18. BIOLOGICAL SPECIES, WATER-MASSES AND CURRENTS

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1. Introduction

Oceanographers have long been aware of the existence in the oceans of areas that can be more or less clearly defined as "water-masses". These areas are recognized because of individual characteristics, particularly with respect to the temperature–salinity relationship as established by T–S curves for sub-surface water. For fullest discussion the reader is referred to *The Oceans* (Sverdrup, Johnson and Fleming, 1942).

It is also recognized by marine biologists that of the vast array of marine organisms many are sensitive to small changes in environmental conditions during all or part of their life history. Salinity and temperature are outstanding factors that are most clearly demonstrated as environmental variables having critical ranges for the lives of many species. In some species, notably the oceanic, the range of tolerance for fluctuations in these factors is relatively small. Such species are known as either stenohaline or stenothermic or both, and the limitations may be most pronounced with respect to reproduction, or during the larval stage. Usually the adult vegetative stage is the most tolerant. Ranges of tolerance may be within different salinity or temperature limits. Thus, an animal may be stenohaline to either high or low salinities. Although the coastal animals are usually considered the more tolerant to environmental changes, still many of these have characteristic limits for reproduction, as shown by investigations carried out by Runnström (1927) on thermal relations. There are also other factors at play that are less well understood which influence endemic distribution, such as non-conservative chemical elements, inter-specific competition and duration of maximum or minimum temperatures.

It is to be expected, then, that bodies of water with distinctive characteristics, such as water-masses, will produce environments for distinctive faunas. This is, indeed, what has been found to be the case in many instances where detailed studies have been made. The preference of certain species for North Sea waters and of others for the adjacent oceanic waters provide classical examples (Russell, 1939). Thus, a biological means is provided to aid in the identification and delineation of water-masses or to trace the source, direction and extent of water currents, and the isolations and pathways they may have provided in speciation of the organisms. It is increasingly realized that the main faunistic regions of the high-oceanic pelagic fauna (certain features of which were heralded by Steuer, 1933) are more strongly characterized taxonomically than they were formerly believed to be (cf. Ekman, 1953, p. 319).

Before discussing representative investigations showing a relationship of species distribution with specific water-masses or currents, it will be useful first to consider some generalizations as to the types of organisms that can best be used as "indicators", and to consider some of their limitations.

Although the geographic distribution of benthic or bottom-living animals is doubtless often dependent directly upon the type of water and the nature of

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prevailing currents, these animals are less used as indicators than the plankton. Therefore, we shall confine our remarks to the latter category. It should be mentioned that certain phytoplankton organisms have also been used as indicators, especially the photosynthetic dinoflagellates. However, the short individual life of unicellular autotrophic organisms and their spontaneous reproductive response to local environmental changes makes their use more complicated, especially as regards indicators of water currents.

A. Zooplankton Indicators

In considering the application of organisms in this category, it is necessary to distinguish first between the "permanent" plankton (holoplankton) and the "temporary" plankton (meroplankton), for each division has its own uses and limitations. The permanent plankton consists of organisms that are planktonic throughout their entire life, and includes especially such abundant forms as the chaetognaths, pteropods, euphausiids and most of the copepods. The relatively long life of many of these forms contributes to their value, particularly as indicators of water movements. In addition to precise identification of the species, a knowledge of the life history and information on the breeding season are of great importance in order to ascertain the area in which the animals find optimal or tolerable conditions for reproduction. This is the "home area", which is either a slowly moving water-mass or a section of a continuing, or more or less well-developed, current system. This system may be one in which there is a semi-closed circulation, with some incoming flow balanced by an outward flow at some other point or depth. Thus, depending upon the tolerance of the organisms being swept into the system but not endemic to it, or of endemic forms swept out with outward flow, zooplankton can serve as an indicator of the exchange of water (Bigelow, 1926). Usually these expatriates, if carried far out of their endemic breeding area, are found only as adults or submature animals, whereas in the "home areas" all stages of development may be found during the reproductive season.

Although no analyses have been made to determine the relative distance expatriates may be carried out of their endemic reproductive area before succumbing to changing conditions, it is reasonable to believe that the border of the endemic area may lie nearer the extreme range of distribution when the transport outward is into gradually increasing temperatures than it would be under cooling conditions; for it is well known that, in general, the optimum temperature lies closer to the lethal high temperature than to the lethal low temperature. The cooler temperatures tend to retard the vital processes but, if not extreme, lead to an extension of the animal's life.

The temporary plankton is made up of floating larval stages of the benthic or nectonic (swimming) animals. Most benthic and nectonic animals pass through a drifting planktonic stage. The duration of this stage does, however, differ greatly in different species, and only larvae of relatively long-floating existence can be useful as indicators of water movements.

Not much study has been made of the tolerance of the temporary plankton

to admixture of other waters, or to changes in temperature, and so forth, experienced during dispersal from the hatching or nursery area. But it should be pointed out here that there is some reason to believe that the larval forms may succumb more readily to changes than do the expatriates of the permanent plankton, although some larvae apparently do survive as drifting organisms for periods longer than considered normal for the species, when conditions favorable to metamorphosis to the benthic stage are not encountered. However, larval stages generally cannot be expected to be found, except as mere stragglers, at very great distances from the distributional range of the adult. The limits of the adult range may be controlled by the tolerance of the planktonic larvae, rather than by that of the benthic stage. However, the floating larvae of some near-shore shallow-water or intertidal adults can be traced to distances ranging up to 150 or more miles offshore over great depths, giving evidence of offshore flow of water.

To illustrate how these biological constituents may be useful as indicators in oceanographic, zoogeographic and ecological studies, the remainder of our discussion will be concerned chiefly with a review of a number of recent surveys, mainly in the North and South Pacific and adjacent seas, that have aided our concepts and understanding of the dynamics of the oceans and of their inhabitants.

The literature contains many reports, largely from the Atlantic, showing the application of this kind of plankton study. Some of these have been reviewed by Hardy (1956) and extended most recently by Tebble (1960). For recent work by Japanese and Russian investigators in the West Pacific see especially Bogorov (1955), Brodskii (1957) and Tokioka (1959).

It is not always possible to distinguish sharply between the application of biological indicators toward identification of water-masses *per se* as opposed to application as indicators of water currents. Often these are one and the same. However, in studies of the terminal extensions of· water-masses or of the more local movements of water intruding from or into separate areas, the application becomes quite distinct. For purpose of discussion, we shall treat the surveys under distinct headings although much overlapping is of necessity implied.

These discussions will not be deeply concerned with the precise physiological or ecological actions of temperature, salinity, etc. that function to confine an organism to a particular water-mass. This is a field that also needs much research, but we shall mainly be occupied in presenting some aspects that contribute to the descriptive phase of oceanography ; these aspects are currently experiencing an upsurge in the less explored Pacific and adjacent waters.

2. Water-Masses and Biological Species

The studies of distribution and systematics are interdependent in the development of biogeographical concepts. Oceanic populations found to be small in range sometimes prove to be ecotypically or genotypically distinct

from other populations of the same morphological type. The apparently broad character of other ranges has prompted study leading also to the recognition of complexes of regional species or subspecies. For example, *Salpa fusiformis* Cuvier, long recognized as cosmopolitan and variable in form, is now seen to consist of four species, two tropical–subtropical, one living south of the subtropical convergence, and one limited to the Pacific sector of the Antarctic (Foxton, 1961). Such forms thereby become meaningful in the framework of oceanic ecology. The discussion in this section will be concerned mainly with the euphausiacian Crustacea and is based on earlier work by Brinton (1962a).

Many of the zooplankton species became known from collections made by exploratory expeditions in the late 19th and early 20th centuries. Classification of plankton at the level of the subspecies or geographical race, requiring exhaustive systematic and ecological data, is a recent consequence of sampling by comprehensive oceanwide surveys and of morphometric comparisons of specimens from different regions. Investigations carried out by various nations in the Atlantic and Antarctic Oceans, and by North American, Japanese and Russian surveys in the Pacific, 1950–1960, provided material from nearly the full extent of the distributional ranges of many species. These surveys have employed improved sampling techniques making possible better quantitative estimates.

The water-mass boundary is recognized as a zone of discontinuity frequently associated with sharp horizontal gradients in temperature. The distributions of subspecific forms (subspecies, races, ecophenotypes), as well as species, may correspond with physical zones. In other instances, two or more closely related forms live in adjoining parts of one well defined water-mass, forming an allopatric complex. Nevertheless, each distribution derives its identity from a system of circulation. The biological evolution of passively drifting organisms is believed to have proceeded according to the availability of habitats that can conserve a stock.

Furthermore, the vertical range of certain planktonic species may correspond with the thickness of the physical water-mass and its contained currents. For example, in temperate and tropical latitudes where the euphausiid and sergestid (decapod) crustaceans perform diurnal vertical migrations between the surface and 300–800 m of depth, the water-masses are identified according to the temperature–salinity characteristic between depths of 150 and 1000 or more meters. The migrations and water-masses are mainly in the mesopelagic zone, a stratum between about 150 to about 700 m. Above this lies the epipelagic or photic zone and below it the bathypelagic and abyssopelagic zones. Bruun (1957) discusses the temperature relations for this zonation and Hedgpeth (1957) has reviewed certain works pertinent to the latitudinal aspects of the epipelagic.

The geographical ranges of species inhabiting the epipelagic zone appear in many cases to be limited by near-surface isotherms, while boundaries of mesopelagic species can be shown to conform with isotherms lying at some greater depth within the vertical range of the species. Inasmuch as many species have an extensive diurnal range that carries them through a vertical

temperature gradient of 10°–12°C, it is not yet possible through the study of distribution to establish that a boundary isotherm can limit a horizontal range of such species.

A. The General Applicability of Zooplankton–Water-Mass Relationships

In each of the several systematic groups thus far studied in the zooplankton of the Pacific (based mainly on samples collected by the California Cooperative Oceanic Fisheries Investigations, The Pacific Oceanic Fisheries Investigations and the Scripps Institution of Oceanography) certain species are recognized as having geographical distributions that are in close agreement with the major water-mass provinces. Pelagic Foraminifera (Bradshaw, 1959), Chaetognatha (Bieri, 1959; Alvariño, 1962), pteropod molluscs (McGowan, MS) and euphausiid crustaceans (Brinton, 1962b) each include species limited to subarctic, subtropical and tropical zones. These three ecological zones are designated *subarctic*, *central* and *equatorial* in this discussion, following the clear role played by water-masses in the zonation of the high seas. Studies of the distribution of polychaetous annelids (Dales, 1957; Tebble, 1962) and certain pelagic tunicates (Berner, 1960) and copepods (Johnson, 1938) in northern and northeastern Pacific waters are in general agreement with the recurring patterns.

A fourth Pacific faunal zone lies in temperate waters at the northern limit of the central region. In the western and mid-Pacific this is a zone of transition between central and subarctic faunas, and occupies water of the North Pacific Drift, 38°–45°N. Toward its eastern limit the zone diverges: a northern branch enters the eastern Gulf of Alaska while a southern branch occupies the California Current, terminating off Baja California. The California Current and the deep and coastal countercurrents which aid in maintaining plankton of the Current lie mainly within this zoogeographic province. However, the characteristic species of the zone are abundant only to the north of about 30°N. A "transition region", distinguished by Sverdrup, Johnson and Fleming (1942) on the basis of physical properties, lies in the California Current where subarctic, central and equatorial waters converge. Certain widely distributed species maintain their highest concentrations in this *transition zone*. Other species are endemic to it.

An analogous zone of transition lies in the Southern Hemisphere, 35°–45°S, reaching northward in offshore waters of the Peru Current. This belt includes the region of the Subtropical Convergence and the northern part of the West Wind Drift. It is the habitat of endemic species and of certain bisubtropical species (i.e. species occurring on each side of the tropics but not within them) found also in the transition zone of the North Pacific.

The quantitative aspects of many of the distributions included in this discussion are based on samples obtained above a depth of 300 m. These generally contained epipelagic populations, including the developmental stages of many species having adults concentrated in the stratum below 200–300 m.

In the case of the strongly migrating euphausiids, sub-adults and larvae of most species are present above 200–300 m during the day-time, while adults are found in the upper layers at night. Samples obtained below 300 m, including those from multiple hauls using opening-closing nets, are used to plot generalized profiles of vertical distribution. Such hauls serve also to establish which of the species distributions can be reliably mapped on the basis of the standard collections—that is, whether presence or absence at a locality can be determined from collections made above 300 m.

B. The Pacific Subarctic Species

The Pacific subarctic sustains a high biomass, although its geographical extent is small (six million square miles) compared with that of the North Pacific central (10 million square miles) and Pacific equatorial zones (15 million square miles). In the northwestern Pacific, the subarctic zone is characterized by the copepod species *Calanus tonsus*, *C. cristatus*, *Eucalanus bungii bungii*, the amphipod *Parathemisto japonica* and the euphausiid *Euphausia pacifica* (Brodskii, 1955; Bogorov and Vinogradov, 1955; Beklemishev and Burkov, 1958). *Eucalanus bungii bungii*, the northern variety of this species, is also characteristic of the eastern portion of this zone and the northern portion of the California Current (Johnson, 1938 *et seq.*), as is *Calanus cristatus*.

The distribution of the euphausiid *Thysanoessa longipes* is representative of the subarctic zone (Fig. 1a). Banner (1949) showed that a large form of *T. longipes* bears spines on the posterior abdominal segments. A smaller form has keels on those segments. The "spined" form is more northern than the "unspined" form. Both occur off Hokkaido, Japan, though their densities diminish sharply at the convergence where the cold water of the Oyashio submerges beneath the Kuroshio system. The "spined" form is predominant in the Gulf of Alaska while only the "unspined" form is found in the California Current, southward to 39°–40°N.

Water-mass envelopes for the two forms of *T. longipes* (Fig. 2) confirm the subarctic nature of the water in which both live. Water inhabited by the "spined" form is more nearly uniform with respect to the *T–S* property than that inhabited by the more southern "unspined" form. The environment of the latter, while remaining nearly subarctic in character below 300 m, is strongly influenced above that depth by admixture of the North Pacific Drift. (The layer of maximum density of *T. longipes* during both day and night is 0–280 m.) Populations of "unspined" *T. longipes* are intermingled with the transition zone species *T. gregaria* (Fig. 4) in the region 41°–45°N.

An area of abundance is evident in the distribution pattern of each of the forms of *T. longipes*. The areas are separated from each other in mid-ocean by a belt of lower density having an east–west axis near 50°N, but converge off northern Japan at the western limit of both ranges. The two forms are regarded as ecophenotypes. It is not known whether they are genetically separate. The morphological distinctions, not evident in the young, appear to be brought
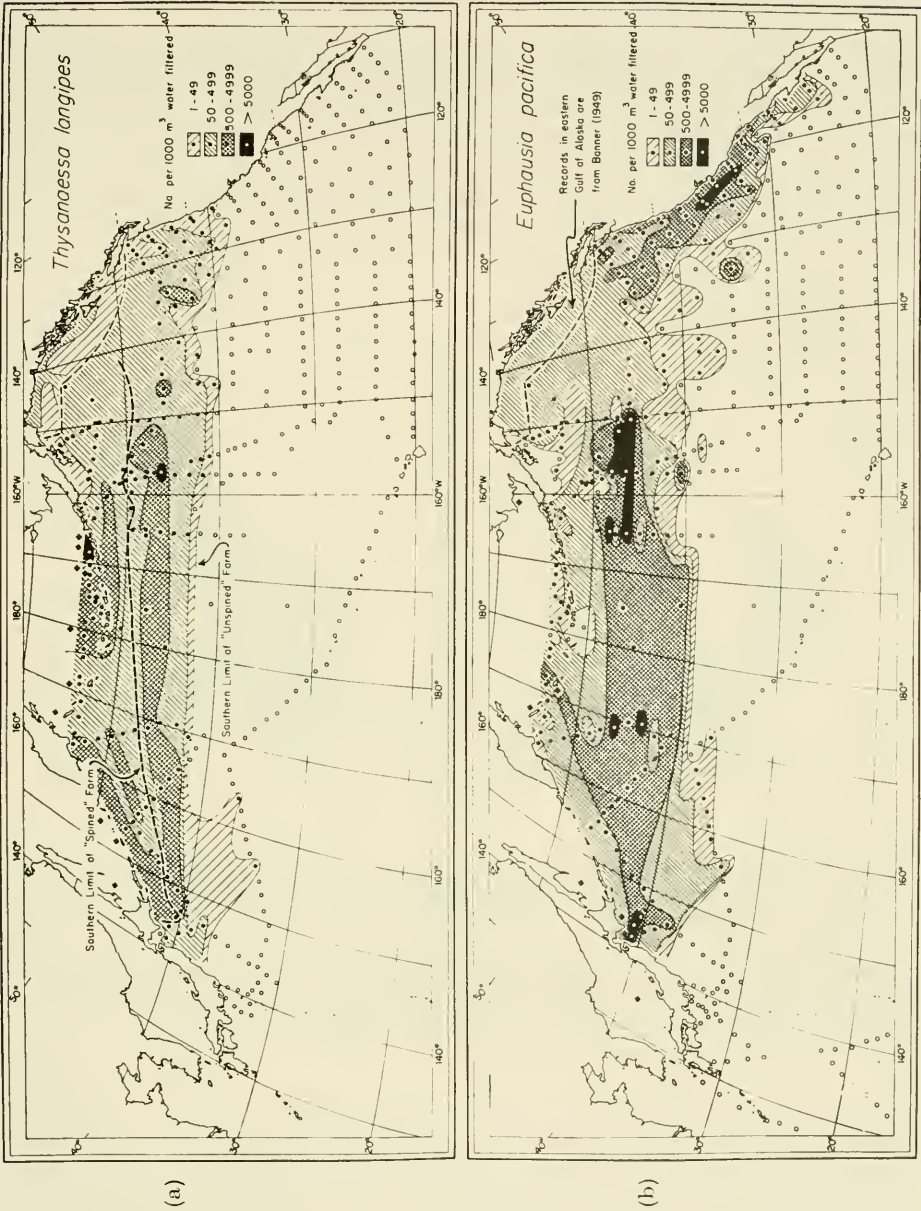
Fig. 1. Euphausiid species inhabiting the subarctic water-mass. (a) *Thysanoessa longipes* and (b) *Euphausia pacifica*. (Based mainly on sampling by the Scripps Institution and the California Cooperative Oceanic Fisheries Investigations between the surface and 270–300 m.)

about by differences between the two optimal environments: the temperature at 200 m is less than 4°C in the range of the "spined" form, but may be as high as 7°C for the "unspined" form.

Other northern species have wider environmental tolerances, permitting them to range southward in the cool coastal waters off California. This group includes *Euphausia pacifica* (Fig. 1b), the copepods *Calanus cristatus*, *Eucalanus bungii bungii*, and the pteropod *Limacina helicina*. Some of these species persist until subarctic and upwelled components of the California Current become thoroughly mixed with equatorial water toward the south, and with central water in the offshore region. McGowan (MS) has shown that a northern
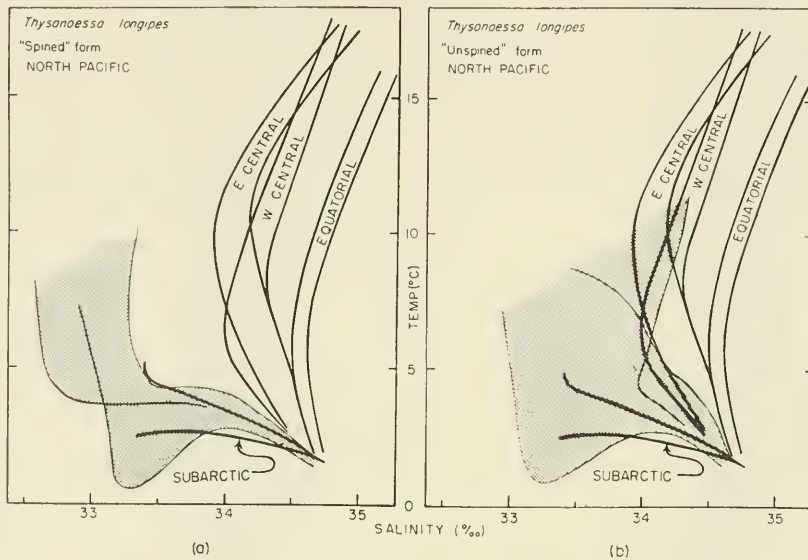

Fig. 2. The shaded part represents temperature–salinity characteristics below about 150 m in the environment of *Thysanoessa longipes*. These observations were made during the "Transpacific" expedition (1953) and the "Norpac" cruise (1955). Certain of the curves that limit the *T–S* envelope for the species are shown as fine lines. The more northern "spined" form (a) is seen to be more typically subarctic than the "unspined" form (b). (The water-mass envelopes are from Sverdrup, Johnson and Fleming, 1942.)

high-spired form of *L. helicina* may be distinguished from a low-spired form occupying the transition zone and the California Current. He regards these as geographical races or ecotypes. The limits of the distribution of *Euphausia pacifica* off Baja California fall where subarctic and equatorial waters are mixed in nearly equal proportions, according to the temperature–salinity characteristics of that region (Tibby, 1943). Seasonal variability in the southward extent of the distribution of *E. pacifica* in the California Current is small (Brinton, 1960). In general, this species is absent from Baja California waters during the winter and recolonizes that region at the onset of spring upwelling.

Distributions like that of *E. pacifica* are included in the subarctic group because the centers of distribution are (1) subarctic water near the northern boundary of the North Pacific Drift, and (2) upwelled subarctic water of the California Current.

A relationship between the distribution of the planktonic worm *Poeobius meseres* and the subarctic water-mass was found by McGowan (1960). Though
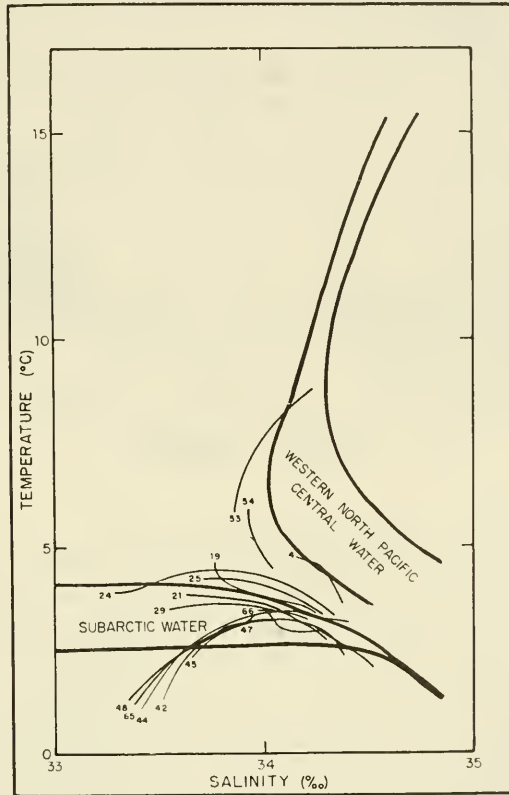

Fig. 3. Temperature–salinity curves from the stations where *Poeobius meseres* was caught during the "Transpacific" expedition, compared with subarctic and North Pacific central *T–S* envelopes. Station numbers are indicated on the fine lines. Only that segment of the curve within the depth range of *Poeobius* is plotted. (After McGowan, 1960.)

widely distributed in the 150–300 m layer in the subarctic region, this species is found at greater depths in the California Current and in the terminal part of the Peru Current between 6°S and the Galapagos Islands (0°). Unlike *Euphausia pacifica*, *Poeobius* submerges toward the southern limits of its range. The tropical records were of specimens believed to be sterile expatriates: it was implied that their occurrence near the equator might be due to a relationship between eastern tropical intermediate water and subarctic water.

McGowan showed that, strictly speaking, the part of a T–S curve which represents a precise depth of capture should be used to identify the water-mass habitat. This procedure is valid where the population maximum is encountered below the mixed layer. Divided hauls carried out at 150-m intervals by the "Transpacific" expedition in 1953 made it possible to show a stratum-of-capture. In the case of *Poeobius*, the segments of T–S curves plotted for these layers generally fell within the envelope of the subarctic water-mass (Fig. 3).

Surface plankton has been related to the surface T–S property (Bary, 1959). Distributions included in the present discussion are based on oblique open-net hauls. These may sample (1) only the upper limits of an extensive vertical range, or (2) a stratum thicker than the local vertical range of the species. In these cases it can be useful to identify the water-mass habitat either by means of the full T–S curve at the locality or by the part relating to the usual vertical range of the species, if this is known.

Recurrent species groups (in the sense of Fager, 1957) were distinguished among certain North Pacific chaetognaths, euphausiids and pteropods (Fager and McGowan, in press) on the basis of the "Transpacific" data of Alvariño, Bieri, Brinton and McGowan. A subarctic group concorded best with shape-of-T–S-curve (50–1000 m), supporting the concept of the water-mass habitat.

C. The Transition Zone Species

The region of transition between subarctic and central populations in the mid-Pacific and between subarctic and equatorial populations in the California Current is regarded as a biogeographical zone because it harbors (1) endemic species, (2) bisubtropical species, limited in the North Pacific to this belt, and (3) maximum densities or regions of dominance of certain species having broader total ranges. A zone between the subantarctic and central regions in the Southern Hemisphere is distinguished in the same way.

In the western Pacific, where the cold subarctic region is in contact with the warm Kuroshio and the Kuroshio Extension, a narrow transition zone was recognized in which the copepod *Calanus pacificus* is particularly abundant (Bogorov and Vinogradov, 1955; Brodskii, 1955). In mid-ocean the transition zone was identified by Hida (1957) as an area of mixed fauna and variable biomass, usually characterized by large numbers of the pteropod *Limacina inflata*. A chaetognath identified by Hida as *Sagitta lyra* was abundant in the transition zone. This form, now distinguished from the more widespread *S. lyra* as *S. scrippsae* (Alvariño, 1962), appears to be endemic to the transition zone.

The euphausiid *Nematoscelis difficilis* lives in this narrow transition belt. A relict population of this species is also maintained in the northern part of the Gulf of California. *N. megalops*, a sibling species close to *N. difficilis*, occupies the transition zone of the Southern Hemisphere, occurring in the Indian and
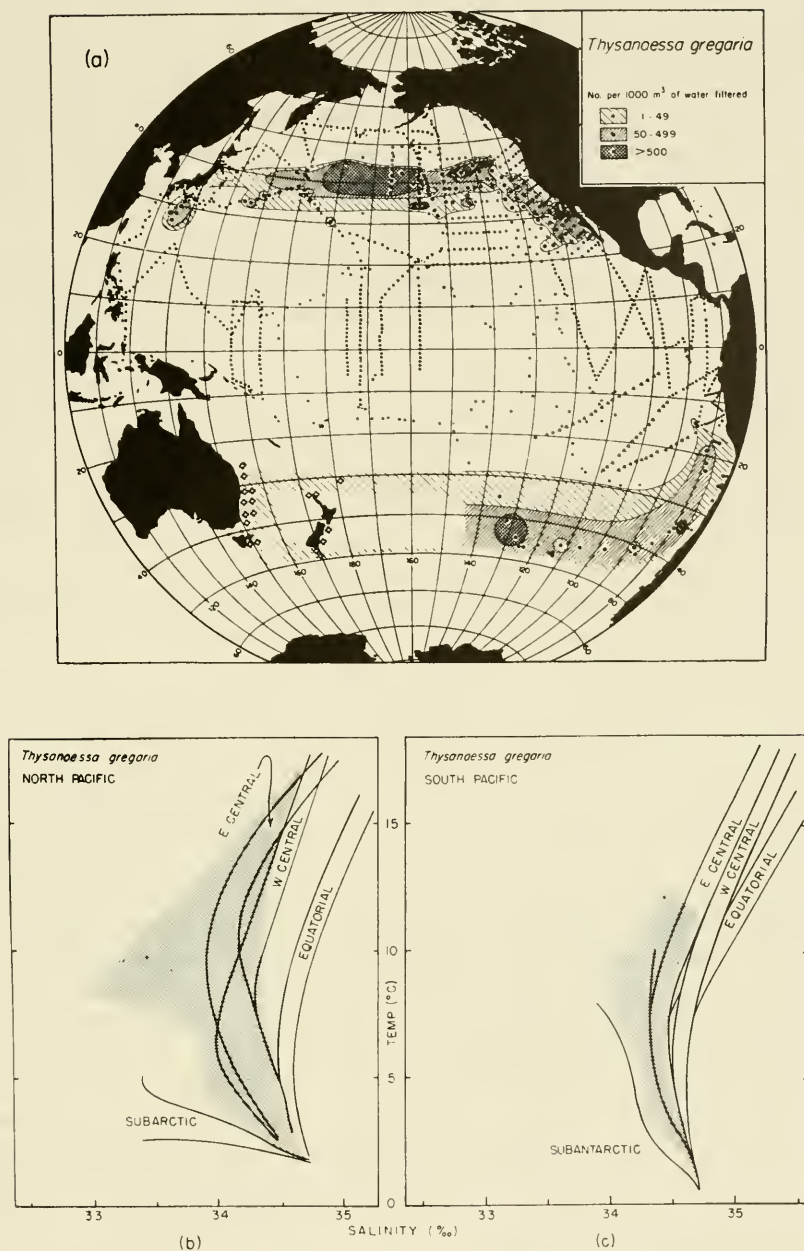
Fig. 4. (a) The Pacific distribution of *Thysanoessa gregaria* within a transition zone between central and subarctic (or subantarctic) water-masses. *T–S* characteristics of water below about 150 m for the North Pacific habitat (b) and the South Pacific habitat (c) of *T. gregaria* are compared with the *T–S* envelopes of the principal Pacific water-masses. South Pacific *T–S* curves for the *T. gregaria* habitat are all from the eastern half of the ocean.

Atlantic Oceans as well. *N. megalops*, rather than *N. difficilis*, occupies the transitional belt in the North Atlantic.

The bisubtropical euphausiid *Thysanoessa gregaria* (Fig. 4) lives in the transition zones of both hemispheres in the Pacific. In mid-ocean its low-latitude boundary is near the 30° parallel in both hemispheres. In the eastern boundary currents the range reaches toward the tropics, terminating in equatorial water. This is near 15°S in the Peru Current and 18°–20°N off Baja California.

The temperature–salinity envelopes for *T. gregaria* (Fig. 4b, c) show that both the northern and southern habitats are intermediate in character between equatorial and subarctic (or subantarctic) waters. In both cases there is overlapping with the central water-masses. In the South Pacific the *T–S* habitat of this species also extends southward into subantarctic water and northward into modified equatorial water. Distributions of the southern transition zone species are closely related to the east–west belt of the Subtropical Convergence, which curves northward as the South American continent is approached and becomes poorly defined in offshore waters of the Peru Current. Northward-reaching tongues in the distributions of *T. gregaria* and *N. megalops* are maintained, in part, by a northward-flowing subantarctic current component and a deeper remnant of southward-flowing equatorial water. *T–S* curves indicate the similarity of the equatorial water to both the South Pacific central water and the subantarctic water.

The term "transition zone" is particularly descriptive of the North Pacific habitat of *T. gregaria* where the *T–S* envelope of the species falls in part between the envelopes of typical subarctic and central water and in part within the central envelopes. In the South Pacific it almost completely overlaps both envelopes. It is to be noted that the *T–S* habitat of *T. gregaria* in the North Pacific differs somewhat from that in the South Pacific. The differences lie mainly in the salinity. The temperatures in the two zones are nearly the same. Apparently a broader range of salinity is found in the northern zone within the range of temperature tolerance. It will be seen that the disjunct habitats of central species, when described in terms of the relationship of temperature to salinity, differ from each other in exactly the same way as those of the transition zone. Salinity *per se* probably has little direct effect in controlling the geographical distributions of oceanic species. Rather, the essential features of the oceanic habitat are (1) continuity in the system of circulation (water-mass) implying a permanent or semi-permanent place of origin of the water, (2) a range of temperature to which the species can adapt, (3) an adequate food supply, and (4) an area sufficiently large to enable restocking despite loss by dispersal.

In an alternative explanation there may be genetic differences, not yet discernible, between the two populations of *T. gregaria*. Such differences are already suggested in the *Nematoscelis difficilis–N. megalops* pair. Geographically separate populations of a species will, in time, diverge genetically as a consequence of selective pressures that differ between the two environments.

D. The Pacific Central Species

Plankton species of the central waters may be grouped according to the extent to which their ranges conform with the distribution of the most typical central water.

The euphausiids *Nematoscelis atlantica, Euphausia brevis* (Fig. 5) and *E. hemigibba* are most numerous in the warm, barren mid-parts of the North Pacific gyrals. *N. atlantica* and *E. brevis* are bisubtropical, occurring also in the South Pacific central zone, while *E. hemigibba* is replaced in the Southern Hemisphere by *E. gibba. T–S* envelopes for these species, as shown for *E. brevis* (Fig. 5b, c), are in agreement with the *T–S* characteristics of the central water-masses.

The distributions of *E. brevis* and *N. atlantica*, unlike those of many other central species, do not extend into the region south and east of Japan, where central water is affected by the warm Kuroshio system and the submerging subarctic water.

A second central group may be represented by *Euphausia mutica, Sagitta pseudoserratodentata*, and the foraminiferan *Globorotalia truncatulinoides*. These species are found in low concentration toward the central parts of the oceanic gyrals, while areas of abundance are associated with the margins of the ranges. These margins are places where the central environment impinges on more fertile waters of the subarctic region, the eastern boundary currents, and the equatorial water-mass.

Ranges of the species of this second central group frequently enter near-shore waters in the southern part of the California Current at 20°–34°N. This is a region south of Pt. Conception, California, where the climate of the northern epipelagic region is modified by the effect of the subtropical latitude and by admixture of southern and offshore water.

The species of a third central group have North and South Pacific zones of distribution, joined in the western Pacific but separated in the eastern Pacific. The eastern region from which these species are excluded lies in the equatorial water-mass, characterized by low sub-surface values for temperature and dissolved oxygen. The chaetognath *Sagitta californica* and the euphausiid *Stylocheiron abbreviatum* are examples of this group that may be showing either incipient bisubtropicality or a coalescence of northern and southern zones of distribution.

The composite range of the species-pair *Thysanopoda aequalis–T. subaequalis* (Boden and Brinton, 1957) falls in the third group. In the North Pacific, *T. subaequalis* is found in the western part of the ocean while *T. aequalis* lives in the eastern part. This is the only known case in which the eastern and western central water-masses of the North Pacific support distinct populations of closely related zooplankton species. (The eastern and western North Pacific central water-masses were distinguished by Sverdrup, Johnson and Fleming (1942), but are not now generally believed to be distinct gyrals.) In the South Pacific the ranges of the two forms overlap; *T. aequalis* lives in cooler water than *T. subaequalis* and is the more widespread form.
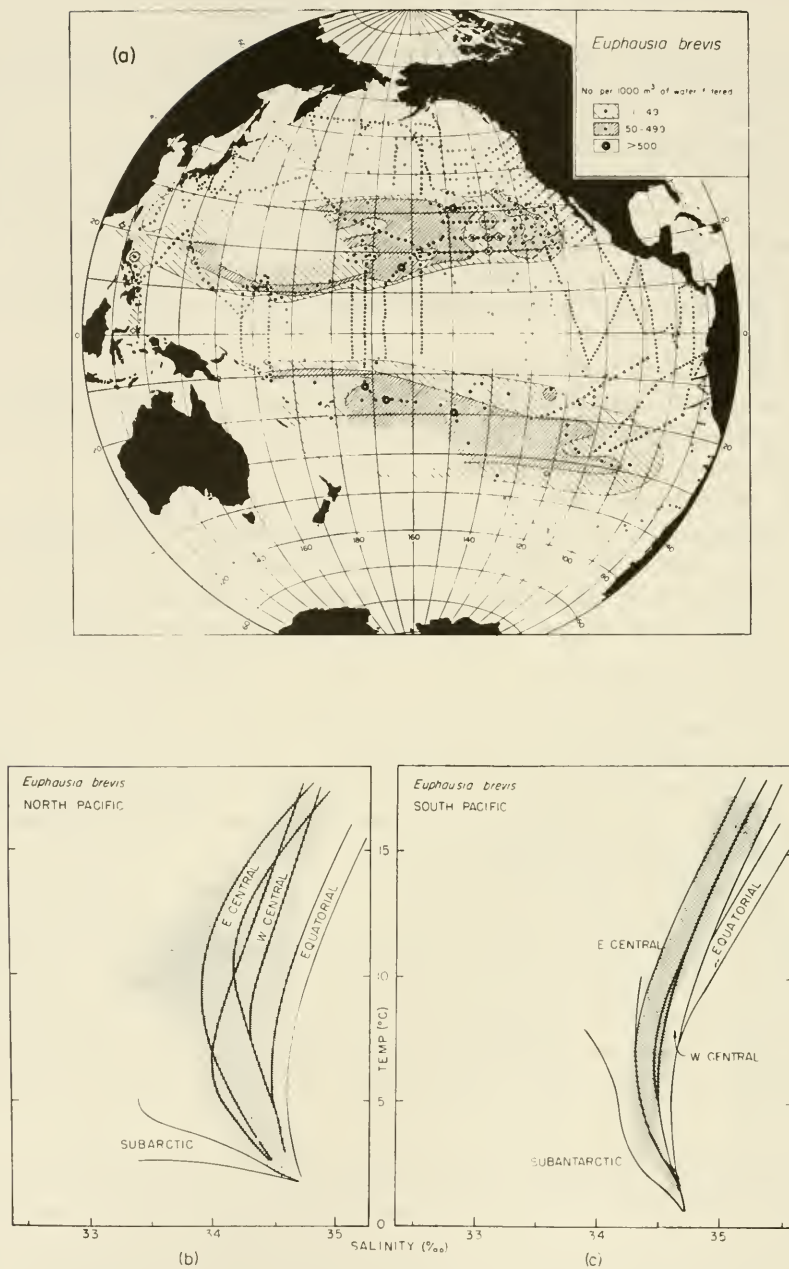
Fig. 5. The Pacific distribution of *Euphausia brevis* in the central water-masses. *T–S* characteristics below about 150 m for the North Pacific habitat of this species (b) and the South Pacific habitat (c) are compared with the *T–S* envelopes of the principal Pacific water-masses. South Pacific *T–S* curves for the habitat of *E. brevis* are all from the eastern half of the ocean.
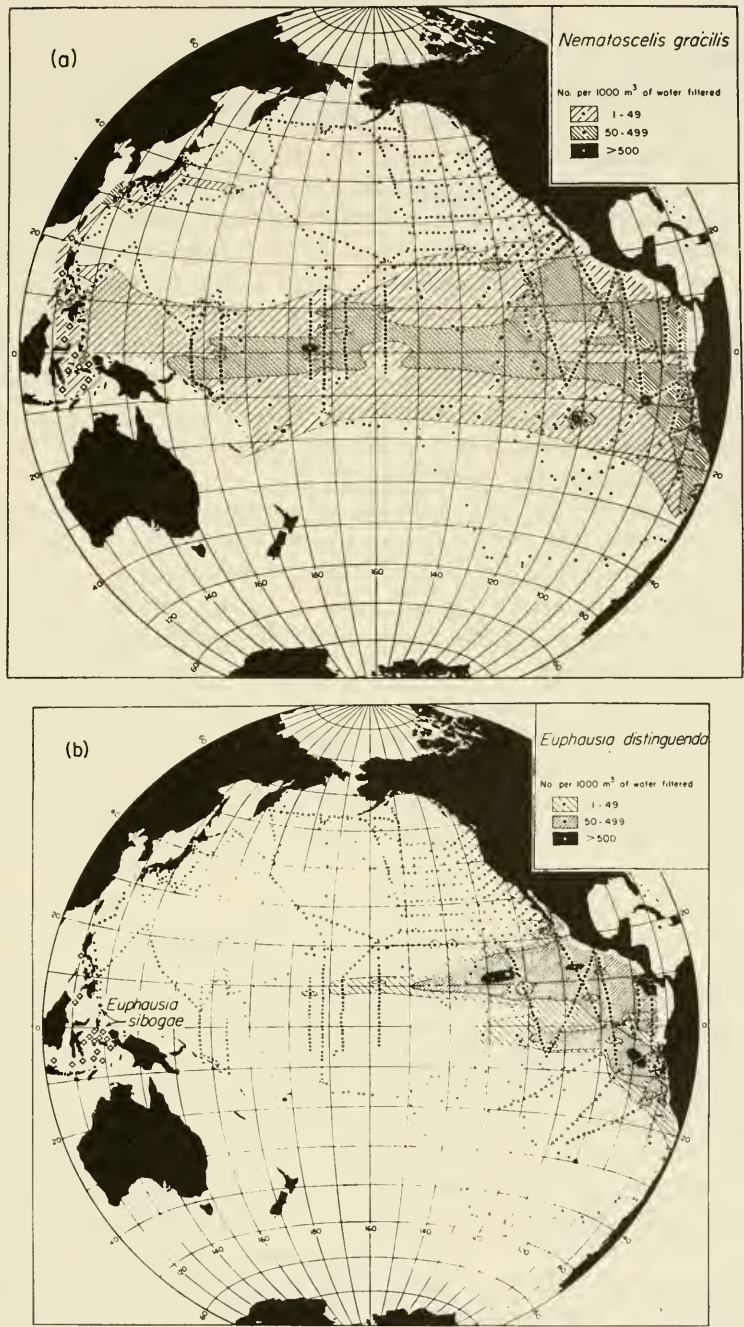
Fig. 6. Geographical distribution of equatorial euphausiid species, *Nematoscelis gracilis* (a) and *Euphausia distinguenda* (b). The only other localities for these two species are in the equatorial water-mass of the Indian Ocean. Crosses in (a) indicate non-quantitative records for *N. gracilis*, and in (b) all known localities for *E. sibogae*, a species related to *E. distinguenda*.

E. The Equatorial Species

The euphausiids *Euphausia distinguenda* and *Nematoscelis gracilis* provide examples of two patterns of distribution (Fig. 6a, b), both related to the region of the Pacific equatorial water-mass. These extend into the Peru and California Currents at the eastern boundary of the ocean. *Euphausia distinguenda* is carried westward by the North and South Equatorial Currents, until the range becomes attenuated in mid-ocean. The influence of the Equatorial Counter-current, 2°–8°N, is evidently a disadvantage to this species. (The distributions of other eastern equatorial species, *E. eximia* and *E. lamelligera*, are completely split along the east–west axis of the countercurrent, according to sampling carried out in 1952 and 1955.) *E. sibogae*, very similar to *E. distinguenda*, is found in the warmer waters of the Indo-Australian Archipelago.

The equatorial water-mass is narrowed in the western Pacific. The range of *Nematoscelis gracilis* narrows in the same way, though this species is carried northward to Japan by the warm Kuroshio.

Four Pacific equatorial euphausiids, including the two just discussed, are found also in equatorial waters of the Indian Ocean but not in the Atlantic. This is in conspicuous agreement with the distribution of equatorial water-masses, recognized in the Pacific and Indian Oceans, but not in the Atlantic.

Each of the planktonic groups thus far studied with respect to distribution contains tropical species which occupy both the equatorial region and the central regions of the western Pacific. The limits of these distributions generally follow the 24°–26°C summer surface isotherm. This assemblage was called the *equatorial-west-central fauna* by Bieri (1959) and Bradshaw (1959), and is made up of numerous epipelagic species including *Sagitta robusta*, *Euphausia tenera*, the foraminiferan *Pulleniatina obiquiloculata* and the pteropod *Limacina inflata*.

F. Species of the Antarctic Ocean

The niches in the Antarctic Ocean appear to have evolved in relation to four boundaries: the Antarctic continent, the edge of the pack ice, the Antarctic Convergence and the Subtropical Convergence. The meridional component of Antarctic circulation, together with sinking at the Antarctic and Subtropical Convergences, partially separates each of the epipelagic zones from its neighbors. Mackintosh (1934) noted that, here, the limits of distribution of species may be controlled by vertical migrations between surface water which has a northward-moving component and southward-moving deep water.

John (1936) showed that *Euphausia crystallorophias* is associated with the coast of the Antarctic Continent, *E. superba* with the zone between the continent and the Antarctic Convergence, and *E. frigida* with the region between the ice edge and the Antarctic Convergence. These may be regarded as species of the antarctic water-mass. Three species of polychaetes, *Rhynchonerella bongraini*, *Vanadis antarctica* and *Tomopteris carpenteri*, are believed to be endemic to waters south of the Antarctic convergence (Tebble, 1960). *Euphausia vallentini*,

E. longirostris and *E. lucens* live in subantarctic water bounded by the Antarctic and Subtropical Convergences. This habitat is comparable in both latitude and temperature to the subarctic habitat of *E. pacifica*, a species related to the *E. lucens–E. vallentini* line of the Antarctic Ocean. A thorough study of *E. triacantha* (Baker, 1959) demonstrated a close relationship between maximum density of this circumpolar species and the position of the Subantarctic Convergence. Smaller numbers were found on either side of the convergence, within the belt of the West Wind Drift. David (1955) described separate races of *Sagitta gazellae*: a "large southern" form is antarctic, while a "small northern" form is subantarctic.

G. Distribution and Speciation

Reference was made in the preceding section to forms that may or may not be sufficiently distinct genetically to be regarded as species. The importance of colonization of neighboring waters as compared with absolute geographical isolation in the differentiation of zooplankton species is an open question.

It may be noted, however, that there are several instances in which forms of uncertain taxonomic rank live on opposite sides of convergences or other oceanographic boundaries, while there are few instances in which closely related, *well defined species* are found in such adjoining regions of the high seas. The forms of *Sagitta gazellae*, *Thysanoessa longipes*, and *Limacina helicina* and the *Vanadis antarctica–V. longissima* and *Thysanoessa aequalis–T. subaequalis* "species pairs" are instances in which the extent of reproductive isolation between closely related forms is not clear. These, and the intergrading forms of the euphausiid *Stylocheiron affine*, discussed in later paragraphs, may be sympatric complexes in which morphological differences between populations are caused by environmental differences across the geographical range of a single genotype. Oceanic forms clearly recognized to be sibling species, as in the cases mentioned above of *Nematoscelis difficilis–N. megalops* and *Euphausia distinguenda–E. sibogae*, are often more widely separated geographically.

In view of the uncertain influence of water-mass boundaries in evolutionary processes, only the three north–south continental land-masses that partition the seas into the Atlantic, Pacific and Indian Oceans can be recognized as absolute barriers between pelagic populations of low latitudes. Certain warm-water species (e.g. *E. brevis*, Fig. 5a) are today split up by these barriers into isolated populations living in the separate oceans.

Similarly, the antitropical pattern of distribution, in which parts of a range are separated by a tropical or subtropical belt, can establish absolute isolation of northern and southern population elements.

The paired roles of continental and tropical barriers in the differentiation of euphausiid species are considered by Brinton (1962b). In that discussion, isotherms that agree with the limits of Recent distributions are used to extrapolate the limits of hypothetical distributions that may have existed during past epochs when the oceans were warmer or cooler.

The positions of ancient water-mass habitats are not mapped as easily. The persistence of belts of oceanic productivity, as measured in the sediments by Arrhenius (1955), suggests that some of the major currents have retained their positions since the close of the Tertiary. If the zones of the water-masses have similarly persisted, it is unlikely that plankton distributions have migrated in strict harmony with postulated latitudinal migrations of isotherms. When ocean-wide warming or cooling compelled a species to occupy a new geographical range, still tolerable with respect to temperature, salinity and food, this new environment had also to include a sufficiently closed current system to maintain the population. Nevertheless, temperature, reflecting obvious responses of the ocean to climatic change, was necessarily used in the euphausiid study.

Of the species with disjunct ranges, those with the widest latitudinal range-split occupy the two transition zones (zones of sinking isohaline and isothermal surfaces, Fig. 7). Given sufficient time, the separated populations of *Thysanoessa gregaria* would be expected to undergo independent selective adaptations. The species pair *Nematoscelis difficilis–N. megalops* is an example of antitropical evolutionary divergence already in an early stage. Compared with *N. difficilis–N. megalops*, *Thysanoessa gregaria* ranges somewhat farther into warm waters, by 1°C, interpreting 100-m isotherms as limiting. The northern and southern populations of *T. gregaria* are morphologically indistinguishable. They may have exchanged genetic material across the tropics more recently than the precursor of *Nematoscelis difficilis–N. megalops*.

Reconstructed Pleistocene distributions for *Thysanoessa gregaria* (Fig. 9) are based on $2\frac{1}{2}$°C warming, or cooling, at a depth of 200 m. Hubbs (1952) suggested that if the surface near-shore waters of the eastern Pacific were 8°C cooler in the winter than during present winters and 3°C cooler in the summer, continuity and exchange between fish faunas now antitropically separated would have been possible. The 7°C and 11°C isotherms at 200 m are associated with the limits of the Recent range of *T. gregaria*. The temperature change required to cool the warm waters west of Central America enough to allow equatorial transgression by *T. gregaria* would have made the California Current extremely cold. The bisubtropical transition-zone fauna would then have moved far offshore into central waters, so that it would no longer have access to prevailing currents entering the eastern equatorial basin. The northern and southern populations might, therefore, have coalesced far offshore in the zone of 0°–12°N (Fig. 9c). With 2°–3°C of cooling, the coastal fauna in the region 20°–30°N would have consisted of subarctic species (*Euphausia pacifica*, *Thysanoessa longipes*, *Tessarabrachion oculatus*). These occur only in the northern hemisphere. It is probable that they have never transgressed the tropics. Similarly, the Peru Current species *Euphausia mucronata* and all subantarctic euphausiids appear to have never crossed the equator.

Thus, during moderately cool epochs, either the transition-zone populations would have coalesced at the equator, or, if the species had previously been present in only one hemisphere, access to a new habitat in the opposite hemi-

sphere would have been provided. During warm epochs the belts of distribution would have moved toward the poles, establishing isolated pockets of distribution in the northern oceans (there, forms would differentiate if they were to remain isolated sufficiently long), while allowing circum-global exchange of genetic material to take place south of the continents.
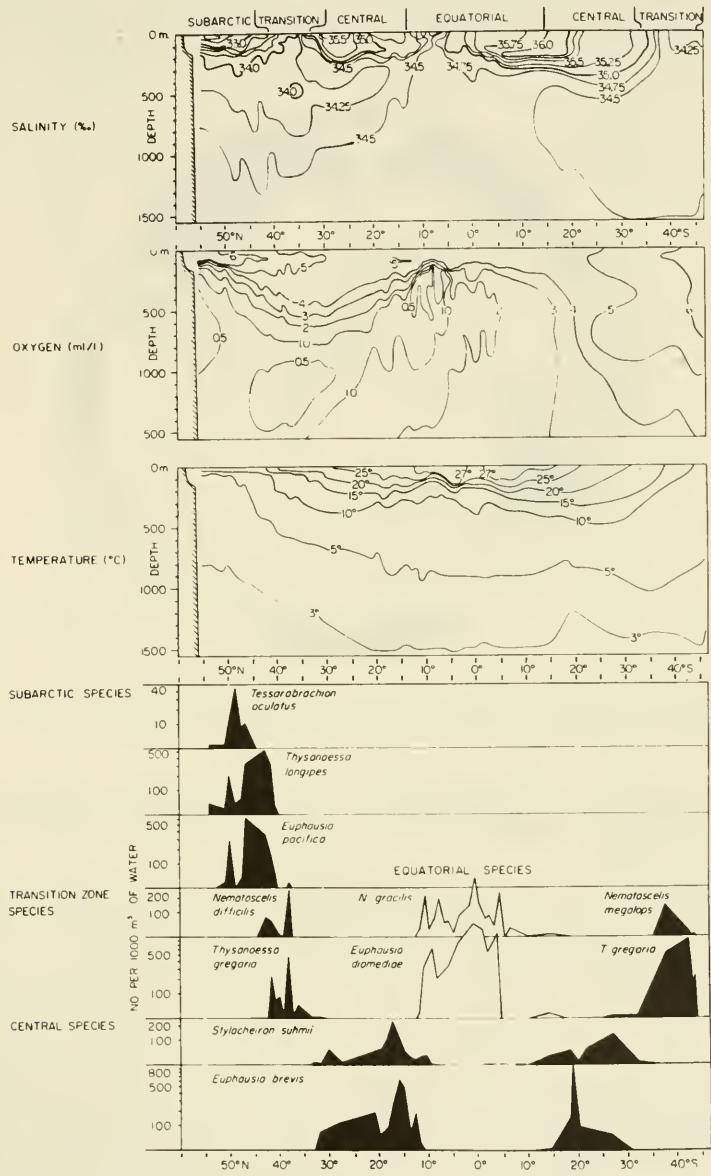

Fig. 7. Abundance of certain euphausiids, belonging to four faunas, from a north–south mid-Pacific track (Fig. 8) compared with salinity, oxygen and temperature profiles from the same stations.

Interglacial warming of the oceans is of equal importance to oceanic cooling in developing or maintaining antitropical distribution. The sub-surface equatorial region is characterized by a belt of cool water (Fig. 7) which extends across the ocean. While species of the transition zone required cooling of the eastern Pacific to accomplish equatorial transgressions, the central species presumably crossed the tropics on the western side of the ocean during epochs of general oceanic warming. Only then would temperatures in the sub-surface equatorial belt become tolerable. *E. mutica* and *Thysanopoda subaequalis*
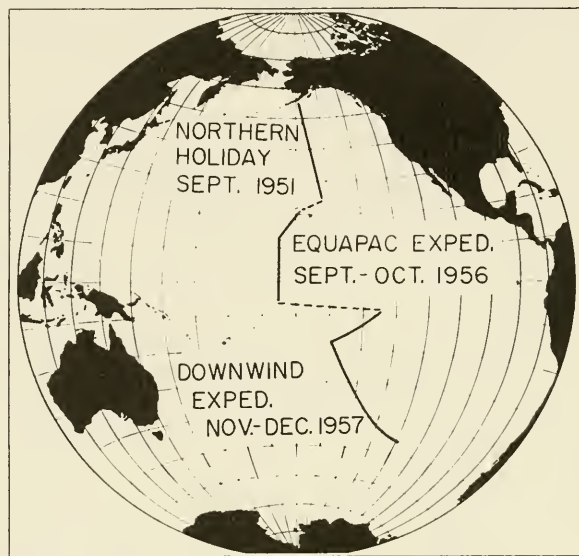

Fig. 8. Composite track of portions of three expeditions on which the physical profiles and species concentrations shown in Fig. 7 are based.

transgress the equator in the western Pacific today. During epochs of oceanic cooling, the central species would be withdrawn into the warm mid-parts of the central gyrals.

It is significant that the bisubtropical euphausiid species, including most of the *Euphausia* species occupying the central water-masses of the oceans, are also panoceanic, occurring in the Atlantic and Indian Oceans as well as the Pacific. In contrast, subarctic euphausiid species (excepting the two most northern species, *Thysanoessa inermis* and *T. raschii*, which appear to have passed between the Atlantic and Pacific Oceans by way of the Arctic Ocean) and the most tropical species, e.g. *Euphausia americana* of the Atlantic and *Nematoscelis gracilis* of the Indo-Pacific equatorial water-mass, do not occur in both the Atlantic and Indian-Pacific Oceans, but are endemic to one or the other. Burkenroad (1936) adduced evidence from penaeid distributions that only shallow water connected the Atlantic with the Pacific at Panama during the Cenozoic. It appears probable that oceanic populations have not crossed

these connections since the Cretaceous. All antarctic and subantarctic species of euphausiids are confined to the Antarctic Ocean and are circumpolar.
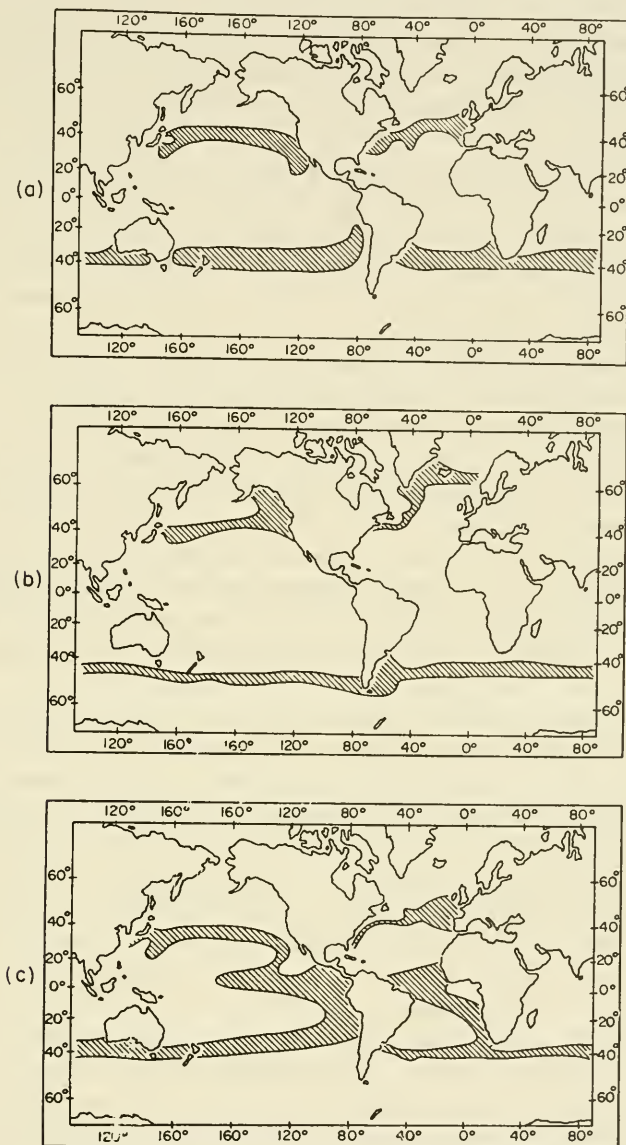

Fig. 9. (a) Present range of the euphausiid *Thysanoessa gregaria* compared with hypothetical circumstances of oceanwide warming (b) and cooling (c), both by $2\frac{1}{2}$°C. The 7°C and 11°C isotherms at 200 m depth, associated with present limits of distribution of *T. gregaria*, are considered limiting for the purpose of the extrapolation. With warming (b), the 7°C isotherm (at the high-latitude boundary) moves to position of present $4\frac{1}{2}$°C isotherm, and the 11°C isotherm (at the low-latitude boundary) moves to position of present $8\frac{1}{2}$°C isotherm. With cooling (c) the limiting 7°C and 11°C isotherms move to positions of present $9\frac{1}{2}$°C and $13\frac{1}{2}$°C isotherms, respectively.

Groups of four related species occur in each of the three major euphausiid genera that inhabit the upper layers—*Euphausia* (2 groups), *Nematoscelis* (1 group), *Stylocheiron* (1 group). These may be explained by postulating long-term isolation of populations, split up from the once-widespread distribution of each parent species, into the four major subtropical oceans—the Atlantic, North Pacific, South Pacific and Indian Oceans. Each quartet of species contains three central and one equatorial Pacific–Indian Ocean species. For example, *Euphausia brevis*, *E. mutica* and *E. recurva* are central, while *E. diomediae* is equatorial. The central species have, in most cases, re-established themselves in the other central regions already occupied by sibling species when these other regions became accessible during Pleistocene periods of latitudinal oscillations of isotherms. The equatorial species remained bound to the equatorial water-masses.

Three closely related mesopelagic species occur in each of three euphausiid genera: the "*Thysanopoda orientalis* group", the "*Stylocheiron maximum* group" and the three species comprising the genus *Nematobrachion*. All occupy depths to 1000 m, mainly in the zone 45°N–45°S. Differentiation from the three parental forms may have followed availability of the three isolated mesopelagic habitats—the low-mid-latitudes of the Atlantic, Pacific and Indian Oceans.

Furthermore, the ten endemic antarctic and subantarctic species of *Euphausia* and *Thysanoessa* may have differentiated within the southern zones of the Atlantic, Pacific and Indian Oceans when circumpolar stocks were split up by the southern continents during cool epochs in the cycles of change in ocean climate.

In this way, latitudinal thermal fluctuations occurring simultaneously within a series of intercommunicating oceans could have led to the rise of groups of euphausiid species. Invasion of equatorial waters and of passageways around the southern tips of continents can account for the present sympatric occurrence of species that initially differentiated as allopatric forms. Earlier transgressions may have brought about the present sympatric occurrence of related genera. Successive climatic revolutions might, therefore, be accompanied by an increasing rate of species formation were it not for the probability that few environmental changes have been of sufficient magnitude or geographical extent to allow the differentiation of species in the partitioned stocks. In addition, successive epochs may not always be enough separated in time to permit allopatric differentiation before coalescence again occurs, either around the tips of continents or across the tropics. Of course, environments may be so altered by climatic change that those species unable to adapt to the changing conditions become extinct.

Less may be inferred about the possible effectiveness of *oceanographic* barriers in isolating planktonic populations from one another. The findings of geographical races or subspecies suggests the possibility that morphological differentiation may arise in segments of the overall population of a species, in each of a series of communicating oceanographic regions. For example, several Pacific variants of the euphausiid *Stylocheiron affine* are distinguished on the

basis of morphometric characteristics (ratios of measurements of the eye and abdomen) (Brinton, 1962b). They appear to be adapted to separate geographical areas and make up a *Rassenkreis* along the anticyclonic pathway of the circulation of the subtropical and tropical North Pacific. The biogeographical sequence includes a "California Current" form, an "Eastern Equatorial" form, a "Western Equatorial" form, and a "Central" form. None are regarded as species because each appears to intergrade with neighboring upstream or downstream forms. Thus, they are sub-species, in the sense that the bulk of the population of each form is morphologically uniform. However, the intergrades have been found only in small parts of the overlapping ranges. The "California Current" and "Central" forms overlap, but are regarded as terminal elements of the cline because they do not intergrade with each other.

In another complex, *Euphausia nana*, occupying the Tsushima water-mass of the East China Sea, is more nearly isolated from *E. pacifica*, its large subarctic counterpart (Brinton, 1962a). *E. pacifica*, ranging eastward from the Japan Sea to the California Current (Fig. 1b), differs conspicuously from *E. nana* in that it is about three times larger at maturity. Morphological differences are small. Though these differences might have ecotypic bases, the absence of intergrading specimens has led to the assignment of specific status to both forms. The partial barriers of the Tsushima Strait and the Kuroshio may be insufficient to have brought about genetic isolation of the two populations; however, it appears possible that unequal maturation rates associated with the different water-mass habitats may have reproductively isolated the large northern adults from the small southern ones. On the other hand, eggs of the large form, after drifting into the southern habitat, might develop into small adults, thereby sustaining a uniform *E. pacifica–nana* gene pool.

It is not possible at present to provide a satisfactory solution of these complex relationships in terms of oceanographic factors. Environmental gradients exert continuing, however variable, pressure on the adaptive capacity of all plankton populations. The populations are thereby constantly subject to both physiological and genetic adaptations, but the implications of these to species formation are clear only when gene pools that are not in communication with each other have been created.

3. Water Currents and Biological Species

Water-masses are conceived of as being sufficiently large in volume to maintain rather steady and uniform conditions throughout circumscribed geographic areas. When these masses are maintained as such over large areas or are confined as semi-closed systems of circulation, a characteristic assemblage of planktonic species may develop. However, these waters are constantly being formed anew by admixtures of water from other systems, each with their own identity. These blended waters, although maintaining their physical-chemical identity for the main body, are changed at their margins and extremities by admixture of yet other waters, or by physical changes resulting from seasonal

changes or from gradual flow into higher or lower latitudes where the effects of temperature or evaporation alter the distinguishing features.

It is often of interest to follow the course of these moving, changing masses, which have now lost part or all of their chemical-physical identities, and exist as modified extensions in the form of currents, tongues or wedges, into other geographic positions. Assuming that the planktonic fauna characterizing the water-mass is well known, it is here that further application of an "indicator species" can serve to corroborate physical-chemical studies, or even provide a clue not otherwise obtainable as to the water's origin or circulation.

Many planktonic species, although dependent on certain waters for reproduction and development, may be swept from these endemic areas and survive for some time as expatriates. Some reproduction may take place at first, but eventually only adults and submature specimens will be found and these, too, finally succumb to changing environmental conditions.

A. Transport from the Bering Sea into the Arctic Ocean

Beginning in 1934 and continuing in the next two decades, considerable oceanographic study, both physical and biological, has been concerned with determining the extent and character of flow of North Pacific and Bering Sea water and its floating life through the Bering Strait into the Arctic Ocean. Parts of these studies will provide some idea of the application of plankton species in following the movement of water-masses, and, conversely, of the kind of dispersal pressure that planktonic species must be subject to under the influence of a current system sweeping them relentlessly downstream into more and more unfavorable living conditions. In this instance, the contrast between the endemic area and the area involuntarily invaded is probably so great that it militates against the evolution and establishment of epiplanktonic species or forms adapted to the more severe environment of the Arctic. However, it has become increasingly evident that some planktonic species hitherto considered common to widely separate areas, such as the North Pacific and the Arctic and boreal waters of the Atlantic, may be distinct species or varieties that have evolved in the Arctic. Outstanding among these is *Calanus glacialis*, established by Jaschnov (1955) as a new species. Although relatively larger than *Calanus finmarchicus* Gunnerus, it was previously identified with that species. Also, Brodskii (1950, 1957) has named a surprising number of new copepod species, some of which are closely allied to common Atlantic or arctic forms. Taxonomically, this affects the present analysis only in that *Metridia lucens* and *Calanus tonsus* as previously recognized by authors for the Pacific form are probably Brodskii's *Metridia pacifica* and Marakawa's *Calanus plumchrus*, both of which are North Pacific and Bering Sea species.

Parts of the arctic areas that we shall be here concerned with were widely surveyed during the short arctic summers by the U.S. Coast Guard cutter *Chelan*, the U.S.S. *Nereus* and H.M.S. *Cedarwood* in the Bering Sea and parts of the Chukchi Sea in 1934, 1947 and 1949 respectively, and by the U.S. ice-

breaker *Burton Island* in the Chukchi and Beaufort Seas in 1950 and 1951. Thus, a seasonal picture of the plankton was obtained which shows its relative stability with respect to occurrence and distribution of certain species for separate years. The study will suffice to illustrate the kind of integrated information that can be gleaned by piecing together oceanographic observations that are applicable to conditions in new or little known areas. Additional details of the plankton analysis made on these surveys is given by Johnson (1953, 1956).

In the eastern portion of the Bering Sea and the southeastern Chukchi Sea, there is a characteristic assemblage of holoplanktonic species of copepods which, while not always abundant, are found at many scattered sampling stations over much of the area. Most of these species are also common along the coast of North America for varying distances south of the Aleutian Islands in subarctic water. To the north in the Chukchi Sea and along the Alaskan coast into the Beaufort Sea, the frequency of catches of these species falls off, and eventually the species disappear in the northern reaches of the Chukchi Sea and in all but the near-shore stations in the Beaufort Sea (Figs. 10 and 11). The abrupt disappearance of *Acartia clausi, Calanus tonsus, Epilabidocera amphitrites, Eucalanus bungii bungii, Eurytemora herdmani, Metridia lucens* and *Tortanus discaudatus* in the region of Point Barrow, Alaska, is interpreted as resulting from an eastward flow along the coast to this area, where it is met by a clockwise flow from the Beaufort Sea as it swings to the northwest in this region. It is obvious that these copepods found off Point Barrow have their main connection with the major population to the southwest in the Chukchi and Bering Seas, where, as a group, they occurred at about 80% of the stations.

Probably the most striking example of this kind in these waters is shown by the distribution of *Acartia longiremis*, a more abundant species of wide distribution in coastal waters of the arctic and subarctic regions (Fig. 11). This is generally considered a coastal species, but with a wide tolerance for offshore conditions. It is abundant in the Bering Sea and southeastern Chukchi Sea, where in 1934 and 1947 it was found at 75% and 85% respectively of the oceanographic stations. From here it may be carried in considerable numbers far into the Arctic Ocean to 74° 17′N, 168° 56′W, where, in 1951, a single station yielded 1040 adult or submature specimens in a 0–100-m haul with a $\frac{1}{2}$-m net. The species was absent from stations north of 76°N, and also totally absent from the many offshore stations in the Beaufort Sea, where in the summer the ice-free water would appear to be as ecologically suitable as the northern Chukchi Sea. This absence in the main part of the Beaufort Sea may be explained by assuming that, except at the near-shore stations, the water entering the Beaufort Sea flows down from high arctic regions as the eastern portion of a large clockwise gyral, the southern part of which is shown in Fig. 10. That such a gyral does exist is also evidenced by physical studies (Worthington, 1953). The offshore portions of the Beaufort Sea affected by such a current could not be expected to harbor any *Acartia longiremis*, which, as shown in
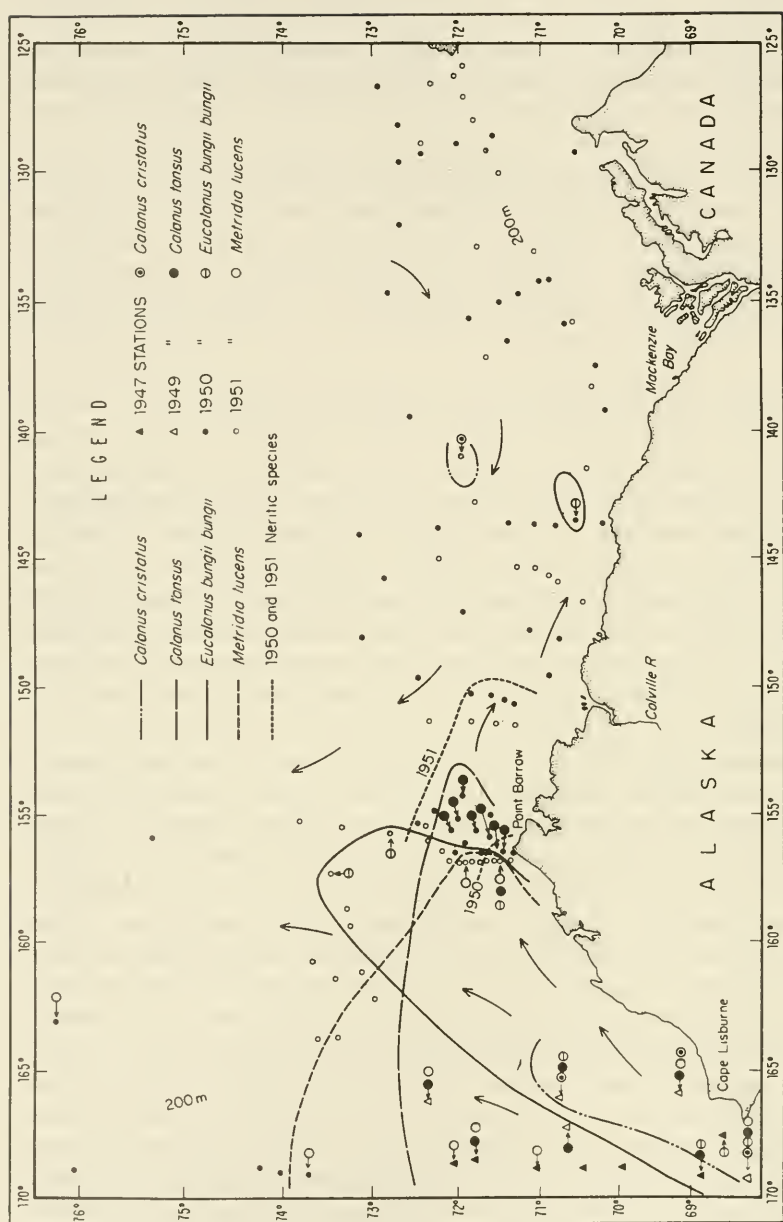
Fig. 10. The extent of Bering Sea and southern Chukchi Sea influence in the arctic region off northern Alaska as indicated by locality records of certain planktonic copepods for the summers of various years. Data are based on vertical hauls with 40 cm (1947, 1949) and 50 cm (1950–51) nets towed from 100–0 m or from bottom to surface at shallower depths. The lines enclose the approximate usual extent of penetration of the species. Note isolated instances.

Shown also are the 1950 and 1951 observed extent of the more strongly neritic species *Acartia clausi, Centropages abdominalis* (syn *mcmurrichi), Epilabidocera amphitrites, Tortanus discaudatus.* The long arrows show general direction of flow based on species distribution.

Fig. 11. was eliminated by either high arctic or oceanic conditions in the northern portion of the Chukchi Sea.

It should be further pointed out that the occurrence of *Metridia lucens* at 73° 42′N, 169° 01′W and 76° 22′N, 163° 16′W in the Chukchi Sea can also be taken to indicate an influx of Bering Sea water into the Arctic Ocean, at least to that latitude. A comparison with Fig. 12 shows this to be farther than reported for penetration of Bering Sea water based on earlier physical-chemical studies (Barnes and Thompson, 1938; LaFond and Pritchard, 1952; Saur,
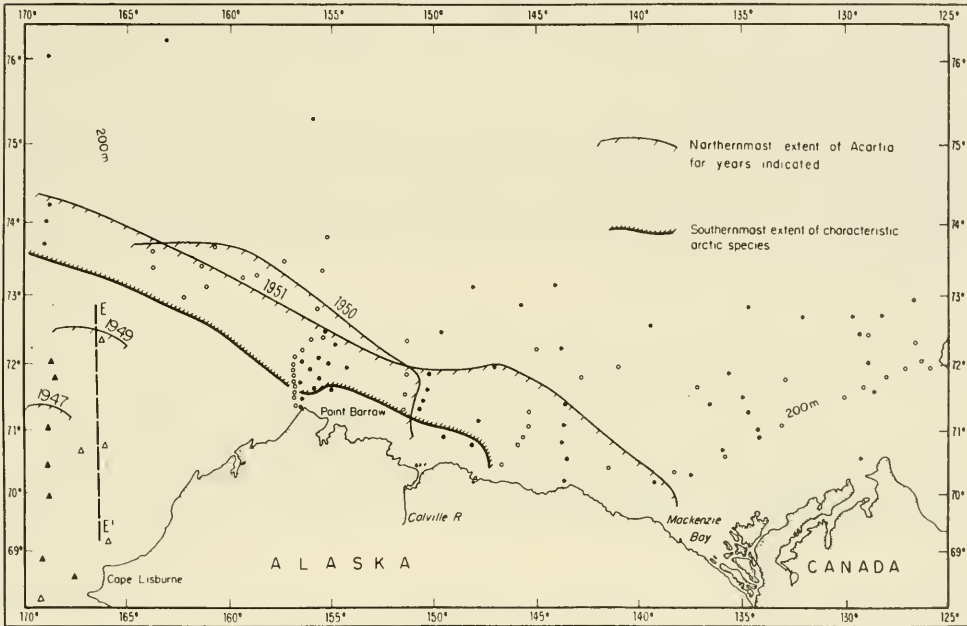

Fig. 11. The extent of observed arctic penetration of *Acartia longiremis* for 1947, 1949, 1950 and 1951. The species occurred at 73%, 100%, 100% and 97% respectively for each year within the distributional areas outlined by light lines. The southernmost observed extent of the two characteristically arctic species, *Calanus hyperboreus* and *Metridia longa*, is shown by the heavy line. The former occurred at 96% of the stations above the line in 1950 and 82% in 1951; and the latter at 83% in 1950 and 82% in 1951. All stations south of the line were negative.

Solid triangles, 1947 stations; open triangles, 1949 stations; open circles, 1950 stations; solid circles, 1951 stations.

Water structure along line E–E′ is shown in Fig. 12.

Tully and LaFond, 1954) made concurrently with plankton collecting. More recent studies (Coachman and Barnes, 1961) do, indeed, indicate the presence in the Arctic Basin of a stratum of water between 50 and 130 m with temperatures as much as 0.5 to 0.8°C warmer than the water immediately above or below it. It diminishes from the Chukchi Sea toward the Pole and toward Ellsmere Island. It is probable that certain hardy expatriates of *Metridia lucens*, found near 74°N in the Chukchi Sea, *Calanus cristatus*, near 72°N in

the Beaufort Sea, and the two species discussed in the next paragraph were transported in such a water stratum.

A recent analysis of zooplankton collected in 1957–58 during the drift of the ice floe "Drift Station Alpha" in latitudes 81° 14'N to 85° 16'N shows additional expatriate species from the North Pacific Ocean–Bering Sea populations (Johnson, MS). Individual adults of *Eucalanus bungii bungii* Giesbrecht were taken at 83° 41'N, 155° 13'W and at 85° 6'N, 167° 40'W. This same species was also reported by Brodskii and Nikitin (1955) at 77° 5'N and 80° 51'N. Another species, *Mimocalanus distinctocephalus* Brodskii, occurred in the ice floe collection taken at 83° 4'N and is probably an expatriate there. Brodskii (1957) found it at 50% of the oceanic stations from 500- to 1000-m depths in the Bering Sea.

Under conditions of cooling associated with northward flow of Pacific and Bering Sea water, the survival of contained southern species far beyond their endemic area would be enhanced by the drop in temperature. That this might occur is supported by the experiments carried out by Clarke and Bonnet (1939) in which the survival of *Calanus finmarchicus* was definitely better at 3°C than at temperatures of 6° and 9°C.
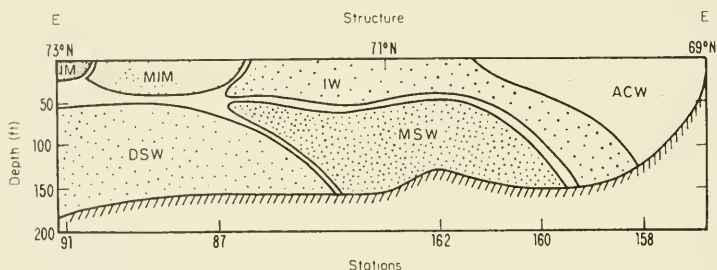

Fig. 12. Water-mass structure from Cape Lisbourne to the ice pack, based on temperature and salinity relations. See Fig. 11 for position of section E–E'.

ACW, Alaskan Coastal Water; MSW, Modified Shelf Water; MIM, Modified Ice Melt; IM, Ice Melt; DSW, Deep Shelf Water. This DSW is not considered continuous with the Bering Sea as are the others. (After Saur, Tully and LaFond, 1954.)

The northward and eastward extensions of the U.S.S. *Burton Island* collections in the Chukchi and Beaufort Seas make it also possible to consider here, in contrast, the distribution of two characteristically arctic species of copepods —*Calanus hyperboreus* and *Metridia longa*. The southern limit of distribution observed for these species shows that a good deal of overlapping of areas may occur (Fig. 11), but the main population of arctic species is held back in the Chukchi Sea by the flow from the Bering Sea. A broad transition zone seems to exist in the northern Chukchi Sea, if one may judge by the 1947 and 1951–1952 collections. The position and extent of this zone doubtless varies somewhat from year to year. In the Beaufort Sea area the truly arctic zone is more sharply defined east of Point Barrow where there is, however, a clear overlapping of the arctic and the more southern species, suggesting considerable

mixing of waters in the coastal part of this area. The line of demarcation between these two faunas may result in part from the width of the Continental Shelf, which is narrow in the Beaufort Sea and relatively broad in the Chukchi Sea as shown by the 200-m depth contour in Fig. 11. This would tend to influence the relative position of the neritic and of the more offshore species such as *Calanus hyperboreus* and *Metridia longa* which occur in deep water but are not characteristically bathypelagic species and were caught regularly in tows from 100 to 0 m depth, and also in a tow from 700 to 430 m depth. Although the geographic limits shown here for these two arctic species appear to be valid for the boundary of their *continuous* distribution, it must be mentioned that both species have been reported far south of this range. Anraku (1954) lumps *M. longa* with *M. lucens* from the Aleutian area; Campbell (1929) reports *M. longa* from the Vancouver Island region; and Wilson (1942) lists *M. longa* from both the North and South Pacific and *Calanus hyperboreus* from the North Pacific. Some of these identifications appear to be in error. Further work on deep-water plankton is needed to determine the extent of subarctic penetration by these and other cold water forms into the deep cold water of the Pacific.

The truly abyssal species found in the Arctic Basin have their main connection with the Atlantic Ocean, since the shallow depth of the Bering Strait permits transport of only the surface species and such bathypelagic forms as also frequent the upper layers.

Parts of the area here covered by the plankton surveys have also been studied by Russian biologists. Their reports substantiate the conclusion that Bering Sea plankton is carried northward through the Bering Strait (Stepanova, 1937; Brodskii, 1957).

B. The Meroplankton

We turn now to illustrate briefly a different aspect of plankton dispersal with emphasis on the floating larval stages of bottom-living invertebrates.

The dispersal of meroplankton has been of interest to marine biological studies mainly because of its importance in the ecology, recruitment and general life cycle of the animals involved. But the extent and pattern of dispersal of these forms can also contribute to the study of water currents, especially on a more restricted scale, although the most widely known and remarkable study ever made on the drift of marine plankton is that of Johannes Schmidt (1925), dealing with the larval drift of the European eel. This eel, after hatching, is carried during its two-to-three-year larval life some 3000 miles by currents across the Atlantic Ocean. The planktonic larval life of most invertebrates is, however, usually much shorter, and their sensitivity to hydrographic changes probably greater. Hence, they are not so likely to be carried great distances away from the spawning area of adult distribution. The usefulness of these larvae as indicators lies in the fact that the spawning area of the adult is often known, and the duration of the larval stage may also be known

within limits. Some information is, therefore, provided that can be of aid in considering the source, direction, time lapse or complexity of currents. During the growth of larvae there is often a succession of well defined stages (or sizes) which, when well known, are further aids in considering the source and time of larval entrance into the waters as floating organisms. The information on water currents that can be gleaned from a study of the distribution of these larvae cannot. as a rule, be expected to indicate a direct line of flow. and thus to provide a clear-cut answer as to the source and time involved. More often, the occurrence of the larvae gives only partial answers and poses problems that need clarification through more detailed oceanographic investigations. They often bring to light oversimplifications that are likely to be introduced in dynamic computations of flow. Thus. more questions about water currents may often be asked than are answered; but this is an important contribution, for it is widely recognized that in oceanographic research questions must first be asked of the sea before answers are obtained.

The implications of a study of this kind are well illustrated by a seven-year investigation of the occurrence of the floating larvae of the California spiny lobster (*Panulirus interruptus*). In this survey it was found that it requires about $7\frac{3}{4}$ months to complete the planktonic larval life in which there are a succession of 11 larval stages (Johnson. 1960). During this relatively long. hazardous time, the larvae are at the mercy of prevailing currents. A characteristic picture of the geographic distribution of various larval stages is given in summary form in Fig. 13.

In the light of this long larval period, it is remarkable that the lobster fishery on the California coast remains as stable as it does. Precisely what are the details of circulation that enable retention of sufficient numbers of larvae to bring about restocking in the area? *A priori*, it appears that the system of eddies and countercurrents that retard outflow from the area is far more complicated than usually pictured on the basis of computations giving dynamic topography. Although major eddies are usually clearly detected by this method, the direction and rate of surface flow suggest that it would be unlikely that any considerable packet of water and its contained larvae would remain for seven to eight months within the distributional area of the adult lobster on the Southern California and Baja California coasts. Only a few drift bottles set adrift 40 miles from the coast to test the currents have been recovered, and the inshore current is said to flow southward from March through October (Reid, Roden and Wyllie, 1958). Nevertheless, the biological data, although evidencing a dispersal from the shore where the larvae are hatched, do show that there must be a fair retention of larvae, and in addition to this retention within the area, a mixture of larval stages does at times occur in a single sample. This would indicate a great deal of mixing within the water by eddy diffusion.

In the interpretation of the meaning of the distribution of these larvae (and, indeed, also of the holoplankton) in terms of water movements, it is important to have in mind at all times that here one is dealing with living creatures that,

unlike inanimate drift bottles, may exercise some degree of modification of their distribution. This could be accomplished mainly by swimming from one depth level to another during vertical diurnal migrations, or even through seasonal migrations of this type. During these shifts of level, which occur under the directive stimulus of light, even weakly swimming animals may conceivably spend a good deal of time alternately in currents flowing in different directions, or at different speeds. In this way a retardation or prevention of
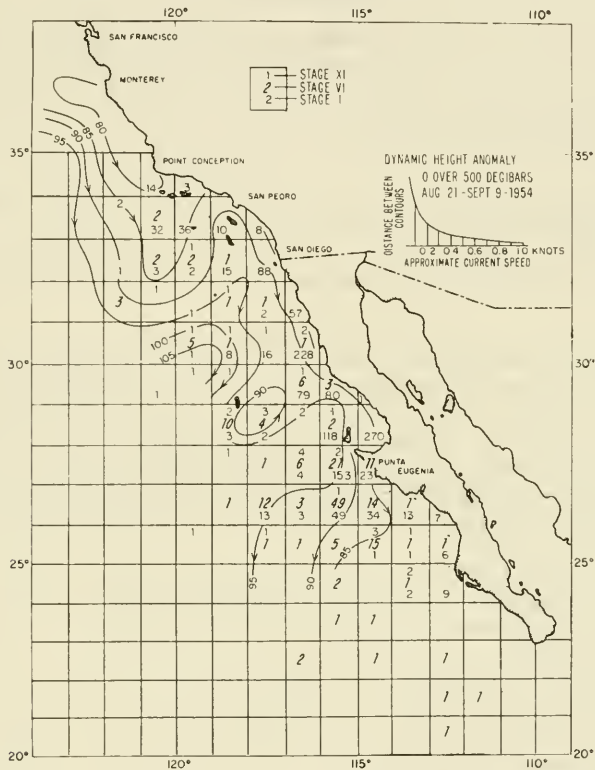

Fig. 13. Summary of the distribution of the Stage I, Stage VI and Stage XI (last) phyllosoma larvae of the spiny lobster *Panulirus interruptus* based on approximately monthly cruises, 1949–1955. Superimposed on the grid is the surface-current pattern for Aug. 21–Sept. 9, 1954. There is considerable variation in currents from month to month but the general flow is to the south. August and September are months with many early and intermediate larvae.

wholesale outwash is effected. That something of this nature occurs in many parts of the sea where a continuous yet drifting population is found is suggested by many studies of both the meroplankton and the holoplankton.

The mystery of how specific planktonic populations can be maintained as such within rather restricted geographical areas is not easy to solve. The answer will most likely be found to include some aspects of water movements correlated with the behavior and life history of the animals. Semi-closed

circulation with horizontal flow, such as exists in the Gulf of Main (Bigelow, 1926; Redfield, 1941) and, on a smaller scale, in coral atoll lagoons, where a semi-closed system is set up in a vertical rather than horizontal plane (Johnson, 1954), provide the more simple and obvious conditions for interpreting the interrelations of species within their ever-moving aquatic environment.

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