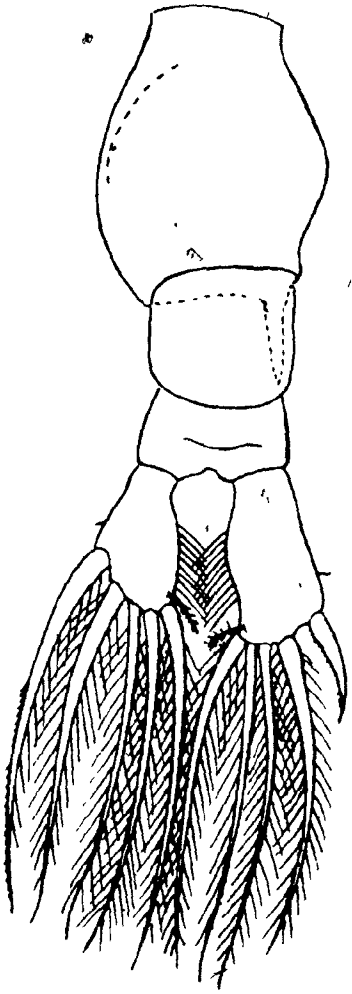
In addition to these samples, many thousands of specimens were examined from the Gulf of St. Lawrence over the three years of the study and no specimens of A. patersoni were found. In the entire study, no specimens were seen which appeared intermediate between the two types as described and shown in the text and drawings above. There were no suggestions of overlap between the types in the measurements of individual specimens in the proportional study.

Figure 4. a) *A. opalus* urosome, dorsal, female

b) *A. patersoni* urosome, dorsal, female



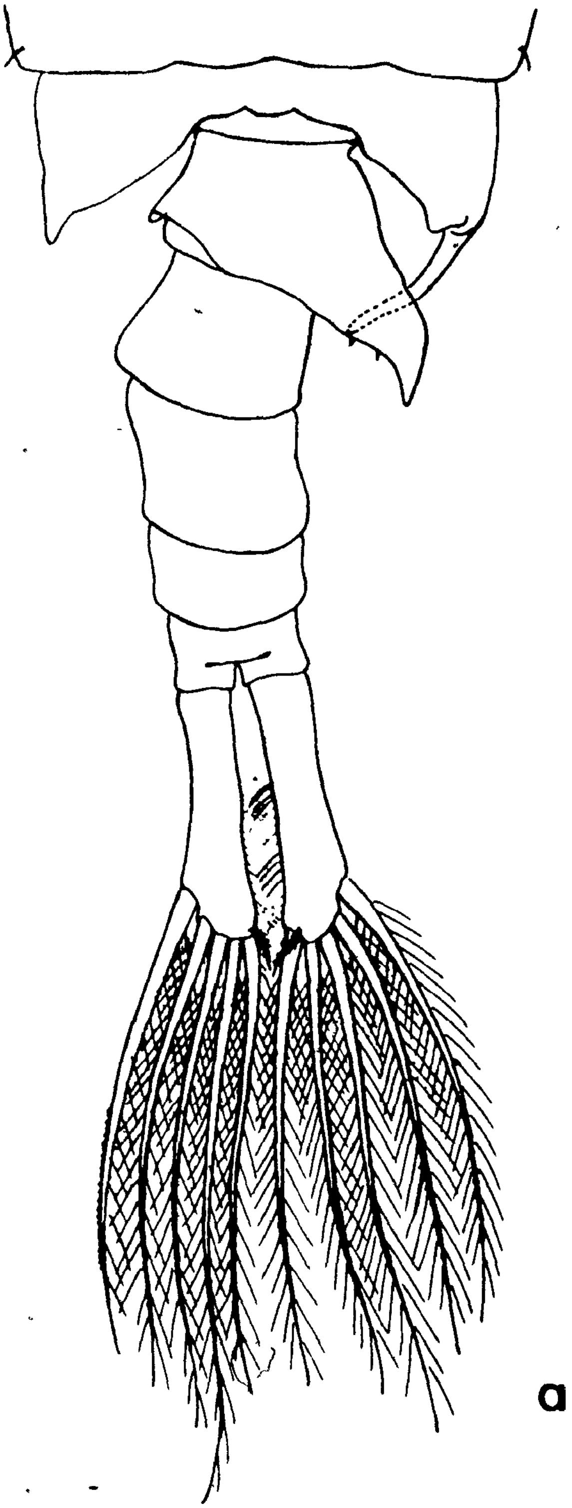
a



b

Figure 5. a) _A._ _opalus_ urosome, dorsal, male

b) _A._ _patersoni_ urosome, dorsal, male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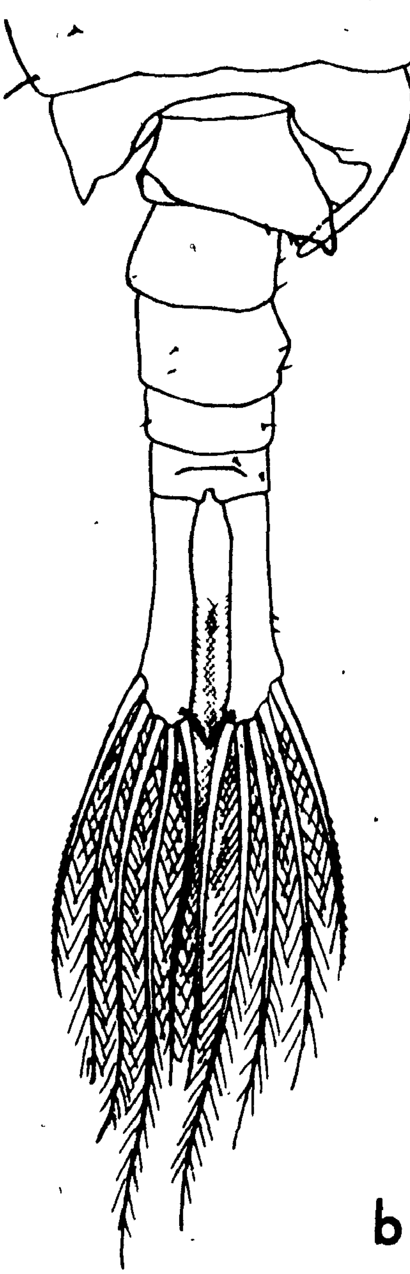
b

Figure 6.
- a) A. opalus urosome, right lateral, male
- b) A. patersoni urosome, right lateral, male
- c) A. opalus urosome, ventral, female
- d) A. patersoni urosome, ventral, female

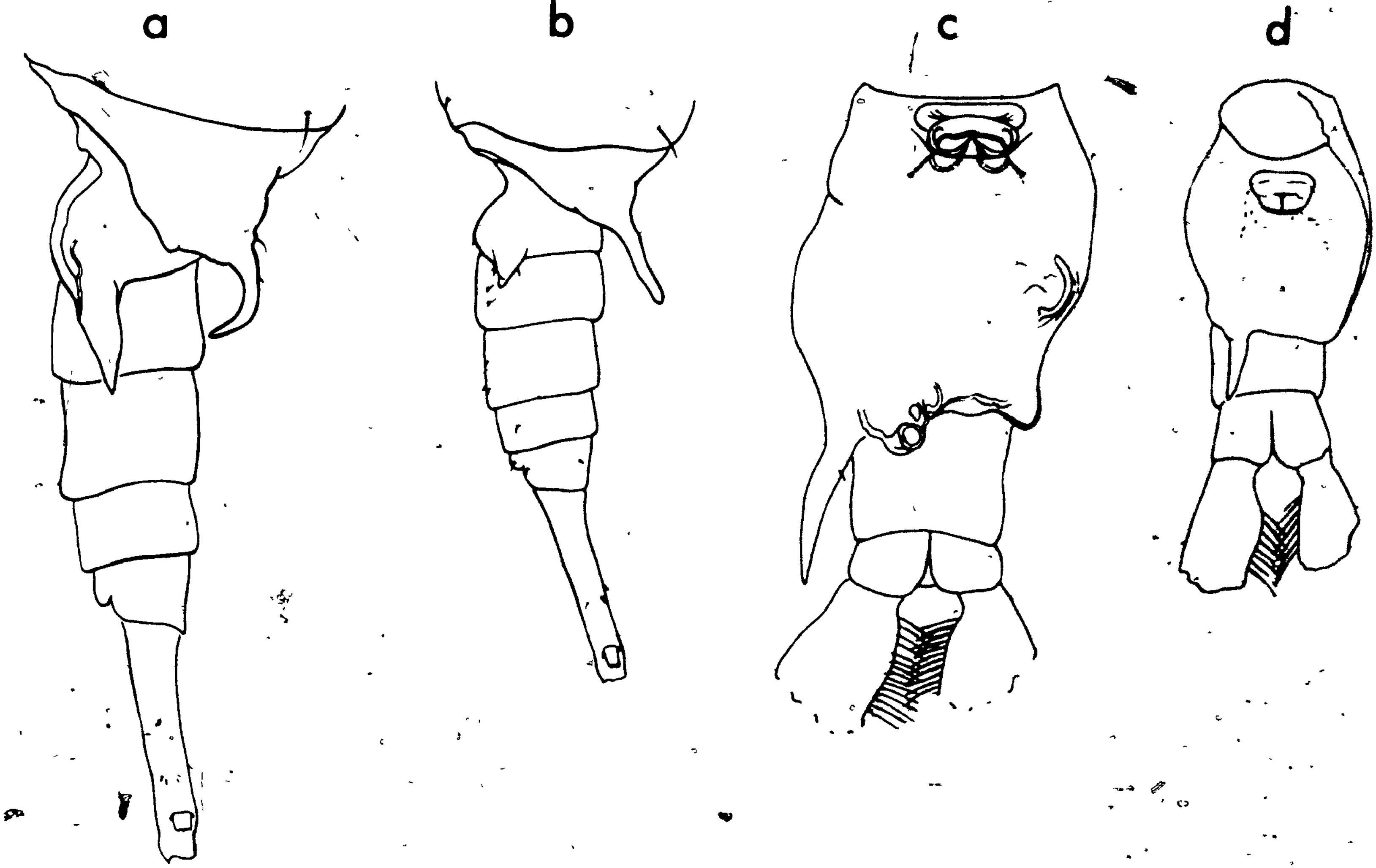
a
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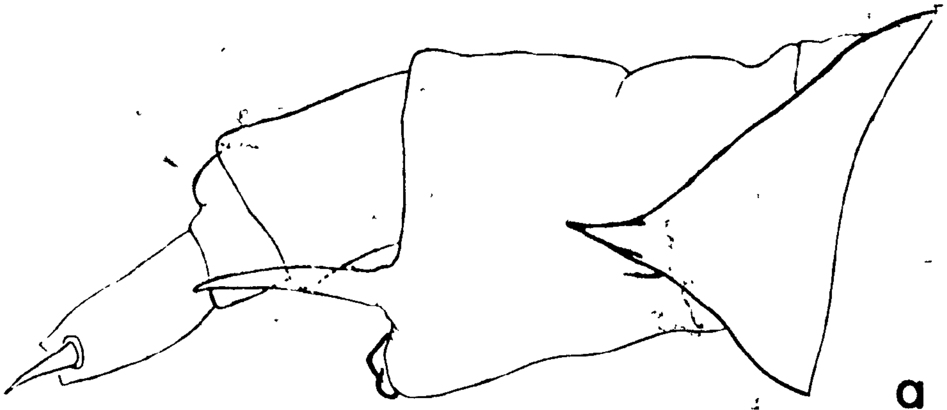
Figure 7. a) *A. opalus* urosome, right lateral, female

b) *A. opalus* urosome, left lateral, female

c) *A. patersoni* urosome, right lateral, female

d) *A. patersoni* urosome, left lateral, female



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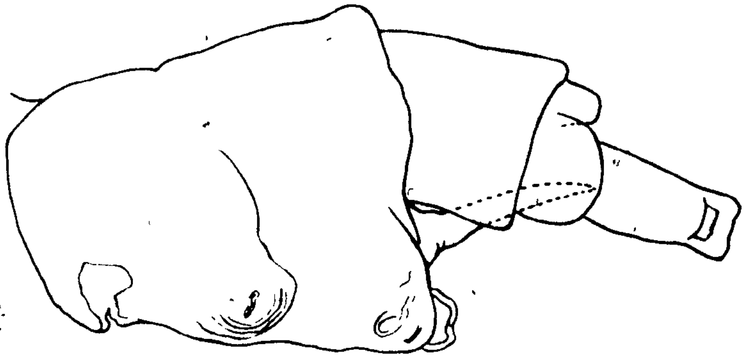

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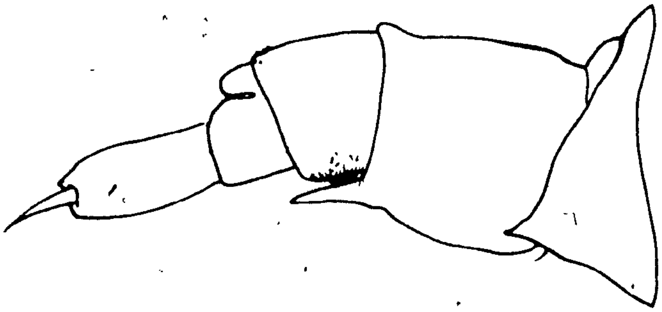

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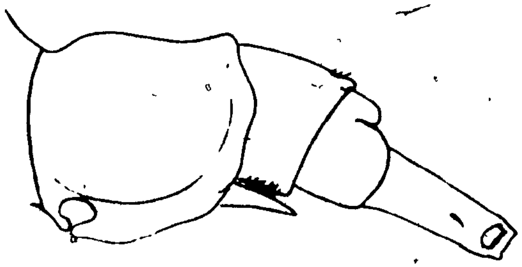

d

Section IV

Geographical distribution of the genus <u>Anomalocera</u>, with emphasis on the North Atlantic

General distribution

The genus Anomalocera comprises three species. A. patersoni was described by Templeton in 1837 from the Irish Sea, A. ornata by Sutcliffe in 1949 from inshore waters of the southern United States, and A. opalus in the present study from the Gulf of St. Lawrence, Gulf of Maine and Scotian shelf waters. Before the present study, the populations, here set up as the new species, A. opalus, were included under the species, A. patersoni. In the following discussion of North Atlantic distributions, these two species will be referred to as A. patersoni sensu lato (s.l.) or simply as Anomalocera, and A. ornata will not be considered unless explicitly mentioned.

A. patersoni s.l. is reported from the Mediterranean Sea (Giesbrecht 1892, Giesbrecht and Schmiel 1898, Rose 1929, Tregouboff and Rose 1957, Vives 1966, Champalbert 1971), the Black Sea (Zaitsev 1961), and the Adriatic Sea (Hure and diCarlo 1968). Wilson (1942) reported it from the Philippines region, but this record has never been substantiated, and there have since been no records of Anomalocera in the Pacific Ocean (Heinrich 1960, Brodski 1950, Mori 1964, Sherman 1964, Tanaka 1964). It is apparently not found in the Indian Ocean (Sewell 1948, Anonymous 1965), nor in the South Atlantic (Brady 1878, Sewell 1948, Bjornberg 1963). It is most often recorded from the North Atlantic Ocean, and its distribution there is discussed below in detail.

Since Templeton's description of A. patersoni from the Irish Sea, there has been confusion whether this species is neritic, oceanic, or intermediate in its distribution, and this has been true on both sides of the Atlantic. Wheeler in 1901, followed by Fish in 1925 and Wilson in 1932, believed that the presence of Anomalocera off Woods Hole, Massachusetts, indicated a Gulf Stream incursion. Deevey (1952) stated that its presence in Block Island Sound was a sign of offshore waters, and she considered it a Gulf Stream copepod. It does not, however, appear to be found in the Gulf Stream (Owre and Foyo 1967, Grice and Hart 1962), or in the Sargasso Sea (Wilson 1936, Moore 1949, Grice and Hart 1952). Sherman and Shaner (1968) have shown it to be most common on the coastal side of Gulf Stream mixing areas near the Gulf of Maine, and Bigelow (1926) presented strong evidence that Anomalocera is an endemic species to the Gulf of Maine, not an immigrant from offshore waters. He considered it to be intermediate between neritic and oceanic.

Similar conflicting opinions are found in reports from European waters. Sars (1903) noted that Anomalocera occurred in Norwegian fjords in the summer after strong onshore gales, and he believed it to be a copepod of the open seas. Farran (1910) and Fleury (1951) both cited it as an oceanic species, and Fraser (1961), on the basis of a sea-ward increase in an area bounded by the Faroe and Shetland Islands, also implied that it was oceanic. Other authors have taken the opposite view and considered Anomalocera a neritic species (Cleve 1900, Wiborg 1905, Murray and Hjort 1912). Colebrooke, John and Brown (1961) and Williamson (1961) considered it to be neither neritic nor oceanic but intermediate. Sewell (1948), using the world distribution map for Anomalocera prepared by Steuer (1933), classified it as neritic but noted that such disputes are common in copepod studies, and that the terms neritic and oceanic may be of limited use as exact natural categories. He cited Dahl (1894), "... many coastal forms occur in isolated instances in the high seas and similarly many oceanic forms occur on the coast." Some species stay well within water mass boundaries while others spread out over wide areas and contribute to overlap in classification schemes (Russell 1935). Such categories are best used only in a very broad sense.

It is noteworthy that most of the workers who have classified A. patersoni s.l. as an oceanic species were shore-based or confined to studies within a limited area (e.g. Wheeler 1901, Fish 1925, Wilson 1932, Deevey 1952, Fraser 1951). Those who considered the species to be neritic or intermediate between neritic and oceanic were more often engaged in broad distributional studies involving large amounts of data over extensive areas (e.g. Bigelow 1926, Sewell 1948, Williamson 1961). The difficulty in determining the distribution of Anomalocera is due in part to its habit of living at the surface interface (Section X); it cannot be well sampled with any of the traditional plankton nets and is frequently under-represented in collections (Zaitsev 1962).

Figure 10 summarizes the North Atlantic distribution of A. patersoni s.l. using data both from the present study and from all available literature. Open ocean cruises from which copepod data have been published or made available are shown in Figure 8 and Table 3. In addition to the plankton gathering cruises, there are extensive data from the Hardy continuous plankton recorder collections both from the open sea and from the shelf waters of the eastern and western North Atlantic (Fig. 9). This material is discussed in the publication, Bulletin of Marine Ecology. The open sea recorder routes are subject to frequent sampling and represent a massive store of data on North Atlantic plankton. Although the recorder does not adequately sample pleuston organisms and is not the best means of studying Anomalocera,

Table 3

Important oceanic cruises in the North Atlantic for which copepod studies are available.

Map symbol (Figure 8)	Ship or cruise designation	Reference to copepod study
A	Challenger	Brady 1883
B	*Continuous plankton samples - transAtlantic	Herdman, Thompson and Scott 1898
C	Fridthjof	With 1915
D	Thor	With 1915
E	Porcupine	With 1915
F	Fram	With 1915
G	Danish Ingolf	With 1915
H	Armourer Hansen	Lysholm and Nordgaard 1921
I	Michael Sars	Strömer 1924 Lysholm and Nordgaard 1945
J	Terra Nova	Farran 1929
K	Prince of Monaco, cruises	Rose 1929
L	Carnegie	Wilson 1942
M	N.Y. - Bermuda, transect	Grice and Hart 1962
N	Oceanographer (1966)	Present study
O	Weather Station M	Kielhorn 1954

* The first continuous plankton samples, taken from ships coolant water across the Atlantic and back again.

Figure 8. Important oceanic cruises in the North Atlantic for which copepod studies are available (see Table 3).

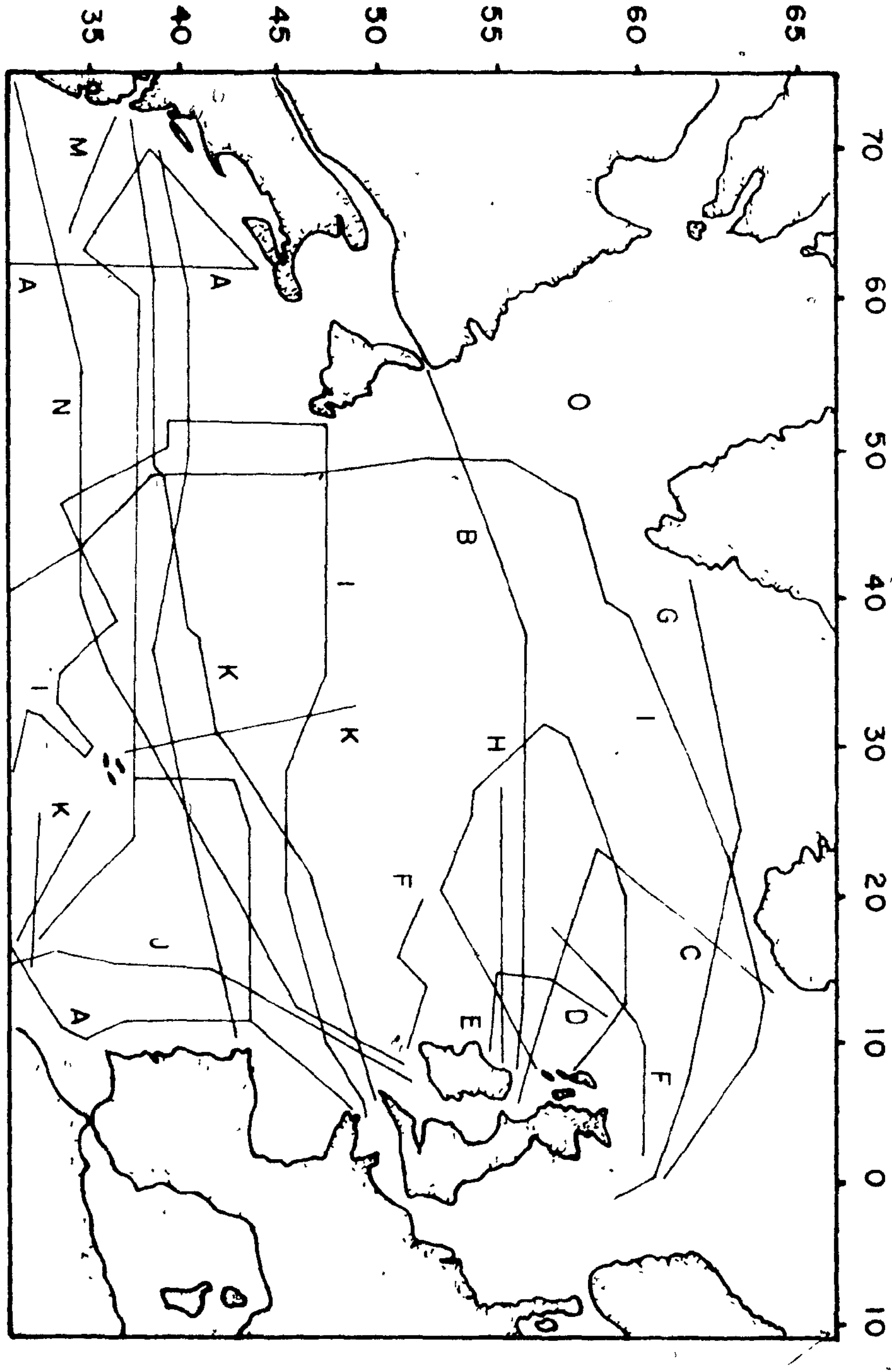
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Figure 9. Hardy continuous plankton recorder cruises in the North Atlantic (repeated regularly). (From Gieskes 1970).

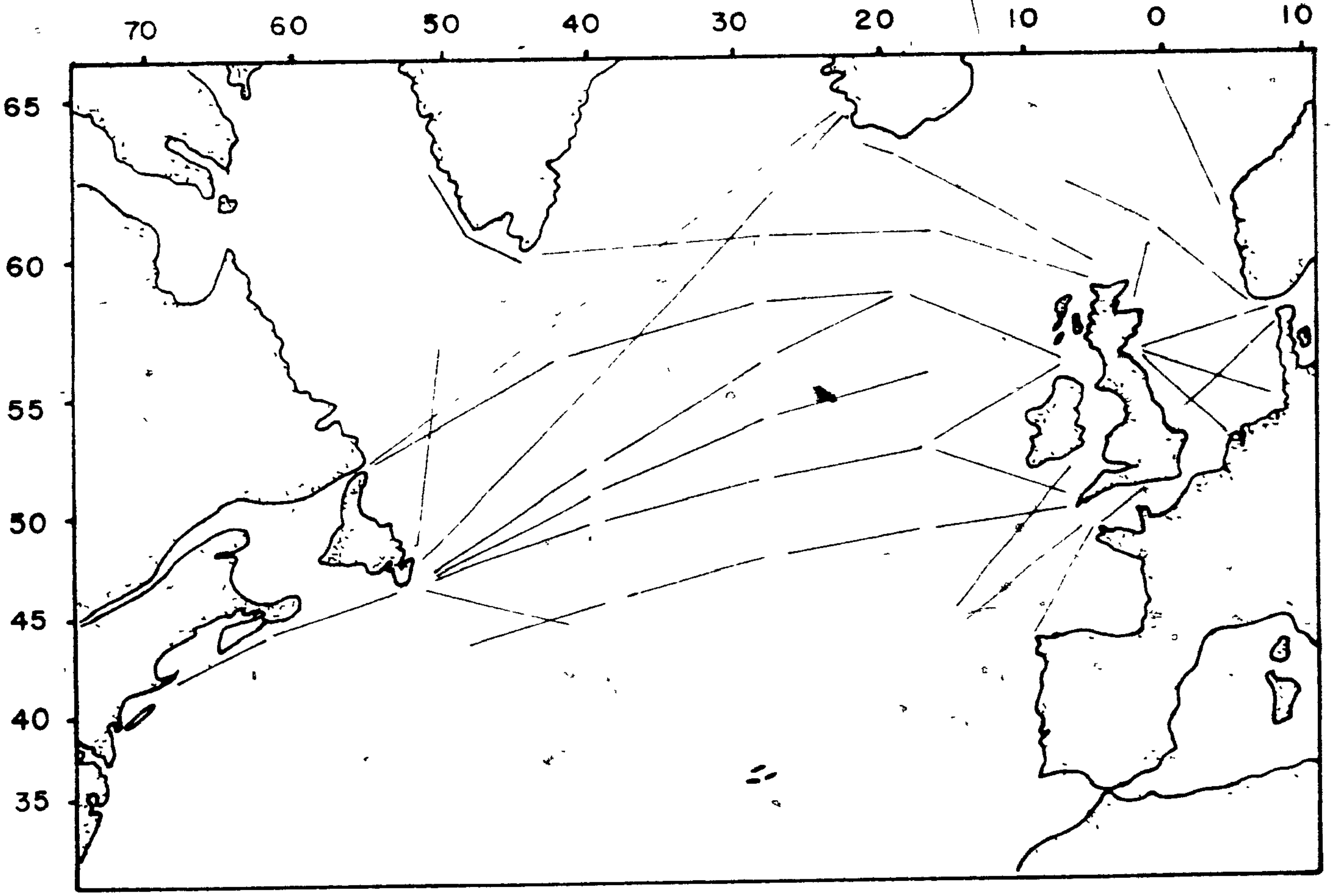
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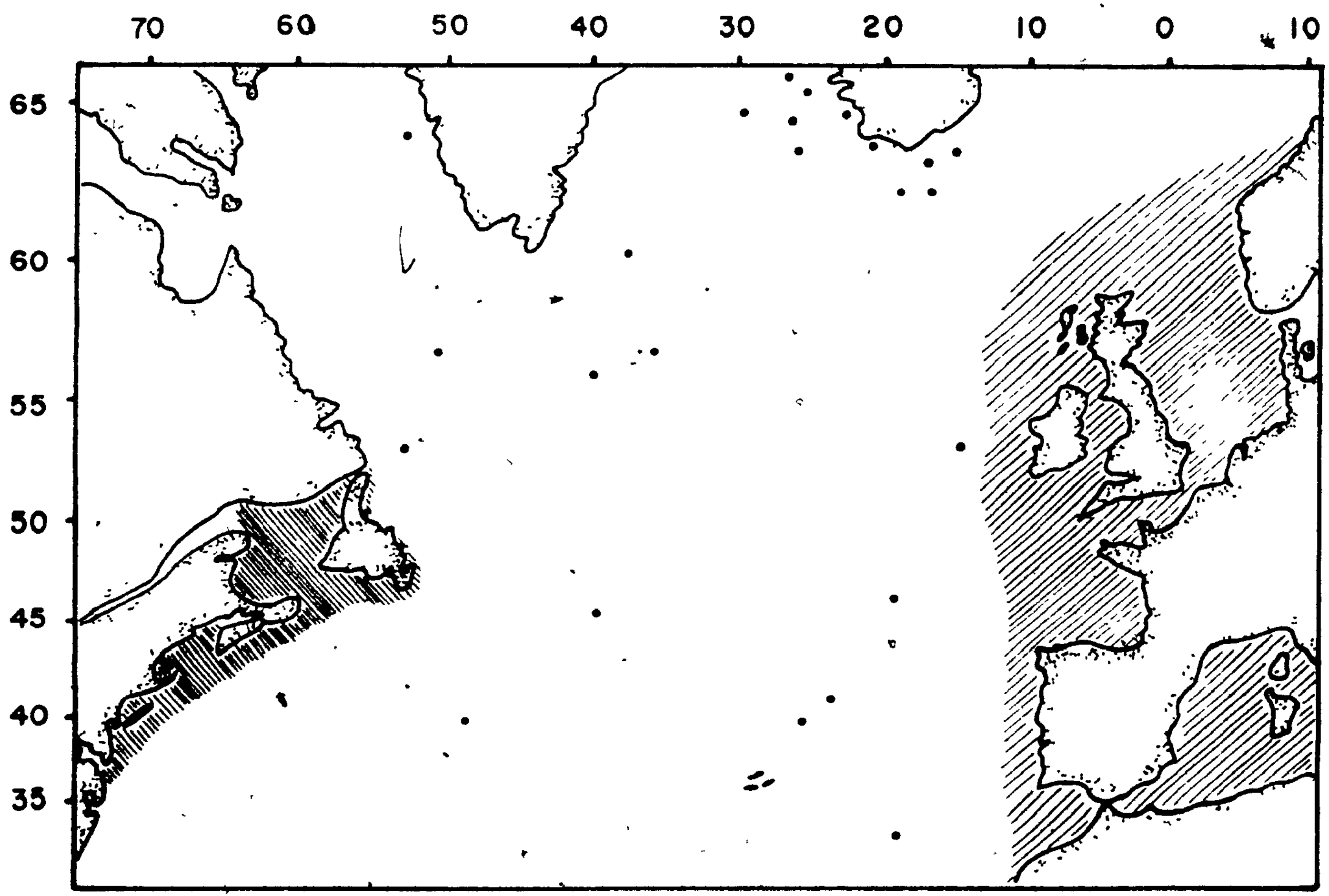
Figure 10. Records of *Anomalocera patersoni* s.l. in the North Atlantic.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it does capture it often in European waters (Colebrooke, John and Brown 1961); in the open ocean samples, *Anomalocera* has been found only three times. Nine additional oceanic records of *Anomalocera* were found in the literature, all consisting of small numbers of adults. In collections from several trans-Atlantic cruises, *Anomalocera* was either over eastern or western shelf waters (or both) but not in the central oceanic waters. One of these cruises, made by the "Oceanographer" in 1966, took many surface plankton samples across the Atlantic. The pontellid copepods from this collection were made available to the present study and were found to contain *Anomalocera* only in samples from waters near the British Isles. Since no immature stages were found in any of the twelve oceanic records, the occasional presence of adults in small numbers far at sea may be attributed to surface drift of shelf waters. The micro-distribution of *Anomalocera* at the very surface renders the animal subject to rapid wind transport (Section VI, p. 98 , Section X, p. 172).

It seems reasonable to conclude that *Anomalocera patersoni* s.l. occurs mainly over shelf waters of the North Atlantic and is found only rarely in the open sea. This point is of considerable importance in the proposal of the new species, *A. opalus*, based on data from inshore collections (Section II) and in the hypothesis of a resting egg in the life cycle in the Gulf of St. Lawrence (Section VI).

Distribution and seasonal occurrence in the eastern North Atlantic

Anomalocera patersoni has long been known from British waters (Baird 1850, Brady 1878, Templeton 1837) and generally from European coastal waters (Steuer 1933), at times in great abundance (Thompson 1889). It has been associated with the onset of the summer fishing season in Norway (Sars 1903), and usually, if only because of its striking appearance, receives mention ~~in~~ the briefest of plankton papers. Its distribution is general over the North Sea, the entrance to the Baltic (but not in the Baltic), and in the Atlantic over the Continental shelf (Colebrook, John and Brown 1961). It is found in mid- to late summer along the coast of Norway (Boeck 1864, Sars 1903, Rose 1929, Wiborg 1934) and has been taken as far north as Latitude 70 at Kval'Sound (T. Scott 1901) and Murmansk (Mrazek 1902).

Jesperson (1940) has reviewed a large body of work on the plankton of Icelandic waters representing thousands of plankton samples and has reported only nine records of *Anomalocera*, all but one along the south coast and all in the summer months. These samples contained only trace amounts of adults, and it seems unlikely that there is a summer breeding population in this region. In the present study, three samples of 30 or more adult *A. patersoni* were examined from the waters just south of Iceland (Fig. 1, Tables 1 and 2). These samples contained no immature forms and probably represent strays from outside the area.

No Anomalocera have been found in East Greenland (Jesperson 1939), and there is only one record from West Greenland (near Godthaab Fjord; Jesperson 1923, 1934). The Greenland material is also large. Kielhorn (1954) found a few adults in Davis Strait after a prolonged S.E. gale; his study from a weather ship consisted of year-round weekly sampling. There do not appear to be summer breeding populations of Anomalocera in the seas of Iceland and Greenland; the small numbers of adults found in these areas in the warmest months probably represent strays from breeding populations further to the south.

In Scottish waters and in the North Sea, Anomalocera makes it first appearance in May but probably not before then (Wolfenden 1904, T. Scott 1911, Fraser and Saville 1948, Fraser 1961). Further to the south, the seasonal distribution seems less well defined, and there is at least the possibility of winter populations in the Irish Sea and off the south coast of England. Anomalocera is a common constituent of the plankton near the Isle of Man (Bruce, Coleman and Jones 1967). Johnston, Scott and Chadwick (1924), reporting on a 14-year study of extensive sampling at Port

Erin, found March to be the month of most usual first occurrence with May and April the months of peak abundance. There were also few winter records. Scattered winter records have been reported for the Irish Sea off Lancashire (Scott 1906) and off Plymouth where there are many more summer records (M.B. Ass. U.K. 1931). These waters may define the northern limit to winter breeding of Anomalocera.

In the Bay of Biscay and off the coast of Portugal, where winter breeding might be expected, there are relatively few records (Candeias 1929, Rose 1929), ~~and it~~ is not possible to determine seasonal distributions of Anomalocera. Rose (1929) found Anomalocera near the Canaries, but Rao (19~~65~~71) and Vervoort (1965) did not find it there. In the Mediterranean and Black Seas, Anomalocera is present the year round, but in the Black Sea it retreats to the south in the winter (Zaitsev, pers. comm.). It has also been found as far south as Latitude 20 off West Africa (Steuer 1933). The breeding range of Anomalocera in the eastern North Atlantic moves northward in the summer at least as far as the North Sea and the waters around Scotland, and possibly to the coasts of Norway. In the winter the range is pushed southward, possibly to the Bay of Biscay and the waters off Portugal. A winter breeding stock in these areas seems probable, but it has not yet been demonstrated.

Distribution and seasonal occurrence in the western North Atlantic

The Gulf of St. Lawrence is the most northern breeding area of Anomalocera in the western North Atlantic; it is found there in the summer months from June to October and is common during late summer (Willey 1919, Pinhey 1927, Filteau 1946, Huntsman, Bailey and Hachey 1954, Lacroix and Bergeron 1953, Lacroix 1966, and the present study, Section VI). Pinhey (1927) showed that it is not found in the Arctic surface waters flowing into the Gulf through the Strait of Belle Isle, but that it is found on the south side of the Strait and along the N.E. coast of Newfoundland south to White Bay. These findings in the Belle Isle region were repeated in the present study during cruises to the area in 1966 and 1967. Anomalocera does not penetrate into the St. Lawrence estuary (Willey 1931, Tremblay 1942, present study).

A. patersoni s.l. is common on the Scotian shelf (Bigelow 1915, Willey 1919, Kearney 1933, Platt and Irwin 1968, and present study), and the south coast of Newfoundland (Lysholm and Nordgaard 1945). It has long been known in the Gulf of Maine in the summer months (Wheeler 1901, Fish 1925, Wilson 1932, Bigelow 1915, 1926, Fish and Johnson 1937, Sherman and Shaner 1968), but never in the winter (the above authors and Sherman, pers. comm.). It also occurs regularly in the Bay of Fundy (Fish and Johnson 1937, Jermolajev 1958, Legaré and Maclellan 1960), although it may occur here a little later in the year than in the Gulf of Maine. Bigelow (1926) found that Anomalocera first appeared in the Gulf of Maine in April and May, but occasionally as early as March. Fish and Johnson (1937), in another very large study, found it from June to September only.

It must be emphasized that there have been no detailed life history studies of Anomalocera outside the Gulf of St. Lawrence (present study), and that the observations taken from the literature refer mainly to late copepodites and adults. This makes possible only the crudest speculations of what the populations are doing. In addition, almost all of the studies used above are based on plankton collections made with gear unsuited to efficient sampling of pleuston animals and such animals will be under-represented in the samples. The loss of precision is great, and these two problems limit the inferences which can be made on the nature of Anomalocera's breeding.

A still more severe problem in the western North Atlantic lies in the southern range of the species; previous to 1949, A. ornata Sutcliffe was not known and, as it has since been reported on several occasions as far north as George's Bank (Sherman and Shaner 1968, Owre and Foyo 1967), it is possible that it was not distinguished from A. patersoni s.l. by earlier authors. Some of the literature discussed below may be misleading for this reason.

Bigelow (1915), in a large summer study of shelf water plankton between Nova Scotia and Chesapeake Bay, found Anomalocera at nearly all stations. Wilson (1932) and Engle and Tan (1965) found it outside Chesapeake Bay in the summer but never inside the bay; Anomalocera is rarely found inside enclosed bays or estuaries (Sars 1903, Bigelow 1915, Deevey 1956, present study). Deevey (1952), in a three-year study of the plankton of Block Island Sound, found it in small numbers from June to October. Bigelow amd Sears (1939) found it in about two percent of 600 stations between Cape Cod and Cape Hatteras in February, and from four to seven percent of the same stations in the spring and summer months. Bigelow (1922) found it widespread in the same area in August. Anomalocera was found in July only during a year long study of a transect between New York and Bermuda (Grice and Hart 1962). Bowman (1971), in an inshore survey between Cape Hatteras and Florida, did not find it, and Sutcliffe (1948), in an extensive study, did not find it in the inshore water off Beaufort, North Carolina.

These scanty records of A. *patersoni*'s southern distribution do not reveal much. There are a few winter citings and somewhat more summer citings between Cape Cod and Cape Hatteras, but there is nothing to firmly demonstrate existence of an over-wintering population or a breeding stock. This is due partly to the lack of data and partly to the taxonomic problem raised by the discovery of the species, A. *ornata*. There is some reason to suspect such winter populations in the warmer waters, but they have yet to be demonstrated. The relevance of southern winter stocks to the life cycle in the Gulf of St. Lawrence and Gulf of Maine bears on the hypothesis of a resting egg as the wintering mechanism in these areas; this is discussed in Section VI.

Temperature and salinity tolerances

In the above review, sea temperature has been alluded to only indirectly, and salinity has not been discussed at all. Although it might be useful to establish *Anomalocera*'s preferences of these variables with respect to breeding, growth and distribution, this is not yet possible, and the range of tolerances to salinity and temperature shown by this copepod are so great that it would be exceedingly difficult to do so. Bigelow (1915) gives a temperature range of 13.5°C (12 - 25.5°C) and 3.15°/oo salinity (32.1 - 35.25°/oo) in the Gulf of Maine alone. He notes that Anomalocera in the eastern North Atlantic lives in "rather saltier water" of high temperature. In the Gulf of St. Lawrence (Tables 8, 9 and 10, and Fig 18), the temperature range was much wider, nearly 18°C (1.7 - 19.4°C), with nauplii occurring in small numbers at the lowest temperature. Salinity ranged from 27.6 to 32.2°/oo. It is probable that both Anomalocera opalus and A. patersoni require temperatures in excess of 12°C in order to increase in numbers, but this is not proven and a more exact temperature requirement cannot be formulated for these eurythermal species. There may also be factors more important to Anomalocera's life cycle than temperature and salinity.

Section V

The speciation of _Anomalocera_ _patersoni_ and _A_. _opalus_

In Sections IV and II on the distribution of Anomalocera in the North Atlantic and the proposal of the new species, A. opalus, efforts were made to demonstrate the improbability of significant contact between A. opalus in the west and A. patersoni in the east. Adults have been found as traces in a few oceanic samples and in northern shelf waters of Iceland and West Greenland; none of these samples is thought to represent a breeding population. In the discussion below of Anomalocera's speciation, the possibility is raised that these northern shelf waters may have been more hospitable to Anomalocera in the past.

Allopatric versus sympatric speciation

In any discussion of species formation, it is necessary to clarify the conceptual model being used. This usually amounts to a distinction between the allopatric and sympatric models of speciation.. Arguments between adherents of these two models have gone on for at least a century, often in a repetitive and non-progressive way (Mayr 1963) which may indicate the state of maturity within this branch of science (Kuhn 1970). At present the overwhelming support of terrestrial biologists goes to the allopatric theory (excluding well-known cases of polyploidy among plants), and there is much evidence to support the consensus. It is to be noted, however, that evidence of speciation is always indirect and arguments often take place on a logical plane which can lead to breakdown over definitions.

When dealing with terrestrial situations, it would not usually be necessary to weigh the relative merits of the two speciation theories except in a few special cases (e.g. White 1968). The allopatric model would be assumed. By contrast, marine life and especially pelagic life seems to offer problems to many workers, and these problems will be briefly discussed below before taking up the speciation of <u>Anomalocera</u>.

Thorpe (1960) notes that Mayr (1942) had initially used the term "sympatric" to mean species formation within a freely interbreeding population. Later (1963), he had changed this to species formation within the cruising range of individuals in the population or within the geographical range of the initial species. Mayr (1963) points out that the allopatric formulation demands the introduction of extrinsic barriers such as distance or relief to separate sub-populations which may genetically diverge during the time of separation. The real issue, however, is that of gene flow and not the particular type of barrier to gene flow; more than one factor may be necessary to adequately slow gene flow between two populations to allow genetic divergence to take place (Thorpe 1960). Nevertheless, there remains a real distinction between the allopatric theory's requirement of an extrinsic barrier and the sympatric theory's lack of such demand. There are also formidable thickets of semantics to be got through.

The sympatric model ultimately supposes that the necessary barriers will arise within the population, but in many cases the nature of the barriers is left to the imagination, and the grounds for choosing this model may be that the allopatric model seems impossible. At other times, extrinsic barriers work their way into supposedly sympatric models; for instance, many proposals of ecological speciation, a variant of sympatric speciation, contain a hidden geographical component which acts as a barrier to gene flow (e.g. Test 1946). Extrinsic barriers form the main obstacle to the acceptance of the allopatric model by marine biologists. In the sea, at least superficially, there seem to be few barriers. Colebrook and Robinson (1963) note, "the epipelagic zone of the sea is, by terrestrial standards, a very uniform environment with few physical barriers to dispersal."

Mayr (1963) remarks, "A rapid process of species formation is implied in most schemes of sympatric speciation." and that if ecological speciation "... led to species formation without geographical isolation, we would have a vastly greater number of species than we actually have." Although the latter statement is logically untenable, it emphasizes a common feeling about the two models of speciation and which, with a curious reverse twist, seems to have motivated many of the workers who are dissatisfied with the theory of allopatric speciation in the sea (e.g. Buzzati-Traverso 1960, Fretter and Graham 1959, Beklemishev 1960, Kohn 1960, Wieser 1960, Dunbar 1972). The proponents of sympatric speciation in the sea hold Mayr's view in reverse; they think that there are more marine species than could have been caused by allopatric speciation alone.

There are in fact many fewer species in the oceans than on land (McGowan 1971) which could indicate a low rate of speciation (a point for the allopatric theory), but which is more likely related to lack of habitat diversity. There is also a high degree of cosmopolitanism in marine pelagic life, as noted by Ekman (1953), "The main faunistic regions of the high-oceanic pelagic fauna are more weakly characterized taxonomically than the main regions of the shelf." This probably indicates a rapid dispersal of pelagic organisms in the face of fewer barriers (a point for the sympatric theory), although other interpretations are possible. Ultimately the weight given these generalizations is subjective and neither diversity nor taxonomic development provides suitable clues to how marine animals speciate.

The allopatric model, in several cases, is as convincing in the marine environment as it has been in terrestrial situations. Brinton (1959) uses an invasion-reinvasion model to explain the speciation of closely related anti-tropical euphausids. Glacial periods which cool ocean temperatures could allow a high latitude species to cross the equatorial zone. Warming periods would divide the population into dimeric isolates through heating the equatorial waters and making them uninhabitable to the species. A further cooling period would allow the isolates to come into contact again after accumulating sufficient genetic divergence to prohibit gene flow. It has been pointed out that this model will not work for equatorial and antarctic forms (McGowan 1963).

Brown (1957) proposes a model of speciation involving alternate expansion and contraction of a species' range due to changes in the environment. After a contraction during unfavourable conditions, only scattered refuge populations of somewhat different genetic make-up will be left in the former peripheral zones. These outlying and cut-off populations will continue to diverge genetically until, by the time of another expansion when they again contact the mother population, they will be reproductive isolates.

McGowan (1963) considers this model free from the need of intervening extrinsic barriers. Geographical barriers are very much involved, however, and it is difficult to see them as anything but extrinsically induced by environmental changes.

Another model of pelagic speciation is proposed by Buzzati-Traverso (1958, 1960) and applied to an actual situation by McGowan (1963). This model is also introduced as being independent of extrinsic barrier formation or spatial isolation of sub-populations. A plankton species is carried by currents from its main population centre to another area of retention of different environmental characteristics. Both en route and upon arrival, there is a strong selection against certain genes which results in an altered gene pool in the new population. Selection continues until the new population is reproductively isolated from the old and from the continuing influx of immigrants. It seems obvious that this theory is the same as the theory of island speciation as proposed by Mayr (1963) and MacArthur and Wilson (1967) (see also Thorpe 1960). It is the amount of gene flow that is important.

David (1963) reviews the speciation of planktonic chaetognaths in allopatric terms and discusses the nature of barriers in the oceans. He concludes that very fine differences in physical parameters such as temperature and salinity may be of great importance in determining distributions, and that an understanding of distributions may clarify the nature of pelagic speciation. David also emphasizes that other factors such as food may be more important than the physical characteristics of water masses. McGowan (1971) makes similar suggestions and cites Macfayden (1957); we must know what factors are relevant from the animal's point of view and often we do not know this. It is likely that the seas are very much less homogeneous than they at first appear (for example see Cooper 1967, and Gregg 1975).

In the main, the sympatric model of speciation has not been successful in the marine environment. Proposals of this model are factually mistaken (e.g. Test 1946, in Kohn 1960), turn out to be variants of allopatric speciation in thin disguise (Brown 1957, Buzzati-Traverso 1958), or they provide no detailed mechanism (Fretter and Graham 1959, Kohn 1960, see discussion of this point in Dunbar 1972). The allopatric model does work, and objections to it are for the most part psychological. It will be assumed in the following discussion of <u>Anomalocera</u>'s speciation.

Climatic change and the speciation of Anomalocera

There is an abundance of climatic changes reported for the Pleistocene era which would have affected North Atlantic water temperatures (Ekman 1953, Denton and Porter 1970, Dansgaard, Johnsen, Clausen and Langway 1971, Ewing 1971, McIntyre, Ruddiman and Jantzen 1972). Dansgaard et al have found a 68-78 year cycling of warming and cooling periods of moderate magnitude. Superimposed on these are longer term changes in climate such as the Little Ice Age of 1600-1740 and the cool period of the fifteenth century which is considered to have broken the connection between the Norse settlements of Greenland and Iceland. Dunbar (1973) notes that such short-term climatic changes can quickly change distributions of marine pelagic life.

Ewing discusses longer term Pleistocene climatic fluctuations from 70,000 to 100,000 years of greater temperature changes. McIntyre et al correlate microplankton facies changes in the mid-Atlantic ridge sediments with latitudinal shifts of North Atlantic water masses over approximately this time scale. The problem with reference to the history of Anomalocera species is that of which time scale to consider.

The time taken to form new species varies greatly and cannot usually be estimated. In some cases, it can be extremely rapid and a few situations have lent themselves to reliable dating. The formation of the Red Sea endemic fauna is known to have taken about one million years (Ekman 1953). Species swarms in fresh water lakes provide the most dramatic instances of rapid species formation (Lake Nabugabo near Lake Victoria, five species of cichlids in 4000 years; Lake Lanao in the Philippines, 18 species of cichlids in 10,000 years) (Myers 1960). Mayr (1963) comments on these findings and gives estimates of about 100,000 years for the formation of certain marine fishes, including a Mediterranean herring. In the case of marine copepods such as Anomalocera it is not realistic to estimate speciation time except to suggest that the events of the Pleistocene provided the climatic fluctuations over adequate periods of time necessary to most hypotheses of allopatric speciation. Periods of climatic change and geographical separation are combined below in a theory of Anomalocera's speciation into _A_. _opalus_ and _A_. _patersoni_.

The temperature requirements of _Anomalocera_ spp. for successful breeding are not known in any detail (Section IV, p. 68). Both _A_. _patersoni_ and _A_. _opalus_ breed in the summer over a large temperature range, in places spanning as much as 18°C (Section IV), and only in the Gulf of St. Lawrence has there been a detailed study of the life history of an Anomalocera species (Section VI). From this study (see Fig. 17, Tables 8, 9 and 10), only a rough estimate of temperature-breeding relationships can be seen; 12-18°C seems to be the range of maximum population size and population growth of A. opalus. As Andrewartha and Birch (1954) have repeatedly pointed out, small variations in temperature can have large effects on population increases or declines. Examination of monthly sea-surface isotherms near the south coast of Iceland (Gieskes 1970, from Krauss 1958) shows that the coastal waters reach 11°C for only two months of the year, July and August. It may be that a slight rise of as little as three degrees centigrade would make possible the establishment of summer breeding populations in these waters, much as a drop in temperature of a similar magnitude eliminated breeding populations of Norsemen in West Greenland.

As noted above (Section III), the strongest distinguishing differences between A. opalus and A. patersoni are to be found in the genital segments of both sexes, which as Mayr (1963) points out is for many species pairs, an indication that previously separated populations have been brought back into contact with each other and that selection has furthered mechanisms to prevent wasteful breeding between two genetic types (wasteful in this context can refer to fruitless use of gametes and energy during mating as well as production of sterile or unfit hybrids). The genital segments of copepods are well known to be highly specific (Fleminger 1967, Geptnev 1968) and are in many instances similar to a lock and key mechanisms ~~in~~ that the male of one species will fit only females of the same species (Lee 197~~1~~2). This would suggest that the original Anomalocera population has been separated, reunited and separated again to create the present day situation. Similar arguments could be made for the formation of A. ornata.

If the history of Anomalocera's speciation involves much guesswork, then the origin of the genus is still more conjectural. Pontellid copepods are predominantly tropical (David 1965, Sherman 1964), although the large genus, Labidocera, is found in temperate regions, and Epilabidocera is found in the Arctic. Ocean systems of the past are difficult to determine, and that plankton species must always spread with dominant current systems is, although plausible, not necessarily true, especially for neritic species. It is possible that the eastern North Atlantic population of Anomalocera once spread to the west by way of Iceland, West Greenland and Newfoundland to the Scotian shelf and down the

North Atlantic coast in westerly currents and gyres north of the North Atlantic Drift. Multiple invasions in this manner could explain the formation of _A_. _ornata_ in southern inshore waters and the Gulf of Mexico.

Section VI

The life cycle of Anomalocera opalus in the Gulf of St. Lawrence

The collections

Facilities for a three-year shore-based field study were provided by the Station de Biologie Marine at Grande-Rivière and at Magdalen Islands field laboratory on Grindstone Islands. Winter cruises on icebreakers were made possible by courtesy of the Canadian Department of Transport. Collections were taken on other cruises made by the Marine Sciences Centre, McGill University, and by the Fisheries Research Board of Canada, Huntsman Biological Laboratory, St. Andrews, New Brunswick. Unless otherwise stated, all field work and cruises were made by the author.

The first series of pleuston samples was begun in March 1966 at Grande-Rivière on the south Gaspé coast. The early samples were taken from very small boats, often during ice conditions. Later samples were taken from a variety of chartered fishing boats, usually 65 foot draggers. The early samples were taken from one to three miles off shore; the later samples were taken at a standard station used by the laboratory (station 112) about five miles offshore over the 60 fathom contour. Several pleuston samples and one or more vertical plankton hauls were taken during each day's sampling. An attempt was made to sample at station 112 at weekly intervals, although this was not always possible. The series was run until mid-November.

A similar program was run in 1967 at the Magdalen Islands from May to September. Four pleuston samples and two vertical hauls were made on each day's sampling and samples were made at approximately weekly intervals. A three-stage pleuston net was used extensively to study micro-vertical distribution. Most of the work was done a few miles offshore from the town of Grindstone but difficulties with the station boat made chartering of boats from other parts of the island necessary. Figure 11 gives the positions of sampling at the Magdalen Islands. In 1968, a third series of pleuston samples and vertical hauls was made by Mr. Martin Weinstein at the station 112 off Grande-Rivière. This series ran from June to October.

Winter plankton work was done from icebreakers and from the Bedford Institute ship, the "Dawson", over different parts of the Gulf. In March of 1967, a cruise was made over the Laurentian Channel on the icebreaker "d'Iberville". Deep vertical hauls were made at several stations. In March 1968, Mr. Weinstein collected plankton from the icebreaker "Labrador", and, in 1969, Mr. G. Tidmarsh made a larger plankton collection from the "Dawson" during a winter of very little ice in the Gulf. The stations made during these cruises are given in Figures 12 and 13 and Tables 4 and 5, which also describe the plankton samples taken.

Additional cruises were made in the Gulf of St. Lawrence during the spring and summer in both 1966 and 1967. Mr. L. Doran made available the Anomalocera found in a larval fish survey made by the RS "A.T. Cameron" in August 1965 over the Magdalen Shallows. In May of 1966, pleuston samples were taken on a similar "A.T. Cameron" cruise over the same area (Fig. 14), with the same equipment used from the shore stations. Other samples made for a fish egg and larva survey on the same cruise were also available for shipboard examination. Another cruise was taken in July of 1966 to the north east area of the Gulf, including the Strait of Belle Isle. The ship used was the "Theta" under charter for the Marine Sciences Centre. Many pleuston samples were taken during this cruise as well as many deep plankton hauls.

In August of 1967, a ten-day cruise over the entire Gulf was made on the C.S. "Hudson" (Fig. 15), with ship-time made available by the Bedford Institute. Similar work was done on this cruise with the addition of observations on live A. opalus and an increased number of micro-distribution samples. These summer cruises provided material that may be of more use to future pleuston work than to the present study. Their main value to this work lay in the opportunity to take many night samples, something not possible from the shore stations, and to examine the micro-distribution of

Figure 11. Map of sampling stations at the Magdalen Islands, summer 1967.

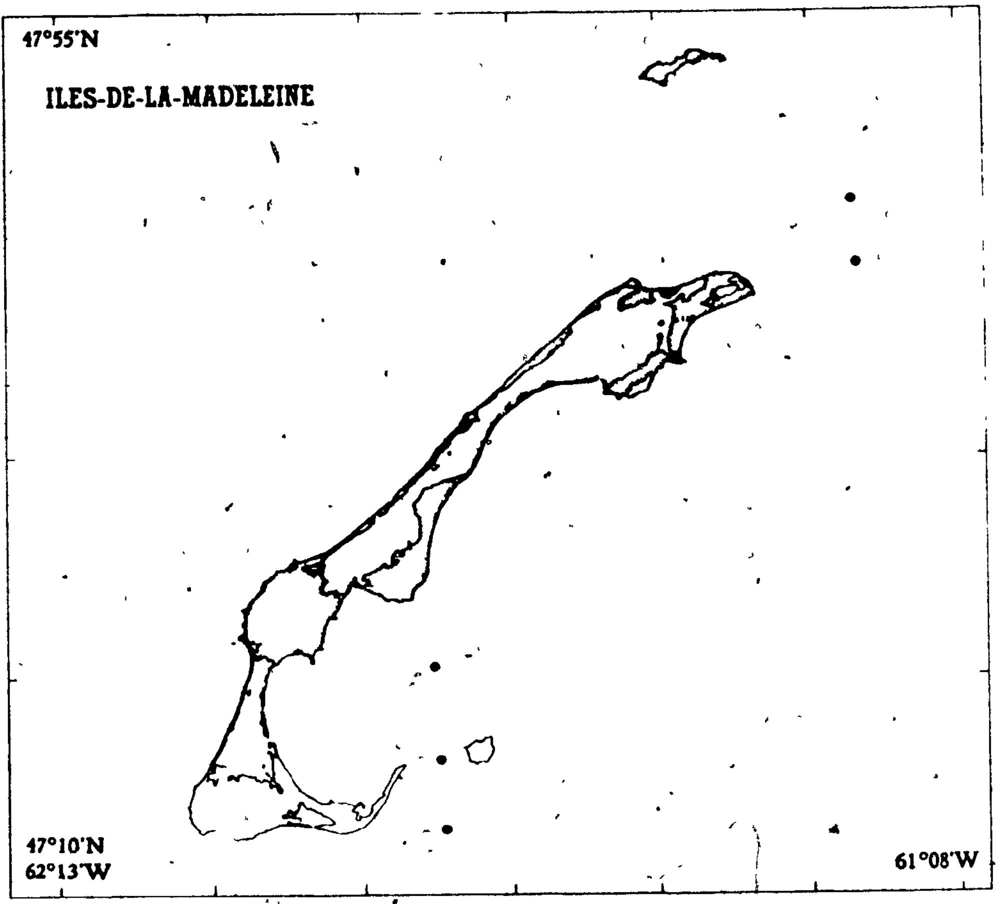

47°55'N
ILES-DE-LA-MADELEINE
47°10'N
62°13'W
61°08'W

Table 4

Late winter cruises in the Gulf of St. Lawrence

Date	Lat. N	Long.W	Type of sample	Depth of sample	E.S.T.
			1967 - d'Iberville		
March 2	49°22'	64°58'	½ meter net #20 mesh Vertical hauls	1st, 20 meters 2nd, 375 meters	0930 hrs
March 3	48°44'	61°26'	" " "	1st, ca 300 m (from bottom) 2nd, ca 300 m (from bottom)	2000 hrs
March 4	47°52'	59°53.5'	" " "	1st, 350-400 m 2nd, " "	2000 hrs
March 5	48°06'	59°53'	" " "	1st, 350-400 m 2nd, " "	1930 hrs
March 6	48°18'	63°55.5'	" " "	1st, 90 m from bottom 2nd, 90 m from bottom 3rd, 90 m from bottom	2300 hrs
			1968 - Labrador		
April	47°52'	60°16	#6 mesh Vertical hauls	1st, 490 m 2nd, "	-
April	48°24'	60°21'	" " "	1st, 440 m 2nd, "	-
April	49°16'	64°08'	" " "	1st, 400 m 2nd, "	-

Table 5

C.S.S. "Dawson" cruise - January 1969*

Date	Lat. N	Long. W	Type of sample	Depth of sample	approx. E.S.T.
Jan. 19	47°06.3'	60°45.0'	Vertical	160 m	2400 hrs
			Horizontal	125 m	
Jan. 10	47°41.0'	63°25.5'	Vertical	65 m	0800 hrs
			Horizontal	26 m	
Jan. 11	49°19.5'	64°50.5'	Vertical	190 m	2000 hrs
Jan. 13	48°58.7'	67°55.7'	Vertical	280 m	0300 hrs
Jan. 14	49°45.3'	65°39.0'	Horizontal	100 m	1300 hrs
	50°02.0'	64°05.0'	Vertical	120 m	1900 hrs
Jan. 15	49°41.3'	61°04.5'	Vertical	250 m	0900 hrs
			Vertical	175 m	
	50°06.5'	59°24.0'	Vertical	150 m	0700 hrs
			Vertical	90 m	
Jan. 16	51°12.0'	57°42.8'	Vertical	145 m	
Jan. 17	49°54.4'	58°52.1'	Vertical	205 m	0000 hrs
			Horizontal	150 m	
			Horizontal	200 m	
	49°02.5'	60°16.0'	Vertical	250 m	1800 hrs
			Horizontal	180 m	
Jan. 18	48°26.1'	62°29.0'	Vertical	350 m	0500 hrs
			Vertical	300 m	
	46°59.0'	62°46.3'	Vertical	250 m	1600 hrs
			Vertical	60 m	
			Horizontal	50 m	
Jan. 19	48°17.9'	61°01.0'	Vertical	400 m	0800 hrs
			Horizontal	250 m	

* All ½ m nets, #6 mesh. All horizontal tows, 10 mins.

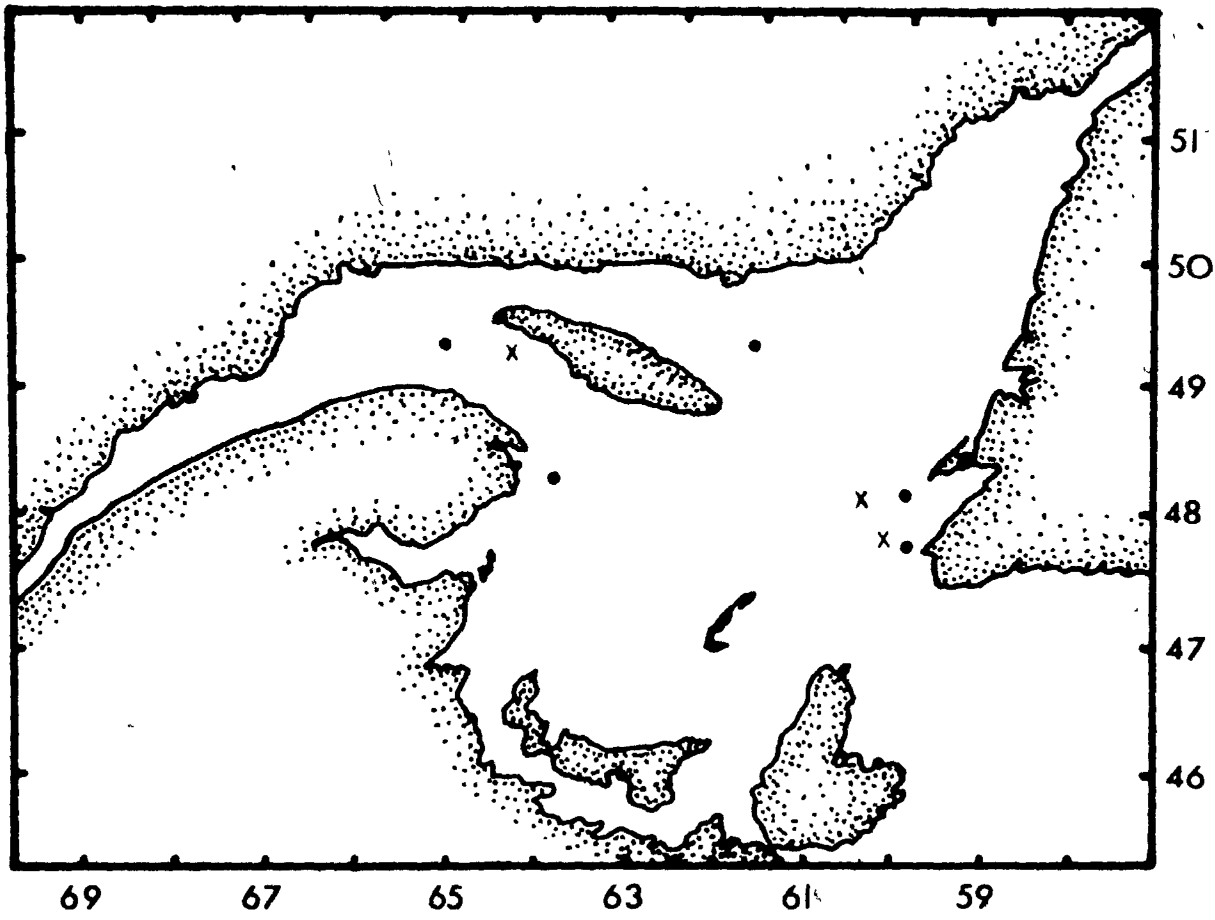
Table 5 (cont'd)

Date	Lat. N	Long. W	Type of sample	Depth of sample	approx. E.S.T.
Jan. 19	47°51.7'	59°58.0'	Vertical	450 m	1700 hrs
			Vertical	275 m	
			Horizontal	200 m	
Jan. 22	47°21.8'	59°47.2'	Vertical	450 m	0200 hrs
			Vertical	300 m	
			Horizontal	200 m	
	47°51.7'	59°25.0'	Vertical	350 m	0500 hrs
			Vertical	200 m	
			Horizontal	125 m	
Jan. 21	47°08.4'	60°12.0'	Vertical	190 m	2200 hrs
			Horizontal	150 m	
	47°08.0'	60°12.0'	Horizontal	200 - 300 m	0300 hrs

Figure 12. Map of two icebreaker cruises:

circles - "d'Iberville", March 1967

crosses - "Labrador", March 1968


51
50
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69
67
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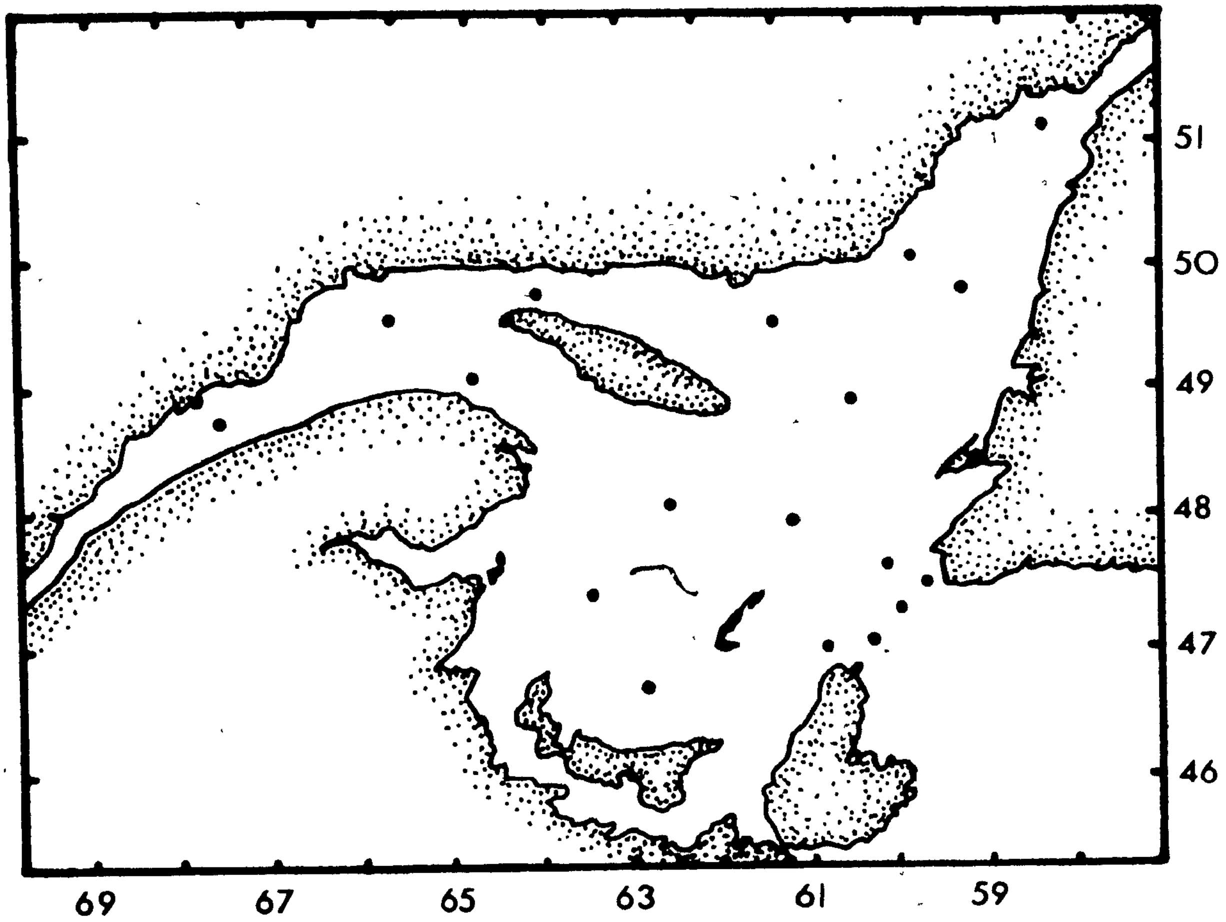
63
61
59
x
x
x

Figure 13. Map of the "Dawson" cruise, January 1969


51
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61
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Figure 14. Map of the "A.T. Cameron" cruise, May - June, 1966.

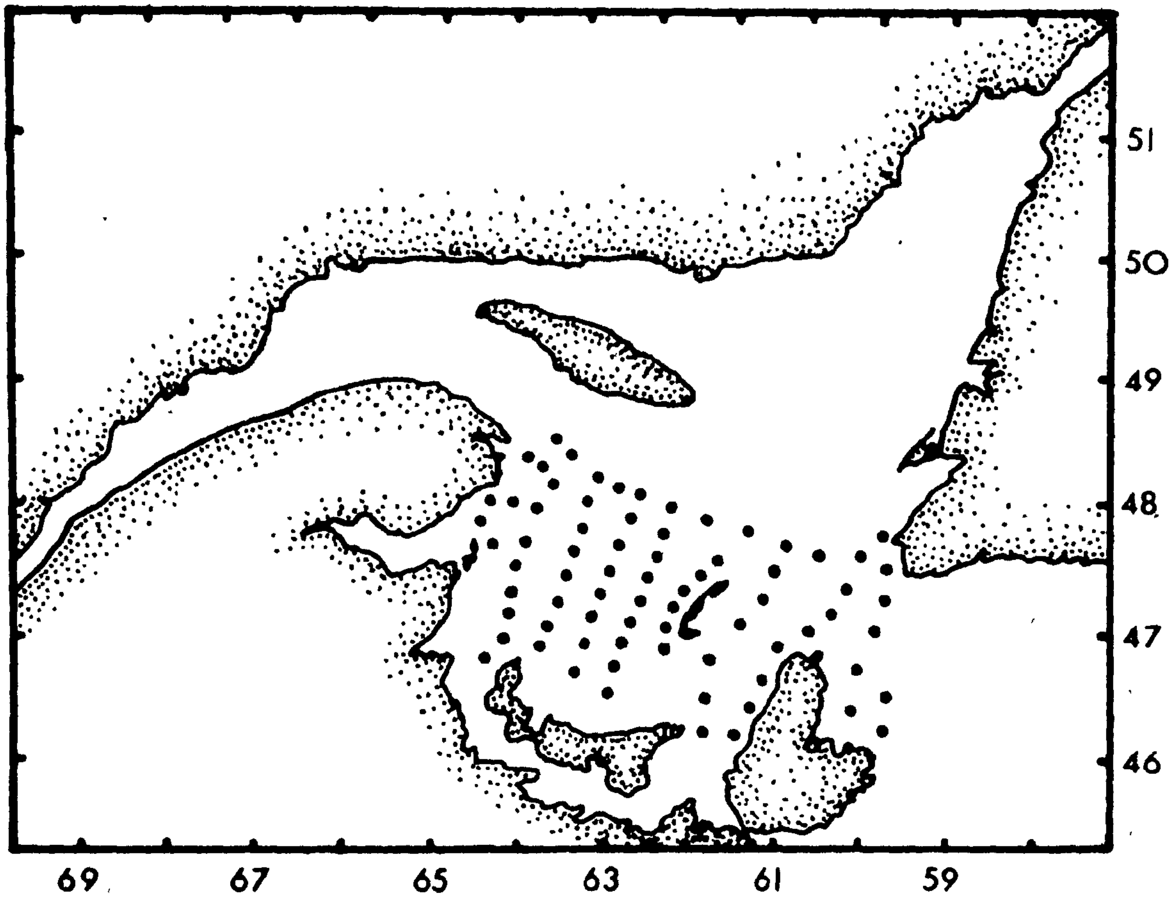
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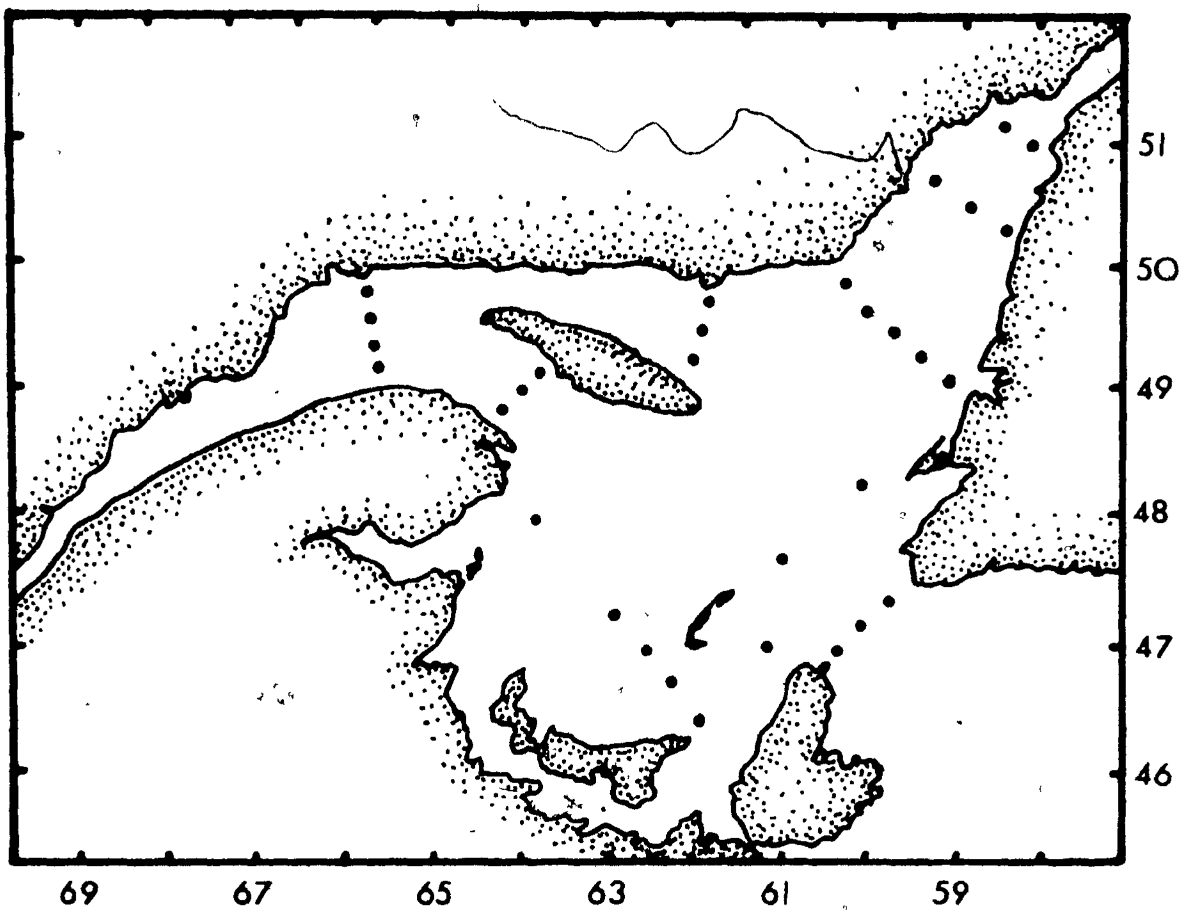
Figure 15. Map of the "Hudson" cruise, August 1967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A. opalus throughout the Gulf of St. Lawrence under different environmental conditions. The "Hudson" cruise of 1967 provided much fresh material for the investigation of the pigment systems of A. opalus. The extreme patchiness of the copepod over both short and long distances and its widespread distribution in the Gulf were demonstrated. The "A.T. Cameron" cruise taken in May 1966 was extremely valuable in that no Anomalocera were found at that time over a wide area of the Gulf, a fact which bears on the argument for a resting egg (see below). Analysis of areal distributions of Anomalocera's abundance and stage composition seemed pointless because the cruises were taken at different seasons, years and areas.

Materials and methods

A pleuston net of the design given by David (1965a) was used initially, but its large size and lack of flotation made it impossible to use from the small boats available at the shore stations, and it was very easily damaged when used from large ships. A smaller model (2/3 scale) of David's net was built and used for most of the study with great success (Fig. 16). The apparatus consists of two wide skiis about 4 feet in length with attached inner keels, joined by two three foot cross members from which the semi-submerged rectangular net frame is suspended. The keel of this scaled down model is relatively deeper (18 inches) than David's, and styrofoam was molded beneath the skiis to increase flotation. (In 1967 an improved model with fibreglass-covered floats was constructed by Mr. Paul Brodie). Bridles are run from the tips of the skiis to a junction set so that the inner bridle is shorter than the outer bridle when the net is towed. This results in a shearing away from the ship's side so that the net can fish in water undisturbed by the ship's bow wave; the deeper keels increase the shearing effect. The plankton nets used had a rectangular mouth 6 x 8 inches and were six feet long. The high ratio of net length to mouth area gives them a very high filtration efficiency. The net was immersed to a depth of about four inches which became reduced to about two or three inches when the net was under way. Slight adjustments of trim were made by attaching weights to the rear of the skiis. The increased buoyancy of the entire system allowed the net to be hauled at slow speeds with only slight variation in net immersion depth. This was not possible with the original design which had to be used at higher speeds and with a sharp cable angle. The larger net also gave trouble when used in heavy seas, but the 2/3 scale net towed perfectly in very rough water.

The pleuston samples taken approximately weekly from the shore stations and during the summer cruises were

Figure 16. Photograph of the pleuston net

standardized as nearly as possible to 15 minute duration at a speed of about two knots. Wind rows, usually composed of seaweeds and eel grasses, were a persistent feature all over the Gulf of St. Lawrence. Samples taken from small manoeuverable boats were always run at an angle to the wind rows (i.e. to the wind direction) to avoid biases due to possible micro-distributions at the wind rows. Samples taken from the larger ships could not always be done in this way but by chance the majority of them were also taken at some angle to the wind rows. In most cases two pleuston samples were taken in one direction followed by two more in the opposite direction along the same line. Usually the last two samples were made with the three stage net, the top net being equal to the standard single pleuston net. The mean number of Anomalocera present was taken for all pleuston samples made during a day's work.

For studies of micro-distribution a net frame was built similar to that described by David (1965a and b) which held three rectangular nets, the top one fishing at the usual 2-3 inches, the middle net sampling the water layer 6 to 12 inches deep, and the bottom net 14 to 20 inches. Attempts were made to use a flow meter attached to the keel bottom to give a measure of distance travelled during the sample, but at nearly every sample seaweed clogged the meter and no reading was possible. Eventually the practise was abandoned and the speed of towing was adjusted as well as possible to two knots and timed for 15 minutes.

The studies of Anomalocera's micro-distribution (Section X, Table 14) show that well over 90% of the population lives within the top 2-3 inches of surface water. The behavioural observations indicated that most of the population was living within the upper few millimeters (Section X), and a review of the literature revealed no instances of any species of Anomalocera caught with a closing net below the surface. It was concluded, on these bases, that the semi-immersed pleuston net sampled the entire population (with the exception of the eggs and first naupliar stages discussed later in this section). This is an unusual circumstance in plankton work where sampling uncertainty is more often the rule. The pleuston net can be watched during the entire sample so that there is no doubt about its functioning properly, again in contrast to deeper plankton hauls. There is a possibility that the later stages of a proportion of Anomalocera might escape the small net aperture, especially since the front sections of the keels would give some warning. This problem is not considered to be more severe with the pleuston net than it is with ordinary plankton nets; it would result in a slight under-estimation of the adults and late copepodite stages.

Salinity samples and surface temperatures were taken at each station. Salinities were determined with a conductivity cell in 1966 and 1968. In 1967, a hydrometer set was used. Two or more pleuston samples and two vertical hauls were taken at each station whenever possible. The vertical hauls were made with a number 20 mesh circular plankton net of either one-half-meter or one-third-meter diameter. Observations were made of wave height, water colour, weather conditions and presence of sea birds or other animals in the vicinity of the station. Plankton samples were preserved in buffered formalin and sea water. Frequently live plankton hauls were made at the end of the regular work for immediate examination in the laboratory. Tables 8, 9 and 10 give temperature, salinity and number of samples for 1966, 1967 and 1968.

The preserved samples were examined during the winters at the Marine Sciences Centre. Samples with large numbers of Anomalocera were sometimes subsampled with a Folsom plankton splitter (McEwen, Johnson and Folsom 1954), or in three cases (in 1968) with an auto-pipette. Otherwise the entire sample was examined. A dissecting microscope was used for these examinations. All the copepods were staged and stages IV, V and VI were sexed. Because of the high degree of irregularity in the samples of both abundance and stage composition (discussed below), much of this detailed information was not useful. The mean numbers of adults, nauplii (stages 2-6), and total of stages for the samples taken on a given day are presented in Tables 5, 6 and 7 for the three years of summer sampling. This information is presented in graphic form in Figure 17. The more detailed information of stage composition is given in the tables in Appendix II.

Precautions were taken to avoid sampling pleuston under a weather shore. In 1967 at the Magdalen Islands, it was noticed that Anomalocera was often lacking or reduced in numbers in such samples, while samples taken further offshore or to one side of an upwind island could contain many Anomalocera. Samples taken early in the 1967 program, which wind data indicated might have been taken under these conditions, were eliminated (before analysis of the samples) and for the rest of the season such conditions were avoided. The Grande-Rivière samples were taken far enough offshore so that this seemed less of a problem.

Results

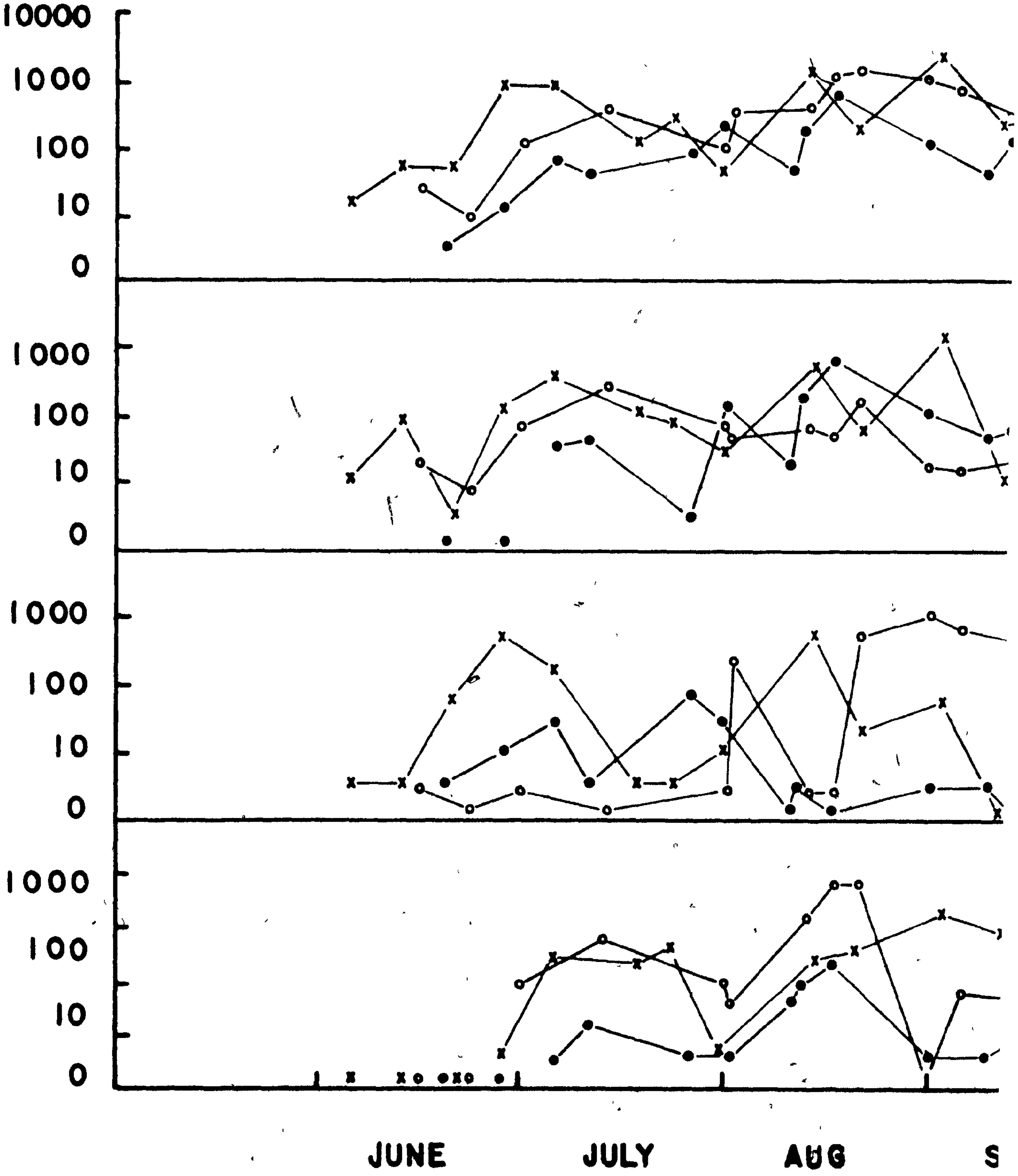
Anomalocera made its first appearance in the study on June 15, 1966 in the form of four stage 6 nauplii and 39 copepodites, mostly early stages but including one stage V

(Table 6). Anomalocera was present from this time on in the 1966 collections. In the months of June and July there was an irregular but general increase in numbers and a dramatic increase of adults in August followed by a decline of adults with a nearly simultaneous appearance of nauplii which reached a peak in early September. From late September on, the entire population declined and at the last sampling date, November 17, there were only 15 nauplii in four pleuston samples. These nauplii probably represent the last of the summer population. Although it is possible that the large numbers of September nauplii were produced by the great concentrations of adults in late August, this is not necessarily so. Results of the summer cruises in the Gulf and of the samples taken from shore stations in 1967 and 1968 showed that the A. opalus population is very patchy, consisting of many different populations which may be swept into or out of a sampling area quite rapidly. Stage composition frequently changes greatly over distances as short as a few miles. Consequently it was never possible to follow the growth of a single brood. Breeding, as evidenced by the presence of young stages and spermatophores on adult females, was continuous and this further reduced clarity in the results.

Similar results were obtained during the summers of 1967 and 1968. The first appearance of A. opalus in these

Figure 17. Graph showing the seasonal abundance of *A. opalus* in the Gulf of St. Lawrence:

1966 - Grande-Rivière
1967 - Magdalen Islands
1968 - Grande-Rivière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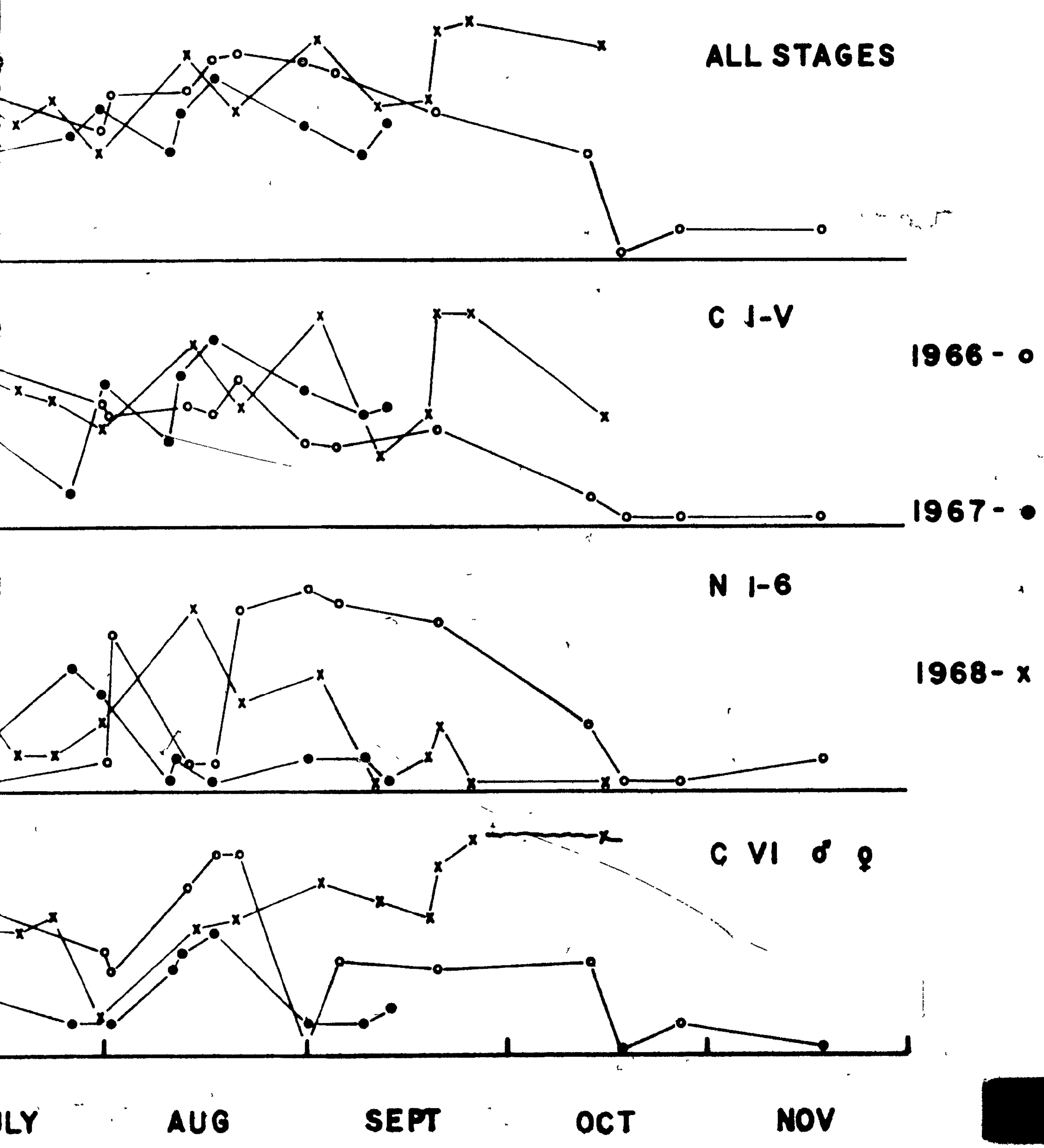

ALL STAGES
C I-V
1966 - ○
1967 - ●
N I-6
1968 - x
C VI ♂ ♀
LY
AUG
SEPT
OCT
NOV

Table 6

The numbers and stage composition of A. opalus on the date of its first appearance in the samples in 1966, 1967 and 1968.

The date of first appearance of adults in the samples in the same years.

Date	Nauplii	Copepodites	Adults	Number of samples
1966, June 15	4 stage 6	7 stage I 7 stage II 11 stage III 13 stage IV 1 stage V (male)	none	2
1967, June 19	7 stage 2 1 stage 3 3 stage 4 1 stage 6	none	none	4
1968, June 5	2 stage 6	9 stage I 3 stage II	none	1

Date of first appearance of adults

1966 - June 30

1967 - July 5

1968 - June 28

Table 7

Pleuston samples taken before the appearance of _Anomalocera_ _opalus_.

Date	No. and type of sample	Salinity	Temperature	Location
		1966 - Grande-Rivière		
March 4	Horizontals(2)	31.94°/oo	-0.5°C	Very near shore
March 16	1 Pleuston	32.00°/oo	-0.7°C	½ mile offshore
April 4	1 "	09.18°/oo	0.6°C	" " "
April 7	1 "	16.04°/oo	0.1°C	" " "
April 12	2 "	30.44°/oo	0.9°C	" " "
April 13	1 "	11.71°/oo	2.8°C	" " "
April 15	1 "	30.53°/oo	0.7°C	3 miles offshore
April 20	2 "	30.72°/oo	2.3°C	" " "
April 22	1 "	27.01°/oo	3.0°C	½ mile offshore
April 29	2 "	30.59°/oo	1.4°C	3 miles offshore
May 3	2 "	30.73°/oo	1.8°C	" " "
May 13	2 "	31.47°/oo	1.9°C	Station 112
May 15	1 "	30.55°/oo	2.2°C	3 miles offshore
May 31*	4 "	-	ca7.0°C	Near Station 112
		1967 - Magdalen Islands		
May 30	4 Pleuston	31.8°/oo	4.1°C	Pleasant Bay
June 2	4 "	31.8°/oo	4.4°C	" "
June 7	4 "	31.6°/oo	6.7°C	" "
June 12	4 "	31.9°/oo	7.5°C	" "

1968 - Grande-Rivière

None - _A_. _opalus_ present in 1st sample

* 4 stations off the Gaspé from the A.T. Cameron cruise. See text page 83, figure 14, Stations 40, 41, 42, 43.

years was in early to mid-June in the form of naupliar and early copepodite stages (Table 6). The adults appeared in the collections two to three weeks later. In the fall of 1968 numbers were still large, and the general decline seen in 1966 had not yet occurred by mid-October when sampling ended. The fate of the last copepods in the fall is not known. Only in 1966 were samples made as late as November and even then fall sampling was not frequent. In 1967 sampling ended in September and a population decline is not readily apparent at this time. Tables 8, 9 and 10 give sampling data for 1966 - 1968, and Tables 11, 12 and 13 give the data used for Figure 17.

The presence of the 15 naupliar stages in mid-November 1966, when the surface sea temperature was 1.6°C, is surprising. During the times of peak population size the surface temperature was between 12 and 14°C and at times of first annual appearance, about 10 - 12°C (1966, 12.8°C; 1967, 9.9°C; 1968, ca 10.5°C; see Fig. 18). Table 6 presents the stage composition and date of first appearance of A. opalus for the three summers of study, and Table 7 gives the number of samples taken before its first appearance.

A rough estimate of the density per m^2 of Anomalocera in the Gulf of St. Lawrence can be determined from the life cycle data. Since the pleuston hauls were taken at an average speed of two nautical miles per hour and were made

Table 8

Table of Station Data for Life Cycle Study: 1966 - Gulf of St. Lawrence

Date	Aliquot	Surface °/oo	T.	No. of Samples
13.5.66	All	31.47	1.9°C	2
15.5.66	all	30.55	2.2°C	1
31.5.66	all	-	6.5°C	4
15.6.66	all	28.12	12.8°C	2
22.6.66	all	28.28	11.1°C	4
30.6.66	all	28.55	14.7°C	4
8.7.66	all	29.51	12.2°C	2
12.7.66	all	-	13.8°C	2
1.8.66	all	30.17	15.0°C	3
2.8.66	½	29.36	16.5°C	2
11.8.66	½	29.81	15.5°C	2
16.8.66	½	29.99	15.9°C	2
20.8.66	½	29.81	13.8°C	2
30.8.66	½	29.99	13.3°C	1
6.9.66	all	30.30	13.9°C	3
20.9.66	all	28.35	11.5°C	2
12.10.66	all	31.49	7.2°C	1
18.10.66	all	32.21	6.6°C	2
26.10.66	all	30.32	5.8°C	3
17.11.66	all	30.10	1.7°C	4

Table 9

Table of Station Data for Life Cycle

Study: 1967 - Gulf of St. Lawrence

Date	Aliquot	Surface °/oo	T.	No. of Samples
2.6.67	all	31.8	4.4°C	4
12.6.67	all	31.8	7.5°C	4
19.6.67	all	30.6	9.9°C	4
27.6.67	all	31.7	13.4°C	4
5.7.67	all	31.2	13.8°C	4
10.7.67	all	31.6	15.0°C	4
26.7.67	all	31.4	17.4°C	4
1.8.67	½	31.2	19.4°C	4
9.8.67	½	-	-	2
10.8.67	½	-	-	2
16.8.67	¼	-	-	2
30.8.67	all	-	17.5°C	4
8.9.67	all	30.6	13.0°C	4
13.9.67	all	-	14.7°C	4

Table 10

Table of Station Data for Life Cycle Study: 1968 - Gulf of St. Lawrence

Date	Aliquot	Surface o/oo	T.	No. of samples
5. 6.68	all	-	-	1
13. 6.68	all	-	-	1
19. 6.68	all	28.60	10.8	1
28. 6.68	½	28.44	11.7	1
5. 7.68	½	28.08	13.5	2
17. 7.68	all	27.62	16.9	1
25. 7.68	½	-	-	1
31. 7.68	all	28.46	15.4	1
14. 8.68	¼	28.58	14.3	1
22. 8.68	½	29.25	11.5	1
3. 9.68	¼	29.68	10.1	1
11. 9.68	½	29.37	15.1	
19. 9.68	all	30.80	12.0	1
20. 9.68	1/8	-	-	1
24. 9.68	1/10	30.12	11.7	2
15. 10.68	1/10	29.38	10.4	1

Table 11

Mean numbers of <u>Anomalocera</u> <u>opalus</u> for each sampling date. Nauplii (Stages 2-6), Adults (Stage VI o and o), all stages.

1966, Grande-Rivière

Date	Nauplii	Adults	All Stages
June 15	2	0	21.5
June 22	0	0	9
June 30	0.3	38	112
July 12	0	180.5	480
August 1	5	35.5	119.5
August 2	237	25	314
August 11	2.5	337	400
August 16	0.5	2202.5	1162
August 20	508	1092.3	1785
August 30	1132	0	1156
September 6	662	29.5	703
September 20	332	24	378
October 12	12	28	40
October 18	0	0	0
October 26	1	2	3
November 17	3.7	0	3.7

Table 12

Mean numbers of <u>Anomalocera</u> <u>opalus</u> for each sampling date. Nauplii (Stages 2-6), Adults (Stage VI o and ^{o}), all stages.

1967, Magdalen Islands

Date	Nauplii	Adults	All Stages
June 19	3	0	3
June 27	11.7	0	11.8
July 5	29.2	0.25	74.8
July 10	1	10.2	49.1
July 26	83.3	2.6	87.3
August 1	28.8	7.8	193.2
August 9	0	20	45
August 10	2	33	225
August 16	0	66	718
August 30	3.5	6.7	110.8
September 8	3.5	1	54.8
September 13	0	60.8	134

Table 13

Mean numbers of *Anomalocera opalus* for each sampling date. Nauplii (Stages 2-6), Adults (Stage VI o and ^{o}), all stages.

1968, Grande-Rivière

Date	Nauplii	Adults	All Stages
June 5	2	0	14
June 13	3	0	53
June 19	71	0	74
June 28	526	1	685
July 5	175	69	642
July 17	3	97	223
July 23	2	130	230
July 31	9	3	49
August 14	552	88	1088
August 22	22	134	316
September 3	56	352	2176
September 11	0	214	234
September 19	1	165	216
September 20	16	712	2648
September 24	0	2075	4100
October 15	0	1990	2030

for 15 minutes, the distance covered during each haul was about one half nautical mile. The rectangular net was eight inches wide and over this distance would filter 193 square meters of surface water. In 1966, the population had a density of about .1 copepods per m^2 in June which rose to about 10 copepods per m^2 in August. This again declined to about the June level of .1 m^2 by October. Densities of up to 20 individuals per m^2 were found in localized patches encountered in August of 1966 off Grande-Rivière and on several occasions in the north eastern Gulf during the "Theta" cruise in 1966.

Zaitsev (pers. comm.) has found Anomalocera patersoni in the Black Sea at densities of 500 per m^2. Huntsman, Bailey and Hachey (1954) report Anomalocera in the north eastern Gulf of St. Lawrence in densities so great that the water was coloured by them. Thompson (1889) reports a huge patch of A. patersoni several miles long near the Isle of Man. He describes the patch, "... the surface of the water literally swarmed with the large and beautiful copepod, Anomalocera patersoni. Each cast of the tow net brought up thousands of them; they were so numerous as to be distinctly visible to the eye on the smooth edge of the waves, and had the appearance of fine dust as seen from the side of the vessel. They were equally abundant during the day and after sundown ...". After a few days this patch disappeared from the area and Anomalocera became rare. The impression of fine dust on the surface probably derives from the dimple made in the surface film by the surface attachment structure. It is curious that no patches with the densities of those described above were ever seen during three years of work on this study. There have been no similar observations elsewhere in recent literature (with the exception of Zaitsev's figure of 500 per m^2 which would not be a great enough concentration to colour water).

Detailed investigations of Anomalocera's relationships to the wind rows was not made. As noted in the discussion of materials and methods in this section, the pleuston net was nearly always towed at an angle to the wind rows to avoid patchiness which might result if the copepods were aggregated at the wind rows. During the observations of living Anomalocera at sea (September 1967, see Section V), the only specimens seen were swimming in the vicinity of floating detritus which seemed to be the remains of old wind rows. On another occasion in August, 1967, Anomalocera was found in moderate numbers in a convergence zone between tidal currents just off Sandy Hook in the Magdalen Islands. The convergence was marked by great amounts of seaweed and floating driftwood. No Anomalocera was found on either side outside this zone. Zaitsev (1970) notes that pontellid copepods in the Black Sea may be concentrated in similar convergences but gives no information of their relation to the smaller wind rows of the Langmuir circulation. Considering the importance of the wind rows to other animals (Section I), this should be an important topic of future research.

Discussion and conclusions

The most interesting and surprising result of the life cycle study was the nearly regular first appearance of A. opalus in June of each of the three years of sampling. At each first appearance the population as seen in the samples was composed of naupliar stages and early copepodites. Adults were not found until two or three weeks later. During the fall of each of the three years' sampling, the Anomalocera population appeared to decline, although only in 1966 was this decline followed as late as November. The analysis of 54 samples from the three winter cruises (Tables 4 and 5), which included samples from the deepest parts of the Gulf of St. Lawrence, yielded no Anomalocera, and no Anomalocera was found in any of the samples taken during the spring at Grande-Rivière (1966) or the Magdalen Islands (1967). In 1966 and 1967 the spring samples were extensive (see Table 7 for a list of the samples taken and examined before the first appearance of Anomalocera. These samples were examined completely). During the spring cruise over the

Magdalen Shallows (May 26 to June 6) on the RS A.T. "Cameron" (Fig. 14, Appendix III), pleuston samples were taken at 85 stations as well as a great many other samples with conventional nets over the entire water column (including samples very near the bottom). Larval fish were sampled with a high speed pleuston net one meter wide. All of the fisheries plankton was given a brief examination during the cruise and Anomalocera was not found; the copepodites would not have been missed because of their large size and bright colour. The pleuston samples were also briefly examined on board and later given a thorough examination on shore and yielded no Anomalocera. It is not possible to conclude definitely that a small stock of this copepod does not exist in the Gulf during the winter and early spring, but it is unlikely considering the large amount of material collected and examined which contained no specimens of this species.

Further evidence on this point comes from the Gulf of Maine. It is noted in Section IV that Anomalocera is not found in this area in the winter. A vast amount of plankton material has been collected and reported on from the Gulf of Maine and it is likely that late copepodites and adults, if present, would have been found. The naupliar stages, however, have only been described in the present work and they could have been overlooked. Naupliar stages of calanoid copepods are unlikely candidates for overwintering at depth because they do not have large stores of oil on which to depend over the months when there is little food. The naupliar stages of A. opalus carry very little oil.

The adults and late copepodites are less likely to overwinter at depth, because of the energy needed to keep them afloat. Koralev (1970) has determined that large pontellids, including Anomalocera patersoni, sink rapidly (ca half meter per minute) when not swimming and have a higher specific gravity than other copepods such as Calanus. The behavioural studies (Section VI) on the use of the surface attachment structure (Section X) revealed the close dependency of the copepodite stages of Anomalocera on the surface film. Although pontellid copepods may carry a thin fat-rich layer beneath the chitin (Heinrich 1969), they are not oil storers to the degree seen in species such as Calanus hyperboreus. It is unlikely that A. opalus could survive below the surface at low temperatures. C. hyperboreus is nearly of neutral density because of its stored fat supply (Conover 1962, 1964); A. opalus is extremely dense and sinks very rapidly when anaesthetized.

In conclusion, if Anomalocera opalus were anywhere in the Gulf of St. Lawrence in the winter and early spring either as nauplii or adults, it should have been found either in the samples taken by the icebreakers during 1967, 1968 and 1969, or in the many samples from the "Cameron" cruise in May of 1966. Either nauplii or adults if present at the surface in the early spring would have been found in the pleuston samples taken on this cruise. The late copepodites and adults are highly specialized for surface life and unlikely to live in deeper water.

Studies in the Gulf of Maine support these conclusions. The congener A. patersoni in the Black Sea and in European waters also disappears in the winter from the northern part of its range and has not been found in these regions in sub-surface collections (Section IV). Herdman and Scott (1908) made observations on the first appearance of A. patersoni near the Isle of Man, which are strikingly similar to results of this study. A large series of plankton samples was taken throughout the year and continued for several years. On March 29 of 1904, Anomalocera made its first appearance in the samples in the form of nearly three hundred metanauplii (in three samples), the first adults appearing on April 9. There were many immature stages found between March 29 and April 9, and after April 9 both adults and young stages occurred together in the samples.

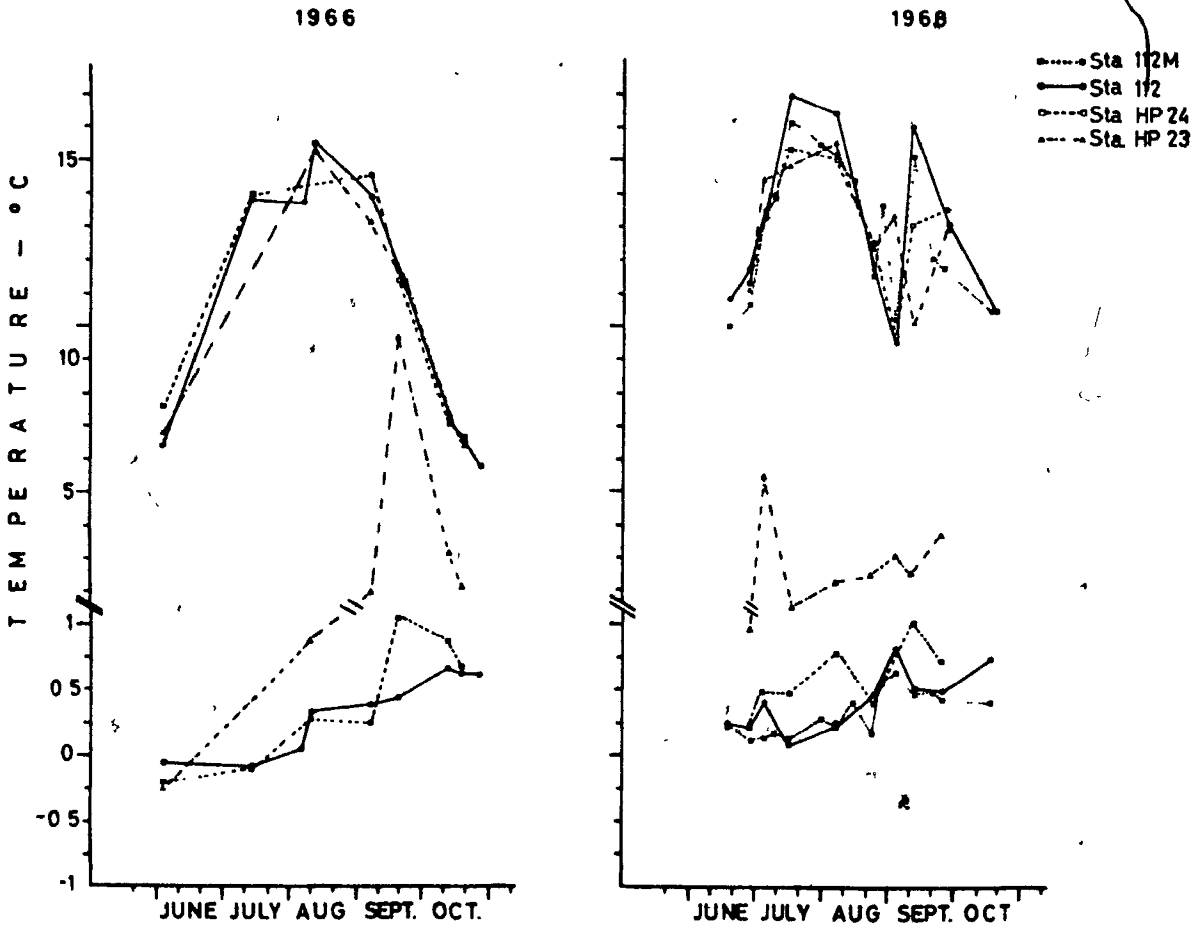
Huntsman in 1919 called Anomalocera a summer visitor to the Gulf of St. Lawrence, thereby implying that it comes into the Gulf each year from outside, presumably through Cabot Strait. This is highly improbable. Anomalocera is absent from the Gulf of Maine in the winter (see above) and a breeding stock south of Cape Cod, although possible, has not been demonstrated. The surface currents along the Scotian Shelf and American Shelf waters flow mainly in a south westerly direction (Bumpus and Lauzier 1965) and in the spring even the flow of surface water across Cabot Strait may be outward. Introduction from the outside would be an extremely irregular process not in keeping with the three year findings of <u>Anomalocera</u>'s appearance in the first half of June. It would be still more difficult to explain the absence of adult copepods in the population at the time of first appearance or the presence of early naupliar stages which should have molted had their journey been from a distant point outside the Gulf.

The hypothesis of a resting egg is better suited to explain the data. Calanoid copepods in fresh waters are well known to aestivate as encysted copepodite stages, with normal eggs which do not develop in low temperatures, and with resistent resting eggs (Hutchinson 1967). Marine calanoids have not been conclusively shown to overwinter in any of these ways, although a resting egg has been indirectly cited for <u>Temora</u> (in Conover 1964). Fish and Johnson (1937) suggest that <u>Centropages</u> <u>typicus</u> may overwinter in the Gulf of Maine with a resting egg, and Conover (1956) proposed a resting egg for Acartia clausi and A. tonsa in Long Island Sound. Recently Grice (pers. comm.) has found a resting egg in Labidocera aestiva, but the details of this study have not yet been given.

The eggs of A. opalus are described in Section VII; those examined did not appear to have special membranes typical of resting eggs. Eggs of Anomalocera were never identified from the plankton and, since they are shed freely into the water, it is not certain that they do not produce special eggs in the fall. The normal egg (.128 - .177 mm) is more dense than cold surface water and either sinks or becomes generally dispersed throughout the water column. As noted above, the first nauplius was rarely found at the surface.

No effort is made here to explain the mechanism for the awakening of a resting egg. Such an egg could be encased in special membranes and equipped with a biological clock, or it could be keyed to slight changes in bottom temperatures if it were overwintering in the sediments. Figure 18 shows the surface and bottom temperatures during 1966 and 1968 at several stations off Grande-Rivière including station 112 used during the life cycle study. The inner station at the 30 fathom contour shows a definite temperature change around early June which could stimulate the hatching of eggs in

Figure 18. Surface and bottom sea temperatures at station 112, Grande-Rivière, 1966 and 1968. Stations HP23 and HP 24 are inshore from Station 112, at about the 30 fathom contour. (From Weinstein 1973).


1966
1968
Sta 112M
Sta 112
Sta HP 24
Sta HP 23
TEMPERATURE — °C
15
10
5
1
0.5
0
-0.5
-1
JUNE
JULY
AUG
SEPT.
OCT.
JUNE
JULY
AUG
SEPT.
OCT

superficial sediments. Possibly the ordinary eggs produced too late in the season to hatch, sink to the bottom and await the spring warming to continue their development (for fresh water examples of this phenomenon, see Hutchinson 1967). It is also possible that the eggs of Anomalocera continue to drift in the water column kept afloat by turbulent mixing.

It is possible that a resting egg is used by *A. opalus* in the Gulf of Maine where the species disappears in the winter. *A. patersoni* might also use this method of overwintering in the northern parts of its range, for instance, in the North Sea and off the Norwegian coast.

Section VII

Description of the developmental stages of *Anomalocera opalus*

The naupliar stages of A. opalus.

Johnson (1935) noted the scarcity of studies of copepod naupliar stages. Faber (1966) produced a key to identification of common nauplii in Naragansett Bay and other studies appearing periodically have further increased the number of species with described developmental stages. Björnberg (1972), however, notes that only about 8% of the known 800 species of planktonic copepods have had their naupliar stages identified. The developmental stages of A. opalus were identified so that the life cycle could be followed in greater detail, but the nature of the population set limits on the precision that could be brought to the life cycle study. The descriptions given in this chapter may be useful to future work, especially laboratory studies of development and growth rates.

Specimens of the stages described here were collected in 1966 from the coastal waters of South Gaspé. The first two naupliar stages were obtained from eggs shed by freshly captured copepods. Later stages could not be obtained in this way and were identified from the surface plankton collections. Pontellid nauplii have been described for other species (Johnson, 1935) and differ markedly from other genera of copepods found in the Gulf of St. Lawrence and in the surrounding waters. Labidocera aestiva, which is found in the Gulf of St. Lawrence in the summer months, has nauplii similar to those of Anomalocera, but so much smaller that they did not cause confusion. There were no apparent morphological contradictions in the usual series of six nauplii and six copepodite stages.

The drawings of entire nauplii show the ventral surface with the limbs in the position most easily seen in actual specimens but twisted slightly for clearer display of the setae. The first antennae are drawn with the dorsal surface outward (lateral). The second antennae and the mandibles are drawn with the dorsal surface anterior to the ventral surface. The drawings of isolated limbs follow the orientation of the whole drawings. Descriptions of each stage often refer to the stage previous but never to the next stage unless explicitly stated. All of the drawings were done with a camera lucens. The organization of the description is based on that of Johnson (1935) in his description of Labidocera jollae.

The eggs of A. opalus are shed directly into the water. Those obtained from captive females averaged .188 mm in diameter (mean of 20 measurements), were brown or pale green coloured, and possessed no outer membranes.

Nauplius Stage 1 (Figure 19a)

Length .22 mm (three measurements)

First antenna - The first two segments are of nearly equal length, the third or distal is longer and bears two long terminal setae and two tiny spines near these but dorsal to them. The second segment bears one bare seta about as long as the segment.

Second antenna - The first basipod bears one small masticatory hook. The second basipod bears a smaller hook and one very small spine ventrally directed near the joining of the endopod. The endopod bears two long setae and one shorter seta. The exopod has five distinguishable segments, the first or proximal is larger than the last four combined. Johnson (1935) finds the exopods of the first nauplius of Labidocera trispinosa and L. jollae to have six segments, the first two being fused. This was not seen in the specimens examined of A. opalus. Each segment bears one seta, and there is a small spine adjacent and dorsal to the terminal seta.

Mandible - The first basipod bears an inner lobe with one small spine; the second basipod bears two very small inner spines. The endopod bears two small bare ventral setae and two longer terminal setae. The exopod has four segments with a seta on each of the first three and two terminal setae on the fourth. The dorsal of these two setae is bare and much smaller than the ventral seta.

<u>Caudal armature</u> - The nauplius is at this stage more rounded in the posterior than in the later stages which are more spindle shaped. There are two stout heavily-barbed setae of nearly equal length.

The labrum is bare.

<u>Nauplius Stage 2</u> (Figures 18b and 21a)

Length .266 - .32 mm (mean .29 mm of 22 measurements)

<u>First antenna</u> - Figure 21a. Three segments. The first segment is now somewhat shorter than the last two which are nearly equal in length. The first segment bears one small spine dorsally near the juncture with the second segment. The second segment bears a small dorsal spine near its midpoint and a longer spine, now plumose, at the juncture of the final segment. The final segment now bears four long setae, one of which, the second from ventral, is smaller and bare. There are rows of fine hairs on the ventral and dorsal margins of this segment; the row on the ventral margin is short and in the centre, the dorsal row is longer and extends along the distal half of the segment.

<u>Second antenna</u> - The first basipod has one curved masticatory hook, more robust than in Stage 1. The second basipod bears one curved masticatory hook, larger than

that of the previous segment, and two spines on the ventral margin, one near the masticatory hook and the other near the juncture with the endopod. The endopod bears a ventral seta midway along the ventral margin and three terminal setae which become longer dorsally. They are spined rather than plumose. The exopod now has six segments. The proximate segment of Stage 1 has apparently divided. The first segment bears no setae; the second segment has added one smaller ventral seta and the rest of the exopod is unchanged.

Mandible - The spination and general form of the two basipods are as in Stage 1, but the spines are more robust and are plumose. The endopod now bears three ventral setae which are plumose and more robust than in Stage 1. There are now four terminal setae, the two most ventral being half the length of the others. The exopod is nearly unchanged but for the addition of one small ventral seta midway along the first segment. The dorsal terminal seta is now larger and plumose.

Labrum - The posterior margin bears a row of fine hairs with a gap in the centre. It does not change in later stages.

Caudal armature - The two terminal setae have diverged in length, the shorter becoming plumose and the longer remaining spined. Both are relatively longer than in

Stage 1. There are two double rows of fine hairs on the ventral surface above the setae.

Eye - The eye is conspicuous as a protuberance above the labrum. It remains so throughout the later naupliar stages.

Nauplius Stage 3 (Figures 19c and 21b)

Length .34 - .44 mm (mean .40 mm of 37 measurements)

First Antenna - Figure 21b. The first two segments remain unchanged. The third, distal segment retains the same four terminal setae and has added one ventral seta about two-thirds of the way toward the terminus and two dorsal marginal setae, a small one at the mid-point of the segment and a longer one between this and the terminal setae. There are two small spines on the outer lateral margin.

Second Antenna - On the first basipod there are two curved masticatory hooks bearing spinules and, on a common base, one small seta. The second basipod is as Stage 2 except that the two central-marginal spines are now plumose. The endopod has added a terminal seta of slightly smaller size than the original three and a fifth very small bare seta. The lateral seta is joined by another small bare seta from the same base. The exopod is as the previous stage but with the addition of small setae on the second and terminal segments.

Mandible - The first basipod is unchanged. The second basipod has a more pronounced inner lateral protuberance and has added a third stout seta. The endopod has added a fifth terminal seta. The exopod is unchanged.

First Maxilla - appears here as a pair of stout spines on the ventral surface midway between the labrum and caudal armature.

Caudal Armature - This consists of four terminal setae, of unequal length (from right to left), an outer right short spined seta, a slender and longer plumose seta, a longer, bare and very slender seta and on the outer left a heavy barbed seta, the longest of the four. Just above the terminal spines are two ventral setae which are stout and spined, and nearly equal in length. Still further anteriorly is a pair of lateral spines, very small and difficult to see.

Nauplius Stage 4 (Figures 19d and 21c)

Length .46 - .53 mm (mean .50 mm of 37 measurements)

First Antenna - Figure 21c. The first two segments are unchanged. On the dorsal margin of the third or distal segment, the two small spines of Stage 3 have disappeared and there are now two setae. On the ventral margin of the distal segment proximal to the lateral seta are two strong curved spines. There are still four terminal setae similar to those of Stage 3.

Second Antenna - The first basipod is unchanged. On the second basipod a new small seta has appeared from the base of the proximal seta on the ventral margin. The endopod is unchanged but for the addition of a third small lateral ventral seta which shares a common base with the other two. Two of these three setae are bare, one is plumose. The exopod has added two small bare terminal setae. There is a total of ten setae on the exopod.

Mandible - A chewing process with two cusps has appeared on the first basipod. It extends under the labrum. The second basipod has added a fourth inner lateral seta. The endopod and the exopod are unchanged.

Caudal Armature - This is nearly the same as Stage 3 except that there is a new pair of tiny lateral spines at the level of the ventral setae. The pair anterior to these has doubled.

First Maxilla - This is now a limb bud of two lobes. On the inner lobe are two small bare setae growing posteriorly. On the outer lobe there are three longer, bare setae.

Nauplius Stage 5 (Figures 19e and 21d)

Length .54 - .70 mm (mean .62 mm of 35 measurements)

First Antenna - Figure 21d. The distal segment of the first antenna has added two small, bare setae on the dorsal margin and one tiny spine on the lower ventral margin. There are no further changes.

Second Antenna - The first and second basipods are unchanged. The endopod is unchanged except for the addition of a fourth small lateral seta. The exopod has added a fourth small seta on the second segment.

Mandible - The chewing process of the first basipod is longer and more robust, and bears a row of delicate nairs on its anterior margin. The lateral setae is longer. The second basipod is unchanged. The inner lobe of the endopod now bears five setae, the rest of the endopod and the exopod are the same as Stage 4.

First Maxilla - This has now developed a series of inner lobes bearing tiny spines and one very small, bare seta. The two larger posteriorly growing lobes are more developed than in Stage 4. There are four setae on the inner and five long setae on the outer lobe. (All are slender and bare). What appears to be the second maxilla is just visible as an inwardly bent hook beneath the first maxilla.

Caudal Armature - The four terminal setae are similar to those of the previous stage. Of the two inner setae, the one to the left is shorter and definitely plumose; the one on the right is longer, bare and more slender. The heavy ventral setae are longer and a new pair of short lateral spines has appeared at the site of the very small lateral spines of Stage 4. Above these there are two paired rows of tiny lateral spines, one anterior to the other.

Nauplius Stage 6

(Figures 20a, 21e, 20c and 20d)

Length .74 - .85 mm (mean .78 mm of 34 measurements)

First antenna - Figure 21 e. The outer lateral surfaces of the first and second segments have clusters of short spines arranged in loose rows. On the terminal segment there are four similar spines on the outer lateral surface. On this segment there are now two more short dorsal marginal setae, making a total of eight, three of which are bare. The two types of setae, bare and plumose, alternate with each other. On the ventral margin are added two small, bare setae. There are now five setae on this margin.

Second Antenna - Figure 20a. Differs from Stage 5 only in the addition of one seta to the second segment of the exopod. This brings the number of exopod setae to twelve.

Mandible - Figure 20 c. The basipods are unchanged. The endopod has added two terminal setae and a row of small spines near the bases of the terminal setae. The exopod is unchanged.

First Maxilla - This has developed further. On the anterior inner lobe are two small spines. On the next posterior lobe there are two spines, one larger than the other. On the inner posterior lobe there are six setae and two spines; on the outer lobe there are seven setae and two spines, one very long. All setae are bare.

Second Maxilla - This is a pronounced, curved bud lying beneath the setae of the first maxilla. It bears five stout setae which are directed inward.

The Maxilliped - This is a small bud near the midline of the ventral body surface not far posterior to the second maxilla. It bears two stout spines.

There are two remaining limb buds which are precursors of the first and second swimming legs. Each bears several irregular stout spines directed posteriorly.

Caudal Armature - This is unchanged.

Along the body, three ridges can be clearly seen which are the precursors of the copepodite segmentation.

Copepodite Stages of *A. opalus*.

The following notes on the copepodite stages present material resulting from the life history study and from the comparative study of the adults. It is not intended as a complete description of all the stages nor as a definitive key to their identification. It will provide information

Figure 19. Naupliar stages of A. opalus:

a) nauplius 1, ventral

b) nauplius 2, ventral

c) nauplius 3, ventral

d) nauplius 4, ventral

e) nauplius 5, ventral

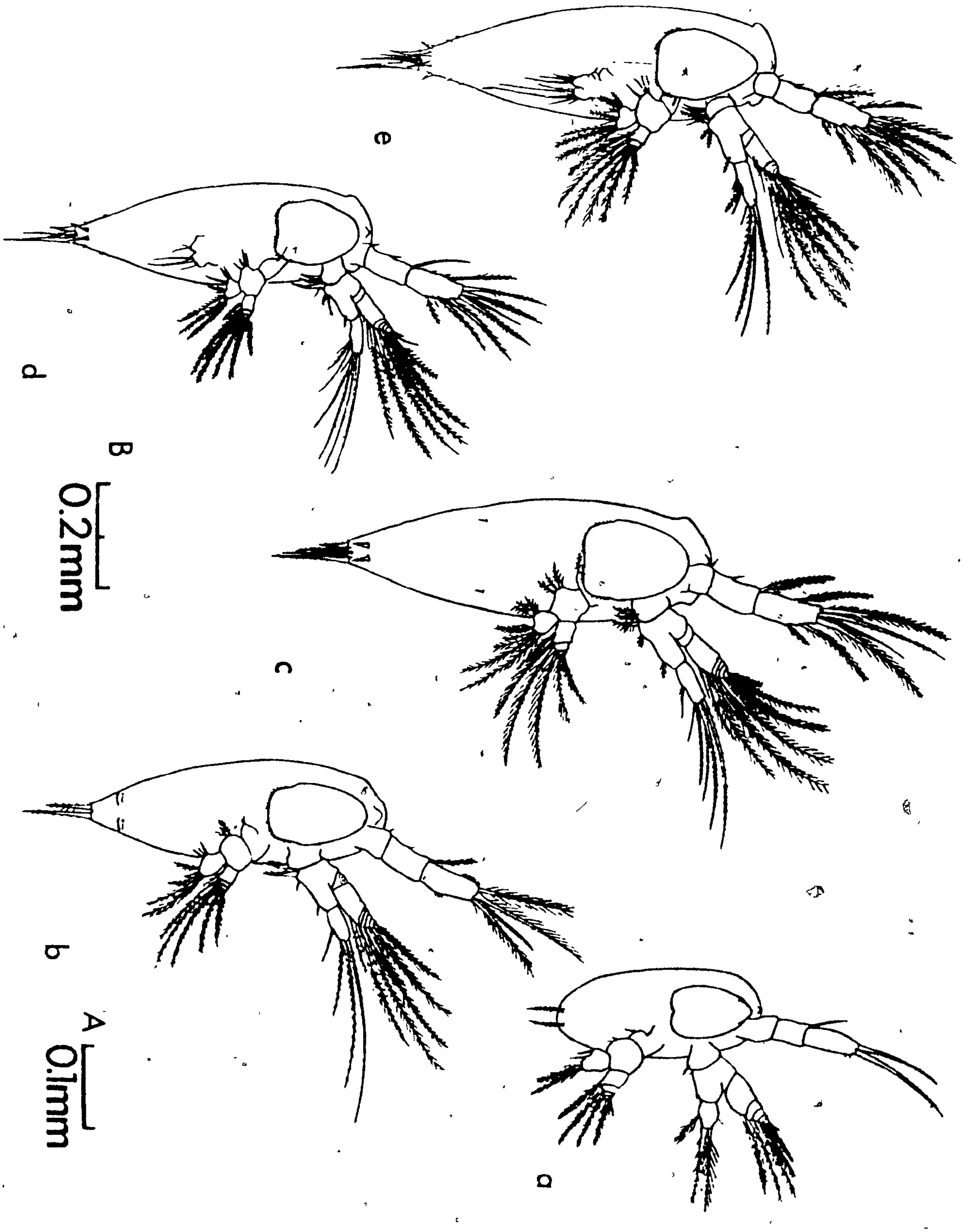

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Figure 20. Naupliar and copepodite stages of

<u>A</u>. <u>opalus</u>:

a) nauplius 6, ventral

b) copepodite I, dorsal

c) nauplius 6, mandible

d) nauplius 6, second antenna

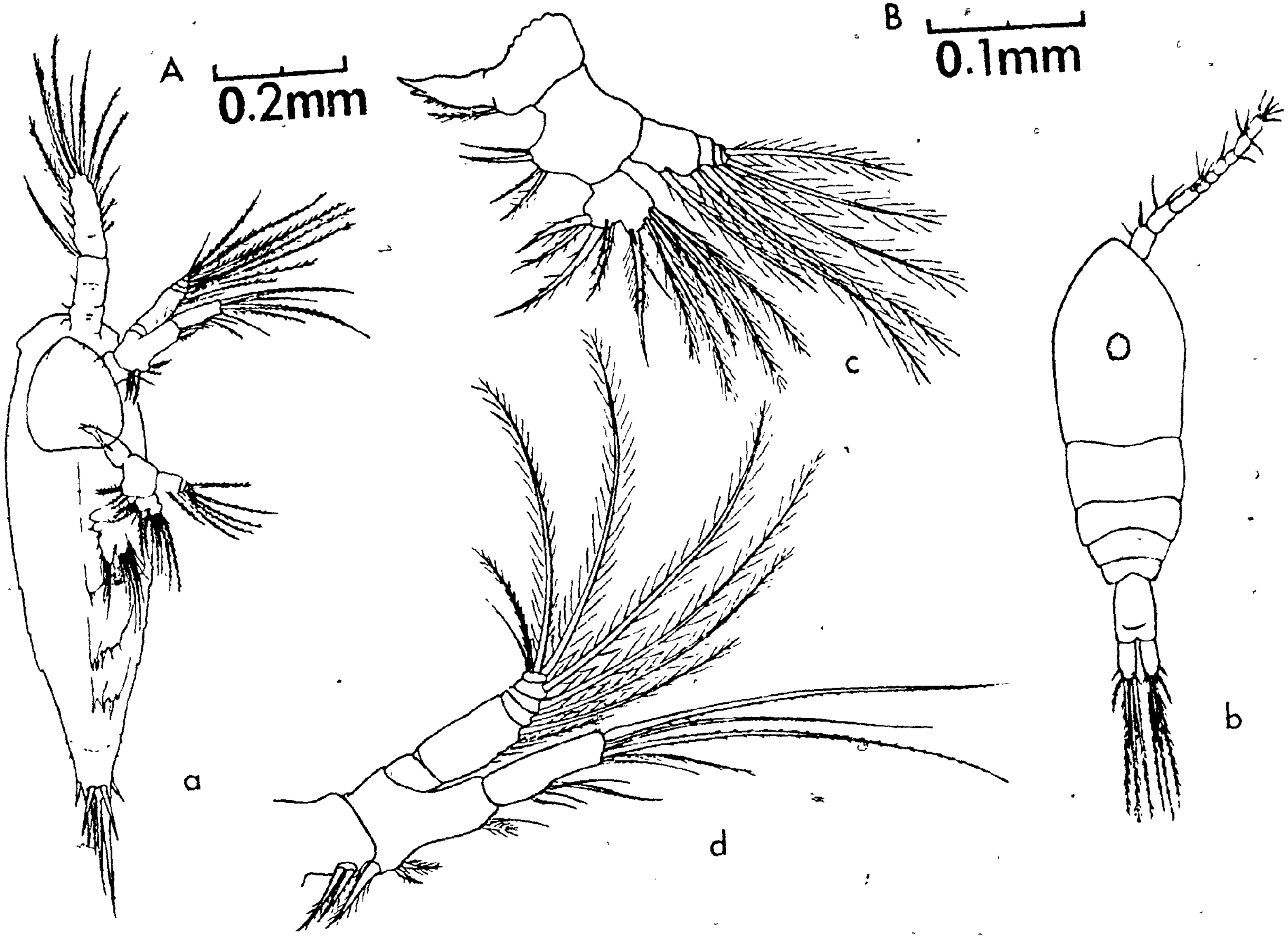
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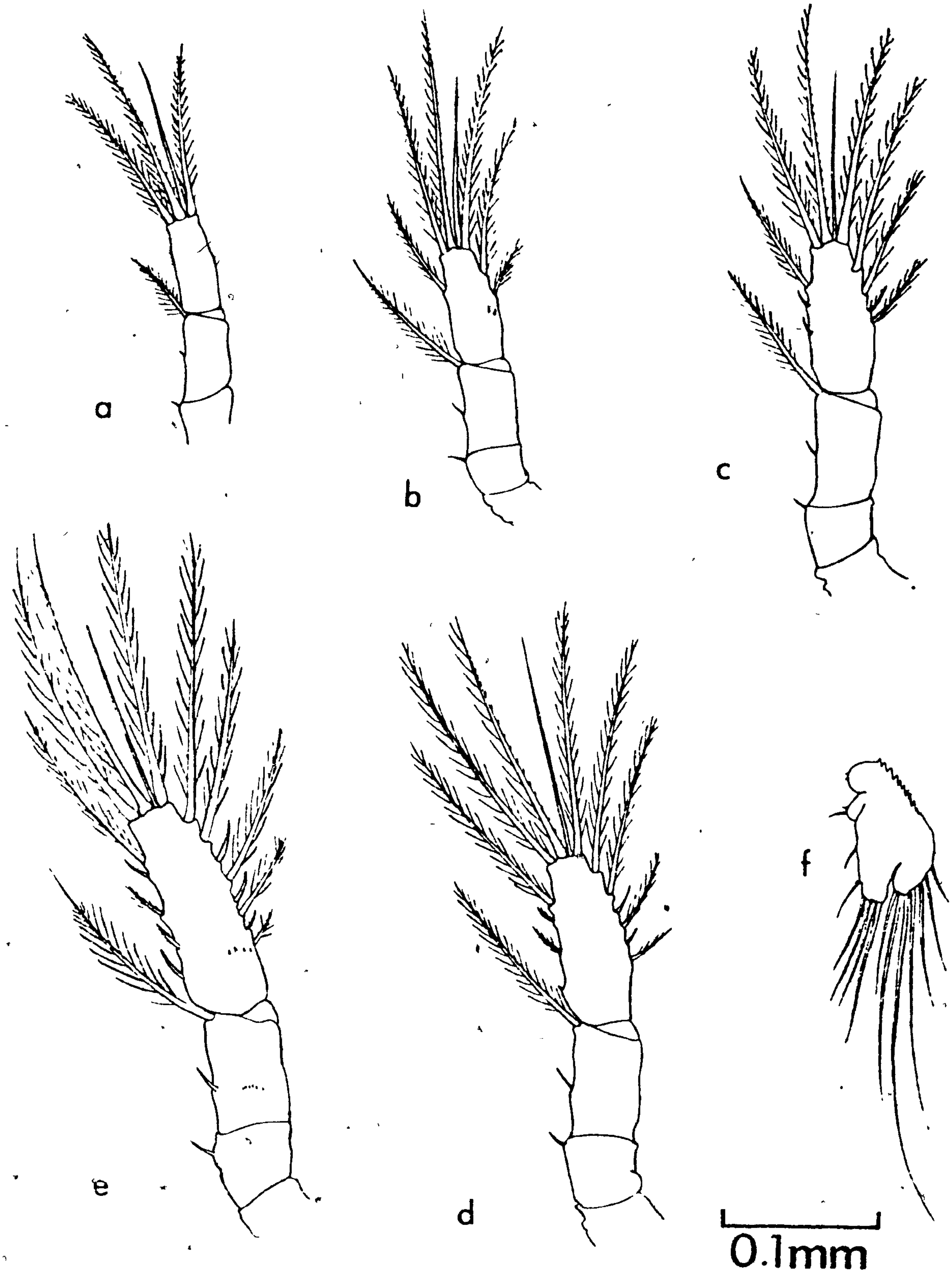
Figure 21. Naupliar stages of A. opalus

a) nauplius 2, first antenna
b) nauplius 3, first antenna
c) nauplius 4, first antenna
d) nauplius 5, first antenna
e) nauplius 6, first antenna
f) nauplius 6, maxilla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adequate for the identification of the stages I, II, and III in many situations, such as the Gulf of St. Lawrence. Stages IV and V are described in detail, with special reference to the fifth swimming legs and sections of the right first antenna. This makes possible taxonomic separation from other species and sexual determination from stage IV on.

Copepodite Stage I (Figure 20b)

Prosome length .68 - .88 mm (mean
.77 mm of 28 measurements)

There is one abdominal segment from which two symmetrical caudal rami extend posteriorly. Each ramus has four terminal setae, one short dorsal seta and one short outer lateral seta. The inner three terminal setae are long and plumose, and of nearly equal length; the outer terminal seta is short and plumose. The prosome has five segments. The first antenna has nine segments each with one or two setae of different types. There are two swimming legs.

Copepodite Stage II (Figure 20i)

Prosome length .99 - 1.09 mm (mean
1.02 mm of 40 measurements)

There are two abdominal segments, five prosome segments and three swimming legs. There are no dorsal eye lenses, but masses of tissue can be seen under the chitin at the sites where the eyes will appear.

Copepodite Stage III (Figure 23h)

Prosome length 1.29 - 1.45 mm (mean
1.34 mm of 43 measurements)

There are two abdominal segments, six prosome segments and four swimming legs. The dorsal eye lenses have appeared, one pair to each side of the first prosome segment, well to the front. These structures resemble simple convex disks of clear chitin.

Copepodite Stage IV (Figures 23g, 22a, b, g, h)

Prosome length - male - 1.80 mm
(mean of 22 measurements)

Prosome length - female - 1.89 mm
(mean of 33 measurements)

Both male and female have three abdominal segments and six prosome segments. There are five swimming legs.

Two features were found which were attributed to sexual differentiation. Both occurred in zones strongly sexually dimorphic in the next two stages. Figures 22a and b show the sixth and seventh segments of the right first antenna (the sixth or most proximate uppermost) of a stage IV female and male respectively. Figures 22c and d show the same features on female and male (Stage V).

The sixth segment of the male antenna bears three setae as does the corresponding segment in the stage V male (Figure 22d). Similarly, the sixth segment of the stage IV female antenna (Figure 22a) bears only two setae as does the same segment in the stage V female (Figure 22c). Both segments in Figures 22b and d (male) are more elongated than those in Figures 22a and c (female).

Other differences were found in the endopodites of the fifth swimming legs. In both sexes the fifth swimming leg of stage IV is biramous and nearly symmetrical. The first basipod bears no setae, the second basipod bears a plumose seta on its posterior surface. The exopod of one segment bears two strong spines and three fine hairs on the lateral margin. The outer margin of the right exopod bears three fine hairs; that of the left exopod bears four. There is one spined, terminal seta and one strong terminal spine lateral to this seta. On the inner lateral margin is a row of fine hairs and below them two small spines.

It is in the endopod that differences were found which corresponded with the sexual differences of the antenna. In the 51 specimens examined the endopods of females bear a heavy hooked process on the inner lateral margin (Figure 22h). The endopods of all males (Figure 22g) were found not to have this hook and to either bear a small spine or no structure at all. The male stage V loses the endopodite entirely while the female retains it.

Copepodite Stage V (Figures 22c, d, e, f)

Prosome length - male - 2.26 - 2.66 mm
(mean 2.46 mm of 23 measurements)
Prosome length - female - 2.46 - 2.86 mm
(mean 2.67 mm of 18 measurements)

This stage is strongly sexually dimorphic. The female has three abdominal segments and six prosome segments. The first abdominal segment is enlarged and will be further enlarged to form the genital segment of the next stage. The male has four abdominal segments all of roughly equal size.

Figures 22d (male) and 22c (female) show the sixth and seventh segments of the first right antenna where the dimorphism is pronounced. The sixth segment of the female bears two lateral setae; the same segment of the male bears one lateral seta and another lateral process which is compound. The seventh of the female segments has three lateral setae, two of these are set in a common base near the juncture with the eighth segment and one of these setae is non-tapered and blunt. The seventh segment of the male has one large process about as long as the segment itself, extending and overlapping in the eighth segment. From its base another much smaller process arises.

The fifth swimming legs are also strongly dimorphic. Those of the female (Figure 22f) are biramous. The first and second basipods are unchanged from stage IV, but the endopods are now irregularly forked, and not strictly symmetrical. The outer lateral margin of the right endopod bears two rows of fine hairs. The exopodite has two segments; the first bears a stout spine on the outer lateral margin near the junction with the second segment, and the second segment bears two lateral spines and two terminal spines of unequal length. The long terminal seta of the right exopodite bears a row of fine hairs. The inner lateral margin bears a slightly irregular process.

The fifth swimming legs of the male (Figure 22e) are asymmetrical and uniramous. The first basipod and second basipod are similar to the female except that the right basipod is smaller than the left second basipod. The exopod is of two segments; those of the right side are smaller than those of the left. Both first basipod segments bear a hook on the lateral outer margin near the junction with the second segment. The second right segment bears two hooks on the outer lateral margin and two terminal hooks, the innermost of which is larger. The second segment of the left exopod is similar but bears an extra spine on the inner lateral margin and bears a much larger inner terminal hook.

Figure 22. Naupliar and copepodite stages of A. opalus

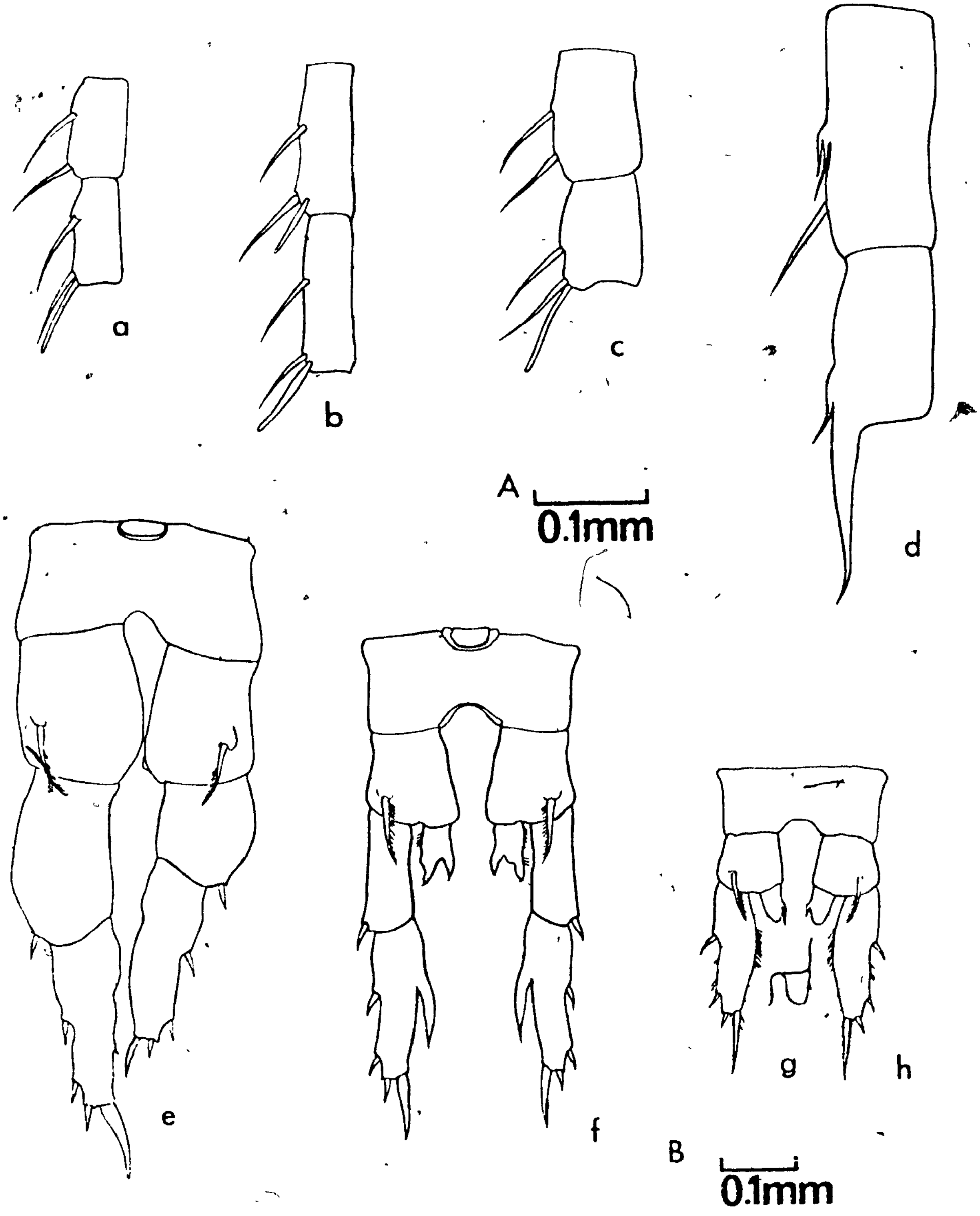
a) copepodite IV, female right first antenna, segments 6 and 7

b) copepodite IV, male, right first antenna, segments 6 and 7

c) copepodite V, female, right first antenna, segments 6 and 7

d) copepodite V, male, right first antenna, segments 6 and 7

d) copepodite V, male, fifth swimming legs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Section VIII

The morphology of the surface attachment structure of *Anomalocera opalus*, and notes on this structure in other pontellid copepods

The use of the surface attachment is described in Section IX on the behaviour of *A. opalus*. It is there made clear that this structure is of great importance to this animal. Very similar structures have been found during this study on a number of other pontellids which probably signifies that these species belong to the pleuston. The structure may prove to have taxonomic value; not all pontellids possess it. No similar structure has been found on other copepods, although Parker (1901) observed *Labidocera aestiva*, which does not have an attachment structure, to attach itself to the surface film with the tips of the first antennae. The structure is very difficult to see at first which may explain why it was missed by so many careful taxonomists who made otherwise exceedingly complete drawings of pontellid copepods (e.g. Sars 1903, Giesbrecht and ~~Schmiel~~ 1898).

Scourfield, in 1894, discovered very similar structures on a species of fresh water cladoceran, *Scapholeberis*, and on a fresh water ostracod, *Notodromus*. In both cases, the structure is a flattened area on the ventral surface covered with fine setae; both animals are dark pigmented. Scourfield notes that the niche of these animals is less competitive and offers a wide variety of food which both species are capable of taking from the interface. In the same paper, two species of dark pigmented cyclopoid copepods (*Cyclops*) are described which attach themselves to the surface with the terminal setae of the second antennae.

In the case of *Anomalocera*, the attachment structure is on the dorsal surface and is seen as a means of saving energy rather than a mode of food gathering, although this may also be important (Section IX). The structure is found on all copepodite stages (Fig. 23), but not on the naupliar stages. The drawings of the structure on stages I-V were made with the aid of a camera lucens using specimens stained with chlorazol black. A scanning electron microscope (s.e.m.) was used to photograph the structure on *A. opalus* and *Pontella atlantica*.

Adult females of *A. opalus* and *Pontella atlantica* were prepared for examination with the s.e.m. by Mr. Gareth Harding with the help of David Walker at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia. Copepods were placed in distilled water to remove salts and then fixed in osmium tetroxide for five minutes. They were again placed in distilled water in which they were frozen solid. In this state the specimens were freeze-dried, mounted in a copper block and coated with gold (Small and Marszalek 1969). Exposures were made on polaroid film four inches square. Magnifications given with the figures refer to the negative and not to the final print.

The surface attachment structure is described below for the copepodites and adults of A. opalus, beginning with stage I.

Stage I - Figures 23a and j

The structure is a small, nearly circular depression in the centre of the first prosome segment. A pair of fine lines runs from the posterior of the depression and seems to reflect a soft structure under the chitin. Although the structure appears functional, it is noted in Section IX that this is the only copepodite stage not seen to attach itself to the surface.

Stage II - Figures 23b and i

The structure is now more elongate and is bounded by two semicircular chitinous ridges. The ends of the posterior semicircle curve abruptly inward and on short horns. Between these horns lies a pair of slightly curved ridges and from the posterior ends of these, the faint line of understructure can be seen. Beneath the anterior semicircle lies a Y-shaped sub-chitinous pattern.

Stage III - Figures 23c and h

The shape of the semicircle is roughly the same as in the last stage, but the ends of both semicircles have developed horns. There is now a pronounced mid-line in the chitin running forward from the base of the posterior semicircle and branching symmetrically within the anterior semicircle. This mid-line is continued posteriorly and anteriorly to the entire attachment structure. At the horns and around the borders of the posterior semicircle there are minor ridges which disappear into the chitin.

Stage IV - Figures 23d and g

Two spines have appeared just anterior and lateral to the forward semicircle. The mid-line is strongly present from the base of the posterior semicircle to the horns of the forward semicircle. Just before this semicircle ends, two curved lines of sub-chitinous structure branch outward. The posterior semicircle is augmented by accessory curves which go out into a shallow canal leading over the surface chitin from the lateral horns, to the sides of the prosome.

Stage V - Figure 23e

The structure is very similar to that of the previous stage, but two new spines have been added lateral to the posterior semicircle. The lateral canals are now continuous with the posterior semicircle, and the lateral horns of both semicircles have disappeared. The sub-chitinous pattern traces an elaborate curve from the mid-line to the beginnings of the lateral canals. The mid-line runs almost the whole way down the attachment structure. At high magnifications very fine hairs can just be seen covering the surface.

In this stage and in the previous one, the entire structure has begun to acquire a distinctive violin shape due to a pinching of the structure at the point of the lateral canals. This is still more apparent in the adult structure.

Stage VI - Figures 3, 24, 25 and 26

Figure 24 shows the entire attachment structure of the adult female. It appears to be essentially like that of stage V with a few changes which may represent the improved definition made possible by the s.e.m.'s increased depth of field. There are two paired openings or pores inside the structure, one pair well to the anterior and the other pair near the lateral edges in about the middle of the posterior section. On the mid-line of the structure near the centre of the anterior section is a whitish oval spot. This is shown at higher magnifications in Figure 25. It appears to be composed of a mass of filaments or tendrils, some of which are also found anterior to the spot scattered over the attachment structure. These may be the fine hairs described for the structure of stage V.

The outer margin of the surface attachment appears raised or crusted (Fig. 24 , 110x and Fig. 27, 3000 x).

At the highest magnification, this crust is seen to be composed of a mass of tentacles or twisted hairs growing like a hedge around the structure. These tentacles seem to grow inward toward the centre of the attachment area. Their exact natural structure might not be well portrayed in the s.e.m. photographs because there may have been some damage or distortion caused during the preparation. The function of these tentacles is uncertain. They could directly repel water from the edges of the attachment structure, or they may actually grip the surface film. Possibly the increased surface area of the tentacles' border greatly increases the surface tension here. Water on the attachment structure could then drain through the lateral canals. The interior of the structure is always dry when the animal is attached to the surface and is apparently water repellent.

Anterior to the attachment structure is the mid-line cleavage of the prosome (Fig. 25). Seen in detail, this is a complicated structure raised in a double fold of chitin, not quite closed over dorsally. It terminates in an enlarged opening which may be a functional pore or the remnant of a chitinous suture. The functions of the several pores and spines associated with the surface attachment structure remain obscure. The pores could be used to release water-repellant substances over the attachment structure.

The following species of pontellid copepods were examined for the presence of surface attachment structures or similar features:

Species	Area taken	With structure	Without structure
Labidocera aestiva, Wheeler	Gulf of St. St. Lawrence		X
Labidocera nerii, Krøyer	Barbados		X
Pontellina plumata, Dana	Barbados		X
Pontellopsis perspicax, Dana	Barbados	X	
Pontella atlantica	Barbados, Bermuda	X	
Anomalocera patersoni, Templeton	E.N. Atlantic	X	
Anomalocera opalus, Pennell	Gulf of St. Lawrence Gulf of Maine	X	
Anomalocera ornata, Sutcliffe	Georges Bank, S. of Gulf of Maine	X	

Figure 23. The surface attachment structure of copepodite stages of A. opalus.

a) copepodite I, attachment structure

b) copepodite II, attachment structure

c) copepodite III, attachment structure

d) copepodite IV, attachment structure

e) copepodite V, attachment structure

f) copepodite V, first prosome segment

g) copepodite IV, first prosome segment

h) copepodite III, first prosome segment

i) copepodite II, first prosome segment

j) copepodite I, first prosome segment

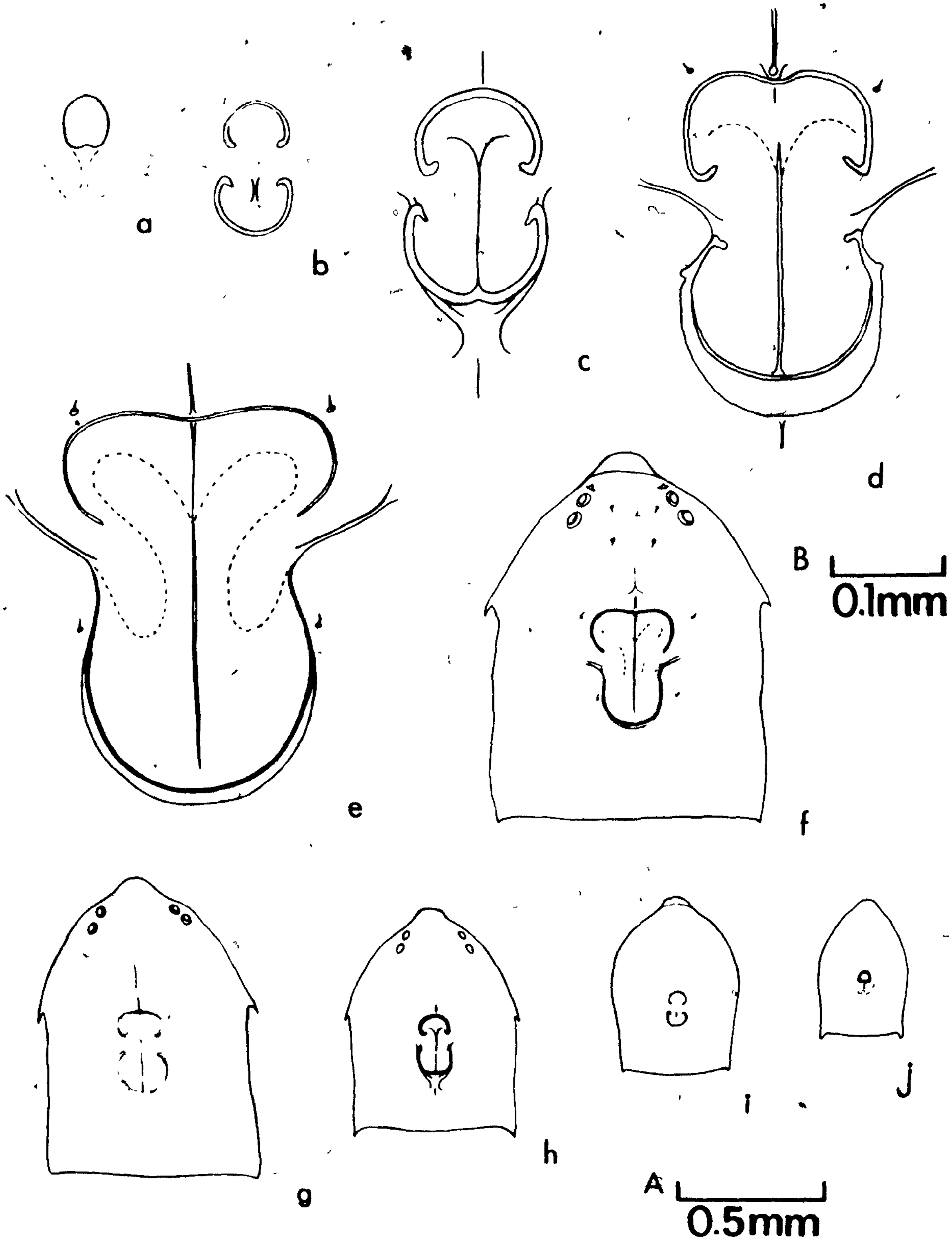
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Figure 24. Surface attachment structure of A. opalus, stage VI, female. S.E.M. photograph, 110x magnification.

Figure 25. Detail of surface attachment structure of _A. opalus_, anterior, stage VI, female. S.E.M. photograph, 3000 x magnification.

Figure 26. Surface attachment structure of <u>Pontella</u> <u>atlantica</u>, S.E.M. photograph, 110x magnification.

Figure 27. Detail of surface attachment structure of *Pontella atlantica*. Lateral edge. S.E.M. photograph, 3000x magnification.

Section IX

The colour of *Anomalocera opalus*

General body colour and its variations

Three pigment systems were observed in the copepod A. opalus; at least one, and possibly all of them, are under the animal's control. Over the dorsal surface of the gut, on or within a peritoneal membrane, is a double row of amoeboid-shaped melanophores of a dense brown colour. These cover a large proportion of the gut and may be a shield against harmful radiation. Their lack of definite shape gives the impression that they may change their shape and become either increased or reduced in area. No observations were made to clarify this.

The second pigment system to be discussed is the general blue and green colour of the entire copepod. Heinrich (1960), Zaitsev (1961) and David (1965) have suggested that the deep blue of many oceanic pontellid copepods may be a form of camouflage. Herring (1965) found that the pigment of Pontella fera was diffused throughout the body in water soluble form as well as concentrated in the chitin and underlying epidermis at specific sites. He found the pigment to be a type of chromoprotein, also called carotenoproteins, a carotenoid with a protein fragment attached. The transmission of this pigment from tropical pontellids is very close to the back-scattered colour of the tropical sea; light corresponding to the ambient light within the surface waters passed through this pigment in solution is relatively unchanged, which reinforces the hypothesis that the blue colour of pontellids is a form of camouflage.

Other possible reasons for the blue colour of pleuston pontellids (as well as the colour of other surface animals) are discussed by Herring (1968). He notes that the blue colour may be used to disguise accumulated red pigments which would otherwise make animals conspicuous, and that transparency even at the surface would perhaps be the best camouflage. Another possibility given by Herring is that carotenoids needed by the animals could be destroyed by light at the surface but are protected by the attached protein. In either of these cases, the blue colour is the lesser of evils and although still an adaptation, one of a second order.

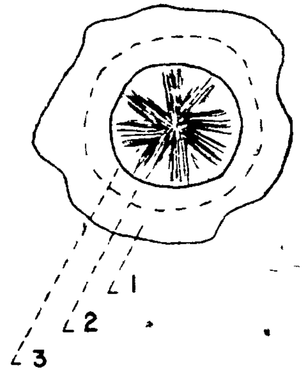
Zaitsev (1961 and pers. comm.) has stated that _Anomalocera patersoni_ in the Black Sea changes its colour from blue to green to match the background colour of the surface waters. Herring (1968) notes that this species in the North Atlantic varies from deep green to blue and notes that the blue is found in specimens from warmer water. He cites David that _A. patersoni_ is nearly always deep green in the northern latitudes, and species of Pontella and Labidocera were found to be green in areas of cold water upwelling. The effects of food, which might be expected to differ geographically, should not be overlooked. Green water usually contains large amounts of phytoplankton as well as dissolved substances.

During the present study, A. opalus was found to differ greatly in general colour from a pale somewhat transparent blue to a very rich and dense emerald green. A deep blue was always present localized in the chitin in large dorsal pigment spots (Figs. 3 and 28) in the ventral eye, in most of the terminal setae, on the ventral surface of the female genital segment, and on the male antennae. This pigment does not fade appreciably in preserved samples, although the diffused colour, either green or blue, very rapidly disappears in sea water-formalin solutions. Living copepods released soluble blue or green liquid when damaged. This is also noted by Herring for other pontellids and is taken as a sign that the pigment may be in the blood (Herring 1968).

The colour variation in A. opalus in the Gulf of St. Lawrence seemed to correspond very well with water colour. Such observations were always subjective but they were never contradicted and appeared convincing. Animals brought into the laboratory (see Section X) usually lost their blue or green diffused hues (but never the deep blues in the chitin described above) and appeared yellow. Observations of the dorsal pigment spots showed that these spots, although usually a deep navy blue, could on occasion be green or purple. Herring (1968) notes that a partial denaturing of blue carotenoproteins could produce a reversible purple colour. In some individuals which had turned yellow, the dorsal pigment spots had a blue centre with a surrounding yellow rim. There was sometimes a third green area between the blue and yellow (Fig. 28). It seems a possibility that the diffused green colour of A. opalus was formed by mixing of the blue pigment with a yellow carotenoid and that the dorsal pigment spots could be the centres of blue pigment manufacture and dispersal or mixing. Herring (1968) makes a similar suggestion, although he does not mention a particular site of control. He cites Keeple and Gamble (1904) who explain the green colour of Hyppolite varians as caused by a mixing of blue and yellow pigments, and Dupraw (1958) who finds that three pigments give the green colour to Cyclops eggs. Whatever the mechanism or cause of Anomalocera's colour variation, it does appear to vary with the colour of the water and would therefore have some beneficial camouflage value. As noted in Section IX, A. opalus observed at sea blended well with its surroundings.

Figure 28. Schematic drawings of _A_. _opalus_ (adult, female)

a) dorsal pigment spot
    1) yellow band
    2) green band
    3) blue spot with underlying tubules
b) animal attached to surface film
c) lateral view through chitin of dorsal pigment spots and underlying opaline collecting tubules
d) laterla, sub-chitinous opaline tubules



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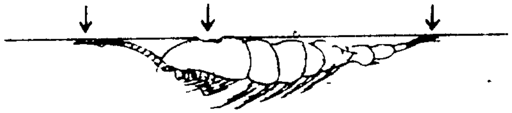

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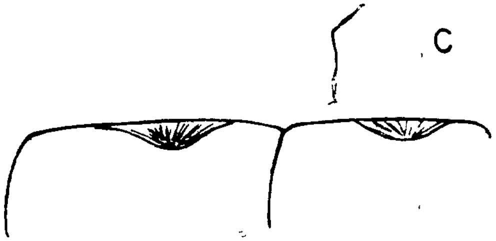

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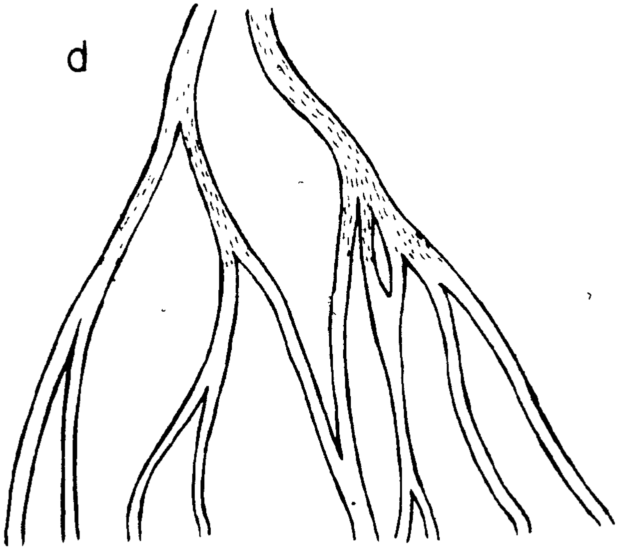

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The opaline pigment system

A third pigment system is the series of opaline organs located beneath each of the four dorsal pigment spots and responsible for a white opalescent sheen seen just under the dorsal and lateral chitin of the prosome (Figs. 3 and 28) in all copepodite stages of living A. opalus. This has not been described in any detail for Anomalocera sp. and in this study it was examined in living A. opalus only, but it is likely that it does occur in A. patersoni and probably other pontellids. Sars (1903) mentions that A. patersoni showed silvery streaks radiating outward from the dorsal pigment spot and Herring (1968) mentions a grey or white metallic sheen over the backs of several other pontellids. A description of this system in A. opalus is given here with some speculations on its use.

Examination of the white patches on the backs of A. opalus revealed that they were composed of many small anastomosing canals which radiate outward and downward just beneath the chitin from small sack-like organs attached to the undersurface of the dorsal pigment spots (Fig. 28). The organs are groups of larger tubules radiating from the centre of the organ and communicating with the finer canals. The outer canals of animals displaying opalescence were found to contain many slender rods, perhaps crystals (approx. .005 mm in length); the canals of animals not showing the opaline patches were empty, but the larger tubules of the central organs were filled with the same rods. Application of pressure to the central tubules sent rods streaming out into the small canals and gave the specimens the characteristic opalescent appearance.

It is not known whether the small rods are actually white or whether they produce the pearly opalescence through interference effects. Attempts were made to preserve them for laboratory study but they rapidly dissolved in all solutions tried, for example, formalin and sea water with and without additional buffering agents, mercuric chloride and fresh water, mercuric chloride with sea water, varying strengths of alcohols, potassium dichromate and formalin, and Bouin's solution. They appeared to dissolve most rapidly in solutions of low ph.

A somewhat similar system of radiating tubules is described by Herring (1968) for the siphonophores *Vellela* sp. and *Portita* sp. Anastomosing canals found in the outer layer of the floats have blue granules within the canal walls. When the blue granules are most frequent the float appears a rich blue; when the blue granules are reduced in number the lumen of the canals is apparent and the float appears whitish. Herring does not mention that there is anything within the lumen of the canals.

Most samples of freshly caught Anomalocera opalus contained some individuals showing varying degrees of opal pigment. Subsequent work with animals in large outdoor holding tanks revealed that almost any disturbance resulted in a contraction of the opal rods from the outer canals (and thus a disappearance of visible opal colour). The time taken to contract the pigment varied between five and fifteen minutes, rendering the usual 15 minute plankton samples useless for determining correlations between the number of animals showing opal colour and environmental variables.

Several schemes were tried to get captive animals to expand their pigment but, although animals readily withdrew their white pigment, it was never possible to get them to do the reverse under controlled conditions. Animals were placed in small containers and subjected to varying degrees of light and to different colour backgrounds, but to no effect. The large outdoor tanks (see Section X) were darkened for various periods but this did not seem to affect the number of animals with extended opal or the degree of opal extension in individuals. During both day and night, there were always some animals in the tank with extended opal pigment, although there was an impression that this was reduced at night. The observations were too few and too imprecise to permit an accurate statement.

During the observations at sea, nearly all of the animals seen had fully extended opal pigment, although the few that did not were very difficult to see initially and there may have been a bias. These observations were made during bright and calm weather. Herring suggests that the silvery patches on the backs of some pontellids are a form of protection against ultraviolet radiation. If this is true, it is hard to understand why the fully extended opal pigment does not cover the entire dorsal surface of the copepods. Much of the anterior nervous sytem and parts of the gonads are left unprotected. The area of the surface attachment structure receives the sun's rays directly without being shielded by water and it is unpigmented.

Despite the apparent conspicuousness of _A_. _opalus_ with extended opal pigment, there is still a possibility of camouflage effect. Zaitsev (1961) (see David 1965b) describes a small fish, _Mugil_ _auratus_, which during rough weather expands white chromatophores to achieve a speckled appearance which Zaitsev feels resembles the froth and bubbles of breaking waves. When the sea is calm, the fish contracts the white colour and becomes blue-green. This could be the case for A. opalus. Although the observations at sea took place during very calm weather, the area was very rich in small bits of floating white detritus and Anomalocera, when not moving, was very difficult to distinguish from these.

Section X

The behaviour and vertical distribution of *Anomalocera opalus*

Vertical distribution

Most plankton workers have considered Anomalocera patersoni s.l. to be a surface copepod (Bigelow 1926, Russell 1925a, 1925b, 1927, Bainbridge 1961), but there has been no detailed study of this genus using closing nets (and it should be noted that only a few of the closing net designs now used avoid contamination of surface life when shot (Harding 1972). Russell's extensive studies of plankton vertical distributions typify the problems arising when the subtractive method is used with a rare animal. Because Anomalocera has essentially a two-dimensional population (see Section I and below in this section), it will usually appear rare in comparison to other species which are more spread out over greater depths in the water column. Russell's work made it probable that Anomalocera is a surface animal, but his non-closing ring nets were unsuited to make finer distinctions. I have found no reference to a subsurface capture of Anomalocera with a closing net, although accidental capture by a deeply towed non-closing net has occurred while the net was at the surface (Bigelow 1915).

There are now several studies of the vertical distribution of A. paternsoni and one given here for A. opalus. These studies show that usually over 90% of the population within the upper meter will be found in the upper five to ten cm (Zaitsev 1961, 1970, Champalbert 1968, Tviete and Danielssen 1969). The specialization of the attachment structure described above and some of the behavioural observations given below combine with studies of micro-distribution to indicate that A. opalus and A. patersoni are surface forms and probably spend their entire lives within the upper few millimeters of the sea.

In 1966, during the first field season in the Gulf of St. Lawrence, several trials were made with a floating three stage net of the type described by David (1965a). A further description of this apparatus is found above in the materials and methods of Section VI. The net was too large to be used from the small boats available at Grande-Rivière stations in 1966, and a temporary system was constructed by suspending a Clarke-Bumpus plankton sampler below the smaller pleuston net used for the weekly collections (Pennell 1967). The depth of the sampler was about 45 cm below the surface and its mouth area about the same as that of the semi-submerged rectangular net above. In 1967, a smaller three stage net was constructed to fit the small towing frame used by this time for all pleuston collections.

It used the same 6 x 8 inches rectangular nets as used on all of the weekly collections for the entire study, and it proved superior to the other two designs. About 50 samples were taken with the Clarke-Bumpus system and about 80 with the small three stage net.

The results from all three systems were the same. Except for the eggs and first nauplius (which was rarely found at all), all stages of A. opalus were found heavily concentrated in the top net. Samples taken off the Gaspé in 1966 showed the same micro-distribution as those taken off the Magdalen Islands in 1967. There were many night samples taken during the course of the study, especially during the summer cruises. No diurnal variation was found and the concentration in the top net persisted. Samples with the three stage net were taken at all stations during the "Hudson" cruise over the Gulf in 1967, all of them showing the same pattern. Table 14 gives the results of 11 representative plankton samples taken with the three stage nets. They were chosen because they contained large numbers of Anomalocera as well as a sampling of the developmental stages. Moderate to heavy seas and steady rainfall did not affect the vertical distribution within limits of accuracy of the nets. Only one first nauplius was found in the plankton during the study and no eggs. The female sheds the eggs directly into the water and observations in the laboratory indicate that the eggs are not buoyant; they must

Table 14

Micro-Distribution - 3 Stage Net

No.	Date	E.S.T.	Copepodites adults	Nauplii (1-6)	Copepodites I-V	Adults	Aliquot
1.	15.8.67	0030	T. - 790	0	6	784	¼
			M. - 38	0	0	38	
			B. - 16	0	0	16	
2.	11.8.67	2124	T. - 224	0	52	172	¼
			M. - 6	2	2	4	
			B. - 2	2	0	2	
3.	12.8.67	2153	T. - 830	0	250	580	1/10
			M. - 30	0	20	10	
			B. - 10	0	0	10	
4.	12.8.67		T. - 2120	0	380	1740	1/10
			M. - 40	0	0	40	
			B. - 20	0	0	20	
5.	16.8.67	2227	T. - 776	0	692	84	1/10
			M. - 30	0	30	0	
			B. - 10	0	10	0	
6.	10.8.67	2225	T. - 270	4	170	100	Total Sample
			M. - 0	0	0	0	
			B. - 20	0	10	10	
7.	26.7.67	1145	T. - 138	56	128	10	Total Sample
			M. - 26	4	26	0	
			B. - 26	10	26	0	
8.	6.9.66	1200	T. - 98	207	55	43	Total Sample
			B. - 7	24	2	5	
			M. - 3	5	3	0	
9.	20.8.66	1300	T. - 6472	0	Not Available	Not available. Total More than 80% adults.	¼
			M. - 940	0			
			B. - 440	0			
10.	20.8.66	1300	T. - 3815	0	"	"	¼
			M. - 413	0	"	"	
			B. - 448	0	"	"	
11.	20.7.66	1500	T. - 977	0	"	"	¼
			M. - 162	0	"	"	
			B. - 66	0	"	"	

either sink or become dispersed through the water column. The first nauplius does not feed and probably is a stage of short duration; it may swim immediately towards the surface. The second nauplius whenever found was concentrated at the surface.

Behaviour

Observations on the behaviour of A. opalus were made on a number of occasions both at sea and ashore in the laboratory or in large outdoor tanks. A. opalus is present in the Gulf of St. Lawrence in large numbers for only a few weeks of the year and its patchiness makes it impossible to plan definitely when to make suitable collections. Limitation of boat time was a problem during all of the study but was especially aggravating to the study of behaviour. In 1966, some observations were made using small numbers of live animals kept in small containers. In 1967, more live animals were available which could be kept for several days at a time in large wooden tanks set up outdoors. Most of the observations at the tanks were made on groups of about 50 adults and a few younger stages. During one day of very calm and sunny weather (September 1967), observations at sea of adult copepods were made for several hours. The account given below derives from all of these observations and is concerned with adults unless otherwise stated.

The surface attachment structure described above in Section VIII was found on all of the copepodites and seen in use by all but stage I. The observations, although limited, suggest that this structure is part of an important adaptation to surface life for A. opalus. By extension, it is probably of equal importance for A. patersoni and several other pontellids which also possess very similar structures as noted in Section VIII.

To attach itself to the surface film, A. opalus appears to bump upward against the film with its dorsal surfaces. There are five points of attachment, the first antennae, the first prosome segment (at the attachment structure) and the ends of the setae of both caudal furcae (Fig. 28). All of these points cause a slight dimpling of the surface film. At times individuals were seen to swim with just the tips of the first antennae in contact with the surface film as described for Labidocera aestiva by Parker (1901). A. opalus is quite flexible through the cephalosome and on each of the dorsal lateral surfaces of the fourth prosome segment there is a single long but very fine hair. These might be used for making very fine adjustments to the surface film. When the attachment spot touches the surface film, it becomes dry, either because it is hydrofuge as is the chitin of hyperiid amphipods and cladocerans or because the borders of the structure are composed of hairs or related structures which in some way repel water. The setae of the first antennae and caudal furcae seem to attach to the surface by means of fine hairs.

The attachment of young stages was seen only occasionally and usually in small containers. The adults, which were better observed, appeared to depend on surface suspension and probably spend much of their time so attached. In the outdoor tanks, most of the animals were always to be found in the attached position, some resting motionless and others swimming both slowly and very energetically. A full range of activities, including feeding attempts, copulation and escape, was seen with animals suspended from the film. The same observations were made at sea, but there the only animals seen were attached and no estimate of the proportions of those not attached could be made.

The most obvious value of the surface attachment behaviour is the saving of energy in place keeping. A. opalus is a large and dense copepod and will sink rapidly if not swimming or attached. It has no means of appreciably slowing descent such as wide or plumose antennae (see discussion in Kovalev 1970). At night in the large outdoor holding tanks, adults could often be seen lying motionless suspended from the interface, thereby exerting no effort for what may be long periods of time. Most of the swimming seen (either with animals attached or not attached to the surface) was done with rhythmic strokes of the second antennae which propel the animal forward in a sequence of tiny jerks (see Gauld 1966, Lukjanova 1940). Very often female adults, swimming without the terminal setae attached to the surface film, showed a pronounced vertical movement of the urosome arising from its junction with the prosome. This may propel the animal forward or may simply result from thrusts of the second antennae. Kovalev (1970) considers the former to be the case and calls the pontellid urosome a "motor". Rapid escape is effected with the four paired swimming legs. Swimming in this manner can be extremely rapid and can take the animal over quite long distances (up to half a meter) in a fraction of a second. In both the tanks and at sea, attached copepods were seen to investigate bits of floating matter, sometimes taking a bit in the feeding limbs. On encountering another <u>A</u>. <u>opalus</u>, both animals frequently executed a rapid whirl about each other and then sprang apart still suspended, or at other times began to mate. A sudden shadow often caused a protean type of behaviour lasting several seconds in which the animals, remaining in contact with the surface, made irregular high speed circles covering several feet in a very short time. At other times, shadows caused diving to several inches depth. The leaps out of the water for distances up to six inches described for A. patersoni by Zaitsev (pers. comm.) and by David (1965) for other pontellids were not seen. Very small jumps clear of the water could be induced by pursuing the copepods with an eye dropper, and under these conditions the jumps were very effective. Often copepods which had been left for the night in small containers were found some distance outside the containers in the morning.

The observations at sea were made during early afternoon sunlight as were many of those at the tanks, and it would seem that insolation does not inhibit attachment to the surface. In the tanks, animals definitely avoided swimming over areas illuminated from below by reflections from sunlight on the tank floor. They neither avoided nor sought those sunlit areas which were shaded on the bottom. In small glass or white porcelain containers in which there was a high degree of reflection from below, copepods were often confused and reversed their positions at the surface, swimming upside down with just the first antennae touching the surface film or lying dorsal surface down on the bottom of the container.

It was not possible to adequately study the response of A. opalus to wind or surface disturbance, to the wind rows or to heavy concentrations of floating matter. In small tanks, considerable waves would not dislodge an attached animal, and in the larger outdoor tanks, a steady breeze with resulting ripples did not seem to inhibit surface attachment. Such a breeze did generate a surface current against which the copepods usually swam. When they did not swim against the current, they were quickly blown along with a thin surface layer. This may explain the very noticeable lack of specimens found under a weather shore as described in the section on the life cycle. During the observations at sea, all copepods seen were in the vicinity of floating detritus which occurred in patches, possibly the remains of wind row convergences.

Copulation was observed on a number of occasions, usually with animals attached to the surface. It appears very similar to that of the calanoid copepod Eudiaptomus gracilis described by Wolf (1905) (in Hutchinson 1967). The male Anomalocera opalus pursues and grasps the female from behind with his geniculate right antenna at about the point of her caudal setae or furcae. He is then pulled behind her in train (dorsal surface of both copepods upward). This phase may last from one to two minutes. Next the male twists and swings around so that he is still dorsal surface up but heading in the opposite direction from the female. He now clasps her about the genital segment with the right fifth pleopod which is modified into a sickle-shaped hook. This differs somewhat from the behaviour of

Eudiaptomus gracilis which during this second phase does not orient with both sexes in the same vertical plane, the male being twisted slightly along his long axis relative to that of the female. For both sexes of Anomalocera to remain in contact with the surface film as they usually are during this phase of copulation, it is necessary for them to have the same alignment. The Eudiaptomus male uses his abdomen against the dorsal surface of the female's urosome to get leverage. This may also be the case with Anomalocera, since the males have a very flexible abdomen. This was not seen however.

The second phase may last from 5 to 8 minutes. The female continues to swim using the second antennae and the male, often swimming against the stronger female, is pulled backwards behind her. Occasionally when the female stops swimming, the male makes some temporary headway. It is presumably during this second phase that the male is extracting the spermatophore and placing it over the genital pore of the female. The left fifth pleopod of the male is equipped with an articulated claw which grasps and positions the spermatophore (details of the positioning were not observed). That this claw or pincer is used to position the spermatophore is inferred from frequently finding spermatophores grasped in the claw of preserved male copepods. On one occasion two males were seen to approach each other, both attached to the surface, and immediately begin copulation which proceeded to the second phase. After 2 or 3 minutes they broke apart. Anomalocera is extremely vulnerable during its lengthy copulation. It is both easy to capture and to see. This is probably an indication that the process has a bearing on inter-specific variation of the genital segments (Section II) (see Lee 1973). After copulation, females frequently were seen to rest quietly for several minutes suspended from the surface tension.

Actual feeding of A. opalus was never observed. Dissection of the gut of adults revealed occasional remains of small crustaceans but no whole, recognizable specimens. This may indicate a rapid digestion. Not enough dissections were made to permit generalizations. Lebour (1925) describes A. patersoni from British waters attacking and eating small fish larvae in laboratory aquaria, and Lillelund, Kurt and Lasker (1971), in a laboratory study, report that the pontellids Labidocera jollae, L. trispinosa and Pontellopsis occidentalis killed and ate large numbers of anchovy larvae. Zaitsev (1970 and pers. comm.) considers A. patersoni in the Black Sea to be chiefly a carnivorous copepod but notes that the gut may contain plant matter as well as occasional remains of insects which have been blown out to see from the land (see Section I). Lebour (1922) noted that guts of A. patersoni contained crustacean remains (including harpacticoid copepods) and at times diatoms such as Rhizosolenia. Gauld (1964) considers A. patersoni carnivorous.

During the observations of A. opalus at sea (Section IX), it was noted that copepods often examined bits of detritus at the surface interface. The bits were held and manipulated with the feeding appendages and then rejected. It is possible that floating detritus constitutes a major food source for this copepod.

Section XI

Notes on other species living at the surface interface in the Gulf of St. Lawrence

In most pleuston samples taken in the course of this study, there were many individuals of plankton species generally known from surface plankton. Some of these were at times conspicuously concen~~tra~~ted at the very surface showing a micro-distribution much like that of A. opalus. Plankton counts from the three stage nets revealed many variations of micro-distribution with different degrees of accumulation at the surface (the top net) or avoidance of the surface, but detailed studies of other organisms were not made. Organisms with very strong surface concentrations are described below. In Section I the absence of conspicuous pleuston animals in the higher latitudes is discussed. It can be seen here that there may be a very significant amount of pleuston in the Gulf of St. Lawrence, at least in the summer months, but that most of it may be quite temporary. Larval forms may predominate.

Phytoplankton was common in samples during the spring and fall increases. One species which appeared to have a surface distribution is Halosphaera sp (Brunel 1962), found in large numbers in 1966 in the months of April and May. It was taken in the top net but was absent from samples in the suspended Clarke-Bumpus net then used. In jars, freshly caught, unpreserved Halosphaera floated upwards to the top. They were found in smaller numbers in the 1967 series in the top net but rarely in the lower two nets.

In both 1966 and 1967, very large numbers of spring cod eggs were found highly concentrated in the top net and nearly absent in the lower nets. At sea on calm days they were seen forming vast clouds at the interface. Plaice eggs were also present at the interface but in lesser numbers.

In May and June 1967, a bloom of an unidentified planktonic rotifer appeared and persisted for several weeks. In all samples the animals were concentrated by the thousands (up to 99%) in the upper net. This distribution persisted in moderate waves and during bright sun.

A larval holothurian, possibly a *Cucumaria* sp., of bright orange colour was frequently captured in the top net but in numbers too small for micro-distribution estimates. Live animals showed a pronounced positive buoyancy and appeared to make contact with the surface film with their podia.

The larvae of the four-bearded rockling, *Enchelyopus cimbrius*, has been reported to have the same micro-distribution as *Anomalocera* (Pennell 1967). This work was not followed up in detail, but many more rockling were caught in 1967 in the upper net. Some observations were made at sea in calm conditions as well as in the large tanks. The rockling larvae were seen to swim at the interface in small schools, often just rippling the film with the dorsal fin. None were seen deeper. When alive, they are speckled metallic green colour on top; the sides and under-surface are white or pale.

Larval _Urophycis_ sp. (Hake) were also found in pleuston samples but were not studied in detail. They occurred in large numbers in high speed pleuston samples taken by the Fisheries Research Board in late summer over the Magdalen Shallows, but were not well represented in the pleuston samples taken with the 6 x 12 inch net used in this study.

As noted in Section VIII on the life cycle of _A_. _opalus_, wind rows composed of seaweeds and coastal grasses were a general feature of the surface waters in the Gulf of St. Lawrence. There were a number of animals associated with these seaweeds and grasses throughout the summer months. Several species of harpacticoid copepods and isopods (_Idotea_ sp.), apparently reproducing themselves, were found in the pleuston samples and were observed to cling to seaweeds (usually _Fucus_ sp.). It is doubtful that these could have maintained themselves without the refuge provided by the weeds.

Larvae of the lumpfish, _Cyclopterus_ _lumpus_, were common in pleuston samples, although usually in small numbers. They appeared to be correlated with seaweed abundance and, although they possessed well developed suckers, observations in aquaria indicated that they often swam near the surface without attachment to floating objects (see Cox and Anderson 1922).

Two species of sticklebacks, the two-spined Gasterosteus wheatlandi, and the three-spined G. aculeatus, were frequently encountered in the southern Gulf and in Northumberland Strait. In the small pleuston net used in this study, they occurred regularly but in very small numbers, presumably because they could escape the smaller net. In the large, high speed pleuston samples made by the Fisheries Research Board from the "A.T. Cameron", they were much more numerous and were perhaps the most important small fish at the very surface in the Magdalen Shallows. They appeared to be associated with floating grasses but were found with seaweed as well.

Sticklebacks, isopods and harpacticoid copepods were also found in the large lagoons on the Magdalen Islands (Anomalocera and many other common Gulf copepods were not found in the lagoons). It is not known to what extent this seaweed - eel grass fauna is distinct from other members of the pleuston in the Gulf of St. Lawrence; it is a little reminiscent of the Sargasso community, although it is not certain that there are any specific adaptations to floating life in this group of animals. It may just be an extension of shore fauna into the pelagic zone during the months when the Gulf surface water is both warmest and most brackish.

Summary of Results

1. Pleuston samples were collected for three seasons in the Gulf of St. Lawrence: March to November 1966, off Grande-Rivière, on the south Gaspé Peninsula; May to September 1967, at the Magdalen Islands; June to October 1968, off Grande-Rivière. Vertical plankton hauls and environmental observations were also made. Three summer cruises were made to different parts of the Gulf and pleuston samples taken. Plankton samples from other cruises were made available to the study. Three winter cruises were made to collect plankton from all depths in the Gulf. This material was used primarily to determine the life cycle of _Anomalocera_ _opalus_ in the Gulf of St. Lawrence.

2. A new species, _Anomalocera_ _opalus_, is described from the Gulf of St. Lawrence. Material from both the east and west North Atlantic shows that _A_. _opalus_ is found in the Gulf of Maine, Scotian Shelf and the shelf waters south of Cape Cod. The range probably extends as far south as Cape Hatteras. _A_. _patersoni_ is found in European shelf waters north along the Norwegian coast and occasionally south of Iceland. It is also found in the Black Sea, the Mediterranean Sea and off the coast of west Africa to latitude 20. A review of the literature suggests that both species are very rare in the open

ocean and that A. patersoni is not likely to breed near Iceland. Anomalocera spp does not breed in west Greenland. The two species are unlikely to have significant contact and the morphological differences described are not extremes of clinal variation.

3. The developmental stages of A. opalus are described.

4. It is suggested that speciation of A. opalus and A. patersoni has proceeded allopatrically as a result of separation of previously united stocks. The separation is suggested to have been caused by climatic fluctuations in the Pleistocene.

5. The terminology of special surface life is discussed as well as the nature of the interface environment and the kinds of animals and plants which may be found there. An abbreviated terminology for interfacial life is suggested and, throughout the work, the term pleuston is used to refer to all such life.

6. Studies of the micro-vertical distribution of A. opalus showed that this species is found in the upper two inches of the sea, and probably is usually found in the top mm. A review of the literature suggests that neither A. patersoni nor A. opalus has been found far below the surface.

A. opalus is a pleuston copepod.

7. A new structure, used for attachment to the surface interface, is described for all copepodite stages; it is located on the dorsal surface of the first prosomal segment. Scanning electron microscope photographs of this structure are presented. The structure was found in this study on several other pontellid copepods. Similar structures are not known for other copepod families.

8. Observations on the behaviour of A. opalus were made both in the laboratory and at sea. The use of the surface attachment structure was observed. This appears to be a very important aspect of the biology of A. opalus; surface attachment seems to be the normal condition of life for this copepod. Other behaviour of A. opalus in relation to the interface is described. The copulation is described in some detail.

9. Three pigment systems in the copepodite stages of A. opalus are described. Brown melanophores form a layer, possibly protective, over the gut wall. A new pigment system called the opal gland is described, and observations made on its use. Its function is obscure, but it may be related to camouflage. The third system is the blue-green colour of the

copepod which appears to match the water colour in which the animals are caught. Dorsal pigment spots may supply both the yellow and blue diffuse pigments which are mixed in the animal's body to produce the correct adaptive shades.

10. The life cycle of A. opalus was determined in the Gulf of St. Lawrence and was the main focus of the study. A. opalus is found from June to November in the Gulf and exhibits continuous breeding over the summer. Its population is extremely patchy and fine details of the cycle could not be determined. The population rose from small numbers in all three years to a peak population size of approximately ten copepods per square meter in mid- to late August. It declined through the fall to extinction. It was not found in any of the winter samples nor in the many early spring plankton samples. Its first appearance was in early to mid-June in each of the three years, in the form of nauplii and early copepodites.

11. To account for the apparently regular June appearance of young forms, a resting egg stage is postulated for the over-wintering of A. opalus in the Gulf of St. Lawrence. It is suggested that a similar method of over-wintering may be used in the Gulf of Maine, and by A. patersoni in the northern part of its North Atlantic range.

12. Several other species of plankton animals were found in the pleuston samples with micro-distributions which suggest that they are pleuston organisms. Larvae of the four-bearded rockling, Enchelyopus cimbrius, were often found in the surface samples and were observed at sea to swim at the interface. Larvae of the hake, Urophysis sp were also common in pleuston samples. A larval echinoderm, Cucumaria sp, was frequently found in interfacial samples and observations were made on its behaviour. The eggs of two important fish, cod and plaice, were found highly concentrated at the surface. An unidentified rotifer formed large blooms at the interface in 1967 with a distribution similar to that of the cod eggs and of A. opalus.

There is the suggestion of a pelagic seaweed-eelgrass community in the Gulf of St. Lawrence, including two species of sticklebacks, Gasterosteus wheatlandi and G. aculeatus, the larvae of the lumpfish, Cyclopterus lumpus, and several small crustaceans. These species were not studied in detail and their relations to the pleuston species are unknown.

Bibliography

Andrewartha, H.G. and L.C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, 782 pp.

Anonymous. 1965. International Indian Ocean Expedition, 1962-3 and 1963-4. Data of oceanographic observations and exploratory fishing. No. 1. Shimonosoki University of Fisheries, Japan, 453 pp.

Bainbridge, R. 1957. The size, shape, and density of marine phytoplankton concentrations. Biol. Revue, 32: 91-115.

Bainbridge, R. 1961. Migrations. In: Physiology of Crustacea, T.H. Waterman (ed.). Vol. II: 431-463, Academic Press, New York and London.

Baird, W. 1850. Natural History of the British Entomostraca. The Ray Society, London, 364 pp.

Banse, K. 1964. On the vertical distribution of zooplankton in the sea. Progress in Oceanography, vol. 2: 53-125.

Barber, R. 1966. Organic aggregates formed from dissolved organic material by bubbling. Second Int. Oceanogr. Congress, No. 17, p. 19.

Bary, B.M. 1953. Sea water discoloration (by living organisms). New Zealand J. Sci. and Tech. Ser. B, 34(5): 393-407.

Bayer, F.M. 1963. Observations on pelagic mollusks associated with the siphonophores Velella and Physalia. Bull. Mar. Sci. Gulf Caribb., 13 (3): 454-466.

Baylor, E.R. and W.H. Sutcliffe, Jr. 1963. Dissolved organic matter in sea water as a source of particulate food. Limn. and Oceanogr., 8: 369-371.

Beebe, W. 1926. The Arcturus Adventure. McClelland and Stewart, Toronto, 439 pp.

Beklemishev, C.W. 1960. Biotope and community in marine plankton. Int. Rev. geo. Hydrobiol., 45 (2): 291-301.

Ben-Yami, M., A. Herzberg, S. Pisantry and A. Lourie. 1970. A side-tracking neuston net. Mar. Biol., 6 (4): 312-316.

Bieri, R. 1959. Dimorphism and size distribution in Velella and Physalia. Nature, 184: 1333.

Bieri, R. and T. Newbury. 1966. Booby II, a quantitative neuston sampler for use from small boats. Publ. Seto marine biol. Lab. 8 (5): 405.

Bigelow, H.B. 1915. Exploration of the coast water between Nova Scotia and Chesapeake Bay, July and August, 1913 by the U.S. Fisheries Schooner, Grampus. Oceanography and Plankton. Bull. Mus. Comp. Zool. 59 (4): 151-359.

Bigelow, H.B. 1922. Exploration of the coastal water off the N.E.U.S. in 1916 by the U.S. Fisheries Schooner, Grampus. Bull. Mus. Comp. Zool., 65 (5): 86-188.

Bigelow, H.B. 1926. The plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bur. Fish., 40 (11): 507 pp.

Bigelow, H.B. and M. Sears. 1939. Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. Mem. Mus. Comp. Zool., 54: 183-278.

Björnberg, T.K.S. 1963. On the marine free living copepods off Brazil. Boletimdo Instituto Oceanographico, Tomo XIII, fasc. 1: 3-142.

Boeck, A. 1864. Oversigt Norges Copepoder. Saerskilt Aftrykt af Vidensk-Selskab Fornandlinger 1864: 226-281.

Bowman, T.E. 1971. The distribution of calanoid copepods off the S.E.U.S. between Cape Hatteras and southern Florida. Smithsonian Contrib. to Zoology, 96: 1-58.

Brady, G.S. 1878. British Copepoda. Vol. I. The Ray Society, London, 148 pp and 33 plates.

Brady, G.S. 1883. Report on the Copepoda obtained by the HMS Challenger during the years 1873-1876. Reports of the Scientific Results of the Voyage of the Challenger, 8 (1): 1-142.

Brinton, E. 1959. Geographical isolation in the pelagic environment. A discussion of the pelagic euphausid crustaceans in the Pacific. Int. Ocean. Conng. Preprints. A.A.A.S.: 255-257.

Brodski, K.A. 1950. Calanoida of the Far Eastern Seas and Polar Basin of the U.S.S.R. Tabl. anal. Faune U.R.S.S., Zool. Inst., Acad. Sci., 35: 1-435. (Translation, Israel program for scientific translation. Jerusalem, 1967).

Brown, W.L. 1957. Centrifugal speciation. Quart. Rev. Biol., 32 (3): 247-278.

Bruce, J.R., J.S. Coleman, and N.S. Jones. 1963. Marine Fauna of the Isle of Man and its Surroundings. Liverpool University Press. 2nd edition, 307 pp.

Brunel, J. 1962. Le Phytoplancton de la Baie des Chaleurs. Contributions du Ministère de la Chasse et des Pêcheries, No. 91: 1-365.

Bull. of Mar. Ecol., and Hull Bull. of Mar. Ecol., A.C. Hardy (ed.), Vol. I (1958) - Vol. VI (1973).

Bumpus, D.F. and L.M. Lauzier. 1965. Surface circulation on the continental shelf off eastern North America between Newfoundland and Florida. Serial Atlas of the Marine Environment, Folio 7. Geogr. Soc. New York.

Buzzati-Traverso, A.A. 1958. Genetishe problems der marinen biologie. Rev. Suisse de Zool., 65 (33): 461-483.

Buzzati-Traverso, A.A. 1960. Discussion. In: Perspectives in Marine Biology, A.A. Buzzati-Traverso (ed.). Berkeley and Los Angeles, Univ. of Calif. Press, p. 585.

Cairns, A. 1969. Seasonal cycles, dynamics and production of copepods in the Arctic. Ph.D. thesis, Marine Sciences Centre, McGill Univ., 57 pp.

Candeias, A. 1929. Première liste des copepodes des côtes du Portugal. (Résumé). Rapp. Proc. Verb. des Réunion. Cons. pour l'Exploration de la Mer, 55: 151.

Carpenter, K.E. 1928. Life in inland waters, with especial reference to animals. New York, MacMillan, xviii + 267 pp.

Cassie, R.M. 1963. Microdistribution of plankton. Oceanogr. Mar. Biol. Ann. Rev., 1: 223-252.

Champalbert, G. 1969. L'hyponeuston dans le Golfe de Marseille. Téthys, 1 (3): 585-666.

Champalbert, G. 1971. Composition de l'hyponeuston du Golfe de Marseille. Rapp. Proc. Verb. Comm. Int. Explor. Scient. Mer Medit., 20 (3): 427-430.

Champalbert, G., and G. Macquart-Moulin, 1970. Les pericardes de l'hyponeuston nocturne du Golfe de Marseille. Cah. Biol. Mar., 11 (1): 1-29.

Cleve, P.T. 1900. Geographical distribution of Atlantic copepods and their physical conditions. Ofversigt af Kongl. Vetenskaps-Akad. Forhandlinger. No. 2. Stockholm.

Colebrook, J.M., D.E. John and W.W. Brown. 1961. Contribution towards a plankton atlas of the north-eastern Atlantic and the North Sea. Part II, Copepods. Bull. Mar. Ecol. 5 (42): 90-97.

Colebrook, J.M. and G.A. Robinson. 1963. Ecological differentiation in the plankton in the waters around the British Isles. In: Speciation in the Sea, pp. 157-169. Systematics Association Publication No. 5.

Conover, R.J. 1956. Oceanography of Long Island Sound, 1952-1954. VI. Biology of <u>Acartia clausi</u> and <u>Acartia tonsa</u>. Bull. Bingham Oceanogr. Coll., 15: 156-233.

Conover, R.J. 1962. Metabolism and growth in <u>Calanus hyperboreus</u> in relation to its life cycle. Rapp. Proc. Verb., 153: 190-197.

Conover, R.J. 1964. Food and nutrition of zooplankton. Symposium on experimental marine ecology. University of Rhode Island, Occ. pub. No. 2: 81-91.

Conrad, J. 1923. The shadow line, a confession. Concord edition. Doubleday, Page & Co., Garden City, N.Y., 133 pp.

Cooper, L.H.M. 1967. Stratification in the deep ocean. In: Sci. Prog. Orf., 55: 73-90.

Cox, P. and M. Anderson. 1922. A study of the lumpfish (Cyclopterus lumpus). Contrib. to Canadian Biol., N.S. I (1): 1-20.

Dahl, M. 1894. Über die horizontale und verticale Verbreitung der Copepoden im Ozean. Verh. d. Deutsch. Zoolog. Ges. Munchen. Vol. 4: 61-80.

Dansgaard, W., S.J. Johnsen, H.B. Clausen and C.C. Langway. 1971. Climatic record revealed by the Camp Century ice core. In: Late Cenozoic Glacial Ages, K.K. Turekian (ed.), pp. 37-56. New Haven and London, Yale University Press.

David, P.M. 1963. The neuston net, a device for sampling the surface fauna of the ocean. Natl. Inst. Oceanogr. Internal Report, No. 33: 1-5.

David, P.M. 1965a. The neuston net, a device for sampling the surface fauna of the ocean. J. mar. biol. Ass. U.K., 45: 313-320.

David, P.M. 1965b. The surface fauna of the ocean. Endeavour, 24 (92): 95-100.

David, P.M. 1967. Illustrations of oceanic neuston. In: Aspects of Marine Zoology, N.B. Marshall (ed.). Symp. Zool. Soc. Lond., 19: 211-213.

Deevey, G.B. 1952. Quantity and composition of the zooplankton of Block Island Sound. Bull. Bingham Oceanogr. Coll., 13 (3): 165-219.

Deevey, G.B. 1956. Oceanography of Long Island Sound. V. Zooplankton. Bull. Bingham Oceanogr. Coll., 15: 113-155.

Della-Croce, N. and L.B. Holthius. 1965. Swarming of <u>Charydis</u> <u>goniohellenus</u> <u>edwardsi</u> Leene and Buitendijk, in the Indian Ocean. (Crustacea, Decapoda, Portunidea). Boll. Dei Mus. E. Degli Inst. Biol. dell' Univ. di Genova, 33 (199).

Della-Croce, N. and T. Sertorio. 1959. Microdistribution of zooplankton. Int. Oceanogr. Cong., 1959, preprints, p. 306, A.A.A.S., Wash., D.C.

Denton, G.H. and S.C. Porter. 1970. Neoglaciation. Sci. Amer., 222 (6): 100-110.

Dietz, R.S. and E.C. LaFond. 1950. Natural slicks on the ocean. J. Mar. Res., 9: 69-76.

Dunbar, M.J. 1957. The determinants of production in northern seas: a study of the biology of <u>Themisto</u> <u>libellula</u> Mandt. Can. J. Zool. 35: 797-819. ("Calanus" series No. 14).

Dunbar, M.J. 1968. Ecological Development in Polar Regions. A Study in Evolution. Concepts of Modern Biology Series, Prentice-Hall Inc., Englewood Cliffs, N.J., 119 pp.

Dunbar, M.J. 1972. The Ecosystem as a unit of natural selection. In: Growth by Intussusception. Ecological Essays in Honour of G. Evelyn Hutchinson, E.S. Deevey (ed.). pp. 115-130.

Dunbar, M.J. 1973. On the West Greenland sea-life area of the Atlantic salmon. Arctic, J. of the Arctic Inst. N. Amer., 26 (1): 3-6.

Dupraw, E.J. 1958. Analysis of egg colour variation in Cyclops vernalis. J. Morph. 103: 31-63.

Edwards, C. 1966. Velella velella: The distribution of its dimorphic forms in the Atlantic Ocean and the Mediterranean, with comments on its nature and affinities. In: Some contemporary studies in marine science, Harold Barnes (ed.). George Allen and Unwin Ltd., pp. 283-296.

Ekman, S. 1953. Zoogeography of the Sea. Sidgwick and Jackson, London, 417 pp.

Engel, W.A. and E.C. Tan. 1965. Investigations of inner continental shelf waters off lower Chesapeake Bay. Part VI, The copepods. Chesapeake Science, 6 (3): 183-189.

Ewing, G.C. 1950. Slicks, surface films and internal waves. J. Mar. Res., 9: 161-187.

Ewing, M. 1971. The late Cenozoic history of the Atlantic Basin and its bearing on the cause of the ice ages. In: The late Cenozoic glacial ages, K. Turekian (ed.). New Haven and London, Yale Univ. Press, pp. 565-573.

Faber, D.J. 1966. Free-swimming copepod nauplii of Naragensett Bay with a key to their identification. J. Fish. Res. Bd. Canada, 23 (2): 189-205.

Fager, E.W. 1957. Determination and analysis of recurrent groups. Ecology, 38 (4): 586-595.

Fager, E.W. 1963. Communities of organisms. The Sea, 2: 415-437. M.N. Hill (ed.). Interscience Pub., New York.

Faller, A.J. 1964. The angle of the windrows in the ocean. Tellus, 16: 363-370.

Faller, A.J. and A.H. Woodcock. 1964. The spacing of windrows of sargassum in the ocean. J. Mar. Res., 22 (1): 22-29.

Farran, G.P. 1910. Resumé des observations des mers explorées par le conseil pendant les années 1902-1908. Copepoda. Bull. Trim. Cons. Explor. Mer, 1910: 60-79.

Farran, G.P. 1929. Crustacea. Part X. Copepoda. Nat. Hist. Rep. Terra Nova Exped. (Zool.), 8: 203-206.

Filteau, G. 1946. Les coépodes marines de la Baie des Chaleurs. Univ. Laval, Sta. Biol. St. Laurent, Rapp. Gen., 1943-1945, Rapp. 5 (App. 4): 88-96.

Fish, C.J. 1925. Seasonal distribution of the plankton of the Woods Hole region. Bull. Bur. Fish. Wash. D.C. Doc. 975, Vol. 41: 91-179.

Fish, C.J. and M.W. Johnson. 1937. The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. J. Biol. Bd. Can. No. 3: 189-322.

Fisher, J. and R.M. Lockley. 1954. Sea Birds. Introduction to the Natural History of British Sea Birds. Collins Pub., London (The New Naturalist Series.). 320 pp.

Fleminger, A. 1967. Taxonomy, distribution, and polymorphism in the <u>Labidocera jollae</u> group with remarks on evolution within the group (Copepoda: Calanoida). Proc. of the U.S. National Museum, 120 (3567): 61 pp.

Fleury, J. 1952. Note planctonique, Atlantic area. Ann. Biol. Cons. perm. Int. Expl. Mer, 8: 65-66.

Fraser, J.H. 1955. The plankton of the waters approaching the British Isles in 1953. Mar. Res. Scot. No. 1: 1-12.

Fraser, J.H. 1961. The oceanic and bathypelagic plankton of the N.E. Atlantic and its possible significance to fisheries. Mar. Res. Scot. No. 4: 1-48.

Fraser, J.H. and A. Saville. 1948. Plankton of the North Western area. Ann. Biol., 5: 29-62.

Fretter, V. and A. Graham. 1963. The origin of species in littoral ~~pro~~sobranchs. In: Speciation in the Sea. Systematics Ass. Pub. N. 5, pp. 99-107.

Frost, N. 1937. Further plankton investigations. Rep. Fish. Res. Inst. Nfld., 1925-1937: p. 25.

Gams, H. 1918. Prinzipienfragen der Vegetationsforschung. Vjschr. Natur. Ges., Zurich, 63: 293-493.

Garrett, W.D. 1965. Collection of slick forming material from the sea surface. Limn. and Oceanogr., 10: 602-605.

Garrett, W.D. and J.D. Bultman. 1963. The damping of water waves by insoluble organic mono-layers. U.S. Naval Res. Lab. Rept., No. 6003: 1-18.

Gauld, D.T. 1964. Feeding in planktonic copepods. In: Grazing in Marine and Terrestrial Environments, D.J. Crisp (ed.). British Ecological Society, symp., Blackwell Sci. Pub., Oxford, pp. 337-249.

Gauld, D.T. 1966. The swimming and feeding of planktonic copepods. In: Some Contemporary Studies in Marine Science, H. Barnes (ed.), Hafner Pub. Co., New York, pp. 313-334.

Geptnev, M.V. 1968. The structure and taxonomic significance of the genital complex in copepods of the family *Euchaetidae* (*Calanoida*). Oceanology, 1968: 543-552.

Giesbrecht, W. 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel. Fauna und Flora des Golfes von Neapel, Vol. 19: 831 pp.

Giesbrecht, W. and O. Schmeil. 1898. *Copepoda*. I. *Gymnoplea*. Das Tierreich, Lief 6: 1-169.

Gieskes, W. 1970. The *Cladocera* of the North Atlantic and the North Sea: Biological and Ecological Studies. Ph.D. thesis, Marine Sciences Centre, McGill Univ., 205 pp.

Gietler, L. 1942. Zur Kentnis der Bewohner des Oberflächen-häutchens einheimischer Gewasser. Biologia gen., 6: 450-475.

Gough, L.H. 1905. Report on the plankton of the English Channel in 1903. Mar. biol. Ass. Intern. Fish. Invest., 1902-1903. Southern Area.

Gregg, M. 1973. The microstructure of the ocean. Sci. Amer., 228 (2): 64-77.

Grice, G.D. 1973. Pers. comm. Woods Hole Oceanographic Inst., Mass., U.S.A.

Grice, G.D. and A.D. Hart. 1962. Distribution, seasonal occurrence and abundance of the epizooplankton between New York and Bermuda. Ecological Monographs, 32: 287-309.

Griffin, D.R. 1963. The fishing bats of Trinidad. Animal Kingdom, 66 (5): 152-158.

Gudkov, V.M. 1962. On interrelation in the distribution of zooplankton, marine birds and baleen whales. Tr. Inst. Okeanol. Akad. Nauk., U.S.S.R., 58: 298-313.

Harding, G. 1972. Ecological observations on North Atlantic deep-sea copepods. Ph.D. thesis, Dalhousie Univ., 201 pp.

Hart, T.J. 1964. Discoloured water due to zooplankton off lower California. The Marine Observer, Jan., 1964. (Nat. Inst. Oceanogr., Wormley, Surrey, Collected reprints, No. 497).

Harvey, G.W. 1966. Microlayer collection from the sea surface. A new method and initial results. Limnol. and Oceanogr., 11 (4): 608-613.

Harvey, G.W. 1971. Aspects of sea surface microlayer ecology. In: Proc. Joint Oceanogr. Cong., "The Ocean World", Tokyo: p. 275.

Heinrich, A.K. 1960. On the surface plankton of the central Pacific. Akademiya Nauk, S.S.S.R. Trudy Inst. Okeanol., 41: 42-47.

Heinrich, A.K. 1969. The ranges of neuston copepods in the Pacific Ocean. Zool. Zh., 48 (10): 1456-1466.

Heinrich, A.K. 1971. The neuston pontellids of the Pacific Ocean. In: Proceed. of Joint Oceanogr. Assembly, "The Ocean World", M. Uda (ed.). Pub., Japan Soc. Prom. Sci., Tokyo, p. 432.

Hempel, G. and H. Weikert. 1972. The neuston of the subtropical and boreal N.E. Atlantic Ocean. A. Review. Mar. Biol. 13 (1): 70-88.

Hentschel, E. 1933. Allegemein Biologie des Südatlantischen Ozeans. 1st Lief. Wiss. Ergebn. Deutsch. Atlant. Exped. "Meteor", 1925-27. Vol. II.

Herdman, W.A. and A. Scott. 1908. An intensive study of the plankton around the south end of the Isle of Man. Proc. & Trans. Liverpool Biol. Soc., 22: 186-289.

Herdman, W.A., I.C. Thompson and A. Scott. 1898. On the plankton collected continuously during two traverses of the North Atlantic, summer of 1897. Trans. Biol. Soc. Liverpool, 12: 33-90, plates 5-7.

Herring, P.J. 1965. Blue pigment of surface living oceanic copepods. Nature, London, 205: 103-104.

Herring, P.J. 1967. The pigments of plankton at the sea surface. In: Aspects of Marine Zoology, N.B. Marshall (Ed.). Zool. Soc. London. Pub. by Academic Press, London, pp. 215-235.

Huntington, C.E. 1966. Bowdoin College, Brunswick, Maine, U.S.A.

Huntsman, A.G. 1919. Some quantitative and qualitative plankton studies of eastern Canadian waters. Canadian Fisheries expedition, 1914-1915, Ottawa, pp. 421-485.

Huntsman, A.G., W.B. Bailey and H.B. Hachey. 1954. The general oceanography of the Strait of Belle Isle. J. Fish. Res. Bd. Canada, 11 (3): 198-260.

Hure, J. and B.S. DiCarlo. 1968. Comparazione tra lo zooplankton del Golfo di Napoli e dell' Adriatico meridional presso Dubrovnik. I Copepoda. Estrato dolle, Pubbl. Staz. Zool. Napoli, 36: 21-102.

Hutchinson, G.E. 1957. A Treatise on Limnology. Volume I. Geography, physics, and chemistry. John Wiley and Sons, New York, 1015 pp.

Hutchinson, G.E. 1965. The Ecological Theater and the Evolutionary Play. Yale University Press, New Haven, 139 pp.

Hutchinson, G.E. 1967. A Treatise on Limnology. Vol. II. Introduction to lake biology and the limnoplankton. John Wiley and Sons, New York. 1115 pp.

Jermolajev, E.G. 1958. Zooplankton of the inner Bay of Fundy. J. Fish. Res. Bd. Canada, 15 (6): 1219-1228.

Jespersen, P. 1923. Dr. Thorild Wulff's Plankton Collections in the Waters of West Greenland. Metazoa. ~~Saertryk af~~ Medd. om Grønland, 62: 1-159. B.L. Bogtrykkeri, Kopenhagen.

Jespersen, P. 1934. The Godthaab Expedition: Copepods. Medd. om Grønland, 79 (10): 1-166.

Jespersen, P. 1939. The zoology of East Greenland: Copepods. Medd. om Grønland, 121 (3): 1-66.

Jespersen, P. 1940. Zoology of Iceland. Non-parasitic Copepoda. Vol. 3 (33). Ejnar Munksgaard, Copenhagen, 116 pp.

Johnstone, J., A. Scott and H.C. Chadwick. 1924. The Marine Plankton, with special reference to the investigation made at Port Erin, Isle of Man, during 1907-1914. Hodder and Stoughton, London, 194 pp.

Kearney, C.E. 1933. The animal plankton of the Halifax area. Biol. Board Canada, Ann. Report (1932): 26.

Keeple, F. and F.W. Gamble. 1904. The colour physiology of higher crustacea. Phil. Trans. R. Soc., 196: 295-298.

Kielhorn, W.V. 1952. Biology of surface zone zooplankton of a boreo-Arctic Atlantic Ocean area. J. Fish. Res. Bd. Canada, 9 (5): 223-264.

Kohn, A.J. 1960. Problems of speciation in marine invertebrates. In: Perspectives in Marine Biology, A.A. Buzzati-Traverso (ed.). Berkeley and Los Angeles, Univ. of Calif. Press, pp. 571-588.

Kovalev, A.V. 1970. Certain ecologo-morphological features of hyponeuston and plankton, Copepoda (Crustacea). Ekologiya, 1: 87-91.

Krauss, W. 1958. Temperatur, Salzgehalt und Dichte an des Oberflache des Atlantischen Ozeans. Wiss. Ergeb. Dtsch. Atlant. Exped., "Meteor", bard V, 3: 251-410.

Kuhn, T.S. 1970. The structure of scientific revolutions. Int. Encyclopedia of Unified Sci. Vol. 2 (2): 1-210. Univ. of Chicago Press, Chicago.

Lacroix, G. 1961. Production de zooplancton dans la Baie des Chaleurs en 1960. Sta. Biol. Mar., Grande-Rivière, Rapp. Ann., 1960: 11-28.

Lacroix, G. and J. Bergeron. 1963. Liste préliminaire des invertébrés du banc de Bradelle, 1962. Sta. Biol. Mar. Grande-Rivière, Rapp. Ann. 1962: 59-67.

Langmuir, I. 1938. The surface motion of water induced by wind. Science, 87: 119-123.

Lebour, M.V. 1922. The food of plankton organisms. J. mar. biol. Ass. U.K., 12: 644.

Lebour, M.V. 1925. Young anglers in captivity and some of their enemies. A study in a plunger jar. J. mar. biol. Ass. U.K., 13: 721-734.

Lee, C.M. 1972. The structure and function of the spermatophore and its coupling device in the Centropagidae (Copepoda, Calanoida). Bull. Mar. Ecol., 8 (1): 1-20.

Légare, J.E.H. and D.C. Maclellan. 1960. A qualitative and quantitative study of the plankton of the Quoddy region in 1957-1958, with special reference to the food of the herring. J. Fish. Res. Bd. Canada, 17 (3): 409-448.

Lillelund, K. and R. Lasker. 1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull. Nat. Mar. Fish. Serv., N.O.A.A., 69 (3): 655-667.

Lukjanova, W.S. 1940. On the maximum velocities of marine plankters. Compt. Rend. (Doklady) Acad. Sci. U.R.S.S. N.S. 28: 641-644.

Lysholm, B. and O. Nordgaard. 1921. Copepoda collected on the cruise of the M/S Armourer Hansen in the N. Atlantic in 1913. Bergen Museum Aarbog, Nature Review, 1 (2): 1-38.

Lysholm, B. and O. Nordgaard. 1945. Copepoda from the "Michael Sars" North Atlantic deep sea expedition, 1910. Reports of the Michael Sars Exped. 1910, 5 (7): 1-60.

MacArthur, R.H. and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton Univ. Press, Princeton, New Jersey. 203 pp.

Mackie, G.O. 1962. Factors affecting the distribution of Velella (Chondrophora). Intern. Revue Hydrobiol., 47 (1): 26-32.

Macfaydēn, A. 1957. Animal Ecology: aims and methods. London. 264 pp.

Marinaro, J. and J. Henry. 1968. Sur un nouvel engin collecteur d'hyponeuston et son utilisation dans la Baie d'Alger. Pelagos, 8: 71-78.

McEwen, G.F., M.W. Johnson and T.R. Folsom. 1954. A statistical analysis of the performance of the Folsom Plankton Splitter, based upon test observations. Arch. J. Meteorol., Geophysik u. Bioklimatol., Ser. A, 7: 502-527.

McGowan, J.A. 1963. Geographical variation in *Limacina helicina* in the N. Pacific. In: Speciation in the Sea. The Systematics Ass., Pub. No. 3: 109-128. London.

McGowan, J.A. 1971. Oceanic biogeography of the Pacific. In: The Micropaleontology of Oceans, B.M. Funnell and W.R. Reidel (eds.), Cambridge Univ. Press, Cambridge, pp. 3-74.

McIntyre, A., W.F. Ruddiman and R. Jantzen. 1972. Southward penetrations of the North Atlantic Polar Front: faunal and floral evidence of large scale surface water mass movements over the last 225,000 years. Deep-Sea Research, 19: 61-77.

Marine Biol. Ass. U.K. 1931. Plymouth Marine Fauna. 2nd edition. M.B.A.U.K., Southwoods Ltd., Exeter, Devon. 328 pp.

Marr, J.W.S. 1962. The natural history of the Antarctic Krill (*Euphausia superba* Dana). Discovery Rept. 32: 33-464.

Marshall, N.B. 1954. Aspects of Deep Sea Biology. Hutchinson's Scientific and Technical Pub., Anchor Press, Tiptree, Essex. 380 pp.

Marshall, S.M. and A.P. Orr. 1955. The Biology of a Marine Copepod, <u>Calanus</u> <u>finmarchicus</u> (Gunnerus). Oliver and Boyd, Edinburgh and London. 188 pp.

Marumo, R., N. Taga and T. Nakai. 1971. Neustonic bacteria and phytoplankton in surface microlayers of the equatorial waters. Bull. Planct. Soc. Japan, 18 (2): 36-41.

Mayr, E. 1942. Systematics and the Origin of Species from the Viewpoint of a Zoologist. Columbia Univ. Press, New York. 334 pp.

Mayr, E. 1963. Animal Species and Evolution. Harvard Univ. Press, Cambridge, Mass. 813 pp.

Mileikovsky, S.A. 1970. The influence of pollution on pelagic larvae of bottom invertebrates in marine near shore and estuarine waters. Mar. Ecol. 6 (4): 350-356.

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

Mori, T. 1964. The Pelagic Copepoda from the Neighbouring Waters of Japan. Soyo Co. Inc., Tokyo. 150 pp, 80 plates.

Mrazek, A., 1902. Arktische Copepoden. Vol. 2: 499-528.

Munk, W.H. 1947. Effects of the earth's rotation upon convection cells. Ann. N.Y. Acad. Sci., 48 (8): 815-820.

Murray, J. and J. Hjort. 1912. The Depths of the Ocean. MacMillan and Co. Ltd., London. Reprint, 1965, Cramer and Weinheim, New York. 821 pp.

Myers, G.S. 1960. The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories. Evolution, 14: 323-333.

Naumann, E. 1917. Beträge zur Kenntnis des Teichnannoplanktons II uber das Neuston des Süsswassers. Biol. Zbl., 37: 98-106.

Nellen, W. 1971. Neuston and plankton observations above and beside the Great Meteor Seamount in the subtropical North Atlantic. In: Proceed. of Joint Oceanogr. Assembly, "The Ocean World", M. Uda (ed.). Japan Soc. for Prom. of Sci., Tokyo. pp. 439-440.

Nishizawa, S. 1971. Concentration of organic and inorganic material in the surface skin at the equator, 155°W. Bull. Plankt. Soc. Japan, 18 (2): 42-44.

Olson, F.C.W. 1951. Plastic envelope substitute for drift bottles. J. Mar. Res., 10(2): 190-193.

Owen, R.W. 1966. Small scale horizontal vortices in the surface layer of the sea. J. Mar. Res., 24 (1): 56-66.

Owre, H.B. and M. Foyo. 1967. Copepods of the Florida Current. Fauna Caribbaea, No. 1. Crustacea, part I, Copepoda. Univ. of Miami, Miami, Fla. 137 pp.

Paine, R.T. 1963. Trophic relationships of eight sympatric predatory gastropods. Ecology, 44: 63-73.

Paine, R.T. 1966. Food web complexity and species diversity. The Amer. Nat., 100 (910): 65-492.

Parker, G.H. 1901. The reactions of copepods to various stimuli and the bearing of this on daily depth migrations. Bull. U.S. Fish. Comm., 21: 103-123.

Parr, A.E. 1939. Quantitative observations on pelagic sargassum vegetation of the western North Atlantic. Bull. Bingham Oceanogr. Coll., 6 (7): 1-94.

Pennell, W.M. 1967. Preliminary report on a study of neuston in the Gulf of St. Lawrence. Sta. Biol. Mar. Grande-Rivière, Rapp. Ann., 1966: 55-61.

Pinhey, K.F. 1927. Entomostraca of the Belle Isle Strait Expedition, 1923, with notes on other planktonic species, Pt. 1. Contrib. Can. Biol. Fish., N.S., 3 (6): 179-234.

Platt, T. and B. Irvwin. 1968. Primary productivity measurements in St. Margaret's Bay, 1967. Fish. Res. Bd. Can. Tech. Rep., 77: 1-23.

Pomeroy, L.R., H.H. Haskin and R.A. Ragotskie, 1956. Observations on dinoflagellate blooms. Limn. and Oceanogr., 1:54.

Riley, G.A. 1963. Organic aggregates in sea water and the dynamics of their formation and utilization. Limn. and Oceanogr., 8 (4): 372-381.

Riley, G.A. 1970. Particulate organic matter in sea water. Advances in Marine Biology, 8: 1-118.

Rivers, J.B. 1966. A nekton ring sampler for use aboard oceanographic research vessels. Comm. Fish. Rev., 28 (2): 9-12.

7.-

Roe, H.S.J. 1965. The vertical distributions and diurnal migrations of calanoid copepods collected on the Sond cruise, 1965. I. The total population and general discussion. J. mar. biol. Ass. U.K., 52: 277-314.

Rose, M. 1929. Copépodes pélagiques, particulièrement de surface provenant des Campagnes Scientifiques Albert I, Prince de Monaco. Résultats Campagnes Scient. Albert I, Prince de Monaco, 78: 1-126.

Rose, M. 1933. Faune de France 26. Copépodes pélagiques. Lechevalier, Paris. 374 pp.

Russell, F.S. 1925. The vertical distribution of marine macroplankton. An observation of diurnal changes. J. mar. biol. Ass. U.K., 13: 769-809.

Russell, F.S. 1926. The vertical distribution of marine macroplankton IV: apparent influence of light intensity as a controlling factor in the behaviour of certain species in the Plymouth area. J. mar. biol. Ass. U.K., 14: 415-440.

Russell, F.S. 1927. The vertical distribution of marine macroplankton V: the distributions of animals caught in the ring trawl in the daytime in the Plymouth area. J. mar. biol. Ass. U.K., 14: 557-608.

Russell, F.S. 1935. On the value of certain plankton animals as indicators of water movements in the English Channel and the North Sea. J. mar. biol. Ass. U.K., 20: 309-332.

Sameoto, D.D. and L.O. Jaroszynski. 1969. Otter surface sampler: a new neuston net. J. Fish. Res. Bd. Canada, 26 (8): 2240-2244.

Sars, G.O. 1903. An account of the crustacea of Norway. Part 4, Copepoda, Calanoida., Bergen Museum, Bergen. 171 pp., 102 plates.

Savage, R.E. and R.S. Wimpenny. 1936. Phytoplankton and the herring, part II, 1933 and 1934. Fish. Invest. Lond., ser. 2, 15 (1): 1-88.

Savilov, A.I. 1956. The pleuston biocenosis of Velella lata in the Pacific. Dokl. Akad. Nauk. S.S.S.R., 110: 476-479.

Savilov, A.I. 1958. Pleuston of the western Pacific. Dokl. Akad. Nauk. S.S.S.R., 122: 1014-1017.

Savilov, A.I. 1959. Pleuston biocenosis of the Pacific Ocean. Int. Oceanogr. Cong., A.A.A.S., Preprints: 322-323.

Savilov, A.I. 1966. Pleuston of the Pacific Ocean. Second Int. Oceanogr. Cong., Moscow: 316-317.

Schroter, C. and O. Kirchner. 1896. Die Vegetation der Bodensees. Lindau, Bodensee Forsch., 9 Tl. I: 1-122, Tl. II: 1-86.

Scott, A. 1906. Report on the tow nettings: Faunistic notes. Trans. Biol. Soc. Liverpool, II: 20-56.

Scott, J.T., G.E. Myer, R. Stewart and E.G. Walther. 1969. On the mechanisms of Langmuir circulation and their role in epilimnion mixing. Limn. and Oceanogr., 14 (4): 493-503.

Scott, T. 1901. On some entomostraca collected in the Arctic Seas in 1898 by William S. Bruce. Ann. Mag. Nat. Hist., ser. 7, vol. 8 (43): 337-356.

Scott, T. 1907. On some entomostraca from the Gulf of St. Lawrence. Trans. Natur. Hist. Soc. Glasgow, N.S. 7: 46-52, pl. 2.

Scott, T. 1911. Copepoda resumé des observations sur le plancton, 1902-1908. Bull. Trim. Cons. Int. Explor. Mer, 2: 106-149.

Scourfield, D.J. 1894. Entomostraca and the surface film of water. J. Linnean Soc., London, Zool., 25: 1-19.

Sewell, S. 1948. The free swimming planktonic Copepoda. Geographical Distribution. The John Murray Expedition, Sci. Reports, 8 (3): 1-592. (British Museum, London).

Sherman, K. 1963. Pontellid copepod distributions in relation to surface water types in the central North Pacific. Limn. and Oceanogr., 8: 214-227.

Sherman, K. 1964. Pontellid copepod occurrence in the central South Pacific. Limn. and Oceanogr., 9: 476-484.

Sherman, K. and E. Schaner. 1968. Pontellid copepods as indicators of an oceanic incursion over Georges Bank. Ecology, 49: 582-584.

Sieburth, J.M. 1965. Bacteriological samples for air-water and water-sediment interfaces. In: Trans. Joint Conf. Ocean Sci., Ocean Eng., MTS-ASLO, Wash., D.C.: 1064-1068.

Sieburth, J.M. 1971. An instance of bacterial inhibition in oceanic surface water. Mar. Biol., 11 (1): 98-100.

Slobodkin, L.B. 1966. Growth and Regulation of Animal Populations. Holt, Rinehart, Winston, New York. 184 pp.

Small, E.B. and D.S. Marszalek. 1969. Scanning electron microscopy of fixed, frozen, and dried protozoa. Science, 163: 1064-1065.

Smith, J.E. 1968. "Torrey Canyon" Pollution and Marine Life. Mar. Biol. Ass. U.K., Cambridge Univ. Press. 196 pp.

Specchi, M. 1969. Influenza della temperatura sulla microdistribution superficiale de plankton rel Golfo di Trieste. Pubbl. Staz. Zool. Napoli, 37: 338-348.

Steeman-Neilsen, E. 1952. Detrimental effects of high light intensities on the photosynthetic mechanism. Physiol. Plant, 5: 334-344.

Steeman-Neilsen, E. 1964. On a complication in marine productivity work due to the influence of ultraviolet light. J. Cons., 24 (2): 130-135.

Steuer, Ad. 1933. Zur planmässigen Erforschung der geographischen Verbreitung des Haliplankters, bersonders der Copepoden. Zoogeographica, Bd. I (3): 269-302.

Stommel, H. 1947. A summary of the theory of convection cells. Annals N.Y. Acad. Sci., 48(8): 515-726.

Stommel, H. 1949. Trajectories of small bodies sinking slowly through convection cells. J. Mar. Res., 8: 24-29.

Störmer, L. 1929. Copepods from the Michael Sars Expedition, 1924. Rapp. Proc. Verb. Res. Cons. Perm. Expl. Mer, 56: 1-57.

Strickland, J.D.H. 1958. Solar radiation penetrating the ocean. A review of requirements, data, and methods of measurement with particular reference to photosynthetic productivity. J. Fish. Res. Bd. Canada, 15 (3): 453-492.

Sutcliffe, W.H. 1948. A list of calanoid copepods from the plankton at Beaufort, North Carolina. J. Elisha Mitchel Soc., 64: 234-236.

Sutcliffe, W.H. 1949. Description of a new species of copepod, Anomalocera ornata. J. Elisha Mitchel Soc., 65 (2): 273-275.

Sutcliffe, W.H., E.R. Baylor and D.W. Menzel. 1963. Sea surface chemistry and Langmuir circulation. Deep Sea Res., 10: 233-243.

Taguchi, S. and K. Nakajima. 1917. Plankton and seston in the sea surface of three inlets of Japan. Bull. Plankton Soc. Japan, 18 (2): 20-36.

Tanaka, O. 1964. The pelagic copepods of the Izu region, middle Japan. Systematic account, 12. Pub. Seto mar. biol. Lab., 12 (3): 231-271.

Templeton, R. 1837. Description of a new Irish crustaceous animal. Trans. Ent. Soc. London, 2: 35-40.

Test, A.R. 1946. Speciation in limpets of the genus Acmaea. Contr. Lab. Vertebrate Biol., Univ. Michigan, 31: 1-24.

Thompson, I.C. 1889. Third Report on the *Copepoda* of Liverpool Bay. Proc. Liverpool Biol. Soc., 3 (Session 1888-89): 181-191.

Thorpe, W.H. 1960. Discussion in: Perspectives in Marine Biology, A.A. Buzzati-Traverso (ed.). Berkeley and Los Angeles, Univ. of Calif. Press, p. 585.

Totton, A.K. 1960. Studies on *Physalia physalia* (L). I. Natural History and Morphology. Discovery Reports, 30: 301-367.

Tregouboff, G. and M. Rose. 1957. Manuel de Planktonologie Mediterranéenne. Tome I, text. Tome II, plates. Centre Nat. Res. Sci., Paris. 587 pp.

Trembley, J.L. 1942. General report of activities, 1936-1942, Trois Pistoles Station. Univ. Laval, Sta. Biol. St. Laurent, Rep. 4: 1-100.

Tsyban, A.V. 1971a. Marine bacterioneuston. Proc. Joint Oceanogr. Assembly, "Ocean World", Tokyo: 276-277.

Tsyban, A.V. 1971b. Sea foam as an ecological niche for bacteria. Gidrobiol. Zh., 7 (5): 14-24.

Tsyban, A.V. and L.N. Polishchuk. 1969. On the interrelation of bacterioneuston. Gidrobiol. Zh., 5 (6): 47-55.

Vervoort, W. 1965. Pelagic *Copepoda*. Part II. Atlantide Reports No. 8. Sci. results of the Danish expeditions to the coasts of tropical West Africa, 1945-1946. Danish Science Press Ltd., Copenhagen.

Vives, F. 1966. Zooplankton neritico de los aguas de Castellon (Mediterraneo occidental). Invest. Pesquera, Tomo 30: 49-166 (Barcelona).

Weiser, W. 1960. Problems of species formation in the benthic micro-fauna of the deep sea. In: Perspectives in Marine Biology, A.A. Buzzati-Traverso (ed.). Berkeley and Los Angeles, Univ. of Calif. Press, pp. 513-518.

Wheeler, W.M. 1901. The free swimming copepods of the Woods Hole region. Bull. of U.S. Fish. Comm., 19: 157-192.

White, M.J.D. 1968. Models of speciation. Science, 159 (3819): 1065-1070.

Wiborg, K.F. 1934. The production of zooplankton in the Oslo Fjord in 1933-1934, with special reference to the copepods. Hvalråd Skr., 21: 1-87.

Wiborg, K.F. 1955. Zooplankton in relation to hydrography. Norwegian Fisk. Skr. Ser. Hvdr., 9 (4): 1-66.

Willey, A. 1919. Report on the <u>Copepoda</u> obtained in the Gulf of St. Lawrence and adjacent waters, 1915. In: Can. Fish. Exped., 1914-1915, J. Hjort (ed.). Dep. Nav. Ser., Ottawa. pp. 173-220.

Willey, A. 1931. Preliminary report on the copepod plankton collected by the Station Biologique du St.-Laurent à Trois Pistoles in July 1931. Univ. Laval St. Biol. St.-Laurent Rapp. 1: 82-84.

Williamson, D.I. 1956. The plankton of the Irish Sea. Bull. Mar. Ecol., 4 (31): 87-114.

Willis, R.P. 1963. A small towed net for ocean surface sampling. N.Z.J. Sci., 6 (1): 120-126. (N.Z. Oceanogr. Inst., Wellington).

Wilson, C.B. 1932. The copepods of the Woods Hole region. Bull. U.S. Nat. Mus., 158, 635 pp.

Wilson, C.B. 1932. The copepod crustaceans of Chesapeake Bay. Proceed. of the U.S. Nat. Mus., 80 (15): 1-54. (Washington, D.C.).

Wilson, C.B. 1936. Plankton of the Bermuda Oceanographic Expeditions. IV. Notes on the Copepoda. Zoologia, 20 (1): 89-93.

Wilson, C.B. 1942. The copepods of the plankton gathered during the last cruise of the "Carnegie". Dept. of Terr. Magni. Carnegie Inst., Wash., Pub. No. 536: 1-237.

Wilson, D.P. 1956. A contribution to the biology of Ianthina janthina (L). J. mar. biol. Ass. U.K., 35: 291-305.

Wilson, D.P. 1958. On some small Ianthina janthina (L) stranded on the Isles of Scilly, 1957. J. mar. biol. Ass. U.K., 37: 5-8.

Wilson, W.B. and A. Collier. 1972. The production of surface active material in marine phytoplankton cultures. J. Mar. Res., 30: 15-26.

With, C. 1915. Copepoda I. Calanoida Amphyascandria. The Danish Ingolf Exped., 3 (4): 1-249. (Copenhagen).

Wolf, E. 1905. Die fort pflanzungs Verhältnisse unserer einheimischen Copepoden. Zool. Jahrb. Abt. Syst., 22: 101-280.

Wolfenden, R.N. 1904. Notes on the Copepoda of the North Atlantic Ocean and the Faroe Channel. J. mar. biol. Ass. U.K., 7 (1): 110-146.

Woodcock, A.H. 1941. Surface cooling and streaming in shallow fresh and salt waters. J. Mar. Res., 4(2): 153-161.

Woodcock, A.H. 1944. A theory of surface water motion deduced from the wind induced motion of Physalia. J. Mar. Res., 5: 196-205.

Zaitsev, Y.P. 1959. The collection of pelagic eggs and fish larvae in parts of the sea not subject to appreciable freshening. Zool. Zhurnal Akad. Nauk., S.S.S.R., 38 (9): 1426-1428.

Zaitsev, Y.P. 1961. Surface-dwelling pelagic biocenosis of the Black Sea. Zool. Zhurn. 40 (6): 818-825.

Zaitsev, Y.P. 1962. Apparatus and technique for studying hyponeuston. Reports of the 4th Ecological Conf., Moscow, pp. 107-109.

Zaitsev, Y.P. 1964. Synopsis of thesis for degree of Doctor of biological science, Odessa (in Russian).

Zaitsev, Y.P. 1968. La neustonologie marine: objet, méthodes, réalisations, principales et problèmes. Pelagos, 8: 1-48.

Zaitsev, Y.P. 1970. Marine Neustonology. Acad. Sci. of the Ukrainian S.S.R., Kovalevskii Inst. of the Biol. of the S. Seas, Odessa·Div., K.A. Vinogradov (ed.). Kiev, 1970. Translation by Israel pro. sci. trans., Jerusalem, 1971. 207 pp.

Zobell, C.E. and G.C. McEwen. 1935. The lethal action of sunlight upon bacteria in sea water. Biol. Bull. Woods Hole, 68: 93-106.

Appendix I

Means of measurements of various body parts of *A. opalus* and *A. patersoni* and selected ratios of these means. N = 30 unless otherwise noted.

Legend for Tables

Description of Ratios given in Tables

A. MALES

No. R1	Length of 1st urosome segment/Width of 1st urosome. segment.
No. R2	Length of 1st urosome segment/Depth of 1st urosome. segment.
No. R3	Width of 1st urosome segment/Depth of 1st urosome. segment
No. R4	Length of 1st prosome segment/Length of last prosome. segment.
No. R5	Length of 1st prosome segment/Length of urosome.

Length of 1st prosome segment refers to length along the dorsal midline.

Length of last cephalothorax segment refers to the right lateral length to the tip of the process.

Width of 1st urosome segment - at the posterior base.

Depth of 1st urosome segment - at the posterior base.

Length of urosome - from anterior margin to tip of caudal rami.

B. FEMALES

No. R1	Genital segment length/Genital segment width.
No. R2	Genital segment length/Genital segment depth.
No. R3	Genital segment length/posterior process.
No. R4	Length 1st prosome segment/Genital segment depth.

Genital segment, depth and length as in male 1st urosome segment.

Genital segment width refers to widest measurement of the segment on line perpendicular to longitudinal body axis.

Posterior process refers to length of the process on the genital segment from its base to the tip.

Legend for Table and (Male and Female)

Key to Measurements Code, Tables

Pro.	Prosome
Sl	Prosome segment 1
CL	Cephalothorax, last segment
U	Urosome
GL	Length, genital segment
GD	Depth, genital segment
GW	Width, gential segment
GP	Length, genital process (posterior process)

Males - measurements (means) and
ratios of means, A. opalus and A. patersoni

		Measurements											
	No.	pro.	Sl	CL	U	Gl	Gd	GW	R1	R2	R3	R4	R5
Specimens, A. opalus	1.	3.44	1.44	.43	1.43	.52	.33	.50	1.04	1.58	1.52	3.35	1.01
	2.	3.42	1.43	.42	1.44	.48	.33	.49	.98	1.45	1.48	3.48	1.01
	3.	3.32	1.42	.44	1.44	.53	.35	.54	.98	1.54	1.57	3.23	.98
	4.	2.97	1.27	.38	1.26	.44	.29	.47	.94	1.52	1.62	3.34	1.01
	5.	2.96	1.28	.35	1.31	.44	.30	.43	1.02	1.47	1.43	3.66	.98
	6.	2.91	1.23	.39	1.27	.45	.29	.45	1.00	1.55	1.55	3.15	.97
	7.	2.83	1.21	.38	1.23	.44	.28	.45	.98	1.57	1.61	3.18	.98
	8.	2.79	1.20	.36	1.22	.45	.28	.43	1.05	1.61	1.54	3.33	.98
Specimens, A. patersoni	9.	3.42	1.47	.39	1.30	.28	.32	.37	.76	.88	1.16	3.77	1.13
	10.	3.22	1.40	.37	1.22	.26	.31	.31	.84	.84	1.00	3.78	1.15
	11.	3.12	1.38	.36	1.20	.26	.35	.29	.90	.74	.83	3.83	1.15
	12.	3.06	1.39	.33	1.19	.25	.31	.36	.69	.81	1.16	4.21	1.17
	13.	3.05	1.34	.36	1.15	.27	.38	.29	.93	.71	.76	3.72	1.17
	14.	2.96	1.23	.35	1.10	.26	.25	.34	.76	1.04	1.36	3.51	1.12
	15.	2.88	1.27	.33	1.16	.25	.34	.28	.89	.74	.82	3.85	1.09
	16.	2.72	1.20	.32	1.10	.24	.26	.33	.73	.92	1.27	3.75	1.09
	17.	2.52	1.11	.28	1.02	.22	.24	.30	.73	.92	1.25	3.96	1.09

Females - measurements (means) and ratios of means, *A. opalus* and *A. patersoni*

		Measurements									
	No.	1 Pro.	2 Sl	3 GL	4 GP	5 GD	6 GW	R1	R2	R3	R4
Specimens, *A. opalus*	1.	3.91	1.63	.63	.32	.60	.61	1.03	1.05	1.97	2.72
	2.	3.72	1.54	.60	.30	.60	.52	1.15	1.03	2.00	2.66
	3.	3.64	1.56	.62	.30	.58	.59	1.05	1.06	2.06	2.69
	4.	3.27	1.40	.53	.29	.56	.53	1.00	.95	1.83	2.50
	5.	3.36	1.43	.57	.27	.57	.50	1.14	1.00	2.11	2.51
	6.	3.09	1.32	.51	.28	.52	.44	1.16	.98	1.82	2.54
	7.	3.05	1.34	.50	.29	.53	.49	1.02	.94	1.72	2.53
	8.	2.99	1.31	.51	.27	.51	.47	1.09	1.00	1.89	2.57
Specimens, *A. patersoni*	9.	3.78	1.64	.45	.11	.39	.45	1.06	1.15	4.09	4.20
	10.	3.60	1.56	.42	.13	.38	.46	.91	1.11	3.23	4.10
	11.	3.46	1.48	.40	.11	.36	.43	.93	1.11	3.64	4.11
	12.	3.37	1.51	.40	.13	.37	.44	.91	1.08	3.08	4.08
	13.	3.31	1.45	.40	.13	.33	.42	.95	1.21	3.07	4.39
	14.	3.09	1.29	.35	.13	.34	.39	.90	1.03	2.69	3.79
	15.	3.16	1.40	.37	.13	.36	.41	.90	1.03	2.85	3.89
	16.	3.02	1.32	.36	.13	.30	.37	.97	1.20	2.77	4.40
	17.	2.73	1.20	.34	.12	.30	.36	.94	1.13	2.83	4.00

Appendix II

Stage composition of A. opalus in the pleuston samples 1966, 1967 and 1968.

This appendix provides a further breakdown of the life cycle data than is found in Section VIII. As in that section numbers of A. opalus are the means of occurrence in the pleuston samples taken on a day of sampling. The number of samples varies from one to four (see tables 8, 9, and 10).

The stage composition has been broken down to naupliar stages 2 to 6 and copepodite stages I to VI (adults). The sexes were determined for stage IV in 1967 and 1968 but not in 1966. When the 1966 samples were analysed, the morphology of sexual differentiation was not known for this stage. The sexes were determined for stages V and VI for all three years.

In three of the six tables the mean numbers have been converted to percentages of the mean total number of <u>A</u>. <u>opalus</u> for each day of sampling.

Stage composition of *A. opalus* in samples, Grande-Rivière, 19[illegible]. Mean numbers.

Date	n 2	3	4	5	6	c I	II	III	IV♂	IV♀	IVt	V♂	V♀	Vt	VI♂	VI♀	VIt
June 15						[illegible]	7.5	5.5			6.5	3.5		[illegible]			
June 22							1.3	4.0			0.[illegible]	0.5	[illegible]	[illegible]			
June 30					3.0		1.0	6.0			24.0	20.0	11.0	[illegible]	1.0	19.0	38.0
July 12					1.5	15.0					74.0	86.5	66.5	153.0	114.0	67.5	180.5
August 1		0.5	1.5	1.0	2.0	51.5	8.5	4.5			8.5	[illegible]	4.0	[illegible]	[illegible]	7.5	45.5
August 2		4.0	75.0	107.0	55.0	20.0	4.0	7.0			8.0	7.0	6.0	13.0	15.0	10.0	125.0
August 11				0.5	1.0	26.5	14.0	6.0			4.5	6.5	3.0	9.5	163.5	173.5	337.0
August 16					0.5			3.0			24.0	25.0	20.0	45.0	544.0	557.5	1101.5
August 20	22.0	20.5	11.5	1.5	2.5	11.0	8.5	54.5			56.0	41.0	31.0	72.0	960.3	137.0	1097.3
August 30	275.0	289.0	282.0	217.0	57.0	23.0	14.0										
September 6	87.0	159.5	180.5	146.5	83.0	5.5	1.5	1.0			4.0	3.0	1.0	4.0	24.5	5.0	29.5
September 20	212.0	46.0	24.0	26.0	10.0	6.0	4.0	4.0			2.0	4.5	7.5	12.0	20.0	4.0	24.0
October 12	6.0	2.0													24.0	4.0	28.0
October 18																	
October 26			1.0												1.0	1.0	2.0
November 17	2.0	1.0	0.8														

Stage composition of *A.* spalus in samples, Grande-Rivière, [illegible].

Percentages of total numbers.

Date	n 2	3	4	5	6	c I	II	III	IV♂	IV♀	IVt	V♂	V♀	Vt	VI♂	VI♀	VIt
June 15					[illegible]	16.27	16.27	5.5			[illegible]	[illegible]					
June 22							14.8	[illegible]			[illegible]	[illegible]	[illegible]	[illegible]			
June 30					(0.03)		1.8	14.3			[illegible]	17.9	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
July 12						0.3	[illegible]	8.5			15.4	[illegible]	[illegible]	[illegible]	[illegible]	11.8	[illegible]
August 1		0.4	1.3	0.83	1.7	43.1	7.1	3.8			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	29.7
August 2		1.3	23.9	32.8	17.5	[illegible]	1.3	2.2			[illegible]	[illegible]	1.9	41.0	4.8	[illegible]	5.0
August 11				0.1	0.5	6.6	[illegible]	1.5			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
August 16				(0.04)				0.3			[illegible]	[illegible]	1.9	[illegible]	[illegible]	[illegible]	94.8
August 20	1.6	1.5	0.9	0.1	[illegible]	[illegible]	[illegible]	[illegible]			[illegible]	[illegible]	[illegible]	5.4	[illegible]	[illegible]	[illegible]
August 30	23.8	25.0	24.4	18.9	4.9	[illegible]	1.2										
September 6	12.4	22.7	25.7	20.8	11.8	0.8	0.2	0.1			0.6	0.4	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
September 20	56.1	12.2	6.3	6.9	2.6	1.6	1.1	1.1			0.5	[illegible]	1.9	[illegible]	[illegible]	[illegible]	6.3
October 12	16.7	5.5													[illegible]	11.1	77.8
October 18																	
October 26			33.3									[illegible]	[illegible]	[illegible]			
November 17	52.6	26.3	21.1														

Stage composition of *A. opalus* in samples, Magdalen Islands, 1967. Mean numbers.

Date	n 2	3	4	5	6	c I	II	III	IV♂	IV♀	IVt	V♂	V♀	Vt	VI♂	VI♀	VIt
June 19	1.8	0.25	0.45	0.0	0.5												
June 27	2.5	3.0	3.0	1.5	1.8												
July 5		0.5	1.5	6.0	21.2	9.8	4.5	6.2	5.8	8.8	14.6	5.2	4.2	9.4		0.25	0.25
July 10				0.8	0.25	11.5	13.5	8.8	0.8		0.8	1.0	2.2	3.2	5.0	5.2	10.2
July 26	20.0	43.0	9.0	6.6	4.3	0.6	0.3								2.3	1.0	3.3
August 1	1.5	5.4	6.5	11.0	4.0	11.8	123.0	20.2		0.5	0.5		0.9	0.9	5.9	2.0	7.9
August 9						0.5	1.0	2.5	1.5	2.0	3.5	10.5	7.0	17.5	10.0	10.0	20.0
August 10					2.0	135.0	34.0	8.0	2.0	2.0	4.0	5.0	4.0	9.0	14.0	19.0	33.0
August 16						54.0	234.0	328.0	6.0	4.0	10.0	16.0	10.0	26.0	52.0	14.0	66.0
August 30		0.5	0.5	0.5	2.0	24.2	38.3	16.8	3.5	10.8	14.3	4.0	2.0	6.0	2.2	4.5	6.7
September 8			0.2	0.2	3.0	19.8	18.5	5.2	2.2	2.2	4.4	1.2	1.0	2.2	0.5	0.5	1.0
September 13							2.8	15.8	10.0	9.2	19.2	17.8	17.8	35.6	37.8	23.0	60.8

Stage composition of A. opalus in samples, Magdalen Islands, 1967.

Percentages of total numbers.

Date	n 2	3	4	5	6	c I	II	III	IV♂	IV♀	IVt	V♂	V♀	Vt	VI♂	VI♀	VIt
June 19	60.0	8.3	15.0		16.7												
June 27	21.2	25.4	25.4	12.7	15.3												
July 5		0.7	2.0	8.0	28.3	13.1	6.0	8.3	7.8	11.8	19.5	6.9	5.6	12.6		3.3	3.3
July 10				1.6	0.6	23.4	27.5	17.9	1.6		1.6	2.0	4.5	6.5	10.2	10.6	20.8
July 26	22.9	49.3	10.3	7.6	4.9	0.7	0.3								2.6	1.1	3.0
August 1	0.8	3.0	3.4	6.7	2.1	6.1	63.7	10.5		0.3	0.3		0.4	0.4	3.0	1.0	4.0
August 9						1.1	2.2	5.6	3.3	4.4	7.8	23.3	15.6	38.9	22.2	22.2	44.4
August 10					0.9	60.0	15.1	3.6	0.9	0.9	1.8	2.2	1.8	4.0	6.2	8.4	14.7
August 16						7.5	32.6	45.7	0.8	0.6	1.4	2.2	1.4	3.6	7.2	1.9	9.2
August 30		0.5	0.5	0.5	1.8	21.8	34.6	15.2	3.2	9.7	12.9	3.7	1.8	5.4	2.0	4.2	6.0
September 8			0.4	0.4	5.5	36.2	33.8	9.5	4.0	4.0	8.0	2.2	1.8	4.0	0.9	0.9	1.8
September 13							2.1	11.8	7.5	6.9	14.3	13.3	13.3	26.6	28.2	17.2	45.4

Stage composition of *A. opalus* in samples, Grande-Rivière, 1968. Mean numbers.

Date	n 2	3	4	5	6	C I	II	III	IV♂	IV♀	IVt	V♂	V♀	Vt	VI♂	VI♀	VIt
June 5					2	9	3										
June 13			1		2	3	14	23	3	3	6	2	2	4			
June 19		24	22	16	12	1		2									
June 28	6	52	142	200	126	79	22	21	6	12	18	13	5	18		1	1
July 5	4	36	28	39	65	43.5	47	78	43	68	111	80	38.5	118.5	22	47	69
July 17					3	42	53	18	3	1	4	2	4	6	96	1	97
July 23					2	72	10	14					2	2	90	40	130
July 31					6	28	8	1							1	2	3
August 14		16	156	192	188	400	36	12							88		88
August 22			2	6	14	108	38	12		2	2				134		134
September 3			4	12	40	124	80	52	252	384	636	436	440	876	260	92	352
September 11									4		4	4	12	16	176	38	214
September 19					1	1	1	11	6	9	15	12	10	22	114	51	165
September 20					8	8	56	32	336	368	704	496	624	1120	456	256	712
September 24						5		45	190	220	410	795	770	1565	1140	935	2075
October 15												10	30	40	1210	780	1990

Stage composition of A. ovalis in samples, Grande-Rivière, 1968.

Percentages of total numbers.

Date	N2	3	4	5	6	I	II	III	IV♂	IV♀	IVt	V♂	V♀	Vt	VI♂	VI♀	VIt
June 5					14.3	4.3	81.4										
June 13			1.9		[illegible]	5.7	26.4	45.4	[illegible]	5.7	11.3	3.8	3.8	7.5			
June 19		28.4	29.7	21.6	16.2	1.4		2.8									
June 25	0.9	7.6	20.7	[illegible]	18.4	11.5	3.2	3.1	0.9	1.7	2.6	1.9	0.7	2.6		0.1	
July 5	0.	5.[illegible]	4.4	6.1	10.1	6.8	7.3	10.1	6.7	10.6	17.3	12.5	6.0	18.5	3.4	7.3	10.7
July 17					[illegible]	18.5	23.8	8.1	1.4	0.5	1.9	0.9	1.8	2.7	43.1	0.5	43.5
July 25					0.9	31.3	4.3	6.1					0.9	0.9	39.1	17.4	56.5
July 31				6.1	12.2	7.0	16.3	2.0							2.0	4.1	6.1
August 14		1.4	14.3	17.7	17.3	36.8	3.3	1.1							8.1		8.1
August 22			0.6	1.9	4.4	34.2	12.0	3.8		0.6	0.6				42.4		42.4
September 3			0.2	0.6	1.8	5.7	3.7	2.4	11.6	17.7	29.3	20.0	20.2	40.3	11.9	4.2	16.2
September 11									1.7		1.7	1.7	5.1	6.8	75.2	16.2	91.5
September 19					0.5	0.5	0.5	5.1	2.7	4.2	6.9	5.6	4.6	10.2	52.8	23.6	76.4
September 20					0.3	0.3	2.1	[illegible]	12.7	13.9	26.6	18.7	23.6	42.3	17.2	9.7	26.9
September 24						0.1		[illegible]	4.6	5.4	10.0	19.4	18.8	38.2	27.8	22.8	50.6
October 15												0.5	1.5	2.0	59.6	38.4	98.0

Appendix III

Positions and sampling data for the "A.T. Cameron" cruise, May 26 - June 6, 1966. 85 stations, one pleuston sample per station (#6 mesh, speed 2 knots, duration 15 minutes). The stations are shown on Figure 14.

"A.T. Cameron" cruise

May 26 - June 6, 1966

Station Number	Lat. N.	Long. W.	Date	Surface Temp. °C
1	46°20'	59°56'	May 26	5.6
2	46°34'	59°34'	May 26	4.7
3	46°45'	59°42'	May 26	4.7
4	46°52'	60°01'	May 27	4.7
5	47°03'	60°09'	May 27	5.6
6	47°17'	59°58'	May 27	3.4
7	47°30'	59°48'	May 27	3.4
8	47°42'	59°41'	May 27	-
9	47°55	59°33'	May 27	-
10	47°48'	59°54'	May 27	3.6
11	47°44'	60°16'	May 27	4.0
12	47°35'	60°11'	May 28	3.2
13	47°24'	60°17'	May 28	3.2
14	47°14'	60°31'	May 28	5.4
15	47°03'	60°45'	May 28	5.8
16	46°51'	60°58'	May 28	6.5
17	46°39'	61°10'	May 28	7.2
18	46°26'	61°21'	May 28	6.7
19	46°22'	61°39'	May 29	6.4
20	46°36'	61°42'	May 29	-
21	46°50'	61°34'	May 29	5.2
22	47°04'	61°27'	May 29	4.7
23	47°13'	61°15'	May 29	-
24	47°23'	60°55'	May 29	5.6
25	47°34'	60°47'	May 29	5.1
26	47°44'	60°39'	May 29	4.3
27	47°39'	60°53'	May 29	4.2

Station Number	Lat. N.	Long. W.	Date	Surface Temp. °C
28	47°55'	61°10'	May 30	4.6
29	48°00'	61°30'	May 30	5.7
30	48°04'	61°50'	May 30	5.8
31	48°09'	61°10'	May 30	6.0
32	48°13'	62°30'	May 30	5.7
33	48°18'	62°50'	May 30	5.4
34	48°22'	63°09'	May 30	5.3
35	48°33'	63°19'	May 30	5.8
36	48°27'	63°20'	May 30	6.7
37	43°29'	63°41'	May 31	5.5
38	48°32'	63°55'	May 31	6.6
39	48°14'	63°58'	May 31	6.2
40	48°20'	64°19'	May 31	–
41	48°15'	64°35'	May 31	7.0
42	48°05'	64°38'	May 31	9.7
43	48°09'	64°32'	May 31	7.8
44	48°05'	64°02'	May 31	7.4
45	48°07'	63°41'	May 31	5.3
46	48°19'	63°38'	June 1	7.2
47	48°16'	63°22'	June 1	7.7
48	48°12'	63°06'	June 1	5.5
49	48°01'	63°09'	June 1	6.4
50	47°58'	63°26'	June 1	6.2
51	47°56'	63°44'	June 1	7.6
52	47°52'	64°04'	June 1	7.4
53	47°41'	64°21'	June 1	8.5
54	47°23'	64°11'	June 1	8.7
55	47°11'	64°25'	June 2	10.3
56	46°53'	64°25'	June 2	10.3
57	47°02'	64°09'	June 2	9.4
58	47°15'	63°56'	June 2	8.5
59	47°28'	63°52'	June 2	7.8
60	47°32'	63°47'	June 2	7.5

Station Number	Lat. N.	Long. W.	Date	Surface Temp. °C
61	47°47'	63°30'	June 2	7.7
62	47°52'	63°12'	June 2	7.1
63	47°38'	63°15'	June 2	7.8
64	47°25'	63°18'	June 3	7.7
65	47°10'	63°20'	June 3	7.9
66	46°55'	63°25'	June 3	8.8
67	46°41'	63°29'	June 3	-
68	46°36'	63°08'	June 3	10.7
69	46°46'	63°05'	June 3	9.1
70	46°58'	63°01'	June 3	9.3
71	47°09'	62°56'	June 3	7.9
72	47°21'	62°51'	June 3	7.3
73	47°32'	62°47'	June 4	7.4
74	47°44'	62°42'	June 4	-
75	47°55'	62°37'	June 4	7.7
76	48°04'	62°35'	June 4	7.0
77	47°59'	62°20'	June 4	7.5
78	47°52'	62°03'	June 4	7.7
79	47°48'	61°49'	June 4	7.5
80	47°37'	62°00'	June 4	7.5
81	47°28'	62°09'	June 4	7.0
82	47°17'	62°20'	June 5	8.1
83	47°07'	62°20'	June 5	7.3
84	47°50'	62°20'	June 5	8.5
85	46°35'	62°19'	June 5	8.8